

RIPARIAN BIRD COMMUNITIES ALONG AN URBAN GRADIENT:
EFFECTS OF LOCAL VEGETATION,
LANDSCAPE BIOPHYSICAL HETEROGENEITY,
AND SPATIAL SCALE

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DEDICATION

*To my Mother and Father whose love and vision
guides me to this day.*

To Mill Creek watershed and the people who vow to restore its integrity.

ABSTRACT

Urbanization is an important driver of ecosystem change that can have deleterious effects on regional native biodiversity. Yet we know little about the potential value of urbanizing areas for maintaining local and regional species diversity. Few studies have explicitly examined how the spatial arrangement and composition of biophysical elements within a metropolitan area contribute to the structure and composition of urban biodiversity. This thesis focuses on avian community responses and uses observational studies that consider local vegetation and landscape factors in order to further understanding of the ecological and conservation implications of urbanization across multiple temporal and spatial scales.

A synthesis of three urban systems demonstrates the usefulness of gradient analysis approach for understanding fine- and coarse-scale processes influencing urban bird distributions. Results illustrate differences between two urban-to-rural gradient paradigms and the importance of conducting investigations at multiple spatial, temporal and biological scales. Recommendations are provided to improve our understanding of urban bird communities using gradient analyses and emphasize the future need to derive a common framework that incorporates the biophysical and social heterogeneity of urban systems.

An urban gradient study of riparian bird communities within metropolitan Cincinnati, Ohio during spring migration found that bird species responses varied based on migratory strategies and across spatial scales. Long-distance Neotropical migrant species density, richness, and evenness responded most strongly to landscape and vegetation measures and were positively correlated with areas of wide riparian forests

and less development within 250 m. Resident Neotropical migrants density, richness, and evenness increased with wider riparian forests (> 500 m) without buildings, while en-route migrants utilized areas having a wide buffer of tree cover (250 to 500 m) regardless of buildings; both resident and en-route landbirds were positively associated with native vegetation composition and mature trees.

To better understand the relative importance of proximate versus landscape features and the influential spatial scales of these landscape features, I focused on breeding riparian bird species and the influences of two biophysical features of the urban environment – vegetation and built elements – within 1 km for the same riparian study area. At the proximate scale, native tree and understory stem frequency were the most important vegetation variables; native tree frequency had a positive influence on 35 species and a negative influence on 13 of the 48 species and native understory frequency had a positive influence on 27 species and a negative influence on 21 species. At the landscape scale, the vegetative features (both tree cover and grass cover) were most important variables included in competitive models across all species; tree cover positively influenced 15 species and negatively influenced 5 species and grass cover positively influenced 22 species and negatively influenced 5 species. Building density was an important variable for 13 species, and positively influenced 6 species and negatively influenced 7 species. In a comparison of multiple scales, models with only landscape variables were adequate for some species, but models combining local vegetation and landscape information were best or competitive for 42 of the 44 species. Local-vegetation-only models were rarely competitive. Combined models at small spatial scales (≤ 500 m) were best for 36 species of the 44 species and these models

commonly included tree cover and building density. Only eight species had best models at larger scales (> 500 m); grass cover was most the important variable at larger scales.

In conclusion, understanding the processes that create repeatable patterns in urban bird distributions is a challenge that requires investigation at multiple spatial, temporal, and biological scales. These findings provide managers and land-use planners with species-specific information and emphasize the importance of acknowledging both proximate and landscape influences in habitat modeling.

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CHAPTER 1

Introduction

Urbanization is one of the leading factors affecting biodiversity (Vitousek et al. 1997, Wilcove et al. 1998, Dale et al. 2000, Pickett et al. 2001), and the development of management strategies aimed at diminishing these impacts will be important for sustaining many of the world's species (Czech 2000, Rosenzweig 2003, Palmer et al. 2004). Urban landscapes are characterized as highly heterogeneous, spatially nested, and hierarchically structured systems of complex interactions among social, economic, and ecological variables (Alberti 2005). The urban spatial structure represents a cumulative and aggregate pattern derived from myriad local decisions involving both socioeconomic and biophysical factors (Pickett et al. 2001). These interactions result in emergent phenomena that fragment, isolate, and degrade natural habitats; simplify and homogenize species composition; alter hydrological systems; and influence nutrient cycling and energy flow (Carreiro et al. 1999, Blair 2001, Meyer et al. 2001). Consequently, an essential research need is identifying the biophysical and socioeconomic factors that are well correlated with specific aspects of ecological structure and function, this requires an integrated approach that combines both landscape monitoring and field studies (Alberti and Marzluff 2004, Cadenasso et al. 2006).

Among taxa, birds have garnered the most attention by ecologists studying urbanization's effects on biodiversity; these feathered vertebrates represent an ideal surrogate because of their conspicuous nature, mobility, and behavioral plasticity that allows some bird species to even occupy the most fragmented urban landscapes (Blair 1999). Over the past decade, urban ecologists have focused their research on questions

examining the patterns and processes structuring urban bird populations and communities by incorporating variations of McDonnell and Pickett's (1990) urban-to-rural gradient methodology (McKinney 2002, see Chace and Walsh 2006 for review). The results from these studies have varied depending on the diversity (or biological) measure. In general, urban areas harbor fewer species than more natural areas (Marzluff 2001, McKinney 2002). Many of the species that do persist in urban areas are typically widespread natives (i.e., cosmopolitan) or non-natives (Blair 2001, McKinney 2002). Yet several studies suggest that intermediate land-use types can support several native species (Blair 1996, Marzluff 2005), suggesting the possibility of designing urban landscapes to sustain local native species diversity.

Urban systems offer a unique ecological situation whereby biophysical and socioeconomic factors interact hierarchically across spatial and temporal scales (Pickett et al. 2001). Urban areas can comprise a diversity of habitats such as large and small patches of greenspace, including intentional (e.g., public parks) and unintentional (e.g., vacant lots), residential and commercial yards, among other habitat types (Blair 1996, Pickett and Cadenasso 2008). The amount and spatial arrangement of these urban habitats within a metropolitan area creates a complex mosaic of both built and vegetative elements – buildings, paved surfaces, and vegetation (Cadenasso et al. 2007, Pickett and Cadenasso 2008). For example, in a forested region a residential area can have varying levels of population or building densities, yet knowing this information does not necessarily reveal how these residential areas can differ in terms of vegetative cover. Some developments can have a continuous canopy of trees, others a few scattered trees along roadways, and still others lack trees entirely.

Riparian areas are systems highlighting interactions between plants, animals, water, and people (Naiman et al. 1993, Groffman et al. 2003, Richardson et al. 2007). People have historically settled near streams and rivers for access to water for drinking, food, irrigation, transportation, and industry. Given this close association, it is not surprising that riparian areas are among the most threatened landscapes (Naiman and Decamps 1997, Richardson et al. 2007); many riparian systems are a part of larger urban systems. Previous studies have demonstrated that upland land use can influence riparian systems for both hydrologic and aquatic biotic measures (Karr and Chu 1999, Paul and Meyer 2001). Riparian areas also support a high diversity of terrestrial plants and animals and serve as corridors between isolated habitat patches within highly fragmented landscapes (Skagen et al. 1998). In order to mitigate the adverse effects of development on riparian birds, it is first necessary to obtain a clear understanding of the potential mechanisms underlying these effects.

Whereas previous research examining the effects of urbanization on riparian avian communities has focused primarily on the breeding season, (Rottenborn 1999, Green and Baker 2003, Rodewald and Bakermans 2006), I examine riparian bird community composition during both the spring migratory and breeding seasons. Riparian areas provide critical habitat for migrating birds (Ohmart 1994), many of which are of interest due to recent declines in some species, especially Neotropical migrants (Robbins et al. 1989). Results from earlier riparian studies have concluded that Neotropical migrant landbirds are the most sensitive to human disturbance and fragmentation during the breeding season (Saab 1999, Hennings and Edge 2003, Miller et al. 2003), yet relatively little is known about the effects of urbanization during the

migratory season (Donovan et al. 2002). During migration, long-distance migrants undergo tremendous energy demands, and require stopover habitat (including both large and small habitat patches) to replenish fat reserves along the way to their breeding grounds (Moore et al. 1995). Consequently, stopover sites are a vital component of a Neotropical migrant's life stage and eventual breeding success (Sillett and Holmes 2002).

This dissertation will emphasize examining avian biodiversity at multiple hierarchical levels, including the species and community levels and enlighten our understanding of gradient analysis. It aims to further our understanding of the degree to which variation in avian community structure and composition can be explained by local habitat characteristics and spatial patterns of fragmentation and development in the surrounding landscape during both the migratory and breeding periods. It will explicitly examine the biophysical heterogeneity – vegetative and built characteristics – of urban landscapes. It also investigates the relative contribution of local vegetation and landscape features to explaining bird distributions to aid future habitat modeling efforts. Finally, it tests the importance of life-history characteristics in determining habitat use during migratory stopover. These topics will be addressed in three chapters.

Chapter 2: *Using gradient analysis to uncover pattern and process in urban bird communities.*

This chapter provides a review and synthesis of urban gradient analysis approaches for understanding urbanization affects on avian biodiversity. I incorporate examples from three urban systems (one from California and two from Ohio) to

illustrate how two new urban gradient paradigms, direct urbanization and urban context, can be used to study fine- and coarse-scale patterns and processes. Based on my review, I provide recommendations for future urban biodiversity studies.

Chapter 3: *The conservation value of urban riparian areas for landbirds during spring migration: land cover, scale, and vegetation effects.*

This chapter describes the relationship between urbanization and bird community composition of Midwestern U.S.A. riparian areas during spring migration. I take a multi-scale approach investigating how local and landscape attributes affect relative density, species richness, and evenness of four migratory guilds: permanent residents, short-distance migrants, and both en-route and summer resident long-distance Neotropical migrants. I measure land cover (percentage tree cover, percentage grass cover, and building area) at four spatial scales (50, 100, 250, and 500 m radii around plots) and local vegetation structure and composition characteristics (within 35 m radius around a plot). With these measures, I estimate the effect development patterns might have on migrating bird communities along urban riparian areas within the Cincinnati metropolitan area.

Chapter 4: *Untangling the relative importance of vegetative and built features on breeding riparian birds within a complex urban environment: local vegetation, landscape, and scale.*

In this chapter, I examine how the spatial arrangement and composition, or heterogeneity, of biophysical structure within a metropolitan area contributes to the

structure and composition of urban riparian biodiversity. Specifically, I examine how two key elements of the biophysical structure – vegetation and built infrastructure – influence the distribution of breeding bird species within urban areas. I compare the relative importance of the structure and composition of these elements on birds across multiple spatial scales within the Cincinnati metropolitan area. I measure breeding birds over a four-year period and measure local vegetation structure and composition within 35 m around a plot and landscape features (percentage tree cover, percentage grass cover, and building density) at multiple spatial scales (at 50, 100, 200, 300, 400, 500, 600, 700, 800, 900, and 1000 m radii around plots). I describe the relative contribution of local vegetation and landscape features for predicting bird distributions and identify the scales at which bird species respond most strongly to landscape biophysical measures.

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Chapter 2

Using gradient analysis to uncover pattern and process in urban bird communities

with Robert B. Blair

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ABSTRACT: Understanding the processes that create repeatable patterns in urban bird distributions is a challenge that requires investigation at multiple spatial, temporal, and biological scales. Based upon our research of urban systems in California and Ohio, we demonstrate how gradient analysis is a useful tool for understanding both fine- and coarse-scaled processes. We also explore how life-history characteristics permit some species to utilize and even thrive in urban areas while others cease to exist. Finally, we provide recommendations to improve our understanding of urban bird communities using gradient analyses and emphasize the need to derive a common framework that incorporates the ecological and social heterogeneity of urban systems.

INTRODUCTION

A primary aim of urban ecology is to enhance our understanding of the structure and function of urban systems (McDonnell and Pickett 1990). Urban systems offer a unique ecological situation whereby biophysical and socioeconomic factors interact hierarchically across spatial and temporal scales. These complex interactions produce dynamic feedbacks resulting in “emergent properties,” such as exacerbated disturbances (e.g., frequent flooding, pollution, climate change, etc.), species turnover, and societal impacts (e.g., health problems, gentrification, etc.) (Machlis et al. 1997, Pickett et al. 2001, Redman and Jones 2005). Insights into these systems allow ecologists to share recommendations with policymakers, land-use planners, and homeowners regarding land-use practices that enhance not only native biodiversity, but also the quality of life for the people living and working within these areas by increasing their opportunities to interact with local wildlife (Miller and Hobbs 2002, Turner et al. 2004).

Urbanization can be defined as the “city construction process” (Gottdiener and Hutchinson 2006), which creates a heterogeneous landscape of varying land uses. From an ecological perspective, urbanization represents the process of converting, degrading, and fragmenting natural habitats (McDonnell and Pickett 1993, Marzluff 2001). The direct ecological impact from urbanization involves the replacement of native vegetation structure by city infrastructure (e.g., buildings, roads, utilities). Indirectly, urbanization alters vegetation composition and structure by the process of fragmentation and degradation, which reduces habitat quality for several native species and increases the quality for early colonizers and non-native species (McKinney 2002). Not

surprisingly, urbanization affects birds in myriad ways (Chace and Walsh 2006).

As a taxonomic group, birds by their conspicuous nature have garnered the greatest attention by urban ecologists. While several vertebrate species fail to persist in urban habitats, birds, through their mobility and plasticity, have been successful at exploiting highly fragmented urban landscapes. Over the past decade, urban ecologists have focused their research on questions examining the patterns and processes structuring urban bird populations and communities by incorporating variations of McDonnell and Pickett's (1990) urban-rural gradient methodology (McKinney 2002, see Chace and Walsh 2006 for review). The results from these studies have varied depending upon the diversity (or biological) measures used. In general, urban areas harbor fewer species than more natural areas (Marzluff 2001, McKinney 2002). Many species that do persist in urban areas are often widespread natives (i.e., cosmopolitan) or non-natives (Blair 2001, McKinney 2002). Yet several studies show that certain urban land-use types can support native species (Blair 1996, Marzluff 2005), suggesting the possibility of designing urban landscapes to sustain local indigenous species diversity.

In this paper, we use multiple urban systems to demonstrate how gradient analysis is a useful tool for understanding both fine-scaled and coarse-scaled processes that influence bird community composition. We also demonstrate how life-history characteristics allow some birds to exist and even thrive in urban settings while limiting the existence of other birds. Finally, we highlight opportunities to improve our understanding of urban bird communities by integrating the ecological and social heterogeneity of urban systems into our studies of urban ecology.

GRADIENT ANALYSIS AS A TOOL FOR STUDYING URBAN BIRDS

The Urban System

Rapid worldwide urbanization presents an immediate challenge to conservationists throughout the world (Berry 1990, Vitousek et al. 1997, Czech et al. 2000, Dale et al. 2000). The current global population exodus from rural areas has placed an unprecedented majority of the Earth's people living within and around urban areas, thus severely testing the limits of not only local infrastructure, but of ecosystems worldwide (Vitousek et al. 1997, Fund 2004). This growing trend is not limited to developing countries, but is happening worldwide as complex global economic "incentives" and cultural "preferences" spur development towards ever larger megametropolises (Berry 1990, Gottdiener and Hutchinson 2006). The growth of megametropolises and metropolitan areas worldwide signifies the increasing importance of understanding urban systems. Specifically, metropolitan areas represent a kaleidoscopic spatial arrangement of biophysical and socioeconomic patterns and processes within a complex hierarchical system (McDonnell and Pickett 1993, Pickett et al. 2005). Hence, metropolitan areas provide a unique opportunity to examine and predict ecological effects across multiple spatial and temporal scales, using a multidisciplinary framework that includes sociology, economics, urban planning, and ecology (Alberti 2005, Cadenasso et al. 2006). Understandably, then, developing a holistic understanding of the dynamic heterogeneity of urban systems represents the new frontier for urban ecology.

URBAN-RURAL GRADIENT ANALYSIS

One goal of urban ecology is to understand how landscape patterns influence ecological process; *how* we describe and define this landscape heterogeneity within urban systems is important (Pickett and Cadenasso 1995, Wu and Loucks 1995). Urban ecologists have struggled to define urbanization in a succinct manner (McIntyre et al. 2000, Marzluff 2001, Theobald 2004, Cadenasso et al. 2007), in part because urban systems are exceptionally complex, and cannot be categorized simply as either “urban” or “natural” habitats (or landscapes) (Pickett et al. 2001, Theobald 2004). Instead, urban systems are an intricate arrangement of varying land uses that result in a mosaic of human modification and built structure. This heterogeneity establishes complex gradients extending from dense central cities (or urban cores), through industrial, transportation, residential, and commercial land covers (Cadenasso et al. 2006). To accommodate such heterogeneity, several urban ecologists have adopted the urban-rural gradient paradigm popularized by McDonnell and Pickett (1990), which is based on well-established models of ecological gradients (Whittaker 1967, Austin 1987, Ter Braak and Prentice 1988). Specified gradients are one reasonable solution to the problem of multiple concepts of urbanization (McIntyre et al. 2000; Theobald 2004). Urban-rural gradients differ from traditional gradient analyses in that they explicitly incorporate people as ecological drivers (e.g., built infrastructure). The urban-rural gradient approach has proven useful for studying the complex spatially varying effects of urbanization on forests (Goldman et al. 1995, Medley et al. 1995, McDonnell et al. 1997, Pickett et al. 2001), terrestrial organisms (Blair 1999), and aquatic systems (Paul and Meyer 2001, Fraker et al. 2002, Groffman et al. 2003).

The urban-rural gradient can be quantified in various ways. Traditionally, the geographic perspective on urbanization has defined these areas as a “dense, highly developed core, surrounded by irregular rings of diminishing development” (from Dickinson 1966 as cited in McDonnell and Pickett 1990:1233; also similar to von Thünen’s location theory; von Thünen 1826). Following this classical definition, the urban-rural gradient paradigm has often been conceived as a linear transect from the inner city to less-altered landscapes across broad spatial scales. For example, McDonnell and Pickett’s (1990) urban-rural gradient was a linear 140 km transect extending north from Central Park in New York City to rural Connecticut. To quantify urbanization in their studies, McDonnell and Pickett included distance from the urban core as one of several landscape factors. However, it is important to note that urban-rural gradients are not necessarily linear transects across the landscape (Austin 1985), especially at smaller spatial scales. Instead, these gradients are “abstract orderings of changes in land cover, land use, human activity, and the fluxes of capital, energy, material, and information in and around cities” (Cadenasso et al. 2006:5). Accordingly, the degree of urbanization can be ordered along conceptual gradients in which scattered sites that can be ordered according to a specific indicator of urbanization, such as human population or vegetation cover (Pickett and Cadenasso 2006). Regardless of the gradient model chosen, it is important to identify the features of the gradient, how they are quantified, and how they change over space for any particular study (McIntyre et al. 2000). To date, no single measure has gained universal approval for quantifying urbanization along gradients. In general, most studies have used measures of human population, building, or road density to quantify increasing urbanization (Marzluff

2001, Pickett et al. 2001).

Scale considerations when using urban-rural gradients

Because urbanization operates across a continuum of different spatial scales, gradient analyses is particularly useful as it can be applied at multiple scales (Whittaker 1967, Pickett and Cadenasso 2006). Conducting multi-scale studies is much needed in order to understand at what scale ecological processes and patterns uniquely appear (Wiens 1989b, Levin 1992, Hostetler 2001). The heterogeneity along a gradient can be distinguished into differing patches at whatever scale is chosen. For example, as the scale of analysis becomes finer, large patches that were internally homogeneous to one another can become a multitude of smaller heterogeneous patches (Cadenasso et al. 2003), thus highlighting the importance of carefully considering the scale(s) in question for a particular study.

Because urban areas are quite heterogeneous, definitions of urbanization will differ depending on the grain (the resolution or detail) and extent (the geographic coverage) of the study (Cadenasso et al. 2007). Most studies have focused on examining large spatial extents ($> 1 \text{ km}^2$), where urbanization has been classified into broad land cover/land use types — wildland, rural/exurban, suburban, and urban (Marzluff et al. 2001). The reasons for using a coarse-scale approach are two-fold: 1) it is a simple way to document the expansion of urban areas, and 2) it often reflects the best possible resolution (e.g., 30 m resolution Landsat data) due to the limited availability of high-resolution land cover/land use data ($< 30 \text{ m}$ resolution, e.g., IKONOS or Quickbird imagery; Hostetler and Holling 2000, Gottschalk et al. 2005,

Cadenasso et al. 2007). Notably, however, as the grain and extent of the study change, so, too, do ecological relationships. For instance, Pautasso (2007) found that correlations between measures of urbanization and species richness turns from positive to negative below a study grain of $< 1 \text{ km}^2$ and extent of $< 10\,000 \text{ km}^2$. With fine-grain studies, researchers are directly measuring the fine-scale heterogeneity of urban systems (i.e., replacement of vegetation by impervious surfaces); the resultant negative coefficients are caused by the direct loss of habitat by urban infrastructure. In contrast, coarse-grain studies are sampling over a diversity of landscapes (i.e., heterogeneity of landscapes); the positive relationships seen at these broader scales are consistent with the concept of species-area curves (Rosenzweig 1995). In other words, by sampling more area there is a greater likelihood of sampling more species because of the greater diversity of habitats surveyed. In addition, using a relatively coarse grain ($> 1 \text{ km}^2$) for environmental variables may result in underestimating the heterogeneity or varied patches in a landscape (Kühn et al. 2004).

Increasingly, ecologists are interested in understanding the ecological function of urban areas themselves, which requires fine-grained studies (Grimm et al. 2000). Traditional coarse-grained approaches make it difficult to separate land cover from land use and often disconnect people from “natural” components. The broad availability of U.S. Geological Survey (USGS) Landsat imagery (e.g., NLCD; Vogelmann et al. 2001) served urban ecologists well for quantifying the array of landscape factors to establish gradients for coarse grained studies, but the 30 x 30 m pixel resolution of the data makes it difficult to tease out fine-grained heterogeneity or habitat patches (e.g., narrow habitat corridors or single trees on parcels) (Gottschalk et al. 2005). Consequently, the

variety and abundance of vegetation within the “urban” classification is neglected (Cadenasso et al. 2007). Since several studies have demonstrated the importance of vegetative cover for native bird diversity (Hennings and Edge 2003, Melles et al. 2003, Donnelly and Marzluff 2004, Rodewald and Bakermans 2006), new methods that incorporate vegetative cover within the varying land-use types of urban systems would improve our understanding of how birds respond to the fine-scale heterogeneity, and therefore improve conservation and management recommendations for these areas.

Direct urbanization and urban context paradigms

For this paper, we introduce two paradigms for thinking about and designing urban-rural gradient studies: *direct urbanization* and *urban context* paradigms. Under the *direct urbanization* paradigm, the gradient is quantified from the study sites themselves, whereas for the *urban context* paradigm, the gradient is quantified by the surrounding landscape of a site (i.e., landscape context). The direct urbanization paradigm involves explicitly examining sites directly located within various land-use types (e.g., sites in wildland, suburban, urban) (Fig. 1a). The urban context paradigm is similar to “ecology in the city” in that sites are embedded within “natural” features or green space (Fig. 1b; Grimm et al. 2000).

EXAMPLES FROM CALIFORNIA AND OHIO: THREE STUDIES

To illustrate how both fine-scale and coarse-scale processes influence bird community composition, we present examples from both previously reported and new research on three urban-rural gradients: two studies using the *direct urbanization paradigm* and one study using the *urban context paradigm*. The two *direct*

urbanization studies are located in Palo Alto, California and Oxford, Ohio (see Table 1). These two studies represent a gradient of land uses ranging from relatively undisturbed to highly developed urban areas to capture a range of human-modified ecosystems based on six sampling sites: a biological preserve, an open-space recreational area, a golf course, single-family detached housing, an industrial-research park (or apartment complex in Oxford), and a business district (see Blair 2004 for details). Each of these sites contained sixteen sampling points, which was surveyed multiple times over at least two breeding seasons to obtain estimates of the relative density of all species. For the Oxford study, Reale and Blair (2005) additionally examined nest fate and nest location at each site along the gradient (see Reale and Blair 2005 for details). These two gradients are located within two different biomes: the coastal chaparral forest shrub in California and the eastern broadleaf forest in Ohio.

The third study area is located in Cincinnati, Ohio and is an example of the *urban context paradigm* – where sites of a particular type of “natural habitat” are surrounded by varying types of land use (see Table 1). Within Cincinnati, our sites are located within a “natural” riparian area that traverses a spectrum of land-use types from relatively undisturbed to highly developed. Many examples of this paradigm have been conducted across broad spatial scales from “urban” to “natural” (McDonnell et al. 1997, Donnelly and Marzluff 2004). But, this fine-scale study differs in that the entire study area is located in what would typically be considered the “urban” land-use type of a broad-scale gradient (human population density $\sim 1,498$ persons/km²). We chose this fine-scale because our objective was to examine the role of fine-scale heterogeneity on riparian bird distributions within the traditional “urban” land-use type. The study area

is situated within the Mill Creek watershed (42 994 ha) and represents all types of land cover associated with densely built regions: a varying array of parks and residential, industrial, and commercial land uses, including both private and public parcels, all within the Cincinnati metropolitan area (for details, see Pennington et al. 2008). We identified 71 sampling points along the streamside edge of two Mill Creek tributaries. At each point, we surveyed multiple times during the spring and summer 2002 to obtain estimates of the relative density of all species. The Cincinnati study area is located in the Eastern deciduous forest biome.

For the Palo Alto and Oxford study areas, we ordinated each site along conceptual gradients (based on % tree cover, % grass, % impervious, and % building) using Principal Component Analysis (PCA) to assess how well we captured variation along the gradient (McCune and Grace 2002). We used the first component axis from the PCA as a surrogate measure of urbanization (eigenvalue, percent variance explained, and significance of the first axis based on a Monte Carlo simulation were $\lambda = 2.85$, % = 57.01, $p = 0.001$ for Oxford and $\lambda = 2.38$, % = 47.66, $p = 0.001$ for Palo Alto). For the Cincinnati study, we did not use a PCA analysis for measuring urbanization, but instead chose to use building area to capture urbanization and examined the biophysical measures of percentage tree cover and percentage grass cover separately.

GENERAL PATTERNS IN BIRD COMMUNITIES ALONG URBAN- RURAL GRADIENTS

Urbanization creates distinct repeatable patterns in bird distributions (Blair 2001, Marzluff 2001, McKinney 2002, Marzluff 2005, Chace and Walsh 2006). In general, studies of bird communities along coarse-scale urban-rural gradients indicate

that abundance increases with urbanization however defined (i.e., building or road density, percent impervious surface, percent forest) and species richness declines with measures of urbanization; however, recent work by Lepczyk et al. (2008) suggests more complex responses to varying measures of urbanization.

Our studies of direct urbanization showed a negative quadratic relationship for species richness and Shannon diversity for Oxford, and reflected a peaking of diversity measures at less developed and more intermediate levels of urbanization (e.g., golf courses and residential areas) (Fig. 2), which has also been documented for European cities (Clergeau et al. 1998, Jokimäki and Suhonen et al. 1998); however, our results for Palo Alto reflected a more linear decline with increasing levels of urbanization across the gradient suggesting potential geographical differences. This curvilinear trend illustrates local extinction and invasion in that minimal development of a site can create a more heterogeneous habitat (e.g., trees and lawn patches) that supports a higher number of species, but intense development can reduce the numbers of both urban avoider and urban adapter species (Blair 1996, McKinney 2002). Based on the urban context paradigm, Cincinnati riparian bird communities displayed a negative curvilinear response for both density and species richness with surrounding forest cover, with diversity measures peaking at ~ 70 % cover (Fig. 3a; also seen in Donnelly and Marzluff 2006). When the proportion of forest cover drops below 30 %, a sharp decline in both density and richness occurs; this appears to be a critical threshold in other studies (Donnelly and Marzluff 2004). For the Cincinnati study, both density and richness declined linearly with increasing building area, our surrogate for urbanization (Fig. 3b). This contrasting trend with what has been generally observed could be due to

a smaller amount of variation captured across the typical urban-rural gradient, as these study sites resided mostly within the “urban” end of the spectrum.

As urbanization creates a gradient of disturbance, it can also create a gradient of homogenization. The blinking in and out of species across the urban gradients implies that some species flourish by exploiting novel resources created from development, while others disappear with increased development (see Table 2; McKinney 2006). At the species level, forest-breeding species, considered the hallmark urban avoiders (Blair 1996, McKinney 2002), displayed a strong pattern of local extinction. Many of the species, and also some of the most abundant, displayed the ability to adjust to moderate levels of disturbance (urban adapters), with densities peaking in sites of intermediate development (e.g., Northern Cardinal (*Cardinalis cardinalis*) and American Robin (*Turdus migratorius*); see Table 2). It is plausible that these patterns result from the changes in the processes of predation and nest survivorship or because of fruit-bearing ornamental plants common in the suburban landscape, especially for urban Northern Cardinals and American Robins (Blair 1996). Non-native species (e.g., European Starling (*Sturnus vulgaris*) and House Sparrow (*Passer domesticus*)), representing urban exploiters, had the highest densities at the most urban sites for Palo Alto, Oxford, and Cincinnati. These two exploiters are among the most common species comprising urban bird communities around the world; unlike urban avoiders and adapters, the abundance of these species is not dependent on vegetation, but instead on exploiting foods and shelter provided by people (Nilon and VanDruff 1987). Consequently, as urbanization expands globally, biological homogenization will increase as many of the same urban adaptable species become increasingly widespread and locally abundant

(McKinney 2006).

EXAMPLES OF FINE-SCALE AND COARSE-SCALE PROCESSES

Fine-scale processes: nesting success and artificial nests

Using the broad scale land-use gradient from our Oxford study area, Reale and Blair (2005) conducted field experiments investigating fine-scale processes including nesting success and nest predation using artificial nests (see Blair 2004, Reale and Blair 2005). They first explored whether increasing levels of urbanization influenced the nesting success of birds, by focusing on Northern Cardinals and American Robins. These two species were selected based on their ubiquitous distribution across land-use types and due to the efficacy of locating their nests (< 3 m above ground). Contrary to expectations and previous research (Jokimaki et al. 2005), the probability of nest predation decreased with increasing urbanization ($W = -2.05$, $P = 0.04$; Blair 2004; Wald's statistic (W) was used to identify significant variables ($P < 0.05$)). However, the decrease in predation with increasing urbanization did not increase the nesting success of American Robins or Northern Cardinals ($W = 3.44$, $P = 0.001$; Blair 2004). Since site, and consequently level of predation, was not a significant predictor of nest fate for robins ($df = 1$, $W = 0.66$, $P = 0.42$; Blair 2004) or cardinals ($df = 1$, $W = 0.002$, $P = 0.96$; Blair 2004), the reason for nest failure in more urban sites is more likely nest abandonment or food unavailability than predation.

Their findings also failed to support the idea that nesting success influences the density of individual species. Even though the nesting success of robins and cardinals varied, it was neither correlated to the density of individuals at a site (for robins: $df = 1$,

$W = 0.08$, $P = 0.67$; and cardinals: $df = 1$, $W = 0.01$, $P = 0.84$; Reale and Blair 2005) nor clearly related to the level of urbanization (for robins: $df = 1$, $W = 0.66$, $P = 0.42$ and cardinals: ($df = 1$, $W = 0.002$, $P = 0.96$; Reale and Blair 2005), suggesting that individuals are unable to select nesting sites based on the suitability of the land use in terms of nesting success. This inability to select sites highlights the importance of conducting fine-scale demographic studies in conjunction with diversity measures in assessing habitat quality, especially in urban systems where density of individuals may not be a good predictor of nesting success (Bock and Jones 2004, Donnelly and Marzluff 2004).

