

INVASION OF RIPARIAN FORESTS BY EXOTIC SHRUBS: EFFECTS OF
LANDSCAPE MATRIX AND IMPLICATIONS FOR BREEDING BIRDS

A Thesis

Presented in Partial Fulfillment of the Requirements for
the Degree Master of Science in the
Graduate School of the Ohio State University

By

Kathi L. Borgmann, B.A.

The Ohio State University
2002

Master's Examination Committee:

Dr. Amanda D. Rodewald, Advisor

Dr. Robert Gates

Dr. Allison Snow

Approved by

Advisor
The School of Natural Resources

ABSTRACT

Landscape-level studies of avian communities have moved beyond investigating simple area and isolation relationships to addressing the complex role of the landscape matrix. The landscape matrix can directly influence habitat availability, dispersal and colonization of organisms, metapopulation dynamics, nest predation, and species abundance and diversity patterns. The landscape matrix also can indirectly affect habitat suitability within a patch by mediating microclimatic conditions and floristic composition. In particular, invasion of forest patches by exotic plants may be closely tied to surrounding land uses, and exotic plants can alter floristic composition and structure. These changes also can affect predator-prey relationships, such as between nesting birds and nest predators, but our understanding of these interactions is limited. I used a multi-scale approach to determine (1) how changes within the landscape matrix influence the extent of exotic shrubs in riparian forests and (2) how exotic shrub species [honeysuckle (*Lonicera* spp) and rose (*Rosa multiflora*)] affect avian nest success.

Twenty sites were selected in mature riparian forests ranging from 63-200 m wide along five major waterways (ca. 20-40 m wide) in central Ohio. In July 2001, site width, volume of exotic shrubs, percent canopy cover, and aspect of forest edge (N/E or S/W) were measured at each site along 3 transects extending from the forest edge to river edge. Within 1 km of each site, coverage by urban development (i.e., paved surfaces and buildings) was determined from 1994 Thematic Mapper Imagery data. Sites occurred

along a rural-urban gradient, ranging from < 1-47% urban land cover within 1 km. From May to August in 2001 and 2002, 231 open-cup nests within the understory (≤ 5 m tall) were monitored at a subset of 12 sites to estimate daily mortality rates. Nest substrate species, nest height, and distance from the forest edge were recorded for each nest, whereas, nest-placement and nest-patch characteristics (0.04 ha circular plot) were measured only for Northern Cardinal (*Cardinalis cardinalis*) nests ($n = 68$). An artificial nest experiment also was conducted using old Northern Cardinal and American Robin (*Turdus migratorius*) nests baited with one clay egg. Artificial nests ($n = 79$) were placed in honeysuckle, rose, and native substrates along a transect 50-75 m from the forest edge at two rural sites.

Potential factors promoting invasion by exotic shrubs were investigated using the information-theoretic approach and Akaike's Information Criterion. I developed 19 *a priori* models consisting of local and landscape level characteristics likely to influence exotic shrub invasion. Exotic shrub volume was best described by the amount of urban land cover within 1 km of my sites. In particular, honeysuckle volume within riparian forests increased with increasing urbanization within the landscape. These results suggest that consideration of landscape matrix characteristics may improve our ability to predict or reduce invasion.

Both natural and artificial nests placed in exotic shrubs were 2-4 times more likely to fail than nests in native nest substrates, regardless of distance from the edge. Moreover, nests in exotic shrubs were especially vulnerable to predation in urban landscapes. These patterns may be explained by differences in nest-placement and nest-

patch characteristics among nest substrates. In particular, nests in native substrates were nearly 1.5-2 m higher than nests in exotic shrubs and higher nests were less likely to fail than nests placed closer to the ground. Northern Cardinal nests in exotic shrubs had fewer and smaller diameter support branches, and were positioned closer to the central axis of the nest substrate. Nests in exotic shrubs also had 6-9 times more exotic shrub volume surrounding the nest (i.e., in the nest patch) than nests in native substrates. Together, these changes may facilitate a predator's ability to locate nests. Of these characteristics, only the number of support branches was directly associated with nest fate, such that failed nests had fewer supporting branches. These findings demonstrate that exotic shrubs can reduce nest success of forest birds. However, the negative effect of exotic shrubs depended on the landscape matrix such that differences in daily mortality rates were most extreme in urban landscapes. This pattern combined with the fact that exotic shrubs were more pervasive in urban areas suggests that exotic shrubs may serve as an underlying mechanism of increased nest failure in fragmented landscapes.

This study is the first to (1) establish a link between the landscape matrix and invasion by exotic shrubs and (2) demonstrate that exotic shrubs impair reproductive success of forest-nesting birds while accounting for edge and landscape matrix effects. These findings suggest that restoring native shrub communities within riparian forests, especially in urban environments may improve avian nest success. An important step in restoring the native shrub community is the identification of land uses that can increase the risk of invasion.

ACKNOWLEDGMENTS

I would like to thank Amanda D. Rodewald for providing invaluable advice and support during my thesis research. Your dedication and assistance is greatly appreciated. Special thanks to my committee members Robert J. Gates and Allison A. Snow for their guidance and support throughout my research. I would also like to thank Marja H. Bakermans and Andrew C. Vitz for their encouragement and moral support during my graduate studies. I am grateful to the following individuals for field assistance: Marja H. Bakermans, Alyssa J. Kornowa, Andrew C. Vitz, Eric Eiben, Bret Graves, Amanda D. Rodewald, Paul G. Rodewald, Melissa J. Santiago, Sarah Hazzard, and Michael R. Nelson, without their help this research would not have been possible. Thanks to Robert J. Gates and Michael G. Brasher for discussions and clarification on the information theoretic approach and Akaike's Information Criteria. Robert J. Gates, Marja H. Bakermans, Nathan J. Stricker, and David Risley assisted with landscape analysis. Finally, I would like to thank Ohio Recreation and Parks Department, Franklin County MetroParks, and private landowners for allowing access to field sites.

This research was supported by The Ohio State University's School of Natural Resources, The Ohio Agriculture and Research Development Center, The C. William Swank Program of Rural-Urban Policy, and The School of Natural Resources GradRoots.

VITA

(Not included in this edition of thesis.)

TABLE OF CONTENTS

	<u>Page</u>
Abstract.....	ii
Acknowledgments.....	v
Vita.....	vi
Table of Contents.....	viii
List of Tables	xi
List of Figures	xiii
Chapters:	
1. Introduction.....	1
1.1 Objectives and hypothesis.....	3
1.2 Thesis format	4
1.3 Background.....	5
1.3.1 Exotic plants.....	5
1.3.1.1 Species profiles	5
1.3.2 Landscape Matrix.....	7
1.3.2.1 Effects on avian communities.....	7
1.3.2.2 Effects on floral communities.....	8
1.3.3 Exotic plants.....	10
1.3.3.1 Effects on nest success.....	10
1.3.3.2 Effects on communities and ecosystems.....	13
1.4 Rationale and significance	14
1.5 Literature cited.....	16
2. Landscape matrix effects on invasion of riparian forests by exotic shrubs	34
2.1 Abstract.....	34
2.2 Introduction.....	35
2.3 Methods.....	37
2.3.1 Study area.....	37
2.3.2 Vegetation sampling	39
2.3.3 Data analysis	40
2.4 Results.....	41
2.5 Discussion.....	42

2.6 Literature cited.....	48
3. Exotic shrubs as an underlying mechanism of increased nest failure in fragmented landscapes	61
3.1 Abstract	61
3.2 Introduction.....	62
3.3 Methods.....	65
3.3.1 Study area.....	65
3.3.2 Nest monitoring	67
3.3.3 Artificial nest experiment	68
3.3.4 Data analysis	69
3.4 Results.....	71
3.4.1 Natural nest study	71
3.4.2 Artificial nest study	74
3.5 Discussion.....	74
3.6 Conservation implications	81
3.7 Literature cited.....	83

APPENDICES

APPENDIX A. Scientific and common names of plants frequently encountered within riparian forest sites in central Ohio, USA. Nomenclature follows Braun (1961). * Indicates exotic species.....	104
APPENDIX B. Location of riparian forest study sites within Franklin and Delaware counties, Ohio, USA	106
APPENDIX C. Location of vegetation sampling sites in central Ohio, USA.....	107
APPENDIX D. Mean \pm SE volume of <i>Lonicera</i> and <i>R. multiflora</i> and local level characteristics measured at 20 riparian forest sites in central Ohio, USA, 2001.....	108
APPENDIX E. Mean \pm SE volume of <i>Lonicera</i> and <i>R. multiflora</i> and landscape level variables. Mean site width and percent land use covered by urban development, agriculture, and forest within 1 km of 20 riparian forest sites in central, Ohio, USA, 2001.....	109
APPENDIX F. Location of nest searching sites and years riparian forests sampled in central, Ohio, USA.....	110

APPENDIX G. Number of understory (≤ 5 m) nests monitored, number of exposure days, and Mayfield's estimate of daily mortality for nests among each nest substrate at 12 riparian forest sites in central Ohio, USA, 2001-2002.....	111
--	-----

Bibliography.....	112
-------------------	-----

LIST OF TABLES

<u>Table</u>	<u>Page</u>
2.1 Mean site width (m) and percent land use covered by urban development, agriculture, and forest within 1 km of 20 riparian forest sites in central, Ohio, USA.....	57
2.2 Model statements describing <i>Lonicera</i> and <i>R. multiflora</i> volume in 20 riparian forests in central Ohio. Models are ranked according to AIC _c and delta AIC (Δ_i) scores. Best-supported models have smaller delta AIC (Δ_i) scores and larger Akaike weights (W_i). Vertical bars represent interactions between variables	58
3.1 Mean site width (m) and percent land covered by urban development, agriculture, and forest within 1 km of nest searching sites. Land use category is based on the percent of urbanization within 1 km (urban > 7% and rural < 2%). Number of understory (≤ 5 m) nests, exposure days, and Mayfield estimates of daily mortality for nests monitored in central Ohio, 2001-2002	95
3.2 Number of understory (≤ 5 m) nests monitored per species at 12 sites in riparian forests in central Ohio, 2001-2002	96
3.3 Results of General Linear Model analysis testing the effects of land use, substrate type, and their interaction on daily mortality rates of understory (≤ 5 m) nesting species in riparian forests in central Ohio, 2001-2002	97
3.4 Mean (SE) and associated P-values of nest-placement and nest-patch characteristics for Northern Cardinal nests (≤ 5 m) within honeysuckle, rose, and native nest substrates in riparian forests in central Ohio, 2001-2002. Nest-placement (Wilks' Lambda $F_{10,108} = 7.97$, $P = < 0.001$)	

and nest-patch characteristics differed significantly among nest substrates (Wilks' Lambda $F_{18,114} = 5.65$, $P = < 0.001$)	98
---	----

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
2.1 (a) Percent <i>Lonicera</i> spp. volume compared to the percentage of urbanization within 1 km of riparian forest sites ($y = 2.6890 + 0.0416x$), (b) Percent <i>R. multiflora</i> volume compared to the percentage of urbanization within 1 km of riparian forest sites ($y = 2.5502 + -0.0067x$).....	59
2.2 <i>Lonicera</i> spp. volume with respect to distance from the forest edge ($r = -0.202$).....	60
3.1 Daily mortality rates for understory (≤ 5 m) nests in honeysuckle, rose, and native nest substrates within rural and urban landscapes ($n = 231$ nests). Land uses were categorized as follows; rural = $< 2\%$ urbanization ($n = 6$), and urban = $> 7\%$ urbanization ($n = 6$) within 1 km of each site. Asterisk indicates significant difference in daily mortality rates among nest substrates within urbanizing landscapes.	100
3.2 Nest-placement characteristics within each nest substrate for understory (≤ 5 m) Northern Cardinal nests ($n = 68$). Nest placement characteristics differed among nest substrates ($F_{10,108} = 7.97$, $P = < 0.001$).	101
3.3 Nest-patch characteristics for understory (≤ 5 m) Northern Cardinal nests ($n = 68$) within 0.04 ha of the center of the nest. Exotic shrub volume ($F_{2,65} = 44.49$, $P = < 0.001$) and native woody vegetation volume ($F_{2,65} = 6.03$, $P = 0.004$) was significantly different among nest substrates. Exotic shrub is volume of exotic shrubs ≤ 3 m in height and native woody vegetation is volume of all native vegetation (trees, shrubs, and vines) ≤ 3 m in height.	102
3.4 Percentage of depredated artificial nests compared to number of days exposed. Artificial nest experiment began on 18 June 2001 at one rural site and on 30 June 2002 at two rural sites in Delaware County, Ohio, USA. Asterisk indicates significant difference among nest substrates.....	103
3.5 Mean (SE) artificial nest characteristics and associated P-values of artificial nests in honeysuckle, rose, and native nest substrates in riparian forests in central Ohio, 2001-2002.....	99

CHAPTER 1

INTRODUCTION

Riparian forests provide critical habitat for many plant and animal species, act as nutrient filters, provide linkages between terrestrial and aquatic systems, and are important dispersal corridors for plants and animals (Lowrance et al. 1984, Peterjohn and Correll 1984, Knopf et al. 1988, Naiman et al. 1993, Machtans et al. 1996, Naiman and Decamps 1997, Mensing et al. 1998). Throughout the Midwest, however, urban and agricultural pressures in concert with rapid land use shifts have accelerated rates of riparian forest fragmentation and degradation (Mensing et al. 1998). Loss of riparian forest habitat in midwestern landscapes is particularly problematic because the majority of intact forests are in riparian areas (Laub 1979, Groom and Grubb 2002).

Fragmentation and land use changes negatively affect flora and fauna in riparian forests by compromising habitat quality. I focused on avian communities because they are sensitive to local and landscape-scale habitat alterations and are often used as indicators of ecosystem health (Martin 1992, Mensing et al. 1998, O'Connell et al. 2000). Forest fragmentation reduces the amount of suitable core habitat for forest interior species, increases the amount of habitat edge and isolation, alters microclimatic conditions, and ultimately reduces avian diversity and abundance (Whitcomb et al. 1981, Saunders et al. 1991, Andren 1994, Askins 1995, 2000, Faaborg et al. 1995, Robinson et al. 1995).

These effects (often termed “edge effects”) negatively impact avian nest success by increasing competition, nest predation, and brood parasitism (Wilcove 1985, Andren 1994, Paton 1994, Murcia 1995, Robinson et al. 1995). The type and extent of surrounding land uses further exacerbates the negative effects of habitat fragmentation on avian communities (Friesen et al. 1995, Flather and Sauer 1996, Donovan et al. 1997, Saab 1999, Trzcinski et al. 1999, Howell et al. 2000, Rodewald and Yahner 2001^{a,b}, Rodewald 2002).

Fragmentation and the landscape matrix also can influence invasion by exotic plants in numerous ways (With 2002). Disturbances that result from fragmentation increase the risk of invasion (Hobbs 1989,1991, Hobbs and Heunneke 1992). Moreover, surrounding land uses facilitate exotic plant invasion (Moran 1984, Rottenborn 1997, Hutchinson and Vankat 1998, Jenkins and Parker 2000). For example, forest patches adjacent to urban areas may contain more exotic species because urban landscapes often support high densities of ornamental exotic plants (Moran 1984, Rottenborn 1997). Once established, exotic plants can alter floristic composition and community structure by reducing herbaceous cover, tree seedling density, and plant species richness (Luken 1988, Woods 1993, Trisel and Gorchoy 1994, Hutchinson and Vankat 1997, Collier et al. 2002). In addition, exotic plants may affect higher trophic levels by altering predator-prey interactions, such as between nesting birds and nest predators. Exotic plants can

increase avian nest predation in several ways. First, exotic plants tend to exhibit early leaf flush (Trisel and Gorchov 1994) and are often concentrated on or near habitat edges (Brothers and Spingarn 1992, Matlack 1993, Luken and Goessling 1995, Hutchinson and Vankat 1997, Goldblum and Beatty 1999). These characteristics may attract birds to nest or forage near habitat edges, where they are more vulnerable to predation (Gates and Gysel 1978, Brittingham and Temple 1983, Wilcove 1985, Paton 1994, King et al. 1996). Second, birds nesting in exotic shrubs may shift nest placement within the nest substrate, which can facilitate the ability of predators to access nests (Best and Stauffer 1980, Martin and Roper 1988, Martin 1988*b*, Schmidt and Whelan 1999). Third, riparian forests that contain numerous patches of exotic shrubs may improve predator search efficiency (Martin 1988*b,c*, 1993*b*, Schmidt 1999, Schmidt and Whelan 1999). Fourth, invasion of exotic plants often degrades or removes habitat altogether (Braithwaite et al. 1989, MacDonald et al. 1989), which may increase overlap of nesting resources among co-existing species (Martin 1993*b*, 1998). However, few empirical data exist that evaluate the nature and severity of these interactions.

OBJECTIVES AND HYPOTHESES

Taken together, invasion by exotic plants may serve as an underlying mechanism of increased nest failure in highly fragmented landscapes. Unfortunately, our knowledge of these interactions is poor because studies fail to examine these factors at multiple spatial scales. I used a multi-scale approach to determine how changes within the landscape matrix influence exotic plant invasion in riparian forests and in turn how exotic plants affect avian nest success. My objectives were to (1) evaluate how local (site level) and landscape level (within 1 km) characteristics influence exotic shrub volume in

riparian forests, and (2) assess how use of exotic shrubs as nesting substrate affects nest success of forest breeding birds in central Ohio.

I hypothesized that the landscape matrix influences invasion of exotic shrubs in riparian forests such that exotic shrubs will be more abundant in urbanized landscapes. I also hypothesized that exotic plants negatively affect avian nest success by (1) reducing average nest height or changing nest placement within the nest substrate (e.g., nest placed further from central axis of shrub), which facilitates predator access, (2) improving predator search efficiency due to changes in nest patch microhabitats, and (3) increasing the number of nest sites, thereby increasing density dependent mortality.

THESIS FORMAT

In Chapter 2, I evaluate how local and landscape-scale characteristics influence invasion by honeysuckle (*Lonicera* spp) and multiflora rose (*Rosa multiflora*) in riparian forests of central Ohio. In particular, I focus on how the landscape matrix influenced exotic shrub volume at my study sites and discuss how this research can be used to develop effective management and reserve design strategies. This chapter is formatted for publication in the journal *Biological Conservation*.

In Chapter 3, I assess how the use of exotic shrubs as nest substrates can negatively affect avian nest success. I also address the specific mechanisms by which exotic shrubs can affect nest fate at local and landscape scales. I contend that exotic shrubs may serve as an underlying mechanism of increased nest failure in highly fragmented landscapes. I end with a discussion on how these findings can be applied to conservation, restoration, and management goals. Chapter 3 is formatted for publication in the journal *Ecology*.

BACKGROUND

EXOTIC PLANTS

Recently, the terms “exotic”, “non-native”, “non-indigenous”, “invasive”, and “alien” have come under scrutiny. Here, the term exotic refers those plant species existing outside of their historic (pre-colonial) native range. Exotic plants are characterized by early leaf expansion (Trisel and Gorchov 1994, Hutchinson and Vankat 1997), high allocation of energy to reproduction, high net primary productivity, plastic growth responses, and efficient dispersal (Bazzaz 1986). Invaders are most successful in climatic conditions and soil types similar to their native ranges (Baker 1986). In addition, an invader is more likely to succeed in a community where the invader has a life-history trait that is absent in that community (Woods 1993). Invasive establishment also is increased by animal-mediated dispersal systems that characterize many exotic plants (Matlack 1994a, Baker 1986, Richardson et al. 2000). Although these features are characteristic of exotic plants, no single factor determines the success of an exotic invader (Noble 1989, Mack et al. 2000). These life history traits give exotic plants an advantage over native plant species, and few mechanisms appear to limit the spread of exotic plants. Typically, only light availability and availability of suitable microsites limit establishment and spread of exotic plants (Brothers and Spignarn 1992, Luken and Goessling 1995, Luken et al. 1995, Richardson et al. 2000).

