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Author(s): Sarah C. Schneider and James R. Miller

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RESEARCH ARTICLE

Response of avian communities to invasive vegetation in urban forest fragments

Sarah C. Schneider¹ and James R. Miller^{1,2*}

¹ Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Champaign, Illinois, USA

² Program in Ecology, Evolution, and Conservation Biology, University of Illinois at Urbana-Champaign, Champaign, Illinois, USA

* Corresponding author: jmillr@illinois.edu

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ABSTRACT

Proliferation of invasive plants in forest understories throughout North America has prompted restoration efforts focused on removal of invasive vegetation. Although the negative impacts of invasives on native plant communities are well documented, effects on forest bird communities remain largely unknown. To address this issue, we examined the response of avian communities to invasive plants in forest fragments across 4 counties in northeastern Illinois, a region characterized by extensive urbanization. We surveyed breeding bird communities in 46 forest plots representing a gradient in abundance of invasive woody plants. We quantified vegetation structure and composition within plots, as well as landscape context. Exotic trees and shrubs were present on all but 3 plots. Although native trees were common, native species represented <7% of total stem density of shrubs. Measures of invasion were weakly correlated with those representing urbanization, yet broad-scale measures of urbanization such as building density and urban cover were strongly associated with avian community structure. At finer scales, measures of invasion were important predictors of the relative abundance of birds in several nesting and foraging guilds. Shrub nesters showed a positive response to invasive vegetation, whereas the relative abundance of aerial salliers and ground nesters decreased with increased proportions of invasive trees. Because restoration strategies aimed at the complete removal of invasive shrubs could diminish habitat quality for some species, thinning of understory vegetation or the removal of invasive trees may confer the greatest benefits to avian communities when few native understory plants are present.

Keywords: avian communities, forest fragments, habitat selection, invasive plants, urbanization

Respuesta de las comunidades de aves a la vegetación invasora en fragmentos urbanos de bosque

RESUMEN

La proliferación de plantas invasoras en el sotobosque de bosques en todo Norte América ha promovido esfuerzos de restauración que se enfocan en la remoción de la vegetación invasora. Aunque los impactos negativos de las plantas invasoras sobre las comunidades nativas de plantas están bien documentados, sus efectos sobre las comunidades de aves de bosque aún no son bien conocidos. Para abordar este tema, examinamos la respuesta de las comunidades de aves a las plantas invasoras en fragmentos de bosque a través de cuatro condados en el nordeste de Illinois, EEUU, una región caracterizada por urbanización extensiva. Hicimos censos de comunidades de aves en 46 parcelas de bosque que representaban un gradiente en la abundancia de plantas leñosas invasoras. Cuantificamos la estructura y composición de la vegetación en las parcelas, así como el contexto del paisaje. Los árboles y arbustos exóticos estuvieron presentes en todas las parcelas, con excepción de tres de ellas. Aunque las especies nativas fueron comunes, representaron menos del 7% de la densidad total de tallos de arbustos. Las medidas de invasión estuvieron débilmente correlacionadas con las medidas de urbanización, aunque las medidas de urbanización a gran escala como la densidad de edificios y la cobertura urbana estuvieron fuertemente asociadas con la estructura de las comunidades de aves. A escalas más finas, las medidas de invasión fueron predictores importantes de la abundancia relativa de aves en varios gremios de anidación y de alimentación. Los anidantes de arbustos mostraron una respuesta positiva a la vegetación invasora, mientras que la abundancia relativa de aves que cazan presas en el aire y de anidantes de piso disminuyó con el incremento en la proporción de árboles invasores. Debido a que las estrategias de restauración que apuntan a la remoción completa de arbustos invasores podrían disminuir la calidad del hábitat de algunas especies, la poda de la vegetación invasora o la remoción de los árboles invasores podría conferir el mayor beneficio para las comunidades de aves cuando hay poca presencia de plantas nativas de sotobosque.

Palabras clave: comunidades de aves, fragmentos de bosque, plantas invasoras, selección de hábitat, urbanización

INTRODUCTION

Negative impacts of exotic invasive species on ecosystem function and biodiversity have emerged as top conservation issues (Wilcove et al. 1998, Pimentel et al. 2000). Recently, some ecologists have advocated that conservationists base management decisions on the environmental effects of exotic species rather than on their origins (Davis et al. 2011), because the ecological impacts of exotics are not exclusively negative. For example, some exotic plants may have positive effects on native vertebrate species via habitat modification (e.g., exotic shrubs can provide cover or nesting structure for birds) or the provisioning of additional food in resource-limited habitats (e.g., frugivores and omnivores can benefit from the fruit provided by exotic vegetation; Reichard et al. 2001). Considerable resources are spent on the eradication of invasive species as part of ecological restoration programs (Pimentel et al. 2000), yet the consequences of these actions are not always well understood.

There is a growing debate within the conservation community regarding potential positive and negative consequences associated with removal of exotic species (Schlaepfer et al. 2011, Rodewald 2012, Simberloff et al. 2013). For instance, some scientists have cautioned against removal of honeysuckle (*Lonicera* spp.) because it could negatively affect frugivorous bird populations (Gleditsch and Carlo 2011), while others assert that this exotic shrub may adversely affect bird species of conservation concern (Rodewald 2012). Eradication of invasives is often accompanied by restoration of native vegetation, but this strategy may not always be feasible because some native plants are not able to persist in soils that have been altered by exotic vegetation (Heneghan et al. 2006, Pavao-Zuckerman 2008). If land managers are to assess potential costs and benefits associated with eradication of exotic plants, a better understanding of the consequences of biological invasions and the removal of exotics is needed.

In North America, studies focusing on the impacts of invasive plants on avian communities have largely been restricted to impacts of saltcedar (*Tamarix* spp.) in riparian areas (Hunter et al. 1988, Ellis 1995, Frost and Powell 2011), exotic herbaceous plants in grasslands (Wilson and Belcher 1989, Sutter and Brigham 1998, Flanders et al. 2006), and ornamental plants in suburban landscapes (Germaine et al. 1998, Burghardt et al. 2008). Results of these investigations show that avian species richness (Ellis 1995, Burghardt et al. 2008, Frost and Powell 2011), diversity (Hunter et al. 1988, Burghardt et al. 2008), and abundance (Hunter et al. 1988, Ellis 1995, Flanders et al. 2006, Burghardt et al. 2008) tend to be highest in areas that lack exotic vegetation. Arthropod abundance is also higher in areas where exotics are absent (Flanders et al. 2006,

Burghardt et al. 2008), which suggests that invasive plants may reduce food availability for birds.