Gering and Blair (1999) compared predation of both real and artificial nests using two Zebra Finch (*Poephila guttata*) eggs and one plasticine egg within the same nest (see Gering and Blair 1999). Artificial nest types had higher probabilities of predation than natural nests ($W = 3.44$, $P = 0.001$; Blair 2004), but both displayed the same general trend of predation decreasing with urbanization ($W = -2.05$, $P = 0.04$; Blair 2004), suggesting that artificial nests can serve as surrogates for real nests (no significant interaction between nest type and site, $W = 0.79$, $P = 0.78$; Blair 2004).

These findings appear to contradict research that has found nest predation increases with urbanization (Jokimäki and Huhta 2000). These other studies were conducted using the urban context paradigm that examined green spaces embedded across an array of surrounding land-use intensities. Jokimäki and Huhta's (2000) findings are verified by studies that estimated higher abundances of nest predators in parks found in urban areas than rural areas (Sorace 2002) and with increasing forest width around green spaces (Sorace 2002, Sinclair et al. 2005). As an example of direct

urbanization paradigm, the Oxford urban-rural gradient examined sites across land-use intensity types and not just patches of “natural” habitat. We expect to see more dramatic responses when examining sites within land-use types versus sites within “parks.” Caution should be taken when drawing conclusions from gradient studies depending on what portion of variation along urban- rural gradient is being evaluated. For example, Thorington and Bowman (2003) found that predation varied greatly in patches when residential housing density was used to determine the urban gradient.

Fine-scale processes: nest site selection

As an example of fine-scale processes elucidated by the Oxford direct urbanization gradient study, Reale and Blair (2005) examined the role of nest site location and height for influencing nesting outcome. In general, the maturity, and consequently the height of trees, is lower in urban areas than in less developed areas (Porter et al. 2001), plausibly providing fewer nesting options for birds. Nest height significantly influenced nesting outcomes for robins and cardinals (robins: $df = 1$, $W = 14.157$, $p < 0.01$; and cardinals: $df = 1$, $W = 9.410$, $p < 0.01$; Reale and Blair 2005), with nests higher off the ground being more likely to succeed. Furthermore, mean nest height decreased with urbanization (robins: $R^2 = 0.23$, $p < 0.001$; cardinals: $R^2 = 0.13$, $p = 0.03$; Reale and Blair 2005), suggesting that birds must select lower quality nesting sites in more developed areas. In addition, examination of the breeding bird community showed that species that characteristically nest higher in trees dropped out completely at the most urban sites, whereas mid- and low-height nesting species increased (Reale and Blair 2005).

Fine-scale processes: local vegetation effects on bird communities

Because local (i.e., fine scale) vegetation structure and composition can influence the habitat quality for birds (Mills et al. 1989, Donnelly and Marzluff 2006), we explored the role of vegetation using the direct urbanization gradient paradigm in Oxford and the urban context gradient paradigm in Cincinnati. For both the Oxford and Cincinnati study areas, we documented predictable changes in vegetation patterns across the urban gradient (see Porter et al. 2001) and how local vegetation influenced riparian bird communities in Cincinnati (see Pennington et al. 2008). Along both urban gradients, native bird species were positively correlated with sites having a high proportion of native woody vegetation, while non-native bird species declined with native woody vegetation. Both bird density and richness were more influenced by vegetation composition whereas the evenness of the bird community was influenced by vegetation structure (Table 3). In other words, both vegetation structure (MacArthur et al. 1966) and composition influence habitat quality (Mills et al. 1991, Rottenborn 1999, Reichard et al. 2001, Fleishman et al. 2003). Forest breeding species, in particular Neotropical migrants, displayed the greatest correlation with native vegetation across species. A plausible mechanism could be that native vegetation provides a higher abundance of food resources and potential higher nesting success (Schmidt and Whelan 1999; Reichard et al. 2001). Notably, just as native birds decrease along the urban gradient, so too does the native vegetation community, with non-native vegetation peaking in the most urban areas for riparian forests in Cincinnati. These similarities across the gradient highlight the difficulty of teasing out process from pattern in a system that has coupled factors influencing ecosystem processes. However, these

findings also suggest that the loss of native vegetation is a major process through which development affects native and non-native birds.

Coarse-scale processes: landscape heterogeneity

As stated earlier, heterogeneity can occur at any scale of investigation, from the individual tree species of a forest at a fine scale to a mosaic of forest types across a landscape at coarse scales. For the Oxford study area, Porter et al. (2001) found that landscape heterogeneity (as measured by percent dissimilarity of woody species) varied across the urban gradient ($\chi^2 = 308.09$, $df = 5$, $P < 0.001$; Porter et al. 2001) and peaked at moderate levels of urbanization (Porter et al. 2001). This intermediate peak corresponds to the pattern we observed for bird community richness and Shannon diversity, suggesting that landscape heterogeneity could be another factor driving community composition. Based on the results of a two-variable regression model, both bird richness and diversity positively correlated with landscape heterogeneity and negatively with the number of canopy patches, implying that bird diversity is highest when there is a mixture of vegetation types in large patches (Blair 2004). One explanation for these patterns is that when woody vegetation is lost due to urbanization it creates a disturbance that facilitates local invasion by pioneer generalists of both plant and bird species, thus temporarily increasing species richness. Over time, this increase is tempered by the loss of species due to habitat loss. Indeed, high loss of woody vegetation associated with development has been shown to facilitate the invasion of non-native woody species (Hutchinson and Vankat 1997).

Coarse scale processes: spatial effects of surrounding land-use

Birds respond to habitat heterogeneity at a variety of scales and the level of response varies for different species (e.g., body size, migrating and foraging habits) (Hostetler 1999), yet few studies have addressed this in urban ecology. Such information is important not only for ecologists, but for city planners as well, since a connection exists between the scales at which birds respond to landscape structure and the scales at which people drive development (Hostetler 2001). Traditionally, urban habitat studies have arbitrarily selected a scale (e.g., local vegetation as a fine-scale measure and a landscape variable (often within 1 km of the site) as the coarse-scale measure) to correlate bird measures to habitat structure. As a few studies have pointed out, these arbitrary scales may not reflect the most important scale to which birds respond (Hostetler and Holling 2000, Hennings and Edge 2003, Hostetler and Knowles-Yanez 2003, Dunford and Freemark 2005). Many of the studies that have examined landscape structure and scale have used broad urban-rural gradients and employed coarse-resolution land use/land cover data (i.e., Landsat satellite imagery). Additionally, bird data is often collected at a much finer resolution (e.g., survey point counts or line transects) than the methods used to quantify the urban gradient (e.g., quantifying habitat with 30 x 30 m pixel resolution landcover data), creating a scale mismatch between remote sensing and bird data that is rarely addressed (Gottschalk et al. 2005). Depending on the species in question, the scale of interest could vary significantly (Hostetler 1999).

In contrast to previous studies, we used fine-resolution IKONOS satellite imagery (4 m² pixel resolution) of the Cincinnati area to classify forest cover and use

digitized building footprints from fine-resolution color orthophotos to calculate building area (see Pennington et al. 2008). We examined bird diversity and landscape structure at 50, 100, 250, and 500 m radii surrounding each riparian site based on *a priori* knowledge that several breeding bird territory sizes are encompassed within smaller scales and the larger scales might be for migrating species. Our findings show that riparian birds respond most strongly to landscape structure at the 250 m scale (see Fig. 4). This implies that to maintain native birds we need to avoid activities that diminish tree cover both near and adjacent to urban streams and that riparian buffers of 250 m are sufficient to protect a reasonable amount of bird diversity.

Another aspect to our investigation addressed how migratory guild as a life history characteristic influenced birds' response to landscape structure. During the spring, Neotropical migrant density and richness peaked with increasing tree cover and fewer buildings at the 250 m and 500 m scale (Fig. 4). In contrast, exotic species density peaked as building area increased and tree cover decreased at the 250 m scale (Fig. 4a,b). Larger areas of forest cover are possibly perceived as having higher habitat quality in terms of food and nesting resources for Neotropical migrants. Short-distance migrants and permanent residents displayed the weakest response to landscape structure across scales with marginal responses to tree cover and grass cover at the 250 m scale and no response to building area (Fig. 4). It is possible that these two groups of species have adjusted to the habitat changes because they live in this location most if not all of the year, yet it is also possible that these groups were responding to scales beyond what we measured (Mayer and Cameron 2003b).

Additionally, the grain of the study can affect how much variation is captured

and may have limited our ability to discern patterns. Another study of Neotropical migrants in Ohio found no relationship between bird abundance and forest cover or urbanization using a 1 km radius and 30 m² Landsat imagery (Rodewald and Matthews 2005). The fact that we did find a relationship between migrants and landscape structure at a finer scale suggests that some spatial relationships may begin to break down at larger scales (> 500 m).

IMPORTANCE OF CONSIDERING LIFE-HISTORY CHARACTERISTICS

Grouping bird communities based on differing life-history guilds can aid in distinguishing process from pattern (Levin 1992) as illustrated above in the spatial section for migratory guilds. In this section, we highlight additional examples from the direct and urban context paradigms from Ohio that underscore the importance of considering life-history traits in discerning pattern and process.

Examining species' brooding strategy (number of broods per year) can provide insights when interpreting ecological patterns. For the Oxford study, Reale and Blair (2005) partitioned the breeding bird community into brooding strategies of single, double, and multiple broods during the breeding season. We then examined if brooding strategy changed across the urban-rural gradient (see Reale and Blair 2005). The proportion of species in the community that rely on multiple brooding sharply increased with urbanization. In contrast, single brooding species displayed a dramatic preference for the least disturbed sites on the gradient. Interestingly, these patterns are similar to the above patterns for the riparian migratory guilds. The shift in the overall community-level brooding strategy is due to the replacement of single brooding

Neotropical migrant species with generalist, multi-brooding species represented by many short-distance and permanent residents of Ohio. Presumably, multiple brooding species are able to compensate for nesting losses in sites with low nesting success by making multiple attempts, while many Neotropical migrants are restricted to one or two broods given the constraints of long-distance migration (Moore et al. 1995). In addition, a change in community-level brooding strategy from low productivity to high productivity at low and highly developed sites suggests a possible change in overall nesting-habitat quality for some species along the gradient. These findings indicate that nesting success over the entire season for the community may provide a better understanding of the distribution of bird species than examining only individual nesting failure alone.

An important aspect of the Cincinnati riparian study is to understand the role of urban areas in providing stopover versus breeding habitat for long-distance migrants species (see Pennington et al. 2008; Pennington unpublished data). Habitat use during migration has been largely overlooked in the development of conservation strategies (Mehlman et al. 2005). Instead, most research has been conducted during the breeding season. However, different life stages can represent periods when birds respond to the landscape in fundamentally different ways. During the breeding season, birds focus on establishing territories and nesting sites, whereas during migration, birds focus on resting and foraging along the way to and from their wintering grounds (Moore and Kerlinger 1987). Hence, food availability could be the most important criteria for selecting suitable stopover habitat en-route (McWilliams et al. 2004, Smith et al. 2007).

We examined riparian bird communities during the spring and summer breeding

seasons of 2002 (surveyed six times during 4 April – 25 May and six times during 30 May – 15 July). To examine migratory season, we divided the Neotropical migrants into en-route (those that are not known to breed within the study area, but do utilize the area during stopover) and potentially breeding species (species known to establish breeding territories within the study area). During the migratory season, we found that several Neotropical species utilize urban riparian forests. Potentially breeding Neotropical migrant density and richness increased with the amount of tree cover and low levels of development surrounding the stream (i.e., less urban sites), while en-route migrant density and richness were highest in areas of high tree cover regardless of the level of development (Fig. 5). This finding suggests that some urban areas with high tree cover (e.g., a residential neighborhood with mature trees throughout) are perceived as “forest” and suitable stopover site to long-distance migrants en-route, but are perceived as unsuitable habitat by potentially breeding individuals. A comparison of response to landscape structure during spring migration and breeding season further supports this finding. During the spring Neotropical migrants respond most significantly to tree cover, but during the breeding season they respond most strongly to building area surrounding a site (Pennington 2003).

NEW DIRECTIONS FOR APPLYING URBAN-RURAL GRADIENT ANALYSES IN AVIAN RESEARCH

Throughout this paper we have provided examples from our own work on urban-rural gradients to highlight how this methodology can provide insights into

complex processes structuring bird communities in urbanizing areas. We recommend the following for future research on birds in urban areas.

Analyze the community in total, as different migratory groups, and by life history traits

Researchers should use partitions of the bird community and not limit their analyses to the entire bird community alone. Dividing the total bird community into functional guilds (e.g., migratory guilds, brooding guilds, foraging guilds) can provide key insights into pattern and process (Levin 1992) (Fig. 4). An important finding from our analyses shows that brooding and migratory guilds respond to urbanization in different ways. A change in species distribution based on brooding strategy from low productivity to high productivity with increased development possibly signifies lower, less predictable, habitat quality and an attempt to overcome this limitation (Reale and Blair 2005). Our analysis of migratory guilds along riparian areas in Cincinnati showed a dramatic decrease in Neotropical migrant abundance and diversity with increasing urbanization (Pennington et al. 2008) in contrast to an overall increase in total bird abundance. These contradictory trends are supported by other studies on breeding bird communities (Friesen et al. 1995, Hennings and Edge 2003, Mayer and Cameron 2003b, Miller et al. 2003). Additionally, studies differentiating the breeding bird community using foraging guilds have shown that urban avoiders tend to be insectivorous leaf gleaners, and urban adapters and urban exploiters comprised of mainly ground foraging seedeaters and omnivores (e.g., Emlen 1974, Miller et al. 2003, McKinney 2006). Further research investigating food availability (e.g., insect abundance and supplemental feeding) and species competition (e.g., foraging efficiency

(Shochat et al. 2004), along urban gradients is needed.

Bird responses differ seasonally

Our examination of riparian bird communities during the spring migratory season highlights the need for more detailed studies on the affects of urbanization on migrant stopover strategies. Conservation strategies have traditionally focused on breeding and overwintering habitat quality, which were often thought to be the primary factors influencing population declines. Consequently, urban areas have been perceived as inhospitable to Neotropical migrants and ignored when devising conservation plans. However, recent evidence suggests that factors experienced during a migrant's journey to and from the wintering and breeding grounds could ultimately be driving some Neotropical migrant population declines (Sillett and Holmes 2002). Our findings imply that certain levels of development, traditionally considered poor habitat for *breeding* Neotropical migrants, are actually important during spring and fall as stopover habitat. In Cincinnati, both surrounding forest cover and native vegetation composition influence en-route migratory species' responses across the gradient; however, building area surrounding the stream is not as important (Pennington et al. 2008). These findings suggest that for stopover conservation, if development must occur, it should incorporate a high degree of vegetative structure (especially mature trees > 70 yr; Donnelly and Marzluff 2006) and native vegetation composition. Measures of habitat-specific demography and dispersal during migration should also be examined along the urban-rural gradient to further improve conservation recommendations. In addition, studies of the effects of urbanization on migrant wintering habitat are also needed. We caution

against the general labeling of Neotropical migrants as “urban avoiders” in the future as this designation depends on whether the bird is breeding, migrating, or overwintering at the time of the study.

Assess species richness, diversity, and evenness for a comprehensive view of the community

There are several indices to measure diversity, yet no single measure includes the number of species and species abundance while revealing how much either contributes to the final value (Hayek and Buzas 1997). Therefore, measures of density, species richness, and evenness are needed to capture different aspects of diversity. Most community-level studies have relied on the community measures of abundance/density or species richness when evaluating bird communities (Marzluff 2001), often ignoring the role of evenness; however, our results from Cincinnati suggest that evenness provides additional information on community processes. Evenness accounts for how evenly partitioned individuals are among species, and is a potentially important measure for urban studies since bird communities are often dominated by a few species (McKinney 2002, Blair 2004). In general, density, species richness, and evenness differed in the magnitude of response to scale and local habitat variables across migratory guilds (Fig. 4) (Pennington et al. 2008). For example, evenness for the total bird community and in particular, permanent residents, decreases with development, indicating that a few synanthropic species dominate the urban bird community (Johnston 2001). Additionally, density and species richness are influenced by the local vegetative composition of riparian forests whereas evenness is influenced

by vegetative structure (Pennington et al. 2008).

Incorporate both experiments and field observations on demographics to understand individual and community dynamics shaping bird distributions

As illustrated earlier, both demographic and community-level studies are important for elucidating process from pattern. Community-level studies that quantify relative species abundance have been, and continue to be, essential for understanding the effects of urbanization on bird community structure and composition. However, the insights derived from these observed patterns regarding the processes driving community change are limited and could be potentially misleading (Marzluff et al. 2001, Shochat et al. 2006). Studies of only species presence/absence or relative abundance cannot determine whether detected individuals of a species are experiencing positive or negative survivorship at a site. Consequently, these studies do not differentiate whether a population is a source, sink or stable (Pulliam 1988). Therefore, field experiments and field observations on population demographics should be incorporated into studies of relative abundance. Given our findings regarding predation, demographic studies should also account for the contribution of food availability, re-nesting, and multiple brooding to better estimate population growth rate, source-sink dynamics, habitat quality, or population viability (Nagy and Holmes 2004).

Recognize that the amount of variation across a gradient will influence the pattern observed

It is important to consider the context of the urban-rural gradient for a particular study when drawing conclusions about process from the patterns observed. The amount

of variation captured across a gradient can vary from study to study with some studies examining only a small portion of the entire urban-rural gradient spectrum (Marzluff et al. 2001). In other words, some studies have focused on the entire gradient at broad scales and others on only one or two land-use types along the gradient, which may explain why it has been difficult to elucidate generalities regarding bird responses to urbanization (McKinney 2002). For example, the curvilinear responses observed for the Palo Alto and Oxford studies may result from an entire array of land-use intensity types (Fig. 2). Observed linear responses of decreasing richness and diversity with increasing measures of urbanization could be due to studies only capturing variation along suburban to urban land-use types, whereas positive linear responses could be due to only capturing variation along exurban to suburban types (Fig. 3). On the other hand, the type of response (i.e., linear vs. curvilinear) may also be due to the urban measure used (Lepczyk et al. 2008).

Recognize that some studies focus on intensifying land use while others focus on intensifying surrounding land use

The two common urban-rural gradient paradigms, direct urbanization and urban context, focus on intensifying land use and on intensifying surrounding land use, respectively. Both are valuable methods for discerning pattern from process at fine and coarse scales. When examining sites within all land-use types comprising the spectrum of the urban-rural gradient, species responses will often be more dramatic than when only examining sites located within “green spaces.” Most urban-rural gradients in urban ecology have followed the urban context paradigm. Although this paradigm

continues to be important, studies that evaluate sites located within differing intensifying land uses are needed to directly measure how species are responding to various types of development. In addition to increasing the number of studies explicitly examining various land-use types, we also need further investigation on the variation within a particular land-use type (e.g., not all suburban residential areas are the same and can vary in size, density, age, etc.).

Analyze land-use/land cover at an array of scales

Processes determining the richness, composition, and dynamics of communities occur at various scales (Wiens 1989a). Consequently, multi-scale analyses should be considered for both demographic and community-level studies along urban-rural gradients (Hostetler 1999). As illustrated by our analyses on migratory stopover, both spatial and temporal scales are important for understanding bird distributions. More studies are needed to address how results vary as a function of scale and to search for consistent patterns in these scale effects (Rahbek 2005). Researchers should also report the spatial grain and extent of their study area since these two constraints can greatly influence conclusions (Mayer and Cameron 2003a). For example, both coarse- (landscape level) and fine- (vegetation level) scale factors influence stopover habitat selection along riparian areas in Cincinnati (Pennington et al. 2008). In addition, researchers should address the issue of using coarse-scale land use/land cover data with fine-scale bird surveys (Gottschalk et al. 2005). The land use/land cover data classifications (e.g., USGS Anderson-derived classifications) used to quantify the gradient influences the amount of fine-scale heterogeneity captured across the urban-

rural gradient (Cadenasso et al. 2007).

The intended audience should also be considered when determining the scale of a particular study. For example, an ecologist may want to know only about a forest patch, a homeowner may only be concerned about the parcel, a land manager may want to know about protected lands, and a planner may want to know effects at the zoning or municipal level. Historically, urban ecologists have been satisfied with focusing on the ecology of urban systems (i.e., an organisms' response to biophysical variables). As we are now realizing, our current understanding of even the ecology is quite limited in the absence of social and economic factors (Pickett et al. 2001, Alberti 2005, Grove et al. 2006a). Recent efforts analyzing socioeconomic and demographic aspects of urban ecology have suggested potential mechanisms by which private landowners influence bird communities (e.g., Lepczyk et al. 2004a,b, Kinzig et al. 2005). We need to move towards a more inclusive interdisciplinary approach to studying the effects of urbanization on organisms as described below.

Incorporate biophysical and socioeconomic factors into gradient analysis

A more inclusive approach to studying urban systems – the ecology *of* cities – addresses the entire range of habitats within metropolitan areas and not just the green spaces that are the focus of the ecology *in* cities described thus far (Pickett et al. 1997a,b, Grimm et al. 2000). In urban systems, people make decisions at multiple scales, from individuals to households to municipalities and agencies, which directly influence the landscape mosaic (Grove et al. 2006b). In this approach, people and their institutions are recognized as a part of the ecosystem and not just outside influences

(Cadenasso et al. 2006). Understanding the feedbacks between socioeconomic and biophysical factors, both spatially and temporally, will allow urban ecologists to more explicitly tease apart finer scale processes driving bird distributions.

To do this, we will need to explore new ways to quantify the complex heterogeneity of these areas. Researchers at the Baltimore Long-Term Ecological Research site (LTER) have developed a new comprehensive method for integrating the built and natural components of urban systems into a high-resolution classification tool, High Ecological Resolution Classification for Urban Landscapes and Environmental Systems (HERCULES) (Cadenasso et al. 2007). This tool provides urban ecologists the opportunity to examine structure and function separately at spatial scales appropriate for urban areas. Incorporating HERCULES, or other land cover models that separate built versus vegetation elements, with urban avian studies promises to aid in illuminating both the biophysical and socioeconomic drivers of bird distributions.

Conclusions

Even though we have highlighted several differences in the ways urban ecologists can, and should, examine patterns and process using gradient analysis, we want to emphasize that we, as researchers, need to focus on the commonalities among studies using similar methods. It is important to understand how our methodological differences influence the patterns observed, but we also need to derive a common framework so that we can compare our studies and findings as illustrated by a comment at a recent professional meeting noting that if ecologists were given the task of discovering the Universal Law of Gravitation, they still would be dropping different

items from the apple tree to see to see how differently they fell under different conditions. In our work as urban ecologists and ornithologists, we need to focus on the universal similarities of our systems and not the picayune differences.

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Table 1. A general description of the three different rural to urban gradient studies: Palo Alto, CA, Oxford, OH, and Cincinnati, OH.

	<u>Direct Urbanization</u>		<u>Surrounding Urbanization</u>
	Palo Alto, CA	Oxford, OH	Cincinnati, OH
Human population density	955.8/km ²	402.8/km ²	1,498.0/km ²
Extent of area sampled	~150 ha	~ 150 ha	~ 100 ha
# of plots sampled	6 sites, 16 points per site	6 sites, 16 points per site	71 points; identified systematically from a random starting point
The amount of the coarse 'rural to urban' gradient measured	Urban, office park, residential, golf course, open space, and nature preserve	Urban, office park, residential, golf course, open space, and nature preserve	Predominately urban (with varying surrounding land uses ranging from 'wildland' to 'urban')
Measure of urbanization	Axis 1 scores from PCA of: % tree/shrubs area, % grassland and lawn, % pavement, % building	Axis 1 scores from PCA of: % tree/shrubs area, % grassland and lawn, % pavement, % building	Building area, % tree/shrubs, and % grassland and lawn cover analyzed as separate variables
Measures of birds	Species richness Relative species density	Species richness Relative species density Nest search Artificial nests	Species richness Relative species density

1

Table 2. Distribution and abundance of summer resident birds in Oxford, Ohio (similar results were found for Palo Alto, CA and Cincinnati, OH). *Notes:* line widths represent ranges of numbers of birds per hectare (x). These ranges are displayed graphically to illustrate the ebb and flow of densities across the gradient for each species. Nomenclature follows the American Ornithologists' Union (1998).

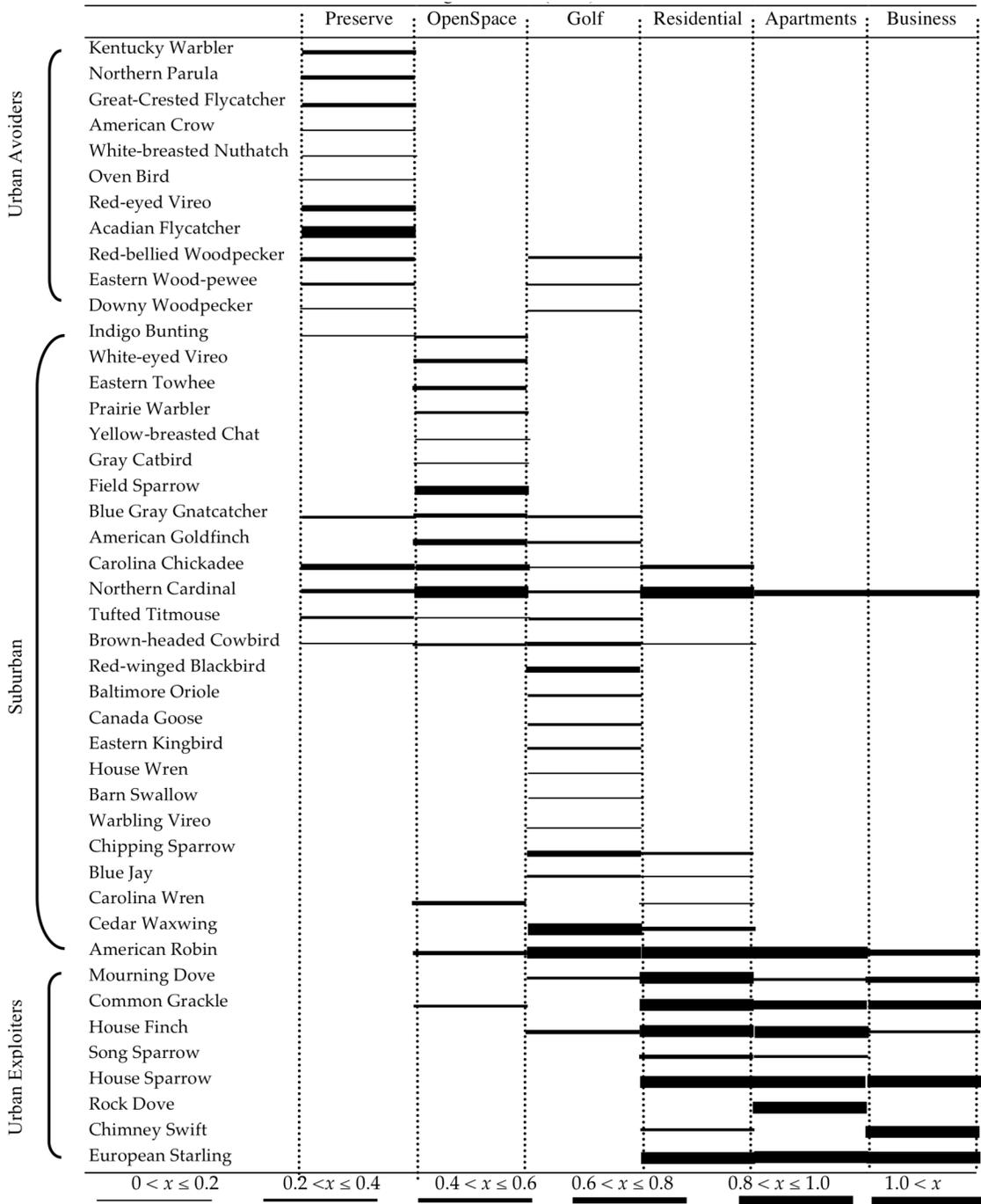


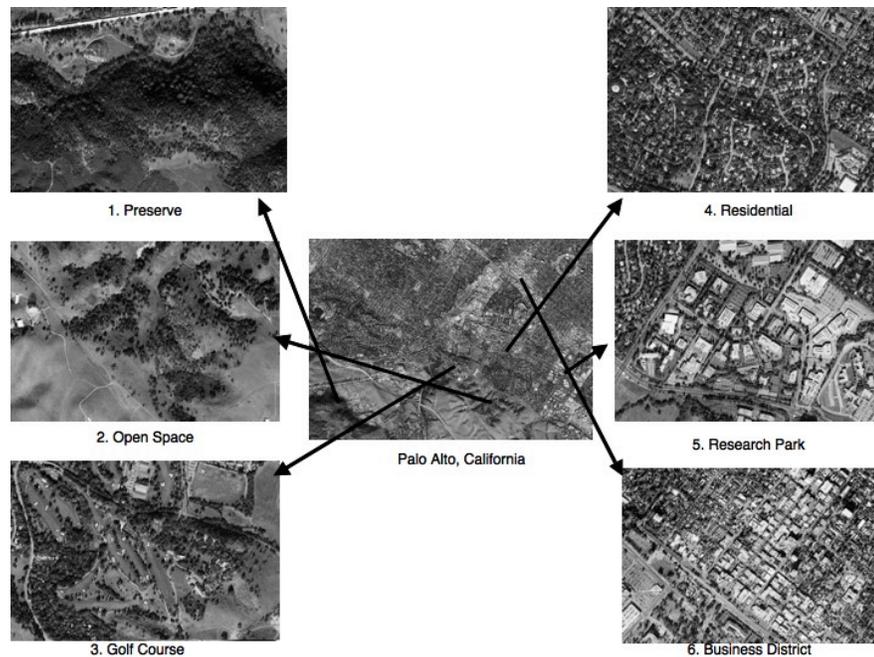
Table 3. Model summary for migratory guild community measures and local vegetation measures from multiple regression analyses.

