INFLUENCES OF A HUMAN-DOMINATED LANDSCAPE ON MIDWESTERN BREEDING BIRD OCCUPANCY AND DIVERSITY

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ABSTRACT

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Human land use dominates the globe, and ecologists and developers are challenged to incorporate effective conservation strategies into human-dominated landscapes that maximize biodiversity and minimize impacts to growth and production. I sought to contribute to general ecological theory by examining the effects of human-dominated landscapes on diversity and distribution patterns of midwestern breeding birds in the Oak Openings Region of northwestern Ohio from 23 May to 2 July 2013 and from 230 point count locations. To better understand the relative importance of matrix, habitat, and localized development, I modeled occurrences of 18 species of birds using an occupancy modeling framework, and occurrences of 10 of those 18 species were best explained by matrix quality over habitat loss and fragmentation. I investigated the importance of habitat structural diversity on diversity patterns of 3 guilds: Neotropical, Nearctic, and exotic species. My diversity models indicated that Neotropical diversity was best explained by habitat amount and secondarily by habitat structural diversity, while the Nearctic guild was best explained by habitat isolation and secondarily to habitat structural diversity. For a subset of survey locations distributed in the urban center, occurrences of native species were best explained by localized habitat amount and habitat structural diversity and not by the proximity to large natural reserves in the area. Finally, I used advances in distribution modeling techniques to predict the spatial distribution of Red-bellied Woodpecker (*Melanerpes carolinus*). My models predicted that habitat isolation and habitat amount were important determinants of occupancy for this species. My work suggests that midwestern breeding bird conservation should focus on conserving matrix quality, restoration of globally unique habitat types, and the addition of localized habitat features in the urban center.

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I thank Dr. Jeffrey Miner and Dr. Shannon Pelini for serving on my examination committee and their dedication to counseling me throughout this project. I am especially grateful for my graduate advisor, Dr. Karen Root. I am proud and deeply grateful to have had the opportunity to work with her. She was an excellent mentor and, in no doubt, will be a lifelong colleague.

I grew up in rural central Ohio, exploring small woodlots and streams, in an environment free to develop my interests in wildlife and ecology. My mother and father, Janet and Timothy Adams, are to be thanked for this. They have encouraged and supported me to pursue my ambitions throughout my life.

I would be remised to not recognize my mother-in-law and father-in-law, Koleen and Daniel Foley, for their support and encouragement throughout this project, as well. They provided writing space and relaxation during academic breaks. I am thankful for their hospitality and generosity.

In closing, this work would not be possible without the support and understanding from my wife, Melissa, and the countless sacrifices she has made for me to pursue my professional aspirations. She has forgone many opportunities to see me succeed. I am deeply indebted to her patience and tolerance throughout this project and my professional development. For this, I cannot describe how appreciative I am for her love and support.

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CHAPTER 1: INTRODUCTION

Natural resource management and conservation depend on accurate information about the distribution and response dynamics of plants and animals; and increasingly, pressing ecological questions have necessitated the need to better understand the effects of the broader landscape on localized ecological patterns and processes (Miller et al. 2004). Understanding the conditions that influence or limit spatial distribution patterns of organisms is central to ecology, as defined as the study of distributions and abundance of plants and animals (e.g., Andrewartha and Birch 1954, Krebs 1972). However, despite decades of research and accumulated knowledge of factors affecting a species' location on the globe or on the landscape, many questions remain. I have sought to examine 4 recent, active areas of research related to the landscape ecology of midwestern breeding birds in human-dominated landscapes: (1) the relative influence of matrix quality vs. habitat loss and fragmentation on bird occupancy; (2) the importance of structural diversity of habitat on bird diversity; (3) the effect of localized habitat in the urban center on bird occupancy; and (4) the extrapolation of fragmentation and structural diversity effects on the broader landscape as reflected by Red-bellied Woodpecker (*Melanerpes carolinus*) occupancy.

Habitat loss and fragmentation (i.e. the breaking apart of habitat independent of habitat loss) are equally recognized as the primary of sources of global biodiversity losses (Fahrig 2003, Fischer and Lindenmayer 2007). Since only a fraction of the entire globe will ever be reserved for biodiversity conservation, many have advocated for the need to better understand the effects of changing anthropogenic land uses on organisms in human-dominated landscapes (Miller and Hobbs 2002, Dearborn and Kark 2010). Changes in land use and land cover have affected species distributions and will continue to affect these patterns (Sala et al. 2000). In highly modified, human-dominated landscapes, much of the remaining native habitat has already been lost or is protected, so most future changes will occur in the matrix in which these remnants are embedded (sensu Driscoll et al. 2013). Thus, the effects of future landscape change are likely to include relatively large changes in matrix quality.

In the Oak Openings Region of northwestern Ohio, where I studied distribution and diversity patterns of breeding birds, several remnant, globally rare vegetative communities exist – which have been shaped by a unique regional glacial history. These communities are distinctive to the region and as such were characterized by early settlers in the name "Oak Openings." It is a gently undulating strip of post-glacial beach sands deposited over dense clay. Dry ridges in close association with wet swales produced a remarkably diverse landscape with patchy forests and savanna, often dominated by oaks (*Quercus* spp.) and broken by prairies and marshes (Anderson 1971). Westward bound settlers must have expressed a sense of relief after having traversed the dense forests of the Great Black Swamp to find themselves in a landscape easily accommodating wagon travel in any direction (Anderson 1971). Local variation in vegetation is highly heterogeneous, and often species such as eastern prickly pear cactus (*Opuntia humifusa*) are often distributed near "wet" sedges (*Carex* spp.; Abella and Jaeger 2004). The local heterogeneity is unlike any other area surrounding the region.

The urban environment provides sanctuary for many organisms in backyard gardens and urban parks (Miller and Hobbs 2002, Dearborn and Kark 2010). As urbanization increases globally, the importance of urban green spaces and environmentally friendly land uses become exceedingly important (Goddard et al. 2010). Some evidence suggests that the restoration of small reserves may be valuable for the conservation of birds in these environments (e.g., Brawn et al. 2002). Many strategies, such as planting native vegetation in lieu of non-native Eurasian grasses in backyards, are relatively undemanding, yet rewarding to people's psychological wellbeing (Gross and Lane 2007). This is an area of active research and many questions are left unanswered, such as the relative importance of localized habitat-effects and disturbance on occupancy patterns of breeding birds in these environments.

The extrapolation of field study across broad landscapes has increasingly been used to address pressing ecological questions (Miller et al. 2004). Distribution modeling can accommodate these questions by combining field study with remotely-sensed data to identify threats to species, focus survey efforts (e.g., Hamer et al. 2008), examine land use or climate change on species (e.g., Pompe et al. 2008), and focus conservation investment appropriately (e.g., Root et al. 2003). For many fragmented landscapes, the independent effects of habitat loss and fragmentation (e.g., reduced mean patch area and increased patch isolation) are unclear. Because some of these variables are also highly correlated, many studies have produced misinterpreted statistics (Smith et al. 2009). Nonetheless, understanding the independent effects of these processes is critical to our understanding of the basic ecology of species and also to invest appropriate conservation efforts. Many empirical studies have addressed questions related to threatened species, but it is important to also consider more common species (Lindenmayer et al. 2011), such as the Red-bellied Woodpecker.

It is critical to recognize several factors when attempting to model distribution and diversity patterns of organisms. Species respond to spatial scale (i.e. the spatial extent with which a variable of importance is measured) and many species respond differently to various processes (Lichstein et al. 2002, Holland et al. 2004). In addition, it is important to recognize that organisms are influenced by variables operating simultaneously at multiple spatial scales (Wiens 1989). False absences (i.e. not detecting a species in a site when in fact it is present) can lead to the over or under-estimation of a variable’s importance, so efforts should be taken to accommodate the detection process in models (MacKenzie et al. 2002). Therefore, I have explicitly examined these factors, where possible, throughout my work.

Study Area

I studied breeding season distribution and diversity of birds within the Oak Openings Region of northwestern Ohio, USA, specifically located in Henry, Fulton, and Lucas counties, from 23 May to 2 July 2013 (Figure 1.1). Today the area remains a biodiversity hotspot and a conservation stronghold. More plants and animals of special conservation interest are found in the Oak Openings Region than any other comparable area in the state, including the federally endangered Karner blue butterfly (*Lycaeides melissa samuelis*). Five globally imperiled plant communities are found here, often in little to no supply elsewhere, including Great Lakes Twig-rush Wet Meadow, Great Lakes Swamp White Oak-Pin Oak Flatwoods, Mesic Sand Prairie, Midwest Sand Barrens, and Black Oak/Lupine Barrens (Faber-Langendoen 2001, EPA 2012). The region is also known for its unique extralimital populations of some breeding birds, sometimes representing the farthest northern or eastern recognized populations for their species; e.g., Lark Sparrow (*Chondestes grammacus*), Summer Tanager (*Piranga rubra*), and Blue Grosbeak (*Passerina caerulea*).

The Oak Openings is within the Eastern Tallgrass Prairie Bird Conservation Region (NABCI 2000) and the Maumee Lake Plains physiographic region of Ohio (ODNR Division of Geologic Survey 2008). The region represents one of the largest and best preserved landscape-scale oak savanna systems in the Midwest and belongs to a suite of globally diminished disturbance dependent ecosystems that exhibits a high percentage of their historic area converted to anthropogenic land use or suppressed of natural disturbance regimes. For this, temperate savanna and prairie are thought to be the most imperiled ecosystems on the planet (Hoekstra et al. 2005). About 73% of the Oak Openings has been converted to human land uses (Schetter and Root 2011). While a quarter of it is thought to be natural/seminatural, much less of this area actually contains great quantities of the rare, endemic vegetative communities due to exotic pine plantations, woody succession, and invasive species. About 10% of the Oak Openings is maintained by public trust for conservation, and partners of the region have set an objective to restore or publicly protect 20% of the area by the year 2025 (Abella et al. 2007).

Restoration and preservation of the Oak Openings embrace many forms, including direct management of the vegetative community, acquiring land, and directing community outreach and education programs (Abella et al. 2007, EPA 2012). Habitat restoration is principally directed towards savanna and wet and dry prairie habitat types (EPA 2012). To alleviate the effects of mesic woody invasions, prescribed fires intended to mimic natural fire disturbance, and to a lesser extend mechanical thinning of woody vegetation, are employed to release senescent oak savanna communities. Fire is necessary in maintaining the unique vegetative structure of oak savanna (Peterson and Reich 2001) through effectively suppressing woody vegetation (Bragg and Hulbert 1976, Sparks et al. 1998) and removing litter to release herbaceous vegetation (Abella et al. 2004).

Perhaps most critical to the mission of conserving the Oak Openings Region is directing further development away from the remaining natural areas and enhancing connectivity between reserves (EPA 2012). While the urban population growth rate in the surrounding Toledo Metropolitan Area has experienced a 10% decrease since 1980, developed land cover has increased by 110% since that time. Regional anthropogenic land cover conversion is expected to rise and understanding its effects on regional wildlife is essential, especially considering the presence of globally rare ecological communities, intense reestablishment of disturbance regimes, expansive human driven alteration, vast confluence of habitat types in the region, and matrix effects on surrounding natural areas.

Study Design

Sampling Sites

I developed a spatially balanced study site design that included the entire Oak Openings Region within my sampling frame. I utilized a 1-km radius circular study site design. I established the 3.14-km^2 circular study sites by circumscribing a 1-km buffer about the centroid of 4-km^2 squares intersected over the 478-km^2 region using ArcGIS ver. 10.1 (ESRI 2012). This design yielded a total sample of 117 study sites within which to randomly position road-based avian surveys (Figure 1.1).

Using the point count method to sample avian response variables (Ralph et al. 1995), I established points alongside roads with a 150-250% oversample (conditional to road density) within each site using ArcGIS. Each point was positioned greater than 250 m from the nearest other point or study site edge. For safety and noise interference concerns, major highways were removed from potential sampling points. I sampled point counts in each site in numerical order until at least 2 points were surveyed, skipping inaccessible or unsuitable (e.g., excessive noise, unsafe to stop) targeted points. In such cases, if the preferred point was unsuitable, I had the flexibility to move to another in favor of more appropriate conditions. Two sites were eliminated during point selection due to a dearth of vehicular access and elevated noise interference, resulting in a total of 115 study sites and 230 points with coverage of 0.48 surveys km^{-2} for my investigation (Figure 1.1).

I used a land cover by Schetter and Root (2011). The map was 0.09 ha in resolution and was produced by a supervised classification of multi-seasonal Landsat-5 Thematic Mapper images, specifically for assessing land cover change for this unique region (Figure 1.2). Fifteen land cover classifications were identified, including cultural or natural/seminatural habitats (Table 1.1). Cultural land cover included dense urban, residential/mixed, turf/pasture, and croplands. Natural/seminatural land cover were swamp forests, floodplain forests, upland deciduous forests, upland coniferous forests, upland savannas, wet shrublands, wet prairies, upland prairies, sand barrens, Eurasian meadows, and perennial ponds.

Cultural land use area dominated over natural/seminatural land area by almost 3:1. Primary land use was developed/built-up at 39.2% of the study area and included residential/mixed (35.4% of land area) and dense urban (3.8%). Agricultural land use (cropland [27%] and turf/pasture [6.6%]) occupied 33.6% of the area. Finally, natural/seminatural land cover accounted for 27.2% of the land area of which 20.4% was forests and woodlands, 0.8% was savannas, 0.4% was shrublands, 5.1% was prairies and meadows, and 0.5% was water.

Avian Sampling

I used the point count method to sample avian response variables (Ralph et al. 1995). I performed all point counts for my investigation in part to reduce observer bias. I adopted a comprehensive point count protocol designed to accommodate multiple statistical approaches for measuring relative abundances and estimating detection probabilities, avian densities, and occupancy probabilities at each point and across the study area. I devised this protocol with occupancy modeling, time-of-detection, and distance sampling techniques specifically in mind. Occupancy modeling uses detection/nondetection data to account for false absences by modeling an expected occupancy rate (Ψ) over repeat sampling (MacKenzie et al. 2002). The time-of-detection method (Alldredge et al. 2007) is used to estimate the proportion of birds missed during a time-limited count, and distance sampling (Rosenstock et al. 2002) estimates the proportion of birds missed as a function of distance from the observer. I formulated point counts to be 6.25 min in length and I sampled birds at an unlimited radius during suitable weather conditions. Although I recorded birds to an unlimited radius, I defined a count radius of 100 m for all of my analyses.

Sampling was dependent on suitable weather conditions. I defined suitable wind speeds to be 0-19 km h^{-1} (Beaufort scale 0-3; calm to leaves and small twigs in constant motion). I ranked the degree of precipitation as none (0), haze or fog (1), drizzle or light rain (2), and moderate to heavy rain (3); and I only abstained from performing counts during moderate to heavy rain. I performed counts from 0.5 hr before sunrise to about 1030 hours EST. Seasonal influences and number of visits to each point can impact the performance of counts (Dettmers et al. 1999, Drapeau et al. 1999). Thus, I sampled each point twice from 23 May through 2 July 2013, corresponding to the region's peak breeding passerine song output period, with approximately 2 weeks separating visits. This repeat survey design also allowed for the application of an occupancy modeling framework. I randomized visits to points and implemented a 1-minute adjustment period to allow birds to acclimate to observer presence after arriving to a site. The temperature (° C) and number of vehicle passes were recorded for all surveys; all vehicular conveyances were treated equally (e.g., motorcycles, buses, cars, trucks, etc).

I recorded each record into 25-m distance and 75-sec time belts for correcting count biases and estimating densities of species following distance sampling (Buckland et al. 2001, Rosenstock et al. 2002, Thompson 2002) and time-of-detection (Alldredge et al. 2007) techniques, respectively. Distances were estimated with aerial photographs and laser rangefinders. For each record, I also counted the number of individuals detected in clusters and the type of detection into 6 detection types, which included song (S), call (C), drum (D), visual (V), air screen (A), and flyover (F). About 18% of records were clusters (i.e. >1 individual record^{-1}) and most often a cluster was composed of a tight association between members of a gregarious species.

Detection types define the cue used to make an observation. I used written voice descriptions from Sibley (2003) to define song and call detection types. Songs (60.2% of total detections) were vocalizations utilized in territory and pair maintenance by males. Calls (29.4%) were general vocalizations made by both sexes and most often frequently observed for non-songbirds or passerines with indistinct songs. Drums (0.2%) were resonant mechanical pecking sounds produced by territorial woodpeckers, similar in purpose to passerine song. All birds seen at the moment of first detection were recorded as visual detections (4.8%). Aerial insectivorous species (swallows and swifts) observed foraging on insects in flight were included in the air screen (1.5%) detection type. Finally, flyovers (3.9%) were defined as any individual observed in flight, generally above tree-line, and not definitively using the local habitat within the count radius. I excluded all flyovers and those species >100 m from the observation point for all analyses.

Local Habitat

Because the land cover map had a pixel resolution of 30 m x 30 m (~3% of a 100-m radius point count) and due to other inherent limitations in remotely sensed images, I opted to quantify fine-scale habitat features of each point count (hereafter local habitat). I also counted the number of human-made structures (e.g., houses, buildings, barns, etc) and the number of snags (i.e. dead or dying trees with the potential to serve as a roost, nest cavity, or foraging substrate for drilling insectivorous species) within the count radius of each point.

I defined 28 local habitat classifications, some adapted from the land cover map and most new, describing both natural and human manipulated features that birds are commonly exposed to in rural and urbanizing settings and features that are not typically picked up from remote sensing, and quantified the relative proportions of each within the 100-m point count circle (Table 1.2). I or a trained observer sketched habitats over 0.5-m resolution aerial photographs by the National Agriculture Imagery Program (NAIP, https://www.fsa.usda.gov/FSA, accessed 9 April 2013) while at each point. Habitat delineation was done during the first visit to each point and examined and corrected for any inaccuracies during the second visit. In most cases more than one observer was able to make adjustments to habitat classifications or boundary limits, reducing haphazard bias in a single observer. The relative proportions (0-1) of each local habitat classification was later quantified by overlaying a half-centimeter dot transparency over each photograph and counting the number of full 0.25-cm^2 squares bounded within each classification.

Preliminary Survey Results

Excluding flyovers and detections >100 m from the point count, I observed 97 species from 5,835 records of 6,975 individuals from 23 May to 2 July 2013 during 460 surveys (230 point count locations surveyed twice; Appendix A). I observed on average, 23.24 species $site^{-1}$ (SD ± 5.84), 8.81 species $point^{-1}$ (SD ± 2.88), and 21.14 individuals ha^{-1} (SD ± 5.84; determined from distance sampling).

Thesis Content

My broad research objective sought to assess typical consequences of anthropogenic land use (e.g., fragmentation, matrix quality, etc.) and to determine the relative importance of these variables on diversity and distribution patterns of breeding birds in the Oak Openings Region. I prepared 4 technical chapters that individually addressed matrix quality on bird occupancy, structural diversity of habitat on bird diversity, localized habitat-effects within the urban center on bird occupancy, and the extrapolation of a predictive model of the effects of habitat loss, fragmentation, and structural diversity as reflected by Red-bellied Woodpecker occupancy.

In Chapter 2, I examined the relative influences of matrix changes vs. habitat changes on breeding bird distributions. I modeled occupancy after controlling for detection bias, individual species responses to spatial-scale, and site variables. My findings support the notion that spatial distributions of midwestern breeding birds are influenced by the matrix, and in highly modified landscapes, the relative influence of these effects are large compared to habitat loss and fragmentation.

For Chapter 3, I assessed the relative contribution of structural diversity, the distribution of area among different land cover types, on diversity patterns of the avian community. I modeled diversity of 3 breeding bird guilds after controlling for scale-dependency of model variables. My results demonstrated that Neotropical and Nearctic diversity can be explained by a diverse array of natural/seminatural land cover types and the presence of globally unique habitats in the landscape in addition to habitat loss and fragmentation.

In Chapter 4, I examined the importance of localized habitat in the urban center of the Toledo Metropolitan Area. I used an occupancy modeling framework to control for detection bias. My findings provided evidence that distributions of breeding birds in the urban center can be best explained by localized habitat features and not to the location of large natural reserves in the landscape.

I developed and validated a predictive habitat occupancy model of Red-bellied Woodpecker in Chapter 5. My objective was to use advances in modeling techniques to assess the relative importance of habitat loss and fragmentation on this species and to extrapolate model-based predictions across the entire region. My results indicated that this species may be responding more strongly to fragmentation over habitat loss and my modeling approach represented an example for future predictive habitat modeling attempts of insectivorous cavity nesting species in the region.

I prepared Chapters 2 – 5 as manuscripts following guidelines from the Central Ornithological Publication Office (https:// http://www.aoucospubs.org, accessed 17 March 2014) for submission in the journals *The Auk: Ornithological Advances* and *The Condor: Ornithological Applications*, and followed recommendations by Anderson et al. (2001) and Messmer and Morrison (2006). I intend to submit Chapters 2 – 5 with coauthors and have written them using plural pronouns. However, I take full responsibility for all content herein. In the final chapter (Chapter 6), I have provided an executive summary and brief conclusion.

Table 1.1. Land use and land cover characteristics of the Oak Openings Region, Ohio, USA, by Schetter and Root (2011).

Class	Subclass	Classification	%
Natural/seminatural	Forests and woodlands	Swamp forests	3.1
		Floodplain forests	8.9
		Upland deciduous forests	6.4
		Upland coniferous forests	1.9
	Savannas	Upland savannas	0.8
	Shrublands	Wet shrublands	0.4
	Prairies and meadows	Wet prairies	0.1
		Upland prairies	1.3
		Sand barrens	0.8
		Eurasian meadows	3.0
	Water*	Perennial ponds	0.5
Cultural	Developed/built-up	Dense urban	3.8
		Residential/mixed	35.4
	Vacant	Turf/pasture	6.6
		Croplands	27.0

% Represents the area occupied by that land cover.

Table 1.2. Mean % and SD of localized habitat area and the number of anthropogenic structures of my 230 point count locations distributed across the Oak Openings Region, Ohio, USA, from 23 May to 2 July 2013.

Habitat	Mean %	SD
Forested residential*	6.32	18.08
Open residential	42.21	35.27
Farm buildings	0.58	3.69
Developed commercial	2.10	9.90
Deciduous forest*	8.89	18.75
Coniferous forest*	0.64	5.03
Mixed deciduous/coniferous*	1.08	6.55
Permanent pasture	1.57	6.86
Hay	0.60	5.22
Meadow/prairie*	0.56	3.29
Row crops	15.37	25.65
Urban grasses	2.35	11.01
Bare soil	0.35	3.29
Woody transitional*	5.57	14.82
Open water	0.35	1.65
Forested wetland*	0.08	0.93
Emergent herbaceous wetland*	0.06	0.85
Linear woody*	0.46	1.86
Riparian*	0.56	2.87
Savanna*	0.79	5.46
Woody ditch/stream*	0.10	1.09
Non-woody ditch/stream*	0.16	1.14
Introduced conifers*	0.10	0.99
Introduced linear woody*	0.29	1.56
Native linear woody*	0.02	0.27
CRP belt*	0.01	0.19
Paved roads	6.61	4.15
Mowed berms	2.19	2.57
No. of structures	6.21	6.20

Localized habitat characteristics were calculated within 100 m from the observation point from aerial images from the NAIP.

*Indicates natural/seminatural land cover considered as suitable breeding bird habitat for the largest number of species.

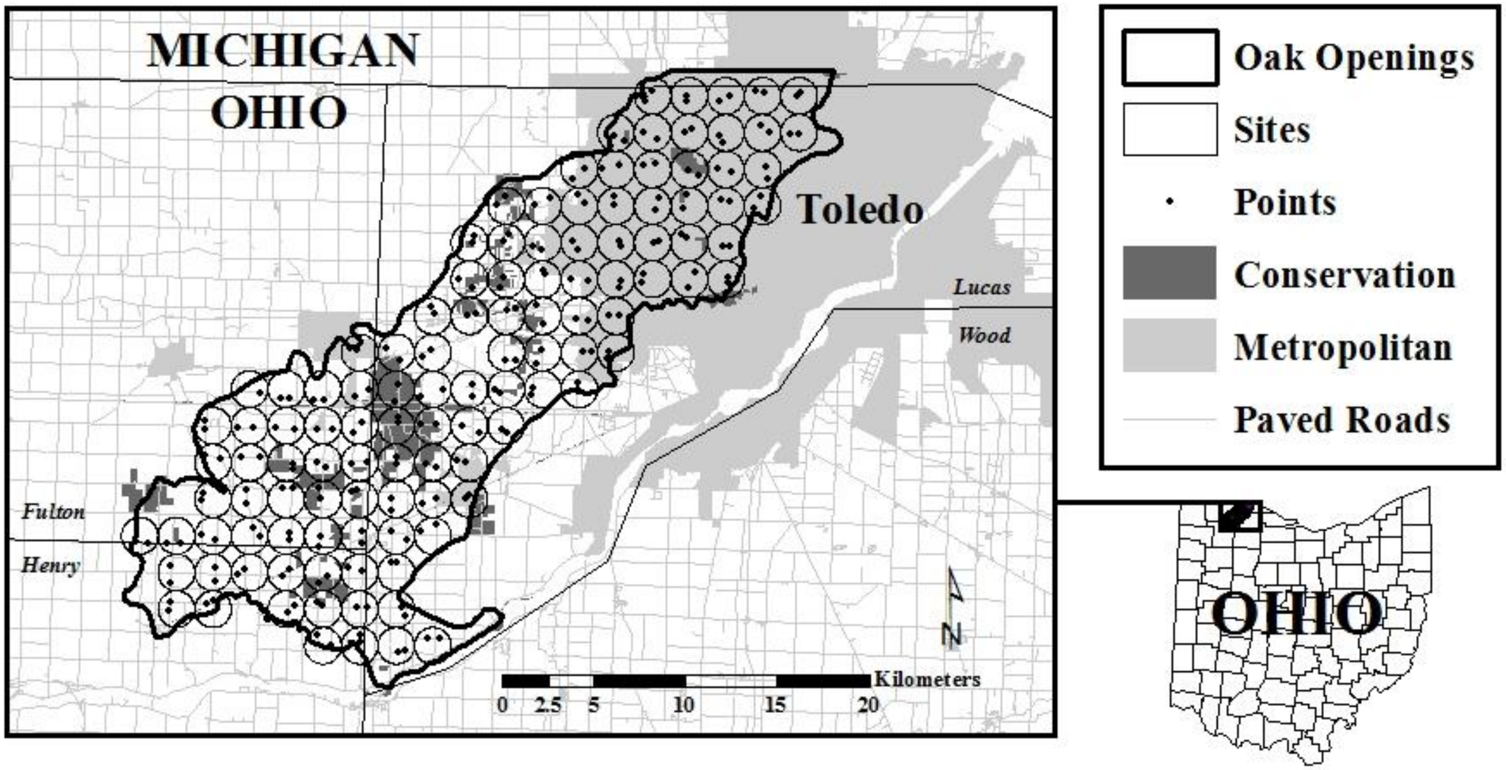

Figure 1.1. Location of the Oak Openings Region, Ohio, USA, including conservation and metropolitan areas.

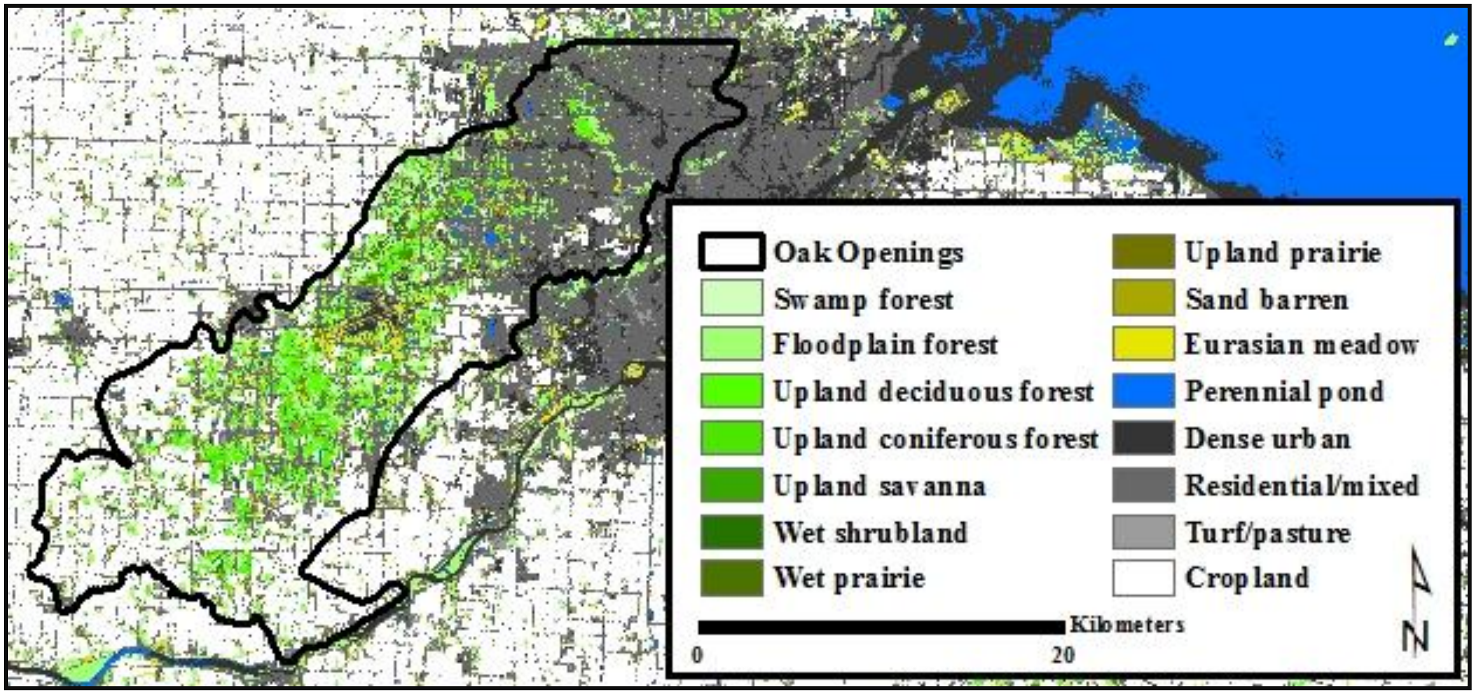

Figure 1.2. Spatial land cover by Schetter and Root (2011) for the Oak Openings Region, Ohio, USA.

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CHAPTER 2: INFLUENCES ON MIDWESTERN BREEDING BIRD OCCUPANCY IN A HUMAN-DOMINATED LANDSCAPE: MATRIX VERSUS HABITAT

Abstract

The rate of future change in habitat is unlikely to exceed changes to the matrix for human-dominated landscapes as most habitat is already lost or protected. We tested the implications of future matrix change relative to habitat loss and fragmentation by extensively surveying midwestern breeding bird species in a mixed-disturbance biodiversity hotspot, the Oak Openings Region of northwestern Ohio, USA, from 23 May to 2 July 2013. We modeled occupancy for several species after controlling for detection bias, individual species responses to spatial-scale, and site variables. While we detected modest effects of habitat loss and fragmentation, occupancy rates were strongly influenced by deteriorating matrix quality, and responses were generally negative for our specialist species and positive for our generalists. Our findings support the notion that spatial distributions of midwestern breeding birds are influenced by the matrix, and in highly modified landscapes, the relative influence of these effects are large compared to habitat loss and fragmentation. We recommend conservation strategies that focus efforts on improving matrix quality.

Introduction

Habitat loss (Dirzo and Raven 2003, Theobald et al. 2010), fragmentation (i.e. the breaking apart of habitat independent of habitat loss; Fahrig 2002, Fischer and Lindenmayer 2007), and matrix alterations (i.e. changes to the often hostile background that habitat patches are embedded within; Driscoll et al. 2013) have affected and will continue to affect distributions and abundance of patch-dependent species in human-dominated landscapes, but the relative importance of each is unclear. Exurban sprawl, low-density residential development and urban fringe development, is becoming the fastest growing land use in the United States (Brown et al.