Research on the impacts of invasive plants on birds in forest habitats has largely been limited to effects on breeding in a few species. Three bird species nesting in honeysuckle experienced higher rates of nest predation, likely due to lower nest heights, the absence of sharp thorns, and branch architecture that could facilitate access to nests by predators (Borgmann and Rodewald 2004, Schmidt and Whelan 1999). Honeysuckle may act as an ecological trap because this shrub may be preferentially selected for nesting because of its early leaf flush (Schmidt and Whelan 1999, Rodewald et al. 2010). However, knowledge of the effects of exotic plant invasions on non-shrub-nesting birds remains limited, and a community-wide perspective is lacking.

We quantified avian community structure (i.e. the number of species and their relative abundances) in forest remnants in the Chicago metropolitan area with varying amounts of invasive vegetation. Specifically, we addressed the following questions: How do measures of invasive vegetation correlate with avian community structure? How do particular avian guilds and individual species respond to exotic vegetation? Finally, how do the effects of exotic vegetation on birds compare in magnitude to those associated with other local and landscape characteristics?

METHODS

Study Area

We conducted fieldwork on public land in Cook, Lake, DuPage, and McHenry counties in the Chicago metropolitan area (Figure 1). Characteristic native tree species in the region include oak (*Quercus* spp.), hickory (*Carya* spp.), elm (*Ulmus* spp.), and ash (*Fraxinus* spp.). Historically, these forests were subjected to frequent fires that maintained open stands characterized by relatively low levels of structural diversity (Sullivan 2011). With settlement in the early 1800s came fire suppression, which facilitated the successful invasion of nonnative shrubs (Sullivan 2011). These invasive plants can shade out native understory plants and prevent regeneration of native tree species (Knight et al. 2007). Because invasion by exotic shrubs is quite pervasive throughout northeastern Illinois, a primary restoration strategy in Chicago's forest remnants has been the removal of these species (Heneghan et al. 2012).

Exotic shrub species in the region include multiflora rose (*Rosa multiflora*), honeysuckle, and European buckthorn (*Rhamnus cathartica*). Multiflora rose is a thorny shrub that was introduced from Asia to the United States several times during the past 200 yr (Rehder 1936). Invasive bush honeysuckle was first introduced from Eurasia during the mid-1700s as an ornamental and had

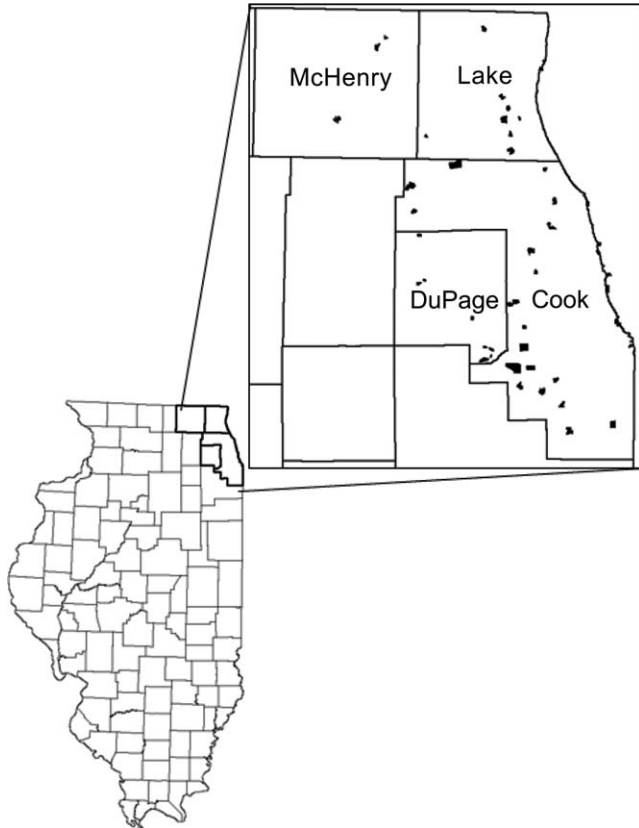


FIGURE 1. Forest fragments ($n = 34$) in which 46 study plots were embedded within 4 counties in northeastern Illinois, USA, 2010–2011.

spread across the eastern United States by the mid-1900s (Pringle 1973, Luken and Thieret 1996). Honeysuckle and multiflora rose are arching shrubs, whereas buckthorn is a spiny shrub or small tree that grows erect to 6 m in height (Gleason and Cronquist 1991). Also native to Eurasia, buckthorn was introduced to North America as an ornamental in the early 1800s (Heimpel et al. 2010) and has since become naturalized throughout much of the Upper Midwest and northeastern United States, displacing native flora (Kurylo et al. 2007). Buckthorn is the dominant exotic shrub in northeastern Illinois and also the most common tree species in the Chicago metropolitan area (McPherson et al. 1997).

Site Selection

We selected 46 study plots in 34 forest remnants to represent a gradient of exotic stem density. Although some fragments were heavily invaded, with exotic vegetation throughout, a few remained relatively uninvaded, and others comprising a mosaic of exotic patches and patches in which invasive plants had been removed at varying time intervals (L. Umek personal communication). Management practices differed by county and by site but typically

involved a combination of cutting, herbicide application, and prescribed burning. The size of woodland fragments in which the study plots were embedded ranged from 8 to 619 ha (mean \pm SD = 96 ± 111.6).

Thirty-five of the plots were originally included in an ongoing study of the effectiveness of biodiversity management practices in the Chicago metropolitan area (Henehan et al. 2012). As part of that study, these plots were assessed by land managers and allocated to one of four restoration categories ranging from degraded to high quality. However, variation in invasion levels among plots within these categories led us to adopt a gradient approach based on a continuous measure of the degree of invasion by woody plants. In addition, we added 11 new plots with varying levels of invasion. Although there were multiple plots within some forest remnants, all plot centers were ≥ 400 m apart and represented different management categories in a given remnant. Further, all plot centers were ≥ 50 m from the nearest nonforest edge.

Bird Surveys

We surveyed bird communities 3 times annually between late May and early July in 2010 and 2011, using standard point-count methodology (Ralph et al. 1993). We conducted 10-min point counts on clear mornings between sunrise and 0930 hours (Hanowski and Niemi 1995). Start times were randomized so that each point was surveyed during different hours of the morning. During each survey, we recorded all birds (excluding waterfowl, raptors, gulls, and shorebirds) seen or heard within 50 m of plot center. We used 50 m as a cutoff for bird observations because of the small size of a few fragments and to maximize the probability that avian habitat use was associated with the vegetation measured at the plot (Martin et al. 1997). Surveys were conducted by 2 observers each year, and observers rotated among points to minimize potential observer bias. Prior to each field season, observers underwent a week-long training period to sharpen identification skills.