Migratory guild	Vegetation Composition			Vegetation Structure				Adj. r^2
	Native tree frequency	Native shrub/sapling frequency	Total tree richness	Overstory stem density	Understory stem density	Dead Trees	Canopy Height	
	Partial r	Partial r	Partial r	Partial r	Partial r	Partial r	Partial r	
Relative density								
AB	+ 0.2646	- 0.1100	- 0.0340	+ 0.1888	- 0.2344	- 0.1494	+ 0.0199	0.07
N	+ 0.4159	+ 0.2007	+ 0.0275	+ 0.2149	- 0.1170	- 0.2100	+ 0.1341	0.34
EN	+ 0.3585	+ 0.0637	+ 0.0184	+ 0.0961	- 0.0472	- .1878	+ 0.1862	0.24
PBN	+ 0.3143	+ 0.2032	- 0.0618	+ 0.2105	- 0.1012	- 0.1719	+ 0.0680	0.22
SD	+ 0.0378	- 0.2872	- 0.0487	- 0.0287	- 0.2346	+ 0.0132	- 0.0346	0.05
P	- 0.0034	- 0.1149	- 0.0573	+ 0.2577	- 0.0814	- 0.1219	- 0.0998	0.00
E	- 0.2339	- 0.2893	- 0.1239	- 0.2373	- 0.1589	+ 0.2281	- 0.1975	0.35
Species richness								
AB	+ 0.4241	- 0.0157	+ 0.0610	+ 0.2733	- 0.2712	- 0.1769	+ 0.0719	0.29
N	+ 0.3974	+ 0.2093	+ 0.0413	+ 0.2576	- 0.1299	- 0.2370	+ 0.1234	0.36
EN	+ 0.3403	+ 0.1121	+ 0.2245	+ 0.1196	- 0.0031	- 0.2163	+ 0.1801	0.28
PBN	+ 0.2932	+ 0.1867	- 0.0635	+ 0.2454	- 0.1362	- 0.1885	+ 0.0565	0.22
SD	+ 0.2842	- 0.2476	+ 0.0511	+ 0.0536	- 0.2981	+ 0.585	- 0.0441	0.05
P	+ 0.1154	- 0.1329	+ 0.0466	+ 0.2516	- 0.1482	- 0.1669	+ 0.0162	0.01
Evenness								
AB	+ 0.3189	+ 0.1418	+ 0.1278	+ 0.1099	- 0.0485	- 0.2269	- 0.0394	0.21
N	+ 0.0438	+ 0.0867	- 0.0467	- 0.4584	- 0.1302	- 0.0003	+ 0.2174	0.29
EN	+ 0.2344	+ 0.1085	+ 0.1019	+ 0.1698	+ 0.0097	- 0.1663	+ 0.1017	0.15
PBN	+ 0.1592	+ 0.1541	- 0.1296	+ 0.3400	- 0.1201	+ 0.1267	+ 0.1211	0.20
SD	- 0.0092	- 0.2108	+ 0.1911	+ 0.0232	+ 0.2543	- 0.2164	- 0.1328	0.12
P	+ 0.2714	+ 0.3162	- 0.0457	+ 0.2619	- 0.2178	- 0.2703	- 0.2441	0.32

^a (+/-) REPRESENTS EFFECT IN RELATIONSHIP; DENOMINATOR DF ARE 70 FOR ALL EFFECTS: ALL BIRDS (AB), NEOTROPICAL MIGRANTS (N), EN-ROUTE NEOTROPICAL MIGRANTS (EN), POTENTIALLY BREEDING NEOTROPICAL MIGRANTS (PBN), SHORT-DISTANCE MIGRANTS (SD), PERMANENT RESIDENTS (P), AND EXOTIC (E; DENSITY ONLY).

Figure 1. Differences in the study design for two urban-rural gradient paradigms: a) example of direct urbanization gradient paradigm where study sites were located within six land-use types (Palo Alto, CA shown; the method was used for the Oxford, OH study); b) example of the urban context gradient paradigm where sites are embedded within “natural” features or green space (represented by forested riparian “corridor”) that are surrounded by myriad land-use-types (Cincinnati, OH shown).

a) Direct urbanization



b) Urban context

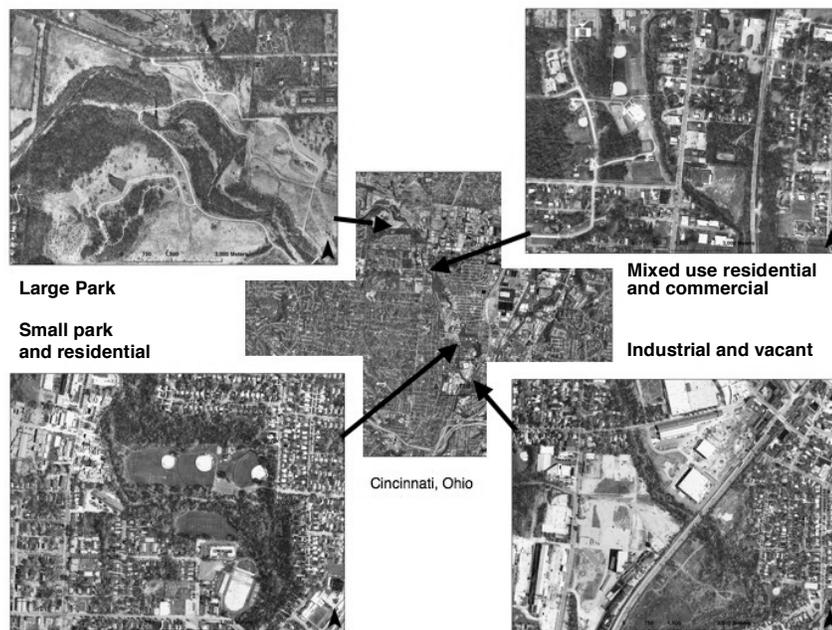


Figure 2. Change in community metrics, species richness and Shannon's diversity, along an intensifying urbanization gradient that was quantified based on the PCA Axis 1 scores (constrained by % tree cover, % grass, % impervious, and % building cover).

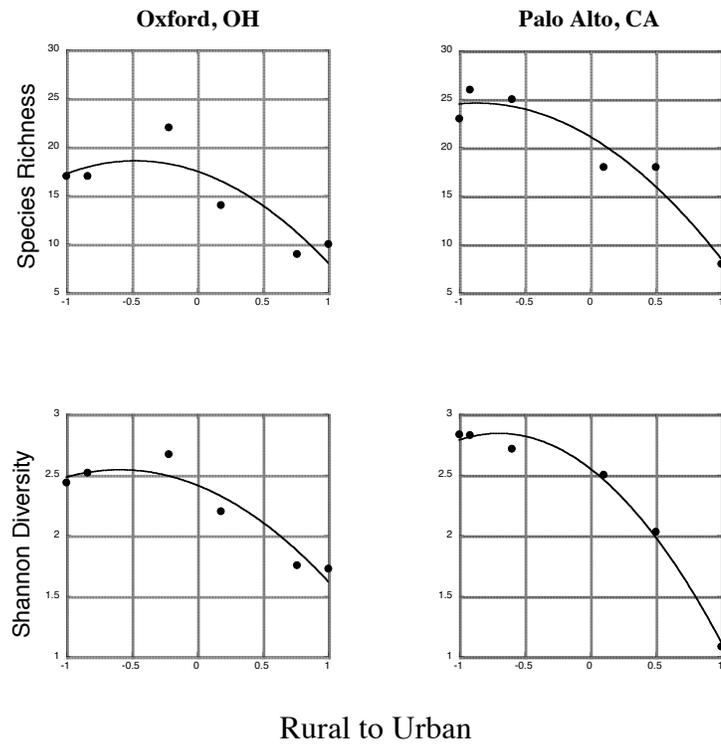


Figure 3. Change in community metrics, relative density and species richness along an intensifying urbanization gradient quantified by examining % tree cover and building area within 250 m separately: a, c) total bird density and richness displayed strong curvilinear responses to the amount of tree cover surrounding a site; a peak or threshold response for density at 60% tree cover (a) and for richness at 70% tree cover (c); and b, d) both total bird density and richness declined linearly with increasing building cover.

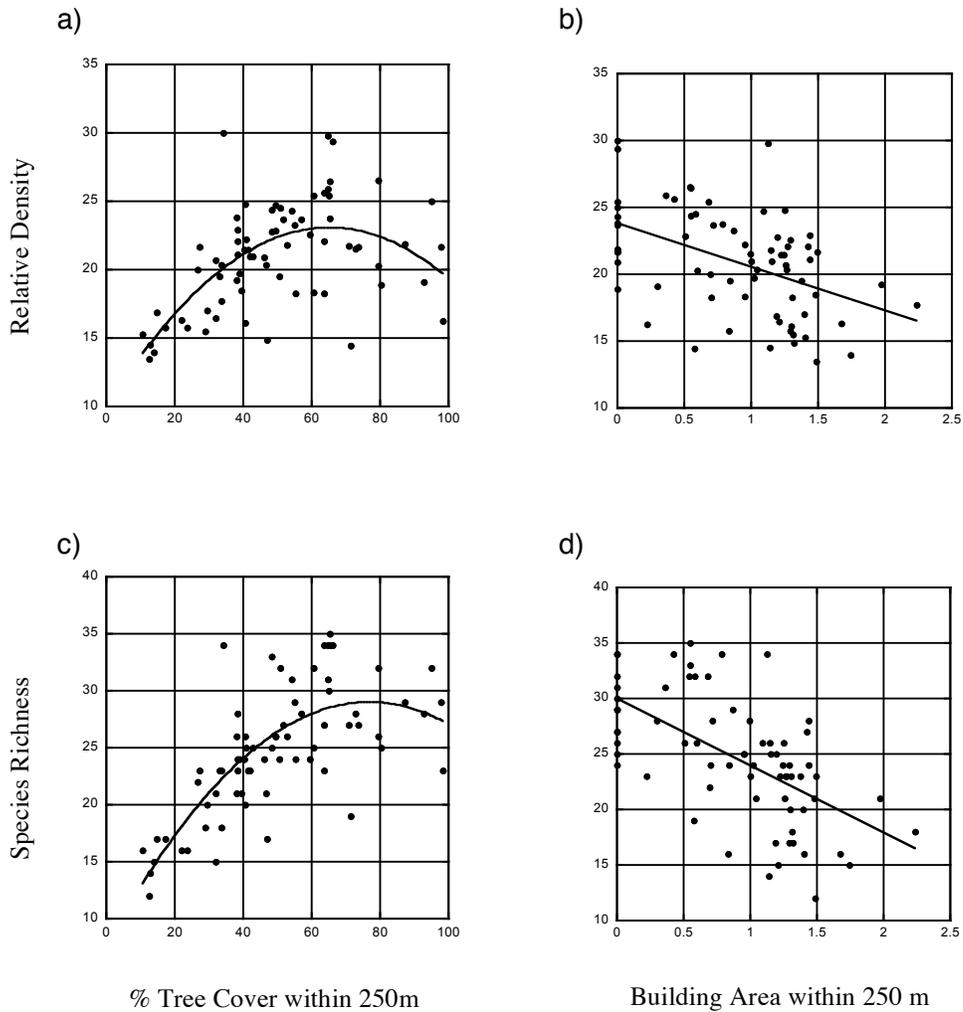


Figure 4. Comparison of the proportion of variance explained in linear regressions by % tree cover (a, c, e) and building area (b, d, f) across four scales (50, 100, 250, 500 m radii) for relative density (a, b), species richness (c, d), and evenness (e, f) for all birds (AB), Neotropical migrants (N), short-distance migrants (SD), permanent residents (P), and exotic (E; density only) during the spring migratory season for tributaries of Mill Creek, Cincinnati, OH; * represents a significant spatial response based on uniqueness index tests ($p < 0.05$). Abundance and richness displayed curvilinear responses (adjusted r^2 values from linear regressions with a quadratic terms; no uniqueness index tests performed). a, c, e) In general, native bird density and diversity measures increased with the amount of tree cover around a plot; exotic species responded oppositely; b, d, f) total birds and Neotropical migrant density and richness decreased sharply with increasing building area; again exotic species responded oppositely. Total species evenness declined sharply with increasing building area. In general, the 250 m scale was the most important scale across guilds and landscape measures (Pennington et al. 2008).

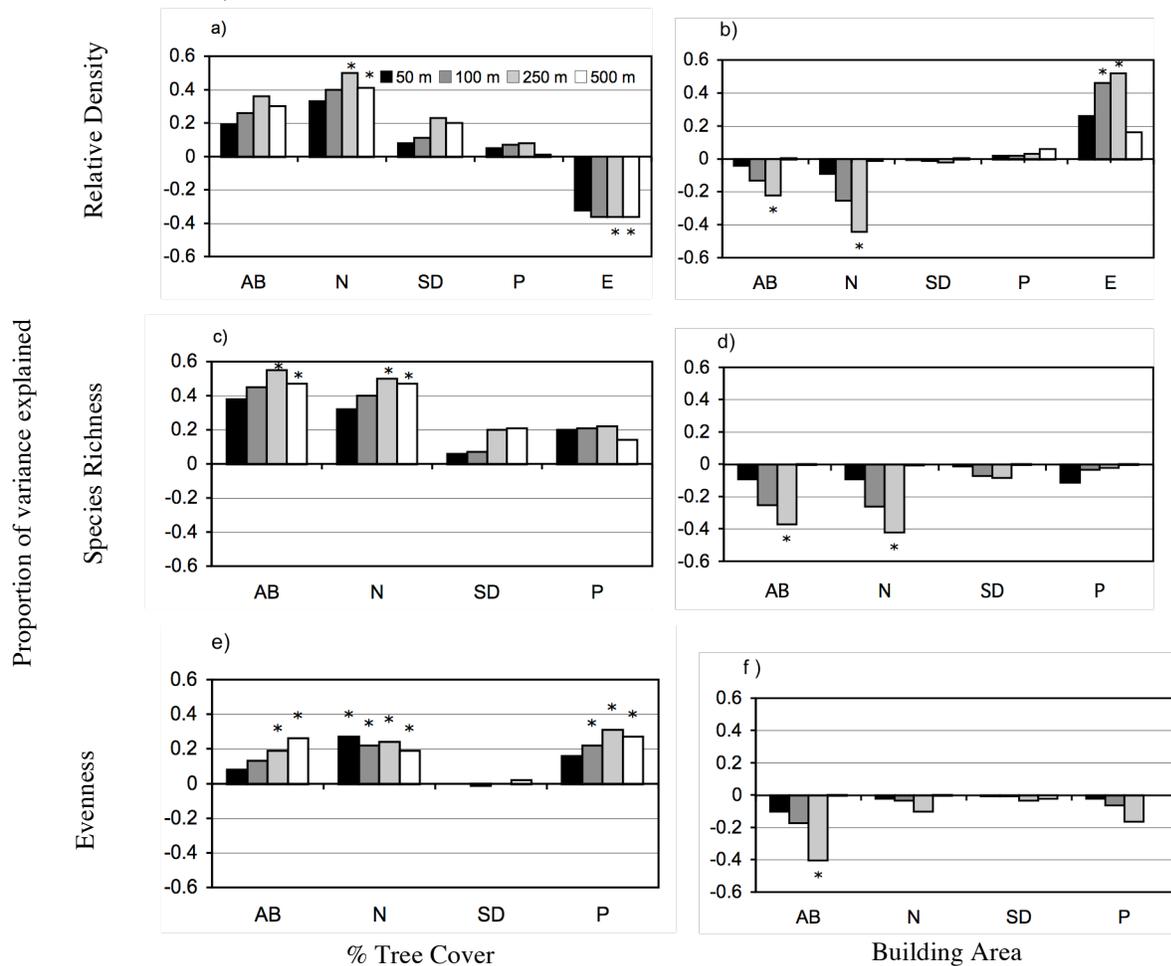
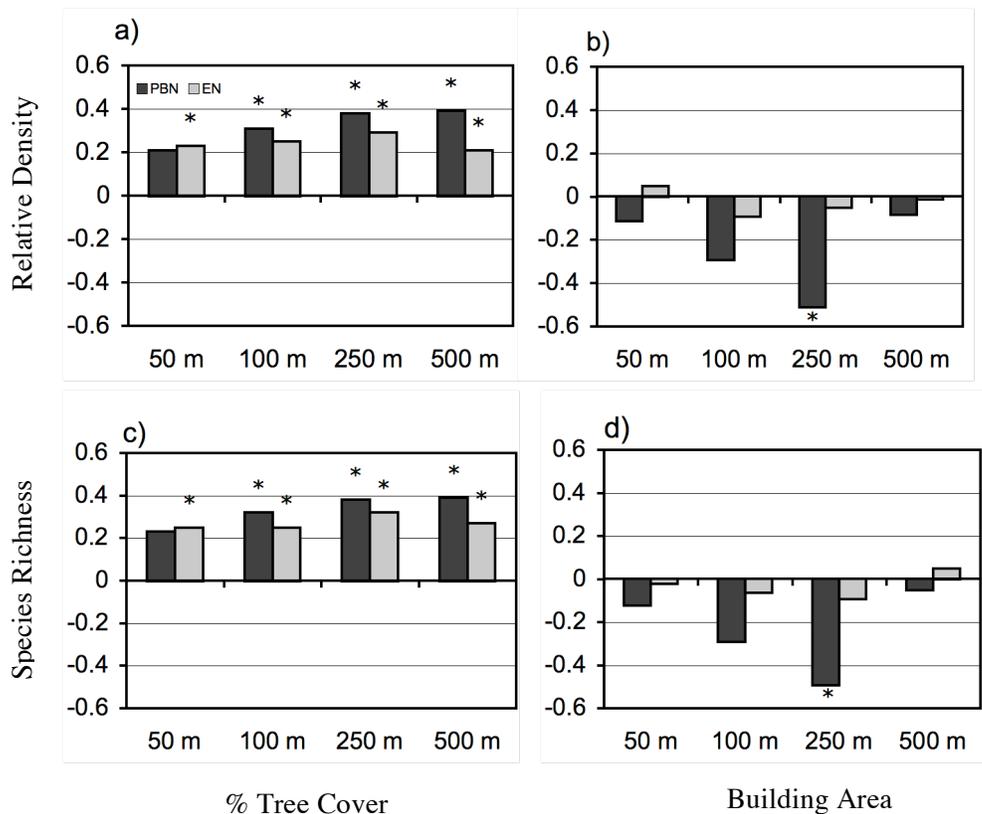


Figure 5. Comparison of the proportion of variance explained in linear regressions by % tree cover (a, c) and building area (b, d) across four scales (50, 100, 250, 500 m radii) for relative density (a, b) and species richness (c, d) of potentially breeding (PBN) and en-route (EN) Neotropical migrants during the spring migratory season for tributaries of Mill Creek, Cincinnati, OH; * represents a significant spatial response based on uniqueness index tests ($p < 0.05$). a, c) Both potentially breeding and en-route Neotropical migrant richness increased with surrounding tree cover; potential breeders displayed a stronger relationship to tree cover > 500 m around stream. b, d) Potential breeding Neotropical migrant richness declines sharply with increasing building area surrounding the stream, whereas en-route richness displayed little or no response to building area (Pennington et al. 2008).



CHAPTER 3

The Conservation Value of Urban Riparian Areas for Landbirds During Spring Migration: Land Cover, Scale, and Vegetation Effects

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ABSTRACT: Urbanization changes bird community structure during the breeding season but little is known about its effects on migrating birds. We examined patterns of habitat use by birds at the local and landscape level during 2002 spring migration at 71 riparian plots along an urban gradient in Cincinnati, Ohio, U.S.A. Using linear regression, we examined variation in relative density, species richness, and evenness of four migratory guilds associated with natural land covers and building area at four scales (50, 100, 250, 500 m radial buffers). We also examined the influence of local vegetation using multiple regression models. As building area increased, riparian forests tended to be narrower and have fewer native trees and shrubs. In general, native birds were positively associated with tree cover (within 250 to 500 m of stream) and native vegetation, and negatively with building area (within 250 m); exotic species responded inversely to these measures. Short-distance migrants and permanent residents displayed the weakest responses to landscape and vegetation measures. Neotropical migrants responded most strongly to landscape and vegetation measures and were positively correlated with areas of wide riparian forests and less development (> 250 m). Resident Neotropical migrants increased with wider riparian forests (> 500 m) without buildings, while en-route migrants utilized areas having a wide buffer of tree cover (250 to 500 m) regardless of buildings; both were positively associated with native vegetation composition and mature trees. Consequently, developed areas incorporating high native tree cover are important for conserving Neotropical migrants during stopover.

INTRODUCTION

Urbanization is one of the leading drivers of native species extirpation at continental (Czech et al., 2000) and regional scales (e.g., Blair, 2001). Urbanization alters and fragments natural habitats through the removal of native vegetation and the introduction of exotic species and novel infrastructure (e.g., buildings, pavement, roads). In general, urban areas support fewer species than natural areas (see Marzluff, 2001); many species that do persist are typically widespread or exotic (Blair, 2001). However, several studies highlight the capacity of certain land uses within urban areas to harbor native species (e.g., Blair, 1996) suggesting that better-designed urban landscapes could sustain more biodiversity in the future. Consequently, urban areas need not be viewed as ‘ecological sacrifice zones’ by conservationists, but ought to be viewed as opportunities to enhance regional biodiversity (Rosenzweig, 2003).

People have historically settled near streams and rivers for access to drinking water, food, irrigation, transportation, and industry. Given this close association, it is not surprising that riparian areas are among the most threatened of landscapes (Groffman et al., 2003). In addition to their benefit to people, riparian areas also support a high diversity of plants and animals (Naiman et al., 1993). These areas also provide important habitat for migrating birds during the spring and fall (Ohmart, 1994; Skagen et al., 1998; Yong et al., 1998; Skagen et al., 2005). This is of particular interest for conservation because of recent declines in some species, especially Neotropical migrants (Robbins et al., 1989; Peterjohn et al., 1995).

The effect of urbanization on riparian bird communities during the breeding season is a relatively recent area of research (e.g., Rottenborn, 1999; Green and Baker, 2003; Hennings and Edge, 2003; Miller et al., 2003; Rodewald and Bakermans, 2006). Habitat characteristics at both the local and landscape scale influenced Western riparian breeding bird communities (Rottenborn, 1999, Miller et al., 2003, Smith and Wachob, 2006). In particular, distance to the nearest urban structure (buildings or bridges) negatively influenced species richness and overall density (Rottenborn, 1999). In Northwestern U.S.A, riparian bird communities of forested parks responded to the intensity of human disturbance at different scales around a stream (Hennings and Edge, 2003). Further, native vegetation composition of riparian forests was an important resource for Western native bird communities (Mills et al., 1989; Rottenborn, 1999; Hennings and Edge, 2003). Native vegetation was correlated with increasing species richness and relative density in these riparian systems (Mills et al., 1989, Rottenborn, 1999); exotic vegetation often lacks the structural and dietary benefits required by many native animal species (Reichard et al., 2001). Additionally, fragmentation and urban intrusion near stream corridors lead to an increase in brood parasitic birds and other predators, such as stray cats and raccoons, and these negatively affect native breeding bird species (Robbins et al., 1989; Gering and Blair, 1999; Reichard et al., 2001; Lepczyk et al., 2004).

Migratory songbirds, because they have complex life histories and range over a wide area, pose a unique challenge to conservation (Levin, 1992; Moore et al., 1995; Hostetler, 2001). Recent research suggesting that some Neotropical landbird populations are limited during their migratory journey, and not on their breeding or

wintering grounds (Sillett and Holmes, 2002), raises the importance of managing stopover habitat for long-distance migratory species. Mechanisms affecting riparian birds during the breeding season may also operate during migration. For example, Yong et al. (1998) noted that loss of native vegetation can negatively influence populations of Wilson's warblers (*Wilsonia pusilla*) during the stopover period. Furthermore, as during the breeding season, forest patch mosaics which are close together or connected by corridors might be best for migrants (Petit, 2000).

Insectivorous migrant songbirds in Western states prefer riparian habitats for refueling (Johnson et al., 1977; Stevens et al., 1977), but were more abundant in contiguous upland forest patches when compared to riparian forests in Columbus, Ohio (Rodewald and Matthews, 2005). In contrast, others report that Midwestern U.S.A. migrants concentrate in forested riparian areas during spring and fall (Winker et al., 1992; Weisbrod et al., 1993). Individual species also differ in the selection of habitat based on patch sizes from spring to summer (Hostetler and Holling, 2000). Given the potential differences between breeding and stopover habitat selection, identifying the types of habitats most important during migration, and how land-use decisions are changing these habitats, is a critical but overlooked aspect to conservation planning (Moore et al., 1995).

Many existing urban studies that have examined the effects of different habitats have ignored community variation across multiple scales (Hostetler and Holling, 2000; Hostetler and Knowles-Yanez, 2003; Mayer and Cameron, 2003). Ecological responses can vary depending on the scale in question (Wiens, 1989; Levin, 1992). Metropolitan areas are comprised of a complex mosaic of different land uses including dense

development, parks, lower-density suburbs, and smaller city centers (Alberti et al., 2001). Consequently, the variation in responses across spatial and temporal scales could be quite dynamic. Studies focusing on these landscape mosaics at varying scales within urban areas will aid in developing management practices that enhance habitat value through better design (Hostetler, 2001).

The purpose of this study was to examine the relationship between urbanization and bird community composition of Midwestern U.S.A. riparian areas during migration. Since different species respond to landscape structure at varying scales, we took a multi-scale approach, investigating how local and landscape attributes affect avian relative density, richness, and evenness of four migratory guilds as well as exotic species. We explored 1) how land cover at four different spatial scales (50, 100, 250, and 500 m radii around a plot) affects the distribution of avian community diversity and composition; and 2) how local vegetation influences habitat selection during the migratory season, in order to predict the effect development patterns might have on migrating bird communities along urban riparian areas.

METHODS

Study region

The 4 243 ha study area within the urbanizing Mill Creek watershed (42 994 ha) is located on the geologically homogeneous Pre-Wisconsinan Drift Plains within the greater Cincinnati metropolitan area (39.2° N 84.5° W) (Fig.1). Pre-European settlement vegetation was comprised of Beech (*Fagus grandifolia*) – Maple (*Acer saccharum*) and mixed-mesophytic forests (Braun, 1950). The area represents one of

the fastest growing areas in Ohio, with more than half a million people living and working in the watershed (U.S. Census Bureau, 2000) and has been designated one of the most polluted and threatened urban rivers in the United States (American Rivers, 1997).

Study design

We sampled birds, vegetation, and environmental variables across a gradient of human settlement intensity following an urban gradient approach (McDonnell and Pickett, 1990). Along Mill Creek and its tributaries of West Fork Mill Creek and Sharon Creek (Fig. 1), we identified 100 plots systematically from a random starting point (Ralph et al., 1995) using ArcGIS 9.1 Geographic Information System (GIS) and the 2002 Cincinnati Area Geographic Information System (CAGIS) dataset (using 2001 color orthophotos at 0.5 m resolution). Plots were located along the streamside edge across myriad land uses including natural areas and lands belonging to municipalities, industries, and homeowners. Stream channel width was similar across plots (~ 10 m). We separated plots by at least 150 m and marked them in the field using a global positioning system (GPS). We excluded 29 plots because of physical difficulties of surveying or lack of permission from private landowners to access the stream.

Bird surveys

We surveyed all 71 plots six times during the spring migratory season (April 4 to May 25, 2002) using variable-radius point-counts (Reynolds et al., 1980; Bibby et al., 2000), except for two plots that we only surveyed five times due to adverse weather. Pennington recorded all individuals heard or seen during 5 minutes within a 50 m radius

during the first 3.5 hours following sunrise. We surveyed 15 to 20 plots daily, allowing all plots to be visited during the same week. Correction for detectability between developed and undeveloped plots was not required because detection functions for most species were relatively constant to 50 m (Schieck, 1997). Additionally, by using small sampling circles with repeated sampling we reduced our likelihood of missing individuals (Ralph et al., 1995; Siegel et al., 2001).

Because migrating landbirds continuously move across the landscape, often spending only a few days at a location while traveling to breeding habitat, we considered a species present at a plot if it occurred once during the six visits. In order to reduce the influence from potentially surveying breeding individuals more than once during the season, we calculated the relative density of each species as the number of individuals divided by the survey effort (number of visits to a site) and plot area (see Reynolds et al., 1980). We did not include birds flying over or through the sampling plot in our analyses. Further, we did not include raptors, shorebirds, waterfowl, nocturnal and crepuscular species, and aerial insectivores in our analyses, because point counts are poor at detecting these species (Bibby et al., 2000).

We examined migratory guilds (Hennings and Edge, 2003; Hurlbert and Haskell, 2003; Rodewald and Bakermans, 2006) to elucidate how migration strategy influences habitat selection during the spring migratory period. We divided species into migratory guilds: resident Neotropical migrants, en-route Neotropical migrants, total Neotropical migrants (the combination of resident and en-route), short-distance migrants, and permanent residents (classified using Ehrlich et al., 1988; Peterjohn and Sauer, 1993; DeGraaf and Rappole, 1995; Keller et al., 1999; see Appendix A for list of

species). Neotropical migrant species spend their winters in Central and South America and migrate long distances in the spring to breed in North America during the summer. Resident Neotropical migrants are known to establish breeding territories within the study area. En-route Neotropical migrants are not known to breed within the study area, but do utilize the area during stopover. Short-distance migrants spend their winters north of the U.S.- Mexico border. Permanent residents remain year-round within the study area. We also examined exotic species separately (defined as those species not present in the area prior to 1850): European starling (*Sturnus vulgaris*), house finch (*Carpodacus mexicanus*), and house sparrow (*Passer domesticus*).

Measures of bird diversity

We measured relative density, species richness, and evenness to capture different aspects of diversity (Magurran, 2004). For each guild, we calculated total relative density (N) (after square root transformation to counteract skewness), species richness (S) and evenness (E) for each of the 71 plots. Only relative density was used for exotic species, since this guild comprised only three species. Evenness was calculated as $E = H'/S$, where H' = Shannon's diversity ($H' = -\sum p_i \log_e p_i$) and S = species richness (Hayek and Buzas, 1997). Evenness ranges from 0 to 1, approaching 1 when individual birds are partitioned equally among species.

Landscape measurements

We measured landscape characteristics within four buffers (i.e. scales) at 50 m, 100 m, 250 m, and 500 m radii around each plot center based on *a priori* knowledge that most breeding bird territory sizes are encompassed within smaller scales and larger

scales might be important to migrating species selecting stopover habitat (e.g., Hutto, 1985; Mayer and Cameron, 2003). We used ArcMAP® GIS version 9.1 and Spatial Analyst software to calculate metrics within a given buffer. For biophysical measures, we used a land-cover classification map derived from 4 m resolution 2001 IKONOS satellite imagery from CAGIS. The classified land-cover data had a 90% accuracy rating when compared to high-resolution color aerial photography (CAGIS; *personal communication*) and included the following land-cover types: trees, grass (e.g. lawns and open meadows), impervious surfaces (e.g., roads, pavement, buildings), agriculture/soil, and water. We included percent tree and percent grass cover as biophysical measures and excluded percent agriculture/soil and percent water (comprised a very small portion of the study area) and percent impervious surface (highly negatively correlated with tree cover; $R^2 > 0.90$).

To measure development, we used an index of building area per hectare, henceforth “building area”, derived from digitized building footprints for each buffer area that was log transformed to counteract skewness. Building density (number of buildings per hectare) is thought to be a good surrogate for settlement intensity (Marzluff et al., 2001). However, our metropolitan study area is comprised of various building types and sizes and the footprint of a single industrial building can have an area several orders of magnitude greater than a typical residential building. Consequently, building density could oversimplify development (Hostetler and Knowles-Yanez 2003). Building area and tree cover correlations were relatively low ($R^2 < 0.60$ for each scale) indicating that the simple presence of buildings was not a surrogate measure for a lack of trees.

Local vegetation measurements

We measured characteristics of the local woody vegetation composition (floristics) and structure (physiognomy) during August to October 2002. In order to capture vegetation data on both sides of the stream, we located a 70-meter diameter plot at the origin of the bird sampling point. We created five 35-meter transects radiating from the origin of the plot, and five 10-meter diameter subplots were centered at randomly selected points 5-35 m from the origin along each transect. If a subplot included the stream, the radial transect was reselected or shifted in 10° increments so no part of the subplot was located in the water. We identified all trees ≥ 10 cm diameter at breast height (dbh) and measured their dbh within the plot and identified dead trees for separate analysis. In each 10-meter diameter subplot, we identified woody plants with stems < 10 cm diameter and calculated total stem density. Also, in each subplot, we measured the height of the tree (≥ 10 cm dbh) located nearest the center using a clinometer. For each plot, we averaged the five height measures to obtain a canopy height measure for the plot. We calculated relative frequency of native canopy and understory species according to Barbour et al. (1987). Exotic or non-native species were defined as those absent from the study area prior to European settlement (Braun 1989).