2005, Hansen et al. 2005), and combined with the public's affinity to reside in close proximity to forested areas (Kaplan and Austin 2004), development is predicted to accelerate near vulnerable remaining habitat in human-dominated landscapes (sensu Driscoll et al. 2013). In these landscapes, we often detect only modest differences in the amount and arrangement of habitat across the broader landscape. However, differences in matrix quality frequently vary widely. The quality of the matrix includes features that may influence dispersal, resource availability, and abiotic edge effects of patch-dependent species and are defined from a species point of view (Driscoll et al. 2013). For many landscapes, any further change in remaining habitat is unlikely to exceed changes to the matrix, as the habitat that remains is already lost or protected. Elucidating the independent effects of these processes is important to understanding the ecology of patch-dependent species and is the focus of this research.

The results of fragmentation per se include a reduction in mean patch size, an increase in distance between patches, an increase in the number of patches, and an increase in the amount of edge (i.e. the abrupt transition between habitat and matrix; Fahrig 2003). Theoretically, based on Island Biogeography Theory (MacArthur and Wilson 1967), fragmentation of remaining habitat is likely to negatively impact many patch-dependent species; the underlying ecological principle of this paradigm being that decreased area and increased isolation of patches will inflate extinction rates and reduce colonization events (e.g., rescue effects) of patch-dependent species, respectively. However, misinterpreted statistical techniques and the misapplication of spatial scale are thought to have influenced our misunderstanding of the independent effects of fragmentation (as reviewed in Fahrig 2003). The consensus from recent reviews indicates that fragmentation, compared to habitat loss, has a weak overall effect on species distribution and abundance, and effects of fragmentation are just as likely to be positive as negative (Fahrig 2003, Fischer and Lindenmayer 2007, Smith et al. 2009). The weak effect of fragmentation is also attributed to a failure to consider the matrix and an assumption that habitat patches exist as islands uninfluenced by the surrounding matrix (Prugh et al. 2008, Franklin and Lindenmayer 2009, Watling et al. 2009).

Within the patch-matrix model, habitat for a particular species is embedded in a complex mosaic of different land cover types and physical features both anthropogenic and natural (Haila 2002). Like habitat quality, species are predicted to respond differently to the quality of the matrix and that these responses may surpass habitat-effects (Fleishman et al. 2002, Prugh et al. 2008, Kennedy et al. 2011). Thus, species may not only be affected by the size and spatial arrangement of primary habitat, but also by the structure and composition of the matrix. Presence and the amount of anthropogenic infrastructure, such as roads, in the landscape can influence the quality of the intervening space between primary habitat patches for a particular species. Roads, in particular, can exhibit predominantly deleterious effects on some species through vehicular collisions (Forman 2000, Forman 2008), restricting dispersal of species, or isolating and subdividing species into smaller more vulnerable populations (Jaeger et al. 2005). The effects of increased roads in human-dominated landscapes may also simultaneous exhibit positive effects on some species through supplemental resources or movement corridors (Norton et al. 2000).

The influence of matrix and habitat-effects are often assessed empirically by relating the presence/absence of species within focal patches or sites to variables serving as correlates of these processes across the broader landscape. Identifying individual species' responses to spatial scale is important to better understanding the relative effects of these factors (Holland et al. 2004). Species respond to spatial scale and failure to not explicitly consider scalar-effects may produce dubious or weak results (Smith et al. 2011). For many species, especially midwestern breeding birds, the selection of resources often begins at broad-scales (i.e. landscape) then proceeds to micro-scales (i.e. patch characteristics or inter-territory responses; Jones 2001).

We examined the relative influence of matrix and habitat-effects on 18 midwestern breeding bird species by accounting for site-level variability, detection bias, and individual species responses to spatial scale. We chose birds as our focal taxa because they are relatively easy to survey and empirical studies suggest that birds in landscapes with modest amounts of habitat respond to habitat loss and fragmentation over patch/site-level attributes (e.g., Mitchell et al. 2001, Betts et al. 2002, Lichstein et al. 2002). Following the line of inquiry established in recent reviews of matrix importance, our overarching objective was to test the hypothesis that matrix features are more important than habitat-effects (i.e. the amount, shape, and spatial arrangement of remnant vegetation) on occurrences of breeding birds within human-dominated landscapes. We expected species to respond differently to matrix quality, and if this hypothesis is corroborated, then efforts in highly modified landscapes should focus conservation investment on improving matrix quality.

Methods

Study Area and Study Sites

Our study area was the 47,800-ha Oak Openings Region of northwestern Ohio, USA (Figure 2.1). The region was formerly composed of patchy oak savanna and floodplain forest broken by wet prairie (Brewer and Vankat 2004, EPA 2012), but is now dominated by urban development (39% of the area) and row-crop production (27%; Schetter and Root 2011). To best examine current land use trends and their effects on occupancy dynamics of midwestern breeding birds, we defined primary habitat as treed canopy, as in many areas of the Midwest development often occurs under a relatively continuous canopy layer (Radeloff et al. 2005). This broad habitat definition especially allowed for the examination of localized development activities and accommodated the direct comparison of site- vs. landscape-level variables on occurrences of birds related to this land use trend. We used canopy data from the 2001 National Land Cover Database (NLCD; Homer et al. 2007) and converted the original data on percentages of canopy to presence/absence of canopy per 30- x 30-m pixel. We compared this data to a local vegetation map by Schetter and Root (2011) and aerial photographs by the National Agriculture Imagery Program (NAIP, https://www.fsa.usda.gov/FSA, accessed 9 April 2013). The treed canopy covered 37% of the study area and occurred as a gradient of natural/seminatural forest (57% of the canopy) to residential development (the remaining 43% of canopy). The canopy hosts a myriad of breeding bird species, and these species may respond to the amount and configuration of canopy within the landscape as well as the relative amount of localized disturbance in the understory. We focused on site occupancy of a wide range of species for this study, including patch-dependent and exotic species.

Our study sites were 51 canopied 100-m point counts selected from our larger investigation of regional bird ecology and conservation. For our larger study, we positioned paired point counts alongside roads with a minimum distance of 250 m from the nearest other point or study site edge within 115 circular study sites 314 ha in size. We surveyed birds ≤100 m from the survey point to ensure the sampled area characterized the habitat being assessed. From this, we used ArcGIS ver. 10.1 (ESRI 2012) to randomly select a series of points with >50% canopy coverage and >1 km apart to control for localized variation in canopy amount and spatial independence, respectively. We arrived at 51 point count locations (hereafter sites) to sample bird occupancy for this study. Our canopied sites were highly diverse in localized anthropogenic disturbance, representing a gradient from closed-canopy native forests to sparsely treed residential developments. The mean (± SD) proportion of canopy coverage across our sites was 0.78 (± 0.14; n = 51).

Bird Surveys

From 23 May to 2 July 2013, we conducted 2 replicate surveys to document the presence/absence of bird species within each site. We surveyed the sites in routes beginning 0.5 hr before sunrise and extending until 1030 EST on precipitation-free and low wind days (<19 km hr^{-1}) with approximately 2 weeks separating visits. Each survey lasted 6.25 min and we implemented a 1- min adjustment period to allow birds to acclimate to observer presence. We randomly generated the order routes were surveyed, attempting to allow each site to be surveyed at least once in the early morning period and another in the late morning period to reduce the effect of time of day on bird detectability. The lead author conducted all surveys to control for observer bias. Although our surveys were restricted to roadsides, all surveys were conducted during low traffic interference with a mean (± SD) of 2.12 (± 3.84) conveyances per survey (n = 102). Roads also likely represent much less of a habitat discontinuity for the habitat being assessed in our system (e.g., patchy forests and residential developments), and a recent investigation (e.g., McCarthy et al. 2011) also detected no difference in model performance between models built from samples from roadsides vs. primary habitat of bird species. Thus we surmise that roadside surveys in our investigation are more-or-less equivalent to off-road surveys.

Matrix and Habitat Variables

We calculated matrix quality, habitat loss, and fragmentation from several spatial extents surrounding each site among the set of buffer radii ranging from 500 m to 2000 m at 500-m increments (i.e. 500, 1000, 1500, and 2000 m distance from each site). Spatial data on canopy cover was derived from the 2001 NLCD. We projected all data in UTM NAD 1983 zone 17 N. For each buffer size class, we used FRAGSTATS ver. 4.2 (McGarigal et al. 2012) to calculate the proportion of canopy within the landscape as a correlate of habitat loss. To examine the effect of a deteriorating matrix, we selected road density (km km^{-2}) as a suitable correlate of matrix quality, as road density was not correlated (i.e. $|r_s| \leq 0.22$) with canopy amount across all spatial extents. We obtained spatial data for road density from the U.S. Census Bureau's TIGER/Line files (topologically integrated geographic encoding and referencing, http://www.census.gov/geo/maps-data/data/tiger-line.html, accessed 9 April 2013) and calculated road density with ArcGIS. We calculated 5 metrics to characterize canopy fragmentation: patch cohesion of canopy, density of canopy/non-canopy edge, mean nearest neighbor distance of canopy patches, mean canopy patch area, and density of canopy patches (Table 2.1, Table 2.2). We also calculated 3 site-level variables within the 100-m count radius of our sites. We calculated the proportion of canopy within each site with the canopy layer and used ground-truthing and aerial photographs to correct any inaccuracies. Similarly, in order to better understand the influence of local anthropogenic disturbance on birds, we also counted the number of anthropogenic structures (e.g., houses, buildings, barns, etc.) within each site and calculated the proportion of natural/seminatural vegetation within the understory using ground-truthing, aerial photographs from NAIP, and half-centimeter dot transparencies.

We tested for collinearity among our 10 predictor variables and detected substantial correlations across all spatial extents (Appendix B). We excluded 4 of our fragmentation correlates (patch cohesion of canopy, density of canopy/non-canopy edge, mean nearest neighbor distance of canopy patches, mean canopy patch area) and 1 of our site-level variables (number of structures) due to redundancy. At the site-level, the number of structures and proportion of natural/seminatural understory vegetation were highly correlated. All of our fragmentation variables were either correlated with the proportion of canopy or road density; however, canopy patch density was relatively less correlated with the proportion of canopy and road density compared across all spatial extents (i.e. $|r_s| \leq 0.75$). Thus, our final statistical model included the proportion of canopy at the site, the proportion of natural/seminatural understory vegetation at the site, the proportion of canopy in the landscape, the density of canopy patches in the landscape, and road density in the landscape to represent the amount of available localized habitat, the amount of localized disturbance, habitat loss, fragmentation, and matrix quality, respectively. We standardized all predictor variables by subtracting by the mean and dividing by the SD for all subsequent analysis so that the estimated parameters could be compared as the influence on response of one SD change on the predictor (Smith et al. 2009). Standardizing predictor variables also helps to reduce any further effects of collinearity among predictor variables and is a useful technique for comparing the influence of habitat loss, fragmentation, and matrix quality on spatial distribution patterns (Smith et al. 2009).

Influence of Matrix and Habitat

We estimated site occupancy and detection probabilities with detection/non-detection histories for each species using logistic regression in program PRESENCE ver. 6.2 to adjust our statistical model for imperfect detection of birds (Hines 2006). While detection is indicative of the site being occupied by the particular species of interest, non-detection does not always imply absence. Occupancy modeling corrects this bias by adjusting the naïve occupancy rate (observed) to the expected occupancy (Ψ) after establishing a detection probability (p) over repeat surveys. Occupancy is based on the probability of detection at each site, $(1 - p)^k$, where k

is the number of surveys at each site. The modeling procedure assumes that sites are closed during the survey period and sites are independent relative to each other (MacKenzie et al. 2002). Habitat variables can then be added to facilitate the estimation of species-habitat relationships (MacKenzie et al. 2006). Because some species in our study had home-ranges larger than our sampling units (e.g., 100-m point count radius, 500-m spatial scale, etc.), our occupancy estimator best represents the "probability of use" of a site in lieu of the "probability of occupancy" (MacKenzie et al. 2006).

We used single-season occupancy models in program PRESENCE, and our modeling proceeded in 3 steps: (1) we identified factors influencing detection for each species; (2) using variables identified to affect detection, we then determined the spatial scale most strongly influencing habitat selection of each species using the 4 buffer radii ranging from 500 m to 2000 m; and (3) using variables affecting detection and best-fit spatial extents, we then built our final statistical model with our 2 site-level and 3 landscape-level variables to examine the relative influence of habitat loss, fragmentation, and matrix quality on site occupancy patterns for each species.

We tested all combinations of our 4 sampling covariates for influences on detection: time of morning (min from sunrise), day of season (number of days since initiation of surveys), temperature (°C), and wind speed (km hr^{-1}). We used the maximum-likelihood statistic, Akaike's Information Criterion adjusted for small sample size (AIC_c), and AIC_c model weights (w_i) to examine covariates affecting detection probabilities (Burnham and Anderson 2002). Covariates in models with a difference in AIC_c value compared to the top-ranked that is less than 2 (i.e. $\Delta AIC_c < 2.0$) were considered to be substantially supported (Burnham and Anderson 2002). The w_i estimates the likelihood of any given model. Covariates identified to affect detection probabilities were included in all subsequent analyses for that species. We next determined the spatial scale that most strongly influenced occupancy patterns of each species for our 3 landscape-level variables: proportion of canopy, density of canopy patches, and road density. We fitted each of these landscape-level variables independently in occupancy models and for each of the 4 buffer radii. We considered our best-fit spatial extent to be the buffer size class that provided the biggest reduction in model deviance (-2 log likelihood) for that variable.

We fit occupancy models for each species using detection models and best-fit spatial extents to examine the relative influence of canopy loss, canopy fragmentation, and matrix quality on site occupancy patterns. Our models were similar in structure (i.e. contained all variables) for each species and included the proportion of canopy to represent habitat loss, density of canopy patches to represent fragmentation, road density to represent matrix quality, and the 2 site-level variables: proportion of canopy at the site to represent localized habitat amount and the proportion of natural/seminatural understory vegetation to represent the amount of localized anthropogenic disturbance. We compared the relative influence of habitat and matrix effects by examining standardized partial regression coefficients and the number of species that responded to these variables. We determined significance of each variable through a likelihood ratio test of the full vs. a reduced model without that variable. A likelihood ratio test is the difference in model deviance from 2 similar models where 1 model is nested inside another model. For variables that strongly influence occupancy patterns, the difference in model deviance between the full vs. reduced model increases relative to variables that do not strongly influence occupancy. The resulting difference and significance of a variable's contribution to a species occupancy pattern can be evaluated with a chi-square distribution with the degrees of freedom equal to the number additional parameters in the model (MacKenzie et al. 2006). We tested for overdispersion for each species' full occupancy model by calculating the variance-inflation factor from 10,000 bootstrap simulations in PRESENCE.

Results

We detected 67 species across all surveys (Appendix C). After excluding those species with small numbers of detections (i.e. detected in <20% of sites), we applied the occupancy modeling procedure to 25 species: Mourning Dove (*Zenaida macroura*), Red-bellied Woodpecker (*Melanerpes carolinus*), Downy Woodpecker (*Picoides pubescens*), Eastern Wood-Pewee (*Contopus virens*), Great Crested Flycatcher (*Myiarchus crinitus*), Red-eyed Vireo (*Vireo olivaceus*), Blue Jay (*Cyanocitta cristata*), Black-capped Chickadee (*Poecile atricapillus*), Tufted Titmouse (*Baeolophus bicolor*), White-breasted Nuthatch (*Sitta carolinensis*), House Wren (*Troglodytes aedon*), Carolina Wren (*Thryothorus ludovicianus*), American Robin (*Turdus migratorius*), Gray Catbird (*Dumetella carolinensis*), European Starling (*Sturnus vulgaris*), Chipping Sparrow (*Spizella passerina*), Song Sparrow (*Melospiza melodia*), Northern Cardinal (*Cardinalis cardinalis*), Indigo Bunting (*Passerina cyanea*), Common Grackle (*Quiscalus quiscula*), Brown-headed Cowbird (*Molothrus ater*), Baltimore Oriole (*Icterus galbula*), House Finch (*Carpodacus mexicanus*), American Goldfinch (*Spinus tristis*), and House Sparrow (*Passer domesticus*). The global detection model was the highest ranked model for measuring variation in detection probabilities for all species (Appendix D). For 22 species (Mourning Dove, Red-bellied Woodpecker, Downy Woodpecker, Eastern Wood-Pewee, Great Crested Flycatcher, Black-capped Chickadee, Tufted Titmouse, White-breasted Nuthatch, House Wren, Carolina Wren, American Robin, Gray Catbird, European Starling, Chipping Sparrow, Song Sparrow, Northern Cardinal, Indigo Bunting, Common Grackle, Baltimore Oriole, House Finch, American Goldfinch, and House Sparrow), models with substantial empirical support (i.e.

$\Delta AIC_c < 2.0$) contained all variables at least once (i.e. time, day, temperature, and wind appeared at least once in models with $\Delta AIC_c < 2.0$); and for 5 species (Eastern Wood-Pewee, Great Crested Flycatcher, White-breasted Nuthatch, American Goldfinch, and House sparrow), the null model (i.e. detection held constant) had a $\Delta AIC_c < 2.0$. Thus, we compared evidence ratios for the global vs. null model (w_{Global}/w_{Null}) to determine whether or not to include the global detection model in conjunction with the habitat modeling. Evidence ratios for the global detection model were not strong relative to holding detection constant (i.e. 1.25 – 1.79) for 3 species (White-breasted Nuthatch, American Goldfinch, and House Sparrow), so we held detection constant for all subsequent analyses for these species (Table 2.3). For all other species, evidence ratios were strong relative to the null detection model, so we modeled detection as a function time, day, temperature, and wind for all subsequent analyses for these species.

We detected variability in response to spatial scale across all species (Table 2.4). For example, Mourning Doves responded most strongly to the proportion of canopy in the 500-m buffer size class and Red-eyed Vireos responded most strongly to the 2000-m buffer. Detectability varied by species with Black-capped Chickadee and House Sparrow having the lowest and highest detection probabilities, respectively (Table 2.5). For the species that received the global detection model, detectability generally decreased with increasing time (i.e. min from sunrise), day (i.e. number of days from beginning of field study), temperature, and wind speed. Thus, detectability was generally higher earlier in the morning and season and during low temperatures and low wind speed.

Our final habitat model failed to reach numerical convergence or produced unlikely parameters (i.e. parameter estimates were suspect because they were at the limits of the parameter space [e.g., zero or one]) for 7 species; thus, we applied the final statistical model to

18 species with varying migratory strategies and habitat requirements (Table 2.5). Of the 18 species, 2 species were not native to North America: European Starling and House Sparrow. We classified 8 species as patch-dependent (i.e. those requiring a relatively continuous treed canopy for breeding habitat) based on habitat descriptions in Sibley (2003; Table 2.5). Variance inflation factors for each species did not indicate overdispersion in our occupancy models (i.e. $\hat{c}$ <3.0; Lebreton et al. 1992). Sixteen species responded most strongly to landscape-level variables over site-level variables based on standardized effect sizes. Matrix quality more strongly influenced occupancy patterns over landscape-level habitat effects, with 10 species responding more strongly to road density and 8 species responding to either proportion of canopy or density of canopy patches (Table 2.5). Matrix quality was significantly associated with occupancy ($P < 0.10$) of 6 species, habitat loss was significantly associated with occupancy for 6 species, and habitat fragmentation was significantly associated with 4 species. For those species that responded significantly to matrix quality, 3 responded negatively to increasing road density, including Tufted Titmouse, Gray Catbird, and Indigo Bunting, and 3 responded positively, including Blue Jay, Common Grackle, and House Sparrow. Three species responding significantly to habitat loss responded negatively to increasing canopy cover, including Red-bellied Woodpecker, Eastern Wood-Pewee, and Red-eyed Vireo, and 3 species positively, including Chipping Sparrow, Indigo Bunting, and Brown-headed Cowbird.

Occupancy of 7 species was significantly influenced by site-level variables. At the site-level, 3 species responded positively to increasing canopy cover within our study sites, including Eastern Wood-Pewee, Red-eyed Vireo, and Tufted Titmouse, and 3 species responded negatively, including Black-capped Chickadee, Chipping Sparrow, and Brown-headed Cowbird. Only one species, House Sparrow, responded significantly to localized anthropogenic disturbance, and this species responded negatively to increasing natural/seminatural understory vegetation. For those species that we could compare standardized effect sizes at the site-level, 6 of 11 species responded more strongly to canopy cover than natural/seminatural understory vegetation.

Discussion

Our data reveals that occupancy dynamics and ultimately species persistence in human-dominated landscapes may depend in part on the quality of the matrix surrounding primary habitat, supporting the hypothesis that matrix influences are important determinants of species occupancy patterns (Prugh et al. 2008, Franklin and Lindenmayer 2009, Watling et al. 2009). Our study also reveals the importance of the application of broad spatial concepts towards understanding species-habitat relationships (Miller et al. 2004), as 16 of the 18 species responded most strongly to landscape-level habitat over site-level variables, corroborating general sentiment that species in landscapes with modest amounts of primary habitat are more strongly influenced by broad spatial scales (e.g., Mitchell et al. 2001, Mitchell et al. 2002, Lichstein et al. 2002, Betts et al. 2002). Also the spatial scale best explaining occurrences of species varied for each landscape-level habitat variable, indicating that these processes are operating simultaneously across multiple spatial scales on species in human-dominated landscapes.

By comparison, more species responded to matrix quality over habitat-effects (i.e. habitat loss and fragmentation). This was true when considering all species and only those that most strongly responded to landscape variables. Examining the effect sizes of landscape variables alone, 5 species responded strongest to habitat loss, 3 species to fragmentation, and 10 to matrix quality. Effect sizes of matrix quality revealed 10 species responded positively to increasing road density and 8 species responded negatively to increasing road density. We considered 8 of our species to be patch-dependent (i.e. dependent on a relatively continuous treed canopy for breeding habitat). For each species group, we detected a similar pattern in effect sizes, with more species responding to matrix quality over habitat-effects. However, of those species that responded strongest to matrix quality, 7 were considered generalists and 3 were considered patch-dependent. By examining effect sizes of matrix quality only, of the 10 generalist species, 9 responded positively to increasing road density; while for the 8 patch-dependent species, 7 species responded negatively to increasing road density.

Our study revealed that species occupancy dynamics, and ultimately species persistence, exists as a complex interplay between matrix and habitat-effects, and not a single combination of responses (e.g., occupancy positively related to amount of canopy, negatively related to patch density of canopy, and negatively to road density) was more or less represented than any other. By only examining effect sizes of matrix quality (i.e. road density), we detected a strong positive effect on generalists species and a negative effect on patch-dependent species with increasing road density. Similar patterns have been observed in other studies (e.g., Friesen et al. 1995, Bolger et al. 1997, Cam et al. 2000, Jokimaki and Huhta 2000, Mortberg 2001). This pattern may, in part, manifest in our study because generalist species are likely to access and/or benefit from anthropogenic matrix-features (e.g., Norton et al. 2000). A possible advantage for generalist species may include supplemental feeding (Brittingham and Temple 1986, Major et al. 1996). Many of the focal species were resident/short-distance migrants and for at least some period of their yearly life cycle, grains account for the majority of their diets. Thus, increased occupancy probability associated with anthropogenic presence could correspond to increased access to bird feeders.

Competitive interactions with non-native species (Churcher and Lawton 1987, Paton 1990) and predation (Major et al. 1996) associated with development (Mitchell et al. 2002) may influence occupancy dynamics of some of these species. Some species may exhibit varying resiliency to traffic exposure (e.g., Underhill and Angold 2000, Forman et al. 2000, Hindmarch et al. 2012). At the site-level more species responded positively to the amount of native understory vegetation. Similarly, this pattern has been encountered in many other studies in human-dominated landscapes (e.g., Emlen 1974, Gavareski 1976, Rosenberg et al. 1987, Mills et al. 1989, Borgmann and Rodewald 2004, Donnelly and Marzluff 2004). The amount of anthropogenic disturbance in the site can also influence occupancy of many species (Lumpkin and Pearson 2013). The structure and floristic attributes of native vegetation likely provide more suitable nesting habitat for many species (Beissinger and Osborne 1982, Emlen 1974, Tweit and Tweit 1986, Green et al. 1989, Borgmann and Rodewald 2004).

Our study also corroborates many principal components of distribution modeling. It is critical to recognize several factors when attempting to model species occurrence. Species respond to spatial scale (i.e. the spatial extent with which a variable of importance is measured) and many species respond differently to various processes (Lichstein et al. 2002, Holland et al. 2004) and species are influenced by variables operating simultaneously at multiple spatial scales (Wiens 1989). False absences (i.e. not detecting a species in a site when in fact it is present) can lead to the over or under-estimation of a variable's importance, so efforts should be taken to accommodate the detection process in models (MacKenzie et al. 2002).

Species Responses

It is now well recognized that the matrix can influence inter-patch dispersal (e.g., Revilla et al. 2004, Bender and Fahrig 2005) and resource availability (e.g., Perfecto and Vandermeer

2002, Brotons et al. 2003) of patch-dependent species occupying fragmented or relictual landscapes, implying a possible mechanism underlying differential occupancy rates of species. Of the 8 species that responded negatively to a deteriorating matrix, 4 species were Neotropical migrants: Eastern Wood-Pewee, Red-eyed Vireo, Indigo Bunting, and Baltimore Oriole. In fact 4 of the 5 Neotropical migratory species in our study revealed a negative relationship with road density; House Wren being the only species within this group that responded positively to road density. This pattern has been detected in other studies (e.g., Rodewald and Bakermans 2006). We suggest that a possible mechanism driving this pattern may relate to resource availability for these largely insectivorous species. It has been demonstrated that arthropod diversity and abundance in native vegetation is negatively influenced by urbanization (Bang and Faeth 2011) with appreciable declines in arboreal arthropods in response to increases in urbanization (Christie et al. 2010, Fattorini 2011). A deteriorating matrix, as observed by increases in road density in our study, likely alters trophic structures and prey abundance for insectivorous, Neotropical migratory species.

Several of our species, including Mourning Dove, Blue Jay, American Robin, European Starling, Chipping Sparrow, Common Grackle, Brown-headed Cowbird, and House Sparrow, were positively influenced by road density. Matrix quality more strongly influenced occupancy of 6 of these 8 species based on parameter effect sizes. These species may be more resilient or able to better access resources in human-dominated landscapes. Some species have even exhibited enhanced reproductive success in these areas. For example, Mourning Dove nests in one study were more likely to fledge young closer to roads in human-dominated landscapes than farther from roads (Muñoz et al. 2008). Interestingly, occupancy of Brown-headed Cowbird was predicted to increase with canopy cover and road density, while occupancy was predicted to be negatively associated with canopy fragmentation. These results are consistent with similar studies where cowbird parasitism is expected to increase in highly fragmented forested areas (Hovick and Miller 2013). Brown-headed Cowbird occupancy was also most strongly associated with decreasing canopy cover at the site-level, indicating that sparsely treed openings may provide suitable sites for perching and surveying for brood-hosts.

Habitat loss best explained occupancy of 3 of our patch-dependent species, while fragmentation best explained occupancy of 2 of these species, and matrix quality for 3 species. For all these species except those strongly influenced by fragmentation, the relationship was significant. For those patch-dependent species responding strongest to canopy amount, the relationship was negative. This perhaps indicates that the canopy within our system may be less desirable as in other such studies. However, our data cannot accommodate this hypothesis. These species, however, also exhibited a significant positive response to canopy amount at the site-level, and this relationship has been observed before for at least Red-eyed Vireo, where canopy coverage was positively selected for breeding habitat (e.g., Siepielski et al. 2001).

Conservation Implications

We have demonstrated that changes to the matrix can affect occurrence of many breeding birds. Our results indicate that a deteriorating matrix quality corresponds to the occurrence of many species and that the effects of these processes are operating on these species at multiple spatial scales. The occurrence of many patch-dependent species is likely to decrease with a deteriorating matrix quality associated with changing land uses, independent of canopy loss and fragmentation in the Oak Openings Region. Exurban development (i.e. low density development on the urban fringe and rural areas) has increased five-fold since 1950 in the United States (Brown et al. 2005), and often this land use is associated with declines in avian diversity across an urban-to-rural gradient (Blair 1996). Future projections of land use change, independent of habitat loss and fragmentation, will continue to be an important driver of ecological patterns and processes. Biodiversity reserves will never cover more than a fraction of the globe, and ecologists and conservation biologists have advocated the need to promote conservation in human-dominated landscapes (Miller and Hobbs 2002, Dearborn and Kark 2010). Processes outside of primary habitat for a given species should be considered for long-term biodiversity conservation, as indicated in previous studies (e.g., Bierregard et al. 1992, Kennedy et al. 2011, Schooley and Branch 2011, Stouffer et al. 2011). Thus, strategies must be implemented to reduce the effects of future landscape change, such as reducing road density and restoring local vegetation.

Table 2.1. Site and landscape variables used to model breeding season occupancy of birds in the Oak Openings Region of northwestern Ohio, USA.

Scale	Variable	Description
Site	Proportion of canopy	proportion of canopy area within site
	No. of structures	number of structures counted within site
	Proportion of natural understory	proportion of natural/seminatural vegetation area in the understory
Landscape	Patch cohesion of canopy	ranges 0-100 and measures the physical connectedness of canopy patches
	Edge density of canopy	density of canopy/non-canopy edge (m/ha)
	Mean nearest neighbor distance	Euclidean mean nearest distance between canopy patches (m)
	Mean patch area of canopy	mean patch area of canopy patches (ha)
	Density of canopy patches	density of canopy patches (no./ km^2)
	Proportion of canopy	proportion of canopy area within landscape
	Road density	density of roads (km/km^2)

Table 2.2. Means, SD, and ranges (i.e. min and max values) of site and landscape variables considered to model breeding season occupancy of birds in the Oak Openings Region of northwestern Ohio, USA, and for 5 spatial extents (site, 500, 1000, 1500, and 2000 m).

Scale	Variable	Mean	SD	Min	Max
Site	Proportion of canopy	0.78	0.16	0.52	1.00
	No. of structures	7.43	6.26	0.00	22.00
	Proportion of natural understory	0.44	0.37	0.00	1.00
Landscape 500 m	Patch cohesion of canopy	97.03	2.65	88.26	99.99
	Edge density of canopy	106.57	45.33	7.95	183.61
	Mean nearest neighbor distance	72.19	16.52	60.00	160.16
	Mean patch area of canopy	18.63	21.76	1.00	71.19
	Density of canopy patches	7.87	5.97	1.39	26.49
	Proportion of canopy	0.60	0.19	0.24	0.99
	Road density	5.43	3.54	0.90	12.28
1000 m	Patch cohesion of canopy	97.26	2.76	88.14	99.95
	Edge density of canopy	98.74	42.61	22.78	175.91
	Mean nearest neighbor distance	87.50	38.47	60.00	246.10
	Mean patch area of canopy	30.58	57.67	1.52	291.33
	Density of canopy patches	6.40	5.18	0.33	20.86
	Proportion of canopy	0.55	0.19	0.15	0.95
	Road density	4.91	3.20	1.01	11.08
1500 m	Patch cohesion of canopy	97.57	2.41	89.94	99.85
	Edge density of canopy	98.25	41.39	25.75	170.55
	Mean nearest neighbor distance	88.18	31.71	64.16	230.26
	Mean patch area of canopy	23.60	33.21	1.69	144.23
	Density of canopy patches	6.13	4.76	0.57	17.42
	Proportion of canopy	0.52	0.17	0.14	0.85
	Road density	4.94	3.22	1.22	11.71
2000 m	Patch cohesion of canopy	97.96	1.92	90.96	99.71
	Edge density of canopy	96.84	39.72	25.57	164.12
	Mean nearest neighbor distance	88.63	28.38	67.35	186.52
	Mean patch area of canopy	17.81	18.31	1.90	80.36
	Density of canopy patches	6.01	4.48	0.98	15.52
	Proportion of canopy	0.50	0.14	0.15	0.78
	Road density	4.87	3.07	1.45	11.82

Table 2.3. Summary of model-selection procedure for variables affecting the probability of detection of 25 breeding bird species (sorted taxonomically) in the Oak Openings Region, Ohio, USA, from 23 May to 2 July 2013.