Vegetation Surveys

Vegetation survey methods were adapted from the BBIRD field protocol (Martin et al. 1997). During the summers of 2010 and 2011, vegetation was measured at 4 sampling locations nested within each plot: 1 at plot center and 3 located 30 m from plot center. The cardinal direction of the first of these latter plots was chosen at random, and the other 2 were placed at 120° in either direction. At plot center, we used a spherical crown densiometer to estimate canopy cover (Lemmon 1956). At each sampling location, we measured vegetation within a 5-m-radius and an 11.3-m-radius subplot.

In each 5-m subplot, all woody stems >1 m in height were identified to genus or species. Woody plants were

classified as shrubs if the diameter at breast height was <7 cm, and otherwise as trees. Shrub cover was estimated visually. To quantify overall groundcover, we randomly placed a 1×1 m quadrat in each of the 5-m subplots and estimated percent grass, forb, litter, and bare ground using the Braun-Blanquet cover abundance scale (Ralph et al. 1993). Increased leaf litter is important for ground-nesting birds because it may improve nest concealment, thus reducing nest predation rates (Mattsson and Niemi 2006). Ground-foraging birds may also benefit from increased leaf litter through positive associations with macroinvertebrate abundance and diversity (Haskell 2000). In each 11.3-m subplot, we counted the total number of trees by species and snags. Snag density was included because standing dead trees not only provide nesting habitat for many cavity nesting birds, but also support different insect species than live trees, potentially affecting bark foraging species (Anderson 1960). All but 2 vegetation measurements were taken in both years. Trees were identified to species during the summer of 2011, and invasive-shrub stem density was measured in 2010. Because no management actions occurred during the course of the study, we assumed that these measures essentially remained constant over the 2-yr period.

Landscape Variables

Landscape composition surrounding each plot was quantified using 2009 high-resolution (0.3 m) satellite imagery obtained from the World Imagery basemap in ArcGIS version 10 (ESRI, Redlands, California, USA). Within 1 km of plot center, we calculated building density (buildings ha^{-1}) and the percentages of forest, agricultural, and urban cover. We delineated forest remnants in which the plots were embedded and calculated the perimeter of each remnant (m) and total contiguous forested area (ha). We also measured the distance between each plot center and the nearest forest edge (m).

Statistical Analyses

Prior to data analysis, we removed environmental variables that were redundant or strongly correlated ($r > 0.70$). Canopy cover was not included because it showed little variation among sites (range: 78–99%, mean \pm SD = 92.53 ± 5.56). We restricted analyses to bird species that typically breed in the region, on the basis of a literature review (Poole 2005). Because there were no interannual effects on bird abundance (paired $t = 1.72$, $P = 0.09$), we pooled abundance data across years. Relative abundance was calculated as the number of individuals detected at a plot averaged over all visits in both years (Nur et al. 1999).

We conducted a Mantel test (Mantel 1967) in PC-ORD version 6 (McCune and Mefford 2011) to determine whether plots that were closer together were more likely to have similar bird communities. Bray-Curtis distance was

used as the measure of ecological dissimilarity, because of its ability to identify ecological gradients (Faith et al. 1987) and because it is less sensitive to differences among rare species. A probability value was derived from 10,000 Monte Carlo simulations.

To examine the dissimilarity of avian communities among forest plots, we conducted an unconstrained distance-based ordination, nonmetric multidimensional scaling (NMDS; Kruskal 1964), using PC-ORD (McCune and Mefford 2011). NMDS is an iterative procedure that is particularly robust to non-normal data, is less prone to spurious results, and has fewer restrictive assumptions than other multivariate methods (Minchin 1987). NMDS graphically arranges samples in ordination space using a measure of dissimilarity (Faith et al. 1987) and a single data matrix composed of the relative abundances of all species detected at each study plot. Points located close together in ordination space represent plots with similar avian community structure. As in the Mantel test, we used Bray-Curtis distance as the ecological dissimilarity measure. In NMDS, goodness-of-fit is measured by the stress value, which is used to determine the number of dimensions needed to adequately portray the sample units in ordination space and to indicate how well the configuration matches the data (Kruskal 1964). To assess how avian community structure was related to environmental variables, we used the vector-fitting procedure in PC-ORD. Vector-fitting maximizes the linear correlation between an explanatory variable and the NMDS axes (Kantvilas and Minchin 1989).

To examine the distribution of individual species in ordination space, we derived correlations of species abundances with ordination axes (Gleditsch and Carlo 2011). Correlation coefficients that expressed both the linear (Pearson's r) and rank (Kendall's τ) relationships between the species and ordination axes (McCune and Grace 2002) were calculated for the 20 most abundant species. Typically, ecologically meaningful relationships have a Kendall's τ value greater than 0.25 or less than -0.25 (McCune and Mefford 2011). These correlations were compared with those of the environmental vectors to gain a better understanding of species-specific responses to measures of invasive vegetation.

To examine the relationship between environmental variables and the foraging and nesting guilds that we assumed were most likely to be influenced by exotic plant invasions, we conducted nonparametric multiplicative regression (NPMR) analyses using HyperNiche version 2.0 (McCune 2011), following Grundel and Pavlovic (2007). Species were assigned to mutually exclusive nesting or foraging guilds based on their life-history characteristics (Ehrlich et al. 1988, Poole 2005; Table 1). We used a subset of environmental variables based on a priori hypotheses

TABLE 1. Observed bird species used in analyses and their foraging and nesting guilds. Guild classifications are based on avian life-history traits and a literature review (Ehrlich et al. 1988, Poole 2005).