Spatial analysis of riparian bird guilds to landscape characteristics

We used simple linear regression to examine the correlations between bird community composition and landscape measures at the four buffer distances. The response variables were relative density, species richness, and evenness, analyzed

separately for each guild and the explanatory variables were percent tree and grass cover and building area within a given buffer. We conducted linear regressions separately for each of the four buffer areas. This resulted in an R^2 statistic measuring the strength of each relationship for increasing buffer distance up to 500 m; we plotted the R^2 statistic against the radial distance from the bird sampling point to assess how these relationships varied spatially. To determine which land cover category most explained bird distributions, we selected the category with the highest R^2 value (> 0.20 ; based on our sample size $N = 71$).

Our goal was to determine if a community measure responded to a land cover category at only one scale or across a range of scales. Generally, we expected collinearity within land cover categories for the four spatial scales. To aid in elucidating which scale or scales for each land cover category was most significant in determining bird distributions, we used a uniqueness index test (SAS Institute, 1994; see Hostetler and Knowles-Yanez, 2003). This test accounts for the potential collinearity among varying buffer areas for a particular land cover category across all 4 spatial scales. First, we selected the land cover category with the highest R^2 value for a given avian community variable ($R^2 > 0.20, P < 0.05$). For buffers having R^2 values within 0.09 of this highest R^2 value, we did not try to determine whether community measures responded to one scale over another. Next, we examined R^2 values smaller by at least 0.10 of the highest R^2 value. For community measures that had at least one R^2 value > 0.20 and at least one R^2 value < 0.10 or more of the highest R^2 for a given land cover category, we conducted a uniqueness index test.

We examined scatterplots prior to these analyses and observed negative quadratic responses between percent forest cover and short-distance migrant relative density and richness and percent forest cover and permanent resident relative density and richness. We included a squared term in these models to account for the curvature. Due to the curvilinear nature of these models, we were not able to perform a uniqueness index test. Under these circumstances, we suggest possible trends, but not significance.

Multiple regression models of local vegetation on riparian bird guilds

To determine the importance of local vegetation during migration, we constructed multiple linear regression models between bird community measures and the seven local vegetation variables (see Table 1); none of the explanatory variables were highly correlated as defined by $r > 0.50$. We report the partial correlations for each vegetation variable and the adjusted R^2 values for all models. For each model, we inspected the partial correlation coefficients to determine the directional and relative importance of each of the seven habitat variables on avian community measures. Because our goal was to look at the relative importance of each explanatory variable on each response variable, we chose not to use a model-selection strategy which would have required considering a limited subset of possible models *a priori* and would not allow the detection of unanticipated relationships.

RESULTS

Bird community

We recorded 7748 detections of 102 species at the 71 sites. For the rest of our discussion, we focus on the 88 species that met our criteria for analysis (see Appendix A). Of these bird detections, most were native species (83%). Half of the detections were short-distance migrants (distributed among 30 species), 39% permanent residents (11 species), 11% Neotropical migrants (47 species), 4% en-route (19 species), and 7% resident Neotropical migrants (28 species). Ten species accounted for 63% of all bird detections; in descending order these were: northern cardinal (*Cardinalis cardinalis*), American robin (*Turdus migratorius*), house sparrow (*Passer domesticus*), European starling (*Sturnus vulgaris*), Carolina chickadee (*Poecile carolinensis*), brown-headed cowbird (*Molothrus ater*), American goldfinch (*Carduelis tristis*), song sparrow (*Melospiza melodia*), Carolina wren (*Thryothorus ludovicianus*), and white-throated sparrow (*Zonotrichia albicollis*). Many species were widespread; 16 species occurred in over half of the plots and 12 species occupied over 75% of the plots (Appendix A). The two most abundant species, northern cardinal and American robin, were present at all plots. The third and fourth most abundant species were exotic: the house sparrow occurred at 62% of the plots, while European starling occurred at more than 90% of the plots. Even less common species, such as downy woodpecker (*Picoides pubescens*) and tufted titmouse (*Baeolophus bicolor*), still occurred at over 80% of the plots. Several species of Neotropical migrants were widespread but to a lesser degree; 6 species

occurred at over 35% of the plots and Baltimore oriole (*Icterus galbula*) and red-eyed vireo (*Vireo olivaceus*) occupied 45% of the plots.

Landscape and local vegetation measures

Based on Spearman's rank correlations, all native tree and shrub measures were negatively correlated with building area at 250 m (Fig 2). Conversely, exotic tree and shrub frequency measures were positively correlated with building area and is consistent with previous findings that habitat disturbance increases the abundance of non-native plant species (Hobbs and Huenneke, 1992; Hutchinson and Vankat, 1997). The amount of dead trees present at a plot also increased with building area. These correlations suggest a development gradient characterized by increased building area and associated environmental changes, particularly increased fragmentation, and a shift within the habitat matrix from riparian landscapes of high forest cover comprised of native tree and shrub species to relatively more building coverage, less forest cover, and non-forest landscape components (e.g., lawns, agricultural pastures, recreational fields) and increased presence of exotic woody species.

Spatial response of birds to landscape characteristics

Three general trends emerged from the spatial analyses. First, the percentage of tree cover was often the most predictive landscape characteristic of bird guilds across scales (Fig. 3) with the exception of the proportion of building area, which was most predictive of resident Neotropical migrants (Fig. 4a, b) and exotic species (Fig. 3b). These two guilds had opposite correlations with respect to building area; resident Neotropical migrants were inversely correlated with building area while exotics were

positively correlated. Secondly, species richness tended to respond most strongly to landscape characteristics followed by relative density and evenness across bird guilds. Finally, birds responded most strongly to the medium and largest scales measured, i.e. 250 m to 500 m scales.

Birds of different migratory guilds displayed varying responses to scale and landscape characteristics. Neotropical migrants responded most predictably to landscape characteristics for all guilds; relative density and richness correlated to broad expanses of surrounding percent tree cover (> 250 m scale; Fig. 3a, c) on the landscape, and evenness correlated less strongly to tree cover across scales (Fig. 3e). Short-distance migrants responded less predictably compared to the other migratory guilds; relative density and richness was weakly positively correlated to the percent grass cover within 100 m to 500 m ($R^2 \leq 0.24$ for all scales) and species richness displayed a negative quadratic response to percent tree cover at the 250 m to 500 m scales (adj. $R^2 \leq 0.21$ for all scales) (Fig. 3a, c). Permanent resident responses varied; richness displayed a negative quadratic response with percent tree cover at 50 to 250 m scales (adj. $R^2 \leq 0.20$ for all scales; Fig. 3c) and evenness was linearly positively correlated with percent tree cover at scales from 100 m to 500 m ($R^2 \leq 0.31$ for these scales; Fig. 3e). Contrastingly, exotic species responded inversely to landscape characteristics compared to the other guilds; their relative densities were best predicted by building area at 100 m and 250 m scale ($R^2 \leq 0.45$ for all scales; Fig. 3a, b).

A closer examination of the Neotropical migrants highlights differences between resident and en-route Neotropical migrant species during migration with respect to scale and landscape characteristics. Both guilds correlated with the amount of tree cover

surrounding a plot, with resident migrants displaying a stronger relationship (Fig 4a, c, e, comparison between guilds highlighted). The two guilds responded differently to the proportion of a site covered by buildings; resident migrants avoided areas with a high proportion of building coverage with relative density and richness strongly negatively associated with building area, most significantly at the 250 m scale ($R^2 = 0.49$; Fig. 4b, d). En-route migrants, in contrast, displayed no significant relationship to building area at any scale (Fig. 4b, d, f).

Multiple regression models of local vegetation on bird guilds

The response of birds to local vegetation composition and structure measures varied (Table 1). In general, native canopy and understory frequency were the most predictive variables across models. Similar to the spatial results, Neotropical migrants responded most predictably to local vegetation measures when compared to the other bird guilds (Table 1). Interestingly, Neotropical migrant relative density and richness were best predicted by the species composition of the riparian forest, responding positively to native canopy and understory stem frequencies and tree species richness, but evenness was best predicted by the vegetation structure as represented by a positive correlation with higher canopy stem densities and taller canopies (Table 1). In contrast, exotic species responded negatively to vegetation; their relative density was inversely predicted by the same vegetation variables (Table 1). Higher native species composition of the canopy and understory vegetation and the vegetation structure (fewer dead trees and higher canopy stem densities) led to higher permanent residents evenness (Table 1). Short-distance migrants displayed weak responses to local

vegetation. Resident and en route Neotropical migrants responded similarly to local vegetation. Their relative densities were best predicted by an increase in native canopy and understory stem frequency and taller canopies (Table 1). In general, native bird measures were weakly negatively correlated with the increasing number of dead trees at a plot (Table 1).

DISCUSSION

Effects of landscape across multiple spatial scales

Our findings underscore the importance of considering the surrounding matrix for managing riparian areas for avian conservation (Table 2). For all spatial scales, native birds tended to be more abundant, have higher numbers of species, and were more evenly distributed in areas of high tree cover and low proportions of building area (Fig. 3). The general effect of urban infrastructure (e.g. buildings and roads) and the associated displacement of tree cover on breeding bird communities has been well documented (e.g., Friesen et al., 1995; Saab, 1999; Hennings and Edge, 2003; Miller et al., 2003; Rodewald and Bakermans, 2006). Even though tree cover was moderately correlated with building area, birds still responded differently to the two landscape characteristics. Because tree cover predicted bird response better than building area, in order to maintain native riparian bird species, activities that diminish the amount of tree cover on adjacent surrounding lands should be avoided (within 250 m of the stream). Interestingly, building area at the 500 m scale never displayed a significant relationship in any of our models (Fig. 3b, d, f). The reason for this loss of a clear signal could have

resulted from our study area being located within a highly modified metropolitan landscape that is extremely heterogeneous in terms of land use and land cover at broad spatial scales.

Examining the riparian bird community based on different migratory guilds illuminated the influence of life-history traits on ecological responses to scale (Levin, 1992). For example, building area was significant for only Neotropical migrants and exotic species and they responded in opposite ways. These two guilds are analogous to previous classifications of bird communities based on urban ecological niches: Neotropical migrants as “urban avoiders” and exotic species as “urban exploiters” (Blair, 1996; McKinney, 2002). Urban avoiders tend to be more sensitive to development and its associated disturbances, such as increased predator abundance and decreased resources. Several of these species are considered specialists, i.e. feeding primarily on insects (e.g., Tennessee warbler (*Vermivora ruficapilla*), scarlet tanager (*Piranga olivacea*), and American redstart (*Setophaga ruticilla*)). Urban exploiters (e.g., European starling and house sparrow), on the other hand, are well adapted to intense development and have co-adapted to utilize human by-products (Johnston, 2001). These species tend to feed on a wide variety of food sources and are capable of having multiple broods during the breeding season, therefore, better equipped to deal with the novel predatory and resource pressures of developed areas (Blair, 2004).

Whereas the Neotropical migrant guild represented species having a specific ecological niche, the other two migratory strategies (short-distance migrants and permanent residents) were comprised of species having myriad ecological strategies (urban adapters and urban exploiters; McKinney, 2002). These variations are likely the

reason for the curvilinear responses of short-distance migrants and permanent residents to tree cover across spatial scales. Short-distance migrants were the only guild that responded to grass cover suggesting the importance of heterogeneous landscapes, consisting of a mix of trees and grassy open spaces (e.g., American robin and brown-headed cowbird), for species in this guild; such areas are abundant in low-density residential and commercial land-uses throughout the study area. Permanent residents' positive correlation to wide tree cover corresponds with the many cavity-nesting species comprising this group (e.g., Carolina chickadee, tufted titmouse, downy woodpecker). In addition, it is also possible that these two guilds were responding to spatial scales beyond what we measured (Mayer and Cameron, 2003; Hostetler and Knowles-Yanez, 2003), and further investigation is needed, especially for understanding short-distance migrant habitat selection in metropolitan areas. In particular, examining species-specific characteristics would aid in interpreting species responses within both the permanent resident and short-distance migrant guilds.

Effects of local vegetation structure and composition

Our findings on how local vegetation influences habitat selection during migration were similar to findings from riparian studies in Western North America; native birds in Cincinnati were associated with riparian areas having high percentages of native woody vegetation, while exotic bird species were negatively associated with native vegetation (e.g., Rottenborn, 1999, Green and Baker, 2003, Hennings and Edge, 2003). Bird densities and species richness were more influenced by the floristic composition of riparian forests whereas evenness tended to be influenced by vegetative

structure (Table 1). This illustrates that birds respond not only to the presence of vegetation structure (MacArthur et al., 1966; MacArthur and Pianka, 1966; Anderson and Shugart Jr, 1974), but also to the composition of the riparian woody vegetation community (Mills et al., 1991; Rottenborn, 1999; Reichard et al., 2001; Fleishman et al., 2003).

Neotropical migrants were, more than any other guild, positively associated with native vegetation. One possible mechanism for this finding could be that native vegetation provides more efficient foraging habitat for Neotropical migrants because it harbors higher abundances of insects than exotic vegetation (Yong et al., 1998; Reichard et al., 2001; Smith et al., 2004). For the same plots, native trees and shrubs decreased as building area increased (Fig. 2). This suggests that loss of native vegetation is a major mechanism through which urban development affects birds. Maintaining or restoring native woody trees and shrubs, and limiting development, can have positive effects on native bird communities in urban riparian forests.

The role of urban areas as stopover habitat for Neotropical migrants

We found that several resident and en-route Neotropical migrant species utilize urban riparian forests. While resident Neotropical migrants did prefer wider riparian forests (> 500 m scale) with low development levels, en-route migrants utilized areas having a wide buffer of tree cover (250 m to 500 m scale) regardless of whether houses or other buildings were present (Fig. 4). Consequently, developed areas incorporating a high amount of tree cover throughout might be perceived as “forest” to certain Neotropical migrants during stopover. In essence, Neotropical migrants act like urban

avoiders when selecting a breeding location or are on a breeding territory, but are more adaptable to urban areas while en-route, utilizing moderately developed areas with significant tree cover. This implies that areas that are not perceived as suitable breeding habitat could nevertheless serve as functional stopover sites. Hostetler et al. (2005) also documented that tree cover was important for migrants during fall stopover.

In contrast to our findings, Rodewald and Matthews (2005) found no relationship between migrant density and the amount of forest cover and urbanization within a 1 km radius, suggesting that relationships may collapse at larger spatial scales (> > 500 m from the stream). This highlights the importance of small-scale studies and the need for examining multiple spatial scales in ecological studies. Furthermore, methodological differences in how landscape variables are calculated could also influence the outcomes of landscape studies. Rodewald and Matthews (2005) used 30 m resolution Landsat imagery while we used 4 m resolution IKONOS imagery, allowing us to examine responses to landscape variables at a finer scale (Hostetler and Holling, 2000). In addition to examining multiple scales, researchers working within urbanizing landscapes should consider how well the resolution of the landscape data used captures the complex heterogeneity of urban areas, separately for biophysical and anthropogenic aspects (Cadenasso et al. 2007).

One mechanism explaining differing patterns between resident and en-route Neotropical migrants could be based on resource needs. Within our study area, a resident Neotropical migrant represents an individual potentially seeking to establish a breeding territory (encompassing a safe nesting site and foraging area); ideally, located within a wide forested area with little or no development. In comparison, en-route

species are selecting for habitat to serve as “pit stops” along their migratory journey northward that provide food (insects) and shelter (i.e. tree cover), and are relatively indifferent to the presence of buildings. Importantly, these stopover sites are also only utilized for few days, compared to an entire summer for residents (Mehlman et al., 2005). It is important to note that en-route migrant community measures increased with the presence of native woody tree and shrubs, suggesting that greater food availability (i.e. insect abundance) may be tied to riparian forest species composition (Herrera et al., 2003).

Most of the current research on riparian bird communities has focused on the North American West during the breeding season. In spite of the differences between North American western and eastern ecological systems (George and Dobkin, 2002), our general results were similar to those of western studies. Because all of these western studies examined forest-breeding species along riparian areas in highly fragmented landscapes, we might expect species with similar resource needs to respond to the landscape in parallel ways. Even though the dominant pre-settlement land cover of our study area was forest (Braun, 1950), present-day urban riparian areas of the Midwest and Eastern U.S.A. are highly fragmented and may functionally mimic the “narrow” riparian corridors of the arid West. More studies on birds in eastern urban riparian systems are needed for further geographical comparisons. Moreover, additional research examining differences in habitat selection during migration in both western and eastern riparian systems is needed (Petit, 2000; Skagen et al., 2005).

Conclusions and management recommendations

Conservation strategies for songbirds must consider temporal scales (breeding vs. wintering vs. migration) in addition to spatial scales when assessing habitat use as different life stages may represent periods when birds are using the landscape in fundamentally different ways. From our results, Neotropical migrants utilize urban vegetation across various land use types; in particular, areas with mature native trees. Maintaining unfragmented forest cover within a 250 m and greater radius surrounding streams is paramount for resident Neotropical migrant conservation; however, en-route Neotropical species do appear to be able to utilize both smaller fragmented or marginal areas of forest cover surrounding urban streams, but we do not know how capable these individuals are in securing adequate food, water, and safe haven from predators. Results from our study highlight the possible conservation benefit of metropolitan areas to Neotropical migrants during stopover, but further research is needed to increase our understanding of resource requirements and survivorship of individuals using these urban stopover sites (Mehlman et al., 2005). In addition, research identifying the urban land-use types that can offer the greatest potential to serve as “convenience store” stopover sites (see Mehlman et al., 2005) will need to incorporate both the social and biophysical aspects of urban heterogeneity (Pickett et al., 2001). Urban areas present a unique challenge to researchers, managers, and land-use planners. Understanding both the potential impacts and the potential benefits of urban areas is critical for avian conservation.

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Table 1. Model summary for migratory guild community measures and local vegetation measures from multiple regressions.

	Vegetation Composition			Vegetation Structure				Adj. R ²
	Native canopy frequency	Native understory frequency	Total tree richness	Canopy stem density	Understory stem density	Dead trees	Canopy height	
Migratory guild	Partial r	Partial r	Partial r	Partial r	Partial r	Partial r	Partial r	
Relative density								
Total Neotropical	+ 0.416	+ 0.201	+ 0.028	+ 0.215	- 0.117	- 0.210	+ 0.134	0.34
En-route Neotrop.	+ 0.359	+ 0.064	+ 0.018	+ 0.096	- 0.047	- 0.188	+ 0.186	0.24
Resident Neotrop.	+ 0.314	+ 0.203	- 0.062	+ 0.211	- 0.101	- 0.172	+ 0.068	0.22
Short-distance	+ 0.038	- 0.287	- 0.049	- 0.029	- 0.235	+ 0.013	- 0.035	0.05
Permanent resident	- 0.003	- 0.115	- 0.057	+ 0.258	- 0.081	- 0.122	- 0.100	0.00
Exotic species	- 0.234	- 0.289	- 0.124	- 0.237	- 0.159	+ 0.228	- 0.198	0.35
Species richness								
Total Neotropical	+ 0.397	+ 0.209	+ 0.041	+ 0.258	- 0.130	- 0.237	+ 0.123	0.36
En-route Neotrop.	+ 0.340	+ 0.112	+ 0.225	+ 0.120	- 0.003	- 0.216	+ 0.180	0.28
Resident Neotrop.	+ 0.293	+ 0.187	- 0.064	+ 0.245	- 0.136	- 0.189	+ 0.057	0.22
Short-distance	+ 0.284	- 0.248	+ 0.051	+ 0.054	- 0.298	+ 0.585	- 0.044	0.05
Permanent resident	+ 0.115	- 0.133	+ 0.047	+ 0.252	- 0.148	- 0.167	+ 0.016	0.01
Evenness								
Total Neotropical	+ 0.044	+ 0.087	- 0.047	- 0.458	- 0.130	- 0.000	+ 0.217	0.29
En-route Neotrop.	+ 0.234	+ 0.109	+ 0.102	+ 0.170	+ 0.010	- 0.166	+ 0.102	0.15
Resident Neotrop.	+ 0.159	+ 0.154	- 0.130	+ 0.340	- 0.120	+ 0.127	+ 0.121	0.20
Short-distance	- 0.009	- 0.211	+ 0.191	+ 0.023	+ 0.254	- 0.216	- 0.133	0.12
Permanent resident	+ 0.271	+ 0.316	- 0.046	+ 0.262	- 0.218	- 0.270	- 0.244	0.32

Table 2. General habitat preferences for the different subsets of the migratory bird community based on landscape analyses. Migratory guilds reflect varied responses to landscape measures, which implies different management needs. Habitat characteristics are listed in order of importance. (*See appendix A for the species composition of each guild*)

	Density	Species Richness	Evenness
Neotropical migrants	Wide forests; undeveloped	Wide forests; undeveloped	Narrow and wide forests
Resident Neotropical migrants	Undeveloped; wide forests	Undeveloped; wide forests	Narrow and wide forests
En-route Neotropical migrants	Narrow and wide forests	Narrow and wide forests	Narrow and wide forests
Short-distance migrants	Wide forests; grassy areas	Wide forests; grassy areas	No relationship
Permanent residents	No relationship	Wide forests; undeveloped	Wide forests; undeveloped
Exotic species	Developed; narrow forests	N/A	N/A

Figure 1. Location of the 71 study plots used to examine the relationship between avian communities in riparian areas and urbanization in the Mill Creek watershed in the greater Cincinnati metropolitan area Hamilton County, Ohio, U.S.A. Land use/land cover map derived from IKONOS satellite imagery area shows land-use classes and survey plots.

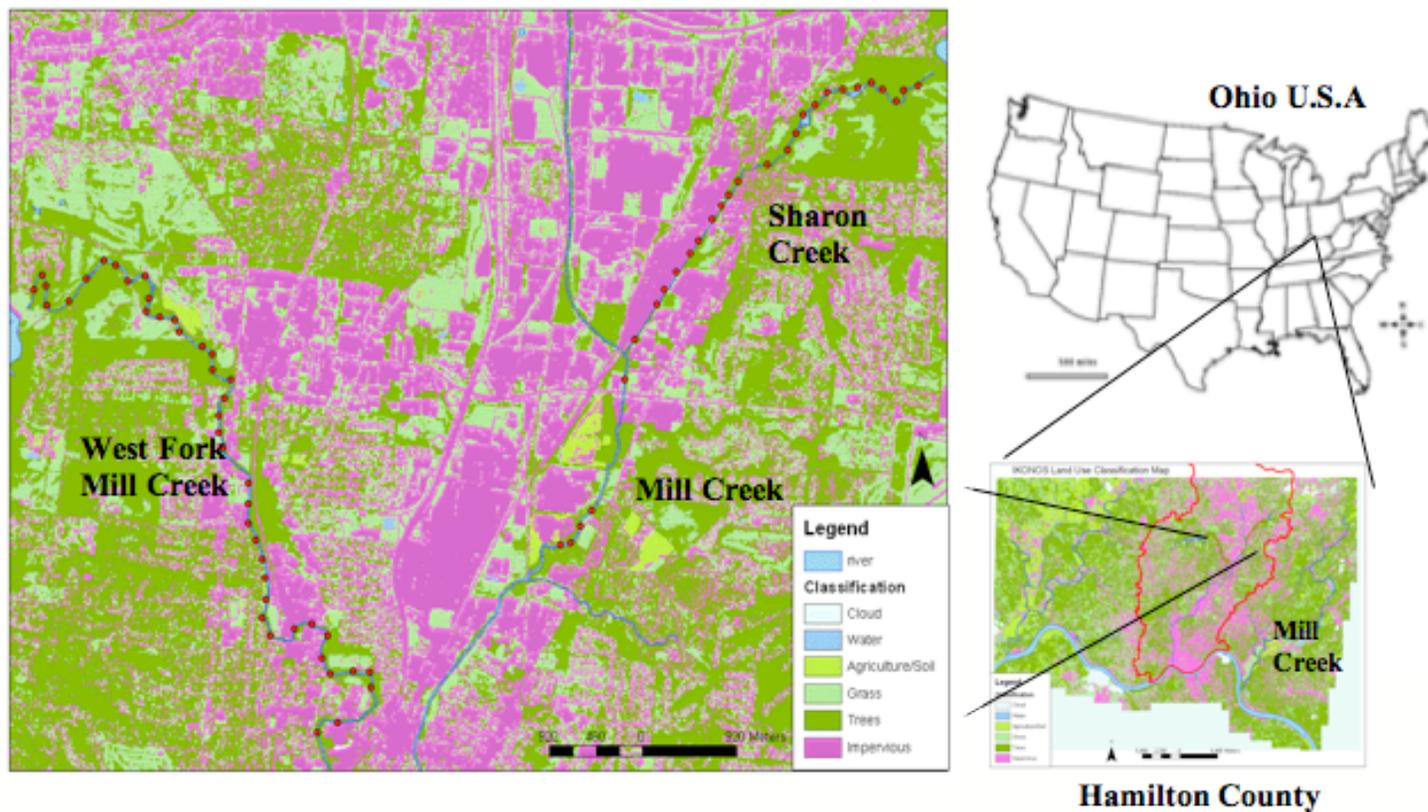


Figure 2. Spearman's rank correlations between urbanization (building area within 250 m) and natural land cover and local vegetation variables ((+/-) represents effect in relationship).

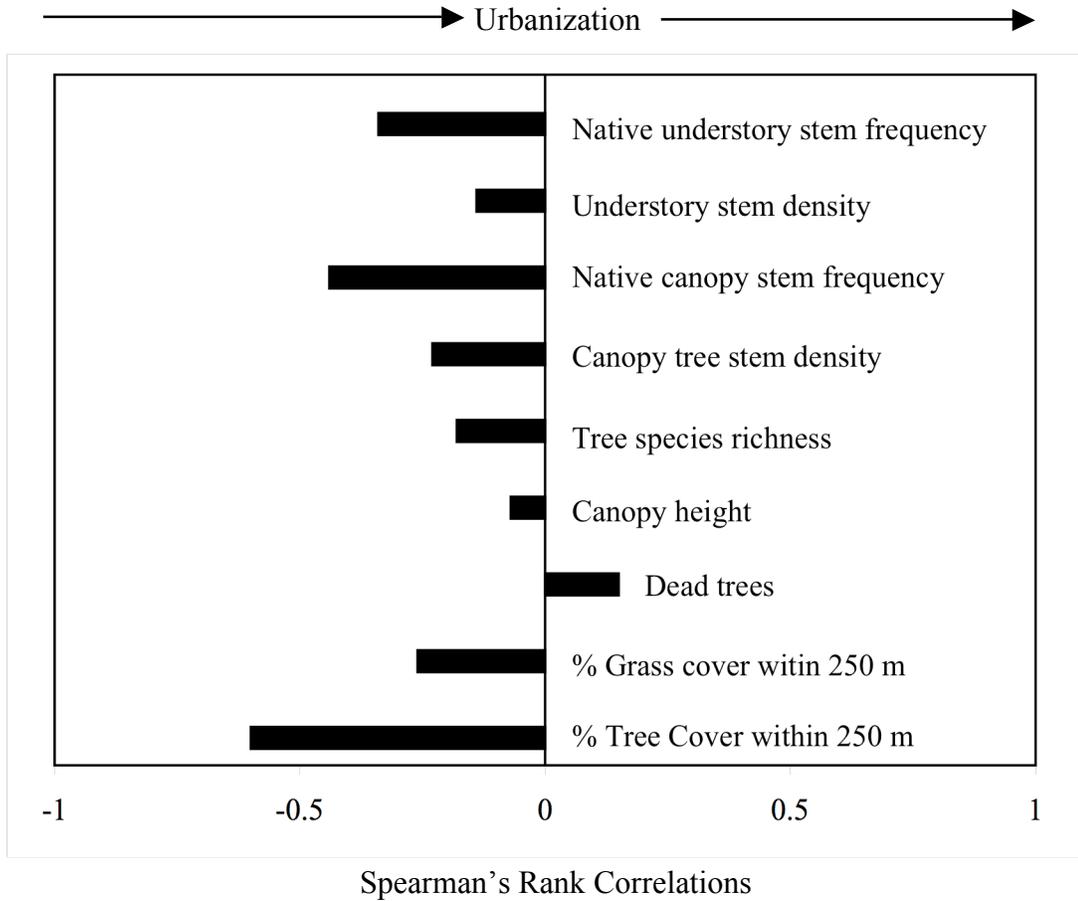


Figure 3. The proportion of variance explained in linear regressions by percent tree cover (a, c, e) and building area (b, d, f) across four scales for relative density (a, b), species richness (c, d), and evenness (e, f) for Neotropical migrants (N), short-distance migrants (SD), permanent residents (P), and exotic (E; relative density only); * represents a significant spatial response based on uniqueness index tests ($p < 0.05$). Relative density and richness for short-distance migrants and permanent residents displayed curvilinear responses (adjusted R^2 values from linear regressions with a squared term; no uniqueness index tests performed).