Species profiles.—Common woody exotic shrubs in riparian forests of central Ohio include *Lonicera* spp. (*L. maackii*, *L. tatarica*, and *L. morrowii*; hereafter *Lonicera*) and *Rosa multiflora* (Braun 1961).

Lonicera maackii (Rupr.) Herder (Caprifoliaceae) was originally introduced to North America in 1896 for its floral and fruit properties. The native range of *L. maackii* includes portions of central and northeastern China, the Amur River and Ussuri River valleys of Korea, and isolated locations in Japan where it typically occupies floodplains, open woodlands, and disturbed areas (Luken and Thieret 1996). *Lonicera maackii* is an upright multi-stemmed shrub that reaches heights > 6 m, produces fruit after 3-5 years (Luken and Thieret 1996) and grows in calcareous soils throughout the Eastern United States and Canada (Luken 1988). *Lonicera maackii* expresses the classic features of invasive plants: morphological and physiological plasticity (Luken et al. 1995, Luken 1988), high reproductive output (Luken and Mattimiro 1991), and zoochrous seed dispersal (Ingold and Craycroft 1983). Light appears to be the only factor limiting *Lonicera* growth, as *Lonicera* is moderately shade-intolerant (Luken and Goessling 1995, Luken and Thieret 1996). The ability of *L. maackii* to escape from garden plantings was first noticed in the 1920s. *Lonicera maackii* was reported in more than 34 counties in Ohio by 1961 (Braun 1961, Luken and Thieret 1996) and now is rapidly spreading west (0.1 km/year) and north (0.5 km/year) (Hutchinson and Vankat 1997, 1998). *Lonicera maackii* also is a predominate shrub in 24 eastern states in the U.S. (Trisel and Gorchov 1994, Luken and Thieret 1996).

Lonicera tatarica L. (Caprifoliaceae) and *L. morrowii* Gray (Caprifoliaceae) have similar reproductive and life history strategies to *L. maackii*, although *L. maackii* and *L. tatarica* are more abundant than *L. morrowii* in central Ohio (Braun 1961). *Lonicera*

tatarica is native to west central Eurasia (Woods 1993) and first appeared in the new world prior to the 1800s (Rehder 1927). *Lonicera morrowii* is native to Japan and likely appeared during the same time period.

Rosa multiflora Thumb (Roseaceae) first arrived in the United States from Japan in 1886 (Wyman 1949). The U.S. Soil Conservation Science Service recommended the use of *R. multiflora* in the 1930s to prevent soil erosion and to act as a “living fence” for livestock (Albaugh 1977). State conservation agencies provided rootstock of *R. multiflora* to landowners as late as the 1960s (Schery 1977). Now *R. multiflora* is considered noxious in several midwestern states (e.g., OH, IN, IA, PA, MI, and WI). *Rosa multiflora* grows in a wide range of edaphic conditions, forming impenetrable thickets. *Rosa multiflora* reproduces by vegetative propagules and by seed (often in the millions), which are dispersed by many bird and mammal species (Martin et al. 1951).

LANDSCAPE MATRIX

Effects on avian communities.—The theoretical relationship between area, isolation, and species richness has been well demonstrated (MacArthur and Wilson 1967) and empirically (Ambuel and Temple 1983, Opdam et al. 1985). Recent focus has shifted toward investigating pressures associated with habitat fragmentation and “edge effects” (Faaborg et al. 1995), largely due to purported declines in some Neotropical migrants (Askins et al. 1990, Rappole and McDonald 1994, Askins, 1995, 2000, Martin and Finch 1995). Despite considerable evidence for edge effects, studies demonstrate contradictory results (see Paton 1994 and Murcia 1995 for review), particularly regarding nest predation and brood parasitism rates near habitat edges (Gates and Gysel 1978, Yahner and Wright 1985, Ratti and Reese 1988, Yahner 1996, Heske et al. 2001).

Recent work suggests that landscape characteristics mediate the effects of area, isolation, and edges on community structure and avian reproductive success (Friesen et al. 1995, Flather and Sauer 1996, Donovan et al. 1997, Saab 1999, Trzcinski et al. 1999, Howell et al. 2000, Rodewald and Yahner 2001^{a,b}, Rodewald 2002). For example, Rodewald and Yahner (2001^a) found that type, rather than amount, of disturbance was the primary factor affecting nesting success of mid-canopy nesting species. In particular, forested landscapes disturbed by agriculture had lower nest success than landscapes disturbed by silviculture (Rodewald and Yahner 2001^a). These reductions may result from abundant and diverse predator assemblages near agricultural areas, especially those that supply consistent food sources (Angelstam 1986, Cubbedge and Nilon 1993, Andren 1994, 1995, Heske 1995, Robinson et al. 1995, Bayne and Hobson 1997, Heske et al. 1999). In addition to agricultural disturbances, several studies have demonstrated that increasing levels of urbanization within the landscape cause avian abundance and diversity to decline (Emlen 1974, Beissinger and Osborne 1982, Mills et al. 1989, Friesen et al. 1995, Reijnen et al. 1995, Bolger et al. 1997, Rottenborn 1997, 1999, Marzluff et al. 1998, Germaine et al. 1998).

Effects on floral communities.—Disturbances such as those that result from fragmentation increase the susceptibility of forest communities to invasion by exotic plants (Hobbs 1989, 1991, Hobbs and Heunneke 1992). Moreover, several studies suggest that the landscape matrix can influence invasion by exotic plants (Mills et al. 1989, Hobbs 1991, Brothers and Spignarn 1992, Luken and Goessling 1995, Rottenborn 1997, Hutchinson and Vankat 1997, Jenkins and Parker 2000, With 2002). Types of disturbance and juxtaposition of habitat patches within the landscape can influence

establishment and dispersal of exotic plants (Rejmanke 1989, Hobbs 1991, Trombulak and Frissell 2000). For example, roads increase dispersal capabilities by acting as movement corridors for exotic plants (Trombulak and Frissell 2000). Forests adjacent to urban areas often contain large numbers of exotic plants due to their proximity to abundant seed sources (Rejmanke 1989, Matlack 1994b, Luken and Goessling 1995, Hutchinson and Vankat 1997, 1998, Rottenborn 1997). Agricultural landscapes also affect the density of exotic plants although results from studies examining forests near agricultural landscapes are inconsistent. Exotic plants may be more abundant near agricultural areas (Jenkins and Parker 2000), but large agricultural fields also can limit distribution and dispersal of exotic plants (e.g., *L. maackii*) because they are unable to disperse across inhospitable crop lands (Brothers and Spingarn 1992, Hutchinson and Vankat 1998). Regional forest cover also influences invasion and establishment. Connectivity increases in regions with extensive forest cover, which can facilitate the spread of *Lonicera* and other woody exotics via animal movement (Hutchinson and Vankat 1998). In contrast, landscapes with low amounts of forest cover may be more vulnerable to exotic plant invasion via habitat edges (Brothers and Spingarn 1992, Matlack 1993, 1994a). Landscape-level effects on invasion may, in part, result from historical factors, such as point of introduction. For example, the primary introduction of *R. multiflora* occurred in agricultural areas, thus elevating the relative abundance of *R. multiflora* in agricultural and rural landscapes. While patterns of occurrence within landscapes will depend on specific plant species, the landscape matrix clearly influences the distribution of exotic plants. Thus, multiple spatial scales need to be examined to understand distribution, abundance, and spread of exotic plants. However, few studies

have explicitly examined landscape matrix characteristics, limiting our ability to determine how landscape characteristics affect distribution and abundance of exotic plant species (but see Moran 1984, Rottenborn 1997, Hutchinson and Vankat 1998).

EXOTIC PLANTS

Effects on nest success.—Floristics and physiognomy are important components that influence habitat choice in birds (Cody 1974, Willson 1974, James and Wamer 1982, Rotenberry 1985, Martin and Karr 1986, Germaine et al. 1998). Indeed, several studies have linked vegetation volume with bird densities (MacArthur and MacArthur 1961, Cody 1974, Willson 1974, Rotenberry 1985, Mills et al. 1991). Increased bird densities near edges were once thought to result from increased vegetation volume at edges and associated food resources (Cody 1981, Bull and Skovlin 1982, Mills et al. 1991, Croonquist and Brooks 1993, Miller and Cale 2000). More recently however, avian abundance patterns have been attributed to nest site availability (Martin 1988*b*, 1993*b*, 1998). Because habitat selection is in part based on the availability of nest sites (Martin 1988*b,c*, 1992, 1993*b*), patches of exotic shrubs may alter habitat selection and use by birds. In fact, studies have found negative correlations between exotic plant densities and bird abundance (Beissinger and Osborne 1982, Mills et al. 1989, 1991, Germaine et al. 1998, Rottenborn 1999). However, most studies have focused only on avian abundance and diversity. Such oversight deserves attention for two reasons. First, nest predation is a major cause of nest failure in birds (Ricklefs 1969, Martin 1992, 1993*b*) and second, studies lacking information on fecundity and survivorship may provide spurious results (Van Horne 1983, Marzluff et al. 2001*a*). Therefore, it is important that future research focus on nest-site availability and suitability and to determine factors that affect nest

success (Martin and Roper 1988, Martin 1992). Exotic plants may negatively affect avian nest success. Birds may be attracted to exotic plants because of early leaf flush (Woods 1993, Trisel and Gorchov 1994), and increased foliage cover for nest sites (Schmidt and Whelan 1999). However, this behavior may ultimately reduce nest success because exotic plants are often concentrated near habitat edges (Brothers and Spingarn 1992, Matlack 1993, Woods 1993, Luken et al. 1995, Luken and Goessling 1995, Hutchinson and Vankat 1997, Goldblum and Beatty 1999). Birds nesting near edges may experience greater predation due to concentration of predators near edges or due to density dependent predation factors (Martin 1988*b,c*, Faaborg et al. 1995, Robinson et al. 1995). Density dependent predation results from a functional response of predators to increased densities of nests (Martin 1988*b,c*, Schmidt and Whelan 1998). Invasion by exotic plants also reduces diversity of nest substrates, which can increase predation rates (Martin 1987, 1988*b*, 1993*b*). For example, Martin (1993*b*) found that nest predation rates dropped when nests were segregated among varying substrates. Moreover, reduced nest substrate diversity may increase nest resource overlap among co-existing species, thereby increasing competition and density-dependent nest predation (Martin 1988*b,c*, 1998, Schmidt and Whelan 1999). Furthermore, nest success of birds utilizing exotic shrubs may be diminished as a result of changes in nest placement within the nest substrate. For example, nests placed lower to the ground may be more vulnerable to predation by small mammals (Schmidt 1999).

The landscape matrix also can exacerbate the negative effects of exotic plants. For example, urban areas often contain higher densities of exotic plants (Beissinger and Osborne 1982, Mills et al. 1989, 1991, Luken and Thieret 1996, Rottenborn 1997, 1999,

Germaine et al. 1998), and have elevated numbers of brood parasites and nest predators (Emlen 1974, Mills et al. 1989, Friesen et al. 1995, Marzluff et al. 1998). Thus, the combined effects of invasion by exotic shrubs and urbanizing landscapes causes birds to be particularly vulnerable to nest predation. Unfortunately, our knowledge of these interactions is limited because studies fail to examine these factors at multiple spatial scales.

In addition to compromising nest success of forest passerines, exotic plants may affect foraging strategies and available food resources in a number of ways. First, differences in foliage structure between native and exotic plants may influence foraging behavior (Maurer and Whitmore 1981, Robinson and Holmes 1984, Whelan 2001) and foraging success rate (Ellis 1995). Foraging success can be further diminished if exotic plants support fewer arthropods relative to native plants (Southwood 1961, Mills et al. 1991). Second, differences in the nutritional value of native and exotic fleshy fruits can impact frugivorous species. Several exotic plants produce fleshy fruits that are consumed by frugivorous birds (Lochmiller 1978, McDonnell and Stiles 1983, Debussche and Iseman 1990, White and Stiles 1992, Sallabanks 1993, Novak and Mack 1995), however these fruits are typically lower in protein and lipid content (Ingold and Craycraft 1983, White and Stiles 1992). Third, increasing the spatial and temporal availability of fruit-producing exotic plants may alter migration patterns, bird distributions, and overwinter survival rates of frugivorous birds (Debussche and Iseman 1990, White and Stiles 1992, Rey 1995, Renne et al. 2002). Future research needs to address issues relating to food abundance and foraging behavior to completely understand the repercussions of exotic plants on the avian community.

Effects on communities and ecosystems.—Exotic plants pose conservation problems worldwide and are implicated in reduced recruitment of some native species and, in some instances, extinction of local flora (MacDonald et al. 1989, Mack et al. 2000). The reproductive attributes and invasive nature of exotic plants allows them to penetrate deep into interior forest patches (Brothers and Spignarn 1992, Matlack 1993, 1994a, Woods 1993, Hutchinson and Vankat 1997), potentially causing long-term negative effects on plant and animal communities. *Lonicera* affects community structure by reducing light and nutrient availability, ultimately changing canopy composition. For example, presence of *Lonicera* is negatively correlated with herbaceous cover, plant species richness, and new seedling establishment (Luken 1988, Woods 1993, Trisel and Gorchov 1994, Hutchinson and Vankat 1997, Collier et al. 2002).

Exotic plants also alter ecosystem properties and/or processes (e.g., *Myrica faya*, and *Mimosa pigra*) by disrupting hydrological cycles (e.g., *Tamarix pentandra*), fire regimes (e.g., *Melaleuca quinquenervia*), and nutrient cycles (e.g., *Myrica faya*) (Neill 1983, Braithwaite et al. 1989, MacDonald et al. 1989, Vitousek 1990, Mack et al. 2000). Several examples throughout the world point to the dramatic effect exotic plants can have on entire ecosystems (see Mack et al. 2000 for review). *Mimosa pigra* in Australia is changing community structure, negatively affecting both plant and animal species in the region (Braithwaite et al. 1989). Areas infested with *Mimosa pigra* retain lower herbaceous biomass and lower diversity of woody plants, birds, and lizards (Braithwaite et al. 1989). Saltcedar (*Tamarix pentandra*) dominated sites in western riparian zones are disrupting avian communities by displacing foraging guilds and altering species composition (Anderson et al. 1977, Hunter et al. 1988, Ellis 1995). Increases in annual

exotic plant species resulting from agricultural conversion have altered historic fire regimes and reduced avian diversity in western shrub-steppe communities (Rotenberry 1998). Finally, urbanized landscapes in the United States with high densities of exotic plants often support depauperate bird communities (Emlen 1974, Hohtola 1978, Beissinger and Osborne 1982, Mills et al. 1989, Friesen et al. 1995, Rottenborn 1997, 1999, Cam et al. 2000).

RATIONALE AND SIGNIFICANCE

Urbanization and invasion by exotic plants threaten many species, communities, and ecosystems (Braithwaite et al. 1989, Vitousek et al. 1997, Schmidt and Whelan 1999, D'Antonio et al. 2001, Marzluff 2001a), yet no study has explicitly investigated the combined effects of these processes on breeding birds. Riparian forests provide an excellent opportunity to examine these interactions because riparian forests typically span the entire gradient of urbanization (e.g., from urban to rural), allowing for rigorous testing of the impacts of urbanization (McDonnell and Pickett 1990, Marzluff et al. 2001b).

Examining how exotic plants affect trophic level interactions, such as between nesting birds and nest predators is critical for several reasons (1) assessing the impacts of exotic plants on nesting songbirds may help improve nesting success especially for birds nesting in highly fragmented landscapes, which may be experiencing population declines (Donovan and Flather 2002), (2) understanding the interactions between nest predation and nest site characteristics is essential for developing effective management plans, (3) evaluating trophic interactions between nesting birds and exotic plants can help land managers assess the potential consequences of exotic plant removal and aid in habitat

restoration practices (Zavaleta et al. 2001), and (4) determining how land uses affect invasion by exotic plants will improve our ability to predict or prevent future invasions (Hobbs and Humphries 1995, Ewel et al. 1999, D'Antonio et al. 2001, Davies et al. 2001, Byers et al. 2002).

LITERATURE CITED

- Albaugh, G. P., W. H. Mitchell, and J. C. Graham. 1977. Evaluation of glyphosate for multiflora rose control. *Proceedings NE Weed Science Society* **31**:283-291.
- Ambuel, B., and S. A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* **64**:1057-1068.
- Anderson, B. W., A. Higgins, and R. D. Omhart. 1977. Avian use of saltcedar communities in the lower Colorado River valley. U.S. Dept. Agric. For. Serv. Gen. Tech. Rep. **RM-43**:128-136.
- Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**:355-366.
- Andren, H. 1995. Effects of landscape composition on predation rates at habitat edges. Pages 225-255 *in* L. Hansson, L. Fahrig, and G. Merriam, editors. *Mosaic landscapes and ecological processes*. Chapman and Hall, New York, New York, USA.
- Angelstam, P. 1986. Predation on ground-nesting birds' nests in relation to predator density and habitat edge. *Oikos* **47**:365-373.
- Askins, R. A. 1995. Hostile landscapes and the decline of migratory songbirds. *Science* **267**:1956-1957.
- Askins, R. A. 2000. *Restoring North America's birds*. Yale University Press, New Haven, Connecticut, USA.
- Askins, R. A., J. F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. *Current Ornithology* **7**:1-57.

- Baker, H. G. 1986. Patterns of plant invasions in North America. Pages 44-55 in H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer Verlag, New York, New York, USA.
- Bayne, E. M., and K. A. Hobson. 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conservation Biology* **11**:1418-1429.
- Bazzaz, F. A. 1986. Life history of colonizing plants: some demographic, genetic, and physiological features. Pages 96-110 in H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.
- Beissinger, S. R., and D. R. Osborne. 1982. Effects of urbanization on avian community organization. *Condor* **84**:75-83.
- Best, L. B., and D. F. Stauffer. 1980. Factors affecting nesting success in riparian bird communities. *Condor* **82**:149-158.
- Bolger, D. T., T. A. Scott, and J. T. Rotenberry. 1997. Breeding bird abundance in an urbanizing landscape in coastal southern California. *Conservation Biology* **11**:406-421.
- Braithwaite, R. W., W. M. Lonsdale, and J. A. Estbergs. 1989. Alien vegetation and native biota in tropical Australia: the impact of *Mimosa pigra*. *Biological Conservation* **48**:189-210.
- Braun, E. L. 1961. The woody plants of Ohio. Ohio State University Press. Columbus, OH, USA.

- Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *Bioscience* **33**:31-35.
- Brothers, T. S., and A. Spingarn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Conservation Biology* **6**:91-100.
- Bull, E. L., and J. M. Skovlin. 1982. Relationships between avian fauna and streamside vegetation. *Transactions of the North American Wildlife and Natural Resources Conference* **47**:496-506.
- Byers, J. E., S. Reichard, J. M. Randall, I. M. Parker, C. S. Smith, W. M. Lonsdale, I. A. E. Atkinson, T. R. Seastedt, M. Williamson, E. Chornesky, and D. Hayes. 2002. Directing research to reduce the impacts of nonindigenous species. *Conservation Biology* **16**:630-640.
- Cam, E., J. D. Nichols, J. R. Sauer, J. E. Hines, and C. H. Flather. 2000. Relative species richness and community completeness: birds and urbanization in the mid-Atlantic states. *Ecological Applications* **10**:1196-1210.
- Cody, M. L. 1974. *Competition and the structure of bird communities*. Princeton University Press, Princeton, New Jersey, USA.
- Cody, M. L. 1981. Habitat selection in birds: the roles of vegetation structure, competitors, and productivity. *BioScience* **31**:107-113.
- Collier, M. H., J. L. Vankat, and M. R. Hughes. 2002. Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. *American Midland Naturalist* **147**:60-71.