Species	Foraging guild	Nesting guild
Mourning Dove (<i>Zenaida macroura</i>)	Ground forager	Tree
Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)	Foliage gleaner	Tree
Red-headed Woodpecker (<i>Melanerpes erythrocephalus</i>)	Aerial sallier	Cavity
Red-bellied Woodpecker (<i>M. carolinus</i>)	Bark forager	Cavity
Downy Woodpecker (<i>Picoides pubescens</i>)	Bark forager	Cavity
Hairy Woodpecker (<i>P. villosus</i>)	Bark forager	Cavity
Northern Flicker (<i>Colaptes auratus</i>)	Ground forager	Cavity
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	Bark forager	Cavity
Eastern Wood-Pewee (<i>Contopus virens</i>)	Aerial sallier	Tree
Acadian Flycatcher (<i>Empidonax vireescens</i>)	Aerial sallier	Tree
Willow Flycatcher (<i>E. traillii</i>)	Aerial sallier	Shrub
Least Flycatcher (<i>E. minimus</i>)	Aerial sallier	Tree
Eastern Phoebe (<i>Sayornis phoebe</i>)	Aerial sallier	Human structures
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	Aerial sallier	Cavity
White-eyed Vireo (<i>Vireo griseus</i>)	Foliage gleaner	Shrub
Yellow-throated Vireo (<i>V. flavifrons</i>)	Foliage gleaner	Tree
Warbling Vireo (<i>V. gilvus</i>)	Foliage gleaner	Tree
Red-eyed Vireo (<i>V. olivaceus</i>)	Foliage gleaner	Tree
Blue Jay (<i>Cyanocitta cristata</i>)	Ground forager	Tree
American Crow (<i>Corvus brachyrhynchos</i>)	Ground forager	Tree
Black-capped Chickadee (<i>Poecile atricapillus</i>)	Foliage gleaner	Cavity
Tufted Titmouse (<i>Baeolophus bicolor</i>)	Foliage gleaner	Cavity
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	Bark forager	Cavity
House Wren (<i>Troglodytes aedon</i>)	Foliage gleaner	Cavity
Carolina Wren (<i>Thryothorus ludovicianus</i>)	Ground forager	Cavity
Blue-gray Gnatcatcher (<i>Polioptila caerulea</i>)	Foliage gleaner	Tree
Veery (<i>Catharus fuscescens</i>)	Ground forager	Ground
Wood Thrush (<i>Hylocichla mustelina</i>)	Ground forager	Tree
American Robin (<i>Turdus migratorius</i>)	Ground forager	Tree
Gray Catbird (<i>Dumetella carolinensis</i>)	Ground forager	Shrub
European Starling (<i>Sturnus vulgaris</i>)	Ground forager	Cavity
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	Foliage gleaner	Tree
Ovenbird (<i>Seiurus aurocapilla</i>)	Ground forager	Ground
Blue-winged Warbler (<i>Vermivora cyanoptera</i>)	Foliage gleaner	Ground
Black-and-white Warbler (<i>Mniotilta varia</i>)	Bark forager	Ground
Prothonotary Warbler (<i>Protonotaria citrea</i>)	Foliage gleaner	Cavity
Kentucky Warbler (<i>Geothlypis formosa</i>)	Ground forager	Ground
Common Yellowthroat (<i>G. trichas</i>)	Foliage gleaner	Shrub
Hooded Warbler (<i>Setophaga citrina</i>)	Foliage gleaner	Shrub
American Redstart (<i>S. ruticilla</i>)	Foliage gleaner	Tree
Cerulean Warbler (<i>S. cerulea</i>)	Foliage gleaner	Tree
Yellow Warbler (<i>S. petechia</i>)	Foliage gleaner	Shrub
Chestnut-sided Warbler (<i>S. pensylvanica</i>)	Foliage gleaner	Shrub
Yellow-breasted Chat (<i>Icteria virens</i>)	Foliage gleaner	Shrub
Eastern Towhee (<i>Pipilo erythrophthalmus</i>)	Ground forager	Ground
Chipping Sparrow (<i>Spizella passerina</i>)	Ground forager	Shrub
Field Sparrow (<i>S. pusilla</i>)	Ground forager	Ground
Song Sparrow (<i>Melospiza melodia</i>)	Ground forager	Shrub
Scarlet Tanager (<i>Piranga olivacea</i>)	Foliage gleaner	Tree
Northern Cardinal (<i>Cardinalis cardinalis</i>)	Ground forager	Shrub
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	Foliage gleaner	Tree
Indigo Bunting (<i>Passerina cyanea</i>)	Foliage gleaner	Shrub
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	Ground forager	Shrub
Common Grackle (<i>Quiscalus quiscula</i>)	Ground forager	Tree
Brown-headed Cowbird (<i>Molothrus ater</i>)	Ground forager	Tree
Baltimore Oriole (<i>Icterus galbula</i>)	Foliage gleaner	Tree
American Goldfinch (<i>Spinus tristis</i>)	Foliage gleaner	Shrub

TABLE 2. Local and landscape-level variables used in analyses of forest bird community structure on our study area in northeastern Illinois, USA, 2010–2011.

Variable description	Variable code	Mean	Range
Local			
Percent honeysuckle cover	HONEY_COV	5.6	0–78.7
Invasive-shrub stem density (stems ha ⁻¹)	INV_STEM	5,392.9	0–17,953.6
Percentage of trees that are buckthorn	BUCK_TREE	14.9	0–84.9
Percentage of trees that are oak	OAK_TREE	34.8	0–87.5
Tree density (trees ha ⁻¹)	TREE_DEN	407.7	59.86–2,062.8
Snag density (snags ha ⁻¹)	SNAG_DEN	40.1	0–174.5
Percent bare ground	AVG_BG	12.7	2.50–50.6
Percent litter cover	AVG_LITTER	40.9	2.50–87.5
Landscape			
Distance to nearest edge (m)	EDGE_DIST	156.9	54.0–375.0
Forest fragment area (ha)	FOREST_AREA	95.5	8.0–619.0
Percent agricultural cover (within 1 km)	AG_COV	4.1	0–45.9
Percent forest cover (within 1 km)	FOREST_COV	41.6	11.4–72.3
Percent urban cover (within 1 km)	URBAN_COV	37.4	1.2–88.1
Building density (number of buildings ha ⁻¹)	BUILD_DEN	1.3	0–8.4

regarding factors that might influence the distribution of each guild.

NPMR has been used in a variety of plant (Engelbrecht et al. 2007, Casazza et al. 2008) and animal studies (Grundel and Pavlovic 2007, Miller et al. 2007). This technique has the ability to model nonlinear relationships, automatically consider potential interactions among environmental variables, and combine the effects of explanatory variables multiplicatively as opposed to additively (McCune 2011). Models derived with this method tend to be more parsimonious and provide better fit than other methods (McCune 2011). NPMR uses the data to specify model form with a local multiplicative smoothing function and a leave-one-out cross-validation, unlike traditional methods that adopt a global model to determine the value of coefficients with a mathematical equation (McCune 2006). We used a local mean estimator and Gaussian kernel weighting function in a stepwise procedure, wherein data points closer to the target point in environmental space are given greater weight. We assessed model quality and fit with a cross-validated R^2 (xR^2) and conducted a sensitivity analysis to assess the relative importance of particular predictors within a selected model (McCune 2006). We examined contour graphs to understand how the independent variables changed in response to the 2 most important variables (i.e. those with the highest sensitivities) selected in the “best” model (i.e. the model with the highest xR^2). Habitat variables can be non-normally distributed (e.g., Grundel and Pavlovic 2007), and a major strength of the NPMR contour graphs is that they explicitly depict the range over which sufficient data are available to make predictions. See McCune (2011) for a more detailed explanation of NPMR.