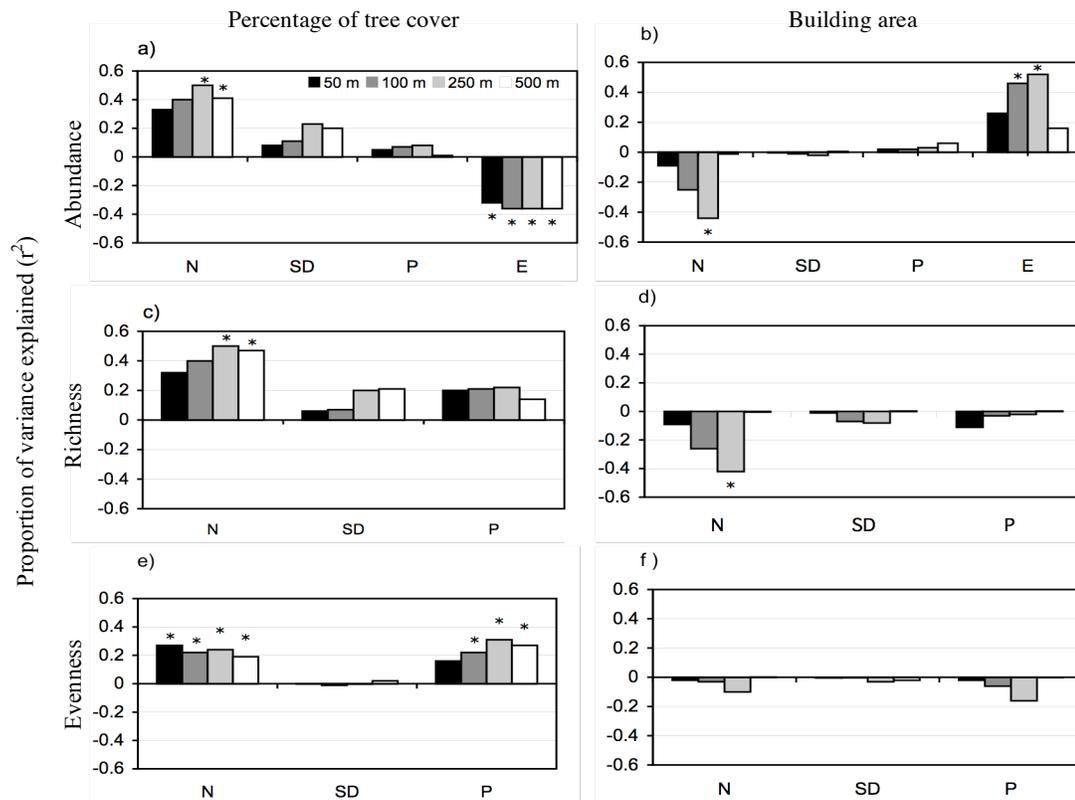
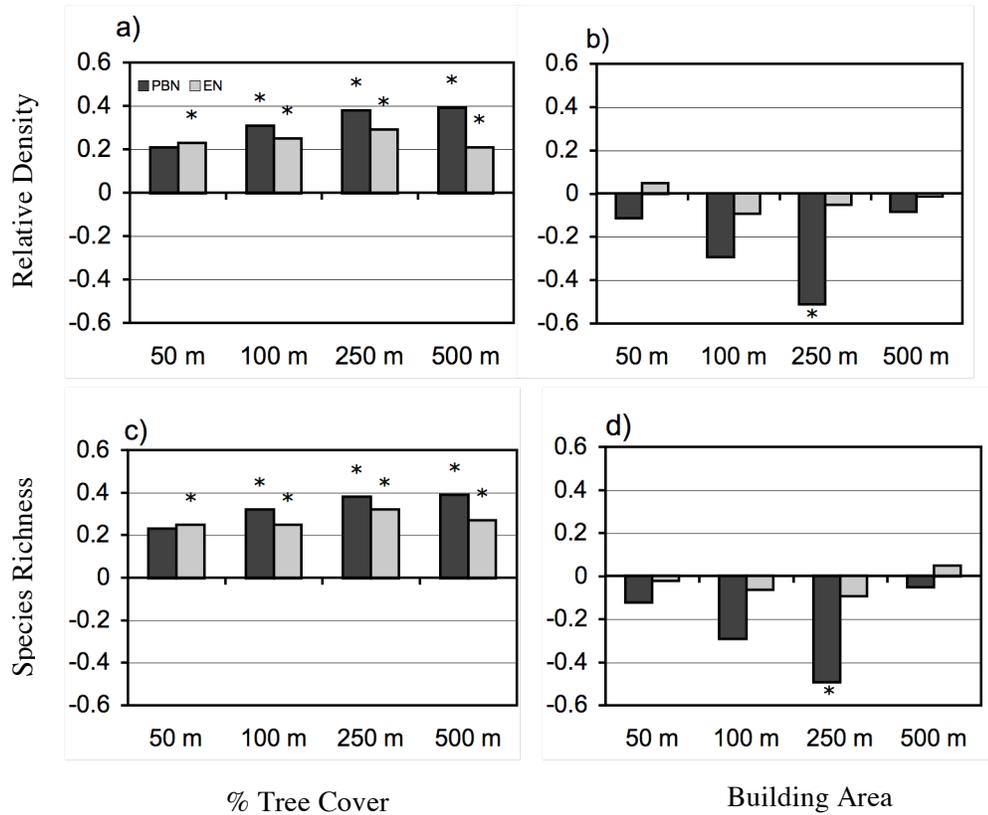


Figure 4. Comparison of the proportion of variance explained in linear regressions by percent tree cover (a, c, e) and building area (b, d, f) across four scales for relative density (a, b), species richness (c, d), and evenness (e, f) of resident and en-route Neotropical migrants; * represents a significant spatial response based on uniqueness index tests ($p < 0.05$).



Appendix A. 88 bird species surveyed during 2002 migratory season in Mill Creek watershed in the greater Cincinnati Metropolitan area used in analyses. N = native, E = exotic, RNM = resident Neotropical migrant, ENM = en-route Neotropical migrant, SD = short-distance migrant, and P = permanent resident (Ehrlich et al. 1988, Peterjohn and Sauer 1993, Keller et al. 1999); see methods for calculation of relative density (birds/hectare).

Common name	Scientific name	Origin	Migratory guild	Relative density	% of 71 plots
American robin	<i>Turdus migratorius</i>	N	SD	2.597	100.0
American goldfinch	<i>Carduelis tristis</i>	N	SD	2.108	90.1
Brown-headed cowbird	<i>Molothrus ater</i>	N	SD	1.882	98.6
European starling	<i>Sturnus vulgaris</i>	E	SD	1.596	87.3
Song sparrow	<i>Melospiza melodia</i>	N	SD	0.838	83.1
White-throated sparrow	<i>Zonotrichia albicollis</i>	N	SD	0.663	74.6
Mourning dove	<i>Zenaida macroura</i>	N	SD	0.569	49.3
Common grackle	<i>Quiscalus quiscula</i>	N	SD	0.520	78.9
Blue jay	<i>Cyanocitta cristata</i>	N	SD	0.424	80.3
American crow	<i>Corvus brachyrhynchos</i>	N	SD	0.380	71.8
Cedar waxwing	<i>Bombycilla cedrorum</i>	N	SD	0.365	12.7
Golden-crowned kinglet	<i>Regulus satrapa</i>	N	SD	0.359	42.3
Red-winged blackbird	<i>Agelaius phoeniceus</i>	N	SD	0.314	26.8
Ruby-crowned kinglet	<i>Regulus calendula</i>	N	SD	0.275	15.5
Yellow-rumped warbler	<i>Dendroica coronata</i>	N	SD	0.263	46.5
Eastern towhee	<i>Pipilo erythrophthalmus</i>	N	SD	0.241	26.8
House finch	<i>Carpodacus mexicanus</i>	E	SD	0.158	31.0
Northern flicker	<i>Colaptes auratus</i>	N	SD	0.144	45.1
Dark-eyed junco	<i>Junco hyemalis</i>	N	SD	0.113	15.5
Eastern phoebe	<i>Sayornis phoebe</i>	N	SD	0.104	7.0
Field sparrow	<i>Spizella pusilla</i>	N	SD	0.080	14.1
Belted kingfisher	<i>Ceryle alcyon</i>	N	SD	0.075	21.1
Brown creeper	<i>Certhia americana</i>	N	SD	0.063	21.1
Eastern bluebird	<i>Sialia sialis</i>	N	SD	0.063	12.7
Eastern meadowlark	<i>Sturnella magna</i>	N	SD	0.027	5.6
Hermit thrush	<i>Catharus guttatus</i>	N	SD	0.025	2.8
Yellow-bellied sapsucker	<i>Sphyrapicus varius</i>	N	SD	0.018	5.6
Winter wren	<i>Troglodytes troglodytes</i>	N	SD	0.015	7.0
Brown thrasher	<i>Toxostoma rufum</i>	N	SD	0.003	1.4
Vesper sparrow	<i>Poocetes gramineus</i>	N	SD	0.003	1.4
Northern cardinal	<i>Cardinalis cardinalis</i>	N	P	5.375	100.0
Carolina chickadee	<i>Poecile carolinensis</i>	N	P	2.130	95.8
House sparrow	<i>Passer domesticus</i>	E	P	1.692	62.0

Carolina wren	<i>Thryothorus ludovicianus</i>	N	P	0.925	91.5
Tufted titmouse	<i>Baeolophus bicolor</i>	N	P	0.628	81.7
Downy woodpecker	<i>Picoides pubescens</i>	N	P	0.430	71.8
Red-bellied woodpecker	<i>Melanerpes carolinus</i>	N	P	0.250	57.7
White-breasted nuthatch	<i>Sitta carolinensis</i>	N	P	0.070	18.3
Hairy woodpecker	<i>Picoides villosus</i>	N	P	0.070	9.9
Pileated woodpecker	<i>Dryocopus pileatus</i>	N	P	0.063	22.5
Northern mockingbird	<i>Mimus polyglottos</i>	N	P	0.059	23.9
American redstart	<i>Setophaga ruticilla</i>	N	RNM	0.541	25.4
Baltimore oriole	<i>Icterus galbula</i>	N	RNM	0.473	49.3
Common yellowthroat	<i>Geothlypis trichas</i>	N	RNM	0.344	18.3
red-eyed vireo	<i>Vireo olivaceus</i>	N	RNM	0.294	45.1
Blue-gray gnatcatcher	<i>Poliophtila caerulea</i>	N	RNM	0.266	33.8
Magnolia warbler	<i>Dendroica magnolia</i>	N	RNM	0.149	35.2
Gray catbird	<i>Dumetella carolinensis</i>	N	RNM	0.126	21.1
Scarlet tanager	<i>Piranga olivacea</i>	N	RNM	0.141	11.3
Indigo bunting	<i>Passerina cyanea</i>	N	RNM	0.108	12.7
Eastern wood-pewee	<i>Contopus virens</i>	N	RNM	0.105	32.4
Yellow warbler	<i>Dendroica petechia</i>	N	RNM	0.103	19.7
Prothonotary warbler	<i>Protonotaria citrea</i>	N	RNM	0.096	11.3
Yellow-throated warbler	<i>Dendroica dominica</i>	N	RNM	0.093	23.9
Yellow-billed cuckoo	<i>Coccyzus americanus</i>	N	RNM	0.075	1.4
Wood thrush	<i>Hylocichla mustelina</i>	N	RNM	0.072	14.1
Acadian flycatcher	<i>Empidonax vireescens</i>	N	RNM	0.072	7.0
Warbling vireo	<i>Vireo gilvus</i>	N	RNM	0.063	16.9
Great crested flycatcher	<i>Myiarchus crinitus</i>	N	RNM	0.056	18.3
Eastern kingbird	<i>Tyrannus tyrannus</i>	N	RNM	0.051	11.3
Louisiana waterthrush	<i>Seiurus motacilla</i>	N	RNM	0.038	8.5
Yellow-throated vireo	<i>Vireo flavifrons</i>	N	RNM	0.036	4.2
Black-and-white warbler	<i>Mniotilta varia</i>	N	RNM	0.033	12.7
House wren	<i>Troglodytes aedon</i>	N	RNM	0.025	4.2
Summer tanager	<i>Piranga rubra</i>	N	RNM	0.024	2.8
Kentucky warbler	<i>Oporornis formosus</i>	N	RNM	0.023	2.8
Yellow-breasted chat	<i>Icteria virens</i>	N	RNM	0.014	2.8
Ovenbird	<i>Seiurus aurocapilla</i>	N	RNM	0.011	4.2
Orchard oriole	<i>Icterus spurius</i>	N	RNM	0.011	4.2
Blackpoll warbler	<i>Dendroica striata</i>	N	ENM	0.242	43.7
Black and white warbler	<i>Mniotilta varia</i>	N	ENM	0.242	12.7
Tennessee warbler	<i>Vermivora peregrina</i>	N	ENM	0.220	38.0
Nashville warbler	<i>Vermivora ruficapilla</i>	N	ENM	0.192	23.9

Magnolia warbler	<i>Dendroica magnolia</i>	N	ENM	0.149	35.2
Palm warbler	<i>Dendroica palmarum</i>	N	ENM	0.121	15.5
Yellow-throated warbler	<i>Dendroica dominica</i>	N	ENM	0.093	23.9
Swainson's thrush	<i>Catharus ustulatus</i>	N	ENM	0.083	28.2
Black-throated blue warbler	<i>Dendroica caerulescens</i>	N	ENM	0.075	1.4
Black-throated green warbler	<i>Dendroica virens</i>	N	ENM	0.066	8.5
Philadelphia vireo	<i>Vireo philadelphicus</i>	N	ENM	0.066	1.4
Chestnut-sided warbler	<i>Dendroica pensylvanica</i>	N	ENM	0.058	8.5
Rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>	N	ENM	0.058	8.5
Blackburnian warbler	<i>Dendroica fusca</i>	N	ENM	0.042	9.9
Bay-breasted warbler	<i>Dendroica castanea</i>	N	ENM	0.034	1.4
Northern parula	<i>Parula americana</i>	N	ENM	0.024	8.5
Willow flycatcher	<i>Empidonax traillii</i>	N	ENM	0.024	1.4
Cape May warbler	<i>Dendroica tigrina</i>	N	ENM	0.018	1.4
Veery	<i>Catharus fuscescens</i>	N	ENM	0.003	5.6

CHAPTER 4

**Untangling the relative importance of vegetative and built features on
breeding riparian birds within a complex urban environment:
local vegetation, landscape, and scale**

with Robert. B. Blair

ABSTRACT: Ecologists increasingly recognize that birds can respond to features beyond their breeding territories, yet little is known about the relative importance of proximate local vegetation characteristics and broader landscape features and the influential spatial scales of these landscape features. We examine the influences of two biophysical elements of the urban environment – vegetation and buildings – at both proximate and landscape scales on breeding riparian bird species. We surveyed birds on 71 sites during 2002, 2004, 2005, and 2006 along an urban gradient within metropolitan Cincinnati, Ohio, U.S.A. We modeled relative density for 48 bird species in relation to local woody vegetation composition and structure and to tree cover, grass cover, and building density within 50 to 1000 m of each site. We used an information-theoretic approach to compare models and variables. At the proximate scale, native tree and understory stem frequency were the most important vegetation variables; native tree had a positive influence on 35 species and a negative influence on 13 species and native understory had a positive influence on 27 species and a negative influence on 21 species. At the landscape scale, the vegetative features (both tree cover and grass cover) were the most important variables across all species; tree cover positively influenced 15 species and negatively influenced 5 species and grass cover positively influenced 22 species and negatively influenced 5 species. Building density was an important variable for 13 species, and positively influenced 6 species and negatively influenced 7 species. In a comparison of multiple scales, models with only landscape variables were adequate for some species, but models combining both local vegetation and landscape information were best or competitive for 42 of the 44 species. Local-vegetation-only models were rarely competitive. Combined models at small spatial

scales (≤ 500 m) were best for 36 species of the 44 species and these models commonly included tree cover and building density. Only eight species had best models at larger scales (> 500 m); grass cover was most the important variable at larger scales. Most native species responded positively to vegetation landscape measures and negatively to building density. Efforts to manage and design urban areas to benefit native birds require both fine-scale (e.g., by individual landowners and landscape design) and larger landscape actions (e.g., by municipal and regional comprehensive planning).

INTRODUCTION

With over half of humanity now residing in cities (UNPF 2007), urban environments present a unique challenge for conserving our planet's biodiversity (Czech et al. 2000). Identifying the habitat requirements for maintaining species' populations within urban areas is essential not only for species conservation (Foley et al. 2005), but for enhancing people's experience with nature as well (Miller 2005). Urbanization or the "city building process" is often portrayed as a leading threat to global biodiversity, causing the elimination of the majority of native species (Czech et al. 2000, McKinney 2002). Indeed, several native species do appear to be urban intolerant, especially many long-distance migrants (Blair 2004, Bakermans and Rodewald 2006). Although urbanization does threaten and impair certain biological elements contributing to habitat for organisms, many studies have documented the persistence of native species diversity and abundance within cities (Chace and Walsh 2006, Pennington and Blair *In press*). An important challenge for ecologists and conservation biologists is to explicitly examine the potential value of urban areas for maintaining local and regional species diversity.

Birds represent an excellent taxonomic group for assessing the effects of urbanization on ecosystem function because bird communities are conspicuous in nature, are of interest to people, and are often used as indicators of habitat quality and availability due to their specialized habitat requirements (Blair 1999). Numerous studies of birds in riparian areas have focused on proximate or microhabitat features, such as territories, nest sites, or song perches (Best and Stauffer 1980, Stauffer and Best

1980, Sallabanks et al. 2000, Smith et al. 2008). Although there is a growing recognition that the extent of habitat beyond nesting territories or landscape-scale patterns can affect bird distributions (Rottenborn 1999, Saab 1999, Rodewald and Bakermans 2006), few studies have attempted to examine the relative importance of proximate and landscape-scale factors (Miller et al. 2003). Fewer still have sought to identify the scales at which different species respond to habitat (i.e., show patterns of selecting for or avoiding habitat features) within an urbanizing landscape (Hostetler and Holling 2000, Hennings and Edge 2003, Pennington et al. 2008).

Identifying the spatial scales at which birds respond most strongly to landscape features would help clarify and explain the processes determining bird distributions (Wiens 1989, Hostetler 1999). Assessing dominant scales would aid our ability to predict species responses within highly heterogeneous areas, such as the varied built and forested landscape of a city. Because people make decisions that directly influence the landscape mosaic at multiple scales, from individuals to households to municipalities and agencies (Grove et al. 2006), information on spatial scale would improve the efficacy of our land-use planning and management decisions by ensuring that these efforts are applied at appropriate scales (Hostetler 1999).

Forested riparian areas harbor a high biodiversity of plants and animals compared to other forest ecosystems (Naiman et al. 1993). However, the integrity of riparian forest communities is vulnerable to the intense land-use modification associated with urbanization (e.g., Richardson et al. 2007), such as changes in proximate vegetation structure and composition habitat features (Burton and Samuelson 2007, Pennington et al. *In review*). Aspects of vegetation composition and structure, such as

the proportion of native vegetation (Rottenborn 1999, Miller et al. 2003) and overstory and understory stem densities (Saab 1999, Bakermans and Rodewald 2006, Smith et al. 2008), have been shown to be important proximate or local vegetation features influencing bird habitat. Indeed, shifts in vegetative species composition from native to exotic can alter habitat quality for native bird species (Borgmann and Rodewald 2004).

Past studies have also demonstrated that proximity and extent of forested habitats can affect the distribution of riparian birds, with greater bird abundance and richness as forest cover increases (Friesen et al. 1995, Saab 1999, Melles et al. 2003, Donnelly and Marzluff 2004, Mason et al. 2007). Whereas some studies found landscape-scale patterns (within 1 km²) to be most significant for determining bird distributions (Saab 1999, Rodewald and Bakermans 2006), others have found proximate features produced the best habitat models (Donnelly and Marzluff 2006), suggesting that responses to landscape-scale features can vary with species, region, and study design.

Efforts to examine relative importance of nested landscape features have found bird responses to vary in magnitude, directionality, and spatial scale (Hennings and Edge 2003, Hostetler and Knowles-Yanez 2003, Dunford and Freemark 2005). For example, previous studies found Neotropical migrant species to be sensitive to housing density within 100-200 m surrounding forest patches (Friesen et al. 1995, Hennings and Edge 2003), yet others recommended limited development within 200-1800 m for Neotropical migrant conservation (Dunford and Freemark 2005). In addition, research has suggested variation in scale responses based on life-history characteristics (e.g.,

habitat selection during migration versus breeding periods for long distance migrants (Pennington et al. 2008)).

Although several studies have demonstrated the importance of urbanization at the landscape-scale for native bird diversity (Hennings and Edge 2003, Melles et al. 2003, Donnelly and Marzluff 2004, Rodewald and Bakermans 2006), few have sought to distinguish the relative importance of built and vegetative elements comprising this “urbanizing” matrix. The dominant paradigm often defines “urban” as an abstract perturbation affecting natural habitats. “Urban” is often measured by reducing several biophysical features, including both land-use and land-cover measures (e.g., building and road density or area, tree cover, grass cover, agriculture, residential) into an index of urbanization (e.g., axes from principal components analysis; Blair 2004, Dunford and Freemark 2005, Rodewald and Bakermans 2006, Smith and Wachob 2006). In contrast, here, we attempt to examine the relative importance of both built and vegetative aspects separately in order to better understand how birds respond to the fine-scale heterogeneity within an urbanizing area.

Few studies have explicitly examined how the spatial arrangement and composition, or heterogeneity, of these biophysical elements within a metropolitan area contributes to the structure and composition of urban biodiversity (Pickett et al. 2008). In this paper we examine how two key elements of the biophysical structure of the urban environment – buildings and vegetation – influence the distribution of breeding bird species within in urban areas. Specifically, we ask what is the relative importance of the structure and composition of these elements on birds across multiple spatial scales within a highly heterogeneous urban area? In order to answer this question we

established three objectives: (1) to examine bird distribution in relation to both proximate local vegetation habitat characteristics and landscape biophysical structure; (2) to compare the relative importance of local vegetation and landscape biophysical structure; (3) to identify scales at which bird species responds most strongly to landscape biophysical measures.

METHODS

Study area

We quantified bird, local vegetation, and landscape variables for riparian forests of the Mill Creek watershed (42 994 ha) located within the Midwestern metropolitan area of Cincinnati, Hamilton County, Ohio (39.2° N 84.5° W) (Fig. 1). The Mill Creek is one of the most polluted and threatened urban rivers in the United States (American Rivers 1997), and its watershed includes some of the fastest growing areas in Ohio, with over half a million people living and working within its boundaries (U.S. Census Bureau 2000).

Within this watershed, we selected a 4 243 ha study area comprised of a portion of the Mill Creek and sections of two tributaries, Sharon Creek and West Fork Mill Creek (human population density $\sim 1,498$ persons/km²), which represents the heterogeneity of land-cover types typically associated with a metropolitan area: diverse public parks, open spaces, residential, industrial, and commercial land uses (Fig. 2). We located 71 sites systematically from a random starting point along Mill Creek, Sharon Creek, and West Fork Mill Creek (Ralph et al. 1995) using ArcView 9.1 and the Cincinnati Area Geographic Information System (CAGIS) dataset (based on 2001 color

orthophotos at 0.5 m resolution). All sites represent “natural” riparian areas within an urban land-use matrix consisting of forest “corridor” widths ranging from narrow (< 100 m) to wide (> 500 m). Plots were placed along the streamside edge and were separated by at least 150 m. Stream channel width was consistent across sites (~ 10 m). Geologically, this area is located on the homogeneous Pre-Wisconsinan Drift Plains ecoregion (Omernik 1997), and prior to European settlement, the area was predominately Beech forest (*Fagus grandifolia*, *Acer saccharum*, *Plantanus occidentalis*, *Populus deltoides*) and mixed mesophytic forest (Gordon 1966).

Field methods

Bird Surveys

We surveyed birds using variable-radius point counts (Reynolds et al. 1980, Bibby et al. 2000) during four breeding seasons (June-July of 2002, 2004, 2005, and 2006) and visited each site three times per season. An observer visited a site during the first 3.5 hours following sunrise and recorded all individuals heard or seen during five minutes within a 50 m radius on days with no rain and wind speeds < 32 km/h. By using a small sampling area and repeated sampling we reduced the likelihood of missing individuals (Ralph et al. 1995, Siegel et al. 2001). We did not correct for detectability across sites because detection functions for most species have been shown to be relatively constant to 50 m (Schieck 1997). For our analyses, we did not include birds flying over or through the sampling plot. Furthermore, we did not analyze raptors, shorebirds, waterfowl, nocturnal and crepuscular species, and aerial insectivores, because point counts are poor at detecting these species (Bibby et al. 2000). We

calculated the relative density of each species as the number of individuals divided by the survey effort (number of visits to a site) and plot area (see (Reynolds et al. 1980); values were square root transformed to adjust for skewness. We averaged relative density values for species over the three visits in each of the four seasons; correlations between relative density and explanatory variables did not vary between years, and thus, we chose to average bird relative density over the four years for each sampling point.

Local vegetation measures

At the origin of each bird sampling point, we placed a 70 m diameter plot (0.38 ha) to assess local woody vegetation structure and composition characteristics on both sides of the stream (see Table 1). Within each of these plots we established five 35 m radial transects equidistant from the plot origin, and centered a 10 m diameter subplot (0.0078 ha x 5 = 0.0395 ha) at randomly selected points 5-35 m from the origin along each transect. The radial transect was reselected or shifted by 10° increments if a subplot included the stream. In the 70 m circular plot, we identified and measured the diameter at breast height (dbh) of all trees > 10 cm dbh, including dead standing trees. In the 10 m diameter subplots, we identified all woody plants with stems < 10 cm diameter and measured the height of the tree (> 10 cm dbh) nearest the subplot center using a clinometer. We averaged the five subplot height measures to obtain a canopy height measure for each plot. We calculated tree or canopy stem densities, canopy basal area, number of dead trees, average canopy height, and understory stem density; all variables were log transformed to adjust for skewness (see Table 1). We also calculated species composition by using relative frequencies of native canopy and understory

species (Barbour et al. 1987; for more details see Pennington et al. *in review*). Exotic or non-native species were defined as those absent from the study area prior to European settlement (Braun 1989).

Biophysical landscape measures

In order to examine the relative importance of vegetative and built features of the urban environment, we used a combination of high-resolution data derived from multispectral satellite imagery and digital orthophotos provided by CAGIS. To assess landscape-scale vegetation metrics, we used a type 1 land cover classification map derived from 4 m resolution IKONOS satellite imagery; the classification map had a 90% accuracy rating compared to high resolution orthophotos (Andy Swift, CAGIS, personal communication) (Fig. 1 and 2). Using ArcView GIS version 9.2 with the spatial analyst extension and FRAGSTATS (version 3.3; McGarigal et al. 2002); raster cell size was 2.43 m), we quantified the relative amount of dominant vegetation types, specifically, percentage of tree cover (e.g., trees and shrubs) and percentage grass cover (e.g., lawns and meadows), surrounding each site at the following radial buffers, henceforth called “spatial scales:” 50, 100, 200, 300, 400, 500, 600, 700, 800, 900, 1000 m (*note*: we take a biological perspective when referring to scale, thus, “large scale” denotes large area and “small scale” denotes small area). Although FRAGSTATS produces several landscape fragmentation metrics (e.g., edge and patch density), we chose to focus on percentage cover, a relative measure of landscape composition, because it is more easily interpreted than many of the other measurements (e.g., patch size, nearest neighbor, interspersion, juxtaposition) (Cunningham and Johnson 2006)

and is a more appropriate measure for comparing among landscapes of varying sizes (McGarigal et al. 2002). Correlations between percentage tree and percentage grass cover were relatively low ($r < 0.60$ across scales; Table 2).

To assess built landscape-scale features, we used building and road footprints derived from 0.5 m resolution color digital orthophotos and ArcView GIS version 9.2 and Hawth Analysis Tools extension, Polygon in Polygon Analyst (Beyer 2004), to quantify road density, building density, and building area surrounding each site for the same spatial scales (all measures log transformed to counteract skewness). Both road and building density were highly correlated ($r > 0.80$); thus we only include building density since this variable is suggested to be a good surrogate of urbanization (Marzluff et al. 2001). We also examined building area because the footprint of a single building can vary greatly within our study area (e.g., a factory versus a residential home) (Pennington et al. 2008), and it is possible that building density alone could misrepresent development (Hostetler and Knowles-Yanez 2003). Correlations between building area and building density to tree cover and grass cover were relatively low for scales ≤ 600 m ($r < 0.60$; Table 2) indicating that the level of vegetative cover and built measures can vary independently of each other; however, for scales > 600 m building area was correlated more strongly with the other metrics ($r > 0.60$; Table 2). Consequently, we chose to only include building density as a measure of the built environment. In general, the lack of both tree and grass cover in our study area is because of habitat loss from the direct conversion of natural habitat to urban infrastructure (e.g., buildings and roads). However, building density, or simply the number of buildings per hectare in the landscape, varied independently of percent tree

cover and grass cover; this measure appears to represent aspects of habitat fragmentation as it was strongly correlated with the number of both grass and tree patches in the landscape ($r > 0.40$).

Statistical methods

We analyzed relative density of each bird species at each point with respect to proximate and landscape-scale biophysical metrics as explanatory variables. We used the mixed model procedure in SAS (PROC MIXED SAS version 9.2, SAS Institute, Cary, NC, U.S.A). At the proximate scale, explanatory variables included seven measures of local woody vegetation structure and composition: native canopy stem frequency, native understory stem frequency, canopy stem density, understory stem density, canopy basal area, canopy height, and number of dead trees. At landscape scales, explanatory variables were percentage of tree cover, grass cover, and building density within 50, 100, 200, 300, 400, 500, 600, 700, 800, 900, and 1000 m.

To reduce concerns about independence among observations or spatial autocorrelation (Legendre 1993), we take a model-ranking approach that does not rely on conventional hypothesis testing and significance to reject variables or models (see Cunningham and Johnson 2006, Diniz-Filho et al. 2008). We ranked models using a multiple-model inference approach rather than trying to determine only a single “best” model that described our data (Burnham and Anderson 2002). Focusing on a single model can lead to a misinterpretation of results, especially when examining several intercorrelated explanatory variables, which can lead to several models that fit the data well. This approach allowed us to rank possible explanatory models and to retain all

models that fit our data well. Our assumption is that several models (and variables) could be similarly important in explaining bird distributions.

We used an information theoretic method to evaluate a set of models based on their explanatory value determined by corrected Akaike's information criterion (AIC_c ; adjusted for small sample-size in relation to number of parameters), and identified the strongest models (or best-fitting) based on ΔAIC_c values (Burnham and Anderson 2002); $\Delta AIC_c = 0$ represented the “best” model and we considered all models with $\Delta AIC_c < 3$ to be competitive candidate models and were considered to be competitive with the best model in explaining the response variable, models having $\Delta AIC_c \geq 3$ were considered to be relatively poorly supported by the data (Cunningham and Johnson 2006). We computed Akaike weights for models to assess the evidence of a particular model based on the observed data. We also computed Akaike weights for each explanatory variable so that we could compare the relative importance of each variable. This prevented us from discarding variables that might be important for explaining bird distributions yet do not appear in the “best” selected model (Burnham and Anderson 2002). For every species we developed three sets of models to evaluate (1) local vegetation characteristics, (2) landscape, and (3) combined proximate and landscape effects. For each analysis, we ranked models by running a model selection routine in SAS that calculated AIC_c , ΔAIC_c , model weights, and variable weights; each model included one or more explanatory variables. We report adjusted R^2 values for the “best” model based on linear regression as a way to evaluate goodness of fit.

To identify competitive local vegetation models, we took an exploratory ‘all possible models’ approach to model selection, which included all seven explanatory

variables characterizing the canopy and understory woody vegetation, which is in contrast to developing a suite of candidate models based on *a priori* hypotheses. Given that our goal was to gain insight into the relative importance of local vegetation variables and to assess unanticipated relationships, not prediction, we felt obliged to take an exploratory approach (Diniz-Filho et al. 2008). From this routine, we identified the strongest local vegetation models and variables for each dependent variable.

We identified competitive landscape-scale biophysical models by running the model selection on groups of 33 candidate models; each candidate model included one of the landscape biophysical metrics at one of the 11 spatial scales (e.g., percentage forest canopy cover for each of the 11 scales (50 m and every 100 m from 100 to 1000 m)). We considered the “best” model and any candidate models within ΔAIC_c of three as representing the most important scale or scales and landscape variables influencing bird distributions.

To compare the relative importance of local vegetation and landscape biophysical structure in explaining bird distributions, we performed a separate model selection routine for each species that included all three landscape-scale biophysical features. Candidate models for each model selection procedure included the “best” proximate model, landscape scale models for each biophysical feature under investigation, and combined models (these included the 'best' local-vegetation model plus one of the landscape variables (e.g., percentage forest canopy cover for each of the 11 scales (50 m and every 100 m from 100 to 1000 m)). We considered the “best” model and any candidate models within ΔAIC_c of three as representing the most important scales and landscape variables influencing bird distributions.

RESULTS

Over a four-year period, observers recorded 21 088 detections representing 68 species. We focus on 48 species and 20 720 detections that met our criteria for analysis (see *Methods*; Appendix A). Of these bird detections, several species were relatively widespread; 26 species were present at more than half the study sites, and 18 species were observed at over 75% of the sites. The ten most abundant species were northern cardinal, American robin, house sparrow, Carolina chickadee, European starling, common grackle, American goldfinch, song sparrow, Carolina wren, and brown-headed cowbird.