- Croonquist, M. J., and R. P. Brooks. 1993. Effects of habitat disturbance on bird communities in riparian corridors. *Journal of Soil and Water Conservation* **48**:65-70.
- Cubbedge, A. W., and C. H. Nilon. 1993. Adjacent land use effects on the flood plain forest bird community of Minnesota Valley National Wildlife Refuge. *Natural Areas Journal* **13**:220.
- D'Antonio, C., L. A. Meyerson, and J. Denslow. 2001. Exotic species and conservation. Pages 59-80 *in* M. E. Soule, and G. H. Orians, editors. *Conservation biology: research priorities for the next decade*. Island Press, Washington, DC., USA.
- Davies, K. F., C. Gascon, and C. R. Margules. 2001. Habitat fragmentation: consequences, management, and future research priorities. Pages 81-97 *in* M. E. Soule, and G. H. Orians, editors. *Conservation biology: research priorities for the next decade*. Island Press, Washington, DC., USA.
- Debussche, M., and P. Iseman. 1990. Introduced and cultivated fleshy-fruited plants: consequences of a mutualistic Mediterranean plant bird system. Pages 399-416 *in* F. diCastri, A. J. Hansen, and M. Debussche, editors. *Biological invasions in Europe and the Mediterranean Basin*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* **78**:2064-2075.

- Donovan, T. M., and C. H. Flather. 2002. Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. *Ecological Applications* **12**:364-374.
- Ellis, L. M. 1995. Bird use of saltcedar and cottonwood vegetation in the Middle Rio Grande Valley of New Mexico, U.S.A. *Journal of Arid Environments* **30**:339-349.
- Emlen, J. T. 1974. An urban bird community in Tucson, Arizona: derivation, structure, regulation. *Condor* **76**:184-197.
- Ewel, J. J., D. J. O'Dowd, J. Bergelson, C. C. Daehler, C. M. D'Antonio, L. D. Gomez, D. R. Gordon, R. J. Hobbs, A. Holt, K. R. Hopper, C. E. Hughes, M. LaHart, R. R. B. Leakey, W. G. Lee, L. L. Loope, D. H. Lorence, S. M. Louda, A. E. Lugo, P. B. McEvoy, D. M. Richardson, and P. M. Vitousek. 1999. Deliberate introductions of species: research needs. *BioScience* **49**:619-630.
- Faaborg, J. F., M. Brittingham, T. Donovan, and J. Blake. 1995. Habitat fragmentation in the temperate zone. Pages 357-380 *in* T. E. Martin and D. Finch, editors. *Ecology and management of Neotropical migratory birds*. Oxford University Press, New York, New York, USA.
- Flather, C. H., and J. R. Sauer. 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. *Ecology* **77**:28-35.
- Friesen, L. E., P. F. J. Eagles, and R. J. Mackay. 1995. Effects of residential development on forest-dwelling Neotropical migrant songbirds. *Conservation Biology* **9**:1408-1414.

- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* **59**:871-883.
- Germaine, S. S., S. S. Rosenstock, R. E. Schweinsburg, and W. S. Richardson. 1998. Relationships among breeding birds, habitat, and residential development in greater Tucson, Arizona. *Ecological Applications* **8**:680-691.
- Goldblum, D., and S. W. Beatty. 1999. Influence of an old field/forest edge on a northeastern United States deciduous forest understory community. *Journal of the Torrey Botanical Society* **126**:335-343.
- Groom, J. D., and T. C. Grubb Jr. 2002. Bird species associated with riparian woodland in fragmented, temperate-deciduous forest. *Conservation Biology* **16**:832-836.
- Heske, E. J. 1995. Mammal abundances on forest-farm edges versus interiors in southern Illinois: is there an edge effect? *Journal of Mammalogy* **76**:562-568.
- Heske, E. J., S. K. Robinson, and J. D. Brawn. 1999. Predator activity and predation on songbird nests on forest-field edges in east-central Illinois. *Landscape Ecology* **14**:345-354.
- Heske, E. J., S. K. Robinson, and J. D. Brawn. 2001. Nest predation and Neotropical migrant songbirds: piecing together the fragments. *Wildlife Society Bulletin* **29**:52-61.
- Hobbs, R. J. 1989. The nature and effects of disturbance relative to invasions. Pages 389-405 in J. A. Drake, H.A. Mooney, F. diCasti, R. H. Groves, F. J. Kruger, M. Rejamek, and M. Williamson, editors. *Biological invasions: a global perspective*. Scope 37. John Wiley and Sons, Chichester, United Kingdom.

- Hobbs, R. J. 1991. Disturbance as a precursor to weed invasion in native vegetation. *Plant Protection Quarterly* **6**:99-104.
- Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* **6**:324-337.
- Hobbs, R. J., and S. E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. *Conservation Biology* **9**:761-770.
- Hohtola, E. 1978. Differential changes in bird community structure with urbanization: a study in Central Finland. *Ornis Scandinavica* **9**:94-100.
- Howell, C. A., S. C. Latta, T. M. Donovan, P. A. Porneluzi, G. R. Parks, and J. Faaborg. 2000. Landscape effects mediate breeding bird abundance in midwestern forests. *Landscape Ecology* **15**:547-562.
- Hutchinson, T. F., and J. L. Vankat. 1998. Landscape structure and spread of the exotic shrub *Lonicera maackii* (Amur honeysuckle) in southwestern Ohio forests. *American Midland Naturalist* **139**:383-390.
- Hutchinson, T. F., and J. L. Vankat. 1997. Invasibility and effects of Amur Honeysuckle in Southwestern Ohio forests. *Conservation Biology* **11**:1117-1124.
- Ingold, J. L., and M. J. Craycraft. 1983. Avian frugivory on honeysuckle (*Lonicera*) in southwestern Ohio in fall. *Ohio Journal of Science* **83**:256-258.
- James, F. C., and N. O. Wamer. 1982. Relationship between temperate forest bird communities and vegetation structure. *Ecology* **63**:159-171.
- Jenkins, M. A., and G. R. Parker. 2000. The response of herbaceous-layer vegetation to anthropogenic disturbance in intermittent stream bottomland forests of southern Indiana, USA. *Plant Ecology* **151**:223-237.

- Knopf, F. L., R. R. Johnson, T. Rich, F. B. Samson, and R. C. Szaro. 1988. Conservation of riparian ecosystems in the United States. *Wilson Bulletin* **100**:272-284.
- Laub, K. W. 1979. Changing land use: forests, farms, and wildlife. Pages 272-281 *in* M.B. Lafferty, editor. Ohio's natural heritage. The Ohio Academy of Sciences, Columbus, OH. USA.
- Lochmiller, R. L. 1978. Privet as a potential winter food supplement for songbirds. *Bird Banding* **49**:279-280.
- Lowrance, R., R. Todd, J. Fail, Jr., O. Hendrickson, Jr., R. Leonard, and L. Asmussen. 1984. Riparian forests as nutrient filters in agricultural watersheds. *Bioscience* **34**:374-377.
- Luken, J. O. 1988. Population structure and biomass allocation of the naturalized shrub *Lonicera maackii* (Rupr.) maxim. in forest and open habitats. *The American Midland Naturalist* **119**:258-267.
- Luken, J. O., and N. Goessling. 1995. Seedling distribution and potential persistence of the exotic shrub *Lonicera maackii* in fragmented forests. *American Midland Naturalist* **133**:124-130.
- Luken, J. O., and D. T. Mattimiro. 1991. Habitat-specific resilience of the invasive shrub Amur honeysuckle (*Lonicera maackii*) during repeated clipping. *Ecological Applications* **1**:104-109.
- Luken, J. O., T. C. Tholemeier, L. M. Kuddes, and B. A. Kunkel. 1995. Performance, plasticity, and acclimation of the nonindigenous shrub *Lonciera maackii*

- (Caprifoliaceae) in contrasting light environments. *Canadian Journal of Botany* **73**:1953-1961.
- Luken, J. O., and J. W. Thieret. 1996. Amur honeysuckle, its fall from grace. *Bioscience* **46**:18-24.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* **42**:594-598.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- MacDonald, I. A. W., L. L. Loope, M. B. Usher, and O. Hamann. 1989. Wildlife conservation and the invasion of nature reserves by introduced species: a global perspective. Pages 215-255 *in* J. A. Drake, H. A. Mooney, F. diCasti, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. *Biological Invasions: a global perspective*. John Wiley & Sons Ltd., New York, New York, USA.
- Machtans, C. S., M. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. *Conservation Biology* **10**:1366-1379.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* **10**:689-710.
- Martin, T. E. 1987. Artificial nest experiments: effects of nest appearance and predator type. *Condor* **89**:925-928.
- Martin, T. E. 1988a. Habitat and area effects on forest bird assemblages: is nest predation an influence? *Ecology*. **69**:74-84.

- Martin, T. E. 1988b. Processes organizing open-nesting bird assemblages: competition or nest predation? *Evolutionary Ecology* **2**:37-50.
- Martin, T. E. 1988c. On the advantage of being different: nest predation and the coexistence of bird species. *Proceedings of the National Academy of Science* **85**:2196-2199.
- Martin, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455-473 *in* J.M. Hagan III and D.W. Johnston, editors. *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Institution Press, Washington, D.C.
- Martin, T. E. 1993a. Nest predation among vegetation layers and habitat types: revising the dogmas. *The American Naturalist* **141**:897-913.
- Martin, T. E. 1993b. Nest predation and nest sites: new perspectives on old patterns. *BioScience* **43**:523-532.
- Martin, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* **79**:656-670.
- Martin, T. E., and J. R. Karr. 1986. Patch utilization by migrating birds: resource oriented? *Ornis Scandinavica* **17**:165-174.
- Martin, T. E., and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the hermit thrush. *Condor* **90**:51-57.
- Martin, T. E., and D. M. Finch, editors. 1995. *Ecology and management of Neotropical migratory birds*. Oxford University Press, New York, New York, USA.
- Martin, A. C., H. S. Zim and A. L. Nelson. 1951. *American Wildlife and Plants: a Guide to Wildlife Food Habits*. Dover, New York, New York, USA.

- Marzluff, J. M., F. R. Gehlbach, and D. A. Manuwal. 1998. Urban environments: influences on avifauna and challenges for the avian conservationist. Pages 283-299 *in* J. M. Marzluff and R. Sallabanks, editors. Avian conservation research and management. Island Press, Washington, DC.
- Marzluff, J. M., R. Bowman, and R. Donnelly, editors. 2001a. Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Boston, USA.
- Marzluff, J. M., R. Bowman, and R. Donnelly. 2001b. A historical perspective on urban bird research: trends, terms, and approaches. Pages 1-17 *in* J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Boston, USA.
- Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the Eastern United States. *Biological Conservation* **66**:185-194.
- Matlack, G. R. 1994a. Vegetation dynamics of the forest edge – trends in space and successional time. *Journal of Ecology* **82**:113-123.
- Matlack, G. R. 1994b. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* **75**:1491-1502.
- Maurer, B. A., and R. C. Whitmore. 1981. Foraging of five bird species in two forests with different vegetation structure. *Wilson Bulletin* **93**:478-490
- McDonnell, M. J. and E. W. Stiles. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* **56**:109-116.

- McDonnell, M. J., and S. T. A. Pickett. 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology* **71**:1232-1237.
- Mensing, D. M., S. M. Galatowitsch, and J. R. Tester. 1998. Anthropogenic effects on the biodiversity of riparian wetlands of a northern temperate landscape. *Journal of Environmental Management* **53**:349-377.
- Miller, J. R., and P. Cale. 2000. Behavioral mechanisms and habitat use by birds in a fragmented agricultural landscape. *Ecological Applications* **10**:1732-1748.
- Mills, G. S., J. B. Dunning, Jr., and J. M. Bates. 1989. Effects of urbanization on breeding bird community structure in southwestern desert habitats. *Condor* **91**:416-428.
- Mills, G. S., J. B. Dunning, Jr., and J. M. Bates. 1991. The relationship between breeding bird density and vegetation volume. *Wilson Bulletin* **103**:468-479.
- Moran, M. A. 1984. Influence of adjacent land use on understory vegetation of New York forests. *Urban Ecology* **8**:329-340.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* **10**:58-62.
- Naiman, R. J., and H. Decamps. 1997. The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics* **28**:621-658.
- Naiman, R. J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* **3**:209-212.
- Neill, W. M. 1983. The tamarisk invasion of desert riparian areas. *Education Bulletin*. 83-84, Desert Protective Council, Spring Valley, California, USA.

- Noble, I. R. 1989. Attributes of invaders and the invading process: terrestrial and vascular plants. Pages 301-313 *in* J. A. Drake, H. A. Mooney, F. diCastri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological Invasions: a global perspective. John Wiley & Sons Ltd., New York, New York, USA.
- Novak, S. J., and R. N. Mack 1995. Allozyme diversity in the apomictic vine *Bryonia alba*: potential consequences of multiple introductions. American Journal of Botany **82**:1153-1162.
- O'Connell, T. J., L.E. Jackson, and R. P. Brooks. 2000. Bird guilds as indicators of ecological condition in the Central Appalachians. Ecological Applications **10**:1706-1721.
- Opdam, P., G. Rijdsdijk, and F. Hustings. 1985. Bird communities in small woods in an agricultural landscape: effects of area and isolation. Biological Conservation **34**:333-352.
- Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology **8**:17-26.
- Peterjohn, W. T., and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. Ecology **65**:1466-1475.
- Rappole, J. H., and M. V. McDonald. 1994. Cause and effect in population declines of migratory birds. Auk **111**:334-345.
- Ratti, J. T., and K. P. Reese. 1988. Preliminary test of the ecological trap hypothesis. Journal of Wildlife Management **52**:484-491.

- Rehder, A. 1927. Manual of cultivated trees and shrubs hardy in North America. MacMillan, New York.
- Reijnen, R., R. Foppen, C. T. Braak, and J. Thissen. 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to proximity of main roads. *Journal of Applied Ecology* **32**:187-202.
- Rejmanek, M. 1989. Invasibility of plant communities. Pages 369-388 in J. A. Drake, F. diCastri, R. Groves, F. Kruger, H. A. Mooney, M. Rejmanek, and M. Williamson, editors. *Biological invasions: a global perspective*. Scope 37. John Wiley and Sons, Chichester, United Kingdom.
- Rey, P. J. 1995. Spatio-temporal variation in fruit and frugivorous bird abundance in olive orchards. *Ecology* **76**:1625-1635.
- Richardson, D. M., N. Allsopp, C. M. D'Antonio, S. J. Milton, and M. Rejmanek. 2000. Plant invasions – the role of mutualisms. *Biological Review* **75**:65-93.
- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* **9**:1-48.
- Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* **267**:1987-1990.
- Robinson, S. K., and R. T. Holmes. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. *Auk* **101**:672-684.
- Rodewald, A.D. and R.H. Yahner. 2001a. Influence of landscape composition on avian community structure and associated mechanisms. *Ecology* **82**:3493-3504.

- Rodewald, A.D. and R.H. Yahner. 2001b. Avian nesting success in forested landscapes: influence of landscape composition, stand and nest-patch microhabitat, and biotic interactions. *Auk* **118**:1018-1028.
- Rodewald, A.D. 2002. Nest predation in forested regions: landscape and edge effects. *Journal of Wildlife Management* **66**:634-640.
- Rotenberry, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics? *Oecologia* **67**:213-217.
- Rotenberry, J. T. 1998. Avian conservation research needs in western shrublands: exotic invaders and the alteration of ecosystem processes. Pages 261-272 *in* J.M. Marzluff and R. Sallabanks, editors. Avian conservation research and management. Island Press, Washington, DC.
- Rottenborn, S. C. 1999. Predicting the impacts of urbanization on riparian bird communities. *Biological Conservation* **88**:289-299.
- Rottenborn, S. C. 1997. The impacts of urbanization on riparian bird communities in central California. Ph.D. dissertation, Stanford University.
- Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. *Ecological Applications* **9**:135-151.
- Sallabanks, R. 1993. Fruiting plant attractiveness to avian seed dispersers: native vs. invasive *Crataegus* in western Oregon. *Madrono* **40**:108-116.
- Sanders, R. E., editor. 2001. A guide to Ohio's streams. Streams Committee, Ohio Chapter of the American Fisheries Society, Columbus, OH. USA.
- Schery, R. 1977. The curious double life of *Rosa multiflora*. *Horticulture* **55**:56-61.

- Schmidt, K. A. 1999. Foraging theory as a conceptual framework for studying nest predation. *Oikos* **85**:151-160.
- Schmidt, K. A., and C. J. Whelan. 1998. Predator-mediated interactions between and within guilds of nesting songbirds: experimental and observational evidence. *American Naturalist* **152**:393-402.
- Schmidt, K. A., and C. J. Whelan. 1999. Effects of exotic *Lonicera* and *Rhamnus* on songbird nest predation. *Conservation Biology* **13**:1502-1506.
- Southwood, T. R. E. 1961. The number of species of insect associated with various trees. *Journal of Animal Ecology* **30**:1-8.
- Trisel, D. E., and D. L. Gorchov. 1994. Regional distribution, ecological impact, and leaf phenology of the invasive shrub, *Lonicera maackii*. *Bulletin of the Ecological Society of American* **75**:231.
- Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* **14**:18-30.
- Trzcinski, M. K., L. Fahrig, and G. Merriam. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications* **9**:586-593.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* **47**:893-901.
- Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* **57**:7-13.

- Vitousek, P. M., C. M. D'Antonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997. Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* **21**:1-16.
- Whelan, C.J. 2001. Foliage structure influences foraging of insectivorous forest birds: an experimental study. *Ecology* **82**:219-231.
- Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 167-190 in R. L. Burgess and D. M. Sharpe, editors. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- White, D. W., and E. W. Stiles. 1992. Bird dispersal of fruits of species introduced into eastern North America. *Canadian Journal of Botany* **70**:1689-1696.
- Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* **66**:1211-1214.
- Willson, M. F. 1974. Avian community organization and habitat structure. *Ecology* **55**:1017-1029.
- With, K. A. 2002. The landscape ecology of invasive spread. *Conservation Biology* **16**:1192-1203.
- Woods, K. D. 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four New England forests. *American Midland Naturalist* **130**:62-74.
- Wyman, D. 1949. *Shrubs and vines for American gardens*. Macmillan Company, New York.

Yahner, R. H. 1996. Habitat fragmentation and habitat loss. *Wildlife Society Bulletin* **24**:592.

Yahner, R. H., and A. L. Wright. 1985. Depredation on artificial ground nests: effects of edge and plot age. *Journal of Wildlife Management* **49**:508-513.

Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution* **16**:454-459.

CHAPTER 2

LANDSCAPE MATRIX EFFECTS ON INVASION OF RIPARIAN FORESTS BY EXOTIC SHRUBS

Abstract

Recently, researchers have suggested that the landscape matrix may provide key insights into the invasion process. However few studies have explicitly examined surrounding land uses making it difficult to assess their effects on invasion. I examined the extent to which local or landscape level characteristics were associated with exotic shrubs in midwestern riparian forests in the United States. Twenty sites were selected in mature riparian forests ranging from 63-200 m wide along 5 major waterways (ca. 20-40 m wide) in Ohio. Sites occurred along a rural-urban gradient, ranging from < 1-47% urban land cover (i.e., paved surfaces and buildings) within 1 km. In July 2001, vegetation volume of exotic shrubs, site width, percent canopy cover, and edge aspect (N/E or S/W) were measured along 3 transects extending from the forest edge to the river edge. I developed 19 *a priori* models based on local and landscape level characteristics I hypothesized to influence exotic shrub volume and used the information-theoretic approach (Akaike's Information Criterion) to determine which model best fit the data. Exotic shrub volume was best described by the amount of urbanization within 1 km

of riparian forests. In particular, honeysuckle (*Lonicera* spp) volume was greater in more urbanized areas perhaps due to abundant seed sources. These results suggest that the landscape matrix is an important component of the invasion process and explicit consideration of land uses may improve our ability to predict or limit invasion. Once land use characteristics that promote invasion are identified (e.g., urbanization), biologists and managers may be able to minimize the impacts of exotic plants on natural areas via local restoration efforts and/or strategic reserve design and planning.