RESULTS

Environmental Variables

Invasive woody plants were present on all but 3 of the study plots, each having recently been the focus of management actions. Buckthorn was present on 37 (80%) of the plots and was the most common tree species, representing 23% of all trees. The native white oak (*Quercus alba*) followed, representing 11.4% of all trees. Buckthorn was also the most dominant invasive shrub, representing 52.5% of the total stem density of exotic shrubs. Honeysuckle and multiflora rose were also prevalent, representing 22.0% and 22.8% of invasive-shrub stem density, respectively. Nearly 18,000 exotic invasive stems were present on just 1 plot. Invasive shrubs were ubiquitous, but native understory vegetation was virtually absent, representing <7% of total stem density of shrubs. This paucity precluded analyses comparing avian responses to exotic versus native plants.

Variables retained for statistical analyses included 8 local and 6 landscape-level factors (Table 2). Of the local variables, 3 were direct measures of invasion: invasive-shrub stem density, percent honeysuckle cover, and proportion of buckthorn trees. Two of the local variables were indirect measures of invasion: tree density, which was positively correlated with proportion of buckthorn trees ($r = 0.53$); and percent bare ground, which was positively correlated with both tree density ($r = 0.44$) and proportion of buckthorn trees ($r = 0.43$). Honeysuckle cover had relatively weak negative correlations with measures of urbanization: urban land cover ($r = -0.23$) and building density ($r = -0.24$). Conversely, urban land cover and building density had weak positive relationships with proportion of buckthorn trees ($r = 0.09$ and $r = 0.13$,

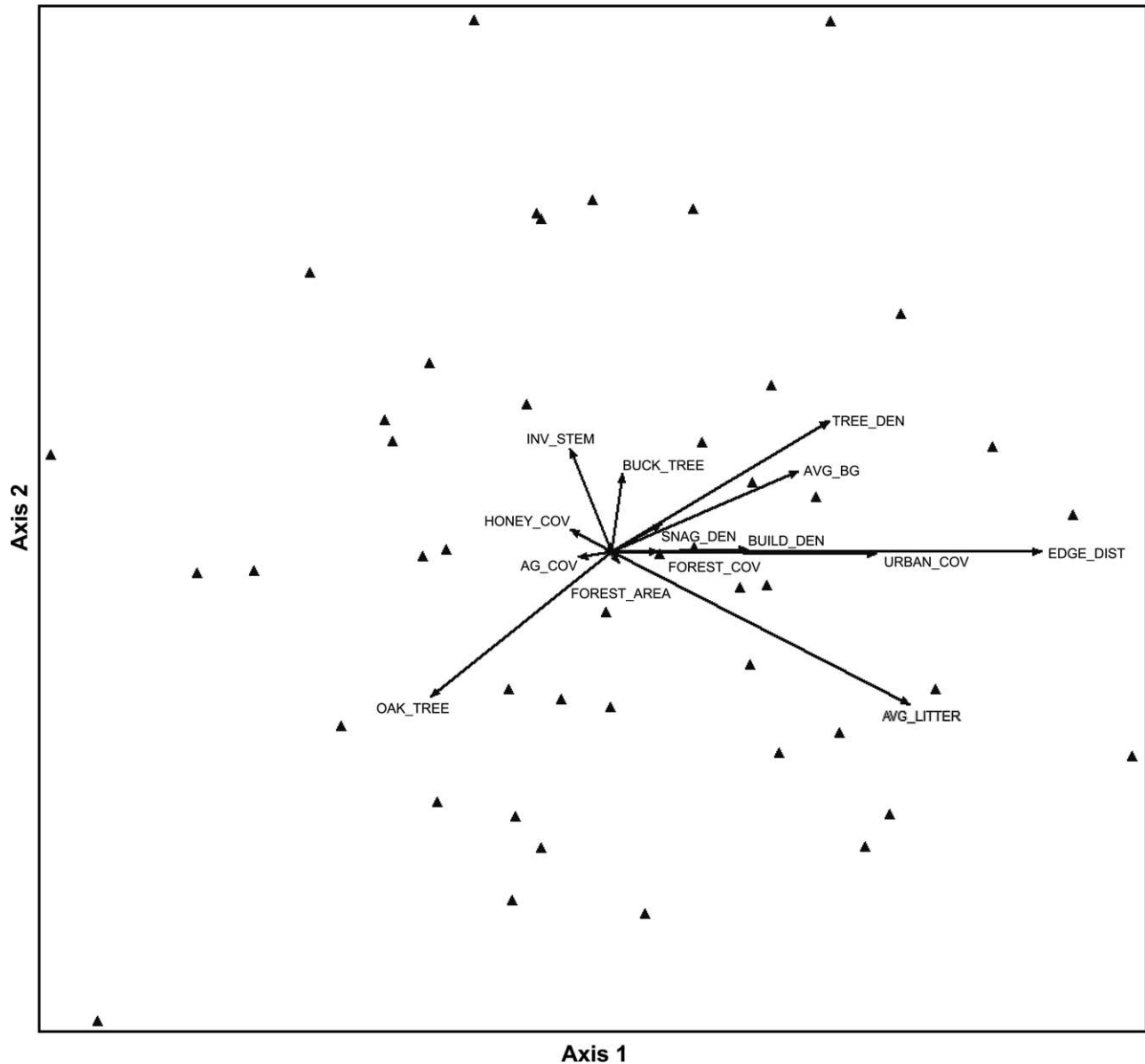


FIGURE 2. Nonmetric multidimensional scaling (NMDS) of avian community structure in 46 study plots in northeastern Illinois, USA, 2010–2011. Environmental vectors are oriented toward the direction of greatest increase for a given variable. The length of an environmental vector is proportional to r^2 with the ordination, and the angle between vectors indicates the correlation between variables. For explanation of environmental variable codes, see Table 2.

respectively) and invasive stem density ($r = 0.12$ and $r = 0.19$, respectively).