Species	No. Sites	Top-ranked detection model	AIC$_c$	w_i	K	w_{Global}/w_{Null}	Selected detection model
Mourning Dove	25	global	120.48	0.10	5	5.00	global
Red-bellied Woodpecker	26	global	114.67	0.24	5	197.83	global
Downy Woodpecker	33	global	128.65	0.13	5	55.96	global
Eastern Wood-Pewee	17	global	98.43	0.09	5	2.49	global
Great Crested Flycatcher	13	global	77.80	0.09	5	2.45	global
Red-eyed Vireo	12	global	73.98	0.25	5	17.11	global
Blue Jay	31	global	122.75	0.29	5	319.56	global
Black-capped Chickadee	18	global	95.65	0.10	5	5.23	global
Tufted Titmouse	22	global	108.88	0.20	5	36.02	global
White-breasted Nuthatch	18	global	94.92	0.08	5	1.79	null
House Wren	34	global	130.66	0.15	5	13.92	global
Carolina Wren	11	global	63.36	0.11	5	9.04	global
American Robin	46	global	101.60	0.13	5	55.04	global
Gray Catbird	24	global	116.57	0.13	5	7.02	global
European Starling	16	global	82.40	0.20	5	976.00	global

Displayed are the number of sites each species was detected, the top-ranked detection model, Akaike's Information Criterion adjusted for small sample size (AIC$_c$), AIC$_c$ model weight (wi), the number of parameters in the model (K), an evidence ratio test of the global model relative to the null model (w_{Global}/w_{Null}), and the selected detection model used for subsequent occupancy modeling.

Continued

Table 2.3 Continued

Species	No. Sites	Top-ranked detection model	AIC$_c$	w_i	K	w_{Global}/w_{Null}	Selected detection model
Chipping Sparrow	28	global	121.77	0.14	5	19.31	global
Song Sparrow	18	global	97.25	0.12	5	4.03	global
Northern Cardinal	48	global	91.43	0.17	5	5.70	global
Indigo Bunting	14	global	86.07	0.10	5	3.67	global
Common Grackle	12	global	73.57	0.21	5	21.01	global
Brown-headed Cowbird	37	global	126.56	0.44	5	162.15	global
Baltimore Oriole	17	global	90.53	0.18	5	45.75	global
House Finch	12	global	69.43	0.11	5	3.43	global
American Goldfinch	20	global	103.92	0.07	5	1.25	null
House Sparrow	20	global	91.39	0.07	5	1.27	null

Table 2.4. Model deviance (-2 log likelihood) for best-fit spatial extent analysis examining the influence of spatial scale (500, 1000, 1500, 2000 m) on 25 breeding bird species (sorted taxonomically).

	Proportion of canopy			
Species	500 m	1000 m	1500 m	2000 m
Mourning Dove	120.71$^{\#}$	121.36	121.55	122.03
Red-bellied Woodpecker	116.41	113.40	110.16$^{\#}$	115.75
Downy Woodpecker	129.90	128.76	127.65$^{\#}$	130.64
Eastern Wood-Pewee	99.70$^{\#}$	100.32	100.32	99.97
Great Crested Flycatcher	79.07$^{\#}$	79.52	79.52	79.60
Red-eyed Vireo	75.51	75.24	73.83	70.64$^{\#}$
Blue Jay	124.21$^{\#}$	124.28	124.28	124.62
Black-capped Chickadee	95.96	92.30	91.86$^{\#}$	93.16
Tufted Titmouse	109.83$^{\#}$	110.22	110.26	110.30
White-breasted Nuthatch	98.08$^{\#}$	98.08	98.08	98.08
House Wren	128.24$^{\#}$	130.81	131.46	132.65
Carolina Wren	64.21	62.98	62.25$^{\#}$	63.16
American Robin	100.33	99.38	94.79$^{\#}$	97.59
Gray Catbird	118.46	116.91$^{\#}$	117.99	118.53
European Starling	83.77	83.64	83.22$^{\#}$	83.60
Chipping Sparrow	122.82	119.08$^{\#}$	121.54	122.34
Song Sparrow	99.21	98.99$^{\#}$	99.13	99.09
Northern Cardinal	86.74	83.23	82.71	80.58$^{\#}$
Indigo Bunting	87.26	84.16$^{\#}$	84.50	86.30
Common Grackle	75.48	75.05$^{\#}$	75.38	75.54
Brown-headed Cowbird	126.43	124.91$^{\#}$	126.25	127.14
Baltimore Oriole	92.46$^{\#}$	92.53	92.52	92.46
House Finch	69.57	69.93	68.29	69.16$^{\#}$
American Goldfinch	106.21$^{\#}$	106.27	106.36	106.36
House Sparrow	93.87	93.48$^{\#}$	93.52	93.84

We selected the spatial scale (#) that provided the biggest reduction in model deviance for further occupancy modeling in the Oak Openings Region, Ohio, USA, from 23 May to 2 July 2013.

Continued

Table 2.4 Continued

	Density of canopy patches			
Species	500 m	1000 m	1500 m	2000 m
Mourning Dove	116.83$^{\#}$	118.37	117.97	117.15
Red-bellied Woodpecker	113.83$^{\#}$	115.67	115.04	114.89
Downy Woodpecker	130.63	128.27$^{\#}$	129.85	130.61
Eastern Wood-Pewee	99.91	98.37$^{\#}$	98.59	99.15
Great Crested Flycatcher	75.43	75.97	70.60	69.95$^{\#}$
Red-eyed Vireo	72.64	72.81	72.65	71.69$^{\#}$
Blue Jay	123.76$^{\#}$	124.65	124.63	124.50
Black-capped Chickadee	97.49	95.56	93.31$^{\#}$	96.09
Tufted Titmouse	108.72	107.82$^{\#}$	109.04	108.85
White-breasted Nuthatch	98.08	97.96	97.88	97.44$^{\#}$
House Wren	125.77$^{\#}$	128.00	126.81	128.34
Carolina Wren	64.58	64.81	62.26$^{\#}$	63.55
American Robin	98.88	98.57	96.92	95.55$^{\#}$
Gray Catbird	115.08	107.68	107.79	106.87$^{\#}$
European Starling	79.06$^{\#}$	80.95	80.94	79.70
Chipping Sparrow	123.76	120.96$^{\#}$	122.18	122.98
Song Sparrow	99.20	97.88	96.65$^{\#}$	97.62
Northern Cardinal	88.87	75.94$^{\#}$	83.26	87.93
Indigo Bunting	82.57	74.76	72.24$^{\#}$	72.43
Common Grackle	71.84	69.54	67.14$^{\#}$	68.06
Brown-headed Cowbird	128.55	128.33$^{\#}$	128.46	128.55
Baltimore Oriole	92.22	90.70$^{\#}$	91.54	91.18
House Finch	71.27	65.84	71.19$^{\#}$	71.33
American Goldfinch	106.36	106.36	106.36	106.25$^{\#}$
House Sparrow	87.44	84.24	77.11	71.97$^{\#}$

Continued

Table 2.4 Continued

	Road density			
Species	500 m	1000 m	1500 m	2000 m
Mourning Dove	113.49	113.52	112.92	112.67#
Red-bellied Woodpecker	113.04#	114.98	116.14	116.41
Downy Woodpecker	130.59	130.64	130.57#	130.60
Eastern Wood-Pewee	97.13#	97.62	98.10	98.28
Great Crested Flycatcher	77.49	75.50#	76.02	77.13
Red-eyed Vireo	70.40	68.12	66.86	66.28#
Blue Jay	122.91	123.15	122.89	122.47#
Black-capped Chickadee	92.24	97.08	91.27	89.99#
Tufted Titmouse	107.16	106.06	105.35	105.30#
White-breasted Nuthatch	93.71	94.63	92.78#	94.63
House Wren	129.84	129.75	129.21	129.19#
Carolina Wren	61.86#	64.88	65.03	64.88
American Robin	93.91#	98.11	98.65	99.37
Gray Catbird	101.82#	104.80	104.57	104.48
European Starling	76.14	76.01#	77.24	78.06
Chipping Sparrow	122.82#	122.95	122.94	123.01
Song Sparrow	95.88	95.10	94.82#	95.12
Northern Cardinal	91.12	90.75	90.34	90.30#
Indigo Bunting	67.92	64.54	63.98	61.91#
Common Grackle	52.76	45.70	45.80	44.94#
Brown-headed Cowbird	128.56	128.55	128.55	128.53#
Baltimore Oriole	91.28#	92.06	92.21	92.23
House Finch	71.33	67.28	66.48#	68.11
American Goldfinch	102.29#	106.36	106.36	106.35
House Sparrow	49.61	49.47#	53.28	54.34

Table 2.5. Standardized parameter estimates predicting occurrence of 18 breeding bird species (sorted taxonomically) in the Oak Openings Region, Ohio, USA, from 23 May to 2 July 2013, including site-level($_S$) and landscape-level($_L$) variables.

Species[¶]	Naïve occupancy	Mean p	Mean Ψ	Prop. of canopy$_S$	Prop. of natural understory$_S$	Prop. of canopy$_L$	Density of canopy patches$_L$	Road density$_L$
Mourning Dove	0.49	0.59	0.57	-0.52	-0.39	-0.13	0.04	0.97
Red-bellied Woodpecker[d]	0.51	0.45	0.73	…	…	-4.39#	-3.16*	-1.01
Eastern Wood-Pewee[d]	0.33	0.52	0.43	1.02#	0.58	-1.30*	-0.79	-0.27
Red-eyed Vireo[d]	0.24	0.66	0.27	0.95#	…	-2.21*	-1.33	-0.81
Blue Jay	0.61	0.59	0.71	0.06	0.23	-0.33	-1.21#	1.95#
Black-capped Chickadee[d]	0.35	0.37	0.54	-1.40*	…	0.19	-1.21	0.73
Tufted Titmouse[d]	0.43	0.45	0.64	1.19*	…	1.52	0.36	-2.86*
House Wren	0.67	0.62	0.77	-0.53	0.57	0.15	1.80	1.24
American Robin	0.90	0.83	0.91	-0.11	0.38	-1.01	0.02	5.88
Gray Catbird[d]	0.47	0.51	0.58	0.32	0.12	0.44	0.03	-1.90#
European Starling	0.31	0.70	0.32	0.18	-0.03	-0.14	0.43	0.70
Chipping Sparrow	0.55	0.65	0.61	-0.89#	-0.35	0.96#	-0.39	0.12
Song Sparrow	0.35	0.72	0.39	0.17	-0.46	0.06	-0.02	-1.08
Indigo Bunting[d]	0.27	0.54	0.36	…	…	2.50*	15.49*	-54.30*
Common Grackle	0.24	0.63	0.29	…	…	-0.46	-0.50	4.11*
Brown-headed Cowbird	0.73	0.63	0.85	-2.64*	1.33	1.74#	-0.14	1.54
Baltimore Oriole[d]	0.33	0.41	0.46	…	…	-0.34	-0.75	-0.00
House Sparrow	0.39	0.89	0.40	0.57	-1.55#	1.50	1.72*	2.53*

Continued

Table 2.5 Continued

… Inestimable parameters not included in the model.

*P <0.05; #P <0.10; Statistical significance determined via likelihood ratio tests between full vs. reduced models without each variable.

¶*Abbreviations: d, patch-dependent.* We defined species that are dependent on a treed canopy as patch-dependent.

Note: Naïve occupancy is the proportion of sites where a species was detected; Mean p is the mean detection probability for a species per survey; Mean Ψ is the mean occupancy probability for a species per site; Seven species with sparse data (Downy Woodpecker, Great Crested Flycatcher, White-breasted Nuthatch, Carolina Wren, House Finch, American Goldfinch) or where "real" occupancy approached 100% (Northern Cardinal) were excluded from analysis; For all species except House Sparrow, a global model including terms for time of morning, day of season, temperature, and wind speed was applied to estimate detection probabilities; For House Sparrow a null detection model (intercept only) was employed.

Scientific names: Refer to Appendix C.

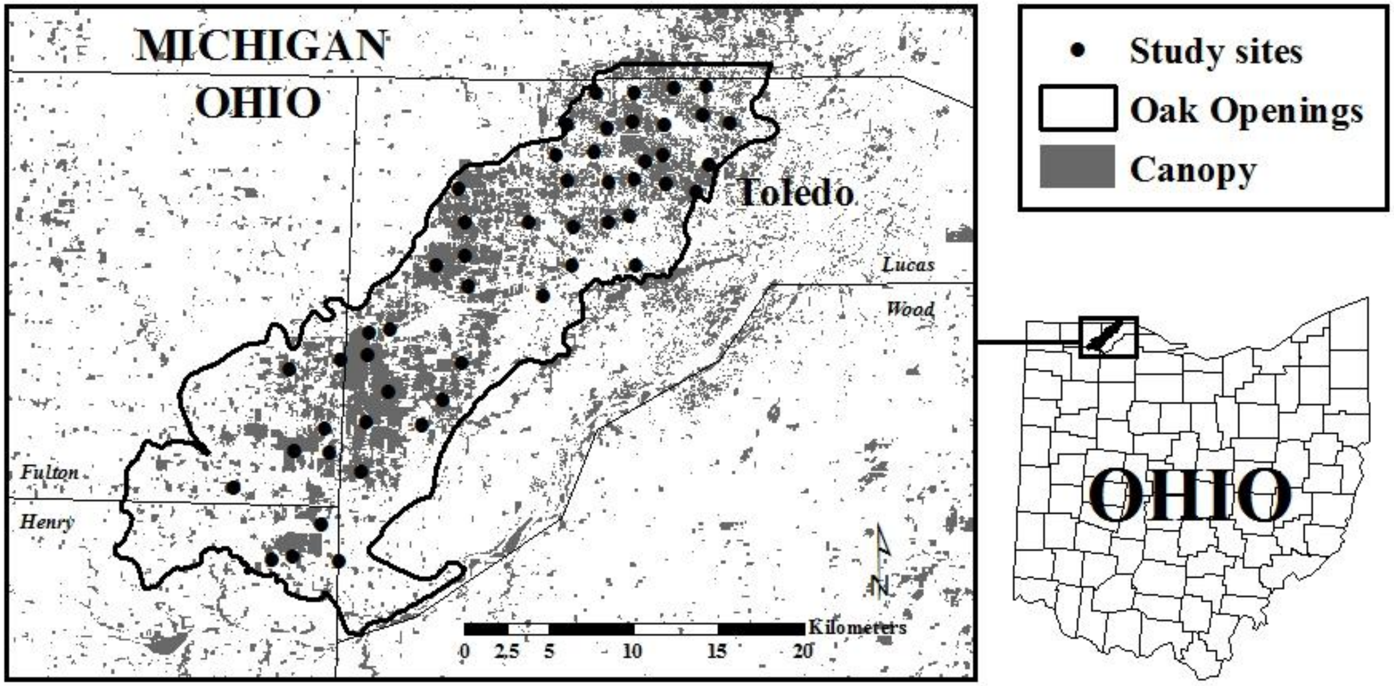

Figure 2.1. Our study area, the Oak Openings Region, Ohio, USA, and locations of 51 study sites used to model breeding bird occupancy from 23 May to 2 July 2013.

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CHAPTER 3: THE RELATIVE IMPORTANCE OF HABITAT STRUCTURAL DIVERSITY: DO RARE HABITATS INFLUENCE MIDWESTERN BREEDING BIRD DIVERSITY?

Abstract

Land use change in the Midwest is especially responsible for losses of many rare ecological communities that are often globally unique and serve as habitat for a variety of threatened species. The Oak Openings Region of northwestern Ohio is home to 5 such habitats that are found in little to no supply elsewhere. These habitats contribute appreciably to the structural diversity (i.e. the distribution of area among different land cover types) of potential midwestern breeding bird habitat. By extensively sampling the birds of the Oak Openings Region, we investigated the importance of structural diversity of remaining natural/seminatural land cover relative to habitat loss and fragmentation on diversity patterns (i.e. species richness) of 3 breeding bird guilds under an information-theoretic framework after identifying the spatial scale most strongly influencing diversity of each guild. Based on variable relative importance and standardized partial regression coefficients, Neotropical diversity was best explained by a combination of habitat amount and structural diversity, while Nearctic diversity was explained by habitat isolation and structural diversity, and exotic diversity by structural diversity and habitat loss. Model-averaged effect sizes of beta coefficients of structural diversity were especially large and positive for all 3 guilds. We validated our final statistical model for each guild with a random subset of our survey points (50%) and mapped our predictions across the entire region. Neotropical and Nearctic diversity were predicted to be greatest in the center of the region corresponding to large core areas of protected habitat, and exotic diversity was predicted to be greatest in the southern and northern portions of the region where agriculture and urban development dominate the matrix, respectively. We have demonstrated that structural

diversity contributes to a diverse breeding bird community and will be an important long-term conservation strategy at preserving both local and global biodiversity.

Introduction

Human use and intensity of Earth's land cover are accelerating globally (Sala et al. 2000, McKinney 2002, Alig et al. 2004, Forman 2008, Pickett et al. 2008, Dearborn and Kark 2010, Ramalho and Hobbs 2012). Remnant natural habitat arranged within human-dominated landscapes provide ecosystem services to surrounding areas and serve as critical reserves for local and global biodiversity conservation (Carpenter et al. 2009). Disturbance-mediated communities, such as prairies and savannas, have almost disappeared from the U.S. Midwest as a result of human expansion and agricultural development (Auclair 1976, Nuzzo 1986). Corresponding to these losses, many disturbance-dependent bird species have suffered precipitous declines. In recent measures, out of 200 species, some 40% have experienced and continue to experience significant losses (as reviewed in Askins 2002). Regional restoration efforts to convert impacted land areas to savanna and prairie habitats are threatened by expanding urban land uses and agricultural intensity.

For the past several thousand years, disturbance-mediated species like oaks (*Quercus* spp.) have dominated many eastern and midwestern landscapes (Abrams 1992). However, as a result of human induced alterations to natural disturbance regimes, shade tolerant species, such as red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), and tulip poplar (*Liriodendron tulipifera*), now threaten the extent and quality of oak forests (Abrams 1992, Abrams and Nowacki 1992); fire suppression, heavy deer browsing, and differing silvicultural practices have been identified as significant contributors to this transition (Lorimer 1984). This represents a challenge for wildlife conservation (Rodewald 2003). Acorn mast provides important forage for many North American wildlife species (VanDersal 1940). Many avian species rely on acorn mast to fulfill fall and winter dietary needs (Smith 1986, Smith and Scarlett 1987). Food resources for species not dependent on acorn mast can also be affected by losses of oaks. This is especially true for many avian species that forage in the mid- to upper-canopies and for many reasons, including differences in the foliage and bark structure between oaks and shade-tolerant species that inhibit the detection and procurement of insects (Holmes and Robinson 1981, Holmes and Schultz 1988, Robinson and Holmes 1984, Whelan 2001, Gabbe et al. 2002). In some cases, the effects of changes in the floristic composition can be quite severe; for example species richness has been reported to be twice as high in oak- relative to maple-dominated stands (Rodewald and Abrams 2002).

In addition to species composition changes, structural transitions have occurred, as well as drastic reductions in many disturbance-mediated habitats, such as grasslands and prairies. For instance, oak dominated, open-canopy communities of the Midwest, predominately oak savannas and grasslands, have been categorized as the most imperiled habitats in the region (Auclair 1976, Nuzzo 1986), and by some measures, temperate savannas and grasslands are considered the most threatened major terrestrial ecosystems globally (Hoekstra et al. 2005). Midwest savanna is defined as a grassland community characterized by sufficiently small or widely spaced oak dominated trees so that the canopy does not close, representing roughly 10 – 80% canopy coverage (Nuzzo 1986, Anderson 1998, Temple 1998). While profound fragmentation, resulting from agriculture, urbanization, and fire exclusion, has contributed to and continues to threaten the existence of oak savanna in the Midwest (Nuzzo 1986, Grossman and Mladenoff 2007), these communities remain as high biodiversity hotspots (Leach and Givnish 1999).

Restoration efforts in the Midwest often target historical species composition and structural attributes indicative of oak savanna or prairie (e.g., Leach and Ross 1995, Abella et al. 2007). Prescribed fire and mechanical thinning are 2 common restoration techniques in the region (Packard 1993). Fire is necessary in maintaining the unique vegetative structure of oak savanna (Peterson and Reich 2001) through effectively suppressing woody vegetation (Bragg and Hulbert 1976, Sparks et al. 1998) and removing litter to release herbaceous vegetation (Abella et al. 2004). Restoration of wet prairie often includes restoring historical hydrological regimes (Bowles and McBride 1998). These efforts transform the floristic composition and stand structure of restoration sites, which are regularly the measures of restoration success (Omerod 2003).

Efforts to restore disturbance-mediated habitats affect bird communities in many ways, especially for habitat specialists. Those species reported to favor disturbance are often identified in many instances as tenants of “open woodland,” “shrubby,” or “old-field” habitat (e.g., Sibley 2003). Brawn (2006) reported avian distribution responses to prescribed burning, of which many species favored restored sites, and among those species considered, 6 exhibited greater nest success. Many species benefit from increased amounts of these habitats within the landscape, especially imperiled grassland communities. The process of burning and mechanical thinning is thought to foster structural advantages unique to many early-succession breeding birds (e.g., Davis et al. 2000, Cunningham and Johnson 2006). In contrast, some species of forest birds display decreases in abundance after prescribed burning (Aquilani et al. 2000, Artman et al. 2001).

We chose to utilize birds as a focal group for our analysis, as bird communities are (a) frequently used as indicators of the availability and quality of habitat, (b) easily surveyed, (c) often exhibit specialized migratory and habitat requirements, and (d) of conservation concern across the region. We examined the diversity (i.e. species richness) of 3 breeding bird guilds in the Oak Openings Region of northwestern Ohio. The region holds one the largest best preserved oak savanna in the Midwest. We sought to examine the independent effects of habitat loss, fragmentation, and structural diversity, the distribution of area among different habitat types, on breeding bird diversity. Our overarching goal was to examine how important the presence and amount of globally unique, often disturbance-mediated, habitats in the Oak Openings Region contributes to the diversity of the breeding bird community. Because the region exhibits intense heterogeneity at both localized and landscape scales, our study helps us better understand how bird diversity is associated with the presence of globally unique habitat types. We hope to contribute generally to ecological theory and help appropriate conservation investment in our unique study area. We expected the diversity of breeding birds to be positively influenced by the structural diversity (i.e. presence of globally imperiled ecological communities) of habitat in the landscape.

Methods

Study Area

Our study area encompassed the 47,800-ha Oak Openings Region of northwestern Ohio, USA (Brewer and Vankat 2004). The region is recognized as a biodiversity hotspot and conservation stronghold; more species of special conservation interest are found here than any other comparable area in the state (as summarized in Schetter and Root 2011). The region contains 5 ecological communities of global significance: Great Lakes Twig-rush Wet Meadow, Great Lakes Swamp White Oak-Pin Oak Flatwoods, Mesic Sand Prairie, Midwest Sand Barrens, and Black Oak/Lupine Barrens (Faber-Langendoen 2001, EPA 2012). The region also hosts an extralimital breeding population of Lark Sparrow (*Chondestes grammacus*), a species typically found in grasslands of the North American West. The region was 20.4% forests and woodlands, 0.8% savanna, 0.4% shrublands, 5.1% prairies and meadows, 0.5% water, 3.8% dense urban, 35.4% residential/mixed, 6.6% turf/pasture, and 27% croplands based on the Schetter and Root (2011) land cover. The region is within the Eastern Tallgrass Prairie Bird Conservation Region (NABCI 2000) and the Maumee Lake Plains physiographic region of Ohio (ODNR Division of Geologic Survey 2008).

Avian Sampling

We conducted a series of repeat roadside surveys using the point count method (Ralph et al. 1995) at 230 point count locations to sample the breeding bird community in the Oak Openings Region. We uniformly intersected a 2-km x 2-km grid pattern over the entire study area and randomly positioned 2 points within each block at most 750 m from the block centroid and greater than 250 m from the nearest other point using ArcGIS ver. 10.1 (ESRI 2012). We used road data from the U.S. Census Bureau's TIGER/Line files (topologically integrated geographic encoding and referencing, http://www.census.gov/geo/maps-data/data/tiger-line.html, accessed 9 April 2013). To account for unforeseen potential safety or noise interference concerns with roadside surveys, we over-distributed the amount of potential survey points within each block by 150-250% (conditional to road density). We surveyed points in each block in numerical order until at least 2 points were surveyed, skipping dangerous or noisy locations. This allowed us for the flexibility to skip unsuitable points for more appropriate conditions while maintaining a randomized sampling design. After eliminating 2 blocks from consideration for potential noise interference concerns or a lack of vehicular access, our sampling design established 115 blocks and 230 points for our investigation.

From 23 May to 2 July 2013, we conducted 2 surveys at each point count location. We surveyed the points in routes beginning 0.5 hr before sunrise and extending until 1030 EST on precipitation-free and low wind days (<19 km hr^{-1}) with approximately 2 weeks separating visits. Each survey lasted 6.25 min and we implemented a 1-min adjustment period to allow birds to acclimate to observer presence. We randomly generated the order routes were surveyed, attempting to allow each point to be surveyed at least once in the early morning period and another in the late morning period to reduce the effect of time of day on bird detectability. The lead author conducted all surveys to control for observer bias. Ensuring that our observations characterized the habitat being assessed, we only analyzed detections within 100 m of the point. Although our surveys were restricted to roadsides, all surveys were conducted during low traffic interference with a mean (± SD) of 3.62 (± 7.05) conveyances per survey (n = 460). Roads also likely represented much less of a habitat discontinuity for the habitat being assessed in our system (e.g., sparsely treed parks, patchy forests, residential developments), and a recent investigation (e.g., McCarthy et al. 2011) also detected no difference in model performance between models built from samples from roadsides vs. primary habitat of bird species. Thus we surmise that roadside surveys in our investigation are more-or-less equivalent to off-road surveys.

Response Variables and Habitat Model

The breeding bird community of the region represents a diverse array of habitat specialists, nesting ecologies, foraging strategies, and migratory guilds. Species with life-cycles that require open-water breeding habitat or species that were not previously documented as breeders in the region were removed from our dataset, and we conducted our analysis on known breeding species with terrestrial life-cycles to eliminate any confounding effects of specialized habitat requirements. We decided to use a guild-based approach to best account for the community's diversity. Because we detected redundancy in guild designations (e.g., most residents were cavity nesters, most resident/short distance migrants consume grains/seeds for some portion of their yearly life-cycle, and most obligate Neotropical migrants were insectivorous), we focused on migratory guilds. We classified the breeding bird community into 3 distinct migratory guilds: Neotropical, Nearctic, and exotic. Neotropical represented the diversity of species that spend the non-breeding period in the Neotropics (i.e. obligate Neotropical-migratory species). Nearctic diversity was those species whose entire life-cycle occurs within the Nearctic region and accounted for resident and short-distance migrants in our study. Because the region also hosts a few non-native species and/or species whose breeding range only recently extended into the area, we also established an exotic guild. For each guild we calculated diversity as the total sum of species (i.e. species richness) detected at each point over our replicated sampling design.

We followed the habitat modeling approach by Guissan and Zimmerman (2000). We proceeded by (1) developing a conceptual model from literature review and preliminary analysis; (2) collecting survey and habitat data; (3) constructing a statistical model; and (4) making predictions and validating the model. We used land cover data from Schetter and Root (2011), a Landsat-5 TM derived land use and land cover classification with a 0.09-ha pixel resolution (see Schetter and Root 2011 for full details on these data). The land cover data included 15 classifications, and we eliminated cultural land uses from consideration for suitable breeding bird habitat. We considered natural/seminatural classes, excluding water, to be suitable breeding bird habitat, and we generated 2 separate raster layers from the original data. For the first raster layer we combined all natural/seminatural classes into a single attribute, and mapped the presence/absence of natural/seminatural land cover per 0.09-ha pixel across our study area. For the second layer we removed cultural land uses and water from the layer by reclassifying those attributes to "no data," creating a raster layer that contained only natural/seminatural types.

Using FRAGSTATS ver. 4.2 (McGarigal et al. 2012) we calculated 4 landscape-level habitat variables within 4 spatial extents from buffer radii ranging from 500 m to 2000 m in 500-m increments around each point: habitat amount, habitat patch area, habitat patch isolation, and habitat structural diversity represented by the proportion of natural/seminatural landcover, mean patch area (ha) of natural/seminatural land cover, Euclidean mean nearest distance (m) of natural/seminatural land cover, and Shannon's diversity of natural/seminatural landcover, respectively (Table 3.1). Using the first raster layer, we calculated habitat amount, habitat patch area, habitat patch isolation within each buffer radii.

Because the landscape is highly heterogeneous in rare globally unique land cover types, we also calculated the structural diversity, the distribution of area of different land cover types, of breeding bird habitat using the second raster layer and Shannon's diversity index in FRAGSTATS:

$$\text{Shannon's diversity} = -\sum_{i=1}^{R} pi \ln pi$$

By generating the second raster layer, we calculated the structural diversity of breeding habitat alone and ignored all other land use/land covers in the landscape for each buffer radii. We selected Shannon's diversity index over other such indices (e.g., Simpson's) because of its sensitivity to richness over evenness. Rare patch types have a disproportionately large effect on Shannon's diversity, and thus, this measure best encapsulated the diversity of rare, globally unique communities in the region. We projected all data in UTM NAD 1983 zone 17 N for all calculations. We also calculated the proportion of habitat within the 100-m point count radius using aerial photographs from the National Agriculture Imagery Program (NAIP, https://www.fsa.usda.gov/FSA, accessed 9 April 2013), ground-truthing, and half-centimeter dot transparencies to control for confounding site-level effects of habitat amount in our statistical model.

For our 4 landscape-level variables (habitat amount, habitat patch area, habitat patch isolation, and habitat structural diversity), we determined the spatial extent from the 4 buffer radii that most strongly correlated with diversity for our 3 breeding bird guilds. We used bootstrapping to obtain Pearson's correlations on 10,000 random samples of 10 points each from the entire set of points (n = 230; Holland et al. 2004) for each guild. Only points in each sample that contained no overlap in buffer radii were selected to eliminate spatial autocorrelation (i.e. only those sites within each sample were selected that possess an inter-plot distance greater than 2x the distance of the buffer). We used Student's *t*-tests to identify statistically dissimilar extents on the mean correlations of each scale. For statistically similar extents, we selected the smaller radius for our calculations to reduce the effect of overlapping extents in each guild's final model. The spatial extent most strongly correlated for each variable to diversity of each guild was included in all subsequent analysis and considered our best-fit spatial extent for that variable. From our entire set of 230 sites we randomly selected 50% of our points (n = 115) >1 km apart to build our statistical model and to serve as our training data set. The remaining half of our points (n = 115) served as our validation data set.

Statistical Analyses

Using our best-fit spatial extents of variables for each breeding bird guild, our entire statistical approach was to construct a series of candidate models containing all possible combinations of our 4 landscape-level variables: amount of natural/seminatural habitat, mean patch area of natural/seminatural habitat, Euclidean mean nearest neighbor distance of natural/seminatural habitat, and Shannon's diversity index of natural/seminatural habitat to represent habitat amount, habitat patch area, habitat patch isolation, and habitat structural diversity, respectively. For all models, including the null model, we also included a term for the proportion of natural/seminatural habitat within the 100-m count radius to control for confounding site-level effects in local habitat amount. We used generalized linear models with a Poisson distribution (log-link function) to build our statistical models with the training data set. We used the maximum-likelihood statistic, Akaike's Information Criterion (AIC), and AIC model weights (w_i) to examine the influence of our variables on each migratory guild's diversity pattern across our study area (Burnham and Anderson 2002). Covariates in models with a difference in AIC value compared to the top-ranked that is less than 2 (i.e. ΔAIC <2.0) are considered to be substantially supported (Burnham and Anderson 2002). The w_i estimates the likelihood of any given model. We standardized all variables by subtracting by the mean and dividing by the SD of each variable to account for collinearity in our covariates before analyses. Standardizing covariates is a useful technique for disentangling unintentional effects of redundancy often associated with fragmentation correlates, and it allows for the comparison of regression coefficients as the influence on response of one SD change on the predictor (Smith et al. 2009). To account for model selection uncertainty and to examine the relative influence of each variable on diversity patterns of each guild, we performed model-averaging for variables in all models with ΔAIC <2.0 and calculated relative variable importance and full model-averaged parameters using conditional model-averaged coefficients as our parameters (Burnham and Anderson 2002):

$$\beta_{\mathrm{j}}^{\Delta}\frac{\sum_{i-1}^{\mathrm{R}} w_i I_j(g_i)\beta_{j+i}}{w+(j)},$$

$$w+(j)=\sum_{i=1}^{R} w_i I_j(g_i)$$

Where $\beta j,i$ is the estimator of βj in model gi. The $w + (j)$ is the sum of Akaike weights over all those models where the predictor j is present. We performed all statistical analyses in program R (R Development Core Team 2008).