Local vegetation and landscape features

The study area represents a gradient of urbanization by capturing areas of relatively high and low levels of development intensity (Table 1). Measures of landscape-scale biophysical features varied across spatial scales. Tree cover ranged from 10.0% to 98.8% at 200 m and grass cover ranged from 0.7% to 41.0%; both percentage tree and grass cover decreased at larger spatial scales (Table 1). Building density ranged from 0.0 to 8.0 buildings per hectare at 200 m, with density of buildings increasing with larger scales (Table 1). Correlations among nested landscape variables of the same kind were strong (e.g., tree cover at 50 – 1000 $r \geq 0.50$; Table 2). Local vegetation measures were partially correlated with all landscape features, but most strongly with tree cover (Table 2). At proximate scales, local vegetation measures were negatively influenced by percentage grass cover and positively at both proximate and larger scales by percentage tree cover. Number of dead trees was positively correlated

and native tree frequency was negatively correlated with building density.

Bird response to local vegetation characteristics

Among best local vegetation models, vegetation composition variables were the most common and often the most heavily weighted variables (Table 3). Best models reflected the variables with the highest cumulative weights across all possible models. Native tree frequency was important for 27 species, and of these species, only six responded negatively: brown-headed cowbird, European startling, house sparrow, northern mockingbird, northern cardinal, and song sparrow. Native understory frequency was important for 22 species; nine of these species responded negatively: American crow, American goldfinch, common grackle, European startling, house finch, house sparrow, mourning dove, song sparrow and warbling vireo. As for vegetation structure measures, tree basal area was important for 10 species; two of these species responded negatively: common grackle and northern mockingbird. Canopy height was important for eight species, and out of these eight only two species responded positively: Louisiana waterthrush and scarlet tanager. Number of dead trees was important for six species; three species responded positively (brown-headed cowbird, house finch, and northern mockingbird) and three negatively (Acadian flycatcher, common yellowthroat, and tufted titmouse). Tree stem density was important for 14 species; three of these species responded negatively: brown-headed cowbird, house finch, and house sparrow. Understory stem frequency was important for 10 species, and none of these species responded positively. Of the 48 species models, 13 species models displayed relatively weak responses to the measured local vegetation variables

(adj. $R^2 \leq 0.10$; Table 3): American crow, belted kingfisher, Carolina wren, cedar waxwing, common yellowthroat, field sparrow, hairy woodpecker, house wren, northern flicker, gray catbird, indigo bunting, red-winged blackbird, and orchard oriole; however, several of these species had good model fits for combined models including local vegetation and landscape-scale.

Local vegetation, landscape-scale, and combined model comparisons

Species responses to local vegetation and landscape biophysical features varied in magnitude, directionality (positive or negative responses), and scale (Table 4; for graphical representation see Appendix B). In general, “best” models ($\Delta AIC_c = 0$) fit observed species data well; however, three species had very weak fits (Carolina wren, gray catbird, and hairy woodpecker; adj. $R^2 \leq 0.10$), and will not be discussed here for brevity.

Combined local vegetation and landscape models were better than local vegetation-only or landscape-only models and represented the best model ($\Delta AIC_c = 0$) for 31 of the 44 species, and were competitive ($\Delta AIC_c < 3$) for the remaining species, except for brown thrasher and great-crested flycatcher (Table 5; Appendix B). A majority of species responded to small scales with best models at ≤ 500 m. Eight species had best models at larger scales > 500 m: blue-gray gnatcatcher, eastern towhee, house sparrow, northern cardinal, northern flicker, pileated woodpecker, yellow-billed cuckoo, yellow-throated warbler. Five species had best models at the smallest scales (50 – 100 m): American crow, American goldfinch, brown-headed cowbird, cedar waxwing, and tufted titmouse (Table 4; Appendix B). Two species, northern cardinal

and pileated woodpecker, had best models at the largest scale (1000 m)(Table 4; Appendix B).

Local vegetation-only models represented the best model for blue jay and Carolina chickadee, and were competitive models for an additional three species: brown-headed cowbird, mourning dove, and scarlet tanager (Table 5; Appendix B); thus measures of local vegetation alone provided adequate information for these species. For the remaining species, landscape data meaningfully improved the predictive power of the models.

Landscape-only models were competitive for 19 species, and represented the best model for ten species (Table 5; Appendix B). For percentage tree cover, landscape-only models were competitive for ten species, and represented the best model for six species: downy woodpecker, great-crested flycatcher, northern mockingbird, red-bellied woodpecker, red-eyed vireo, and white-breasted nuthatch (Table 4; Appendix B). All ten species responded positively to tree cover, except for northern mockingbird and song sparrow. Landscape-only models including percent tree cover at small spatial scales (≤ 500 m) were competitive for seven species. Two species, American crow and downy woodpecker, had competitive models including percent tree cover at both small and large scales (> 500 m) (Table 4; Appendix B).

For percentage grass cover, landscape-only models were competitive for seven species, and represented the best model for four species, brown thrasher, common yellowthroat, orchard oriole, and red-winged blackbird (Table 4; Appendix B). All seven species responded positively with percentage grass cover. Percentage grass cover landscape-only models at smaller spatial scales (≤ 500 m) were competitive for two

species, eastern bluebird and northern flicker. Percentage grass cover landscape-only models at larger spatial scales (> 500 m) were competitive for five species: brown thrasher, common yellowthroat, orchard oriole, yellow-billed cuckoo, and yellow-throated warbler. Red-winged blackbird had competitive percentage grass cover models at both small and large scales (Table 4; Appendix B).

Landscape-only models for building density were only competitive for one species, indigo bunting, and also represented the best model for that species (Table 4; Appendix B). Indigo bunting responded negatively to building density landscape-only models at smaller spatial scales (≤ 500 m).

Combined models including local vegetation and percentage tree cover measures were competitive for 19 species, and was the best model for nine species: Acadian flycatcher, common grackle, eastern phoebe, Louisiana waterthrush, northern cardinal, scarlet tanager, song sparrow, tufted titmouse, and wood thrush (Table 5; Appendix B). Three of the 19 species responded negatively to percentage tree cover: brown-headed cowbird, common grackle, and northern mockingbird (Table 4; Appendix B). Combined models including local vegetation and percentage tree cover at smaller spatial scales (≤ 500 m) were competitive for nine species: blue-gray gnatcatcher, brown-headed cowbird, downy woodpecker, northern mockingbird, red-bellied woodpecker, red-eyed vireo, song sparrow, tufted titmouse, and white-breasted nuthatch. Combined models including percentage tree cover at larger scales (> 500 m) were competitive for two species: American crow and northern cardinal. Nine species had competitive combined models including percentage tree cover at both small and large scales: Acadian flycatcher, blue jay, Carolina chickadee, cedar waxwing, common

grackle, eastern phoebe, Louisiana waterthrush, scarlet tanager, and wood thrush (Table 4; Appendix B).

Combined models including local vegetation and percentage grass cover were competitive for 26 species, and was the best model for seventeen species: American goldfinch, Baltimore oriole, blue-gray gnatcatcher, brown-headed cowbird, eastern bluebird, eastern towhee, European starling, field sparrow, house finch, house sparrow, house wren, mourning dove, northern flicker, pileated woodpecker, warbling vireo, yellow-billed cuckoo, and yellow-throated warbler (Table 4; Appendix B). Of the 26 species, five responded negatively to percentage grass cover: Carolina chickadee, house finch, house sparrow, northern cardinal, and scarlet tanager. Combined models including percentage grass cover at smaller spatial scales (≤ 500 m) were competitive for seven species: American goldfinch, Baltimore oriole, eastern bluebird, European starling, scarlet tanager, song sparrow, and warbling vireo. Combined models including percentage grass cover at larger scales (> 500 m) were competitive for nine species: blue-gray gnatcatcher, brown-headed cowbird, eastern towhee, common yellowthroat, field sparrow, house sparrow, pileated woodpecker, red-winged blackbird, and yellow-billed cuckoo. Nine species had competitive models including percentage grass cover at both small and large scales: blue jay, Carolina chickadee, eastern kingbird, house finch, mourning dove, northern cardinal, northern flicker, orchard oriole, white-breasted nuthatch (Table 4; Appendix B).

Combined models including local vegetation and building density were competitive for 15 species, and represented the best model for five species: American crow, American robin, cedar waxwing, eastern kingbird, and eastern wood-pewee

(Table 4; Appendix B). Eight species responded positively to building density: American crow, American robin, brown-headed cowbird, eastern phoebe, house finch, house sparrow, mourning dove, and northern cardinal. Combined models including building density at smaller spatial scales (≤ 500 m) were competitive for seven species: Acadian flycatcher, brown-headed cowbird, cedar waxwing, eastern kingbird, house finch, house sparrow, and indigo bunting. Eight species had competitive combined models including building density at both small and large scales (> 500 m): American crow, American robin, blue jay, Carolina chickadee, eastern phoebe, eastern wood pewee, mourning dove, and northern cardinal (Table 4; Appendix B).

DISCUSSION

Habitat selection is a challenging process to understand (Jones 2001), especially within human-dominated areas (Pennington and Blair *in press*). Our study is among the first to explicitly explore how local habitat and landscape biophysical heterogeneity within the “urban” land-use type influence habitat selection in birds. Because birds select habitat hierarchically across a variety of scales (Hostetler 1999), it is important to note the relative importance of local versus landscape features. Our results provide important insights into the hierarchical habitat-selection process by birds within an urban area. For a majority of species the composition of landscape features within 500 m of streams was the most important landscape scale; however, several birds also responded to larger scales (Table 4; Appendix B). Furthermore, our results emphasize the importance of untangling the relative effects of vegetative and built features within urban systems (Hostetler and Knowles-Yanez 2003, Cadenasso et al. 2007). For the

majority of species, the amount of vegetation in the landscape (percentage tree cover and percentage grass cover) was more important than settlement intensity (building density); in general, tree cover and building density were more important at small scales and grass cover was more important at large scales (for summary, see Table 6-8). Finally, fine-scale habitat elements based on local vegetation characteristics (e.g., composition and structure measures) were also important for a majority of birds (Table 3). The importance of combined landscape-scale and local vegetation features illustrates the need for considering the hierarchical decision-making process employed by birds when selecting breeding habitat (Table 4; Appendix B)(Hostetler and Holling 2000).

Local vegetation versus landscape influences

The majority of bird species responded to both local vegetation and surrounding landscape scales, so that combined models, incorporating both local vegetation and landscape features, were good for many species (Table 4; Appendix B). Others have also noted the benefit of combining both local vegetation and landscape features in habitat studies (e.g., Miller et al. 2003, Donnelly and Marzluff 2006, Luther et al. 2008). At proximate scales, local vegetation or small-scale landscape-only models (≤ 100) were competitive for more than one-third of the species, which emphasizes the importance of considering local habitat characteristics. However, when taken alone, landscape-only models were better candidate models than local vegetation-only models. Over half of the species had landscape-only models that were competitive. This runs counter to the conclusions of previous riparian bird studies of urbanizing regions

comparing local vegetation and landscape features (Rottenborn 1999, Miller et al. 2003, Bakermans and Rodewald 2006, Donnelly and Marzluff 2006).

Even though landscape-scale models were important for several species, they often provided poorer predictive power when taken alone. For several species, such as eastern phoebe, eastern kingbird, eastern wood pewee, Louisiana waterthrush, tufted titmouse, and wood thrush, landscape-only models poorly explained bird distributions; however, landscape features contributed to very good combined models that were often competitive with the best models in explaining the data. Consequently, the addition of landscape scales contributed meaningful information to the local vegetation model. Further research is needed to untangle the specific mechanisms at play between within-territory local vegetation and surrounding landscape features.

Results from goodness-of-fit models show that our models predicted most species well. Even for species where few individuals were surveyed, best models were still biologically meaningful. Species with poorer fits were Carolina wren, gray catbird, and hairy woodpeckers; all of these species vary in terms of life-history characteristics and territory sizes. It is possible that these species were responding to broader spatial scales or to different aspects of the local vegetation not considered in our study (Mayer and Cameron 2003).

Most influential local vegetation characteristics

Species' responses to vegetation composition and structure measures varied widely, emphasizing the importance of species-specific management (Table 3). Native species composition of both canopy and understory vegetation were the most important

habitat variables influencing bird distributions (Table 3). Most species responded positively to the presence of native vegetation; exceptions, or species that increased with exotic vegetation, included edge-associated or synanthropic species: American crow, American goldfinch, brown-headed cowbird, common grackle, European startling, house finch, house sparrow, mourning dove, northern cardinal, and song sparrow. Positive effects from native trees were most important for blue-gray gnatcatcher, brown thrasher, Carolina chickadee, eastern towhee, red-bellied woodpecker, and white-breasted nuthatch, whereas native understory vegetation was most important for increases in the abundance of Acadian flycatcher, eastern phoebe, Louisiana waterthrush, scarlet tanager, and wood thrush. These species were also positively associated with percentage tree cover, except for brown thrasher and eastern towhee, both of which are more commonly associated with edge and open habitats (Ehrlich et al. 1988).

In general, many forest-associated species increased in abundance with higher tree densities and declined with higher understory stem densities. Specifically, local tree densities positively affected red-bellied woodpecker, red-eyed vireo and tufted titmouse; conversely, American goldfinch, brown-headed cowbird, house finch and house sparrow were strongly negatively affected. These latter species are often associated with more open areas (Ehrlich et al. 1988). The majority of bird species were negatively associated with increasing understory stem density. For our study, understory stem density was positively correlated with the exotic shrub, Amur honeysuckle (*Lonicera maackii*) ($r > 0.70$), whose presence is strongly predicted by habitat fragmentation (Hutchinson and Vankat 1998). Furthermore, one of most

common species in our study, American robin, has been suggested to be an important dispersal vector for this shrub in southwestern Ohio (Bartuszevige and Gorchoff 2006).

Possible mechanisms for these observed patterns in bird distributions include the notion that native trees and shrubs may provide superior food resources and nesting opportunities compared to exotic vegetation (Reichard et al. 2001). Numerous other investigations have documented the negative effects of exotic vegetation on reproductive performance of many native birds (Schmidt and Whelan 1999, Borgmann and Rodewald 2004, Ortega et al. 2006). In particular, the exotic shrub Amur honeysuckle (*Lonicera maackii*) negatively influences the breeding success of some native species (Schmidt and Whelan 1999); however, recent evidence suggests that the reproductive success of some widespread native species, such as the northern cardinal, is not dependent on exotic vegetation (Leston and Rodewald 2006).

Because local riparian vegetation in our urban system was influenced by changes in the surrounding landscape features (Table 2; see Pennington et al. *in review* for details), impacts of human activity on bird species were also indirectly expressed through changes in vegetation composition and structure. Modification in riparian vegetation from surrounding landscape has been also noted by other studies (e.g., Beissinger and Osborne 1982, Miller et al. 2003, Burton and Samuelson 2007). Consequently, habitat restoration efforts aimed at maintaining both native trees and shrubs at the site level must also attend to landscape context.

Most influential landscape features and spatial scales

Species responses to landscape features and spatial scale varied greatly in both importance and effect (Figure 2; Appendix B). Our approach to examining the influences of different aspects of urban heterogeneity – built and vegetation features – across multiple scales did uncover nuanced responses by individual species. A majority of the species in our study are not regionally listed as a species of conservation concern; however, several of these species, often labeled “urban avoiders” and “urban adapters” (McKinney 2002), did show distinct habitat preferences within the metropolitan landscape, emphasizing the importance of considering species-specific management actions to prevent possible local extinctions within metropolitan areas of what are considered regionally widespread species. Additionally, management and planning efforts focused within metropolitan areas that emphasizes native species diversity (not just species of concern) can help ensure common species stay common (McKinney 2006) and that people have opportunities to experience a biologically diverse landscape where they live, work, and play (Miller 2005).

Based on combined and landscape-scale competitive models, vegetative landscape features were important for 40 species (Table 5 and 6; percentage tree cover and grass cover, respectively), while surrounding building density was important for 13 species (Table 7). Between the two vegetative landscape features, percentage grass cover was more commonly included in competitive models than percentage tree cover. For the majority of species, the amount of vegetation in the landscape was more important than building density. In general, the percentage tree cover and building density were most important at smaller spatial scales (≤ 500 m; Table 5 and 7,

respectively) whereas increasing percentage grass cover was more important at larger scales (> 500 m; Table 6). A similar pattern was reported for an area of much greater spatial extent (5000 m) in Ottawa, Canada (Dunford and Freemark 2005). Others have emphasized the importance of small spatial scales (≤ 200 m) for structuring riparian bird communities (Portland, Oregon; Hennings and Edge 2003), yet we found both small and large scales to be important depending on the species in question.

Most native bird species were positively associated with surrounding tree and grass cover and negatively with building density; in contrast, exotic species (European starling, house finch, and house sparrow) responded oppositely (however, European starling did respond positively to grass cover). This general trend is consistent with both western and eastern North American riparian bird studies (Rottenborn 1999, Miller et al. 2003, Mason et al. 2007). However, the spatial response of both native and exotic bird species did vary. For example, European starlings responded to primarily smaller spatial scales while house sparrows responded to both small and large scales. Two nest predators, American crow and blue jay, had best models at small scales. The only nest parasite, brown-headed cowbird, was best predicted by small scale (50 m) features comprised of a mixture of grass and few trees, or in other words, a patchy and fragmented habitat; however, others have reported broad scales being most important for this species in developed (Hennings and Edge 2003) and undeveloped areas (Cunningham and Johnson 2006).

For 10 species, the lowest AIC_c values for combined or landscape-only models included variables at the largest scales, 700 to 1000 m. Percentage grass cover was important for eight of these species and building density for the remaining two. Two

species that responded to grass cover, pileated woodpecker and red-winged blackbird, have large range sizes, and are likely responding to broad expanses of open space with scattered trees. Many of the species showing sensitivity to the largest spatial scales are thought to have small breeding territories and remain near nest sites (Erhlich et al. 1988). The body size of individuals of a species has been suggested to correspond with the scale at which a species responds; however, further work is needed to clarify this relationship (Hostetler and Holling 2000). Four of these species (brown thrasher, common yellowthroat, eastern towhee, and yellow-billed cuckoo) prefer large expanses of open or patchy habitats. One ubiquitous species, American robin, increased with areas of increasing building density at the largest scale, apparently demonstrating its preference for exploiting the resources associated with dense residential areas (Donnelly and Marzluff 2006). Several species responded to both small and large scales further emphasizing the difficulty of generalizing species responses.

Interestingly, 14 species responded to multiple landscape features, often at different spatial scales. For example, the Neotropical migrant Acadian flycatcher responded positively to the amount of tree cover within 100 to 1000 m and negatively to the number of buildings within 100 to 300 m, suggesting the importance of an undeveloped forest corridor at least 300 m wide and the influence of tree cover beyond 300 m regardless of the number of buildings. In contrast, the exotic species house sparrow responded positively to building density at 100 to 200 m and negatively to grass cover at 500 to 900 m. The ubiquitous native species northern cardinal responded positively to building density and less grass cover at 300 to 600 m and to less tree cover at larger scales from 700 to 1000 m. Such complexity in species' responses to both

landscape feature and scale suggests that the aggregation of biophysical measures into simplified urban indices could mask potential mechanisms.

Management and research implications

Riparian habitats within metropolitan areas can provide important breeding habitat for a variety of native species. We accentuate the importance of untangling the role of built and vegetative features in order to further our understanding of the biophysical composition and structure of these complex urban environments. Our results provide landowners, managers, and land-use planners with species-specific information to begin addressing both local and landscape conservation needs. Human decisions that alter the landscape at different scales (e.g., individual landowner, municipality, and regional land-use planning) can affect species differently (Hostetler 1999). Human-mediated processes occurring at the individual landowner scale (e.g., design and management of a backyard) are often considered too fine-scaled to have much impact on many species within urban areas. However, a few species were affected by fine-scale landscape decisions; for example, American goldfinch, brown-headed cowbird, and European starling benefit from individual landowners that manage for lawns with a few trees. In contrast, blue-gray gnatcatcher, downy woodpecker, red-bellied woodpecker, and tufted titmouse benefit from landowners managing for less lawn and more trees (Table 5 and 6).

Yet most birds would be more affected by a city's long-range comprehensive development plan that considers landscapes at larger scales. Many of the most urban-sensitive species require the broad-scale maintenance of natural habitat within urban

areas, such as maintaining large grassy open areas with few trees (e.g., common yellowthroat, eastern towhee, and yellow-billed cuckoo; Table 6), while others require the broad-scale maintenance of forest cover (e.g., Acadian flycatcher, Louisiana waterthrush, scarlet tanager, and wood thrush; Table 5). Still others, often the most abundant and widespread species, such as American robin, blue jay, and northern cardinal, can co-exist with varying levels of development and vegetation (Table 7).

Consideration of both local and landscape-scale features is important for studies of habitat selection in urbanizing areas. Researchers of small study areas should attend to the larger landscape context, and those focused on landscape modeling efforts should acknowledge the role of local vegetation characteristics. Landscape-scale studies should evaluate habitat conditions at scales less than 1 km, especially when high resolution remotely-sensed data are available. In general, the large-scale responses we report could be applied to regional level habitat modeling efforts; however, we stress that for most species best models were based on the combination of both local and landscape information. Therefore, investigators utilizing regional scale modeling should acknowledge the potential limitations of these habitat models (Cunningham and Johnson 2006). Additional studies are needed to parse out the contributions of specific biophysical features within the urban landscape and provide additional insights regarding the complexity of urban systems. Futures studies should focus on how specific life-history characteristics explain the possible mechanisms behind the pattern in bird distributions presented here; suggested approaches would include demographic and functional group responses. Such insights will benefit not only our understanding

of species management, but also deepen our understanding of the structure and function of these novel ecosystems (Hobbs et al. 2006).

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Table 1. Summary values for explanatory variables for the Cincinnati study area in southwestern Ohio, USA.

Variable	Maximum	75% quartile	Median	25% quartile	Minimum
<i>Local vegetation</i>					
N_T_FRQ	1.0	0.9	0.90	0.8	0.7
N_U_FRQ	0.8	0.1	0.0	0.0	0.00
TOT_BA	12.6	12.3	11.8	11.6	10.1
CANOPYH	28.6	18.4	15.4	12.0	7.2
DEAD_T	23.0	8.0	5.0	3.0	0.0
T_DEN	6.0	5.7	5.5	5.3	4.4
U_DEN	10.6	9.8	9.5	9.1	7.9
<i>Landscape</i>					
%T_50	100.0	99.5	77.2	59.6	8.3
%T_100	100.0	80.0	61.0	44.2	7.9
%T_200	98.8	65.7	48.1	34.5	10.0
%T_300	96.2	60.5	44.2	34.0	9.1
%T_400	89.3	53.3	44.3	31.0	9.2
%T_500	81.8	53.6	42.6	30.6	11.9
%T_600	77.3	52.7	40.1	31.4	15.5
%T_700	71.1	50.5	38.8	31.0	19.6
%T_800	65.4	51.3	39.1	31.7	21.0
%T_900	61.4	50.3	39.3	30.9	22.0
%T_1000	59.5	48.7	39.7	30.6	21.2
%G_50	43.8	9.0	8.9	0.8	0.0
%G_100	48.0	23.0	15.2	7.4	0.0
%G_200	41.0	26.9	20.4	13.3	0.7
%G_300	41.3	26.6	21.6	14.0	2.2
%G_400	39.9	26.2	21.4	15.4	9.2
%G_500	34.1	25.0	20.6	14.7	12.5
%G_600	37.0	23.8	20.3	17.9	14.8
%G_700	37.8	23.9	20.5	18.8	14.1
%G_800	39.3	23.9	21.1	18.6	15.7
%G_900	40.6	23.5	21.0	19.1	15.1
%G_1000	41.1	24.4	21.1	19.6	14.8
BDEN_50	17.8	1.3	0.0	0.0	0.0
BDEN_100	10.8	2.6	0.6	0.0	0.0
BDEN_200	8.0	3.7	1.6	0.3	0.0
BDEN_300	9.0	4.4	2.0	0.7	0.0
BDEN_400	9.1	4.4	2.4	0.4	0.0
BDEN_500	9.3	4.5	2.4	1.2	0.0
BDEN_600	8.7	4.6	2.4	1.4	0.2
BDEN_700	9.0	4.8	2.2	1.4	0.4
BDEN_800	9.2	5.3	2.2	1.4	0.6
BDEN_900	8.7	5.4	2.4	1.5	0.8
BDEN_1000	8.4	5.6	2.4	1.7	0.9

Note: Variable codes: N_T_FRQ = native tree frequency, N_U_FRQ = native understory frequency, TOT_BA = basal area, CANOPYH = avg. canopy height, DEAD_T = number dead trees, T_DEN = tree or canopy stem density, U_DEN = understory stem density, %T = percentage tree cover (e.g., %T_50 is percentage tree cover within 50 m), %G = percentage grass/shrub cover, BDEN = building density (#/ha).

Table 2. Correlations between explanatory variables (see Table 1 for codes).

	N_FRQ_U	TOT_BA	TOT_T_DEN	CANOPYH	DEAD_T	TOT_U_DEN	T_50	T_200	T_400	T_800	G_50	G_200
N_FRQ_T	0.2493	0.215	0.3151	0.0578	-0.099	0.3484	0.5145	0.4917	0.459	0.3836	-0.2703	0.0126
N_FRQ_U		0.0068	0.0625	-0.0162	-0.1726	-0.1592	0.2135	0.4328	0.4692	0.3754	-0.0797	-0.358
TOT_BA			0.4585	0.5184	0.1771	0.1517	0.4755	0.3802	0.3048	0.1452	-0.309	0.0914
TOT_T_DEN				0.0704	0.3542	0.3831	0.5116	0.4879	0.4658	0.3998	-0.3112	0.0606
CANOPYH					-0.0181	-0.1639	0.2842	0.1872	0.1662	0.0405	-0.2763	-0.0825
DEAD_T						0.2267	0.0036	-0.1616	-0.1555	-0.1174	0.0717	0.1284
TOT_U_DEN							0.0547	-0.0336	-0.0501	-0.1253	-0.1038	0.0714
T_50								0.7606	0.666	0.544	-0.6734	0.0081
T_200									0.9189	0.7813	-0.4465	-0.1964
T_400										0.8801	-0.3382	-0.1431
T_800											-0.1751	-0.0151
G_50												0.3052
G_200												
G_400												
G_800												
BDEN_50												
BDEN_200												
BDEN_400												
BDEN_600												
BDEN_800												
B_50												
B_200												
B_400												
B_600												

Table 2 (continued). Correlations between explanatory variables (see Table 1 for codes).

Continued...	G_400	G_800	BDEN_50	BDEN_200	BDEN_400	BDEN_600	BDEN_800	B_50	B_200	B_400	B_600	B_800
N_FRQ_T	0.1162	0.206	-0.0909	-0.1585	-0.2572	-0.3194	-0.3738	-0.2891	-0.4098	-0.3276	-0.4087	-0.3871
N_FRQ_U	-0.2275	-0.1076	-0.1214	-0.1707	-0.1589	-0.1525	-0.1476	-0.1369	-0.226	-0.2554	-0.2657	-0.2326
TOT_BA	0.0263	0.0594	0.0798	0.1257	0.1484	0.1097	0.0425	-0.13	-0.2217	-0.0721	-0.0572	-0.0412
TOT_T_DEN	0.1673	0.2531	0.1636	0.1848	0.1743	0.1016	0.0367	0.0745	-0.1372	-0.3526	-0.286	-0.2725
CANOPYH	-0.1422	-0.1536	0.1168	0.0377	-0.0251	-0.066	-0.0938	-0.116	-0.236	0.0052	-0.0374	-0.0002
DEAD_T	0.0673	-0.0229	0.1341	0.3072	0.4131	0.3987	0.3612	0.0794	0.2052	0.0826	0.1632	0.2184
TOT_U_DEN	-0.0406	0.1435	0.0925	-0.0201	-0.0396	-0.0418	-0.0746	0.0253	0.0095	-0.1124	-0.0946	-0.0736
T_50	0.2177	0.2781	-0.0988	0.0276	-0.0367	-0.1033	-0.1699	-0.3037	-0.4262	-0.3894	-0.378	-0.3764
T_200	0.0926	0.3184	-0.0906	-0.2014	-0.2749	-0.3298	-0.3598	-0.3159	-0.5748	-0.5807	-0.5978	-0.6128
T_400	0.1167	0.3744	-0.1219	-0.2688	-0.3477	-0.3718	-0.3908	-0.2639	-0.5575	-0.6866	-0.6975	-0.7099
T_800	0.3131	0.4512	-0.1572	-0.3275	-0.4727	-0.4864	-0.4837	-0.2542	-0.5349	-0.6969	-0.7942	-0.8441
G_50	0.1474	0.049	-0.093	-0.151	-0.1452	-0.0726	0.007	-0.1418	0.0204	0.0773	0.0662	0.0044
G_200	0.7331	0.2867	-0.0756	-0.0558	0.0213	0.072	0.0964	-0.1826	-0.2875	-0.1511	-0.0251	-0.0412
G_400		0.6691	-0.1432	-0.1215	-0.1521	-0.1142	-0.0834	-0.2138	-0.3408	-0.4806	-0.4073	-0.3894
G_800			-0.2271	-0.3334	-0.3954	-0.339	-0.3016	-0.2195	-0.3843	-0.6455	-0.6515	-0.684
BDEN_50				0.593	0.4607	0.4296	0.4082	0.4812	0.3209	0.2315	0.2437	0.2055
BDEN_200					0.8406	0.7293	0.6856	0.3473	0.5276	0.4256	0.552	0.5224
BDEN_400						0.9411	0.8721	0.338	0.5516	0.5181	0.6934	0.7018
BDEN_600							0.9748	0.3481	0.5726	0.4926	0.6982	0.7122
BDEN_800								0.3649	0.5726	0.4624	0.69	0.7035
B_50									0.5616	0.2734	0.2587	0.3009
B_200										0.6809	0.6533	0.5934
B_400											0.8771	0.7634
B_600												0.9237

Table 2 (continued). Correlations between explanatory variables (see Table 1 for codes).