1. Introduction

Exotic plants have invaded many ecosystems and communities throughout the world, disrupting ecosystem properties, reducing native biodiversity, and altering hydrologic and fire regimes (Vitousek, 1990; Vitousek et al., 1997; Mack et al., 2000). In fact, exotic species are the second leading cause of species loss and endangerment (Wilcove et al., 1998). Although exotic plants are now recognized as a serious threat to many ecosystems, the mechanisms behind the invasion process are poorly understood. Consequently, our ability to predict invasion is minimal at best (Hobbs and Humphries, 1995; Lonsdale, 1999; Mack et al., 2000). Several researchers have identified characteristics of successful invaders (Baker, 1986; Bazzaz, 1986; Noble, 1989; Rejmanek and Richardson, 1996; Richardson et al., 2000), but these characteristics offer little predictive power, as no one trait determines the success or failure of an invader (Noble, 1989; Hobbs and Humphries, 1995; Mack et al., 2000). Other researchers have examined the susceptibility of specific communities and ecosystems to invasion, however their findings fail to consistently predict the vulnerability of specific sites (Elton, 1958; Baker, 1986; Rejmanek, 1989; Pysek and Prach, 1993; Hobbs and Humphries, 1995;

Mack et al., 2000). The difficulty may be, in part, due to the variation in the landscape context of ecological communities. Landscape context is known to be an important determinant of plant (Hobbs, 2000), bird (Flather and Sauer, 1996) and mammal (Dijak and Thompson, 2000) communities. Thus, investigating how landscape-level patterns affect the process of invasion is a critical component in predicting invasion and consequently limiting the spread of exotic plants (Hobbs and Humphries, 1995; Mooney, 1999; Hobbs, 2000; Byers et al., 2002; Pysek et al., 2002).

Previous studies have focused on local-scale mechanisms that affect exotic plant invasion and persistence (Ranney et al., 1981; Luken, 1988; Brothers and Spingarn, 1992; Matlack, 1993, 1994a; Woods, 1993; Luken and Goessling, 1995; Goldblum and Beatty, 1999). Several of these studies have shown that abundance of exotic species decreases with increasing distance from the edge, which suggests that the type of edge and/or adjacent land uses may contribute to the observed patterns. In fact, Moran (1984) found that forest patches adjacent to urban areas contained more exotic herbs and shrubs than did forests adjacent to agricultural areas. Although Rottenborn (1997,1999) examined the association between land uses and exotic plant and avian abundance in California he did so at relatively small spatial scales. Few studies have specifically investigated the role of the landscape matrix and, in particular, how the degree of urbanization affects invasion by exotic plants. Instead, investigators have inferred landscape associations based on subjective categorization or anecdotal evidence (Moran, 1984; Brothers and Spingarn, 1992; Luken et al., 1995; Planty-Tabacchi et al., 1996), past herbarium collections (Mack, 1981), historical records (Pysek and Prach, 1993; Luken and Thieret, 1996), or aerial photos (Lonsdale, 1993; Hutchinson and Vankat, 1998). Without

specifically quantifying the surrounding landscape matrix we lack the ability to control invasion and subsequently reduce our ability to design effective reserves. Moreover, understanding how the landscape matrix influences invasion risk will greatly improve our ability to buffer reserves from invasion by exotic plants.

There is an urgent need to assess how land use patterns influence exotic plant invasion (Hobbs and Humphries, 1995; D'Antonio et al., 2001; Davies et al., 2001; Byers et al., 2002) especially as the rate of urbanization and new introductions increases (Ewel et al., 1999; Mack et al., 2000). Landscape level studies of plant invasion are particularly relevant for species whose establishment is inextricably linked to human activities (e.g., *Lonicera* spp and *Rosa multiflora*). Moreover, riparian forests provide an excellent opportunity to examine these interactions because riparian areas (1) are influenced to a large degree by external pressures, such as encroachment of exotic plants (Rejmanek, 1989; Planty-Tabacchi et al., 1996) (2) typically span the entire gradient of urbanization (e.g., from rural to urban), which allows for rigorous testing of the impacts of urbanization (McDonnell and Pickett, 1990; Marzluff et al., 2001), and (3) receive substantial attention from local and regional conservation groups. In this study, I explicitly test if local and/or landscape matrix characteristics influence the extent of exotic shrub invasion in riparian forests.

2. Methods

2.1. Study area

I studied invasion of exotic shrubs in riparian forests within the Scioto River Watershed located in the Till Plains physiographic region of Ohio. Sites are located

within Franklin and Delaware counties on publicly and privately owned lands. Land cover within these two counties is primarily agriculture (44%) and urban/residential development (41%), whereas only 8.5% of the land cover within these two counties is forested (USGS EROS Data Center, 2000). Remnant forests persist mainly in riparian areas (Laub, 1979; Groom and Grubb, 2002) and generally consist of three forest types: beech-maple, swamp (silver maple-American elm), and floodplain (cottonwood-sycamore) (Forsyth, 1979). Dominant tree species include hickory (*Carya* species), black cherry (*Prunus serotina*), white ash (*Fraxinus americana*), sugar maple (*Acer saccharum*), silver maple (*Acer saccharinum*), American elm (*Ulmus americana*), cottonwood (*Populus deltoides*), sycamore (*Platanus occidentalis*), honeylocust (*Gleditsia triacanthos*), Ohio buckeye (*Aesculus glabra*), and boxelder (*Acer negundo*). Dominant shrubs include honeysuckle (*Lonicera* spp.), multiflora rose (*Rosa multiflora*), spicebush (*Lindera benzoin*), and hawthorn (*Crataegus* spp.) (Appendix A).

Potential riparian forest study sites (approximately > 40 m wide and > 250 m long) within the watershed were identified from digital orthophoto quadrangle images (USGS DOQ 1994-95, 1:24,000) and detailed maps of Franklin and Delaware counties. From these, I selected 20 sites that met the following criteria (1) mature riparian forest, (2) ≥ 40 m wide, (3) ≥ 250 m long, (4) ≥ 2 km between sites, (5) negligible slope ($< 5\%$), and (6) river width of approximately 20-40 m (Appendix B, C). I calculated the percent land area containing urban, forest, and agricultural cover types within a 1 km radius for each site using Thematic Mapper Imagery data and ArcView geographic information software (Table 2.1). Land covered by pavement, or buildings was classified as urban

development, and open (non-forested lacking wetlands or water) vegetation was classified as agriculture. The amount of forest within the landscape was not confounded with the amount of urban land cover, as the two were unrelated ($r = -0.075$).

2.2. Vegetation sampling

Exotic shrub volume was sampled using modified line point methodology (Barbour et al., 1987) along three transects separated by 50 m within each site. Transects were placed perpendicular to the forest edge and extended the entire width of the site, from the forest edge to the river. I defined an edge as the center of the outermost canopy tree (Brothers and Spingarn, 1992). I sampled vegetation volume from 0 to 4 m above the ground in 0.5 m intervals using an extendable aluminum pole positioned at successive 5 m points along each transect. At each of these points, I recorded the number of times exotic shrub species touched the pole within each 0.5 m interval (Chase, 2002). All tree and shrub species contacting the pole were identified to species, while all other vegetation hits were categorized as either native or exotic forb, grass, or vine.

Other local level variables collected include density of human trails, edge aspect (N/E vs. S/W), site width, and canopy cover (Appendix D). Assessment of relative trail density within each site was determined by counting the number of times a trail intersected each vegetation transect. Site width was determined by taking the mean length of three vegetation transects per site. Canopy cover also was recorded every 5 m along each transect using an ocular tube (James and Shugart, 1970). In addition, I recorded the type of adjacent edge, noted any unusual site characteristics, and documented each edge with a photograph (35mm).

2.3. Data Analysis

Exotic shrub volume was calculated as the total number of hits among all 0.5 m intervals at each point, divided by the number of points sampled per transect. I then averaged volume estimates over all three transects to obtain vegetation volume estimates per site.

To determine if exotic shrub volume is greater near the forest edge than away from it, I summed the number of hits over all intervals at each point and averaged each point over three transects and over all sites. Pearson correlation coefficients were used to determine if exotic shrub volume was correlated with the distance from the forest edge.

Exotic shrubs in the 20 riparian forest sites consisted mainly of *Lonicera maackii*, *L. tatarica*, and *Rosa multiflora*, thus I focused my analyses on these species. Because *L. maackii* and *L. tatarica* were introduced in a similar manner and exhibit similar life history characteristics, I grouped these two species in my analysis. In contrast, I analyzed *Lonicera* spp (hereafter *Lonicera*) and *R. multiflora* separately because both points of introduction and life histories differ substantially.

I developed a set of *a priori* models based on previous studies and on what I hypothesized would influence exotic plant invasion. These models incorporated landscape and site level variables as well as interactions between variables (Table 2.2). To reduce the number of initial model statements, I removed variables that were redundant or strongly correlated ($r > 0.70$) with other terms and those that lacked adequate variation across sites. I used the information-theoretic approach (Burnham and Anderson, 1998) to determine which candidate model of exotic shrub volume was best

supported by the data. I calculated Akaike's Information Criterion (AIC) and bias-corrected AIC_c (Burnham and Anderson, 1998) from log-likelihood values generated using the GENMOD procedure (SAS Institute, 1990). Because the distribution of *Lonicera* and *R. multiflora* cover fit a negative binomial distribution (i.e., the variance was greater than the mean, Fowler and Cohen, 1990), I specified the negative binomial distribution in GENMOD. Differences in AIC_c values, delta AIC (Δ_i) and Akaike weights (w_i) among models were used to identify the model that was best supported by my data. Models with large delta AIC (Δ_i) values are less plausible given the data and Akaike weights (w_i) provide an additional measure of strength of evidence for a model (Burnham and Anderson, 1998).

3. Results

Relative trail density at each site was positively correlated with the amount of urbanization within 1 km ($r = 0.70$, $p = < 0.001$), and therefore, I dropped trail density from the analysis. The amount of agriculture in the landscape was negatively correlated with the amount of urban land cover ($r = -0.75$, $p = < 0.001$) and also was dropped from subsequent analyses. Because canopy cover showed little variation among sites (range = 78 - 97%, mean = 89.32 ± 1.30 SE, CV = 6.51), it was not included in the model statements. In total, 19 candidate models were created separately for *Lonicera* and *R. multiflora* using the variables site width, amount of urban land cover within 1 km, amount of forest cover within 1 km, edge aspect (N/E vs. S/W), and interactions between variables (Table 2.2 and Appendix E). Of these 19 candidate models, delta AIC (Δ_i) and Akaike weights (w_i) identified the model containing percent urban land cover within 1 km as the best model describing both *Lonicera* and *R. multiflora* volume within riparian

forests (Table 2.2). *Lonicera* volume was positively associated with the degree of urban land cover within the landscape (Fig. 2.1a), whereas the amount of *R. multiflora* volume was negatively associated with urban land cover (Fig. 2.1b). Several models were closely ranked with delta AIC (Δ_i) < 2 for *Lonicera* (Table 2.2). However, the sums of the Akaike's weights (w_i) for all models containing the urban variable suggested that the most important variable among those tested was the percent of urban land cover (*Lonicera* = 0.573, *R. multiflora* = 0.812). At a smaller scale, vegetation volume of *Lonicera* was negatively correlated with distance from the forested edge ($r = -0.202$, $p = < 0.001$, Fig. 2.2), whereas *R. multiflora* showed no association with distance from edge ($r = -0.026$, $p = 0.520$).

4. Discussion

I found that invasion of riparian forests by exotic shrubs was best explained by the landscape matrix rather than local characteristics, such as aspect of edge or forest width. Specifically, the amount urban development within 1 km of riparian forests was associated with the extent of both *Lonicera* and *R. multiflora* volume. The association between urbanized landscapes and exotic shrub volume is consistent with observations from previous studies (Moran, 1984; Nilsson et al., 1989; Timmins and Williams, 1991; Planty-Tabacchi et al., 1996; Luken and Thieret, 1996; Hutchinson and Vankat, 1997; Rottenborn, 1997; Pysek et al., 2002). For example, Nilsson et al. (1989) and Planty-Tabacchi et al. (1996) both suggested that the proportion of exotic plants within riparian areas increased as the distance to heavily urbanized landscapes decreased. Moreover, Pysek et al. (2002) found that exotic plants increased with human population density. Luken and Thieret (1996) also suggested that *Lonicera* populations occur most often in

urban landscapes. Although these studies suggested that urban areas contain higher densities of exotic plants, composition of the matrix or of surrounding land uses were not explicitly tested, and this limited their ability to examine the nature of the association. An important distinction between my study and others is that I quantified the degree of urbanization along a gradient from areas with < 1% to > 40% development. Using the gradient approach improves our ability to make management decisions and improves our ability to limit or prevent invasion (McDonnell and Pickett, 1990; Marzluff et al., 2001).

Urban areas can facilitate invasion by exotic shrubs because developed lands often maintain high densities of exotic ornamental shrubs, particularly *Lonicera*, which provide ample seed sources. The proximity of a forest patch to a seed source greatly increases dispersal probabilities, and consequently influences the risk of invasion (Rejmanke, 1989; Matlack, 1994b; Mack et al., 2000). The positive association between urbanized landscapes and trail densities in my study also suggests that urban forest patches may have higher levels of human activity, which can exacerbate the invasion process by providing additional dispersal agents (e.g., humans) and disturbance (Lonsdale, 1999). Moreover, trails can create suitable microsites similar to those created by tree fall gaps, which may promote further encroachment of exotic plants (Goldblum and Beatty, 1999).

Interestingly, *R. multiflora* showed the opposite pattern of *Lonicera* as its distribution was negatively associated with urbanization. This difference is likely explained by points of introduction. *Rosa multiflora* was first introduced into agricultural areas to prevent soil erosion and to act as a “living fence” for livestock (Albaugh, 1977;

Schery, 1977). Thus, I expected to find elevated levels in rural landscapes. In this way, past as well as current land uses can be useful predictors of the extent of exotic shrubs (Timmins and Williams, 1991; Ruesink, 1998).

In addition to the effects of urbanization, I originally hypothesized that the amount of forest cover within the landscape might explain the degree of invasion by exotic shrubs as it is inversely related to the amount of anthropogenic disturbance in my study area. However, the percent of forest cover within 1 km was not strongly related to the extent of exotic shrub volume. Yet, a model statement for *Lonicera* that contained the forest cover variable was ranked as the third best model given the data, but in an unexpected way. Sites with a higher percentage of forest cover often had more *Lonicera* volume relative to sites with less forest cover. The amount of forest cover and degree of connectivity can serve as an effective means of exotic shrub expansion at a regional level (Hutchinson and Vankat, 1998) and perhaps at the local level as well.

Unlike other studies (Brothers and Spingarn, 1992; Matlack, 1993; Luken et al., 1995; Luken and Goessling, 1995), I found no evidence that canopy cover or edge aspect influenced invasion of riparian forests by exotic plants (Appendix D). Light availability is often a factor limiting exotic plant establishment and canopy cover and edge aspect are often used as indicators of light availability. Canopy cover did not seem to be an important factor determining the extent of invasion given that it did not vary across my sites. Edge aspect may also indicate available light, as light penetration into forests is typically higher along S/W edges than N/E edges. However, edge aspect apparently did not influence the amount of either *Lonicera* or *R. multiflora* volume. Although I did not quantify light availability (e.g., Luken and Goessling, 1995), light may not be a major

factor determining the presence of exotic plants at my sites. For example, forest-growing *Lonicera* populations could allocate resources towards stem regrowth that requires less photosynthetic activity while still allowing for self-perpetuating populations (Luken, 1988).

Surprisingly, site width was not identified as the major factor determining extent of exotic shrubs at my sites. Although the influence of size and perimeter to area ratio on abundance of exotic plants is somewhat unclear (Timmins and Williams, 1991; Pysek et al., 2002), one would predict that narrower sites are more likely to be completely invaded and thus have elevated cover (Timmins and Williams, 1991; Planty-Tabacchi et al., 1996). This pattern is evident in that site width in my study was ranked as the second best model for *Lonicera* (i.e., narrower sites contained greater quantities of *Lonicera*), but ultimately the landscape matrix explained more of the variation.

Although site width did not appear to affect invasion, I found that at a smaller scale, volume of exotic shrubs was negatively related to the distance from the forested edge. Specifically, *Lonicera* volume was much greater near the forested edge than away from it (Fig. 2.2). This relationship further suggests that edge type and adjacent land uses can influence the degree of invasion. If the surrounding edge contains dense patches of exotic shrubs, then edges may contribute to elevated levels of exotic shrubs within the forest, especially if the surrounding landscape provides sufficient structure and foraging resources for animal dispersers such as frugivorous birds (Beissinger and Osborne, 1982).

Limiting the spread of exotic shrubs, such as *Lonicera*, is essential as many species are reaching noxious weed status in some areas. *Lonicera* can have long-term negative effects on plant community structure by causing local extinction of herbaceous

species and by suppressing new seedling establishment, ultimately changing canopy composition (Woods, 1993; Trisel and Gorchov, 1994; Luken and Goessling, 1995; Hutchinson and Vankat, 1997; Collier et al. 2002). *Rosa multiflora* may even cause the decline of some native moth species that feed on grasses in areas where it dominates (Eckardt, 1987). The presence of exotic plants within communities also may be permeating to higher trophic levels by altering predator-prey interactions, such as between breeding birds and nest predators (Schmidt and Whelan, 1999). In another study, I found that birds nesting in exotic shrubs were more vulnerable to nest predators than those nesting in native substrates (Borgmann and Rodewald, in review). In addition, exotic plants may alter arthropod abundance (Southwood, 1961; Mills et al., 1989), fruiting resources (Ingold and Craycraft, 1983; Debussche and Isenmann, 1990), and structural resources (Maurer and Whitmore, 1981; Meents et al., 1984; Whelan, 2001) for bird species. Clearly, exotic plants are negatively impacting plant and animal communities, therefore efforts need to be directed toward predicting or preventing further spread.

Overall, these results suggest that the landscape matrix significantly impacts the extent of exotic plant invasion. In particular, urbanization seemed to promote the invasion of *Lonicera* in riparian forests. Moreover, *Lonicera* was more likely to dominate the understory in riparian forests that were surrounded by urban development (A. D. Rodewald, unpublished data). Because *Lonicera* and *R. multiflora* can adapt to a wide variety of environmental conditions (Schery, 1977; Luken, 1988; Woods, 1993; Luken and Goessling, 1995), their spread is most likely influenced by dispersal mechanisms and proximity to a seed source, which are ultimately linked with land use

patterns. Thus incorporating landscape scale features is a critical component in understanding the invasion process, which may allow us to increase our ability to minimize future invasions. Moreover, because eradication of exotic species has proven to be both laborious and economically challenging, efforts may be better directed toward predicting or preventing future invasions (Hobbs and Humphries, 1995; Ewel et al., 1999). Once land use characteristics that promote invasion are identified, biologists and managers may be able to minimize the impacts of exotic plants via local restoration efforts and/or strategic reserve design and planning (Luken, 1997; Byers et al., 2002). Promoting low-development buffer zones in areas surrounding reserves may reduce the risk of invasion by ornamental exotic plants (Hobbs and Humphries, 1995; Pysek et al., 2002). Strategically placed reserves also can increase the potential for native plant recolonization (Matlack, 1994b). For example, establishing forest reserves near old growth or older second growth stands can increase capacity of native herbs and shrubs to establish (Matlack, 1994b). In addition, community developers and can advocate planting native shrubs and herbs within metropolitan areas to limit spread into nearby forest patches.