Using model-averaged coefficients from models with ΔAIC < 2.0, we applied our models to the validation data set. To validate each guild's diversity model, we performed paired Student's *t*-tests on observed diversity patterns in the validation dataset and model-based predicted values. We tested for spatial autocorrelation of the model-averaged residuals from the validation data set using Moran's *I* to determine if independence of errors was met. We also extrapolated our predictions and mapped the diversity pattern of each migratory guild across the Oak Openings Region using coefficients derived from our 4 landscape variables. We did not include our site-level variable as we only included this variable in our models to control for confounding site-level effects in local habitat amount. We used the "moving window" analysis in FRAGSTATS to generate raster layers of each variable. We then imported each raster into in ArcGIS and standardized each 0.09-ha pixel to the mean and SD of each variable. We then used the spatial analyst tool "raster calculator" and model-averaged coefficients to produce diversity maps of each breeding bird guild.

Results

We detected 97 species across our investigation (Appendix A). After removing all species not known to breed in the region and those species with predominately open-water life histories, we arrived at 87 species to perform our analysis. Forty of these species were considered Neotropical, 43 were Nearctic, and 4 were exotic: Eurasian Collared-Dove (*Streptopelia decaocto*), European Starling (*Sturnus vulgaris*), House Finch (*Carpodacus mexicanus*), and House Sparrow (*Passer domesticus*). The mean (± SD) numbers of species detected per point (n = 230) was 3.06 (± 2.28) for the Neotropical guild, 8.92 (± 2.73) for Nearctic, and 1.21 (± 1.06) for exotic.

Our landscape-level habitat variables tended to vary by spatial scale based on effect sizes of means and SD calculated in each buffer radii (Table 3.2). Diversity patterns of each guild tended to respond to this scalar variability in our spatial bootstrapping analysis (Table 3.3). For example, Neotropical diversity was most correlated to habitat patch area in the 500 m buffer, while Nearctic diversity was most correlated to the 2000 m buffer, and exotic diversity was most correlated to the 500 m buffer. Diversity of all guilds was best explained by the 500 m buffer for habitat amount in the landscape. Our model results revealed differing responses of our guilds to each variable (Table 3.4). The top-ranked model for Neotropical diversity included habitat amount and habitat structural diversity. The top-ranked model for Nearctic diversity included habitat patch isolation. For exotic diversity, the top-ranked model included habitat patch area. The null model that included a term for the proportion of habitat within the 100-m point count radius did not appear in any of the best-competing models (i.e. those models exhibited a ΔAIC value >2.0 Table 3.4).

Nine models exhibited a ΔAIC <2.0 for Neotropical, 4 models for Nearctic, and 3 for the exotic guild (Table 3.5). According to variable relative importance (RI), habitat amount (RI = 0.58) best explained diversity of the Neotropical guild, while habitat patch isolation (RI = 0.45) best explained Nearctic diversity, and habitat structural diversity (RI = 0.42) best explained exotic diversity (Table 3.6). Based on model-averaged coefficients, the diversity of each guild tended to respond negatively to fragmentation (i.e. to the area and isolation of habitat patches) and positively to habitat amount in the landscape (i.e. the proportion of natural/seminatural habitat) and habitat structural diversity (i.e. Shannon's diversity). However, exotic diversity tended to respond negatively to increased habitat in the landscape. The effect sizes of coefficients for Neotropical and Nearctic diversity were largest for our site-level variable (i.e. proportion of natural/seminatural habitat in the 100-m point count radius) and largest for habitat patch area for exotic diversity. Only considering our 4 landscape variables, effect sizes of coefficients were greatest for the habitat amount for Neotropical diversity and habitat patch isolation for Nearctic diversity. Habitat structural diversity was ranked second based on effect sizes for Neotropical and Nearctic diversity.

We validated our diversity models, as model-based predictions were statistically insignificant from observed diversity patterns in the validation dataset for all 3 guilds based on paired Student's *t*-tests: Neotropical ($t = -0.72$, df = 114, $p = 0.47$), Nearctic ($t = -0.75$, df = 114, $p = 0.46$), and exotic ($t = -0.29$, df = 114, $p = 0.78$). We detected no evidence of spatial autocorrelation in model-averaged residuals for each guild in the validation data set: Neotropical (Moran's $I = 0.000103$, $p = 0.91$); Nearctic (Moran's $I = 0.05$, $p = 0.43$); and exotic (Moran's $I = 0.03$, $p = 0.57$).

The predicted diversity of the Neotropical guild was greatest in the center of the Oak Openings Region where large core areas of protected breeding bird habitat exist (Figure 3.1). The lowest predicted values were found in the southern and northern extremes of the region where the dominant matrix was agricultural and urbanized land uses, respectively. Nearctic diversity followed a similar pattern, where larger predicted values were centered on large core areas of protected habitat in the middle of the Oak Openings Region. Predicted values for Neotropical and Nearctic diversity were especially low in the northern portion of the region where urbanized land use dominates the landscape. Predicted exotic diversity exhibited a pattern that was nearly the inverse of Neotropical and Nearctic diversity. Exotic diversity was predicted to be largest in the southern and northern portions of the region.

Discussion

Each breeding bird guild in the Oak Openings Region responded differently to scale and to each habitat variable. Neotropical diversity was best explained by the amount of habitat in the landscape, while diversity of the Nearctic community was best explained by isolation of habitat. The structural diversity of habitat was the second most important variable to diversity patterns. The globally unique habitats in the region in part contribute greatly to the diversity of these guilds. This has also been observed elsewhere, where diversity and population persistence of some species was best explained by the numbers and relative proportions of non-dominant habitat types in the landscape. Rittenhouse et al. (2012) associated diversity and population declines of many bird species along breeding bird survey (BBS) routes to losses in non-dominant habitats, such as wetlands and prairies. In our study system, many of the non-dominant habitat types are wetlands and prairies and the persistence of these habitats may be beneficial not only to the many declining species associated with these habitats but also to the conservation of other species with different habitat preferences, as also observed in Rittenhouse et al. (2012).

The relative isolation of habitat was particularly important in explaining diversity of Nearctic species. This guild responded negatively to increasing Euclidean mean nearest neighbor distance of habitat patches, which means that the highest diversity was found in areas that were in close proximity to similar habitats. This group contained many resident species that may exhibit relatively shorter dispersal capabilities than Neotropical migratory species; however, recent evidence by Tittler et al. (2009) suggests that dispersal distances of many midwestern breeding birds may be much larger than previously reported in the literature and likely ranges from 15 to 95 km, depending on the species. Although we cannot substantiate this claim further with our data, we consider it an important aspect of future research in our study area.

Another possible mechanistic explanation for this relationship could be related to daily resource use as measured through seed dispersal (Whelan et al. 2008). Most species likely require a multitude of habitat patches to obtain daily dietary needs with less connected sites receiving less visits than more continuous habitats (Garcia et al. 2010), forcing many species to make exploratory movements through the hostile matrix to obtain resources through a myriad of habitat patches. Increasing isolation of habitat patches would then increase the time an individual would need to spend in the hostile matrix searching for resources. Experimentally connecting habitat patches with corridors can enhance seed dispersal of many North American breeding birds (e.g., Evans et al. 2013); thus, providing a mechanistic link to the strong negative association of the Nearctic species to habitat isolation.

General consensus from reviews of the fragmentation literature (see Fahrig 2002, Fahrig 2003, Smith et al. 2009) suggest that habitat loss is always more important than habitat configuration (i.e. the area and isolation of habitat). Based on Island Biogeography Theory, extinction and colonization rates of species occupying relictual habitats are predicted to a function of the relative area and isolation of the habitat patches (MacArthur and Wilson 1967). Neotropical diversity was best explained by habitat loss and not fragmentation in our study, corroborating general sentiment in fragmentation reviews. We also detected scale-dependent responses to these processes across the broader landscape (Smith et al. 2011). For example, Neotropical diversity was most correlated with habitat patch area calculated in the 500 m buffer, while Nearctic diversity was most correlated with patch area in the 2000 m buffer. Likewise we detected differing correlations between diversity and habitat patch isolation: Neotropical diversity was most correlated at 1500 m and Nearctic at 2000 m. We agree with concerns from other investigations (e.g., Holland et al. 2005) that researchers must utilize multiple spatial scales when attempting to discern species-habitat relationships.

Exotic diversity, not surprising, exhibited a negative relationship with habitat amount and mean patch area. However, more surprising, diversity of this community shared a positive relationship with structural diversity. This is surprising, as many highly modified landscapes are often dominated by low species richness and high relative abundance of exotic species (Chase and Walsh 2006). However, most of these studies looked at the entire bird community as a whole and not the diversity of exotic species alone. Thus, at least through our study, we have shown that even exotic breeding bird diversity may be enhanced through habitat structural diversity in the landscape.

Disturbance-mediated habitats in our study area contributed appreciably to the structural diversity of breeding bird habitat in our study area. Prairies and oak savanna have been implicated as some of the most globally imperiled ecosystems (Hoekstra et al. 2005). Corresponding to losses in disturbance-mediated habitats, such as savannas, grasslands, or shrublands, many disturbance-dependent avian species have suffered significant precipitous declines in the United States, prompting concern among conservation organizations (Askins 1993, Askins 2001, Brawn et al. 2001, Hunter et al. 2001, Askins 2002, Sauer et al. 2012, and the citations therein). These species include Vesper Sparrow (*Pooecetes gramineus*), Lark Sparrow (*Chondestes grammacus*), Baltimore Oriole (*Icterus galbula*), Eastern Kingbird

(*Tyrannus tyrannus*), and Red-headed Woodpecker (*Melanerpes erythrocephalus*; Askins 1993, Peterjohn and Sauer 1994). We observed each of these species in our study. The fate of grassland birds, in particular, has periodically been cited as a significant conservation crisis (e.g., Brennan and Kuvlesky 2005).

Many disturbance-dependent birds in the Midwest might be relativity area insensitive (Brawn et al. 2002). Limited empirical exploration of area insensitivity in disturbance-dependent birds has provided some evidence for this claim, especially shrubland birds in forested landscapes (e.g., Lehnen and Rodewald 2009). This contradicts popular rhetoric dominating ecological literature, often concerning mature forest specialist's response to patch size (e.g., Ambuel and Temple 1983, Blake and Karr 1987, Annand and Thompson 1997, Burke and Nol 1998). In theory, patch size has a negligible effect on generalist species (Bender et al. 1998). Many grassland species, such as Upland Sandpiper (*Bartramia longicauda*) are also reported to select large unbroken grasslands (Cunningham and Johnson 2006). Responses of many of these species, often collectively described as open-country specialists, to restoration practices over an intensifying urban landscape are not known, however. Disturbance-dependent birds in general may be responding to past selection pressures indicative of a dynamic mosaic of frequently transitioning successional communities across historic landscapes (Balmford 1996, Brawn et al. 2001).

Isolation better explained diversity of Nearctic and Neotropical diversity over mean patch area, based on our analysis. This may suggest that effective conservation of the breeding birds in our study area should focus more efforts on connecting patches than expanding current reserves. We have also demonstrated that there are no universally applicable conservation strategies that can reverse the effects of changing land use. Based on our analysis, we conclude that diversity of Neotropical and Nearctic species was best explained by habitat amount, isolation of habitat, and structural diversity of habitat. Restoring and increasing the total amount of habitat within the landscape is relatively difficult and other approaches such as increasing permeability through management efforts or compatible land use may be more feasible (Theobald et al. 2012). We recommend focusing efforts on restoring many of the globally unique habitats in the Oak Openings Region and increasing connectivity between patches as a more applicable solution to conserving biodiversity in the region.

Table 3.1. Site and landscape variables used to model diversity patterns (i.e. species richness) of 3 breeding bird guilds in the Oak Openings Region of northwestern Ohio, USA, from 23 May to 2 July 2013.

Scale	Variable	Description
Site	Local habitat	proportion of natural/seminatural habitat area in the 100-m point count radius
Landscape	Habitat amount	proportion of natural/seminatural habitat area in the landscape
	Patch area	mean patch area (ha) of natural/seminatural patches in the landscape
	Patch isolation	Euclidean mean nearest distance (m) between natural/seminatural patches
	Structural diversity	Shannon's diversity of natural/seminatural habitat in the landscape

Table 3.2. Means and SD for variables quantified from natural/seminatural land cover and calculated within 5 spatial scales (site, 500, 1000, 1500, and 2000 m) used to model the influences of habitat amount, area, isolation, and structural diversity on 3 breeding bird guilds in the Oak Openings Region of northwestern Ohio, USA, from 23 May to 2 July 2013.

Scale	Variable	Mean	SD
Site*	Proportion	0.26	0.30
500#	Proportion	0.26	0.30
	Mean patch area (ha)	5.03	11.98
	Mean nearest neighbor (m)	110.12	64.00
	Shannon's diversity	1.25	0.45
1000	Proportion	0.27	0.15
	Mean patch area (ha)	8.78	37.00
	Mean nearest neighbor (m)	99.79	36.25
	Shannon's diversity	1.48	0.30
1500	Proportion	0.27	0.15
	Mean patch area (ha)	6.77	26.39
	Mean nearest neighbor (m)	100.13	28.81
	Shannon's diversity	1.53	0.30
2000	Proportion	0.27	0.15
	Mean patch area (ha)	4.13	5.91
	Mean nearest neighbor (m)	98.03	20.47
	Shannon's diversity	1.57	0.30

*Indicates habitat quantified using aerial photographs from the NAIP within the 100-m point count radius.

#Indicates landscape-level habitat variables derived from Schetter and Root (2011) and calculated within 4 buffer radii from the point count: 500, 1000, 1500, and 2000 m.

Table 3.3. Means and 95% confidence intervals for Pearson's correlation coefficients between 3 breeding bird guilds and habitat variables measured in buffer radii from 500 m to 2000 m in 500-m increments used to identify the spatial scale best explaining diversity (i.e. species richness) for each guild.

		Neotropical		Nearctic		Exotic	
Variable	Scale	Mean	95%	Mean	95%	Mean	95%
Proportion	500	0.604#	0.005	0.362#	0.005	-0.490#	0.005
	1000	0.552	0.005	0.341	0.006	-0.436	0.005
	1500	0.527	0.005	0.334	0.006	-0.415	0.005
	2000	0.511	0.005	0.339	0.006	-0.396	0.005
Mean patch area	500	0.535#	0.005	0.259	0.006	-0.444#	0.004
	1000	0.499	0.005	0.252	0.006	-0.400	0.005
	1500	0.494	0.005	0.273	0.006	-0.397	0.005
	2000	0.531	0.005	0.286#	0.006	-0.409	0.005
Mean nearest neighbor	500	-0.327	0.005	-0.238	0.006	0.158	0.007
	1000	-0.404	0.005	-0.284	0.006	0.268	0.006
	1500	-0.419#	0.005	-0.337	0.006	0.274#	0.006
	2000	-0.404	0.005	-0.348#	0.006	0.251	0.006
Shannon's diversity	500	0.353	0.005	0.256	0.006	-0.264	0.006
	1000	0.363	0.005	0.259#	0.006	-0.260	0.006
	1500	0.390	0.005	0.254	0.006	-0.289#	0.006
	2000	0.394#	0.005	0.247	0.006	-0.268	0.006

We used bootstrapping on 10,000 random samples of 10 points each from our entire set of point count locations (n = 230) with an inter-plot distance greater than twice the buffer radii distance for each spatial extent.

#Spatial extent, calculated as distance from observation point, selected and used in subsequent habitat modeling for each guild. We used Student's *t*-tests to identify statistically dissimilar extents, and for statistically similar extents, we selected the smaller buffer radii to minimize overlap in the final habitat model for each guild.

Table 3.4. Model results examining the effects of habitat amount, area, isolation, and structural diversity on 3 breeding bird guilds in the Oak Openings Region, Ohio, USA, from 23 May to 2 July 2013.

		Neotropical			Nearctic			Exotic		
Model#	*K*	AIC	ΔAIC	w_i	AIC	ΔAIC	w_i	AIC	ΔAIC	w_i
prop + shdi	4	447.40	0.00	0.15	539.77	3.42	0.05	292.41	7.63	0.01
prop + emnn	4	448.44	1.04	0.09	538.34	1.99	0.09	292.08	7.30	0.01
prop + mpa	4	448.45	1.05	0.09	541.27	4.92	0.02	286.54	1.76	0.15
shdi	3	448.51	1.10	0.09	538.18	1.82	0.10	307.18	22.39	0.00
prop + mpa + shdi	5	448.52	1.12	0.09	541.79	5.43	0.02	288.12	3.33	0.07
prop	3	448.53	1.12	0.09	539.21	2.85	0.06	291.42	6.63	0.01
emnn	3	448.74	1.33	0.08	536.36	0.00	0.25	306.94	22.15	0.00
emnn + shdi	4	448.81	1.41	0.08	538.10	1.75	0.11	308.93	24.15	0.00
prop + emnn + shdi	5	449.15	1.75	0.06	540.24	3.88	0.04	293.81	9.02	0.00
prop + mpa + emnn	5	449.54	2.14	0.05	540.46	4.10	0.03	288.21	3.42	0.06
mpa + shdi	4	450.51	3.11	0.03	540.31	3.96	0.04	286.67	1.89	0.14
global	6	450.57	3.16	0.03	542.35	5.99	0.01	290.11	5.32	0.02
mpa + emnn	4	450.81	3.41	0.03	538.49	2.14	0.09	286.80	2.02	0.13
mpa + emnn + shdi	5	450.94	3.54	0.03	540.24	3.88	0.04	288.84	4.05	0.05
null¶	2	455.45	8.04	0.00	539.91	3.55	0.04	305.72	20.93	0.00
mpa	3	457.02	9.61	0.00	541.71	5.35	0.02	284.79	0.00	0.35

#prop (habitat amount: proportion of habitat), mpa (habitat area: mean patch area [ha] of habitat), emnn (habitat isolation: Euclidean mean nearest neighbor distance [m]of habitat), and shdi (habitat structural diversity: Shannon's diversity index of habitat).

¶All models, including the null model, also included a term for the proportion of habitat within the 100-m point count radius to control for confounding site-level attributes.

Table 3.5. Summary of model-averaging procedure of parameters appearing in the top-competing models (i.e. ΔAIC <2.0) examining the effects of habitat amount, area, isolation, and structural diversity on 3 breeding bird guilds in the Oak Openings Region, Ohio, USA, from 23 May to 2 July 2013.

Guild	Proportion	Mean patch area	Mean nearest neighbor	Structural diversity	Site proportion	ΔAIC_c	w_i
Neotropical	0.15			0.14	0.23	0.00	0.15
	0.14		-0.13		0.23	1.04	0.09
	0.30	-0.09			0.21	1.05	0.09
				0.21	0.32	1.10	0.09
	0.22	-0.06		0.12	0.22	1.12	0.09
	0.22				0.21	1.12	0.09
			-0.22		0.31	1.33	0.08
			-0.13	0.13	0.30	1.41	0.08
	0.12		-0.07	0.11	0.23	1.75	0.06
Nearctic			-0.09		0.10	0.00	0.25
			-0.07	0.03	0.10	1.75	0.11
				0.07	0.11	1.82	0.10
	0.02		-0.08		0.09	1.99	0.09
Exotic		-2.92			-0.01	0.00	0.35
	-0.16	-2.31			0.01	1.76	0.15
		-3.07		0.05	-0.01	1.89	0.14

Table 3.6. Estimated variable relative importance (RI) and model-averaged standardized partial regression coefficients (averaged β) for parameters appearing in top-competing models (i.e. ΔAIC <2.0) predicting diversity of 3 migratory guilds of breeding birds in the Oak Openings Region, Ohio, USA, from 23 May to 2 July 2013.

	Neotropical		Nearctic		Exotic	
Variable	RI	Averaged β	RI	Averaged β	RI	Averaged β
Proportion	0.58	0.19	0.09	0.02	0.27	-0.16
Mean patch area	0.18	-0.08			0.06	-2.81
Mean nearest neighbor	0.31	-0.14	0.45	-0.08		
Shannon's diversity	0.47	0.15	0.21	0.05	0.42	0.05
Site proportion*	1	0.25	1	0.10	1	0.00
Intercept		0.97		2.16		-5.72

*Site proportion was included in every model, including the null model, to control for confounding site-level effects.

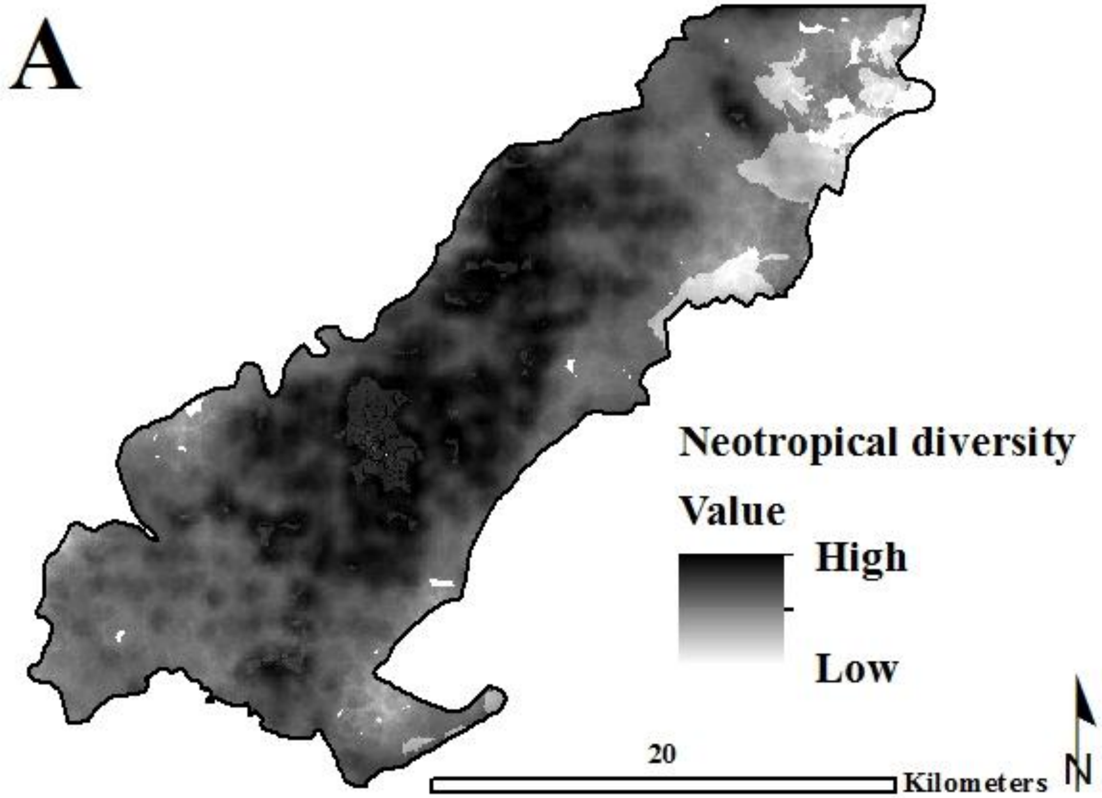

Figure 3.1. Predicted low to high diversity (i.e. species richness) of 3 breeding bird guilds in the Oak Openings Region of northwestern Ohio, USA: (**A**) Neotropical, (**B**) Nearctic, and (**C**) exotic.

Continued

Figure 3.1 Continued

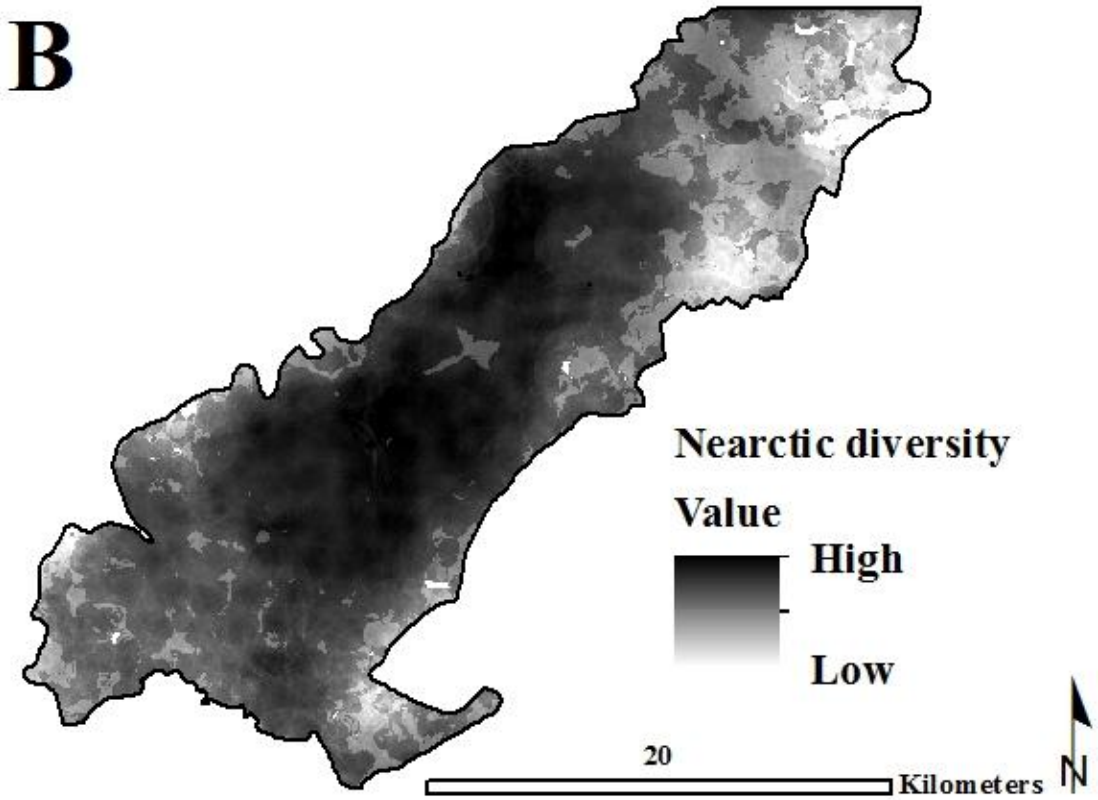

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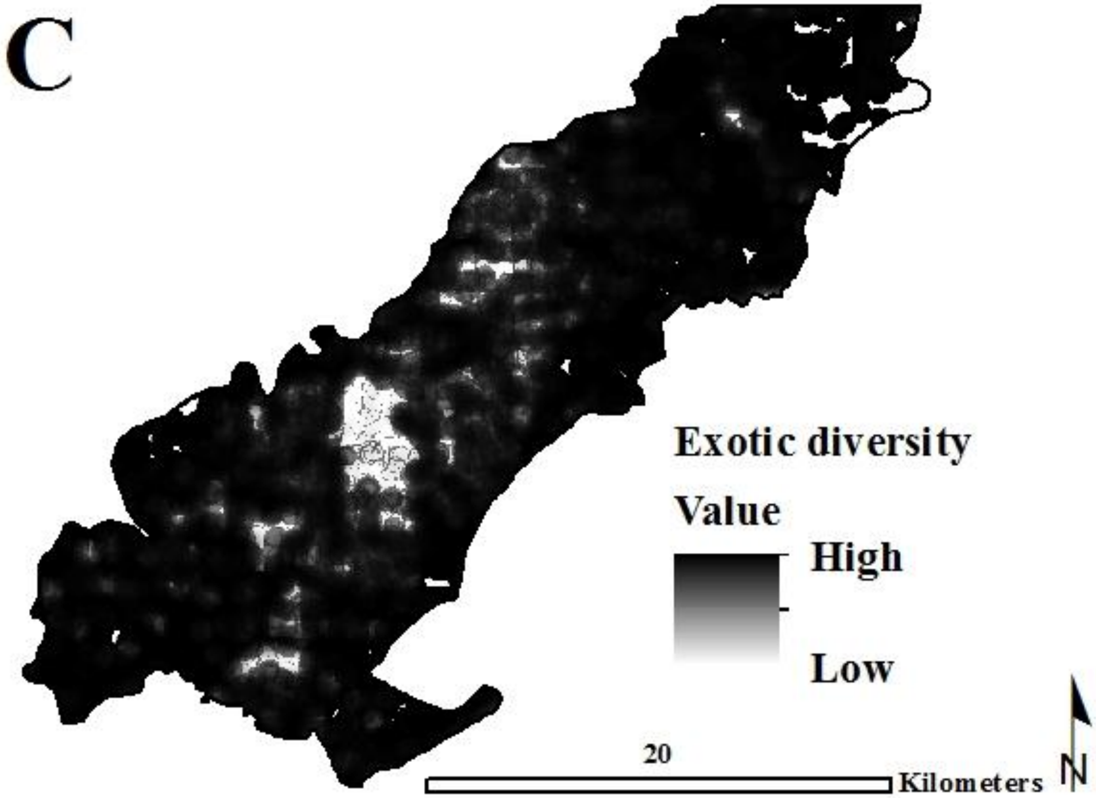
Figure 3.1 Continued



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CHAPTER 4: DOES MIDWESTERN BREEDING BIRD OCCUPANCY IN THE URBAN CENTER VARY ACCORDING TO LOCALIZED HABITAT AMOUNT AND STRUCTURAL DIVERSITY?

Abstract

Urban land use dominates the globe and an emphasis has emerged on better understanding the ecology and conservation of birds in these environments. Many studies have related species presence and abundance to the size and spatial arrangement of habitat patches in human-dominated landscapes, but can fine-scale localized habitat features across the urban center drive occupancy dynamics of urban birds? We sought to quantify the amount of habitat, structural diversity (i.e. the distribution of area among different cover types) of habitat, and the amount of anthropogenic disturbance within a series of 100-m point counts distributed across the Toledo Metropolitan Area and the Oak Openings Region of northwestern Ohio and determine how occurrences of urban breeding birds vary in relation to these features using an occupancy modeling framework. Because a few large parks containing large core areas of natural habitat that are maintained in part for conservation existed in our study area, we also examined if distributions of birds could be explained by the distance to large habitat reserves. We fit a model of similar structure to 15 species, and determined how individual species' responses varied to habitat features. Native species tended to respond positively to habitat amount, structural diversity, and development. Exotic species tended to respond positively to development and large reserves. We attributed generally positive responses of some native species to development from potential supplemental feeding sources. Our results indicate that while large reserves in the broader urban landscape no doubt contribute significantly to biodiversity conservation in these landscapes, occurrences of many species are largely driven by localized amounts in habitat and structural diversity in the urban center. Efforts to conserve urban biodiversity should attempt to

integrate a network of localized natural sources of habitat, which may be more reasonable to accomplish and broader in appeal to urban planners than to construct or expand large habitat reserves.

Introduction

For many reasons, emphasis in understanding ecological patterns and processes within human settlement has emerged (Miller and Hobbs 2002, Dearborn and Kark 2010). Human land use dominates the globe (Sala et al. 2000), and urbanization is quickly becoming a dominant, pervasive land cover in the midwestern United States (Alig et al. 2004). Ecologists and developers are challenged to incorporate effective conservation strategies into these areas that maximize biodiversity, such as avian diversity, and minimize impacts to growth and production. Most studies of urban bird ecology are broad in spatial scale and often focus attention towards the spatial arrangement and size of patches across the urban center (e.g., Melles et al. 2003). While it is true that broad-scale habitat features are important determinants of diversity and distribution of birds, especially in fragmented or relictual landscapes (e.g., Mitchell et al. 2001, Lichstein et al. 2002, Betts et al. 2002), implementing strategies focused on increasing the amount of localized habitat may be broader in appeal or more realistic to urban developers than constructing or expanding large habitat reserves.

Studies of this kind often use presence/absence data to relate a species' occurrence to some ecological pattern or process of interest. A common challenge, however, is accounting for false absences of species (MacKenzie et al. 2002). While detection is indicative of occupancy of a site by the particular species of interest, non-detection does not always imply absence. Imperfect detection of a species can lead to the over- or under-estimation of a particular variable of interest and thus can bias our understanding of even the most basic ecology of species in urban environments. Occupancy modeling can overcome this bias by adjusting the naïve occupancy rate (observed) to the expected occupancy (Ψ) after establishing a detection probability (p) over repeat surveys. Occupancy is based on the probability of detection at each site, $(1 - p)^k$, where k is the number of surveys at each site. The modeling procedure assumes that sites are closed during the study period and sites are independent relative to each other (MacKenzie et al. 2002). Habitat variables can then be added to facilitate the estimation of species-habitat relationships (MacKenzie 2006).