Continued...	G_400	G_800	BDEN_50	BDEN_200	BDEN_400	BDEN_600	BDEN_800	B_50	B_200	B_400	B_600	B_800
N_FRQ_T	0.1162	0.206	-0.0909	-0.1585	-0.2572	-0.3194	-0.3738	-0.2891	-0.4098	-0.3276	-0.4087	-0.3871
N_FRQ_U	-0.2275	-0.1076	-0.1214	-0.1707	-0.1589	-0.1525	-0.1476	-0.1369	-0.226	-0.2554	-0.2657	-0.2326
TOT_BA	0.0263	0.0594	0.0798	0.1257	0.1484	0.1097	0.0425	-0.13	-0.2217	-0.0721	-0.0572	-0.0412
TOT_T_DEN	0.1673	0.2531	0.1636	0.1848	0.1743	0.1016	0.0367	0.0745	-0.1372	-0.3526	-0.286	-0.2725
CANOPYH	-0.1422	-0.1536	0.1168	0.0377	-0.0251	-0.066	-0.0938	-0.116	-0.236	0.0052	-0.0374	-0.0002
DEAD_T	0.0673	-0.0229	0.1341	0.3072	0.4131	0.3987	0.3612	0.0794	0.2052	0.0826	0.1632	0.2184
TOT_U_DEN	-0.0406	0.1435	0.0925	-0.0201	-0.0396	-0.0418	-0.0746	0.0253	0.0095	-0.1124	-0.0946	-0.0736
T_50	0.2177	0.2781	-0.0988	0.0276	-0.0367	-0.1033	-0.1699	-0.3037	-0.4262	-0.3894	-0.378	-0.3764
T_200	0.0926	0.3184	-0.0906	-0.2014	-0.2749	-0.3298	-0.3598	-0.3159	-0.5748	-0.5807	-0.5978	-0.6128
T_400	0.1167	0.3744	-0.1219	-0.2688	-0.3477	-0.3718	-0.3908	-0.2639	-0.5575	-0.6866	-0.6975	-0.7099
T_800	0.3131	0.4512	-0.1572	-0.3275	-0.4727	-0.4864	-0.4837	-0.2542	-0.5349	-0.6969	-0.7942	-0.8441
G_50	0.1474	0.049	-0.093	-0.151	-0.1452	-0.0726	0.007	-0.1418	0.0204	0.0773	0.0662	0.0044
G_200	0.7331	0.2867	-0.0756	-0.0558	0.0213	0.072	0.0964	-0.1826	-0.2875	-0.1511	-0.0251	-0.0412
G_400		0.6691	-0.1432	-0.1215	-0.1521	-0.1142	-0.0834	-0.2138	-0.3408	-0.4806	-0.4073	-0.3894
G_800			-0.2271	-0.3334	-0.3954	-0.339	-0.3016	-0.2195	-0.3843	-0.6455	-0.6515	-0.684
BDEN_50				0.593	0.4607	0.4296	0.4082	0.4812	0.3209	0.2315	0.2437	0.2055
BDEN_200					0.8406	0.7293	0.6856	0.3473	0.5276	0.4256	0.552	0.5224
BDEN_400						0.9411	0.8721	0.338	0.5516	0.5181	0.6934	0.7018
BDEN_600							0.9748	0.3481	0.5726	0.4926	0.6982	0.7122
BDEN_800								0.3649	0.5726	0.4624	0.69	0.7035
B_50									0.5616	0.2734	0.2587	0.3009
B_200										0.6809	0.6533	0.5934
B_400											0.8771	0.7634
B_600												0.9237

Table 3. Species, number of sites species were detected, best local vegetation model, and variable weights (for codes refer to Appendix A).

Species code	N	Best local vegetation model	Weights for variables in local vegetation models							Adj R ²
			Vegetation composition			Vegetation structure				
			Native canopy frequency	Native understory frequency	Canopy basal area	Canopy Height	# Dead trees	Canopy stem density	Understory stem density	
MODO	66	- CANOPYH - TOT_U_DEN - N_FRQ_U	-0.31	-0.86	-0.32	-0.85	+0.40	-0.26	-0.60	0.17
YBCU	28	+ N_FRQ_T + TOT_T_DEN - CANOPYH	+0.61	-0.83	-0.37	-0.65	-0.26	+0.27	+0.40	0.18
BEKI	32	+ N_FRQ_T - TOT_U_DEN	+0.81	+0.25	+0.40	-0.25	-0.36	-0.48	-0.52	0.07
RBWO	56	+ N_FRQ_T + TOT_T_DEN - TOT_U_DEN	+0.99	+0.27	+0.46	-0.27	-0.44	+0.82	-0.46	0.28
DOWO	71	+ N_FRQ_T + TOT_BA	+0.72	+0.31	+0.72	+0.26	+0.27	+0.49	-0.28	0.14
HAWO	19	+ N_FRQ_T + N_FRQ_U	+0.49	+0.65	+0.36	+0.41	-0.44	+0.48	-0.25	0.08
NOFL	50	+ TOT_BA	+0.43	+0.25	+0.60	+0.33	+0.27	+0.33	-0.34	0.04
PIWO	14	+ N_FRQ_T + N_FRQ_U	+0.84	+0.66	+0.24	-0.24	-0.44	+0.41	-0.28	0.14
EWPE	21	+ N_FRQ_T + TOT_BA - TOT_U_DEN + N_FRQ_U	+0.83	+0.67	+0.73	+0.43	-0.24	-0.25	-0.80	0.24
EAPH	11	+ N_FRQ_U	+0.31	+1.00	+0.24	+0.26	-0.24	+0.24	-0.24	0.23
ACFL	10	+ N_FRQ_T + TOT_T_DEN + N_FRQ_U	+0.87	+1.00	+0.31	+0.49	+0.28	+0.56	+0.33	0.29
GCFL	32	+ N_FRQ_T + TOT_BA - DEAD_T + N_FRQ_U	+0.83	+0.63	+0.74	-0.32	-0.79	+0.47	-0.30	0.24
EAKI	17	+ N_FRQ_T + TOT_BA - TOT_T_DEN - CANOPYH + N_FRQ_U	+0.76	+0.77	+0.50	-0.58	-0.28	-0.59	+0.26	0.18
WAVI	37	+ N_FRQ_T - TOT_U_DEN - N_FRQ_U	+0.60	-0.66	+0.41	+0.25	-0.59	-0.26	-0.59	0.09
REVI	26	+ N_FRQ_T + TOT_T_DEN	+0.77	+0.41	+0.26	+0.38	-0.38	+0.80	-0.32	0.14

BLJA	66	+ N_FRQ_T + TOT_BA + TOT_T_DEN - TOT_U_DEN	+0.83	+0.48	+0.78	-0.26	-0.39	+0.69	-0.39	0.24
AMCR	54	- CANOPYH - N_FRQ_U	-0.59	-0.58	-0.32	-0.57	+0.31	-0.25	+0.44	0.06
CACH	71	+ N_FRQ_T + TOT_T_DEN	+0.96	+0.27	+0.58	+0.26	+0.33	+0.49	+0.44	0.21
ETTI	57	+ N_FRQ_T + TOT_BA + TOT_T_DEN - DEAD_T	+0.88	+0.38	+0.72	-0.30	-0.80	+1.00	-0.36	0.41
WBNU	36	+ N_FRQ_T + TOT_T_DEN - TOT_U_DEN	+1.00	+0.40	+0.44	-0.32	+0.25	+0.64	-0.88	0.28
HOWR	6	+ N_FRQ_U	+0.31	+0.47	-0.27	+0.27	-0.27	-0.34	+0.28	0.02
CARW	71	- N_FRQ_U	+0.36	-0.29	-0.27	+0.31	+0.26	+0.43	+0.31	0.00
BGGN	64	+ N_FRQ_T + CANOPYH	+0.94	-0.25	+0.31	+0.62	-0.41	+0.58	-0.30	0.17
EABL	10	+ N_FRQ_U	+0.37	+0.27	+0.27	-0.27	-0.30	-0.34	-0.37	0.00
WOTH	10	+ TOT_T_DEN + CANOPYH + N_FRQ_U	+0.36	+1.00	+0.28	+0.67	-0.31	+0.61	+0.29	0.38
AMRO	71	+ TOT_T_DEN - TOT_U_DEN - N_FRQ_U	-0.35	-0.96	+0.35	-0.26	+0.46	+0.73	-0.88	0.19
GRCA	30	- N_FRQ_U	-0.29	-0.85	+0.25	+0.36	-0.25	-0.25	-0.33	0.06
BRTH	5	+ N_FRQ_T + TOT_BA + TOT_T_DEN - TOT_U_DEN	+0.83	+0.48	+0.78	-0.26	-0.39	+0.69	-0.39	0.24
NOMO	35	- N_FRQ_T - TOT_BA + DEAD_T	-0.74	-0.38	-0.79	+0.34	+0.73	-0.33	+0.39	0.16
EUST	70	- N_FRQ_T - N_FRQ_U	-0.98	-1.00	-0.35	-0.25	+0.26	-0.42	-0.33	0.33
CEDW	55	- TOT_T_DEN + TOT_U_DEN	+0.32	+0.25	+0.28	+0.40	+0.30	-0.58	+0.73	0.05
LOWA	3	+ CANOPYH + N_FRQ_U	+0.36	+1.00	-0.40	+0.90	-0.26	+0.36	+0.40	0.28
COYE	15	+ TOT_T_DEN - DEAD_T	+0.37	-0.26	+0.31	-0.32	-0.53	+0.39	+0.27	0.02
YTWA	27	+ N_FRQ_T + TOT_U_DEN	+0.60	-0.30	+0.48	-0.29	-0.42	+0.38	-0.83	0.08
SCTA	8	+ CANOPYH + N_FRQ_U	+0.37	+1.00	-0.25	+0.99	-0.25	-0.26	+0.24	0.42
EATO	16	+ N_FRQ_T - CANOPYH	+0.94	-0.26	+0.30	-0.90	-0.25	+0.31	-0.29	0.16
FISP	7	+ N_FRQ_U	+0.28	+0.37	-0.30	-0.37	+0.28	+0.28	-0.29	0.00
SOSP	61	- N_FRQ_T - N_FRQ_U	-0.98	-0.95	-0.34	-0.38	+0.25	-0.38	+0.32	0.28
NOCA	71	- N_FRQ_T + TOT_U_DEN	-0.70	-0.24	+0.31	-0.24	-0.26	-0.31	-0.99	0.15
INBU	49	- TOT_T_DEN	-0.28	+0.28	+0.33	+0.31	-0.30	-0.33	-0.27	0.00
RWBL	23	- CANOPYH	+0.36	+0.26	-0.28	-0.61	-0.26	+0.28	-0.26	0.02

COGR	70	-TOT_BA - N_FRQ_U	+0.24	-1.00	-0.62	-0.27	-0.25	-0.58	+0.28	0.27
BHCO	70	-N_FRQ_T - TOT_T_DEN + DEAD_T	-0.58	-0.24	+0.40	+0.27	+0.69	-0.98	-0.37	0.21
OROR	14	+N_FRQ_T	+0.42	+0.30	-0.27	-0.41	+0.26	+0.27	-0.28	0.00
BAOR	49	+TOT_BA - TOT_U_DEN	+0.37	-0.48	+0.94	-0.33	-0.25	+0.28	-0.87	0.14
HOFI	27	+TOT_BA - TOT_T_DEN + DEAD_T - TOT_U_DEN - N_FRQ_U	-0.26	-0.58	+0.66	-0.26	+0.81	-0.82	-0.83	0.22
AMGO	68	-N_FRQ_U	-0.34	-1.00	-0.28	+0.24	+0.44	-0.32	-0.37	0.38
HOSP	69	-N_FRQ_T - TOT_T_DEN - N_FRQ_U	-0.92	-0.89	-0.36	-0.23	+0.29	-0.84	-0.25	0.31

Note: For best local vegetation models, variables and signs of coefficients (positive or negative effects) are shown. For example, the best proximate model for eastern towhee (EATO) included a positive response to native tree frequency and a negative response to canopy height. Strengths of effects are indicated by cumulative weights. Variable weights are the cumulative Akaike weights of models in which a variable occurred. In general, the best proximate models include the most important variables. Where secondary variables have comparable weights, omitted variables may contribute to alternative competitive models.

Table 4. The most important scales and landscape variables influencing bird distributions. Candidate models for species based on model selection procedure including the “best” local vegetation model, landscape-scale models for each biophysical feature, and combined models (these included the 'best' local-vegetation model plus one of the landscape variables (e.g., percentage forest canopy cover for each of the 11 scales (50 m and every 100 m from 100 to 1000 m)). See Appendix A for species codes.

Species code	Best local Vegetation model	Combined models											Landscape-only models										Adj. R ²	
		50 m	100 m	200 m	300 m	400 m	500 m	600 m	700 m	800 m	900 m	1000 m	50 m	100 m	200 m	300 m	400 m	500 m	600 m	700 m	800 m	900 m		1000 m
MODO	X	B+	G+	<u>G+</u>	G+	G+	G+	G+	G+	0.20
YBCU	G+	<u>G+</u>	G+	G+	G+	0.34
RBWO	T+	<u>T+</u>	0.39
DOWO	...	T+	<u>T+</u>	T+	0.20
NOFL	G+	<u>G+</u>	G+	G+	G+	0.21
PIWO	G+	<u>G+</u>	G+	G+	T+	T+	0.33
EWPE	B-	B-	B-	B-	B-	B-	B	<u>B-</u>	0.31
EAPH	X	...	B+	T+	<u>T+</u>	T+	T+	T+	T+	0.27
ACFL	T+	T+	<u>T+</u>	T+	T+	T+	T+	...	T+	T+	T+	T+	0.36
GCFL	B-	B-	B-	T+	<u>T+</u>	0.34
EAKI	<u>B-</u>	G+	...	G+	G+	0.28
WAVI	G+	0.25
REVI	T+	T+	<u>T+</u>	0.21
BLJA	<u>X</u>	B-	B-	B-	G+	G+	G+	G+	B-	B-	B-	B-	...	T+	T+	0.24
AMCR	T+	T+	T+	T+	T+	T+	G+	G+	T+	T+	T+	T+	T+	T+	0.18
CACH	<u>X</u>	T+	T+	B-	T+	...	G-	G-	G-	G-	G-	G-	0.21
		G-	B-	T+	B-																			

CACH	X	T+	T+	B-	T+	...	G-	G-	G-	G-	G-	B-	0.21	
		G-	B-	T+	B-						B-	G-												
			G-	G-								T+												
ETTI	...	T+	T±	T+	0.48	
WBNU	...	T+	T+	T+	T+	G+	G±	G+	G+	G+	G+	G+	T+	T+	T+	T+	0.34	
HOWR	G±	G+	0.22	
BGGN	...	T+	G+	G+	G±	G+	G+	T+	0.25	
EABL	G±	G+	G+	G+	G+	...	G+	G+	0.14	
WOTH	T+	T±	T+	T+	0.46	
AMRO	B+	B+	B+	B+	B+	B+	B+	B±	B+	B+	0.29	
BRTH	G+	G±	G+
NOMO	T-	T-	T-	0.19	
EUST	G±	0.38	
CEDW	B-	B-	T+	T+	T+	B-	B-	0.12	
					T+																			
LOWA	T±	T+	T+	T+	T+	T+	T+	0.33	
COYE	G+	G+	G+	G±	G+	...	0.37	
YTWA	G+	G±	G+	0.14	
SCTA	X	G-	...	T+	T+	T±	T+	T+	T+	T+	0.45	
					G-																			
EATO	G+	G±	G+	G+	0.39	
FISP	G±	G+	0.32	
SOSP	G+	T-	T-	0.38	
			T-																					
NOCA	B+	B+	B+	B+	T-	T-	T-	T-	0.23	
					G-	G-	G-																	
INBU	B-	...	B-	B-	B-	B-	B-	B-	0.15	
RWBL	G+	G+	G+	G+	G+	G+	G±	G+	...	0.23	
COGR	T-	T-	T-	T-	T-	T-	T-	T-	T-	T-	0.32	
BHCO	X	G±	B-	...	B-	B-	B-	0.25	
		T-	G+																					
OROR	G+	G+	G±	G+	0.25	
BAOR	G±	G+	0.29	
HOFI	G-	G-	G-	G-	G-	G-	0.29	
					B+	B+																		

Notes: Biophysical features are represented by the following symbols: T = percentage tree cover, G = percentage grass cover, B = building density, X = local vegetation. The “best” explanatory models for the relative density of a species ($\Delta AIC_c = 0$; boldface and underlined type) varied greatly; for each scale, biophysical features are listed in order of importance. Non-highlighted type represents candidate models ($\Delta AIC_c < 3$). For example, house sparrow (HOSP) responded negatively to the amount of grass cover within 500 to 900 m of the stream and positively to building density within 100 to 200 m of the stream. Overall, combined models and landscape scales ≤ 500 m were most important across species. Goodness of fit is based on adj. R^2 from linear regression for best model. See Appendix B for graphical representation of modeling results.

Table 5. Competitive models based on local-vegetation only, landscape-scale only, and combined models ($\Delta AIC_c < 3$) for each species. XX represents “best” models ($\Delta AIC_c = 0$).

Common name	Local vegetation	Combined	Landscape
blue jay	XX	X	X
Carolina chickadee	XX	X	
eastern phoebe	X	XX	
scarlet tanager	X	XX	
brown-headed cowbird	X	XX	
mourning dove		XX	
eastern-wood pewee		XX	
eastern kingbird		XX	
warbling vireo		XX	
tufted titmouse		XX	
wood thrush		XX	
American robin		XX	
European starling		XX	
Louisiana waterthrush		XX	
yellow-throated warbler		XX	
eastern towhee		XX	
field sparrow		XX	
song sparrow		XX	
northern cardinal		XX	
common grackle		XX	
Baltimore oriole		XX	
house finch		XX	
American goldfinch		XX	
house sparrow		XX	
yellow-billed cuckoo		XX	X
northern flicker		XX	X
pileated woodpecker		XX	X
Acadian flycatcher		XX	X
American crow		XX	X
white-breasted nuthatch		XX	X
blue-gray gnatcatcher		XX	X
eastern bluebird		XX	X
cedar waxwing		XX	X
red-bellied woodpecker		X	XX
downy woodpecker		X	XX
red-eyed vireo		X	XX

northern mockingbird	X	XX
common yellowthroat	X	XX
indigo bunting	X	XX
red-winged blackbird	X	XX
orchard oriole	X	XX
great crested flycatcher		XX
brown thrasher		XX

Table 6. Summary of species response to scale for percentage tree cover based on both combined-models and landscape-only models. Positive relationships represented by solid black bars and negative relationships represented by slashed bars.

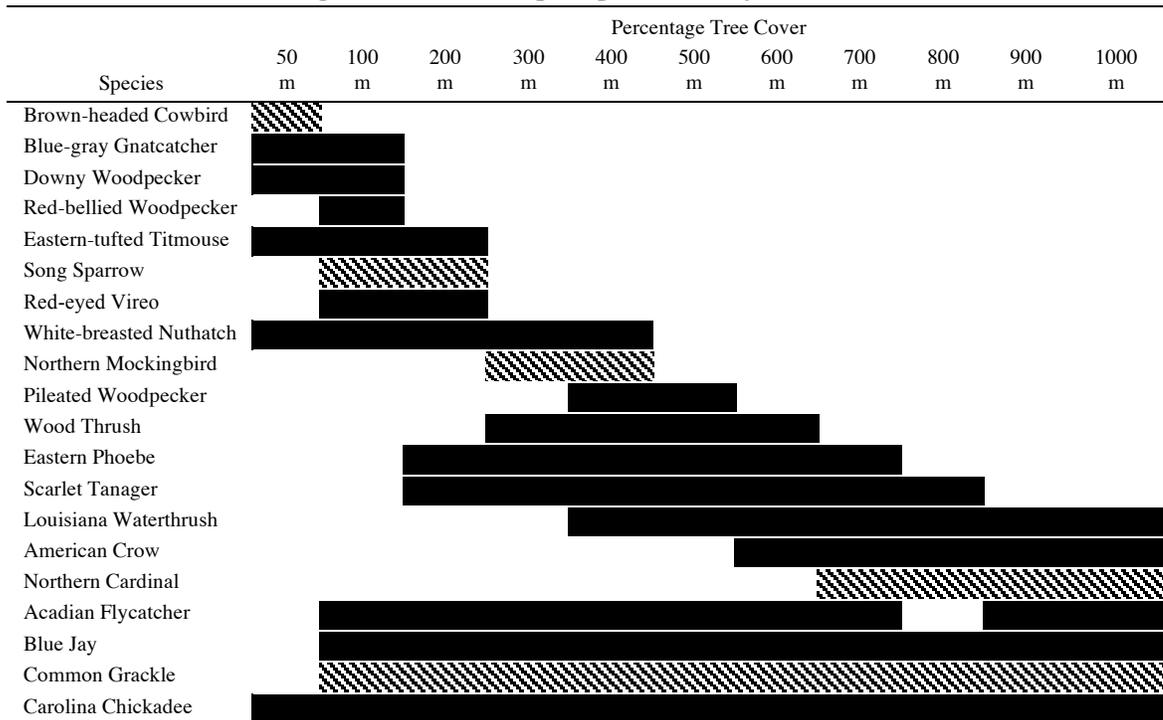


Table 7. Summary of species response to scale for percentage grass cover based on both combined-models and landscape-only models. Positive relationships represented by solid black bars and negative relationships represented by slashed bars.

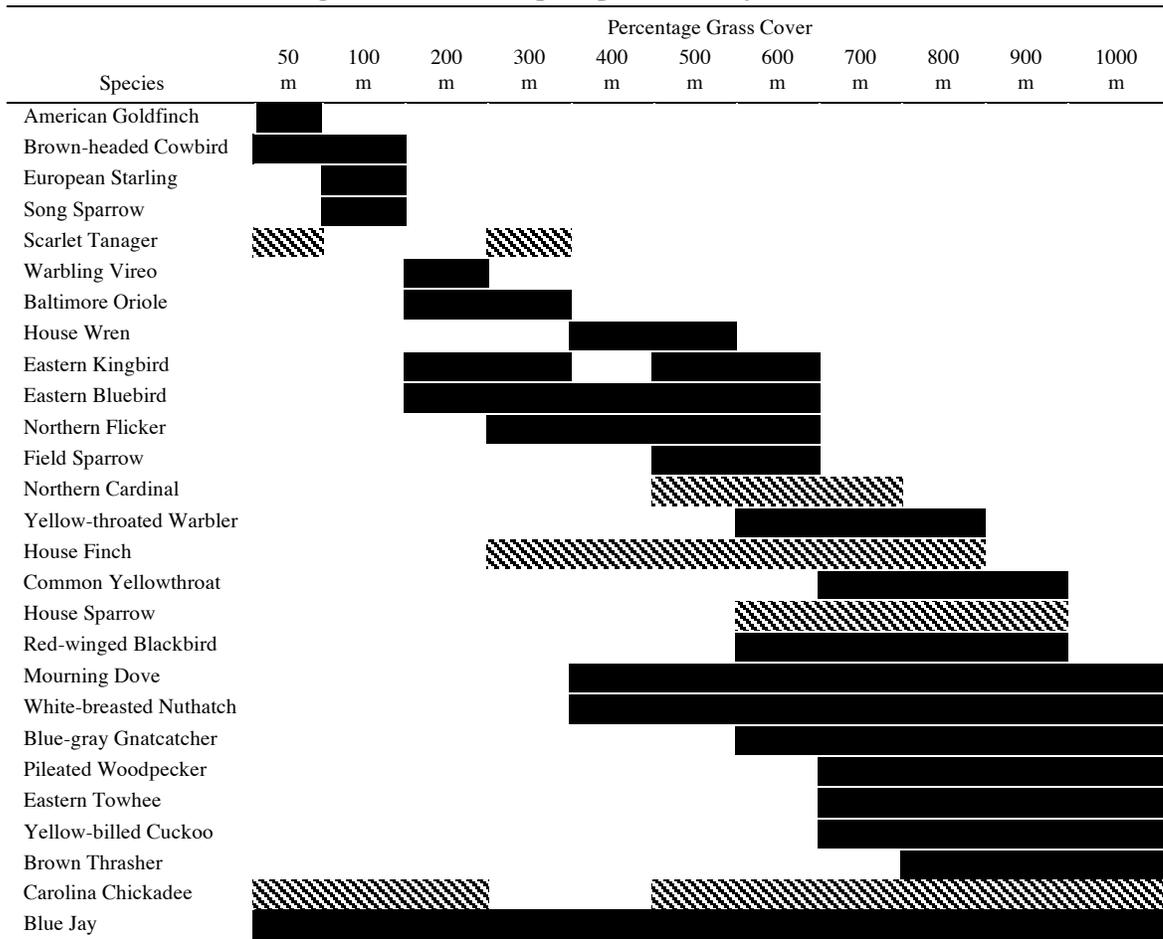


Table 8. Summary of species response to scale for building density based on both combined-models and landscape-only models. Positive relationships represented by solid black bars and negative relationships represented by slashed bars.

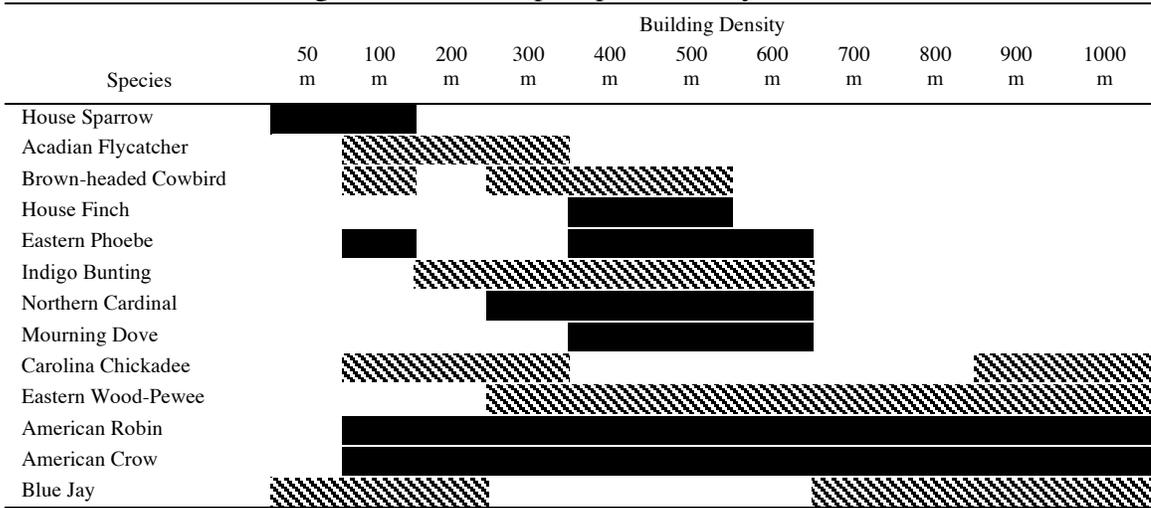


Figure 1. Location of the 71 study plots used to examine bird distributions in riparian areas within the Mill Creek watershed in the greater Cincinnati metropolitan area Hamilton County, Ohio, U.S.A. Land use/land cover map derived from IKONOS satellite imagery courtesy of Space Imaging, LLC and Cincinnati Area Geographical Information Systems.

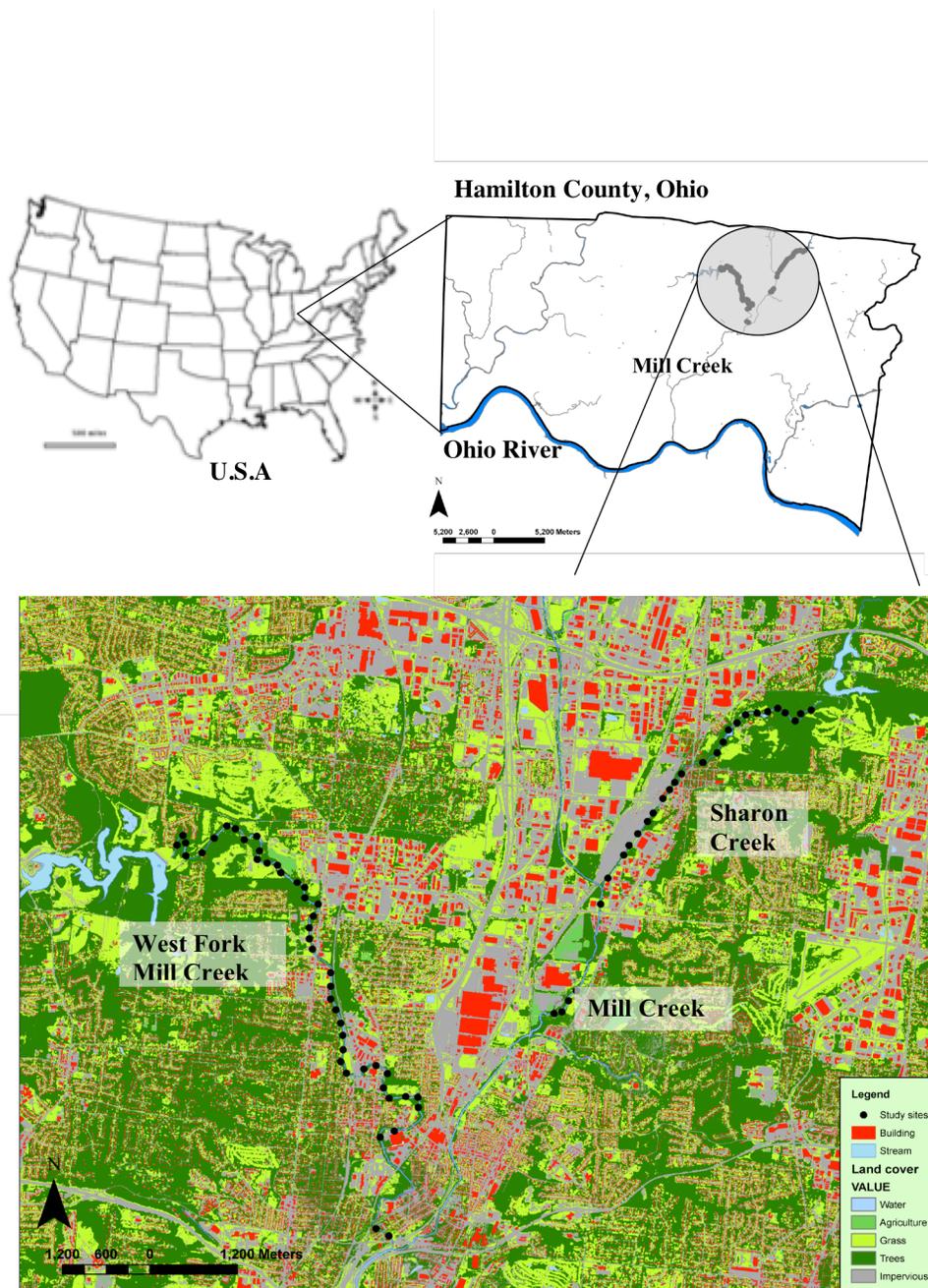
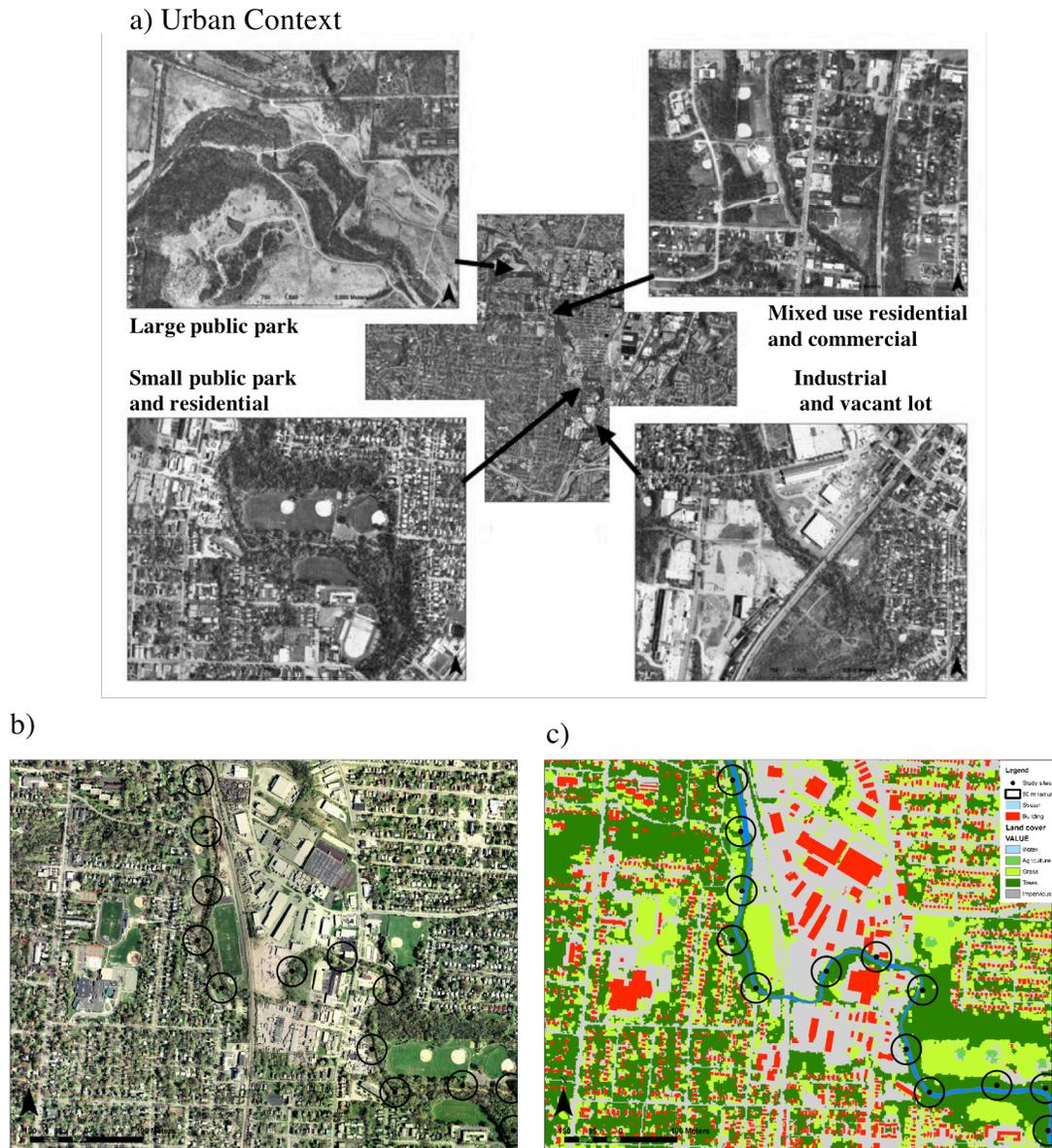


Figure 2. Examples of the variety of land-use types within Cincinnati, OH, U.S.A. study area for West Fork Mill Creek (a). Close-up example of fine-scale landscape biophysical heterogeneity – built and vegetative elements – based on fine-scale digital orthophotos (1:10,000) (b) and IKONOS derived land cover data (c). Black circles represent 50-m radius study plots where birds and woody vegetation were surveyed. IKONOS imagery courtesy of Space Imaging, LLC and Cincinnati Area Geographical Information Systems.