Literature cited

- Albaugh, G. P., Mitchell, W. H., Graham, J. C., 1977. Evaluation of glyphosate for multiflora rose control. *Proceedings NE Weed Science Society* 31, 283-291.
- Baker, H. G., 1986. Patterns of plant invasions in North America. In: Mooney, H. A., Drake, J. A. (Eds.), *Ecology of Biological Invasions of North America and Hawaii*. Springer-Verlag, New York, pp. 44-55.
- Barbour, M. G., Burk, J. H., Pitts, W. D., 1987. *Terrestrial Plant Ecology*. Second Edition. The Benjamin/Cummings Publishing Company, Inc., Menlo Park.
- Bazzaz, F. A., 1986. Life history of colonizing plants: some demographic, genetic, and physiological features. In: Mooney, H. A., Drake, J. A. (Eds.), *Ecology of Biological Invasions of North America and Hawaii*. Springer-Verlag, New York, pp. 96-110.
- Beissinger, S. R., Osborne, D. R., 1982. Effects of urbanization on avian community organization. *Condor* 84, 75-83.
- Borgmann, K. L., Rodewald A. D., In review. Exotic shrubs as an underlying mechanism of increased nest failure in fragmented landscapes. *Ecology*.
- Braun, E. L., 1961. *The Woody Plants of Ohio*. Ohio State University Press. Columbus.
- Brothers, T. S., Spingarn, A., 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Conservation Biology* 6, 91-100.
- Burnham, K. P., Anderson, D. R., 1998. *Model Selection and Inference: a Practical Information-theoretic Approach*. Springer-Verlag, New York.

- Byers, J. E., Reichard, S., Randall, J. M., Parker, I. M., Smith, C. S., Lonsdale, W. M., Atkinson, I. A. E., Seastedt, T. R., Williamson, M., Chornesky, E., Hayes, D., 2002. Directing research to reduce the impacts of nonindigenous species. *Conservation Biology* 16, 630-640.
- Chase, M. K., 2002. Nest site selection and nest success in a song sparrow population: the significance of spatial variation. *Condor* 104, 103-116.
- Collier, M. H., Vankat, J. L., Hughes, M. R., 2002. Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. *American Midland Naturalist* 147, 60-71.
- D'Antonio, C., Meyerson, L. A., Denslow, J., 2001. Exotic species and conservation. In: Soule, M. E., Orians G. H. (Eds.), *Conservation Biology: Research Priorities for the Next Decade*. Island Press, Washington, DC, pp. 59-80.
- Davies, K. F., Gascon, C., Margules, C. R., 2001. Habitat fragmentation: consequences, management, and future research priorities. In: Soule, M. E., Orians G. H. (Eds.), *Conservation Biology: Research Priorities for the Next Decade*. Island Press, Washington, DC, pp. 81-97.
- Debussche, M., Iseman, P., 1990. Introduced and cultivated fleshy-fruited plants: consequences of a mutualistic Mediterranean plant bird system. In: di. Castri, F., Hansen, A. J., Debussche, M. (Eds.), *Biological Invasions in Europe and the Mediterranean Basin*. Kluwer Academic Publishers, Dordrecht, pp. 399-416.
- Dijak, W. D., Thompson, F. R., 2000. Landscape and edge effects on the distribution of mammalian predators in Missouri. *Journal of Wildlife Management* 64, 209-216.

- Eckardt, N., 1987. Element stewardship abstract, *Rosa multiflora*. Unpublished report for The Nature Conservancy, Arlington.
- Elton, C., 1958. The Ecology of Invasions by Plants and Animals. Methuen. London.
- Ewel, J. J., O'Dowd, D. J., Bergelson, J., Daehler, C. C., D'Antonio, C. M., Gomez, L. D., Gordon, D. R., Hobbs, R. J., Holt, A., Hopper, K. R., Hughes, C. E., LaHart, M., Leakey, R. R. B., Lee, W. G., Loope, L. L., Lorence, D. H., Louda, S. M., Lugo, A. E., McEvoy, P. B., Richardson, D. M., Vitousek, P. M., 1999. Deliberate introductions of species: research needs. *BioScience* 49, 619-630.
- Flather, C. H., Sauer, J. R., 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. *Ecology* 77, 28-35.
- Forsyth, J. L., 1979. Tills plains. In: Lafferty, M. B. (Ed.), Ohio's Natural Heritage. The Ohio Academy of Sciences, Columbus, pp. 198-213.
- Fowler, J., Cohen, L., 1990. Practical Statistics for Field Biology. Open University Press, Philadelphia.
- Goldblum, D., Beatty, S. W., 1999. Influence of an old field/forest edge on a northeastern United States deciduous forest understory community. *Journal of the Torrey Botanical Society* 126, 335-343.
- Groom, J. D., Grubb, T. C., Jr., 2002. Bird species associated with riparian woodland in fragmented, temperate-deciduous forest. *Conservation Biology* 16, 832-836.
- Hobbs, R. J., 2000. Land-use changes and invasions. In: Mooney, H. A., Hobbs, R. J. (Eds.), *Invasive Species in a Changing World*. Island Press, Washington, DC, pp. 55-64.

- Hobbs, R. J., Humphries, S. E., 1995. An integrated approach to the ecology and management of plant invasions. *Conservation Biology* 9, 761-770.
- Hutchinson, T. F., Vankat, J. L., 1998. Landscape structure and spread of the exotic shrub *Lonicera maackii* (Amur honeysuckle) in southwestern Ohio forests. *American Midland Naturalist* 139, 383-390.
- Hutchinson, T. F., Vankat, J. L., 1997. Invasibility and effects of Amur Honeysuckle in Southwestern Ohio forests. *Conservation Biology* 11, 1117-1124.
- Ingold, J. L., Craycraft, M. J., 1983. Avian frugivory on honeysuckle (*Lonicera*) in southwestern Ohio in fall. *Ohio Journal of Science* 83, 256-258.
- James, F. C., Shugart, H. H., Jr., 1970. A quantitative method of habitat description. *Audubon Field Notes* 24, 727-736.
- Laub, K. W., 1979. Changing land use: forests, farms, and wildlife. In: Lafferty, M.B. (Ed.), *Ohio's Natural Heritage*. The Ohio Academy of Sciences, Columbus, pp. 272-281.
- Lonsdale, W. M., 1993. Rates of spread of an invading species *Mimosa pigra* in northern Australia. *Journal of Ecology* 81, 513-521.
- Lonsdale, W. M., 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80, 1522-1536.
- Luken, J. O., 1988. Population structure and biomass allocation of the naturalized shrub *Lonicera maackii* (Rupr.) maxim. in forest and open habitats. *American Midland Naturalist* 119, 258-267.

- Luken, J. O., 1997. Management of plant invasions: implicating ecological succession. In: Luken, J. O., Thieret S. W. (Eds.), Assessment and Management of Plant Invasions. Springer-Verlag, New York, pp. 133-144.
- Luken, J. O., Goessling, N., 1995. Seedling distribution and potential persistence of the exotic shrub *Lonicera maackii* in fragmented forests. American Midland Naturalist 133, 124-130.
- Luken, J. O., Tholemeier, T. C., Kuddes, L. M., Kunkel, B. A., 1995. Performance, plasticity, and acclimation of the nonindigenous shrub *Lonicera maackii* (Caprifoliaceae) in contrasting light environments. Canadian Journal of Botany 73, 1953-1961.
- Luken, J. O., Thieret, J. W., 1996. Amur honeysuckle, its fall from grace. Bioscience 46, 18-24.
- Mack, R. N., 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. Agro-ecosystems 7, 145-165.
- Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., Bazzaz, F. A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10, 689-710.
- Marzluff, J. M., Bowman, R., Donnelly, R., 2001. A historical perspective on urban bird research: trends, terms, and approaches. In: Marzluff, J. M., Bowman, R., Donnelly, R. (Eds.), Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic Publishers, Boston, pp. 1-17.
- Matlack, G. R., 1993. Microenvironment variation within and among forest edge sites in the Eastern United States. Biological Conservation 66, 185-194.

- Matlack, G. R., 1994a. Vegetation dynamics of the forest edge – trends in space and successional time. *Journal of Ecology* 82, 113-123.
- Matlack, G. R., 1994b. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* 75, 1491-1502.
- Maurer, B. A., Whitmore, R. C., 1981. Foraging of five bird species in two forests with different vegetation structure. *Wilson Bulletin* 93, 478-490.
- McDonnell, M. J., Pickett, S. T. A., 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology* 71, 1232-1237.
- Meents, J. K., Anderson, B. W., Ohmart, R. D., 1984. Sensitivity of riparian birds to habitat loss. In: Warner, R. E., Hendrix, K. M. (Eds.), *California Riparian Systems: Ecology, Conservation and Productive Management*. University of California Press, Berkeley, pp. 619-625.
- Mills, G. S., Dunning, J. B., Jr., Bates, J. M., 1989. Effects of urbanization on breeding bird community structure in southwestern desert habitats. *Condor* 91, 416-428.
- Moran, M. A., 1984. Influence of adjacent land use on understory vegetation of New York forests. *Urban Ecology* 8, 329-340.
- Mooney, H. A., 1999. A global strategy for dealing with alien invasive species. In: Sandland, O. T., Schie, P. J., Viken, A. (Eds.), *Invasive Species and Biodiversity Management*. Kluwer Academic Publishers, Netherlands, pp. 407-418.
- Nilsson, C., Grelsson, G., Johansson, M., Sperens, U., 1989. Patterns of plant species richness along riverbanks. *Ecology* 70, 77-84.

- Noble, I. R., 1989. Attributes of invaders and the invading process: terrestrial and vascular plants. In: Drake, J. A., Mooney, H. A., di. Castri, F., Groves, R. H., Kruger, F. J., Rejmanek, M., Williamson, M. (Eds.), *Biological Invasions: a Global Perspective*. John Wiley & Sons Ltd., Chichester, pp. 310-313.
- Planty-Tabacchi, A., Tabacchi, E., Naiman, R. J., Deferrari, C., Decamps, H., 1996. Invasibility of species-rich communities in riparian zones. *Conservation Biology* 10, 598-607.
- Pysek, P., Prach, K., 1993. Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. *Journal of Biogeography* 20, 413-420.
- Pysek, P., Jarosik, V., Kucera, T., 2002. Patterns of invasion in temperate nature reserves. *Biological Conservation* 104, 13-24.
- Ranney, J. W., Bruner, M. C., Levenson, J. B., 1981. The importance of edge in the structure and dynamics of forest islands. In: Burgess, R. L., Sharpe, D. M. (Eds.), *Forest Island Dynamics in Man-dominated Landscapes*. Springer-Verlag, New York, pp. 67-95.
- Rejmanek, M., 1989. Invasibility of plant communities. In: Drake, J. A., Mooney, H. A., di. Castri, F., Groves, R. H., Kruger, F. J., Rejmanek, M., Williamson, M. (Eds.), *Biological Invasions: a Global Perspective*. John Wiley & Sons Ltd., Chichester, pp. 369-388.
- Rejmanek, M., Richardson, D. M., 1996. What attributes make some plant species more invasive? *Ecology* 77, 1655-1661.

- Richardson, D. M., Allsopp, N., D'Antonio, C. M., Milton, S. J., Rejmanek, M., 2000. Plant invasions – the role of mutualisms. *Biological Review* 75, 65-93.
- Rottenborn, S. C., 1997. The impacts of urbanization on riparian bird communities in central California. Ph.D. dissertation, Stanford University.
- Ruesink, A., 1998. Links between land use and *Lonicera*: patterns of honeysuckle invasion in a post-agricultural landscape. M.S. Thesis. University of Vermont, Burlington.
- SAS Institute., 1990. SASSTAT User's Guide. SAS Institute, Cary, North Carolina.
- Schery, R., 1977. The curious double life of *Rosa multiflora*. *Horticulture* 55, 56-61.
- Schmidt, K. A., Whelan, C. J., 1999. Effects of exotic *Lonicera* and *Rhamnus* on songbird nest predation. *Conservation Biology* 13, 1502-1506.
- Southwood, T. R. E., 1961. The number of species of insect associated with various trees. *Journal of Animal Ecology* 30, 1-8.
- Timmins, S. M., Williams, P. A., 1991. Weed numbers in New Zealand's forest and scrub reserves. *New Zealand Journal of Ecology* 15, 153-162.
- Trisel, D. E., Gorchov, D. L., 1994. Regional distribution, ecological impact, and leaf phenology of the invasive shrub, *Lonicera maackii*. *Bulletin of the Ecological Society of American* 75, 231.
- USGS EROS Data Center., 2000. MRLC regional land cover characterization project land cover data for Ohio early 1900s (version 2000-03). Multi-resolution land characteristics consortium. National Land Cover Data Program.
- Vitousek, P. M., 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57, 7-13.

Vitousek, P. M., D'Antonio, C. M., Loope, L. L., Rejmanek, M., Westbrooks, R., 1997.

Introduced species: a significant component of human-caused global change. *New*

Zealand Journal of Ecology 21, 1-16.

Whelan, C. J., 2001. Foliage structure influences foraging of insectivorous forest birds:

an experimental study. *Ecology* 82, 219-231.

Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying

threats to imperiled species in the United States. *Bioscience* 48, 607-615.

Woods, K. D., 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree

seedlings in four New England forests. *American Midland Naturalist* 130, 62-74.

Site	Mean site width (m)	Urban (%)	Agriculture (%)	Forest (%)
Big Walnut Park	83	45.78	15.51	36.72
Casto Park	142	47.17	26.71	24.57
Cherrybottom Park	150	31.22	35.38	28.87
Darby Public Hunting	141	0.95	58.27	39.66
Elkrun Park	160	12.64	66.56	17.76
Galena	200	1.23	42.06	42.53
Gardner Rd.	111	1.23	54.01	43.28
Innis Park	63	7.61	39.86	51.09
Kilbourne	116	0.41	62.52	35.54
Lockbourne Park	158	2.68	68.77	24.48
North Galena	110	0.14	45.97	53.15
North Olentangy	88	29.47	22.55	45.04
Prairie Oaks	117	0.98	65.03	29.69
Prindle	140	0.12	83.75	12.92
Smith Farm	71	14.88	71.30	61.02
South Galena	158	0.13	50.22	12.01
Three Creeks	113	7.81	73.28	15.36
Whetstone Park	95	30.59	15.17	48.18
Whitehall Park	77	35.42	34.23	49.91
Woodside Green Park	106	17.80	47.68	29.22

Table 2.1. Mean site width (m) and percent land use covered by urban development, agriculture, and forest within 1 km of 20 riparian forest sites in central Ohio, USA.

Model statements	Log likelihood	K	AIC _c	Δ_i	w_i
<i>Lonicera</i> spp.					
Urban ^a	2124.415	3	-4241.33	0.000	0.347
Width ^b	2123.735	3	-4239.97	1.361	0.176
Forest ^c	2123.727	3	-4239.95	1.378	0.174
Urban width	2124.474	4	-4238.28	3.050	0.075
Urban forest	2124.422	4	-4238.18	3.153	0.072
Urban forest	2125.648	5	-4237.01	4.320	0.040
Forest width	2123.789	4	-4236.91	4.419	0.038
Aspect ^d	2123.627	4	-4236.59	4.743	0.032
Urban forest width	2135.663	9	-4235.33	6.006	0.017
Urban width	2124.626	5	-4234.97	6.364	0.014
Urban forest width	2124.495	5	-4234.70	6.627	0.013
Aspect urban	2124.431	5	-4234.58	6.754	0.012
Forest width	2123.921	5	-4233.56	7.774	0.007
Forest aspect	2123.767	5	-4233.25	8.083	0.006
Width aspect	2123.749	5	-4233.21	8.119	0.006
Urban forest width aspect	2124.547	6	-4230.63	10.698	0.002
Aspect urban	2125.530	7	-4227.73	13.605	0.000
Width aspect	2124.021	7	-4224.71	16.622	0.000
Forest aspect	2123.960	7	-4224.59	16.745	0.000
<i>Rosa multiflora</i>					
Urban	242.343	3	-477.187	0.000	0.443
Urban width	242.912	4	-475.157	2.029	0.161
Urban forest	242.429	4	-474.191	2.996	0.099
Width	240.527	3	-473.554	3.633	0.072
Forest width	241.651	4	-472.636	4.551	0.046
Urban forest width	243.460	5	-472.634	4.553	0.045
Forest	239.860	3	-472.220	4.967	0.037
Urban width	242.969	5	-471.653	5.534	0.028
Forest width	242.694	5	-471.101	6.086	0.021
Urban forest	242.678	5	-471.069	6.118	0.021
Aspect urban	242.618	5	-470.949	6.238	0.020
Urban forest width aspect	243.839	6	-469.215	7.971	0.008
Width aspect	241.680	5	-469.073	8.114	0.008
Aspect	239.607	4	-468.546	8.640	0.006
Aspect urban	244.820	7	-466.307	10.880	0.002
Forest aspect	239.863	5	-465.440	11.746	0.001
Width aspect	241.808	7	-460.283	16.904	0.000
Forest aspect	240.058	7	-456.782	20.405	0.000
Urban forest width	246.150	9	-456.300	20.887	0.000

^a Percent urbanization within 1 km of each site

^b Mean width (m) of riparian forest measured at 3 transects

^c Percent forest cover within 1 km of each site

^d Edge orientation (North/East or South/West)

Table 2.2. Model statements describing *Lonicera* and *Rosa multiflora* volume in 20 riparian forests in central Ohio. Models are ranked according to AIC_c and delta AIC (Δ_i) scores. Best-supported models have smaller delta AIC (Δ_i) scores and larger Akaike weights (w_i). Vertical bars represent both main effects and interactions between variables.

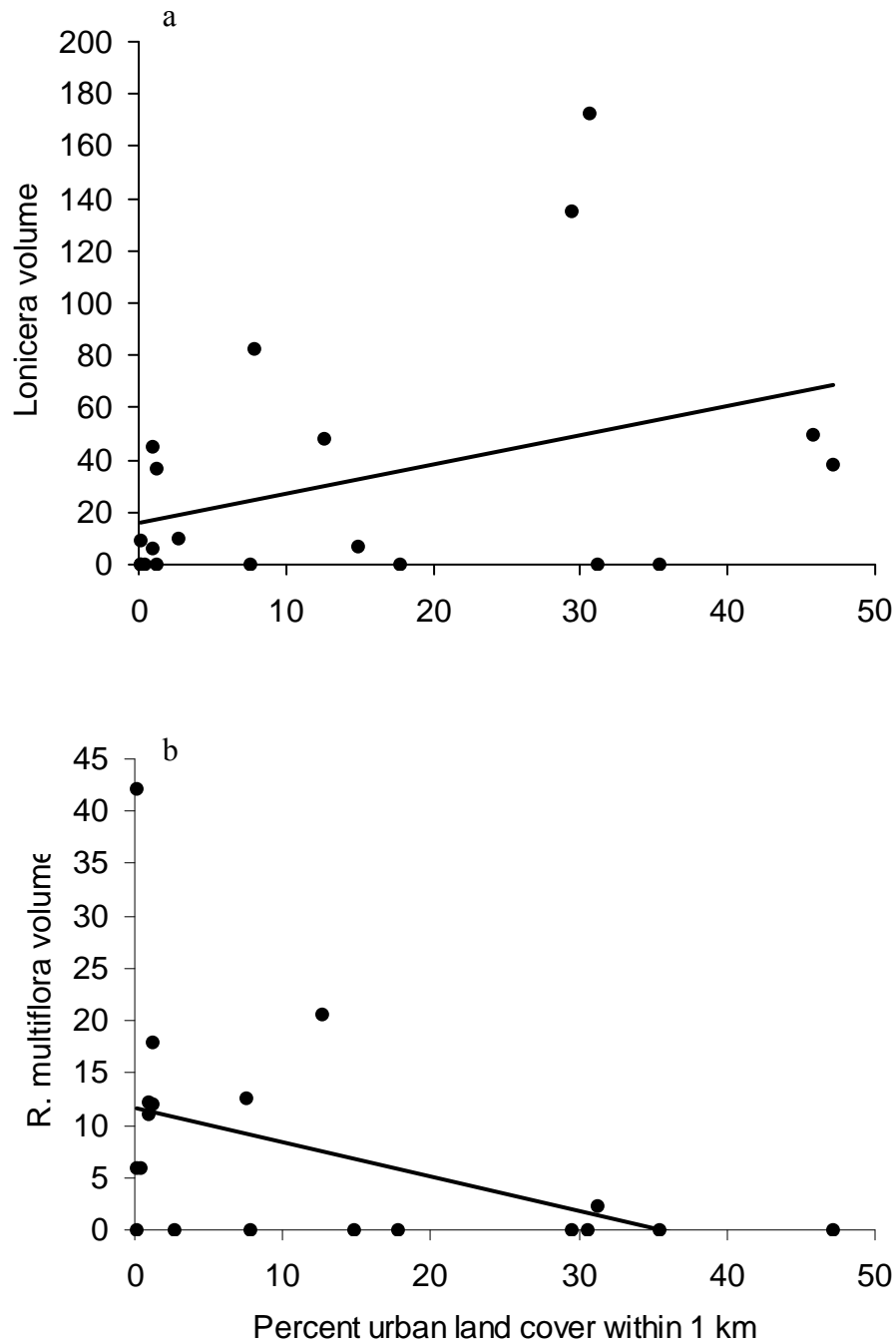


Figure 2.1. (a) Percent *Lonicera* spp. volume compared to the percentage of urbanization within 1 km of riparian forest sites ($y = 2.6890 + 0.0416x$). (b) Percent *R. multiflora* volume compared to the percentage of urbanization within 1 km of riparian forest sites ($y = 2.5502 + -0.0067x$).