Urbanization results in the reduction and fragmentation of native vegetation across a landscape mosaic that includes large increases in impervious surfaces (Beissinger and Osborne 1982, Arnold and Gibbons 1996, Germain et al. 1998). A few studies of urban birds have examined small-scale vegetation (e.g., Daniels and Kirkpatrick 2006a, b), but most investigate the size and spatial arrangement of habitat patches within urban environments (e.g., Lichstein et al. 2002, Evans et al. 2009). Bird occurrence within these patches often increases when patches are closer to large parks or preserves (Sandström et al. 2006). Bird communities in urban areas often exhibit low species richness and high densities of just a few species, generally exotic species (Emlen 1974). Native plant abundance in suburban landscapes tends towards a positive relationship with bird diversity (Burghardt et al. 2009). However, other activities associated with urban landscapes (e.g., supplemental feeding) may also contribute to diversity or occurrence of some birds in these areas and distort our understanding (Lepczyk et al.2004). This is especially true when considering predation of free ranging pets, such as cats (*Felis catus*; Lepczyk et al. 2003). Species also respond to the amount of localized development, with some species occurring in areas with less development while others in areas with more development (e.g., Lumpkin and Pearson 2013).

Species living in these urban areas may respond differently to localized effects based on their individual conservation risk. Partners in Flight (PIF; Panjabi et al. 2012) have developed a scientifically objective criteria used to assess the relative risk of species persistence in North America based on the following factors: Population Size (PS), Breeding Distribution (BD), Non-breeding Distribution (ND), Threats to Breeding (TB), Threats to Non-breeding (TN), and Population Trend (PT). Each factor is scored from “1” for low vulnerability to “5” for high vulnerability, reflecting the species risk of population decline or global extinction for each factor. A combined conservation score for each species is then tallied with the addition of each factor, taking the highest between TB and TN and between BD and ND, for a total of 0 (low risk) to 20 (high risk). Species assessment scores continue to be updated over time to address new insights in population patterns and issues addressed by reviewers and partners (Panjabi et al. 2005, Panjabi et al. 2012). The process has been examined thoroughly and reviewed externally (Beissinger et al. 2000, Carter et al. 2000, Nuttle et al. 2003). The conservation scores of species represent a valuable tool for assessing a variable’s importance to a particularly species’ global conservation.

Because of pressing interest in developing an empirical understanding of localized urban effects on biodiversity, we sought to determine how occurrences of several breeding birds vary in relation to habitat amount, structural diversity of habitat, development, and distance from large core areas of native habitat. We used point counts and occupancy modeling to correct detection bias to fit a model of similar structure to several breeding birds in our study area. We hypothesized that species would exhibit varying responses to our covariates based on functional groups (e.g., native vs. exotic). We predicted that occurrence of native species would be positively influenced by the amount of localized natural/seminatural habitat, structural diversity of habitat, and proximity large reserves. We expected the opposite to be true of exotic species, and we expected exotics to be positively influenced by the amount of development in the area.

Methods

Study Area

We conducted our study within the 14,843-ha portion of the Toledo Metropolitan area that overlaps the Oak Openings Region in northwestern Ohio, USA (Figure 4.1). The region's characteristic flora was recognized by early European settlers in the name "Oak Openings." Five ecological communities of global significance, including Great Lakes Twig-rush Wet Meadow, Great Lakes Swamp White Oak-Pin Oak Flatwoods, Mesic Sand Prairie, Midwest Sand Barrens, and Black Oak/Lupine Barrens, reside in the region (Faber-Langendoen 2001, EPA 2012). The region is especially distinguished for its biodiversity and presence of at-risk species. More species of conservation interest occur in the region than any other comparable area in the state. A few extralimital breeding populations of birds also occur in the region; e.g., Lark Sparrow (*Chondestes grammacus*). Anthropogenic land use of our study area was primarily dense urban (23.1% of area) and residential/mixed (18.7%; Schetter and Root 2011). The estimated 2012 Toledo population size was 284,012 individuals (U.S. Census Bureau 2014). The long-term mean annual temperature was 10.2° C and the long-term mean temperature during the study period (June –July) was 19.8° C (NCDC 2014). Mean annual total precipitation was 87.6 cm and mean precipitation for the study period was 25.9 cm (NCDC 2014).

Site Selection and Bird Occurrence

For this study, we selected a subset of survey locations from our larger investigation of regional bird ecology and management. We conducted a series of roadside bird surveys using the point count method (Ralph et al. 1995) from paired points within 115 blocks 400 ha in size positioned across the Oak Openings Region. Our points were positioned randomly alongside roads greater than 250 m from the nearest other point or study site edge. From this, we selected all those points that were within the greater Toledo Metropolitan Area; we then eliminated points that occurred within parks or near the boundary of our study area; and finally we arrived at 65 survey locations for this study.

From 5 June to 2 July 2013, we conducted 2 replicate roadside surveys at each point count location (hereafter site) with approximately 2 weeks separating visits. We surveyed sites in routes beginning 0.5 hr before sunrise and extending until 1030 EST on precipitation-free and low wind days (<19 km hr^{-1}). Each survey lasted 6.25 min and we implemented a 1-min adjustment period to allow birds to acclimate to observer presence. We randomly generated the order routes were surveyed, attempting to allow each site to be surveyed at least once in the early morning period and another in the late morning period to reduce the effect of time of day on bird detectability. The lead author conducted all surveys to control for observer bias. Ensuring that the site characterized the habitat being assessed, we only analyzed detections within 100 m of the point. Although our surveys were restricted to roadsides, all surveys were conducted during low traffic interference with a mean (± SE) of 1.48 (± 0.26) conveyances per survey (n = 130).

Habitat, Structural Diversity, Development, and Park Proximity

We quantified the relative proportions of 12 habitat types within each site (Table 4.1). We selected 4 covariates to model occurrences of breeding bird species in our study. We selected the proportion of natural/seminatural habitat within the 100-m count radius of our point counts to represent the amount of available breeding habitat. We calculated the structural diversity of habitat types using Shannon's diversity index:

$$\text{Shannon's diversity} = -\sum_{i=1}^{R} pi \ln pi$$

Where p_i indicates the proportion of the site occupied by habitat type *i*. We selected Shannon's diversity index to represent the structural diversity of habitat over other such indices (e.g., Simpson's) because of its sensitivity to richness over evenness. We counted the number of anthropogenic structures (e.g., houses, buildings, etc.) within each site to represent the amount of localized development on the breeding bird community. To calculate relative proportions of the 12 habitat types and the number of anthropogenic structures in each site, we used aerial photographs from the National Agriculture Imagery Program (https://www.fsa.usda.gov/FSA, accessed 9 April 2013), ground-truthing, and half-centimeter dot transparencies. Using ArcGIS ver. 10.1 (ESRI 2012), we used the spatial analyst tool "near" to calculate the distance (m) to the nearest large reserve >1 km^2 to represent the distance to large core areas of native habitat. The large reserves within of our study were all managed and owned by the Metroparks of the Toledo Area and were the following: Secor (41.6638 N; -83.7880 W), Wildwood Preserve (41.6817 N; -83.6688 W), and Swan Creek Preserve (41.6269 N; -83.6652 W). The mean (± SE) across our 65 study sites was 0.13 (± 0.03) proportion natural/seminatural habitat, 0.49 (± 0.04) Shannon's diversity of habitat, 12.69 (± 0.71) no. of anthropogenic structures, and 3267.26 (± 229.47) Euclidean distance (m) to large reserves. We did not detect any considerable collinearity among our 4 habitat variables (Table 4.2).

Occupancy Modeling and Statistical Analyses

We used single-season occupancy models and logistic regression in PRESENCE ver. 6.2 (Hines 2006) to fit an occupancy model of similar structure to each species detected in >10% of our sites. Our occupancy model included 3 survey-level variables, time of morning (min from sunrise), day of season (days since beginning of study), and temperature (°C), affecting the probability of detection (*p*) and our 4 habitat variables, proportion of natural/seminatural habitat, Shannon's diversity of habitat, number of structures, and Euclidean distance to a large reserve, representing habitat amount, habitat structural diversity, development, and proximity to large core areas of habitat, respectively, affecting the probability of occupancy (Ψ). The occupancy modeling procedure simultaneously accounts for factors influencing p and Ψ. All covariates were standardized by subtracting by the mean and dividing by the SD of each variable, so that the estimated beta coefficients could be compared as the influence on response of one SD change on the predictor. When a species' model failed to reach numerical convergence, we attempted to alter the order of covariates and their initial starting values. When this did not work, we concluded that our data for the species in question was too sparse or where real occupancy reached 100%, and we eliminated that species from consideration in our study. This was true for at least one of our species, where it was detected at every survey: American Robin (*Turdus migratorius*). Because some species in our study had home-ranges larger than our sampling units (e.g., 100-m point), our occupancy estimator best represents the "probability of use" and our detection parameter is best interpreted as the probability of a species using a site and being detected given that it was present (MacKenzie et al. 2006).

We compared the relative influence of our habitat variables by examining standardized beta coefficients and the number of species that responded to these variables. For our occupancy model, proportion of natural/seminatural habitat represented the amount of habitat present in a site, Shannon's diversity indicated the structural diversity of habitat within a site, number of structures represented the amount of development within a site, and Euclidean distance to large reserves represented the distance to large core areas of potential midwestern breeding bird habitat. We tested for overdispersion for each species' full occupancy model by calculating the variance-inflation factor ($\hat{c}$) from 10,000 bootstrapped simulations, and considered $\hat{c} < 3.0$ as indication of suitable fit (Lebreton et al. 1992). We averaged beta coefficients and calculated 95% confidence intervals of native and exotic species to compare responses in these 2 groups. We also tested for correlation of the beta coefficients of our 4 habitat variables with PIF conservation scores (Panjabi et al. 2012) to determine if conservation risk explained species responses.

Results

We detected 51 species in our sites during surveys (Appendix E). We modeled occurrence of 15 species (Table 4.3). Of the 15 species, Northern Cardinal (*Cardinalis cardinalis*) and Cedar Waxwing (*Bombycilla cedrorum*) were the most and least frequently detected species, with naïve occupancy of 91% and 12% respectively. House Sparrow (*Passer domesticus*) had the highest mean detection probability (80%) and Cedar Waxwing had the lowest mean detection probability (16%). Twelve species were native and 3 species were exotic: European Starling (*Sturnus vulgaris*), House Finch (*Carpodacus mexicanus*), and House Sparrow. Two of the 12 species were Neotropical migrants: Eastern Wood-Pewee (*Contopus virens*) and Baltimore Oriole (*Icterus galbula*). Our detection models generally indicated that detectability was negatively influenced by increasing time, day, and temperature, such that detectability was highest in the early morning, early season, and during lower temperatures. Variance-inflation factors indicated no overdispersion in our models for each species (i.e. $\hat{c} < 3.0$; Lebreton et al. 1992).

For individual species, we detected varying responses to habitat amount, structural diversity, development, and proximity to parks. Based on effect sizes of beta coefficients, occurrences of 6 species were most strongly influenced by development, 4 species were most influenced by structural diversity of habitat, 3 species by habitat amount, and 2 species by proximity to large reserves (Table 4.3). Considering each variable independently, 6 species responded positively to habitat amount, 7 species to structural diversity of habitat, 7 species to development, and 8 species to distance to large reserves.

Mean beta coefficients and 95% confidence intervals indicated high variability in response to covariates (Table 4.3, Figure 4.2). For habitat amount, mean betas were positive for total and native species and negative for exotic species, indicating native species generally responded positively to increasing natural/seminatural habitat in the sites. We also found the same relationship for habitat structural diversity. Mean betas indicated that on average all species tended to respond positively to development in the sites with exotic species exhibiting the largest parameter estimate but also the highest variability in 95% confidence intervals. Total and native species tended to respond negatively to proximity to large reserves, based on mean betas, indicating that the probability of occupancy of native species was greatest in sites further from large reserves. The opposite was revealed for exotic species with occupancy probability, on average, being higher in sites nearer to large reserves.

Conservation scores of species were not correlated with beta coefficients of any predictor. However, we detected a modest positive linear relationship between PIF score and our beta coefficients (Figure 4.3). Beta coefficients for species' responses tended to increase with PIF score for habitat amount (Pearson's $r = 0.31$, df = 13, $p = 0.26$), habitat structural diversity ($r = 0.08$, df = 13, $p = 0.78$), development ($r = 0.16$, df = 13, $p = 0.57$), and distance to large parks ($r = 0.25$, df = 13, $p = 0.36$). Our results tended to indicate that responses of more imperiled species were stronger than those less imperiled, such that species with greater PIF scores were predicted to occur in areas with more localized habitat, more structural diversity, more residential development, and farther from large parks (Figure 4.3).

Discussion

Our results indicate that occurrences of individual species vary widely in response to the amount of habitat, structural diversity of habitat, development, and distance to large core areas of native habitat in urban environments. This study highlights the need for an occupancy estimator in urban studies, as in many cases the estimated occupancy of some species was greater than twice the observed occupancy rate (e.g., Cedar Waxwing). Overall occurrence of native species tended to increase with increasing habitat, structural diversity of habitat, and development. Occurrences of exotic species tended to increase with development and with decreasing distance to large reserves.

One explanation for the positive relationship for native species in response to development may relate to supplemental resources in urban settings. Many of these species consume grains for a large portion of their yearly life cycle; thus a large positive response to development for some species could correspond to supplemental feeding at bird feeders (Lepczyk et al. 2004). In contrast, for Eastern Wood-Pewee, an insectivorous Neotropical migratory species, the response was much stronger for the amount of habitat rather than development. Occurrence of this species could in part be explained by a strong positive influence of natural/seminatural habitat in the sites and not from supplemental feeding. However, we do not have any other largely insectivorous species in our study to further test this hypothesis. Downy woodpecker (*Picoides pubescens*), a wood-boring species, like many of the grain consuming species responded positively to development. This could be because it is a resident species that will utilize supplemental feeders in the non-breeding period (i.e. winter). Similarly, Lepczyk et al. (2013) demonstrated that occurrences of Ovenbird (*Seiurus aurocapillus*), a Neotropical migratory species, in Massachusetts were largely negatively influenced by development independent of habitat loss. Thus, Neotropical, insectivorous species may be less tolerant of development overall in comparison other such functional groups.

Across our functional groups we generally detected a positive relationship with occurrence of birds and development. In addition to supplemental food sources, other possible mechanistic links may have also occurred in our study, such as differences in ground cover (e.g., Norton et al. 2014) and tree diversity (e.g., Bourne et al. 2014) associated with urban development. For example, cultured grass cover in urban landscapes has been shown to have greater diversity and abundance of arthropods to other such covers, such as bare ground or leaf litter (Norton et al. 2014). Tree species diversity is often greatest in areas of highest human population density in the urban center (Bourne et al. 2014) and may correspond to high arthropod diversity and abundance as well (Stamps and Linit 1998). We did not measure these processes, but we cannot rule out these patterns discovered in other studies as possible mechanistic links to positive relationships of breeding birds to development in our investigation.

For our Neotropical migratory species, Eastern Wood-Pewee and Baltimore Oriole, occupancy was positively correlated to habitat amount and structural diversity of habitat. Our results indicate that even small increases in native vegetation, often associated with native gardens, can increase the likelihood of these species being present at a site (Daniels and Kirkpatrick 2006a, b, Evans et al. 2009). The structural diversity of habitat was particularly important for Tufted Titmouse (*Baeolophus bicolor*), Song Sparrow (*Melospiza melodia*), and House Finch – the latter being an exotic species. Song Sparrow is a transitional, edge species and Tufted Titmouse depends on deciduous, evergreen species. These species were also predicted to occur in areas further from large reserves in our study. This may be that resources for these species were similar between residential developments and large parks. In fact some investigations have determined that bird diversity is no different, or in some cases greater, in residential habitats than non-residential parks after controlling for local habitat amount (e.g., Smith et al. 2014).

Although we obtained insignificant statistical results in our correlation analysis between beta coefficients and PIF scores, we detected a modest positive linear relationship between PIF score and for each variable. Our results anecdotally suggest that species of greater conservation risk may benefit from increased habitat, increased structural diversity of habitat, and localized development in the urban center. Interestingly, species of greatest conservation concern were predicted to occur in areas farther from large parks. We echo concerns from recent reviews of urban conservation (e.g., Goddard et al. 2010) and suggest that conservation in the urban center may be more effective by increasing the amount connectivity of fine-scale habitat resources, as our study generally indicated that species of greatest conservation risk responded positively to these processes.

Land use is expected to accelerate and more increasingly will there be a need to provide sanctuary for biodiversity in urbanized landscapes. More specifically, localized efforts undertaken by those living within the urban center could help offset the costs of altered land use by promoting localized conservation for many bird species in lieu of the restoration or expansion of large habitat reserves (Kostyack et al. 2011). Increased development, especially on the urban fringe or in rural areas, is expected to reduce the occurrence of many species (Lumpkin and Pearson 2013). Thus strategies should be undertaken to help maintain biodiversity during this land use transition (such as promoting small-scale habitat and diversity of habitats). We have demonstrated that habitat amount and structural diversity are positively associated with occurrence of some species in our study. More importantly, while the public has an affinity to develop near scenic natural areas (Kaplan and Austin 2004), the likelihood of many species occurring more within sites close in proximity to large reserves was not improved. Thus, while large reserves in the urban landscape certainly contribute significantly to overall biodiversity in the landscape, there are yet many localized activities that can also contribute to the viability of urban populations of breeding birds.

Table 4.1. Means and SE proportions of 12 localized habitat types within 65 study sites (100-m point counts) used to model occurrences of breeding bird species in Toledo Ohio, USA, from 5 June to 2 July 2013.

Habitat	Mean	SE
Forested residential*	0.067	0.025
Open residential	0.730	0.036
Deciduous forest*	0.041	0.017
Permanent pasture	0.010	0.007
Row crops	0.010	0.007
Urban grasses	0.031	0.018
Woody transitional*	0.006	0.004
Open water	0.005	0.003
Linear woody*	0.003	0.002
Riparian*	0.008	0.005
Paved roads	0.085	0.007
Mowed berms	0.003	0.001

*Indicates natural/seminatural land cover considered as suitable midwestern breeding bird habitat combined into a single class: habitat amount. All habitats were used in calculating Shannon's diversity to represent habitat structural diversity.

Table 4.2. Spearman's correlation matrix describing relationships between predictor variables used to model occurrences of breeding bird species in Toledo Ohio, USA, from 5 June to 2 July 2013.

Variable	Proportion of natural/seminatural	Shannon's diversity	No. of structures
Euclidean nearest distance	-0.02	-0.09	0.07
Proportion of natural/seminatural		0.66	-0.55
Shannon's diversity			-0.54

Table 4.3. Estimated beta coefficients predicting occurrences (Ψ) of 15 midwestern breeding bird species (sorted taxonomically) in Toledo, Ohio, USA, from 5 June to 2 July 2013.

Species	Naïve Ψ	Mean *p*	Mean Ψ	Proportion of natural/semi.	Shannon's diversity	No. of structures	Euclidean distance	Migration[1]	PIF[2]
Mourning Dove	0.62	0.59	0.77	-0.53	-0.21	2.11	-0.27	R	5
Downy Woodpecker	0.52	0.40	0.81	1.12	1.30	2.22	-1.60	R	7
Eastern Wood-Pewee	0.14	0.26	0.29	4.21	0.03	0.06	0.07	N	10
Blue Jay	0.58	0.53	0.75	-0.08	-0.39	-0.40	-0.33	R	6
Tufted Titmouse	0.20	0.43	0.32	2.39	4.21	1.80	0.90	R	8
Carolina Wren	0.14	0.21	0.35	11.56	-2.50	0.88	-1.31	R	8
European Starling	0.55	0.55	0.70	-0.51	-0.59	-0.26	0.51	E	7
Cedar Waxwing	0.12	0.16	0.37	-0.12	-0.60	-1.03	1.04	R	7
Chipping Sparrow	0.63	0.70	0.69	-0.05	-0.02	-0.40	-0.05	R	7
Song Sparrow	0.26	0.41	0.39	-0.67	0.78	-0.30	0.59	R	8
Northern Cardinal	0.91	0.77	0.94	2.08	-1.36	-0.57	-3.36	R	5
Baltimore Oriole	0.15	0.18	0.49	0.44	0.14	0.48	-0.22	N	11
House Finch	0.40	0.45	0.58	-0.49	0.75	-0.05	0.48	E	6
American Goldfinch	0.49	0.39	0.72	-7.09	2.14	-2.10	1.62	R	6
House Sparrow	0.80	0.80	0.84	-1.00	-0.87	2.70	0.33	E	8

Continued

Table 4.3 Continued

[1] Migratory guild: R = resident/short-distance migrant; N = Neotropical migrant; E = exotic.

[2] Partners in Flight combined conservation scores (Panjabi et al. 2012).

Note: Naïve Ψ (occupancy) is the proportion of sites detected; Mean p is the mean probability of detection at any given survey; Mean Ψ is the corrected mean proportion of sites being occupied, accounting for detection probability in occupancy modeling (MacKenzie et al. 2002).

Scientific names: Refer to Appendix E.

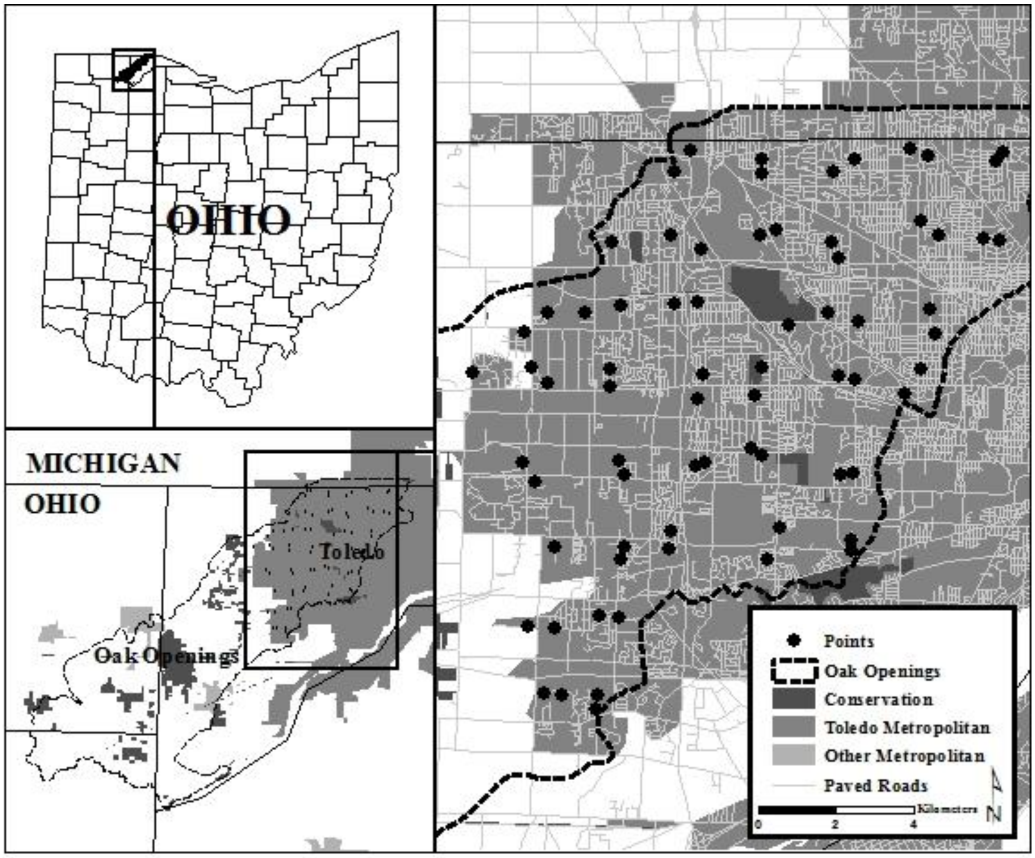
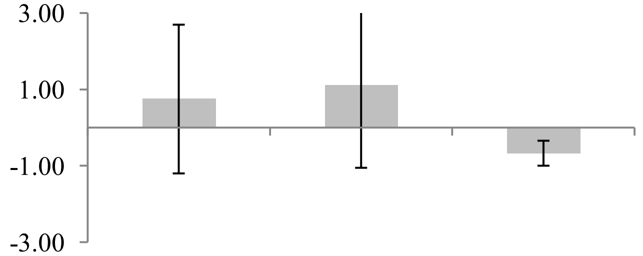
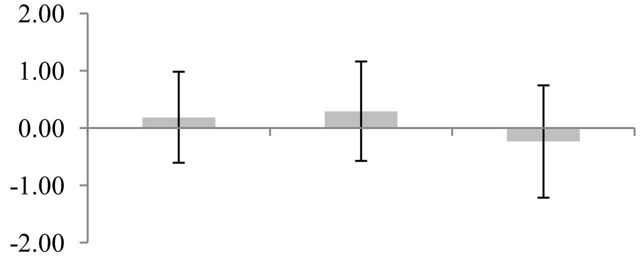


Figure 4.1. Location of our study area and 65 roadside point counts used to sample midwestern breeding bird species in the Toledo Metropolitan Area and the Oak Opening Region, Ohio, USA, from 5 June to 2 July 2013.

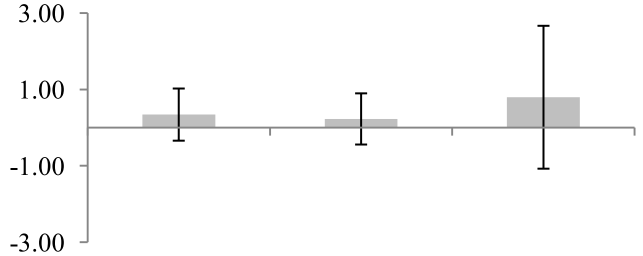
A) Proportion of natural/seminatural



B) Shannon's diversity



C) No. of structures



D) Euclidean distance

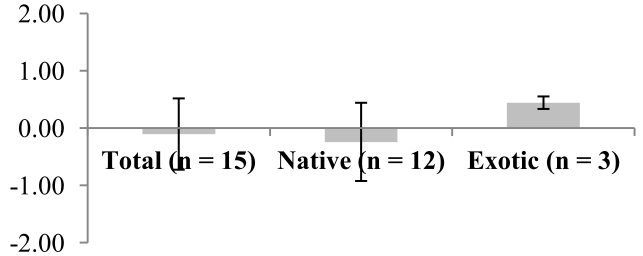


Figure 4.2. Mean and 95% confidence intervals of beta coefficients for (**A**) proportion of natural/seminatural habitat, (**B**) Shannon's diversity of habitat, (**C**) no. of structures, and (**D**) Euclidean distance (m) to large reserve >1 km^2 for total species, native species, and exotic species.

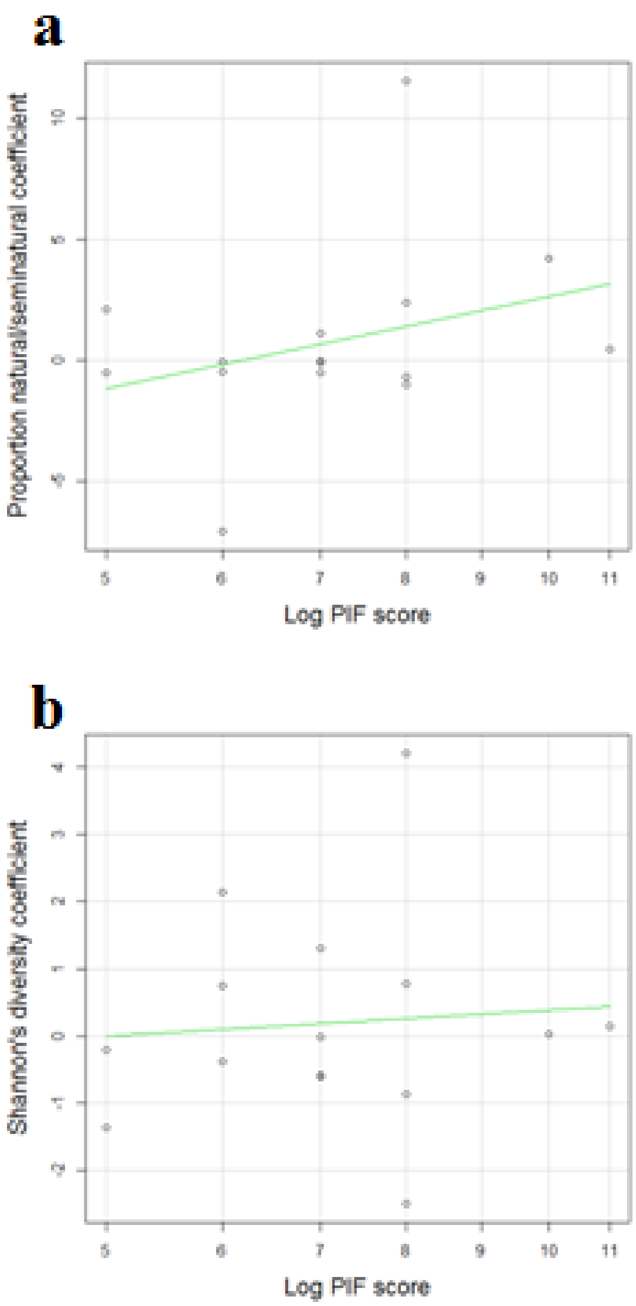
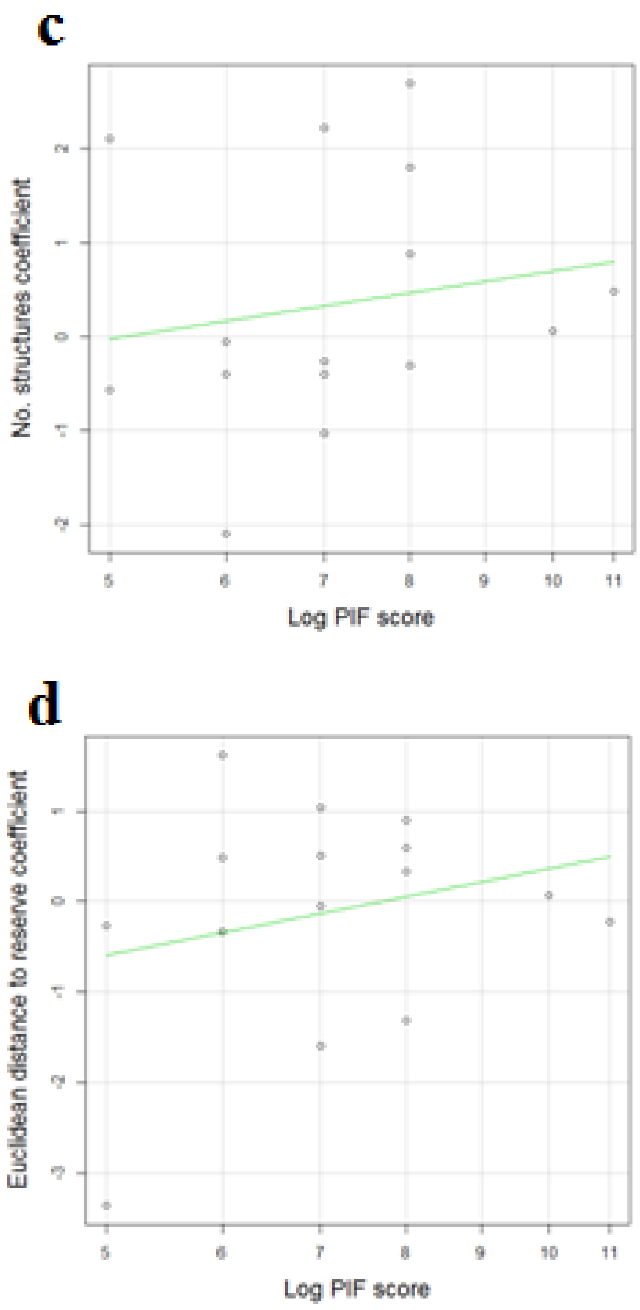


Figure 4.3. Beta coefficients for (**A**) proportion of natural/seminatural habitat, (**B**) Shannon's diversity of habitat, (**C**) no. of structures, and (**D**) Euclidean distance to large reserve >1 km^2 as a function of the Partners in Flight (PIF) conservation score of each species (n = 15).