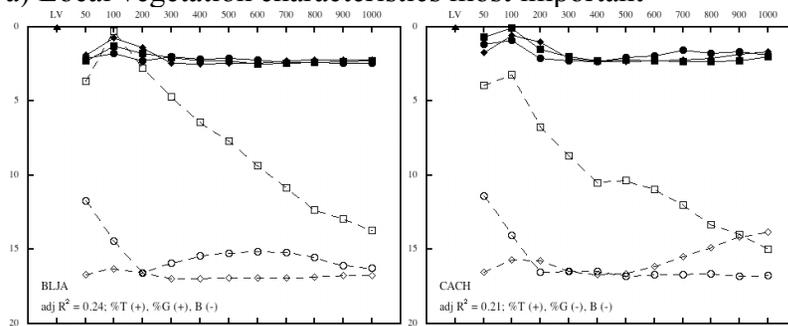
Appendix A. Forty-eight bird species surveyed during 2002 migratory season in Mill Creek watershed in the greater Cincinnati Metropolitan area used in analyses (see methods for calculation of relative density (birds/hectare)).

Species code	Common name	Scientific name	Origin	Mig. status	Mean relative density	% of 71 plots
MODO	mourning dove	<i>Zenaida macroura</i>	N	SD	0.527	93.0
YBCU	yellow-billed cuckoo	<i>Coccyzus americanus</i>	N	N	0.120	39.4
BEKI	belted kingfisher	<i>Ceryle alcyon</i>	N	SD	0.153	45.1
RBWO	red-bellied woodpecker	<i>Melanerpes carolinus</i>	N	P	0.492	78.9
DOWO	downy woodpecker	<i>Picoides pubescens</i>	N	P	0.710	100.0
HAWO	hairy woodpecker	<i>Picoides villosus</i>	N	SD	0.072	26.8
NOFL	northern flicker	<i>Colaptes auratus</i>	N	SD	0.266	70.4
PIWO	pileated woodpecker	<i>Dryocopus pileatus</i>	N	P	0.073	19.7
EWPE	Eastern-wood pewee	<i>Contopus virens</i>	N	N	0.172	29.8
EAPH	eastern phoebe	<i>Sayornis phoebe</i>	N	SD	0.040	15.5
ACFL	Acadian flycatcher	<i>Empidonax virescens</i>	N	N	0.101	14.1
GCFL	great crested flycatcher	<i>Myiarchus crinitus</i>	N	N	0.171	45.1
EAKI	eastern kingbird	<i>Tyrannus tyrannus</i>	N	N	0.052	23.9
WAVI	warbling vireo	<i>Vireo gilvus</i>	N	N	0.172	52.1
REVI	red-eyed vireo	<i>Vireo olivaceus</i>	N	N	0.148	36.6
BLJA	blue jay	<i>Cyanocitta cristata</i>	N	SD	0.597	93.0
AMCR	American crow	<i>Corvus brachyrhynchos</i>	N	SD	0.207	76.1
CACH	Carolina chickadee	<i>Poecile carolinensis</i>	N	P	1.295	100.0
ETTI	tufted titmouse	<i>Baeolophus bicolor</i>	N	P	0.421	80.3
WBNU	white-breasted nuthatch	<i>Sitta carolinensis</i>	N	P	0.267	50.7
HOWR	house wren	<i>Troglodytes aedon</i>	N	N	0.070	8.5
CARW	Carolina wren	<i>Thryothorus ludovicianus</i>	N	P	0.823	100.0
BGGN	blue-gray gnatcatcher	<i>Poliophtila caerulea</i>	N	N	0.570	90.1
EABL	eastern bluebird	<i>Sialia sialis</i>	N	SD	0.047	14.1
WOTH	wood thrush	<i>Hylocichla mustelina</i>	N	N	0.156	14.1
AMRO	American robin	<i>Turdus migratorius</i>	N	SD	1.730	100.0
GRCA	gray catbird	<i>Dumetella carolinensis</i>	N	N	0.123	42.3
BRTH	brown thrasher	<i>Toxostoma rufum</i>	N	N	0.016	7.0
NOMO	northern mockingbird	<i>Mimus polyglottos</i>	N	SD	0.145	49.3
EUST	European starling	<i>Sturnus vulgaris</i>	E	SD	0.963	98.6
CEDW	cedar waxwing	<i>Bombycilla cedrorum</i>	N	SD	0.469	77.5
LOWA	Louisiana waterthrush	<i>Seiurus motacilla</i>	N	N	0.029	4.2
COYE	common yellowthroat	<i>Geothlypis trichas</i>	N	N	0.072	21.1

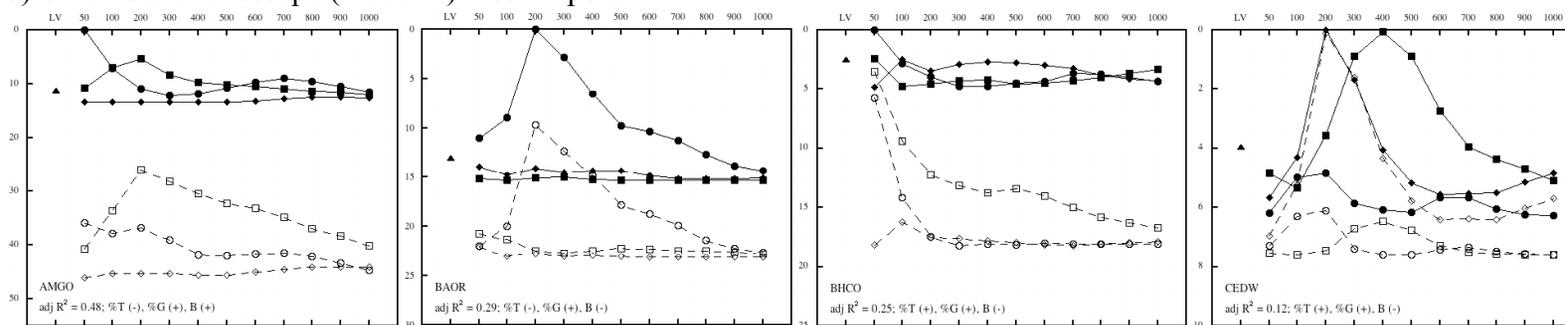
YTWA	yellow-throated warbler	<i>Dendroica dominica</i>	N	N	0.146	38.0
SCTA	scarlet tanager	<i>Piranga olivacea</i>	N	N	0.057	11.3
EATO	Eastern towhee	<i>Pipilo erythrophthalmus</i>	N	SD	0.104	22.5
FISP	field sparrow	<i>Spizella pusilla</i>	N	SD	0.031	9.9
SOSP	song sparrow	<i>Melospiza melodia</i>	N	SD	0.743	85.9
NOCA	northern cardinal	<i>Cardinalis cardinalis</i>	N	P	1.955	100.0
INBU	indigo bunting	<i>Passerina cyanea</i>	N	N	0.369	69.0
RWBL	red-winged blackbird	<i>Agelaius phoeniceus</i>	N	SD	0.135	32.4
COGR	common grackle	<i>Quiscalus quiscula</i>	N	SD	0.853	98.6
BHCO	brown-headed cowbird	<i>Molothrus ater</i>	N	SD	0.722	98.6
OROR	orchard oriole	<i>Icterus spurius</i>	N	N	0.043	19.7
BAOR	Baltimore oriole	<i>Icterus galbula</i>	N	N	0.247	69.0
HOFI	house finch	<i>Carpodacus mexicanus</i>	E	SD	0.148	38.0
AMGO	American goldfinch	<i>Carduelis tristis</i>	N	SD	0.805	95.8
HOSP	house sparrow	<i>Passer domesticus</i>	E	P	1.047	97.2

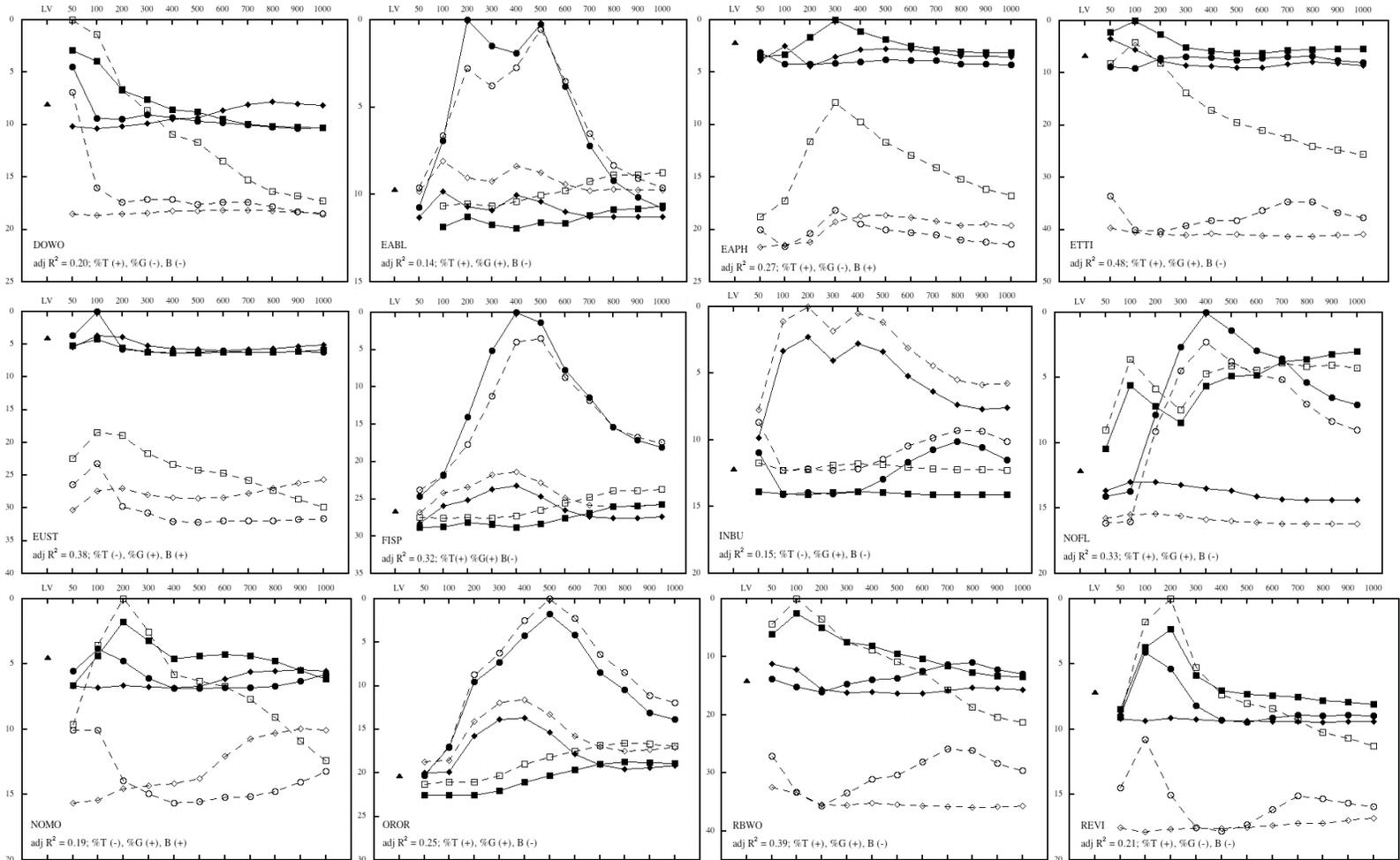
Appendix B. Plots of $\Delta AICc$ show scales of response and comparisons between landscape features as well as comparisons between local vegetation, landscape, and combined models. Graphs of ΔAIC compare models within a set. Best models have $\Delta AIC = 0$, but models with $\Delta AIC < 3$ can be considered competitive with the best model. Triangles indicate ΔAIC for local vegetation models: LV = \blacktriangle . Dashed lines show ΔAIC across scales for models containing only one landscape variable: % Tree = \square , % Grass = \oplus , Building density = \diamond . Solid lines show ΔAIC for combined (local vegetation and landscape) models at 50 to 1000 m scales: % Tree + LV = \blacksquare , % Grass + LV = \bullet , Building density + LV = \blacklozenge . Goodness of fit for the “best” model based on adjusted R^2 and the relationship for each landscape feature are reported.

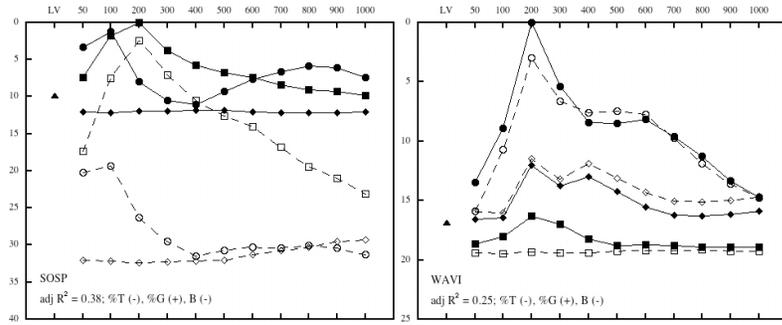
a) Local vegetation characteristics most important



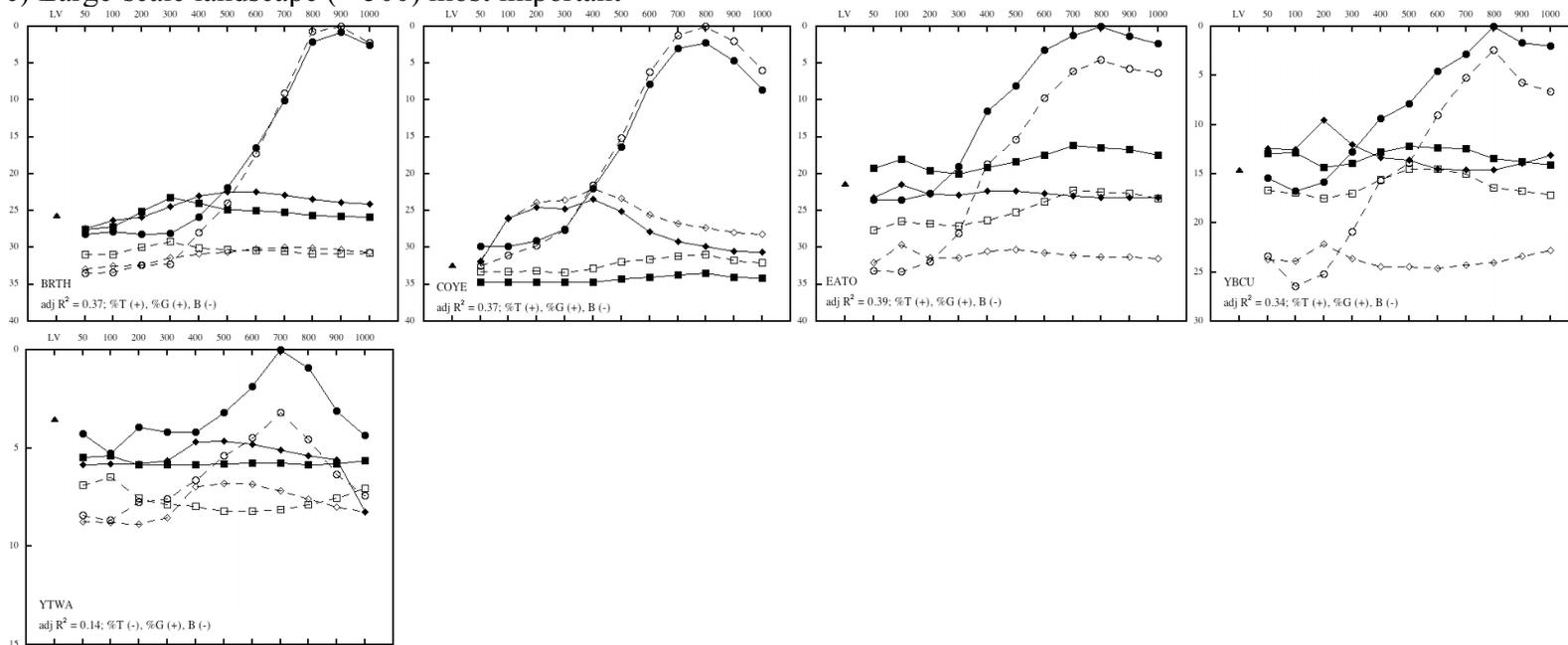
b) Small-scale landscape (≤ 500 m) most important



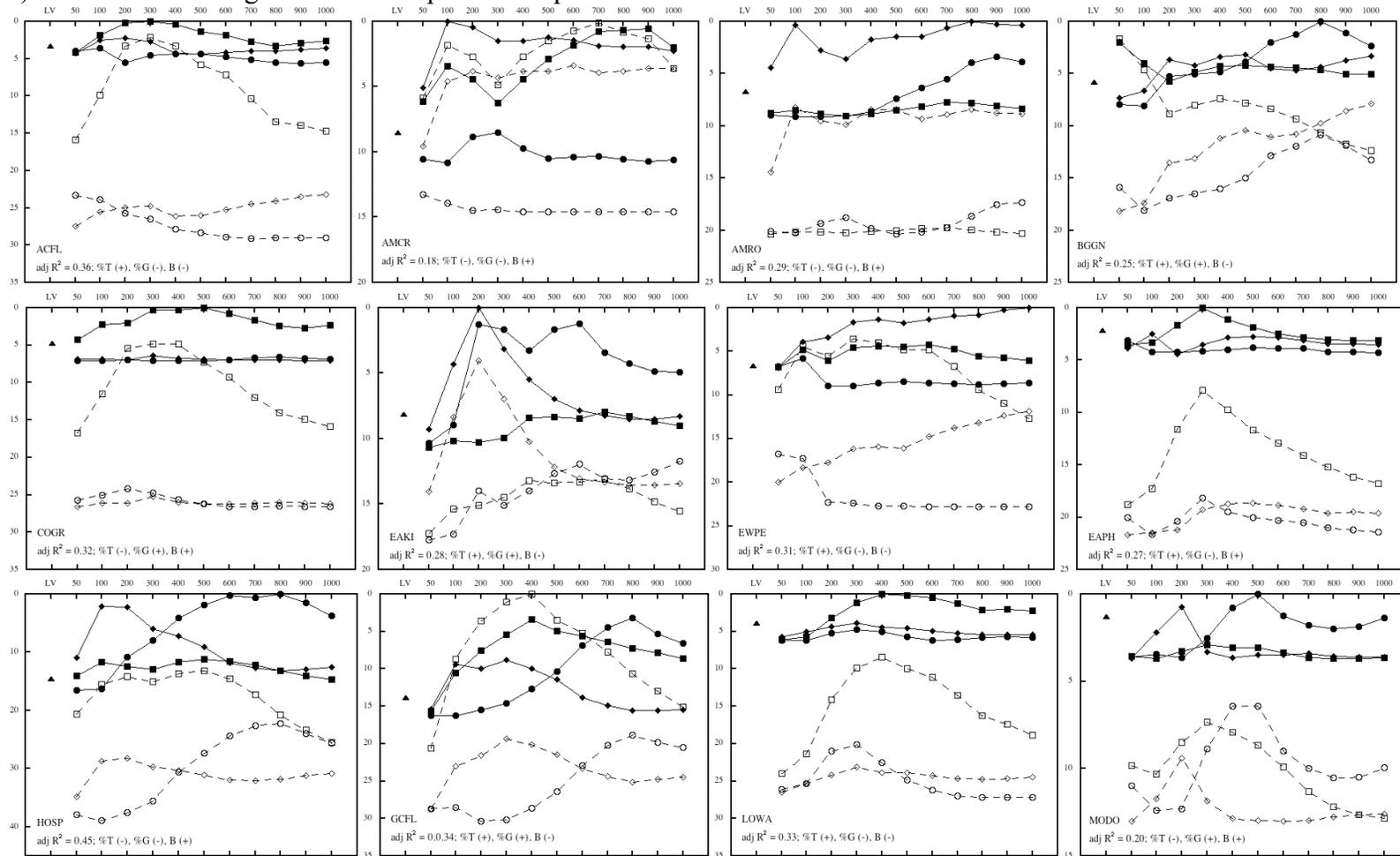


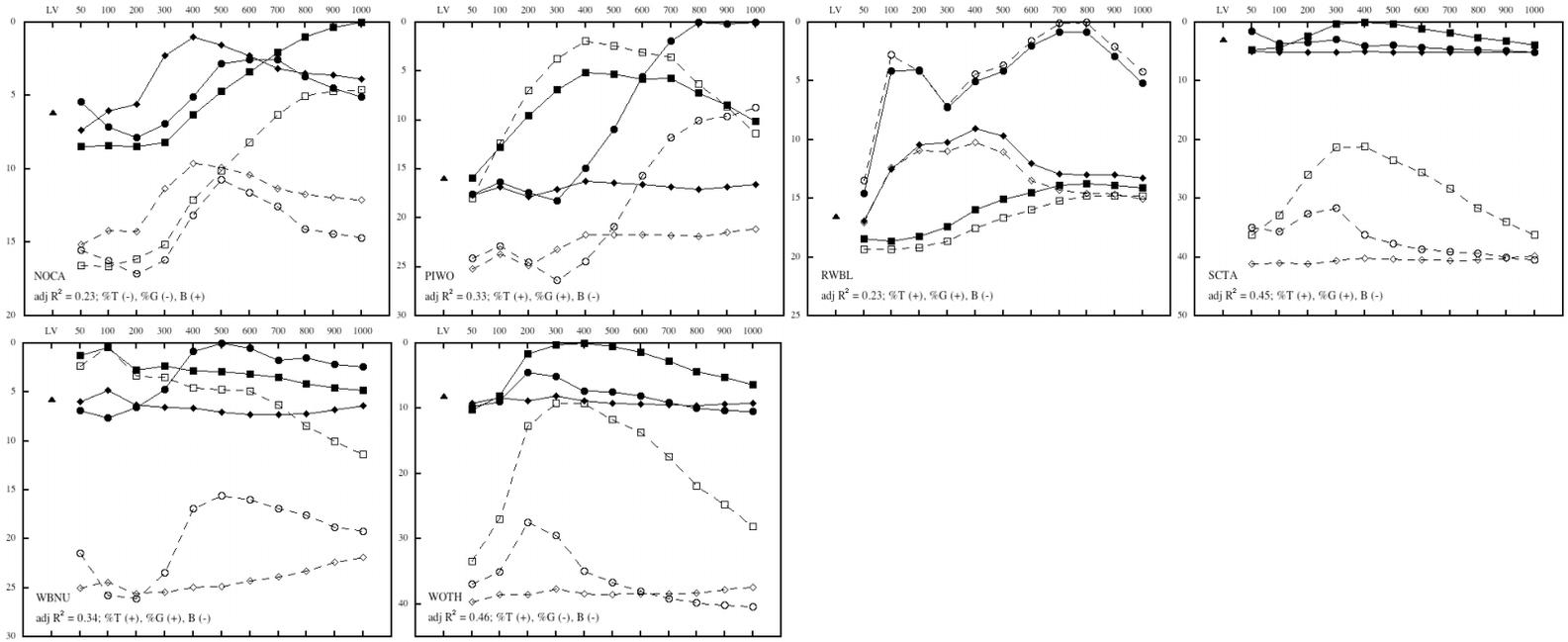


c) Large-scale landscape (> 500) most important



d) Both small and large-scale landscape scale important





CHAPTER 5

Conclusions

My research in the Cincinnati metropolitan region advances our knowledge on the effect of both local and landscape biophysical features – vegetation and built infrastructure – on the distribution of birds in urban riparian areas. Birds are distributed differently in urban areas depending on their individual life history characteristics and migratory strategies. The vegetative and built features of urban areas affect bird distributions differently. Finally, birds respond differently to features in the urban environment at varying spatial scales.

Habitat selection during spring migration

Tree cover and building area are the most important landscape features affecting the habitat selection of native birds during spring migration. Native forest bird species are more abundant, more diverse, and more evenly distributed in riparian areas with greater tree cover and less urban development (e.g., buildings) within the surrounding landscape. Synanthropic and exotic species show the opposite response and are more numerous in riparian areas with less tree cover and more urban development.

During spring migration, native birds rely on native trees and shrubs. Most native bird species are dependent on riparian forests comprised of native woody vegetation and with a structurally diverse canopy. Again, synanthropic and exotic species respond oppositely, and are found in areas comprised of more exotic trees and shrubs and less structure.

Long-distance migrant songbirds are most affected by changes in the biophysical features. Riparian forests with a high percentage of tree cover and fewer buildings within 250-500 m surrounding the streams are important for retaining long-distance migrant songbirds. Permanent resident species are most strongly associated with areas of high

tree cover within 250 m of the stream, and short-distance migrants are positively correlated with grass cover within 500 m of the stream.

Native woody plant composition is the most important local vegetation characteristic for determining habitat selection by long-distance migrants. Native vegetation is also important for permanent resident species, but to a lesser degree. Short-distance migrants do not show a clear preference for the local vegetation characteristics measured.

Stopover habitat selection dependent on native vegetation surrounding streams

En-route Neotropical migrants occur in more urbanized sites than locally breeding Neotropical species. During spring migration, en route or stopover migrants settle into urban landscapes without regard to degree of urbanization, but do select certain habitat attributes once on the ground. Specifically, en-route migrants utilize areas with of a wide (250-500 m) buffer of tree cover regardless of whether buildings are present. Locally breeding species preferred wider riparian forests (> 500 m) with little or no development.

Riparian forests that include native woody species and high canopies are important for both en-route and locally breeding Neotropical species.

Breeding habitat selection dependent on both proximate and landscape

Bird distributions are best described by both the amount of vegetation (amount of tree and grass cover) in the surrounding landscape and the woody plant composition of the riparian forest. Native breeding species select habitat based on vegetation features within the surrounding landscape with little regard for building density. Habitat selection for most birds is dependent on the biophysical features present within small spatial scales

(≤ 500 m) based on the amount of tree cover and building density; grass cover is most important at larger scales (500-1000 m).

Most breeding bird species select riparian habitats comprised of native canopy and understory vegetation. However, habitat selection by several species is also dependent on structural vegetation measures such as tree and shrub stem densities, tree basal area, and canopy height.

Management and conservation recommendations

Past large-scale urban gradient studies have documented that urban riparian forests are more impaired than their “natural” or rural counterparts (e.g., Paul and Meyer 2001, Rodewald and Bakerman 2006); and consequently, their conclusions often diminish the perceived ecological value of small remnant vegetation within highly modified landscapes. Yet it is becoming increasingly important for researchers, managers, planners, and citizens to understand the potential ecological and societal value of remnant urban vegetation (Miller and Hobbs 2002, Turner et al. 2004). Given that over 60 % of the world’s population will reside in urban areas by 2030 (UNPD 2003), my study illustrates how the “less than pristine” forested habitats can provide an opportunity to support critical ecosystem services for both people and other species (Miller 2005, Bernhardt and Palmer 2007).

A majority of the bird species examined in my study are not regionally listed as species of conservation concern; however, several of these species did show distinct habitat preferences within the metropolitan landscape, emphasizing the importance of considering species-specific management actions to prevent possible local extinctions within metropolitan areas of what are considered regionally widespread species.

To maintain native birds, management activities should aim to avoid activities that diminish tree cover both near and adjacent to urban streams. Riparian buffers of 250 m are sufficient to protect a reasonable amount of bird diversity. Efforts are also needed to restore and maintain native riparian vegetation of both tree and shrub species.

Managing for stopover habitat

Birds that use urban landscapes during migration are often constrained by habitat availability and have few options when selecting areas for feeding and resting as they finish migratory flight. Management efforts should focus on protecting and restoring the remaining wide and undeveloped riparian forests within metropolitan areas, especially within 250 to 500 m within the surrounding landscape of a stream. Because developed areas incorporating a high amount of tree cover appear to be perceived as “forest” to en route long-distance migrant songbirds during stopover, efforts should aimed at increasing native tree and shrub cover with residential and commercial developments should be strongly encouraged.

Managing for breeding habitat

Management actions should acknowledge the species-specific habitat requirements of birds within urban environments. Efforts should be made to attend to local vegetation and landscape considerations, as some species require wide riparian forests and others require more open areas. The effect of spatial scale on individual species can greatly influence the extent of management activities for a species.

Future directions

Future work should examine the role of urban biophysical features on bird distributions in other metropolitan areas. Additional studies comparing migration and breeding habitat selection within urban areas are needed to better design urban areas for bird conservation. Both energetic and demographic investigations are needed to further understanding into the mechanisms behind these patterns described here.

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CHAPTER 6

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