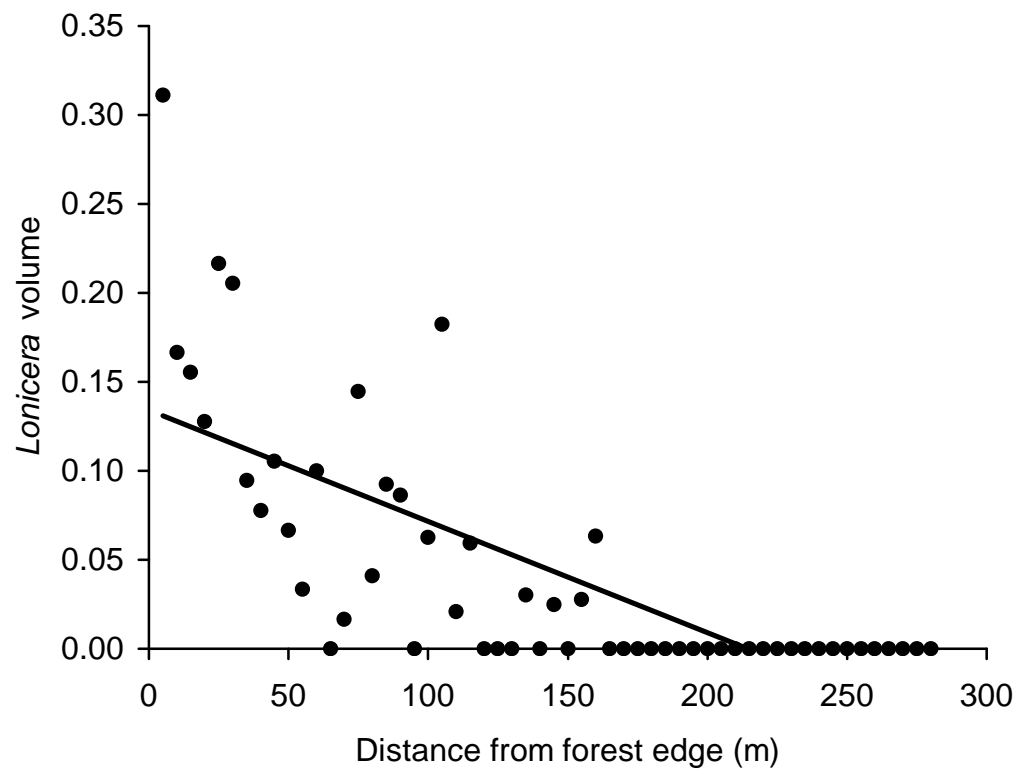


Figure 2.2. *Lonicera* spp volume with respect to distance from the forest edge ($r = -0.202$).

CHAPTER 3

EXOTIC SHRUBS AS AN UNDERLYING MECHANISM OF INCREASED NEST FAILURE IN FRAGMENTED LANDSCAPES

Abstract. Nest predation is considered a primary force shaping avian communities, and landscape-scale features are generally recognized as factors mediating nest predation. However, these same landscape-scale features may promote invasion by exotic plants, which may, in turn, increase risk of nest predation. I used a multi-scale approach to examine if use of exotic shrubs (*Lonicera* spp and *Rosa multiflora*) as nesting substrates affects nest predation. I selected 12 riparian forest sites (100-200 m wide) along a rural-urban gradient, ranging from < 1-47% urban land cover within 1 km. From May to August in 2001-2002, 231 open-cup nests within the understory (≤ 5 m tall) were monitored. Nest substrate species, nest height, and distance from the forest edge were recorded for each nest, whereas, nest-placement and nest-patch characteristics were measured only for Northern Cardinal (*Cardinalis cardinalis*) nests ($n = 68$). At two rural sites, artificial nests ($n = 79$) were placed at similar heights in honeysuckle, rose, and native nest substrates along a transect 50-75 m from the forest edge. Both natural and artificial nests in exotic shrubs were 2-4 times more likely to fail than nests in native nest substrates, irrespective of distance from the edge. Moreover, nests in exotic shrubs were especially vulnerable in urban landscapes. These patterns may be explained by

differences in nest-placement and nest-patch characteristics among nest substrates. Nests in exotic shrubs were 1.5-2 m lower to the ground and within patches containing 6-9 times more exotic shrub volume. Together, these differences may improve predator search efficiency and increase predation risk. In fact, nests lower to the ground had higher daily mortality rates than higher nests. These findings demonstrate that exotic shrubs can reduce nesting success of forest birds. However, the magnitude of the effect depends on the landscape matrix, such that differences in daily mortality rates were most extreme in urban landscapes. Because exotic shrubs appear to exacerbate high levels of nest predation, exotic shrubs may serve as an underlying mechanism of increased nest failure in fragmented landscapes. Results suggest that restoring the native shrub community especially in urban environments may reduce nest predation.

INTRODUCTION

Nest predation is a common source of nest failure in birds (Ricklefs 1969, Martin 1992, 1993*a*) and is thought to be a primary selective force shaping nest-site selection (Martin and Roper 1988, Martin 1992, 1993*b*, Schmidt and Whelan 1998*a*), nest-site suitability (Martin 1988*a*), life history traits (Martin 1995), and patterns of avian distribution (Martin 1988*b,c*, Sieving and Willson 1998, Rodewald and Yahner 2001*a*). Because nest predation exerts such a strong selective force on birds, research has focused on identifying factors that govern the intensity and frequency of nest predation. Recent work suggests that landscape-scale factors can mediate nest predation (Andren 1992, Flather and Sauer 1996, Trzcinski et al. 1999, Rodewald and Yahner 2001*a,b*, Rodewald 2002). For example, Rodewald and Yahner (2001*a*) found that types of disturbance within the landscape matrix influenced nest predation, such that predation was higher in

forested landscapes disturbed by agriculture than by silviculture. However, many of the same landscape-scale factors (e.g., land uses) that are associated with increased nest predation also may facilitate invasion by exotic plants (Moran 1984, Rottenborn 1997, Hobbs 2000, Borgmann and Rodewald, *in review*). In riparian forests in Ohio, exotic shrub volume was closely associated with land uses within the landscape matrix, such that, volume of *Lonicera* spp was positively associated with urbanization (Borgmann and Rodewald, *in review*). Associations between the landscape matrix and invasion have important implications because exotic shrubs may reduce nesting success of birds that are already vulnerable due to fragmentation and habitat degradation (Schmidt and Whelan 1999a, Donovan and Flather 2002). Unfortunately, few empirical data exist to assess how these interactions affect nest success and predator-prey relationships (D'Antonio et al. 2001, Reichard et al. 2001, Byers et al. 2002). Because most landscape-scale studies have not sufficiently addressed potential contributions of exotic plants to the observed patterns of nest predation, increased nest predation in fragmented landscapes cannot be entirely attributed to landscape features. Instead, exotic shrubs may serve as a mechanism contributing to increased nest failure in highly fragmented landscapes (Schmidt and Whelan 1999a).

Exotic plants threaten communities by disrupting nutrient cycling (Vitousek 1986), fire regimes (Schmitz et al. 1997), wildlife community composition (Hunter et al. 1988, Braithwaite et al. 1989, Fraser and Crowe 1990, Morrow et al. 2001), and species interactions (Braithwaite et al. 1989, Fraser and Crowe 1990, Reichard et al. 2001, Renne et al. 2002). In fact, studies have found negative correlations between density of exotic plants within sites and avian abundance and diversity in Arizona (Mills et al. 1989,

Germaine et al. 1998) and California (Rottenborn 1999). Exotic plants also alter composition of avian guilds and trophic-level interactions. For example, in saltcedar (*Tamarix* spp) dominated communities, timber gleaners, cavity nesting species, breeding insectivores, and Neotropical migrants were either absent or present in lower numbers compared to native cottonwood (*Populus fremontii*) stands (Anderson et al. 1977, Hunter et al. 1988, Ellis 1995).

In the eastern United States, *Lonicera* and *Rosa multiflora* are among the most common woody exotic shrubs (Trisel and Gorchov 1994, Luken and Thieret 1996). *Lonicera* spp (*L. maackii* and *L. tatarica*) are present in 66 % of Ohio's counties, where they are often the dominant understory shrub (Hutchinson and Vankat 1997, 1998, R. Gardner and J. Hillmer, *unpublished report*). Similarly, *R. multiflora* is present in 88% of Ohio's counties (R. Gardner and J. Hillmer, *unpublished report*). Invasion of forest patches by these species frequently alters habitat structure and floristic composition (Schery 1977, Eckardt 1987, Woods 1993, Hutchinson and Vankat 1997, Gould and Gorchov 2000, Collier et al. 2002). For example, herbaceous cover, plant species richness, and tree seedling density were negatively correlated with *Lonicera* presence (Woods 1993, Hutchinson and Vankat 1997, Gould and Gorchov 2000, Collier et al. 2002). Ultimately, these changes in habitat structure may weaken the ability of birds to adapt to new nest-sites, resulting in increased predation risk (Gates and Gysel 1978, Chase 2002). Moreover, exotic shrubs may act as an ecological trap by compromising avian nest success in seemingly suitable nest sites (Gates and Gysel 1978, Schmidt and Whelan 1999a).

Schmidt and Whelan (1999a) provided the first evidence that exotic shrubs negatively affect nest success of forest birds in one Chicago area woodlot. They demonstrated that daily mortality rates were nearly three times higher for nests in exotic shrubs than nests in native species. Because other factors (e.g., distance from edge) may have produced similar results, I expanded upon their research by using a multi-scale approach to evaluate how the use of exotic shrubs [*Lonicera* spp (hereafter honeysuckle) and *R. multiflora* (hereafter rose)] as nest substrates affects nest success. The goals of my study were to compare nesting success among exotic and native nest substrates across a range of landscapes and to identify the mechanisms by which exotic shrubs may be responsible for increased nest predation. Specifically I addressed the following questions: (1) do daily mortality rates differ among understory (≤ 5 m tall) nests located in honeysuckle, rose, and native nest substrates? (2) does nest placement (within the nest substrate) and vegetation within the nest patch differ among nests in exotic and native nest substrates? (3) do differences in nest-patch and nest-placement characteristics among nests influence predation risk? (4) does location of exotic shrubs within the forest contribute to edge related predation?, and (5) does the landscape matrix mediate these patterns?

METHODS

Study area

The study area is located within the Scioto River Watershed in central Ohio. Sites are located within Franklin and Delaware counties on publicly and privately owned lands. Land cover within these two counties is primarily agriculture (44%) and urban/residential development (41%), whereas only 8.5% of the land cover is forest (USGS EROS Data

Center 2000). Remnant forests persist mainly in riparian areas (Laub 1979, Groom and Grubb 2002) and generally consist of three forest types: beech-maple, swamp (silver maple-American elm), and floodplain (cottonwood-sycamore) (Forsyth 1979). Dominant tree species include hickory (*Carya* spp), black cherry (*Prunus serotina*), white ash (*Fraxinus americana*), sugar maple (*Acer saccharum*), silver maple (*Acer saccharinum*), American elm (*Ulmus americana*), cottonwood (*Populus deltoides*), sycamore (*Platanus occidentalis*), honeylocust (*Gleditsia triacanthos*), Ohio buckeye (*Aesculus glabra*), and boxelder (*Acer negundo*). Dominant shrubs include honeysuckle (*Lonicera* spp), multiflora rose (*Rosa multiflora*), spicebush (*Lindera benzoin*), and hawthorn (*Crataegus* spp) (Appendix A).

Potential riparian forest study sites (approximately ≥ 100 m wide and > 250 m long) within the watershed were identified from digital orthophoto quadrangle images (USGS DOQ 1994-95, 1:24,000) and detailed maps of Franklin and Delaware counties. From these, I selected 12 sites that met the following criteria: (1) mature riparian forest, (2) ca. 100 - 200 m wide, (3) ≥ 250 m long, (4) ≥ 2 km between sites, (5) negligible slope ($< 5\%$), and (6) river width of approximately 20-40 m. Only eight sites were studied in both years due to time constraints; four additional sites were studied in either 2001 or 2002 (Appendix F). I calculated percent land area containing urban, forest, and agricultural cover types within a 1 km radius for all sites using 1994 Thematic Mapper Imagery data and ArcView geographic information software (Table 3.1). Land covered by pavement or buildings was classified as urban development and open (non-forested areas lacking wetlands or water) vegetation was classified as agriculture. The amount of forest within the landscape was not confounded with urbanization, as the two were not

significantly related ($r = -0.28$, $P = 0.38$). Because percent cover by agriculture and urban land cover were negatively correlated ($r = -0.60$, $P = 0.04$), only percent urban land cover was used in analyses.

Nest monitoring

My field crew and I searched for and monitored nests of all open-cup nesting species but emphasized common shrub and mid-story canopy nesting species such as Northern Cardinal, Wood Thrush (*Hylocichla mustelina*), Acadian Flycatcher (*Empidonax virescens*), American Robin (*Turdus migratorius*), and Gray Catbird (*Dumetella carinensis*). Each site was searched for active songbird nests from May to early August in 2001 and 2002. Nests were located primarily by observing adult behavior (e.g., carrying nesting material or food) and secondarily by systematic searching nest substrates. Nest fate was monitored every 3-5 days following Martin et al. (1997). A nest was considered successful if one young fledged from the nest. Nests were considered failed when either the nest or eggs were destroyed or when nest activity ceased prior to expected fledging date (after incubation was confirmed). Abandoned nests, in which nest activity ceased prior to confirmed incubation or where eggs remained intact, were removed from analyses.

Vegetation characteristics describing the nest patch (0.04 ha circular plot) were measured for the most common understory nesting species (Northern Cardinal) following a modified Breeding Bird Survey Protocol (BBIRD) from late July through August in 2001 and 2002 (Martin et al. 1997). Nest-patch characteristics were measured within a 0.04 ha circular plot centered on the nest (11.3 m radius) including the number and diameter (1.4 m above the ground) of tree species, number of snags, amount of course

woody debris [logs (≥ 7.5 cm diameter and ≥ 1 m long) and stumps], understory vegetation volume (≤ 3 m), and percent canopy cover (measured with an ocular tube) (James and Shugart 1970, Martin et al. 1997). We measured nest-placement characteristics within each nest substrate including, nest height, nest substrate species, number of branches supporting the nest, diameter of support branches, distance of the nest from the central axis of the nest substrate, and distance of the nest from the nearest foliage edge. We also measured nest height and the distance of nests from the nearest forest edge for all understory nests monitored ($n=231$).

Artificial nest experiment

Artificial nests were placed within a rural ($< 2\%$ urban land cover within 1 km) landscape at one site in 2001 ($n = 29$ nests) and two sites in 2002 ($n = 50$ nests). Because of the biases associated with artificial nests (Martin 1987), I used old Northern Cardinal and American Robin nests. Prior to use in the experiment, nests were allowed to air dry for at least one week. Each nest was baited with one clay egg (Van Aken International, CA) shaped to resemble a Northern Cardinal egg (ca. 25 x 18 mm). Eggs were fashioned while wearing latex gloves and exposed for at least 2 days prior to the start of the experiment to dissipate some of the clay odor (Major and Kendal 1996). Nests were placed every 25 m along one transect, 50 m from and paralleling the river (Wilcove 1985, Haskell 1995), and 50-75 m from the forest edge. I placed nests in the nearest substrate along the transect alternating between honeysuckle ($n = 24$), rose ($n = 28$), and native ($n = 27$) nest substrates when possible. To control for the effect of nest height, each nest was placed at similar heights (mean nest height ranged from 0.89 to 1.58 m). The experiment began on 18 June 2001 and 30 June 2002 when many other breeding birds in

my sites were in the incubating stage. High rates of nest predation led to desynchronized nesting, thus nests were at all stages of development throughout the breeding season (Filliater et al. 1994, Halkin and Linville 1999). After the initial placement, nests were checked every 3 days over a 12-day period; the average number of incubation days for Northern Cardinals. Latex gloves and rubber boots were worn during nest placement and at each subsequent nest check (Rudnický and Hunter 1993, Whelan et al. 1994). Artificial nest characteristics were measured for all nests placed in 2001 and 2002 including amount of visual concealment [measured at eye level 1 m from the nest in four cardinal directions (Martin et al. 1997)], nest height, distance of the nest from the nearest foliage edge of the nest substrate, and distance of the nest from the central axis. A nest was considered depredated if the egg was missing, scratched, punctured, or bitten.

Data analysis

Prior to running analyses, variables not meeting the assumption of normality were transformed [$\log(x + 1)$ and $\sqrt{x + 1}$] and highly correlated variables ($r \geq 0.70$ and $P \leq 0.05$) were removed from analyses (i.e., one of the highly correlated variable pairs was removed). A critical level of 0.10 was used due to the low associated power with small sample sizes and to reduce the likelihood of making Type II errors (Peterman 1990, Schmiegelow et al. 1997).

Daily mortality rates (DMR) were calculated per site and per nest substrate (honeysuckle, rose, and native species) following Mayfield's (1961) method. To avoid confounding nest height with nest substrate only nests ≤ 5 m tall were used in analyses. Within this understory layer, both native and exotic plants were relatively common, whereas native species dominated the midstory and canopy layers. A general linear

model (GLM) was used to test for between year differences in DMR (Proc GLM; SAS 1990). Nest data were pooled across both years as DMR did not differ between years ($F_{1,20} = 1.36, P = 0.257$). To determine if use of exotic nest substrates changed over the nesting season, date of nest initiation was tested against nest substrate with a general linear model. I used the program CONTRAST (Hines and Sauer 1989) to test for differences in DMR among nest substrates. CONTRAST performs multiple comparison contrasts using chi-square tests of independence (Hines and Sauer 1989). A general linear model was used to examine differences in nest height among nest substrates for all understory nests monitored. The influence of nest height and edge effects (i.e., distance of nest from the forest edge) on nest fate (successful vs. failed) was examined using logistic regression (Proc Logistic; SAS 1990) for each of the nest substrates. A logistic regression also was used to test if nest fate varied throughout the nesting season.