Continued

Figure 4.3 Continued



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CHAPTER 5: PREDICTING THE SPATIAL DISTRIBUTION OF RED-BELLIED WOODPECKER AS INFLUENCED BY HABITAT LOSS AND FRAGMENTATION

Abstract

In this study we develop and validate a predictive distribution model of Red-bellied Woodpecker (*Melanerpes carolinus*). Our objective was to investigate the relative effects of habitat loss and fragmentation on occupancy dynamics of this charismatic species. From a series of 230 sites we conducted repeat-visit surveys from 23 May to 2 July 2013 in the Oak Openings Region of northwestern Ohio to sample the presence of woodpecker. After determining the spatial scale of model variables most correlated with the presence of woodpecker, we applied an occupancy modeling framework to a random subset of half of our sites to model scale-dependent habitat-relationships. Accounting for model selection uncertainty, we model-averaged parameters appearing in our top-competing models and fit the final averaged habitat-occupancy model to the remaining validation dataset. Our model produced an area under the receiver operating characteristic curve value of 0.73, indicating good discriminatory power. Woodpecker occupancy was positively associated with the proportion of natural/seminatural land cover in a buffer radius of 500 m from the site, mean patch area of natural/seminatural cover at 500 m, and the proportion of natural/seminatural cover in the site (100-m point count). Woodpecker occupancy was negatively related to the Euclidean mean nearest neighbor distance (m) of natural/seminatural cover at 500 m and Shannon's diversity of natural/seminatural cover at 1500 m. Standardized partial regression coefficients revealed that mean patch area most strongly affected occupancy of Red-bellied Woodpecker in our study, indicating that fragmentation may act more strongly on occupancy dynamics over habitat loss in this species and perhaps other insectivorous cavity nesting species in our study area. Our distribution map predicted occupancy to be greatest in the center of the region where large core areas of natural/seminatural land cover

remain. Our results will help to direct conservation investment in our unique area and serve as an example for future habitat-occupancy modeling.

Introduction

Increasing awareness of global biodiversity losses and the misapplication of research and management towards biologically inconsequential spatial scales has prompted the examination of ecological patterns and processes on the broader landscape to better focus conservation investment (Miller et al. 2004). Also, the recognition of increasing land use transitions to human-dominated types often with only modest human population growth rates has warranted an emphasis on describing these relationships in urbanizing landscapes and private lands (Miller and Hobbs 2002, Dearborn and Kark 2010). Effective species management plans should be based on our best understanding of species-habitat relationships. Species distribution modeling can accommodate these efforts by deriving avian-habitat relationships through remotely sensed data and mapping habitat occupancy of species for a wide use of applications in addition to conservation planning.

Species distribution modeling may be especially useful for assessing habitat relationships for charismatic species that may function in multiple environmental roles, including keystone and umbrella species concepts, and broader marketable appeal, such as flagship species. In the Midwest, woodpeckers are keystone species, serving as primary cavity excavators for many other secondary cavity-nesting species (Virkkala 2006). Woodpeckers also provide considerable ecosystem services to surrounding anthropogenic land areas through consumption of insect pests (Virkkala 2006, Whelan 2008, Wenny 2011). Several of these species are known to consume emerald ash borer (*Agrilus planipennis*), an invasive wood-boring beetle from Asia known for causing widespread mortality in midwestern Ash trees (*Fraxinus* spp.; Lindell et al. 2008, Koenig et al. 2013).

Habitat loss and fragmentation are recognized as the primary sources of global biodiversity losses, and these processes are occurring at multiple spatial scales, including scales broader than the focus of traditional research and management. Understanding the effects of these processes and of multi-scale habitat relationships are important for improving woodpecker management, in general, as well as in our unique study area. Our approach was to develop and validate a predictive distribution model of Red-bellied Woodpecker (*Melanerpes carolinus*; hereafter woodpecker) in the Oak Openings Region of northwestern Ohio. The Oak Openings is contained within the Eastern Tallgrass Prairie Bird Conservation Region (NABCI 2000) and the Maumee Lake Plains physiographic region of Ohio (ODNR Division of Geologic Survey 2008). It is a biodiversity hotspot and conservation stronghold, threatened by encroaching anthropogenic land use. Our objective was to investigate the relative effects of habitat loss and fragmentation on occupancy dynamics of this charismatic species. Following the line of inquiry established in recent reviews of habitat loss and fragmentation (e.g., Fahrig et al. 2003, Smith et al. 2009), we predicted woodpecker to be most strongly influenced by habitat loss than fragmentation.

Methods

Sampling Coverage and Woodpecker Surveys

We conducted a series of repeat roadside surveys using the point count method (Ralph et al. 1995) at 230 sites to sample the presence of woodpecker in the Oak Openings Region (Figure 5.1). We uniformly intersected a 2-km x 2-km grid pattern over the study area and randomly positioned 2 sites within each block at most 750 m from the block centroid and greater than 250 m from the nearest other site using ArcGIS ver. 10.1 (ESRI 2012). We used road data from the U.S. Census Bureau's TIGER/Line files (topologically integrated geographic encoding and referencing, http://www.census.gov/geo/maps-data/data/tiger-line.html, accessed 9 April 2013). To account for unforeseen potential safety or noise interference concerns with roadside surveys, we over-distributed the amount of potential survey sites within each block by 150-250% (conditional to road density). We surveyed sites within each block in numerical order until at least 2 sites were surveyed, skipping dangerous or noisy sites. This allowed us for the flexibility to skip unsuitable sites for more appropriate conditions while maintaining a randomized survey design. After eliminating 2 blocks from consideration for potential noise interference concerns or a lack of vehicular access, our sampling design established 115 blocks and 230 sites for our investigation.

From 23 May to 2 July 2013, we conducted 2 replicate surveys at each site with approximately 2 weeks separating visits. We surveyed sites in routes beginning 0.5 hr before sunrise and extending until 1030 EST on precipitation-free and low wind days ($<$19 km hr^{-1}). Each survey lasted 6.25 min, and we implemented a 1-min adjustment period to allow woodpecker to acclimate to observer presence. We alternated the order routes were surveyed, attempting to allow each site to be surveyed at least once in the early morning period and another in the late morning period to reduce the effect of time of day on woodpecker detectability. The lead author conducted all surveys in part to control for observer bias and to ensure that the observations characterized the habitat being assessed, we only analyzed detections within 100 m of the observation point. Although our surveys were restricted to roadsides because of large holdings of private property, all surveys were conducted during low traffic interference with a mean (± SD) of 3.62 (± 7.05) conveyances per survey ($n = 460$), and a recent investigation (e.g., McCarthy et al. 2011) also detected no difference in model performance between models built from samples from roadsides vs. primary habitat of bird species. Thus we surmise that roadside surveys in our investigation are more-or-less equivalent to off-road surveys.

Habitat Model Development

We followed the predictive distribution modeling approach by Guissan and Zimmerman (2000). We proceeded by (1) developing a conceptual model from literature review and preliminary analysis; (2) collecting survey and habitat data; (3) constructing a statistical model; and (4) making predictions and validating the model. We used land cover data from Schetter and Root (2011), a Landsat-5 TM derived land use and land cover classification with a 0.09-ha pixel resolution (see Schetter and Root [2011] for full details on these data). The land cover data included 15 classifications, and we eliminated cultural land uses from consideration for suitable breeding woodpecker habitat (Table 5.1, Table 5.2). We considered natural/seminatural classes, excluding water, to be suitable breeding woodpecker habitat, and we generated 2 separate raster layers from the original data. For the first raster layer we combined all natural/seminatural classes into a single attribute, and mapped the presence/absence of natural/seminatural land cover per 0.09-ha pixel across our study area. For the second layer we removed cultural land uses and water from the layer by reclassifying these attributes to “no data,” creating a layer that contained only natural/seminatural types.

Using FRAGSTATS ver. 4.2 (McGarigal et al. 2012) and the first raster layer, we calculated the proportion of natural/seminatural land cover within 4 spatial extents from buffer radii ranging from 500 m to 2000 m in 500-m increments around each site. We calculated the proportion of natural/seminatural land cover to represent habitat amount. We also calculated 2 correlates of fragmentation: mean patch area of natural/seminatural land cover (ha) and

Euclidean mean nearest neighbor distance (m) of natural/seminatural land cover to represent the relative area and isolation of habitat, respectively, within each buffer radii.

Because the landscape is highly heterogeneous in rare globally unique land cover types, we also calculated the structural diversity, the distribution of area of different land cover types, of breeding woodpecker habitat using the second raster layer and Shannon's diversity index in FRAGSTATS:

$$\text{Shannon's diversity} = -\sum_{i=1}^{R} pi \ln pi$$

By generating the second raster layer, we calculated the structural diversity of breeding habitat alone and ignored all other land use/land covers in the landscape for each buffer radii. We selected Shannon's diversity index over other such indices (e.g., Simpson's) because of its sensitivity to richness over evenness. Rare patch types have a disproportionately large effect on Shannon's diversity, and thus, this measure would best encapsulate the diversity of rare, globally unique communities in the region. We projected all data in UTM NAD 1983 zone 17 N for all calculations. We also calculated the proportion of habitat within the 100-m count radius using aerial photographs from the National Agriculture Imagery Program (NAIP, https://www.fsa.usda.gov/FSA, accessed 9 April 2013), ground-truthing, and half-centimeter dot transparencies to control for confounding site-level effects in our statistical model.

For each of our landscape-level variables, we determined the spatial extent from the buffer radii that most strongly correlated with woodpecker presence. We used bootstrapping to obtain Spearman's correlations on 10,000 random samples of 25 sites each from the entire set of sites (n = 230; Holland et al. 2004). We selected sites that contained no overlap within each sample to eliminate spatial autocorrelation (i.e. only those sites within each sample were selected that possess an inter-plot distance greater than 2x the distance of the buffer). We used Student's *t*-tests to identify statistically dissimilar extents on the mean correlations of each scale. The spatial extent most strongly correlated for each variable to woodpecker presence was included in all analysis and considered our best-fit spatial extent for that variable. From our entire set of 230 sites we randomly selected 50% of our points (n = 115) >1 km apart to build our statistical model and to serve as our training data set. The remaining half of our points (n = 115) served as our validation data set.

Statistical Analyses

We estimated site occupancy and detection probability following MacKenzie et al. (2002), using single-season occupancy models with PRESENCE (Hines 2006) to adjust the habitat model for imperfect detection of woodpecker. While detection is indicative of that site being occupied by the particular species of interest, nondetection does not always imply absence. Occupancy modeling corrects this bias by accounting for the probability of a species occupying a site and being detected by adjusting the naïve occupancy rate (observed) to an expected occupancy rate (Ψ) after establishing a detection probability (p) over repeat surveys. The modeling procedure assumes that sites are closed during the survey period and sites are independent relative to each other (MacKenzie et al. 2002). Habitat variables can then be added to the occupancy models to facilitate the estimation of avian-habitat relationships (MacKenzie 2006, MacKenzie et al. 2006).

We first modeled factors influencing detectability of woodpecker. We considered time (min since sunrise), day (number of days since surveys began), and temperature (°C) as factors influencing detection. We modeled detection as a function of all combinations of our detection variables. We selected our best model from that analysis to control for detection bias for subsequent habitat-modeling. Using detection variables and our best-fit spatial extents of habitat variables, we constructed a series of candidate models containing all possible combinations of our 4 landscape variables: amount of habitat, mean patch area of habitat, Euclidean mean nearest neighbor distance of habitat, and Shannon's diversity index of habitat to represent the amount, mean patch area, isolation of patches, and structural diversity of habitat, respectively. For all models, including the null model, we also included a term for the proportion of natural/seminatural habitat within the 100-m count radius to control for confounding site-level effects. We built our statistical model with the training data set.

We used the maximum-likelihood statistic, Akaike's Information Criterion corrected for small samples (AIC_c), and AIC_c model weights (w_i) to examine the influence of our variables on woodpecker occupancy (Burnham and Anderson 2002). Covariates in models with a difference in AIC_c value compared to the top-ranked model that is less than 2 (i.e. $\Delta AIC_c < 2.0$) are considered to be substantially supported (Burnham and Anderson 2002). The w_i estimates the likelihood of any given model. We standardized all variables by subtracting by the mean and dividing by the SD of each variable to account for collinearity in our covariates before analyses. Standardizing covariates is a useful technique for disentangling unintentional effects of redundancy often associated with fragmentation correlates, and it allows for the comparison of regression coefficients as the influence on response of one SD change on the predictor (Smith et al. 2009). To account for model selection uncertainty, we performed model-averaging for all variables in models with $\Delta AIC < 2.0$ and calculated full model-averaged parameters using a conditional model-averaging technique (Burnham and Anderson 2002):

$$\beta_{\mathrm{j}}^{\Delta} \frac{\sum_{i-1}^{\mathrm{R}} w_i I_j(g_i)\beta_{j+i}}{w+(j)},$$

$$w + (j) = \sum_{i=1}^{R} w_i I_j(g_i)$$

Where *βj,i* is the estimator of *βj* in model *gi*. The *w + (j)* is the sum of Akaike weights over all those models where the predictor *j* is present.

Using model-averaged coefficients from models with ΔAIC <2.0, we applied our final habitat occupancy model to the validation data set and fit a receiver operating characteristic (ROC) area under the curve (AUC) to our model-based predictions. We evaluated the AUC as previously recommended: 0.50 = no discriminatory power; 0.50-0.69 = poor power; 0.70-0.89 = good power; >0.90 = excellent discriminatory power (Manel et al. 2001). We also extrapolated our predictions and mapped the probability of woodpecker occupancy across the Oak Openings Region using our landscape-level habitat variables. We used the "moving window" analysis in FRAGSTATS to generate raster layers of each variable. We then imported each raster into in ArcGIS and standardized each 0.09-ha pixel to the mean and SD of each variable. We then used the spatial analyst tool "raster calculator" and model-averaged coefficients to produce our map.

Results

We detected Red-bellied Woodpecker at 64 of the 230 (27.8%) sites (Figure 5.1). Mean (± SD) detection probability at a given survey was 0.33 ± <0.01 and mean occupancy at a given site was 0.46 ± 0.04. Presence of woodpecker was most correlated with habitat amount, mean patch area, and Euclidean mean nearest neighbor distance in the 500 m buffer and at the 1500 m buffer for structural diversity (Figure 5.2, Figure 5.3). The global model was our top-ranked detection model and each detection variable appeared at least once in our top-competing models, so we modeled subsequent habitat-occupancy with the global detection model, including time, day, and temperature as variables affecting detection of woodpecker (Table 5.3).

The global habitat model was our top-ranked model, and all habitat variables appeared at least once in our top-competing models, so we model-averaged all variables from all models $\Delta AIC_c < 2.0$ (Table 5.4). Our final habitat model was logit (woodpecker presence) = 1.83 (proportion of natural/seminatural habitat) + 2.05 (mean patch area of habitat) + -0.19 (Euclidean mean nearest neighbor of habitat) + -0.89 (Shannon's diversity of habitat) + 0.35 (site-level proportion of natural/seminatural habitat) + 0.28. We fit our final habitat model to the validation data set and the AUC value was 0.73, indicating good discriminatory power (Figure 5.4; Manel et al. 2001).

Woodpecker occupancy was positively associated with the proportion of natural/seminatural land cover in a buffer radius of 500 m from the site, mean patch area of natural/seminatural cover at 500 m, and the proportion of natural/seminatural cover in the site (100-m point count). Woodpecker occupancy was negatively related to the Euclidean mean nearest neighbor distance of natural/seminatural cover at 500 m and Shannon's diversity of natural/seminatural cover at 1500 m. Standardized partial regression coefficients revealed that mean patch area most strongly affected occupancy of Red-bellied Woodpecker in our study. Our distribution map predicted occupancy to be greatest in the center of the region where large areas of natural/seminatural land cover remain (Figure 5.5). Given the presence of suitable localized habitat, only ~32% of the Oak Openings Region was predicted to have habitat not well suited for woodpecker (<0.20; Table 5.5), while ~68% was predicted to be well suited for breeding woodpecker habitat.

Discussion

We found that habitat loss, fragmentation, and structural diversity of habitat all influenced Red-bellied Woodpecker occupancy. In addition, our woodpecker occupancy model included support for variables calculated from 2 different spatial extents, highlighting the need for multi-scale approaches in research and management (Wiens 1989). Based on our results, 3 of 4 of our landscape habitat variables influenced occupancy of woodpecker more strongly than our site-level variable, which supports the need to incorporate broad spatial scales in research and management (Miller et al. 2004). Broad-scale habitat variables tend to influence the local distribution and abundance of birds in landscapes with moderate amounts of habitat compared to landscapes with greater, more contiguous amounts of habitat (Mitchell et al. 2001, Lichstein et al. 2002, Betts et al. 2002). Our study also continues to provide support for the effective management of species through GIS-derived variables of habitat relationships on the broader landscape (e.g., Carter et al. 2006, Thogmartin and Knutson 2007).

The predictive capability of our model was good (AUC = 0.73; Manel et al. 2001). AUC is a single measure of accuracy and interpretation of the statistic is straightforward: AUC ranges from 0.50 (no discriminatory power) to 1.0 (full, perfect discriminatory power), and for our habitat model, 73% of the time a site randomly selected from those predicted to have a high occupancy probability would be correctly classified as present given observed presence rates from those where woodpecker was not present (Pearce and Ferrier 2000). Although detectability cannot be incorporated in the ROC analysis for the validation dataset, the analysis is considered a powerful tool for assessing the predictive power of habitat models (Guisan and Zimmerman 2000).

At least ~68% of our study area was predicted to be suitable for breeding woodpecker habitat. Presence of woodpecker was correlated to habitat variables at 2 spatial scales: 500 m and 1500 m. To our knowledge, no previous published studies have attempted to model multi-scale habitat associations for this species. However, knowledge of multi-scale habitat selection has existed for some time in the avian literature (e.g., Jones 2001). Spatial scaling is also becoming more common in game and natural resource management (e.g., Williams et al. 2004). On the basis of our results and other habitat studies of various woodpecker species (e.g., Dorresteijn et al. 2013), we recommend a multi-scale approach to examining habitat associations of other insectivorous cavity nesting species.

We have provided evidence that fragmentation may be more important than habitat loss in determining distributions of woodpecker in our study area. This contrasts with general consensus that habitat loss is always more important than fragmentation for Temperate bird species (see review by Fahrig 2003). Woodpecker responded strongest to mean patch area, with larger patches being more likely to be occupied or used by woodpecker over smaller patches. This may in part be related to differing resource availability relative to patch size in our study system. For example, insect density has been shown to increase relative to patch size in some studies (e.g., Pasinelli et al. 2013, Soga and Koike 2013). Based on these relationships, we believe that resource availability may serve as a possible mechanism for driving occupancy of woodpecker in the Oak Openings Region.

Interestingly, our models predicted a negative relationship between woodpecker occupancy and structural diversity of habitat. This could be interpreted as woodpecker being less sensitive to the globally rare habitats found in this region; many of them, excluding oak savanna, likely do not accommodate snags, an important foraging (Whelan 2001) and cavity substrate (Bull 1983). This negative association in part suggests that restoration practices commonly used to open the canopies of woodlands to resemble wet prairies may result in reduced occurrence of some insectivorous cavity nesting species in the region.

Our habitat occupancy model produced robust results that discriminated with good power, indicating that we overcame at least some of the limitations often connected with distribution modeling, such as coarse spatial resolution, biotic errors associated with the selection of biologically irrelevant habitat variables, model-selection uncertainty, and the selection of biologically inconsequential spatial scales. We have demonstrated the usefulness of distribution modeling. Interestingly and contrasting recent reviews of fragmentation, our expectations were not fulfilled in that fragmentation appeared to more strongly influence occupancy of woodpecker over habitat loss. We recommend conservation strategies that attempt to increase the patch size of suitable habitat for insectivorous cavity nesting species. Our modeling approach can serve as an example for future habitat modeling of wildlife in this unique area.

Table 5.1. Reclassified and % area of original land use/land cover by Schetter and Root (2011) used to model breeding season occupancy of Red-bellied Woodpecker in the Oak Openings Region of northwestern Ohio, USA, from 23 May to 2 July 2013.

	Original Schetter and Root (2011) land use/land cover			
Reclassified land cover	Class	Subclass	Classification	%
Breeding habitat*	Natural/seminatural	Forests and woodlands	Swamp forests	3.1
			Floodplain forests	8.9
			Upland deciduous forests	6.4
			Upland coniferous forests	1.9
		Savannas	Upland savannas	0.8
		Shrublands	Wet shrublands	0.4
		Prairies and meadows	Wet prairies	0.1
			Upland prairies	1.3
			Sand barrens	0.8
			Eurasian meadows	3.0
Non-habitat		Water	Perennial ponds	0.5
	Cultural	Developed/built-up	Dense urban	3.8
			Residential/mixed	35.4
		Vacant	Turf/pasture	6.6
			Croplands	27.0

*Natural/seminatural land cover types, excluding water, were combined into a single land cover: breeding woodpecker habitat; all other land cover was excluded from analysis.

We calculated structural diversity of breeding habitat using Shannon's diversity index, using only natural/seminatural classes excluding water.

Table 5.2. Means and SD for variables quantified from natural/seminatural land cover and calculated within 5 spatial scales (site, 500, 1000, 1500, and 2000 m) used to model breeding season habitat occupancy of Red-bellied Woodpecker in the Oak Openings Region of northwestern Ohio, USA, from 23 May to 2 July 2013.

Scale	Variable	Mean	SD
Site*	Proportion	0.26	0.30
500#	Proportion	0.26	0.30
	Mean patch area (ha)	5.03	11.98
	Mean nearest neighbor (m)	110.12	64.00
	Shannon's diversity	1.25	0.45
1000	Proportion	0.27	0.15
	Mean patch area (ha)	8.78	37.00
	Mean nearest neighbor (m)	99.79	36.25
	Shannon's diversity	1.48	0.30
1500	Proportion	0.27	0.15
	Mean patch area (ha)	6.77	26.39
	Mean nearest neighbor (m)	100.13	28.81
	Shannon's diversity	1.53	0.30
2000	Proportion	0.27	0.15
	Mean patch area (ha)	4.13	5.91
	Mean nearest neighbor (m)	98.03	20.47
	Shannon's diversity	1.57	0.30

*Indicates habitat quantified using aerial photographs from the NAIP within the 100-m point count radius.

#Indicates landscape-level habitat variables derived from Schetter and Root (2011) and calculated within 4 buffer radii from the point count: 500, 1000, 1500, and 2000 m.

Table 5.3. Model results for examination of Red-bellied Woodpecker detectability in the Oak Openings Region, Ohio, USA, from 23 May to 2 July 2013.

Model	ΔAIC_c	w_i	K	-2LL
Global	0.00	0.21	4	199.58
Time, temperature	0.17	0.19	3	199.75
Day, temperature	0.29	0.18	3	199.87
Temperature	0.56	0.16	2	200.14
Time, day	1.71	0.09	3	201.29
Time	1.72	0.09	2	201.30
Day	3.29	0.04	2	202.87
Null	3.35	0.04	1	202.93

We report small sample corrected Akaike's Information Criterion (AIC_c), the relative distance in AIC_c values from each model to the highest-ranked model (ΔAIC_c), the Akaike model weight (w_i), the number of model parameters (K), and the model deviance (-2LL). AIC_c of the top model is 197.58.

Table 5.4. Model results for examination of Red-bellied Woodpecker occupancy in the Oak Openings Region, Ohio, USA, from 23 May to 2 July 2013.

Model[#]	ΔAIC_c	w_i	K	-2LL
global	0.00	0.18	10	178.90
prop, mpa, shdi	0.16	0.17	9	179.06
prop, emnn, shdi	0.23	0.16	9	179.13
prop, shdi	0.31	0.16	8	179.21
mpa, emnn, shdi	1.53	0.09	9	180.43
mpa, shdi	2.17	0.06	8	181.07
prop, mpa, emnn	3.77	0.03	9	182.67
mpa, emnn	3.81	0.03	8	182.71
prop, mpa	4.05	0.02	8	182.95
emnn, shdi	4.14	0.02	8	183.04
mpa	4.22	0.02	7	183.12
shdi	4.74	0.02	7	183.64
prop, emnn	5.02	0.01	8	183.92
prop	5.10	0.01	7	184.00
emnn	6.51	0.01	7	185.41
null	6.96	0.01	6	185.86

We report small sample corrected Akaike's Information Criterion (AIC_c), the relative distance in AIC_c values from each model to the highest-ranked model (ΔAIC_c), the Akaike model weight (w_i), the number of model parameters (K), and the model deviance (-2LL). AIC_c of the top model is 176.90.

[#] prop (habitat amount: proportion of habitat), mpa (habitat area: mean patch area of habitat), emnn (habitat isolation: Euclidean mean nearest neighbor distance of habitat), and shdi (habitat structural diversity: Shannon's diversity index of habitat).

Table 5.5. Predicted probability of occurrence of Red-bellied Woodpecker in the Oak Openings Region, Ohio, USA, from 23 May to 2 July 2013.

Probability of occurrence	No. of 0.09 ha cells	Percent of study area
0.00 - 0.20	169337	31.9
0.20 - 0.40	123304	23.2
0.40 - 0.60	69796	13.1
0.60 - 0.80	54350	10.2
0.80 - 1.00	114208	21.5

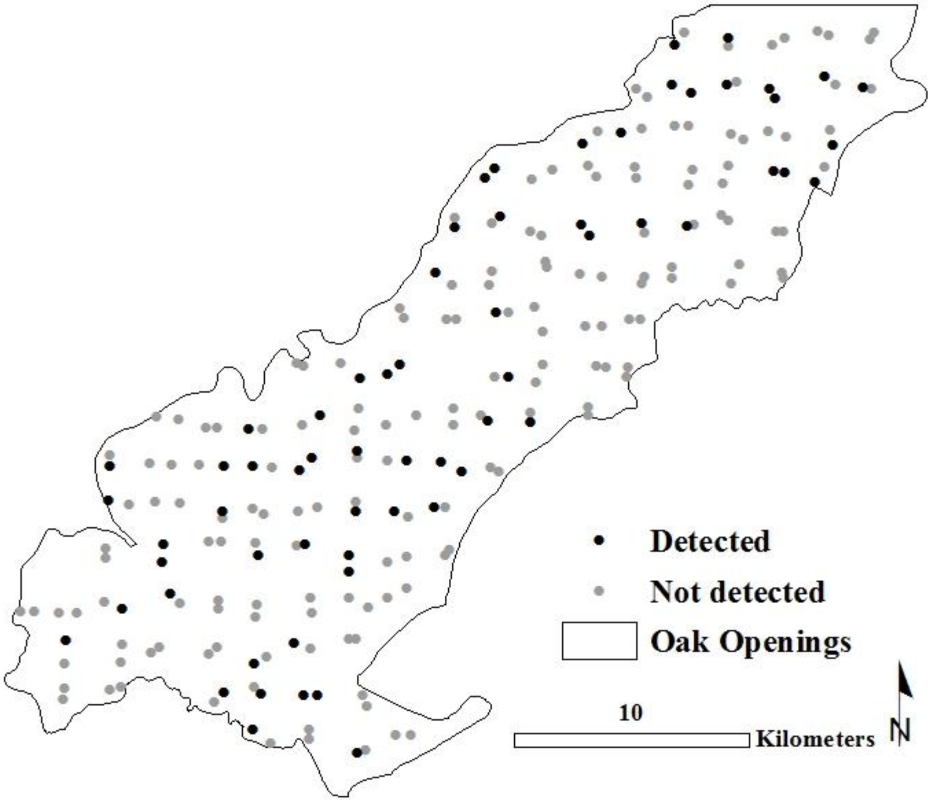

Figure 5.1. Locations of 230 sites (100-m point counts) used to sample the presence of Red-bellied Woodpecker in the Oak Openings Region of northwestern Ohio, USA, from 23 May to 2 July 2013.

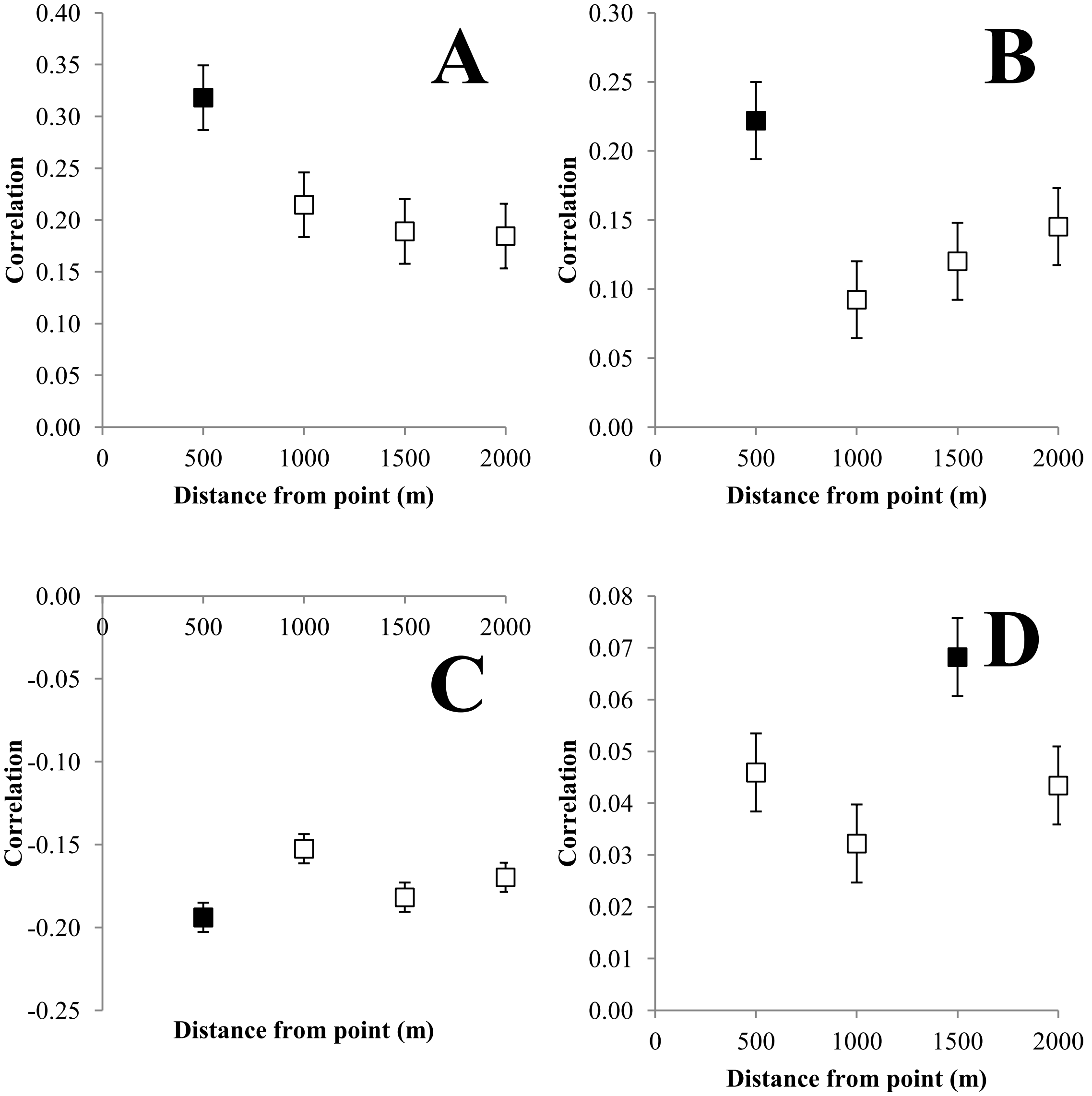

Figure 5.2. Spatial scales for habitat variables, (**A**) habitat amount, (**B**) habitat patch area, (**C**) habitat patch isolation, and (**D**) habitat structural diversity, selected to model Red-bellied Woodpecker occupancy (filled boxes) in the Oak Openings Region, Ohio, USA, from 23 May to 2 July 2013.