Bird Responses

We observed 1,962 individual birds representing 57 species that met our criteria for inclusion in data analyses. The most common species were American Robin (16.3% of all observations), Red-eyed Vireo (7.6%), and Northern Cardinal (7.4%) (scientific names of species are given in Table 1). The Mantel test indicated no significant spatial autocorrelation in bird community structure among our

study plots (Mantel $r = -0.08$, $P = 0.11$). Thus, we considered the plots to be statistically independent.

NMDS reached a convergent three-dimensional solution with a stress of 18.6% (Kruskal 1964). We chose to display axes 1 and 2 (Figure 2) because they had the highest coefficients of determination and explained 49% of the variation in the community data. At the local scale, litter cover was the variable most strongly correlated with the arrangement of avian assemblages in ordination space (Figure 2 and Table 3). The 2 indirect measures of invasive vegetation, tree density and percent bare ground, were

TABLE 3. Pearson correlations of environmental variables and the 20 most abundant bird species on our study area in northeastern Illinois, USA, 2010–2011, with nonmetric, multidimensional-scaling ordination axis scores. See Table 1 for explanation of environmental variable codes. Birds are listed in descending order of abundance. Relationships that have $|\text{Kendall's } \tau| \geq 0.25$ (in bold) are considered ecologically meaningful (McCune and Mefford 2011).

Environmental and species variables	Axis		
	1	2	3
Local environmental variables			
AVG_LITTER	0.486	-0.315	-0.113
TREE_DEN	0.391	0.325	0.052
AVG_BG	0.359	0.254	-0.031
SNAG_DEN	0.190	0.147	-0.004
BUCK_TREE	0.082	0.243	0.040
HONEY_COV	-0.174	0.110	0.468
INV_STEM	-0.179	0.272	0.093
OAK_TREE	-0.355	-0.333	-0.120
Landscape environmental variables			
EDGE_DIST	0.567	-0.007	-0.015
URBAN_COV	0.446	-0.037	-0.028
BUILD_DEN	0.316	0.063	-0.011
FOREST_COV	0.193	0.036	-0.076
FOREST_AREA	0.085	-0.091	0.102
AG_COV	-0.155	-0.083	0.150
Species			
American Robin	0.521	-0.603	-0.079
Red-eyed Vireo	0.516	0.517	-0.519
Northern Cardinal	-0.224	0.647	0.311
Indigo Bunting	-0.575	-0.088	-0.489
Blue Jay	-0.118	-0.342	0.462
Eastern Wood-Pewee	-0.309	-0.024	-0.220
Black-capped Chickadee	-0.051	0.031	0.313
Red-bellied Woodpecker	0.266	-0.242	0.325
Downy Woodpecker	0.404	-0.141	0.069
White-breasted Nuthatch	-0.115	-0.214	0.052
Blue-gray Gnatcatcher	-0.084	0.314	-0.254
Great Crested Flycatcher	0.139	0.220	0.354
Brown-headed Cowbird	-0.109	-0.091	0.018
Red-winged Blackbird	-0.355	-0.373	0.085
House Wren	-0.388	0.163	-0.177
Gray Catbird	-0.163	-0.122	0.518
Eastern Towhee	-0.402	0.003	-0.036
Hairy Woodpecker	0.304	0.136	0.194
Common Yellowthroat	-0.610	-0.238	0.003
Cedar Waxwing	0.134	-0.012	-0.006

strongly correlated with both axis 1 and axis 2. All measures of invasive vegetation, both direct and indirect, were positively correlated with axis 2. Honeysuckle cover was the only variable to show a strong association with axis 3. At the landscape scale, distance-to-edge was the variable most strongly correlated with the arrangement of avian assemblages in the ordination, followed by the 2 measures of urbanization—urban land cover and building density. All 3 of these variables were strongly associated with axis 1. Contiguous forest area, forest cover, and agricultural cover

had the weakest associations with the arrangement of avian assemblages in ordination space.

Correlations between the relative abundances of individual species and NMDS axis scores revealed several trends (Table 3). The relative abundance of the most common species, American Robin, was positively correlated with axis 1 and negatively correlated with axis 2. These correlations reflected a positive relationship with the litter cover vector and a negative association with the vectors representing honeysuckle cover and invasive-shrub stem density. Several species, including Common Yellowthroat, Indigo Bunting, Eastern Towhee, House Wren, and Eastern Wood-Pewee, had strong negative associations with distance-to-edge and urban cover. The relative abundances of common shrub-nesting species, such as Northern Cardinal and Gray Catbird, had positive associations with the honeysuckle cover vector. The second most abundant species, Red-eyed Vireo, had a negative association with this vector.

All of the best NPMR guild models contained either a direct or indirect measure of invasion (Table 4). The model with the highest xR^2 was that of the shrub-nesting guild, which included a direct measure of invasion (invasive stem density) and an indirect measure (tree density). The contour graph revealed that the abundance of shrub nesters decreased with increased tree density and distance-to-edge (Figure 3B). Foliage gleaners were most sensitive to changes in these same variables but reached their highest abundances in areas with high tree density, 200–300 m away from the forest edge (Figure 3E). Aerial salliers also responded to the metric distance-to-edge, although this model was the weakest overall. The abundance of aerial salliers generally increased with distance from the edge and decreased as the proportion of buckthorn trees in a plot increased (Figure 3D). Ground nesters were also sensitive to changes in the proportion of buckthorn trees. This guild reached its highest abundance in areas with low proportions of buckthorn trees and intermediate amounts of honeysuckle cover (Figure 3C). Both tree nesters and ground foragers were sensitive to invasive stem density. Tree nesters reached their highest abundances in areas with lower invasive stem densities and moderate amounts of forest cover in the landscape (Figure 3A). Ground foragers reached their highest abundances in areas with moderate proportions of oak trees and numbers of invasive shrub stems (Figure 3F). It is important to note that the relative abundance of ground foragers and tree nesters were highly dependent on American Robin abundance.

DISCUSSION

Native understory plants were rare on our study plots, perhaps because of management activities, competition with exotics, or decreased light availability associated with

TABLE 4. Best nonparametric multiplicative regression (NPMR) models for estimating the relative abundances of birds in different nesting and foraging guilds on our study area in northeastern Illinois, USA, 2010–2011. Models are sorted in descending order by their cross-validated r -square value (xR^2) within each response-variable category. Direct measures of invasive vegetation are italicized. Sensitivities are the average estimated absolute standardized changes in the relative abundance of a response variable per standard change in the predictor, and they represent the relative importance of each predictor variable within a given multivariate model. Tolerances are the standard deviation of the Gaussian weighting function expressed in the same units as the environmental variables and therefore have ready ecological interpretation. For explanation of environmental variable codes, see Table 1.