Land cover data were categorized into two distinct categories based on the percent of urban land cover within 1 km of each site. Urbanizing landscapes ($n = 6$) were classified as those containing $> 7\%$ urban land cover within 1 km. Landscapes containing $< 2\%$ urban land cover, were classified as rural ($n = 6$; Table 3.1). These landscapes also differed qualitatively, such that rural landscapes contained only dispersed single-family homes, while urbanizing landscapes contained strip malls, industrial developments, and concentrated residential developments. I used a general liner model with an interaction term to determine if the landscape matrix affected the differences in DMR among nests in honeysuckle, rose, and native nest substrates (model; DMR = land use + substrate + land use*substrate). Within each land use, program CONTRAST was used to test for differences in DMR among nest substrates.

I compared the differences in nest-placement and nest-patch characteristics among nests in honeysuckle, rose, and native nest substrates for both the natural nest study and the artificial nest study with Multiple Analysis of Variance (MANOVA; SAS Institute 1990), which controlled experiment wise error at $\alpha = 0.05$. Differences in nest-placement and nest-patch characteristics for both the natural and artificial nest study also were compared to nest fate (success vs. failure) with MANOVA. If Wilks' Lambda was significant ($P < 0.05$), *a posteriori* univariate F tests were used to identify which nest characteristic differed significantly among the nest substrates.

Chi-square approximations were used to test for differences in the number of depredated artificial nests among nest substrates for each exposure day (Proc Freq; SAS 1990). Chi-square tests also were used to test for differences in the number of depredated artificial nests between years and between sites. Artificial nest data were pooled across years and sites, because the number of depredated nests did not differ between years ($\chi^2 = 1.12$, $df = 1$, $P = 0.289$) or between sites ($\chi^2 = 2.09$, $df = 1$, $P = 0.148$). To determine if characteristics of the nest substrate influenced the length of time each artificial nest survived, the mean number of days each artificial nest survived was tested against nest characteristics (lateral concealment, distance from central axis, and distance from foliage edge of the nest substrate) with a general linear model.

RESULTS

Natural nest study

A total of 231 understory nests (≤ 5 m tall) were monitored during 2001 and 2002 (3,489 exposure days) (Table 3.1). Of these nests, 38 nests were in honeysuckle, 46 in rose, and 147 in native nest substrates. Nests in native substrates were primarily located

in saplings (86%), of which 55% were box elder and 16% were Ohio buckeye. Seventy-seven percent of the nests monitored were Northern Cardinal, American Robin, Acadian Flycatcher, and Wood Thrush (Table 3.2). American Robins, Northern Cardinals, and Wood Thrushes most commonly nested in both native and exotic nest substrates (49% and 51% respectively). Use of exotic and native nest substrates did not vary throughout the nesting season ($F_{2,230} = 1.57$, $P = 0.209$). However nests were more successful as the season progressed ($\chi^2 = 4.21$, $df = 1$, $P = 0.040$) but only nests in rose showed an effect of date on nest fate (rose: $\chi^2 = 3.46$, $df = 1$, $P = 0.063$; honeysuckle: $\chi^2 = 2.33$, $df = 1$, $P = 0.127$; native: $\chi^2 = 0.285$, $df = 1$, $P = 0.594$). Daily mortality rates (mean \pm SE) of all understory nests (≤ 5 m) differed significantly among nests in honeysuckle (0.078 ± 0.049), rose (0.186 ± 0.046), and native (0.047 ± 0.040) nest substrates ($\chi^2 = 5.45$, $df = 2$, $P = 0.066$), such that DMR was nearly 2-4 times higher for nests in exotic shrubs. The most extreme differences in DMR were between nests in rose and native species ($\chi^2 = 5.20$, $df = 1$, $P = 0.023$) and between nests in rose and honeysuckle ($\chi^2 = 2.58$, $df = 1$, $P = 0.108$). These differences in DMR among nest substrates were not artifacts of edge effects. Nest fate for all of the nests was unrelated to the distance from the forest edge ($\chi^2 = 0.69$, $df = 1$, $P = 0.407$). Nest fate within each nest substrate also was unrelated to the distance from the forest edge (honeysuckle: $\chi^2 = 0.84$, $df = 1$, $P = 0.360$; rose: $\chi^2 = 1.64$, $df = 1$, $P = 0.201$; native: $\chi^2 = 0.03$, $df = 1$, $P = 0.858$). Nest height was significantly different among nest substrates ($F_{2,230} = 62.95$, $P = < 0.001$). In particular, nests in native nest substrates were nearly two and a half times higher than nests in exotic shrubs [(mean \pm SE) honeysuckle: 1.83 ± 0.18 ; rose: 1.32 ± 0.16 ; native: 3.23 ± 0.09]. In addition, nest fate varied with nest height ($\chi^2 = 2.73$, $df = 1$, $P = 0.099$), such that higher nests were

more successful [(mean \pm SE) successful: 2.81 m \pm 0.15; failed: 2.50 m \pm 0.11].

Interestingly, the effect of exotic shrubs varied between landscapes, such that nests in exotic shrubs in urbanizing landscapes were particularly vulnerable to predation.

Although the interaction between the landscape matrix and the nest substrate was not significant ($F_{2,28} = 2.02$, $P = 0.155$), differences in DMR among nest substrates were different between rural and urbanizing landscapes (Table 3.3 and Fig. 3.1).

Based on 68 Northern Cardinal nests (≤ 5 m tall), both nest-placement (Wilks' Lambda $F_{10,108} = 7.97$, $P < 0.001$) and nest-patch (Wilks' Lambda $F_{18,114} = 5.65$, $P < 0.001$) characteristics differed among nests in honeysuckle, rose, and native nest substrates. All nest-placement characteristics measured within the nest substrate differed among nests in honeysuckle, rose, and native nest substrates (Table 3.4, Fig. 3.2).

Northern Cardinal nests in native nest substrates were nearly two and a half times higher than nests in either rose or honeysuckle ($F_{2,58} = 28.16$, $P < 0.001$). Distance of the nest from the central axis of the nest substrate also differed, with nests in exotic shrubs placed closer to the central axis of the shrub ($F_{2,58} = 5.25$, $P = 0.008$). Nests in native substrates were supported by more ($F_{2,58} = 3.81$, $P = 0.028$) and larger diameter branches ($F_{2,58} = 8.94$, $P < 0.001$) than nests in either rose or honeysuckle. Only exotic shrub volume ($F_{2,65} = 44.49$, $P < 0.001$), native woody vegetation volume ($F_{2,65} = 6.03$, $P = 0.004$), and number of small (≤ 23 dbh) trees ($F_{2,65} = 2.61$, $P = 0.081$) differed among nests in rose, honeysuckle, and native nest substrates (Table 3.4, Fig 3.3). Differences were such that nests in exotic shrubs had 6-9 times more exotic shrub volume surrounding the nest (i.e., in the nest patch) than nests in native nest substrates. Nests in exotic shrubs also contained more small trees within the nest patch compared to nests in native nest

substrates. Of the nest vegetation characteristics measured, only number of support branches was directly associated with nest fate ($F_{1,59} = 6.50, P = 0.013$). Failed nests had fewer numbers of supporting branches [(mean number \pm SE); 3.04 ± 0.12 vs. 3.73 ± 0.28].

Artificial nest experiment

The number of artificial nests depredated differed among nests in honeysuckle, rose, and native nest substrates after the third exposure day ($\chi^2 = 6.54, df = 2, P = 0.038$), but did not differ thereafter (day 6: $\chi^2 = 2.33, df = 2, P = 0.312$; day 9: $\chi^2 = 1.67, df = 2, P = 0.435$; day 12: $\chi^2 = 0.886, df = 2, P = 0.642$), as the majority of nests already were depredated (Fig. 3.4). More nests in honeysuckle were predated than nests in rose or native nest substrates after the third exposure day (Fig 3.4). Differences among honeysuckle, rose, and native nest-substrate growth form lead to differences in horizontal concealment and distance of the nest from the central axis ($F_{2,67} = 17.99, P < 0.001$; $F_{2,67} = 4.61, P = 0.01$ respectively) (Table 3.5). However, these differences failed to account for the mean number of days each nest survived (honeysuckle: $F_{3,21} = 0.93, P = 0.446$; rose: $F_{3,25} = 0.75, P = 0.535$; native: $F_{3,21} = 1.09, P = 0.379$).

DISCUSSION

Both natural and artificial nests demonstrated that exotic shrubs negatively affected nest success of understory (≤ 5 m) nesting birds. Nests in honeysuckle and rose suffered higher daily mortality rates (DMR) than nests in native nest substrates and this pattern was unrelated to distance from edge. However, the negative effect of exotic shrubs varied with the landscape matrix. Nests in exotic shrubs in urbanizing landscapes were particularly vulnerable to nest predation. Although exotic shrubs in the natural nest

study did not appear to negatively impact nest success in rural landscapes, results from the artificial nest experiment indicate that exotic shrubs in rural landscapes can still reduce nest success. Interestingly, DMR was higher for artificial nests in honeysuckle, while DMR was higher for natural nests in rose. These discrepancies may have resulted from the absence of parental defense in the artificial nest study. Because nests in honeysuckle are generally less well concealed (K. L. Borgmann, *personal observation*), parental defense may reduce predation in natural nests (Major and Kendal 1996, King et al. 1999).

Several studies suggest that exotic plants negatively affect avian communities by altering species abundance (Anderson et al. 1977, Braithwaite et al. 1989, Mills et al. 1989, Rottenborn 1997, 1999, Germaine et al. 1998, Benoit and Askins 1999), species guilds (Hunter et al. 1988, Fraser and Crowe 1990, Ellis 1995), brood parasitism rates (Anderson et al. 1977, Reichard et al. 2001), and nest success (Schmidt and Whelan 1999a). For example, abundance of three tidal wetland species [Seaside Sparrow (*Ammodramus maritimus*), Saltmarsh Sharp-tailed Sparrow (*Ammodramus caudacutus*), and Willet (*Catoptrophorus semtipalmatus*)] in Connecticut was reduced in marshes dominated by common reed (*Phragmites australis*) (Benoit and Askins 1999). Foraging guilds and species composition shifted in saltcedar-dominated communities, such that timber gleaners, breeding insectivores, and some riparian species [e.g., Summer Tanager (*Piranga rubra*)] were either present in lower numbers or absent from saltcedar stands (Ellis 1995). Similarly, invasion of Australian acacia (*Acacia cyclops*) in South Africa has displaced nectarivorous birds (Fraser and Crowe 1990). Avian communities in saltcedar-dominated communities may experience reduced fecundity as Brown-headed

Cowbird (*Molothrus ater*) abundance increased in saltcedar dominated areas (Anderson et al. 1977, Reichard et al. 2001). Finally, Schmidt and Whelan (1999a) found that American Robin and Wood Thrush nests in honeysuckle suffered higher DMR than nests in comparable native species. However, these findings are not entirely conclusive because (1) measures of nest success were not always collected (but see Schmidt and Whelan 1999a) and (2) other local and landscape level factors were not measured (e.g., distance from edge and surrounding land uses), potentially confounding their results.

Because exotic shrubs are more abundant near forest edges in many systems (Brothers and Spingarn 1992, Luken et al. 1995, Luken and Goessling 1995, Goldblum and Beatty 1999), it is necessary to address how edge effects influence nest success. Reduced nest success could result from increased edge-related nest predation (Gates and Gysel 1978, Paton 1994, King et al. 1996), rather than from the exotic nest substrate. Although honeysuckle volume was negatively related to distance from the forest edge (Borgmann and Rodewald, *in review*), there was no edge-related pattern in nesting success within each of the nest substrates. Therefore, my results provide compelling evidence that the nest substrate itself, rather than its location within a site, is responsible for increased predation.

Although specific mechanisms of increased vulnerability of nests in exotic shrubs are unclear, there have been several proposed hypotheses. Differences in nest placement and shrub growth form between native and exotic nest substrates have been suggested to increase predation risk in exotic substrates (Braithwaite et al. 1989, Schmidt and Whelan 1999a). I found that understory nesting birds nested lower to the ground when nesting in exotic nest substrates relative to native ones. Nest height can be an important factor

affecting nest success (Best and Stauffer 1980, Filliater et al. 1994) as ground foraging mammals, such as raccoons (*Procyon lotor*) and small mammals, are more likely to encounter nests lower to the ground (Schmidt 1999). Because nests in native nest substrates in my study were placed nearly two and a half times higher they may have been less vulnerable to mammalian predation. In fact, I found that failed nests were lower to the ground than successful nests. This may, in part, explain the pronounced differences in DMR among nest substrates in urbanizing landscapes, where domestic cats (*felis domesticus*) were regularly observed (K. L. Borgmann, *personal observation*).

Vegetation characteristics within the nest patch are thought to affect nest success in a number of ways (Martin and Roper 1988, Martin 1992, 1993b). First, nests within dense patches of vegetation may be at a higher risk of predation (Chase 2002, Schmidt and Whelan 1998). Nests in exotic shrubs were surrounded by relatively dense patches of exotic vegetation as opposed to native nest substrates, allowing predators to concentrate search efforts on dense patches of exotic shrubs. Second, exotic shrubs often reduce the diversity of nest substrates, resulting in less nest-site partitioning. This uniformity can increase predation because predators can focus their efforts on specific nest sites (Martin 1987, 1988b, 1993b). For example, Martin (1988b, 1993b) found that predation rates dropped when nests were segregated among different substrates and placed at varying heights. At my sites, honeysuckle and rose were the dominant understory shrubs and nest height of all understory species nesting in exotic shrubs was similar. These similarities may have facilitated predator search image and allowed predators to focus their efforts on specific nest types (Bowman and Harris 1980, Martin 1987, 1988b,c, 1993b, Schmidt and Whelan 1998, Chase 2002). In addition, lower

diversity of nesting substrates can lead to use of non-preferred nest sites (Martin 1993*b*, 1998). Use of non-preferred nest sites can increase overlap of nest resources, increasing predation risk (Martin 1993*b*). Third, dense patches of vegetation may have a higher probability of containing nests, which can increase density dependent predation (Martin and Roper 1988, Martin 1988*b,c*, Schmidt and Whelan 1998, 1999*a*). Martin (1988*c*) suggests that predators can alter their search behavior, increasing effort when more nests are encountered.

Exotic shrubs also have been hypothesized to act as an ecological trap (Gates and Gysel 1978, Schmidt and Whelan 1999*a*). Exotic shrubs provide seemingly suitable nest sites with appropriate cover yet birds nesting within them experienced reduced nest success (Schmidt and Whelan 1999*a*, Reichard et al. 2001). An ecological trap occurs when a species is attracted to a specific area in which it experiences reduced fitness (Gates and Gysel 1978). Typically an ecological trap is attributed to increased vegetation volume and predation rates at edges. However in my study, exotic shrubs may be acting as an ecological trap that is driven primarily by landscape-scale processes. Urban landscapes typically support high densities of exotic shrubs (Rottenborn 1997, Moran 1984, Borgmann and Rodewald *in review*), which may increase the number (but not diversity) of available nest sites for shrub nesting species. Thus, birds may be attracted to nest in exotic substrates within urban landscapes making them more vulnerable to predation as urban landscapes typically maintain higher numbers of nest predators (Matthiae and Stearns 1981, Oehler and Litvaitis 1996). Urban landscapes contained nearly three times the number of nest predators than rural landscapes in my study

area (A. D. Rodewald, *unpublished data*), including American Crows (*Corvus brachyrhynchos*), Blue Jays, (*Cyanocitta cristata*), domestic cats, eastern gray squirrels (*Sciurus carolinensis*), eastern chipmunks (*Tamias striatus*), and raccoons.

Although exotic shrubs may not directly affect nest success of some species, invasion of exotic shrubs can negatively affect community wide predation pressures via apparent competition (Barber and Martin 1997, Schmidt 1998, Schmidt and Whelan 1998, 1999b, Gazda et al. 2002). Invasion of riparian forests by exotic shrubs often results in a new structural component to areas previously lacking a dense shrub layer. For example, a well-developed native shrub community was historically lacking in many southwestern Ohio forests (Braun 1916). Now many of these forest patches contain a dense *L. maackii* shrub layer (Luken et al. 1995, Luken and Goessling 1995, Hutchinson and Vankat 1997, 1998). An increase in the number of shrub nesting sites provides additional nesting opportunities for generalist nesting species such as the Northern Cardinal and American Robin. These increases can enhance apparent competition with other understory nesting species (e.g., Wood Thrush) (Schmidt and Whelan 1998, Schmidt 1998, 1999). Moreover, additional nest sites can provide suitable nest sites for avian nest predators (Gazda et al. 2002).

Nest-placement and nest-patch characteristics for understory Northern Cardinal nests varied among nest substrates, although few of these characteristics significantly influenced nest success. One feature did however influence nest success. Nests with more support branches succeeded more often than nests with fewer branches. This may suggest that nests with more support branches are located in nest substrates with a more complex branching structure, reducing the ability of predators to access nests. Although

few characteristics affected nest fate, birds may not have had enough time to respond to recent changes in habitat structure that result from invasion by exotic plants (Gates and Gysel 1978, Siepielski et al. 2001, Chase 2002). Moreover, gene flow from nearby forest patches also can prevent or reduce adaptation (Misenhelter and Rotenberry 2000). In addition, the lack of association between nest-site characteristics and nest fate may result if the predator community is diverse, as different search behaviors can preclude “safe” nest sites (Filliater et al. 1994, Misenhelter and Rotenberry 2000, Chase 2002).

An important finding that distinguishes my study from others is that the landscape matrix appeared to mediate the influence of exotic shrubs, such that nests in exotic shrubs were particularly vulnerable in urbanizing landscapes. This may be, in part, be explained by several important differences between riparian forests in rural and urbanizing landscapes. First, exotic shrubs, especially honeysuckle, are more likely to dominate the understory shrub community in urbanizing landscapes (Borgmann and Rodewald, *in review*). Thus in urbanizing landscapes exotic shrubs decrease nest-site partitioning, which can increase predation risk. The level of predation risk however may depend on the density of exotic shrubs within a site, such that above a particular level, predation increases for all nests regardless of nest substrate. Predators may show a functional response, increasing search effort in areas with patches of exotic shrubs, thereby increasing incidental predation on nests within the same vicinity (Schmidt and Whelan 1999b). Second, mammalian nest predators differed between landscapes with higher numbers in urbanizing landscapes (A. D. Rodewald, *unpublished data*). Increased numbers of mammalian predators in urbanizing landscapes may cause increased vulnerability to predation for nests in exotic shrubs because they are lower to the ground.

In addition, mammalian predators can focus their efforts on dense patches of exotic shrubs that often occur in urban landscapes. Third, prey (i.e., bird) density could differ between landscapes such that density-dependent factors would contribute to differences in DMR among nest substrates. However, surveys of breeding birds at my sites indicate that the number of understory-nesting birds did not differ between rural and urbanizing landscapes (A. D. Rodewald, *unpublished data*). Therefore, density-dependent predation is likely not responsible for increased daily mortality although density dependence was not directly tested. In sum, birds nesting in exotic shrubs are more vulnerable to predation, particularly in urbanizing landscapes where exotic shrubs and mammalian nest predators are more abundant because differences in nest-placement and nest-patch characteristics can facilitate the ability of mammals to locate nests in exotic shrubs.