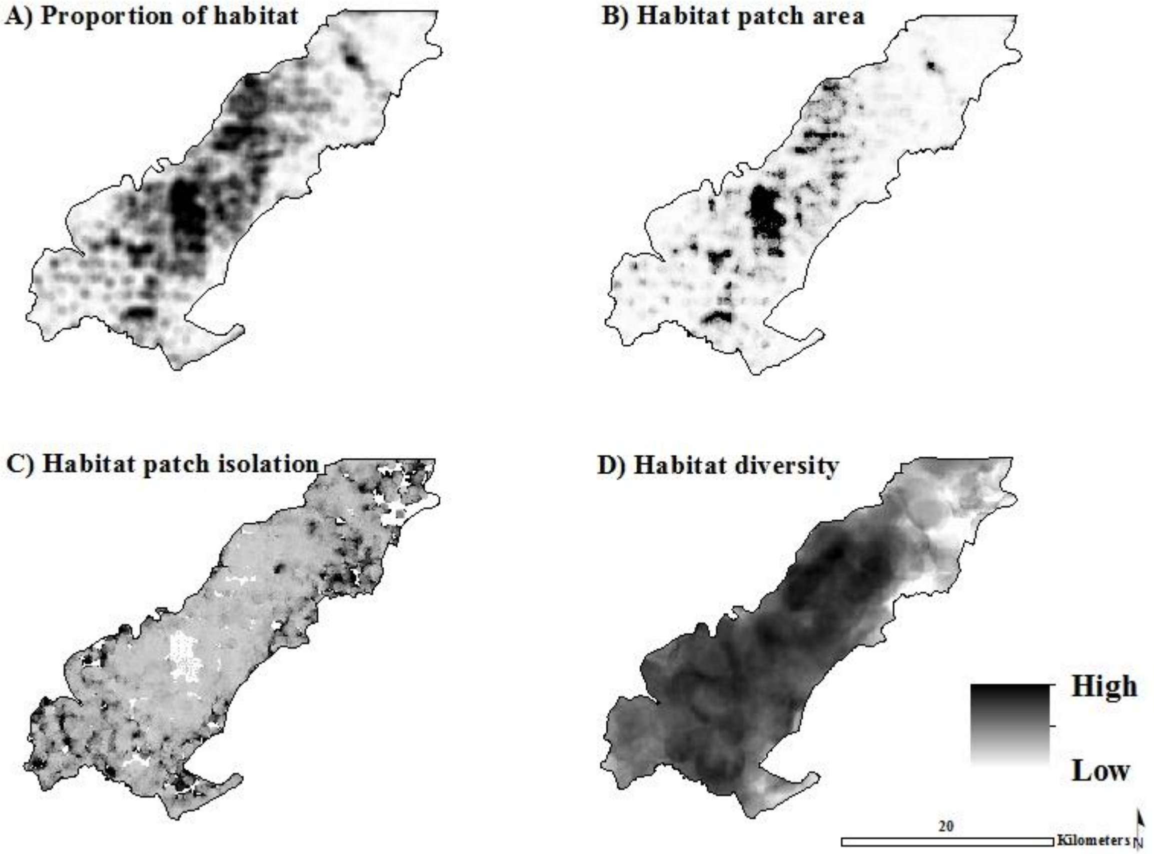

Figure 5.3. Distribution, low to high value, of habitat variables used to model breeding season occupancy of Red-bellied Woodpecker in the Oak Openings Region, Ohio, USA, from 23 May to 2 July 2013: (**A**) proportion of natural/seminatural landcover (500 m radius), (**B**) mean patch area (ha) of natural/seminatural land cover (500 m radius), (**C**) Euclidean mean nearest neighbor distance (m) of natural/seminatural land cover (500 m radius), and (**D**) Shannon's diversity of natural/seminatural land cover (1500 m radius).

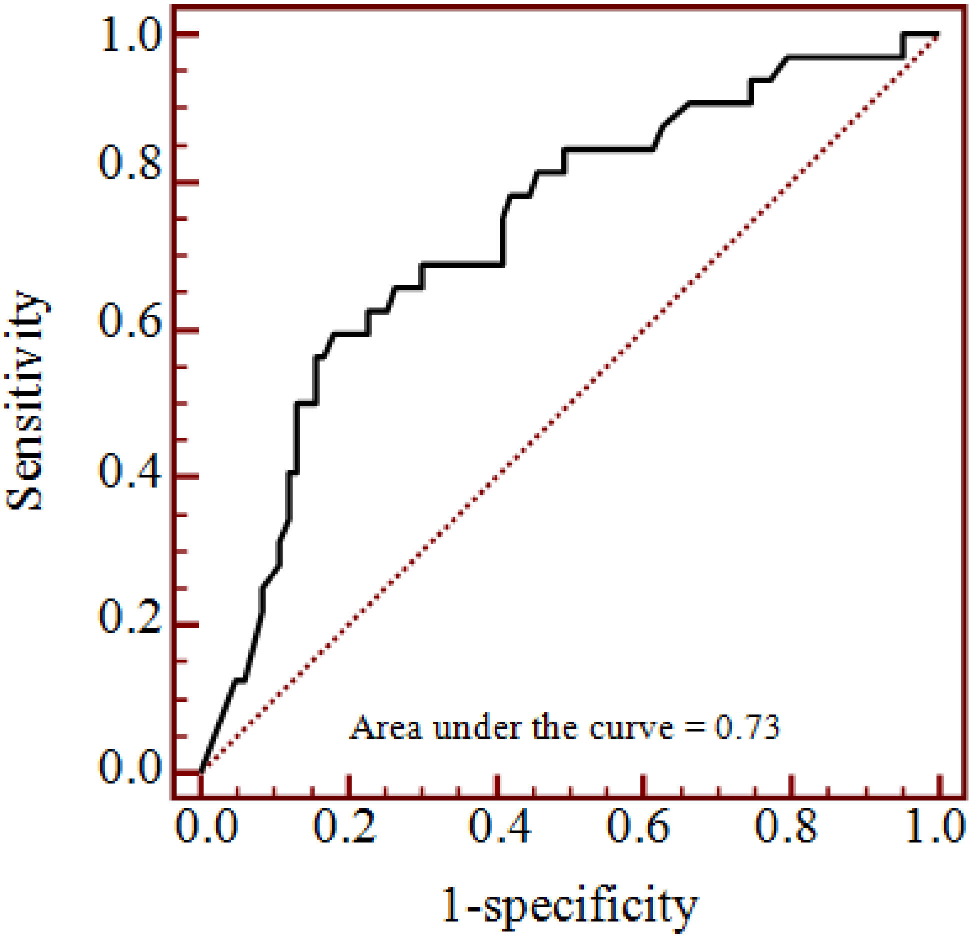

Figure 5.4. Receiver operating characteristic curve of validation sites (n = 115) of Red-bellied Woodpecker occupancy in the Oak Openings Region of northwestern Ohio, USA, from 23 May to 2 July 2013.

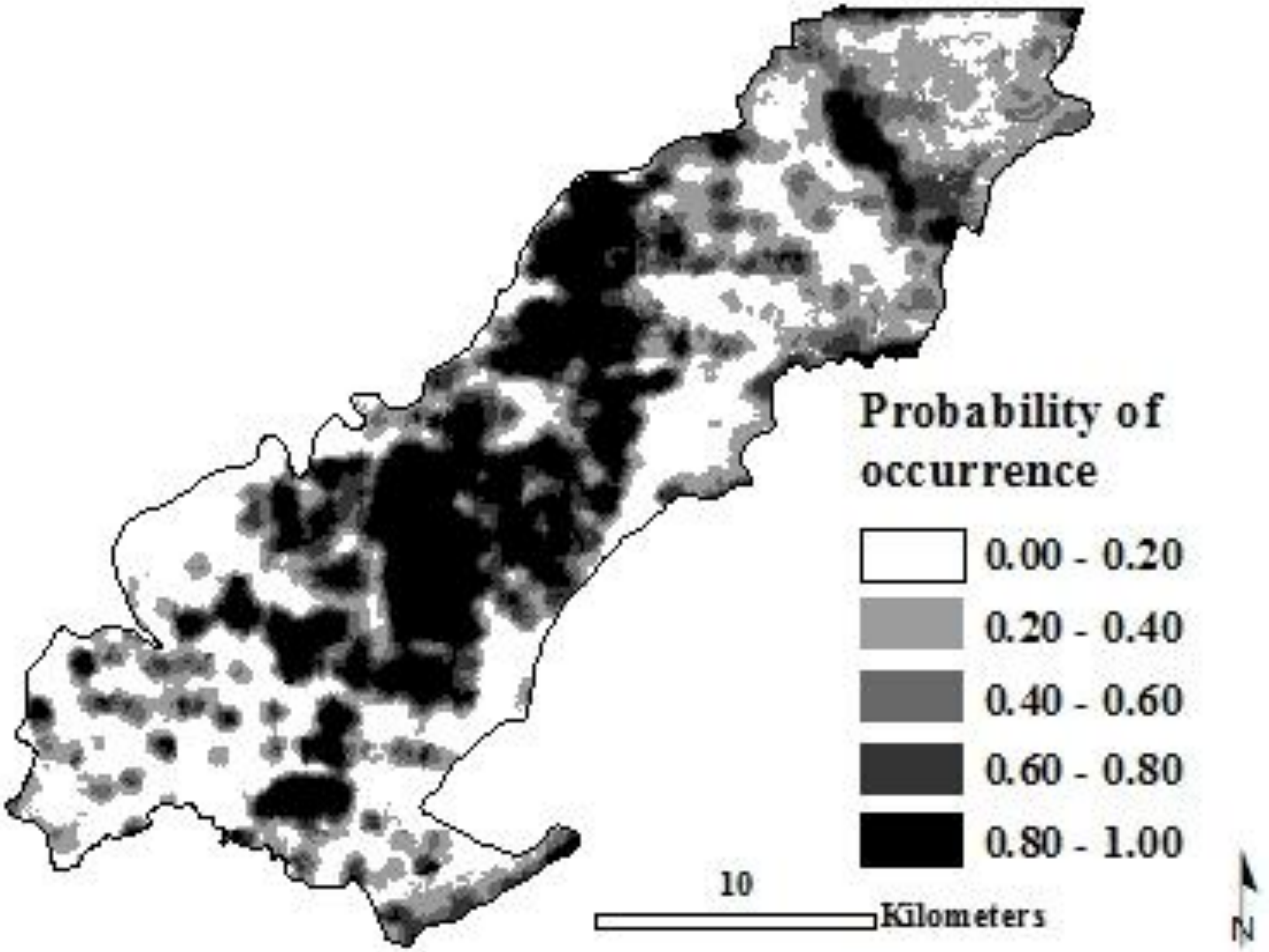

Figure 5.5. Predicted probability of breeding season occupancy of Red-bellied Woodpecker in the Oak Openings Region of northwestern Ohio, USA, from 23 May to 2 July 2013.

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CHAPTER 6: EXECUTIVE SUMMARY

"To build a better motor we tap the
uttermost power of the human
brain; to build a better countryside we
throw dice." Leopold (1933)

Aldo Leopold dedicated much of his work to small farmsteads in human-dominated landscapes and observed that the oldest task in human history was to live off the land sustainably (Leopold 1933). In human-dominated landscapes, anthropogenic land use change will continue to affect ecological communities through habitat loss, fragmentation, and matrix transitions; and these processes will interact simultaneously on species populations and at broad spatial scales often greater than those used in traditional research and management.

Biodiversity conservation requires detailed information on the responses of populations to these processes. Land use change will continue to occur with or without input from ecologists and conservation biologists. In this thesis I have examined the relative importance of habitat loss, fragmentation, and matrix quality on the breeding bird community of the Oak Openings Region of northwestern Ohio across multiple spatial scales. I have used advances in modeling techniques to incorporate the detection process in my work. I will review the objectives and findings of each chapter. I will then provide general conclusions from each chapter.

Chapter 2: Influences on midwestern breeding bird occupancy in a human-dominated landscape: matrix versus habitat

Objectives

1. Select a subset of my points to model the importance of matrix quality on patch-dependent species.
2. Account for detection bias in modeling occurrences of breeding birds.
3. Determine the best-fit spatial extent for model variables.

4. Examine the relative importance of matrix vs. habitat effects on occupancy dynamics of midwestern breeding birds in human-dominated landscapes.

Implications and Findings

1. Detection probabilities of species varied.
2. Species responded differently to spatial scale.
3. Landscape variables were more important than site-level variables in determining occurrences of several species of birds.
4. More species responded to matrix quality over habitat loss and fragmentation and the response was generally stronger for matrix quality.
5. Generalist species responded positively to deteriorating matrix quality.
6. Patch-dependent species responded negatively to deteriorating matrix quality.

Chapter 3: The relative importance of habitat structural diversity: Do rare habitats influence midwestern breeding bird diversity?

Objectives

1. Understand the influence of the diversity of land cover of the Oak Openings Region on diversity of the breeding bird community.
2. Calculate the diversity of breeding birds (i.e. species richness) at every point count location.
3. Model the relative influence of habitat loss, fragmentation, and structural diversity of habitat on 3 breeding bird guilds in the Oak Openings Region.
4. Account for scale-dependency in model variables.
5. Randomly select 50% of my data to build my model and use the remaining data to validate my model-based predictions.
6. Predict the spatial distribution of diversity across the entire Oak Openings Region using a Geographic Information System (GIS).

Implications and Findings

1. Each guild responded differently to the spatial scale of model variables.
2. Neotropical diversity responded strongest to habitat amount and secondarily to structural diversity of habitat.
3. Nearctic diversity responded strongest to fragmentation and secondarily to structural diversity.
4. Exotic diversity response was greatest for fragmentation and secondarily to habitat amount.
5. Neotropical and Nearctic species tended to respond positively to habitat amount and structural diversity of habitat and negatively to fragmentation, while exotic diversity responded negatively to habitat amount and positively to fragmentation and structural diversity.
6. Neotropical and Nearctic diversity were predicted to be greatest in the center of the region where large areas of natural habitat remain, and exotic diversity was predicted to be greatest in the southern and northern portions of the region where anthropogenic land use dominates the area.

Chapter 4: Does midwestern breeding bird occupancy in the urban center vary according to localized habitat amount and structural diversity?

Objectives

1. Understand the influence of fine-scale habitat on occurrences of breeding birds in the urban center of the Toledo Metropolitan Area, Ohio.
2. Account for detection bias in models.
3. Utilize a subset of my point count locations in Toledo.
4. Calculate fine-scale habitat attributes of each point count location.

5. Determine the importance of the proximity to large parks in the urban center on occurrences of breeding birds.

Implications and Findings

1. Species tended to respond positively to fine-scale habitat, structural diversity of habitat, and development.
2. Native species especially responded positively to habitat amount and structural diversity.
3. I detected a negative response of many species, including combining predictions of all native species, to proximity to large reserves.
4. Exotic species were predicted to occur in sites closer to large reserves.
5. The results indicate that fine-scale habitat amount and structural diversity may be a useful conservation tool in highly modified urban environments.

Chapter 5: Predicting the spatial distribution of Red-bellied Woodpecker as influenced by habitat loss and fragmentation

Objectives

1. Build a broad multi-scale, predictive model to determine the probability of presence of Red-bellied Woodpecker (*Melanerpes carolinus*) in the Oak Openings Region.
2. Validate the model with an independent data set.
3. Determine the scale most correlated between woodpecker presence and each habitat variable measured in buffers from 500 m to 2000 m at 500-m increments.
4. Use occupancy modeling to account for imperfect detection.
5. Apply my model within a GIS to produce a map of breeding season habitat suitability for woodpeckers in the Oak Openings Region.

Implications and Findings

1. Landscape habitat loss, fragmentation, and configuration all explained the occupancy of woodpecker.
2. Woodpecker presence was best explained by habitat loss and fragmentation in the 500-m buffer and structural diversity of habitat in the 1500-m buffer.
3. We applied our statistical model to an independent data set and it discriminated good with a receiver operating characteristic (ROC) area under the curve (AUC) value of 0.73.
4. Woodpecker occupancy was especially affected by fragmentation based on standardized partial regression coefficients.
5. Our map predicted woodpecker occupancy to be greatest in the center of the region where large core areas of habitat remain.

General Conclusions

The first technical chapter in my thesis (Chapter 2) followed the line inquiry in recent reviews of matrix-effects on wildlife (e.g., Driscoll et al. 2013). I hypothesized that matrix quality is more important than habitat effects (i.e. habitat loss and fragmentation) in determining spatial distributions of wildlife in human-dominated landscapes. My results indicated that more species responded the matrix quality over habitat loss and fragmentation and that the size of the response was generally greater for matrix quality. I also detected varying responses of species to matrix quality, with more generalists species responding positively to a deteriorating matrix and patch-dependent species responding negatively to a deteriorating matrix. This suggests that future changes in the matrix will influence biodiversity and spatial distributions of organisms in human-dominated landscapes.

Regarding the changes in bird life at the western end of Lake Erie in the last century, Mayfield (1989) describes the loss of many-disturbance dependent birds as a result of anthropogenic land use change. He suggested that losses in prairies and savannas were driving the loss of avian diversity in Northwest Ohio. Results from my Chapter 3 corroborate this sentiment. After considering habitat loss and fragmentation, my results indicated that the structural diversity of habitat, the distribution of area of different land cover types, was positively related to avian diversity in the Oak Openings Region. The landscape of the Oak Openings is highly heterogeneous in small globally unique ecological communities and the presence of these communities establishes a diverse array of potential breeding habitat for birds in the area.

In Chapter 4, I determined that fine-scale amounts of habitat and structural diversity of habitat corresponded to occurrences of many breeding bird species in the urban center. Interestingly, I found that for many native species, occupancy was negatively related to proximity to large reserves in the area. I also found that many species were positively associated with fine-scale levels of urban development, suggesting that some species were able to access and/or utilize supplemental resources provided by development. My results suggest that urban bird conservation may be augmented by the addition of fine-scale, diverse habitats in the urban center, instead of focusing on large contiguous reserves.

I utilized advances in modeling techniques to develop and validate a predictive distribution model of Red-bellied Woodpecker in the Oak Openings Region in Chapter 5. I determined that woodpecker occupancy was affected most strongly by the patch area of habitat and that occupancy was negatively related to patch area, suggesting that this species may be relatively sensitive to fragmentation. My model predicted that woodpecker occupancy would be greatest in the center of the region where large core areas of natural habitat remain.

Through my work I have demonstrated that matrix-effects are important determinants of occupancy patterns of patch-dependent species. I have also provided evidence that the diversity of the Oak Openings' breeding bird community is positively influenced by the diversity and presence of globally unique ecological communities in the region. In the urban center breeding bird occupancy was positively influenced by localized habitat amount and diversity. Thus, in conclusion, breeding bird conservation in this region should include efforts that minimize anthropogenic land use transitions in the matrix and increases in the connectivity and restoration of globally unique ecological communities endemic to this region.

"This quiet decline has proceeded
almost without notice in this area and
many others." Mayfield (1989)

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APPENDIX A: TOTAL SPECIES DETECTED FROM ALL SURVEYS

Table A.1. Numbers of bird species detected in the Oak Openings Region of northwestern Ohio, USA, from 23 May to 2 July 2013 from 230 randomized roadside point counts replicated twice (n = 460 surveys) ranked by number of detections <100 m. We do not report flyovers; including flyovers would add one additional species to the list: turkey vulture (*Cathartes aura*).

Common Name	Scientific Name	# <100 m	# Total
American Robin	*Turdus migratorius*	1002	1321
House Sparrow	*Passer domesticus*	825	1144
Northern Cardinal	*Cardinalis cardinalis*	445	605
Chipping Sparrow	*Spizella passerina*	396	536
Brown-headed Cowbird	*Molothrus ater*	324	343
Song Sparrow	*Melospiza melodia*	266	422
House Wren	*Troglodytes aedon*	265	373
European Starling	*Sturnus vulgaris*	263	281
Mourning Dove	*Zenaida macroura*	224	251
Blue Jay	*Cyanocitta cristata*	221	331
Common Grackle	*Quiscalus quiscula*	195	211
Red-winged Blackbird	*Agelaius phoeniceus*	171	316
Gray Catbird	*Dumetella carolinensis*	146	170
American Goldfinch	*Spinus tristis*	134	147
Tufted Titmouse	*Baeolophus bicolor*	122	173
Downy Woodpecker	*Picoides pubescens*	121	131
Cedar Waxwing	*Bombycilla cedrorum*	101	104
House Finch	*Haemorhous mexicanus*	98	124
Red-bellied Woodpecker	*Melanerpes carolinus*	93	145
Indigo Bunting	*Passerina cyanea*	92	167
Barn Swallow	*Hirundo rustica*	91	91
Black-capped Chickadee	*Poecile atricapillus*	89	111
Baltimore Oriole	*Icterus galbula*	86	108
Chimney Swift	*Chaetura pelagica*	84	84

Continued

Table A.1 Continued

Common Name	Scientific Name	# <100 m	# Total
Horned Lark	*Eremophila alpestris*	69	101
White-breasted Nuthatch	*Sitta carolinensis*	62	64
Eastern Bluebird	*Sialia sialis*	61	70
Eastern Wood-Pewee	*Contopus virens*	59	74
Purple Martin	*Progne subis*	56	56
American Crow	*Corvus brachyrhynchos*	55	269
Red-eyed Vireo	*Vireo olivaceus*	54	67
Blue-gray Gnatcatcher	*Polioptila caerulea*	38	39
Field Sparrow	*Spizella pusilla*	37	76
Common Yellowthroat	*Geothlypis trichas*	37	47
Eastern Kingbird	*Tyrannus tyrannus*	36	52
Warbling Vireo	*Vireo gilvus*	36	50
Carolina Wren	*Thryothorus ludovicianus*	36	46
Wood Thrush*	*Hylocichla mustelina*	32	40
Yellow Warbler	*Setophaga petechia*	29	34
Great Crested Flycatcher	*Myiarchus crinitus*	28	37
Northern Mockingbird	*Mimus polyglottos*	27	42
N. Rough-winged Swallow	*Stelgidopteryx serripennis*	23	23
Eastern Towhee	*Pipilo erythrophthalmus*	22	25
Canada Goose	*Branta canadensis*	19	27
Killdeer	*Charadrius vociferu*	18	42
Red-headed Woodpecker*	*Melanerpes erythrocephalus*	18	34
Tree Swallow	*Tachycineta bicolor*	18	18
Vesper Sparrow	*Pooecetes gramineus*	16	21
Eastern Phoebe	*Sayornis phoebe*	15	17
Ovenbird	*Seiurus aurocapilla*	15	16
Northern Flicker	*Colaptes auratus*	14	20
Scarlet Tanager	*Piranga olivacea*	13	14
Ruby-throated Hummingbird	*Archilochus colubris*	13	13
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	11	16
Savannah Sparrow	*Passerculus sandwichensis*	11	14
Yellow-billed Cuckoo	*Coccyzus americanus*	10	13
Brown Thrasher	*Toxostoma rufum*	10	11
Hairy Woodpecker	*Picoides villosus*	9	13
Willow Flycatcher*	*Empidonax traillii*	9	12

Continued

Table A.1 Continued

Common Name	Scientific Name	# <100 m	# Total
Yellow-throated Vireo	*Vireo flavifrons*	9	11
Acadian Flycatcher	*Empidonax virescens*	8	8
Pine Warbler	*Setophaga pinus*	7	7
Mallard	*Anas platyrhynchos*	6	8
Red-shouldered Hawk	*Buteo lineatus*	5	6
American Redstart	*Setophaga ruticilla*	5	5
Bank Swallow	*Riparia riparia*	5	5
Blue-winged Warbler*	*Vermivora cyanoptera*	5	5
Veery	*Catharus fuscescens*	5	5
Pileated Woodpecker	*Dryocopus pileatus*	4	8
Cooper’s Hawk	*Accipiter cooperii*	4	4
Orchard Oriole	*Icterus spurius*	3	5
Yellow-throated Warbler	*Setophaga dominica*	3	3
Eastern Meadowlark	*Sturnella magna*	2	5
Blackpoll Warbler	*Setophaga striata*	2	4
Swamp Sparrow	*Melospiza georgiana*	2	3
Broad-winged Hawk	*Buteo platypterus*	2	2
Chestnut-sided Warbler*	*Setophaga pensylvanica*	2	2
Great Blue Heron	*Ardea herodias*	2	2
Hooded Warbler*	*Setophaga citrina*	2	2
Lark Sparrow	*Chondestes grammacus*	2	2
Northern Parula	*Setophaga americana*	2	2
White-eyed Vireo	*Vireo griseus*	2	2
Wood Duck	*Aix sponsa*	2	2
Ring-necked Pheasant	Phasianus colchicus	1	13
Red-tailed Hawk	*Buteo jamaicensis*	1	5
Summer Tanager	*Piranga rubra*	1	2
Wild Turkey	*Meleagris gallopavo*	1	2
Yellow-breasted Chat	*Icteria virens*	1	2
Alder Flycatcher	*Empidonax alnorum*	1	1
Caspian Tern	*Hydroprogne caspia*	1	1
Eastern Screech-Owl	*Megascops asio*	1	1
Eurasian Collared-Dove	*Streptopelia decaocto*	1	1
Green Heron	*Butorides virescens*	1	1
Grasshopper Sparrow	*Ammodramus savannarum*	1	1

Continued

Table A.1 Continued

Common Name	Scientific Name	# <100 m	# Total
Ring-billed Gull	*Larus delawarensis*	1	1
Swainson's Thrush	*Catharus ustulatus*	1	1
Tennessee Warbler	*Oreothlypis peregrina*	1	1
Bald Eagle	*Haliaeetus leucocephalus*	0	1
Belted Kingfisher	*Megaceryle alcyon*	0	1
Rock Pigeon	*Columba livia*	0	1
	Total	6975	9346

*Partners in Flight regional species of conservation interest (Panjabi et al. 20112).

APPENDIX B: CORRELATION MATRIX OF OCCUPANCY PREDICTOR VARIABLES (CHAPTER 2)

Table B.1. Spearman's correlation coefficients among 3 predictor variables at the site-scale ($_S$) and 7 at the landscape-scale ($_L$) in spatial extents (500, 1000, 1500, 2000 m) surrounding each site used to characterize the amount and configuration of canopy habitat for 51 canopied 100-m point counts in the Oak Openings Region, Ohio, USA. Note: Only landscape-level variables were recalculated for the 4 spatial scales.

Scale	Variable	No. of structures$_S$	Proportion of natural understory$_S$	Patch cohesion of canopy$_L$	Edge density of canopy$_L$	Mean nearest neighbor dist.$_L$	Mean patch area of canopy$_L$	Density of canopy patches$_L$	Proportion of canopy$_L$	Road density$_L$
500 m	Proportion of canopy$_S$	-0.05	0.22	0.29	-0.02	0.08	0.21	-0.14	0.31	0.26
	No. of structures$_S$	1.00	-0.77	-0.18	0.79	-0.21	-0.50	0.57	-0.16	0.78
	Proportion of natural understory$_S$		1.00	0.30	-0.64	0.10	0.53	-0.59	0.25	-0.67
	Patch cohesion of canopy$_L$			1.00	-0.18	-0.46	0.82	-0.69	0.93	-0.13
	Edge density of canopy$_L$				1.00	-0.19	-0.57	0.68	-0.17	0.74
	Mean nearest neighbor dist.$_L$					1.00	-0.37	0.25	-0.48	-0.20
	Mean patch area of canopy$_L$						1.00	-0.96	0.81	-0.45
	Density of canopy patches$_L$							1.00	-0.64	0.55
	Proportion of canopy$_L$								1.00	-0.10

Continued

Table B.1 Continued

Scale	Variable	No. of structures$_S$	Proportion of natural understory$_S$	Patch cohesion of canopy$_L$	Edge density of canopy$_L$	Mean nearest neighbor dist.$_L$	Mean patch area of canopy$_L$	Density of canopy patches$_L$	Proportion of canopy$_L$	Road density$_L$
1000 m	Proportion of canopy$_S$	-0.05	0.22	0.18	0.06	-0.15	0.11	-0.08	0.26	0.15
	No. of structures$_S$	1.00	-0.77	-0.29	0.76	-0.31	-0.64	0.71	-0.33	0.78
	Proportion of natural understory$_S$		1.00	0.27	-0.65	0.25	0.52	-0.61	0.32	-0.69
	Patch cohesion of canopy$_L$			1.00	-0.16	-0.32	0.82	-0.69	0.90	-0.22
	Edge density of canopy$_L$				1.00	-0.49	-0.56	0.73	-0.16	0.85
	Mean nearest neighbor dist.$_L$					1.00	-0.04	-0.16	-0.49	-0.40
	Mean patch area of canopy$_L$						1.00	-0.95	0.82	-0.60
	Density of canopy patches$_L$							1.00	-0.64	0.70
	Proportion of canopy$_L$								1.00	-0.22

Continued

Table B.1 Continued

Scale	Variable	No. of structures$_S$	Proportion of natural understory$_S$	Patch cohesion of canopy$_L$	Edge density of canopy$_L$	Mean nearest neighbor dist.$_L$	Mean patch area of canopy$_L$	Density of canopy patches$_L$	Proportion of canopy$_L$	Road density$_L$
1500 m	Proportion of canopy$_S$	-0.05	0.22	0.20	0.08	-0.12	0.16	-0.11	0.30	0.13
	No. of structures$_S$	1.00	-0.77	-0.32	0.76	-0.56	-0.71	0.79	-0.38	0.78
	Proportion of natural understory$_S$		1.00	0.25	-0.66	0.54	0.55	-0.63	0.28	-0.68
	Patch cohesion of canopy$_L$			1.00	-0.15	-0.10	0.80	-0.64	0.88	-0.21
	Edge density of canopy$_L$				1.00	-0.81	-0.57	0.74	-0.13	0.87
	Mean nearest neighbor dist.$_L$					1.00	0.24	-0.44	-0.21	-0.73
	Mean patch area of canopy$_L$						1.00	-0.95	0.81	-0.61
	Density of canopy patches$_L$							1.00	-0.64	0.74
	Proportion of canopy$_L$								1.00	-0.18

Continued

Table B.1 Continued

Scale	Variable	No. of structures$_S$	Proportion of natural understory$_S$	Patch cohesion of canopy$_L$	Edge density of canopy$_L$	Mean nearest neighbor dist.$_L$	Mean patch area of canopy$_L$	Density of canopy patches$_L$	Proportion of canopy$_L$	Road density$_L$
2000 m	Proportion of canopy$_S$	-0.05	0.22	0.17	0.09	-0.20	0.08	-0.04	0.29	0.12
	No. of structures$_S$	1.00	-0.77	-0.41	0.72	-0.52	-0.76	0.81	-0.30	0.78
	Proportion of natural understory$_S$		1.00	0.28	-0.66	0.52	0.56	-0.62	0.16	-0.70
	Patch cohesion of canopy$_L$			1.00	-0.16	-0.07	0.79	-0.66	0.83	-0.21
	Edge density of canopy$_L$				1.00	-0.75	-0.59	0.74	0.03	0.88
	Mean nearest neighbor dist.$_L$					1.00	0.29	-0.46	-0.39	-0.73
	Mean patch area of canopy$_L$						1.00	-0.96	0.68	-0.62
	Density of canopy patches$_L$							1.00	-0.50	0.73
	Proportion of canopy$_L$								1.00	0.00

APPENDIX C: NUMBER OF SITES AND SPECIES DETECTED DURING MATRIX INVESTIGATION (CHAPTER 2)

Table C.1. Number of sites (100-m point count; n = 51) species detected for investigation of matrix vs. habitat-effects on midwestern breeding birds in the Oak Openings Region of northwestern Ohio from 23 May to 2 July 2013. Species ranked by number of sites detected.