Response variable	Environmental variables	Sensitivities	Tolerances	xR^2
Nesting guild				
Shrub	TREE_DEN and <i>INV_STEM</i> and EDGE_DIST	0.86; 0.03; 0.20	100.65; 12,566.84; 32.50	0.51
Ground	<i>BUCK_TREE</i> and <i>HONEY_COV</i> and AG_COV	0.04; 0.44; 0.03	21.22; 0.04; 13.77	0.26
Tree	<i>BUCK_TREE</i> and <i>INV_STEM</i> and FOREST_COV	0.02; 0.15; 0.45	55.18; 4,488.16; 6.08	0.18
Foraging guild				
Foliage gleaners	OAK_TREE and TREE_DEN and EDGE_DIST	0.09; 0.89; 0.25	30.63; 100.65; 32.50	0.27
Ground foragers	OAK_TREE and <i>INV_STEM</i> and FOREST_COV	0.40; 0.25; 0.05	8.75; 2,692.90; 36.51	0.22
Aerial salliers	<i>BUCK_TREE</i> and EDGE_DIST	0.08; 0.28	21.22; 32.50	0.10

mesophication (Nowacki and Abrams 2008). Thus, the understory in these plots was largely dominated by invasive woody vegetation. Of the direct measures of invasion, honeysuckle cover was the most highly correlated with avian community structure. The architecture of honeysuckle is considerably different than that of other shrubs in the region, so perhaps the arching structure and high cover provided by honeysuckle attracted some species (e.g., Gray Catbird) and deterred others (e.g., Red-eyed Vireo). Surprisingly, 2 other direct measures of invasion, invasive-shrub stem density and proportion of buckthorn trees, were weakly correlated with avian community structure. Nevertheless, all direct measures of invasion were important predictors of the relative abundance of birds in several avian nesting and foraging guilds.

Guilds exhibited positive and negative responses to increases in invasive vegetation. The relative abundance of both ground nesters and aerial salliers decreased with increases in the proportion of buckthorn trees. Rapid litter decomposition can result in bare ground beneath buckthorn (Knight et al. 2007), degrading a crucial substrate for ground-nesting birds. The positive relationship between buckthorn trees and tree density may explain the decrease in aerial insectivores, a guild that tends to decline with high densities of small trees (Kotliar et al. 2002). The foraging ability of aerial salliers is likely inhibited by the dense understory created by buckthorn invasions.

Lower abundance of aerial insectivores with increased abundance of invasive trees and shrubs may also be explained by reduced food availability, because exotics generally support less diverse insect communities than native plants (Wu et al. 2009, Litt and Steidl 2010). The Eastern Wood-Pewee, a common aerial sallier in our study region, exhibited a strong positive response to increases in oak trees and a negative association with honeysuckle. This same pattern was reported by McCusker et al. (2010), who also observed lower densities of this species in sites heavily

invaded by honeysuckle than in sites with native shrub understories.

Unlike aerial insectivores, foliage-gleaning species reached their greatest abundances in plots with the highest tree densities, an indirect measure of invasion. Similarly, the abundance of foliage-gleaning birds is known to increase with the density of another invasive, Chinese privet (*Ligustrum sinense*; Wilcox and Beck 2007). Taken together, these findings suggest that foliage-gleaning species may prefer invaded areas because foraging substrates are more prevalent.

Like foliage gleaners, shrub nesters responded positively to the amount of invasive vegetation. Because several shrub nesters are also foliage gleaners, these similar responses may be influenced by guild overlap. Nevertheless, the relative abundance of several common shrub-nesting birds (e.g., Northern Cardinal and Gray Catbird) was positively associated with the density of exotic-shrub stems and honeysuckle cover. These positive associations may be influenced by hatch-year birds seeking cover in the denser vegetation provided by this plant. Indeed, fledgling Northern Cardinals appear to prefer microhabitats with abundant honeysuckle, and this preference has been positively associated with survivorship (Ausprey and Rodewald 2011). Others have reported positive associations between the relative abundance of understory bird species and invasive shrubs (Leston and Rodewald 2006, McCusker et al. 2010), even though selecting exotic shrubs as nest sites when natives are available may be evolutionarily maladaptive. In our system, shrub nesters have little choice but to select exotics, given the rarity of native species. These findings are consistent with our expectation that shrub-nesting species would prefer invaded forests over areas that lack understory vegetation.

The relative abundance of shrub nesters also decreased with increased tree density. In our study area, plots with