Common Name	Scientific Name	# Sites
Northern Cardinal	*Cardinalis cardinalis*	48
American Robin	*Turdus migratorius*	46
Brown-headed Cowbird	*Molothrus ater*	37
House Wren	*Troglodytes aedon*	34
Downy Woodpecker	*Picoides pubescens*	33
Blue Jay	*Cyanocitta cristata*	31
Chipping Sparrow	*Spizella passerina*	28
Red-bellied Woodpecker	*Melanerpes carolinus*	26
Mourning Dove	*Zenaida macroura*	25
Gray Catbird	*Dumetella carolinensis*	24
Tufted Titmouse	*Baeolophus bicolor*	22
American Goldfinch	*Spinus tristis*	20
House Sparrow	*Passer domesticus*	20
Black-capped Chickadee	*Poecile atricapillus*	18
Song Sparrow	*Melospiza melodia*	18
White-breasted Nuthatch	*Sitta carolinensis*	18
Baltimore Oriole	*Icterus galbula*	17
Eastern Wood-Pewee	*Contopus virens*	17
European Starling	*Sturnus vulgaris*	16
Indigo Bunting	*Passerina cyanea*	14
Great Crested Flycatcher	*Myiarchus crinitus*	13
Common Grackle	*Quiscalus quiscula*	12
House Finch	*Haemorhous mexicanus*	12
Red-eyed Vireo	*Vireo olivaceus*	12
Carolina Wren	*Thryothorus ludovicianus*	11
Eastern Bluebird	*Sialia sialis*	10
Cedar Waxwing	*Bombycilla cedrorum*	9
Chimney Swift	*Chaetura pelagica*	9
American Crow	*Corvus brachyrhynchos*	8

Continued

Table C.1 Continued

Common Name	Scientific Name	# Sites
Blue-gray Gnatcatcher	*Polioptila caerulea*	8
Eastern Towhee	*Pipilo erythrophthalmus*	7
Field Sparrow	*Spizella pusilla*	7
Red-winged Blackbird	*Agelaius phoeniceus*	7
Wood Thrush	*Hylocichla mustelina*	7
Scarlet Tanager	*Piranga olivacea*	6
Eastern Phoebe	*Sayornis phoebe*	5
Ruby-throated Hummingbird	*Archilochus colubris*	5
Common Yellowthroat	*Geothlypis trichas*	4
Eastern Kingbird	*Tyrannus tyrannus*	4
Northern Flicker	*Colaptes auratus*	4
Warbling Vireo	*Vireo gilvus*	4
Mallard	*Anas platyrhynchos*	3
Ovenbird	*Seiurus aurocapilla*	3
Pine Warbler	*Setophaga pinus*	3
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	3
Red-headed Woodpecker	*Melanerpes erythrocephalus*	3
Red-shouldered Hawk	*Buteo lineatus*	3
Yellow-throated Vireo	*Vireo flavifrons*	3
Great Blue Heron	*Ardea herodias*	2
Hooded Warbler	*Setophaga citrina*	2
Yellow Warbler	*Setophaga petechia*	2
Acadian Flycatcher	*Empidonax virescens*	1
Alder Flycatcher	*Empidonax alnorum*	1
American Redstart	*Setophaga ruticilla*	1
Barn Swallow	*Hirundo rustica*	1
Blackpoll Warbler	*Setophaga striata*	1
Broad-winged Hawk	*Buteo platypterus*	1
Blue-winged Warbler	*Vermivora cyanoptera*	1
Chestnut-sided Warbler	*Setophaga pensylvanica*	1
Hairy Woodpecker	*Picoides villosus*	1
Horned Lark	*Eremophila alpestris*	1
Northern Parula	*Setophaga americana*	1
Orchard Oriole	*Icterus spurius*	1
Tree Swallow	*Tachycineta bicolor*	1
Wild Turkey	*Meleagris gallopavo*	1
Yellow-breasted Chat	*Icteria virens*	1
Yellow-throated Warbler	*Setophaga dominica*	1

APPENDIX D: SUMMARY OF MODEL RESULTS FOR DETECTION PROBABILITIES (CHAPTER 2)

Table D.1. Model results, including Akaike's Information Criterion adjusted for small sample size (AIC_c), relative difference in AIC_c to the top-ranked model (ΔAIC_c), AIC_c model weight (*wi*), the number of parameters in the model (*K*), and the -2 log-likelihood (-2LL) of the model, examining factors affecting detection probabilities with occupancy modeling of 25 bird species in the Oak Openings Region of northwestern Ohio, USA, from 23 May to 2 July 2013.

Species	Model	AIC_c	ΔAIC_c	w_i	*K*	-2LL
Mourning Dove	Global	120.48	0.00	0.10	5	122.48
	Day, temperature, wind	120.57	0.09	0.10	4	122.57
	Time, day, wind	120.65	0.17	0.10	4	122.65
	Day, wind	120.66	0.18	0.10	3	122.66
	Time, temperature, wind	120.97	0.49	0.08	4	122.97
	Temperature, wind	120.98	0.50	0.08	3	122.98
	Time, wind	121.02	0.54	0.08	3	123.02
	Wind	121.02	0.54	0.08	2	123.02
	Time, day, temperature	122.10	1.62	0.05	4	124.10
	Day, temperature	122.11	1.63	0.05	3	124.11
	Time, day	122.11	1.63	0.05	3	124.11
	Day	122.14	1.66	0.05	2	124.14
	Time, temperature	123.18	2.70	0.03	3	125.18
	Time	123.27	2.79	0.03	2	125.27
	Temperature	123.52	3.04	0.02	2	125.52
	Null	123.53	3.05	0.02	1	125.53
Red-bellied Woodpecker	Global	114.67	0.00	0.24	5	116.67
	Time, day, wind	114.67	0.00	0.24	4	116.67
	Time, day, temperature	116.28	1.61	0.11	4	118.28
	Day, temperature, wind	116.32	1.65	0.10	4	118.32
	Time, day	116.40	1.73	0.10	3	118.40
	Day, temperature	116.95	2.28	0.08	3	118.95
	Day, wind	117.59	2.92	0.06	3	119.59
	Day	118.16	3.49	0.04	2	120.16

Continued

Table D.1 Continued

Species	Model	AIC$_c$	ΔAIC$_c$	w_i	K	-2LL
	Time, temperature, wind	120.30	5.63	0.01	4	122.30
	Time, temperature	121.10	6.43	0.01	3	123.10
	Time, wind	121.61	6.94	0.01	3	123.61
	Time	121.83	7.16	0.01	2	123.83
	Temperature, wind	125.15	10.48	0.00	3	127.15
	Wind	125.20	10.53	0.00	2	127.20
	Temperature	125.27	10.60	0.00	2	127.27
	Null	125.31	10.64	0.00	1	127.31
Downy Woodpecker	Global	128.65	0.00	0.13	5	130.65
	Time, temperature, wind	128.65	0.00	0.13	4	130.65
	Day, temperature, wind	128.67	0.02	0.13	4	130.67
	Temperature, wind	128.68	0.03	0.13	3	130.68
	Time, day, temperature	129.03	0.38	0.11	4	131.03
	Time, temperature	129.08	0.43	0.11	3	131.08
	Day, temperature	129.15	0.50	0.10	3	131.15
	Temperature	129.30	0.65	0.10	2	131.30
	Time, day, wind	133.79	5.14	0.01	4	135.79
	Time, day	133.91	5.26	0.01	3	135.91
	Time, wind	134.58	5.93	0.01	3	136.58
	Time	134.59	5.94	0.01	2	136.59
	Day, wind	135.91	7.26	0.00	3	137.91
	Wind	136.45	7.80	0.00	2	138.45
	Day	136.49	7.84	0.00	2	138.49
	Null	136.73	8.08	0.00	1	138.73
Eastern Wood-Pewee	Global	98.43	0.00	0.09	5	100.43
	Time, day, wind	98.61	0.18	0.09	4	100.61
	Time, temperature, wind	98.80	0.37	0.08	4	100.80
	Time, day, temperature	98.84	0.41	0.08	4	100.84
	Time, day	98.95	0.52	0.07	3	100.95
	Time, temperature	99.08	0.65	0.07	3	101.08
	Day, wind	99.09	0.66	0.07	3	101.09
	Day, temperature, wind	99.09	0.66	0.07	4	101.09
	Time, wind	99.24	0.81	0.06	3	101.24
	Day	99.31	0.88	0.06	2	101.31
	Day, temperature	99.31	0.88	0.06	3	101.31

Continued

Table D.1 Continued

Species	Model	AIC$_c$	ΔAIC$_c$	w_i	K	-2LL
	Time	99.40	0.97	0.06	2	101.40
	Temperature, wind	100.19	1.76	0.04	3	102.19
	Temperature	100.21	1.78	0.04	2	102.21
	Wind	100.23	1.80	0.04	2	102.23
	Null	100.25	1.82	0.04	1	102.25
Great Crested Flycatcher	Global	77.80	0.00	0.09	5	79.80
	Time, temperature, wind	77.80	0.00	0.09	4	79.80
	Time, day, temperature	77.83	0.03	0.09	4	79.83
	Time, temperature	77.84	0.04	0.09	3	79.84
	Time, day, wind	78.43	0.63	0.07	4	80.43
	Time, day	78.49	0.69	0.07	3	80.49
	Time, wind	78.57	0.77	0.06	3	80.57
	Time	78.75	0.95	0.06	2	80.75
	Day, temperature, wind	78.85	1.05	0.05	4	80.85
	Temperature, wind	78.94	1.14	0.05	3	80.94
	Day, wind	78.96	1.16	0.05	3	80.96
	Day, temperature	79.04	1.24	0.05	3	81.04
	Day	79.14	1.34	0.05	2	81.14
	Wind	79.16	1.36	0.05	2	81.16
	Temperature	79.30	1.50	0.04	2	81.30
	Null	79.59	1.79	0.04	1	81.59
Red-eyed Vireo	Global	73.98	0.00	0.25	5	75.98
	Time, day, temperature	74.17	0.19	0.23	4	76.17
	Day, temperature, wind	76.25	2.27	0.08	4	78.25
	Day, temperature	76.33	2.35	0.08	3	78.33
	Time, temperature, wind	76.38	2.40	0.08	4	78.38
	Temperature, wind	77.68	3.70	0.04	3	79.68
	Time, day, wind	78.33	4.35	0.03	4	80.33
	Day, wind	78.39	4.41	0.03	3	80.39
	Time, temperature	78.47	4.49	0.03	3	80.47
	Time, day	78.61	4.63	0.03	3	80.61
	Time, wind	78.61	4.63	0.03	3	80.61
	Wind	78.62	4.64	0.03	2	80.62
	Temperature	78.79	4.81	0.02	2	80.79
	Day	78.84	4.86	0.02	2	80.84

Continued

Table D.1 Continued

Species	Model	AIC_c	ΔAIC_c	w_i	K	-2LL
	Time	79.54	5.56	0.02	2	81.54
	Null	79.66	5.68	0.01	1	81.66
Blue Jay	Global	122.75	0.00	0.29	5	124.75
	Time, day, wind	122.93	0.18	0.26	4	124.93
	Day, temperature, wind	125.01	2.26	0.09	4	127.01
	Day, wind	125.13	2.38	0.09	3	127.13
	Time, day, temperature	125.45	2.70	0.07	4	127.45
	Time, day	125.46	2.71	0.07	3	127.46
	Day, temperature	126.51	3.76	0.04	3	128.51
	Day	126.69	3.94	0.04	2	128.69
	Time, temperature, wind	129.30	6.55	0.01	4	131.30
	Time, wind	129.93	7.18	0.01	3	131.93
	Temperature, wind	130.05	7.30	0.01	3	132.05
	Wind	131.77	9.02	0.00	2	133.77
	Time, temperature	132.27	9.52	0.00	3	134.27
	Temperature	132.35	9.60	0.00	2	134.35
	Time	133.64	10.89	0.00	2	135.64
	Null	134.36	11.61	0.00	1	136.36
Black-capped Chickadee	Global	95.65	0.00	0.10	5	97.65
	Day, temperature, wind	95.65	0.00	0.10	4	97.65
	Time, day, wind	95.68	0.03	0.10	4	97.68
	Day, wind	95.70	0.05	0.10	3	97.70
	Time, day, temperature	95.77	0.12	0.10	4	97.77
	Time, day	95.78	0.13	0.10	3	97.78
	Day, temperature	95.79	0.14	0.10	3	97.79
	Day	95.84	0.19	0.09	2	97.84
	Time, temperature, wind	97.89	2.24	0.03	4	99.89
	Temperature, wind	98.07	2.42	0.03	3	100.07
	Time, wind	98.14	2.49	0.03	3	100.14
	Wind	98.19	2.54	0.03	2	100.19
	Time, temperature	98.32	2.67	0.03	3	100.32
	Temperature	98.75	3.10	0.02	2	100.75
	Time	98.79	3.14	0.02	2	100.79
	Null	98.96	3.31	0.02	1	100.96
Tufted Titmouse	Global	108.88	0.00	0.17	5	110.88

Continued

Table D.1 Continued

Species	Model	AIC$_c$	ΔAIC$_c$	w_i	K	-2LL
	Day, temperature, wind	109.07	0.19	0.15	4	111.07
	Time, day, wind	109.37	0.49	0.13	4	111.37
	Day, wind	109.37	0.49	0.13	3	111.37
	Time, day, temperature	110.01	1.13	0.10	4	112.01
	Day, temperature	110.08	1.20	0.09	3	112.08
	Time, day	110.54	1.66	0.07	3	112.54
	Day	110.58	1.70	0.07	2	112.58
	Time, temperature, wind	112.97	4.09	0.02	4	114.97
	Time, temperature	113.35	4.47	0.02	3	115.35
	Temperature, wind	114.27	5.39	0.01	3	116.27
	Temperature	114.38	5.50	0.01	2	116.38
	Time, wind	115.74	6.86	0.01	3	117.74
	Wind	115.94	7.06	0.00	2	117.94
	Time	115.95	7.07	0.00	2	117.95
	Null	116.05	7.17	0.00	1	118.05
White-breasted Nuthatch	Global	94.92	0.00	0.08	5	96.92
	Time, day, wind	94.93	0.01	0.08	4	96.93
	Day, wind	94.95	0.03	0.08	3	96.95
	Day, temperature, wind	94.95	0.03	0.08	4	96.95
	Time, day, temperature	95.44	0.52	0.07	4	97.44
	Time, day	95.48	0.56	0.06	3	97.48
	Day, temperature	95.59	0.67	0.06	3	97.59
	Day	95.59	0.67	0.06	2	97.59
	Time, temperature, wind	95.72	0.80	0.06	4	97.72
	Temperature, wind	95.73	0.81	0.06	3	97.73
	Time, wind	95.80	0.88	0.05	3	97.80
	Wind	95.80	0.88	0.05	2	97.80
	Time, temperature	96.02	1.10	0.05	3	98.02
	Temperature	96.03	1.11	0.05	2	98.03
	Time	96.04	1.12	0.05	2	98.04
	Null	96.08	1.16	0.05	1	98.08
House Wren	Global	130.66	0.00	0.15	5	132.66
	Time, temperature, wind	130.67	0.01	0.15	4	132.67
	Time, day, temperature	131.43	0.77	0.10	4	133.43
	Time, temperature	131.52	0.86	0.10	3	133.52

Continued

Table D.1 Continued

Species	Model	AIC$_c$	ΔAIC$_c$	w_i	K	-2LL
	Day, temperature, wind	132.08	1.42	0.08	4	134.08
	Temperature, wind	132.26	1.60	0.07	3	134.26
	Time, day, wind	132.43	1.77	0.06	4	134.43
	Day, wind	132.85	2.19	0.05	3	134.85
	Time, wind	133.11	2.45	0.05	3	135.11
	Day, temperature	133.57	2.91	0.04	3	135.57
	Wind	133.57	2.91	0.04	2	135.57
	Time, day	133.58	2.92	0.04	3	135.58
	Temperature	134.12	3.46	0.03	2	136.12
	Day	134.38	3.72	0.02	2	136.38
	Time	134.93	4.27	0.02	2	136.93
	Null	135.93	5.27	0.01	1	137.93
Carolina Wren	Global	63.36	0.00	0.11	5	65.36
	Time, day, temperature	63.36	0.00	0.11	4	65.36
	Day, temperature, wind	63.55	0.19	0.10	4	65.55
	Day, temperature	63.57	0.21	0.10	3	65.57
	Time, temperature, wind	64.09	0.73	0.08	4	66.09
	Time, temperature	64.12	0.76	0.08	3	66.12
	Temperature, wind	64.13	0.77	0.08	3	66.13
	Temperature	64.14	0.78	0.07	2	66.14
	Time, day	64.32	0.96	0.07	3	66.32
	Time, day, wind	64.32	0.96	0.07	4	66.32
	Day, wind	65.29	1.93	0.04	3	67.29
	Day	65.37	2.01	0.04	2	67.37
	Time, wind	66.99	3.63	0.02	3	68.99
	Time	67.23	3.87	0.02	2	69.23
	Wind	67.70	4.34	0.01	2	69.70
	Null	67.76	4.40	0.01	1	69.76
American Robin	Global	101.60	0.00	0.13	5	103.60
	Time, day, temperature	101.60	0.00	0.13	4	103.60
	Time, temperature	101.62	0.02	0.13	3	103.62
	Time, temperature, wind	101.62	0.02	0.13	4	103.62
	Day, temperature, wind	101.94	0.34	0.11	4	103.94
	Temperature, wind	101.95	0.35	0.11	3	103.95
	Day, temperature	102.02	0.42	0.11	3	104.02

Continued

Table D.1 Continued

Species	Model	AIC$_c$	ΔAIC$_c$	w_i	K	-2LL
	Temperature	102.05	0.45	0.11	2	104.05
	Time, day, wind	107.22	5.62	0.01	4	109.22
	Time, day	107.33	5.73	0.01	3	109.33
	Day, wind	107.65	6.05	0.01	3	109.65
	Day	107.67	6.07	0.01	2	109.67
	Time, wind	109.12	7.52	0.00	3	111.12
	Wind	109.34	7.74	0.00	2	111.34
	Time	109.53	7.93	0.00	2	111.53
	Null	109.60	8.00	0.00	1	111.60
Gray Catbird	Global	116.57	0.00	0.13	5	118.57
	Day, temperature, wind	116.58	0.01	0.13	4	118.58
	Time, day, temperature	117.26	0.69	0.09	4	119.26
	Day, temperature	117.28	0.71	0.09	3	119.28
	Time, day, wind	117.57	1.00	0.08	4	119.57
	Time, temperature, wind	117.93	1.36	0.06	4	119.93
	Time, day	118.03	1.46	0.06	3	120.03
	Temperature, wind	118.03	1.46	0.06	3	120.03
	Day, wind	118.05	1.48	0.06	3	120.05
	Time, wind	118.26	1.69	0.05	3	120.26
	Day	118.76	2.19	0.04	2	120.76
	Wind	118.82	2.25	0.04	2	120.82
	Time, temperature	119.32	2.75	0.03	3	121.32
	Time	119.38	2.81	0.03	2	121.38
	Temperature	119.91	3.34	0.02	2	121.91
	Null	120.47	3.90	0.02	1	122.47
European Starling	Global	82.40	0.00	0.20	5	84.40
	Time, day, wind	82.48	0.08	0.19	4	84.48
	Day, temperature, wind	82.63	0.23	0.17	4	84.63
	Day, wind	83.27	0.87	0.13	3	85.27
	Time, day	83.83	1.43	0.10	3	85.83
	Time, day, temperature	83.83	1.43	0.10	4	85.83
	Day, temperature	84.44	2.04	0.07	3	86.44
	Day	84.97	2.57	0.05	2	86.97
	Time, temperature, wind	95.33	12.93	0.00	4	97.33
	Temperature, wind	95.90	13.50	0.00	3	97.90

Continued

Table D.1 Continued

Species	Model	AIC$_c$	ΔAIC$_c$	w_i	K	-2LL
	Time, wind	95.92	13.52	0.00	3	97.92
	Wind	96.01	13.61	0.00	2	98.01
	Time, temperature	96.45	14.05	0.00	3	98.45
	Time	96.45	14.05	0.00	2	98.45
	Temperature	96.47	14.07	0.00	2	98.47
	Null	96.48	14.08	0.00	1	98.48
Chipping Sparrow	Global	121.77	0.00	0.14	5	123.77
	Time, day, temperature	121.77	0.00	0.14	4	123.77
	Time, temperature, wind	122.01	0.24	0.12	4	124.01
	Time, temperature	122.05	0.28	0.12	3	124.05
	Time, day, wind	122.68	0.91	0.09	4	124.68
	Time, day	122.71	0.94	0.09	3	124.71
	Time, wind	123.21	1.44	0.07	3	125.21
	Time	123.61	1.84	0.05	2	125.61
	Day, temperature, wind	124.14	2.37	0.04	4	126.14
	Temperature, wind	124.15	2.38	0.04	3	126.15
	Day, temperature	124.29	2.52	0.04	3	126.29
	Temperature	124.30	2.53	0.04	2	126.30
	Day, wind	127.47	5.70	0.01	3	129.47
	Day	127.51	5.74	0.01	2	129.51
	Null	127.68	5.91	0.01	1	129.68
	Wind	127.68	5.91	0.01	2	129.68
Song Sparrow	Global	97.25	0.00	0.12	5	99.25
	Time, day, temperature	97.34	0.09	0.11	4	99.34
	Day, temperature, wind	97.53	0.28	0.10	4	99.53
	Day, temperature	97.59	0.34	0.10	3	99.59
	Time, temperature, wind	98.00	0.75	0.08	4	100.00
	Temperature, wind	98.07	0.82	0.08	3	100.07
	Time, temperature	98.25	1.00	0.07	3	100.25
	Temperature	98.27	1.02	0.07	2	100.27
	Time, day, wind	99.65	2.40	0.04	4	101.65
	Time, wind	99.69	2.44	0.03	3	101.69
	Day, wind	99.70	2.45	0.03	3	101.70
	Wind	99.76	2.51	0.03	2	101.76
	Time, day	99.80	2.55	0.03	3	101.80

Continued

Table D.1 Continued

Species	Model	AIC_c	ΔAIC_c	w_i	K	-2LL
	Time	99.89	2.64	0.03	2	101.89
	Day	99.90	2.65	0.03	2	101.90
	Null	100.04	2.79	0.03	1	102.04
Northern Cardinal	Global	91.43	0.00	0.17	5	93.43
	Time, temperature, wind	92.54	1.11	0.10	4	94.54
	Time, day, temperature	92.60	1.17	0.09	4	94.60
	Time, day, wind	92.72	1.29	0.09	4	94.72
	Time, wind	93.09	1.66	0.07	3	95.09
	Day, temperature, wind	93.64	2.21	0.06	4	95.64
	Time, day	93.69	2.26	0.05	3	95.69
	Day, wind	93.86	2.43	0.05	3	95.86
	Day, temperature	93.96	2.53	0.05	3	95.96
	Temperature, wind	94.09	2.66	0.05	3	96.09
	Wind	94.14	2.71	0.04	2	96.14
	Day	94.24	2.81	0.04	2	96.24
	Time, temperature	94.38	2.95	0.04	3	96.38
	Time	94.58	3.15	0.04	2	96.58
	Temperature	94.88	3.45	0.03	2	96.88
	Null	94.91	3.48	0.03	1	96.91
Indigo Bunting	Global	86.07	0.00	0.10	5	88.07
	Time, temperature, wind	86.08	0.01	0.10	4	88.08
	Time, day, wind	86.12	0.05	0.10	4	88.12
	Time, wind	86.20	0.13	0.09	3	88.20
	Time, day, temperature	86.25	0.18	0.09	4	88.25
	Time, day	86.28	0.21	0.09	3	88.28
	Time, temperature	86.35	0.28	0.09	3	88.35
	Time	86.54	0.47	0.08	2	88.54
	Day, temperature, wind	87.61	1.54	0.05	4	89.61
	Day, temperature	87.65	1.58	0.04	3	89.65
	Temperature, wind	87.86	1.79	0.04	3	89.86
	Temperature	87.88	1.81	0.04	2	89.88
	Day, wind	88.65	2.58	0.03	3	90.65
	Day	88.66	2.59	0.03	2	90.66
	Wind	88.66	2.59	0.03	2	90.66
	Null	88.67	2.60	0.03	1	90.67

Continued

Table D.1 Continued

Species	Model	AIC$_c$	ΔAIC$_c$	w_i	K	-2LL
Common Grackle	Global	73.57	0.00	0.21	5	75.57
	Time, day, temperature	74.15	0.58	0.16	4	76.15
	Day, temperature, wind	75.50	1.93	0.08	4	77.50
	Day, temperature	75.51	1.94	0.08	3	77.51
	Time, day, wind	75.63	2.06	0.08	4	77.63
	Time, day	75.66	2.09	0.07	3	77.66
	Time, temperature, wind	76.08	2.51	0.06	4	78.08
	Day, wind	76.29	2.72	0.05	3	78.29
	Day	76.39	2.82	0.05	2	78.39
	Time, temperature	76.44	2.87	0.05	3	78.44
	Time, wind	78.21	4.64	0.02	3	80.21
	Time	78.24	4.67	0.02	2	80.24
	Temperature, wind	78.37	4.80	0.02	3	80.37
	Wind	78.88	5.31	0.01	2	80.88
	Temperature	78.92	5.35	0.01	2	80.92
	Null	79.66	6.09	0.01	1	81.66
Brown-headed Cowbird	Global	126.56	0.00	0.44	5	128.56
	Time, temperature, wind	127.90	1.34	0.22	4	129.90
	Time, day, temperature	129.58	3.02	0.10	4	131.58
	Time, temperature	130.00	3.44	0.08	3	132.00
	Time, day, wind	130.41	3.85	0.06	4	132.41
	Time, day	132.27	5.71	0.03	3	134.27
	Time, wind	133.30	6.74	0.02	3	135.30
	Time	133.90	7.34	0.01	2	135.90
	Day, temperature, wind	133.96	7.40	0.01	4	135.96
	Day, wind	134.09	7.53	0.01	3	136.09
	Day, temperature	134.77	8.21	0.01	3	136.77
	Day	134.91	8.35	0.01	2	136.91
	Temperature, wind	136.05	9.49	0.00	3	138.05
	Temperature	136.15	9.59	0.00	2	138.15
	Wind	136.66	10.10	0.00	2	138.66
	Null	136.72	10.16	0.00	1	138.72
Baltimore Oriole	Global	90.53	0.00	0.18	5	92.53
	Time, day, wind	90.93	0.40	0.15	4	92.93
	Time, day, temperature	91.19	0.66	0.13	4	93.19

Continued

Table D.1 Continued

Species	Model	AIC$_c$	ΔAIC$_c$	w_i	K	-2LL
	Day, temperature, wind	91.54	1.01	0.11	4	93.54
	Day, temperature	91.81	1.28	0.10	3	93.81
	Time, day	91.88	1.35	0.09	3	93.88
	Day, wind	92.55	2.02	0.07	3	94.55
	Day	93.02	2.49	0.05	2	95.02
	Time, temperature, wind	94.26	3.73	0.03	4	96.26
	Temperature, wind	94.39	3.86	0.03	3	96.39
	Time, wind	94.99	4.46	0.02	3	96.99
	Wind	95.71	5.18	0.01	2	97.71
	Time, temperature	96.30	5.77	0.01	3	98.30
	Temperature	96.45	5.92	0.01	2	98.45
	Time	98.16	7.63	0.00	2	100.16
	Null	98.18	7.65	0.00	1	100.18
House Finch	Global	69.43	0.00	0.11	5	71.43
	Time, temperature, wind	69.82	0.39	0.09	4	71.82
	Time, day, temperature	69.88	0.45	0.09	4	71.88
	Day, temperature, wind	70.08	0.65	0.08	4	72.08
	Time, temperature	70.13	0.70	0.08	3	72.13
	Day, temperature	70.29	0.86	0.07	3	72.29
	Time, day, wind	70.71	1.28	0.06	4	72.71
	Day, wind	70.76	1.33	0.06	3	72.76
	Temperature, wind	70.85	1.42	0.06	3	72.85
	Temperature	70.89	1.46	0.05	2	72.89
	Time, day	70.91	1.48	0.05	3	72.91
	Day	70.92	1.49	0.05	2	72.92
	Time, wind	71.75	2.32	0.04	3	73.75
	Time	71.78	2.35	0.03	2	73.78
	Wind	71.88	2.45	0.03	2	73.88
	Null	71.89	2.46	0.03	1	73.89
American Goldfinch	Global	103.92	0.00	0.07	5	105.92
	Day, temperature, wind	103.94	0.02	0.07	4	105.94
	Time, day, wind	103.96	0.04	0.07	4	105.96
	Day, wind	104.05	0.13	0.07	3	106.05
	Day, temperature	104.06	0.14	0.07	3	106.06
	Time, day, temperature	104.06	0.14	0.07	4	106.06

Continued

Table D.1 Continued

Species	Model	AIC$_c$	ΔAIC$_c$	w_i	K	-2LL
	Time, day	104.12	0.20	0.06	3	106.12
	Day	104.17	0.25	0.06	2	106.17
	Time, temperature, wind	104.20	0.28	0.06	4	106.20
	Time, wind	104.20	0.28	0.06	3	106.20
	Time, temperature	104.27	0.35	0.06	3	106.27
	Time	104.28	0.36	0.06	2	106.28
	Temperature, wind	104.31	0.39	0.06	3	106.31
	Wind	104.33	0.41	0.06	2	106.33
	Temperature	104.34	0.42	0.06	2	106.34
	Null	104.36	0.44	0.06	1	106.36
House Sparrow	Global	91.39	0.00	0.07	5	93.39
	Day, temperature, wind	91.39	0.00	0.07	4	93.39
	Time, day, wind	91.41	0.02	0.07	4	93.41
	Time, temperature, wind	91.43	0.04	0.07	4	93.43
	Day, wind	91.43	0.04	0.07	3	93.43
	Temperature, wind	91.44	0.05	0.07	3	93.44
	Time, wind	91.45	0.06	0.07	3	93.45
	Wind	91.47	0.08	0.07	2	93.47
	Time, day, temperature	91.71	0.32	0.06	4	93.71
	Time, temperature	91.73	0.34	0.06	3	93.73
	Day, temperature	91.79	0.40	0.06	3	93.79
	Temperature	91.80	0.41	0.06	2	93.80
	Time, day	91.84	0.45	0.06	3	93.84
	Time	91.85	0.46	0.06	2	93.85
	Day	91.86	0.47	0.06	2	93.86
	Null	91.87	0.48	0.05	1	93.87

APPENDIX E: NUMBER OF SITES AND SPECIES DETECTED DURING URBAN INVESTIGATION (CHAPTER 4)

Table E.1. Number of sites (100-m point count; n = 65) species detected for urban investigation of local habitat-effects on midwestern breeding birds in the Toledo Metropolitan Area, Ohio, USA, from 23 May to 2 July 2013. Species ranked by number of sites detected.

Common Name	Scientific Name	# Sites
American Robin	*Turdus migratorius*	65
Northern Cardinal	*Cardinalis cardinalis*	59
House Sparrow	*Passer domesticus*	52
House Wren	*Troglodytes aedon*	49
Brown-headed Cowbird	*Molothrus ater*	45
Chipping Sparrow	*Spizella passerina*	41
Mourning Dove	*Zenaida macroura*	40
Blue Jay	*Cyanocitta cristata*	38
European Starling	*Sturnus vulgaris*	36
Downy Woodpecker	*Picoides pubescens*	34
American Goldfinch	*Spinus tristis*	32
Common Grackle	*Quiscalus quiscula*	30
House Finch	*Haemorhous mexicanus*	26
Red-bellied Woodpecker	*Melanerpes carolinus*	19
Chimney Swift	*Chaetura pelagica*	18
Song Sparrow	*Melospiza melodia*	17
Black-capped Chickadee	*Poecile atricapillus*	16
White-breasted Nuthatch	*Sitta carolinensis*	15
Tufted Titmouse	*Baeolophus bicolor*	13
Gray Catbird	*Dumetella carolinensis*	11
Baltimore Oriole	*Icterus galbula*	10
Eastern Wood-Pewee	*Contopus virens*	9
Carolina Wren	*Thryothorus ludovicianus*	9
Red-winged Blackbird	*Agelaius phoeniceus*	8
Cedar Waxwing	*Bombycilla cedrorum*	8

Continued

Table E.1 Continued

Common Name	Scientific Name	# Sites
Ruby-throated Hummingbird	*Archilochus colubris*	7
Great Crested Flycatcher	*Myiarchus crinitus*	6
Eastern Bluebird	*Sialia sialis*	6
American Crow	*Corvus brachyrhynchos*	6
Red-eyed Vireo	*Vireo olivaceus*	5
Indigo Bunting	*Passerina cyanea*	5
Mallard	*Anas platyrhynchos*	4
Barn Swallow	*Hirundo rustica*	3
Cooper's Hawk	*Accipiter cooperii*	2
Wood Thrush	*Hylocichla mustelina*	2
Northern Flicker	*Colaptes auratus*	2
Eastern Phoebe	*Sayornis phoebe*	2
Blue-gray Gnatcatcher	*Polioptila caerulea*	2
Yellow Warbler	*Setophaga petechia*	1
Yellow-throated Warbler	*Setophaga dominica*	1
Warbling Vireo	*Vireo gilvus*	1
Vesper Sparrow	*Pooecetes gramineus*	1
Savannah Sparrow	*Passerculus sandwichensis*	1
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	1
Killdeer	*Charadrius vociferus*	1
Horned Lark	*Eremophila alpestris*	1
Hairy Woodpecker	*Picoides villosus*	1
Great Blue Heron	*Ardea herodias*	1
Caspian Tern	*Hydroprogne caspia*	1
Canada Goose	*Branta canadensis*	1
Broad-winged Hawk	*Buteo platypterus*	1