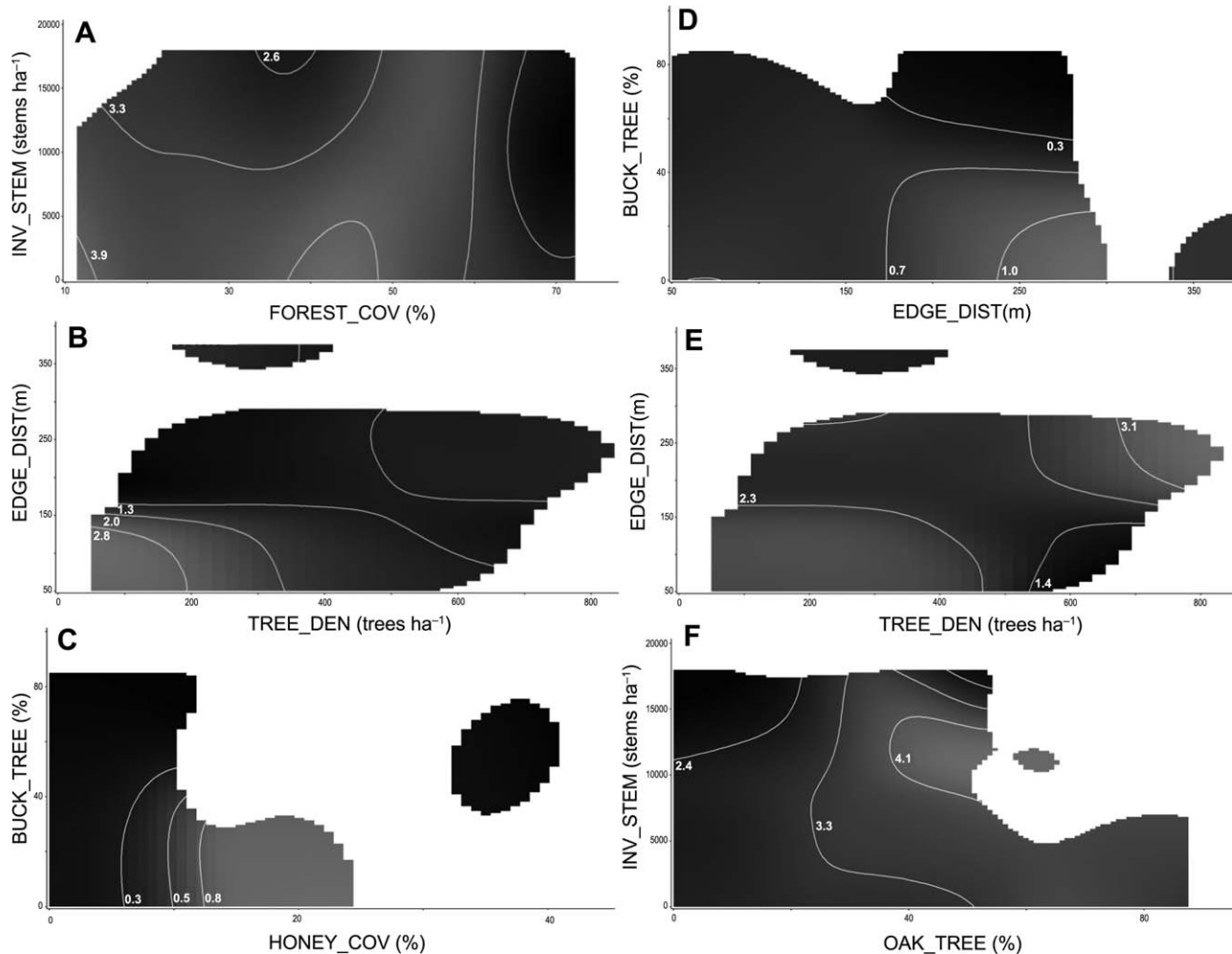


FIGURE 3. Estimated average abundance for 6 avian guilds on our study area in northeastern Illinois, USA, 2010–2011, as determined by nonparametric multiplicative regression (NPMR). Guilds include (A) tree nesters, (B) shrub nesters, (C) ground nesters, (D) aerial salliers, (E) foliage gleaners, and (F) ground foragers. The contour graphs illustrate the predicted average avian abundance as a function of the 2 environmental variables selected in the best model (Table 4). The particular variable to which a guild is most sensitive is displayed on the x-axis. Lighter shading corresponds to higher average abundances, and white areas in the graphs indicate locations in the environmental space where predictions were not made because of insufficient data. For explanation of environmental variable codes, see Table 2.

low tree density often had greater honeysuckle cover and tended to be in edge-dominated fragments located in less urban landscapes. Proximity to edges can play a major role in structuring avian communities (Sisk et al. 1997, Brand and George 2001), and distance-to-edge was included in half of the top NPMR models. Shrub nesters showed the clearest response, their relative abundance increasing as distance-to-edge decreased. Shrub-dependent birds, such as the Northern Cardinal, are often attracted to forest edges that typically have more shrub cover than adjacent areas (Mills et al. 1991). In our study, invasive shrub cover decreased with distance into the forest, but this relationship was weak. Anecdotally, exotic shrubs appeared to be most dense within 5 m of the forest edge. It is possible that

our vegetation sampling method did not capture the fine-scale variation in shrub cover within plots.

In addition to distance-from-edge, the 2 measures of urbanization were highly correlated with avian community structure. Urbanization can indirectly influence forest bird communities in a variety of ways, including increased human activity, more food resources via supplemental feeding or fruits on ornamental shrubs, and greater invasion potential. Invasive plants are often highly successful colonizers of natural habitats within urban environments (Borgmann and Rodewald 2005) because of increased seed movement and disturbance (Hobbs 2000). Furthermore, exotic shrub invasions have been positively associated with increases in urban land cover (Borgmann

and Rodewald 2005). In our study, however, measures of urbanization were weakly associated with measures of invasion. This seeming contradiction may stem from the ubiquity of invasive plants throughout the Chicago metropolitan area. Indeed, heavily invaded fragments were located in both urban and more rural landscapes. Despite the fact that building density and urban cover were highly correlated with avian community structure, neither was selected in any top NPMR guild models. One explanation for the different outcomes in these 2 analyses is that species from several guilds were sensitive to urbanization and avoided fragments embedded within more developed areas. This pattern is particularly common for many Neotropical migrants (Friesen et al. 1995, Kluza et al. 2000, Miller et al. 2001). This would have influenced community structure, but the impacts on guilds could have been diluted by increases in the abundance of other guild members with increasing housing density in the surrounding landscape matrix.

The primary goal of our study was to investigate the impacts of invasive plant abundance on forest bird communities. Because the gradient of invasion was, to some extent, a function of management history, we were unable to completely separate the effects of plant invasions and restoration activities on avian communities in our analyses. Nonetheless, our results indicate that while removal of invasive vegetation may benefit some avian species, it may be detrimental for others, such as shrub nesters and foliage gleaners. One strategy that would appear to have unambiguous results is the control or removal of buckthorn trees. No species or guild responded positively to increases in the proportion of buckthorn trees. Indeed, the relative abundance of birds in several guilds, including aerial salliers, increased with a decline in the proportion of buckthorn trees or overall tree density. Aerial insectivores, including aerial salliers, are of particular conservation concern because they are experiencing widespread population declines in North America (Sauer et al. 2007) and are especially vulnerable in urban areas (Chace and Walsh 2006).

Habitat quality might be maintained or improved if the removal of the exotic understory plants was accompanied by restoration of native shrubs. Other studies have demonstrated that honeysuckle can act as an ecological trap for shrub-nesting songbirds (Schmidt and Whelan 1999, Borgmann and Rodewald 2004). Hence, this restoration strategy would likely benefit this guild and provide needed resources for other species. Implementing this strategy may be challenging, however, because some native plants are not able to persist in soils that have been altered by exotic vegetation (Heneghan et al. 2006, Pavao-Zuckerman 2008). If native shrubs cannot be reestablished, thinning the understory would likely be more beneficial to the entire avian community than complete clearing of

understory vegetation. Thinning would decrease invasive stem density, yet still provide nesting and foraging substrates for certain birds. Historically, low-intensity fires maintained relatively open forest understories in this region, but prescribed fires may only top-kill invasive shrub species (Post and McCloskey 1989), rendering mechanical and chemical removal the method of choice.

Ultimately, land managers need to be explicit about their goals for habitat improvement by identifying target species of conservation concern. Large volunteer bases in metropolitan areas can render restoration of habitat remnants more feasible there (Miller 2005), but the limitations of restoration that consists only of removing invasive plants should be recognized.

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