CONSERVATION IMPLICATIONS

It is critical that ecologists and land managers understand the interactions among exotic plants and wildlife species especially as exotic plants become more prevalent (Reichard et al. 2001, Zavaleta et al. 2001, Byers et al. 2002). This study was the first to demonstrate that exotic shrubs can negatively impact avian nest success while taking into account both distance from edge and the landscape matrix. In my study area, DMR of nests in exotic shrubs exceeded 4% and DMR less than 4% are generally needed to allow self-sustaining populations of Neotropical migrants (Donovan et al. 1995*a,b*, Robinson 1996). Thus exotic shrubs could be considered population sinks, in areas already experiencing high rates of predation (A. D. Rodewald, *unpublished data*). These findings have several important implications for land managers and biologists. First, because invasion of exotic shrubs is tied to the landscape matrix (Borgmann and Rodewald, *in*

review), and landscape matrix characteristics (i.e., urbanization) exacerbated the negative impacts of exotic shrubs, managers can identify forest reserves where avian communities may be especially vulnerable and require additional conservation attention. Second, landscape models could be developed to predict (1) the disturbance level at which invasion increases (With 2002) and (2) the level of exotic shrub volume at which nest predation increases. Third, city planners and managers can take a proactive approach by addressing land uses that increase invasion risk. For example, low-development buffer zones surrounding forest reserves may reduce invasion by exotic plants (Hobbs and Humphries 1995, Pysek et al. 2002). Managers also can promote the use of native plants in urban areas to limit future invasions. Fourth, at the local scale, restoring the native shrub community, especially in urban landscapes, may prove to be a viable strategy to improve nest success for species already at risk (Donovan and Flather 2002). Moreover, replacing exotic with native vegetation is an important and effective management tool that will likely benefit many wildlife and native plant species (Germaine et al. 1998, Schmidt and Whelan 1999a, Marzluff and Ewing 2001). Although this study is the first to examine the effects of exotic plants on breeding birds at multiple scales, additional research is needed to (1) determine if exotic shrubs impact annual productivity, (2) better identify underlying mechanisms of decreased nesting success in exotic shrubs, (3) determine if selection of exotic shrubs is adaptive or non-adaptive, and (4) determine if a threshold in the amount of exotic vegetation exists, at which nest predation increases.

LITERATURE CITED

- Anderson, B. W., A. Higgins, and R. D. Ohmart. 1977. Avian use of saltcedar communities in the lower Colorado River valley. U.S. Dept. Agriculture Forest Service General Technical Report **RM-43**:128-136.
- Andren, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* **73**:794-804.
- Barber, D. R., and T. E. Martin. 1997. Influence of alternate host densities on Brown-headed Cowbird parasitism rates in Black-capped Vireos. *Condor* **99**:595-604.
- Benoit, L. K., and R. A. Askins. 1999. Impacts of the spread of *Phragmites* on the distribution of birds in Connecticut tidal marshes. *Wetlands* **19**:194-208.
- Best, L. B., and D. F. Stauffer. 1980. Factors affecting nesting success in riparian bird communities. *Condor* **82**:149-158.
- Borgmann, K. L., and A. D. Rodewald. *In review*. Landscape matrix effects on invasion of riparian forests by exotic shrubs. *Biological Conservation*.
- Bowman, G. B., and L. D. Harris. 1980. Effect of spatial heterogeneity on ground-nest depredation. *Journal of Wildlife Management* **44**:806-813.
- Braithwaite, R. W., W. M. Lonsdale, and J. A. Estbergs. 1989. Alien vegetation and native biota in tropical Australia: the impact of *Mimosa pigra*. *Biological Conservation* **48**:189-210.
- Braun, E. L. 1916. The physiographic ecology of the Cincinnati region. *Ohio Biological Survey Bulletin* 7, **2**:137.
- Brothers, T. S., and A. Spingarn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Conservation Biology* **6**:91-100.

- Byers, J. E., S. Reichard, J. M. Randall, I. M. Parker, C. S. Smith, W. M. Lonsdale, I. A. E. Atkinson, T. R. Seastedt, M. Williamson, E. Chornesky, and D. Hayes. 2002. Directing research to reduce the impacts of nonindigenous species. *Conservation Biology* **16**:630-640.
- Chase, M. K. 2002. Nest site selection and nest success in a song sparrow population: the significance of spatial variation. *Condor* **104**:103-116.
- Collier, M. H., J. L. Vankat, and M. R. Hughes. 2002. Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. *American Midland Naturalist* **147**:60-71.
- D'Antonio, C., L. A. Meyerson, and J. Denslow. 2001. Exotic species and conservation. Pages 59-80 in M. E. Soule and G. H. Orians, editors. *Conservation biology: research priorities for the next decade*. Island Press, Washington, D.C., USA.
- Donovan, T. M., R. H. Lamberson, A. Kimber, F. R. Thompson III, and J. Faaborg. 1995a. Modeling the effects of habitat fragmentation on source and sink demography of neotropical migrant birds. *Conservation Biology* **9**:1396-1407.
- Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995b. Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology* **9**:1380-1395.
- Donovan, T. M., and C. H. Flather. 2002. Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. *Ecological Applications* **12**:364-374.
- Eckardt, N. 1987. Element stewardship abstract, *Rosa multiflora*. Unpublished report for The Nature Conservancy, Arlington, Virginia, USA.

- Ellis, L. M. 1995. Bird use of saltcedar and cottonwood vegetation in the Middle Rio Grande Valley of New Mexico, U.S.A. *Journal of Arid Environments* **30**:339-349.
- Filliater, T. S., R. Breitwisch, and P. M. Nealen. 1994. Predation on Northern Cardinal nests: does choice of nest site matter? *Condor* **96**:761-768.
- Flather, C. H., and J. R. Sauer. 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. *Ecology* **77**:28-35.
- Forsyth, J. L. 1979. Tills plains. Pages 198-213 *in* M.B. Lafferty, editor. Ohio's natural heritage. The Ohio Academy of Sciences, Columbus, Ohio, USA.
- Fraser, M. W., and T. M. Crowe. 1990. Effects of alien woody plant invasion on the birds of Mountain Fynbos in the Cape of Good Hope Nature Reserve. *South African Journal of Zoology* **25**:97-108.
- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* **59**:871-883.
- Gazda, R. J., R. R. Meidinger, I. J. Ball, and J. W. Connelly. 2002. Relationships between Russian olive and duck nest success in southeastern Idaho. *Wildlife Society Bulletin* **30**:337-344.
- Germaine, S. S., S. S. Rosenstock, R. E. Schweinsburg, and W. S. Richardson. 1998. Relationships among breeding birds, habitat, and residential development in greater Tucson, Arizona. *Ecological Applications* **8**:680-691.
- Goldblum, D., and S. W. Beatty. 1999. Influence of an old field/forest edge on a northeastern United States deciduous forest understory community. *Journal of the Torrey Botanical Society* **126**:335-343.

- Gould, A. M. A., and D. L. Gorchov. 2000. Effects of the exotic invasive shrub *Lonicera maackii* on survival and fecundity of three species of native annuals. *American Midland Naturalist* **144**:36-50.
- Groom, J. D., and T. C. Grubb Jr. 2002. Bird species associated with riparian woodland in fragmented, temperate-deciduous forest. *Conservation Biology* **16**:832-836.
- Halkin, S. L., and S. U. Linville. 1999. Northern Cardinal (*Cardinalis cardinalis*). Pages 1-32 *In* A. Poole and F. Gill, editors. The Birds of North America, Number. 440. The Academy of Natural Sciences, Philadelphia Pennsylvania, and the American Ornithologists' Union, Washington, D.C., USA.
- Haskell, D. G. 1995. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. *Conservation Biology* **9**:1316-1318.
- Hines, J. E., and J. R. Sauer. 1989. Program CONTRAST: a general program for the analysis of several survival or recovery estimates. Technical report **24**. U.S. Fish and Wildlife Service, Laurel, Maryland, USA.
- Hobbs, R. J. 2000. Land-use changes and invasions. Pages 55-64 *in* H. A. Mooney and R. J. Hobbs, editors. Invasive species in a changing world. Island Press, Washington, D.C., USA.
- Hunter, W. C., R. D. Ohmart, and B. W. Anderson. 1988. Use of exotic saltcedar (*Tamarix chinensis*) by birds in arid riparian systems. *Condor* **90**:113-123.
- Hutchinson, T. F., and J. L. Vankat. 1997. Invasibility and effects of Amur Honeysuckle in Southwestern Ohio forests. *Conservation Biology* **11**:1117-1124.

- Hutchinson, T. F., and J. L. Vankat. 1998. Landscape structure and spread of the exotic shrub *Lonicera maackii* (Amur honeysuckle) in southwestern Ohio forests. *American Midland Naturalist* **139**:383-390.
- James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. *Audubon Field Notes* **24**:727-736.
- King, D. I., C. R. Griffin, and R. M. DeGraaf. 1996. Effects of clearcutting on habitat use and reproductive success of the ovenbird in forested landscapes. *Conservation Biology* **10**:1380-1386.
- King, D. I., R. M. DeGraaf, C. R. Griffin, and T. J. Maier. 1999. Do predation rates on artificial nests accurately reflect predation rates on natural bird nests? *Journal of Field Ornithology* **70**:257-262.
- Laub, K. W. 1979. Changing land use: forests, farms, and wildlife. Pages 272-281 in M.B. Lafferty, editor. *Ohio's natural heritage*. The Ohio Academy of Sciences, Columbus, Ohio, USA.
- Luken, J. O., and N. Goessling. 1995. Seedling distribution and potential persistence of the exotic shrub *Lonicera maackii* in fragmented forests. *American Midland Naturalist* **133**:124-130.
- Luken, J. O., T. C. Tholemeier, L. M. Kuddes, and B. A. Kunkel. 1995. Performance, plasticity, and acclimation of the nonindigenous shrub *Lonicera maackii* (Caprifoliaceae) in contrasting light environments. *Canadian Journal of Botany* **73**:1953-1961.
- Luken, J. O., and J. W. Thieret. 1996. Amur honeysuckle, its fall from grace. *Bioscience* **46**:18-24.

- Major, R. E., and C. E. Kendal. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis* **138**:298-307.
- Martin, T. E. 1987. Artificial nest experiments: effects of nest appearance and predator type. *Condor* **89**:925-928.
- Martin, T. E. 1988*a*. Habitat and area effects on forest bird assemblages: is nest predation an influence? *Ecology* **69**:74-84.
- Martin, T. E. 1988*b*. Processes organizing open-nesting bird assemblages: competition or nest predation? *Evolutionary Ecology* **2**:37-50.
- Martin, T. E. 1988*c*. On the advantage of being different: nest predation and the coexistence of bird species. *Proceedings of the National Academy of Science* **85**:2196-2199.
- Martin, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455-473 *in* J. M. Hagan III and D. W. Johnston, editors. *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Institution Press, Washington, D.C., USA.
- Martin, T. E. 1993*a*. Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist* **141**:897-913.
- Martin, T. E. 1993*b*. Nest predation and nest sites: new perspectives on old patterns. *BioScience* **43**:523-532.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* **65**:101-127.

- Martin, T. E., and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the hermit thrush. *Condor* **90**:51-57.
- Martin, T. E., C. Paine, C. J. Conway, and W. M. Hochachka. 1997. BBIRD field protocol. Montana Cooperative Wildlife Resource Unit, Missoula, Montana, USA.
- Marzluff, J. M., and K. Ewing. 2001. Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. *Restoration Ecology* **9**:280-292.
- Matthiae, P. E., and F. Stearns. 1981. Mammals in forest islands in southeastern Wisconsin. Pages 55-66 *in* R. L. Burgess and D. M. Sharpe, editors. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, New York, USA.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* **73**:255-261.
- Mills, G. S., J. B. Dunning, Jr., and J. M. Bates. 1989. Effects of urbanization on breeding bird community structure in southwestern desert habitats. *Condor* **91**:416-428.
- Misenhelter, M. D., and J. T. Rotenberry. 2000. Choices and consequences of habitat occupancy and nest site selection in sage sparrows. *Ecology* **81**:2892-2901.
- Moran, M. A. 1984. Influence of adjacent land use on understory vegetation of New York forests. *Urban Ecology* **8**:329-340.

- Morrow, J. L., J. H. Howard, S. A. Smith, and D. K. Poppel. 2001. Habitat selection and habitat use by the box turtle (*Clemmys muhlenbergii*) in Maryland. *Journal of Herpetology* **35**:545-552.
- Oehler, J. D., and J. A. Litvaitis. 1996. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. *Canadian Journal of Zoology* **74**:2070-2079.
- Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology* **8**:17-26.
- Peterson, R. M. 1990. Statistical power analysis can improve fisheries research and management. *Canadian Journal of Fisheries and Aquatic Sciences* **47**:2-15.
- Pyšek, P., V. Jarosik, and T. Kucera. 2002. Patterns of invasion in temperate nature reserves. *Biological Conservation* **104**:13-24.
- Reichard, S. H., L. Chalker-Scott, and S. Buchanan. 2001. Interactions among non-native plants and birds. Pages 179-223 in J. M. Marzluff, R. Bowman, and R. Donnelly, editors. *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston, Massachusetts, USA.
- Renne, I. J., W. C. Barrow Jr., L. A. Johnson Randall, and W. C. Bridgers Jr. 2002. Generalized avian dispersal syndrome contributes to Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasiveness. *Biodiversity Research* **8**:285-295.
- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* **9**:1-48.

- Robinson, S. K. 1996. Threats to breeding neotropical migratory birds in the Midwest. Pages 1-21 in F. R. Thompson, III, editor. Management of midwestern landscapes for the conservation of neotropical migratory birds. U.S. For. Serv. Gen. Tech. Rep. NC-**187**. North Central For. Exp. Sta., St. Paul, MN, USA.
- Rodewald, A. D., and R. H. Yahner. 2001*a*. Influence of landscape composition on avian community structure and associated mechanisms. *Ecology* **82**:3493-3504.
- Rodewald, A. D., and R. H. Yahner. 2001*b*. Avian nesting success in forested landscapes: influence of landscape composition, stand and nest-patch microhabitat, and biotic interactions. *Auk* **118**:1018-1028.
- Rodewald, A. D. 2002. Nest predation in forested regions: landscape and edge effects. *Journal of Wildlife Management* **66**:634-640.
- Rottenborn, S. C. 1997. The impacts of urbanization on riparian bird communities in central California. Ph.D. dissertation, Stanford University, Stanford, California, USA.
- Rottenborn, S. C. 1999. Predicting the impacts of urbanization on riparian bird communities. *Biological Conservation* **88**:289-299.
- Rudnický, T. C., and M. L. Hunter. 1993. Avian nest predation in clearcuts, forests, and edges in a forest-dominated landscape. *Journal of Wildlife Management* **57**:358-364.
- SAS Institute. 1990. SASSTAT user's guide. SAS Institute, Cary, North Carolina, USA.
- Schery, R. 1977. The curious double life of *Rosa multiflora*. *Horticulture* **55**:56-61.
- Schmidt, K. A. 1998. The consequences of partially directed search effort. *Evolutionary Ecology* **12**:263-277.

- Schmidt, K. A. 1999. Foraging theory as a conceptual framework for studying nest predation. *Oikos* **85**:151-160.
- Schmidt, K. A., and C. J. Whelan. 1998. Predator-mediated interactions between and within guilds of nesting songbirds: experimental and observational evidence. *American Naturalist* **152**:393-402.
- Schmidt, K. A., and C. J. Whelan. 1999a. Effects of exotic *Lonicera* and *Rhamnus* on songbird nest predation. *Conservation Biology* **13**:1502-1506.
- Schmidt, K. A., and C. J. Whelan. 1999b. Nest predation on woodland songbirds: when is nest predation density dependent? *Oikos* **87**:65-74.
- Schmiegelow, F. K. A., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology* **78**:1914-1932.
- Schmitz, D. C., D. Simberloff, R. H. Hofstetter, W. Haller, and D. Sutton. 1997. The ecological impacts of nonindigenous plants. Pages 39-61 *in* D. Simberloff, D. C. Schmitz, and T. C. Brown, editors. *Strangers in paradise*. Island Press, Washington, D. C., USA.
- Siepielski, A. M., A. D. Rodewald, and R. H. Yahner. 2001. Nest site selection and nesting success of the red-eyed vireo in central Pennsylvania. *Wilson Bulletin* **113**:302-307.
- Sieving, K. E., and M. F. Willson. 1998. Nest predation and avian species diversity in Northwestern forest understory. *Ecology* **79**:2391-2402.

- Trisel, D. E., and D. L. Gorchov. 1994. Regional distribution, ecological impact, and leaf phenology of the invasive shrub, *Lonicera maackii*. Bulletin of the Ecological Society of American **75**:231.
- Trzcinski, M. K., L. Fahrig, and G. Merriam. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecological Applications **9**:586-593.
- USGS EROS Data Center. 2000. MRLC regional land cover characterization project land cover data for Ohio early 1900s (version 2000-03). Multi-resolution land characteristics consortium. National Land Cover Data Program.
- Vitousek, P. M. 1986. Biological invasions and ecosystem properties: can species make a difference? Pages 163-176 in H. A. Mooney, and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.
- Whelan, C. J., M. L. Dilger, D. Robson, N. Hallyn, and S. Dilger. 1994. Effects of olfactory cues on artificial-nest experiments. Auk **111**:945-952.
- Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology **66**:1211-1214.
- With, K. A. 2002. The landscape ecology of invasive spread. Conservation Biology **16**:1192-1203.
- Woods, K. D. 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four New England forests. American Midland Naturalist **130**:62-74.

Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution* **16**:454-459.

Site	Mean site width (m)	Urban (%)	Agriculture (%)	Forest (%)	Land use category	Number of nests	Exposure days	Daily mortality rate
Casto Park	142	47.17	26.71	24.57	Urban	30	399.0	0.059
Cherrybottom Park ^a	150	31.22	35.38	28.87	Urban	8	83.5	0.052
Darby Public Hunting	140	0.95	58.27	39.66	Rural	36	648.0	0.036
Elkrun Park	160	12.64	66.56	17.76	Urban	23	343.0	0.140
Galena	200	1.23	42.06	42.53	Rural	11	206.0	0.041
Kilbourne ^a	116	0.41	62.52	35.54	Rural	11	104.5	0.061
North Galena	110	0.14	45.97	53.15	Rural	28	408.0	0.046
Prairie Oaks ^a	117	0.98	65.03	29.69	Rural	7	132.5	0.030
Rush Run	150	21.01	9.63	61.02	Urban	8	54.0	0.293
South Galena	158	0.13	50.22	12.01	Rural	26	393.5	0.040
Three Creeks	113	7.81	73.28	15.36	Urban	31	549.0	0.036
Woodside Green Park	106	17.80	47.68	29.22	Urban	12	168.3	0.032

^a nests monitored only in one year of the study.

TABLE 3.1. Mean site width (m) and percent land covered by urban development, agriculture, and forest within 1 km of nest searching sites. Land use category is based on the percent of urbanization within 1 km (urban > 7% and rural < 2%). Number of understory (≤ 5 m) nests, exposure days, and Mayfield estimates of daily mortality for nests monitored in central Ohio, 2001-2002.

Species	Number of nests
Mourning Dove (<i>Zenaida macroura</i>)	5
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)	8
Acadian Flycatcher (<i>Empidonax virescens</i>)	43
Red-eyed Vireo (<i>Vireo olivaceus</i>)	8
Blue Jay (<i>Cyanocitta cristata</i>)	5
Wood Thrush (<i>Hylocichla mustelina</i>)	24
American Robin (<i>Turdus migratorius</i>)	36
Gray Catbird (<i>Dumetella carolinensis</i>)	9
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	1
Hooded Warbler (<i>Wilsonia citrina</i>)	2
Eastern Towhee (<i>Pipilo erythrophthalmus</i>)	2
Song Sparrow (<i>Melospiza melodia</i>)	2
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	1
Northern Cardinal (<i>Cardinalis cardinalis</i>)	76
Indigo Bunting (<i>Passerina cyanea</i>)	9
Total	231

TABLE 3.2. Number of understory (≤ 5 m) nests monitored per species at 12 sites in riparian forests in central Ohio, 2001-2002.

Source	df	SS	MS	F	P
Model	5	0.232	0.046	2.85	0.038
Error	23	0.374	0.016		
Total	28	0.605			
Type					
Substrate ^a	2	0.085	0.043	2.62	0.094
Land use ^b	1	0.077	0.077	4.74	0.040
Substrate * Land use	2	0.066	0.033	2.02	0.155

^a Honeysuckle, rose, or native nest substrates

^b Rural (< 2 % urbanization) and urban (> 7 % urbanization) land uses within 1 km of the site.

TABLE 3.3. Results of General Linear Model analysis testing the effects of land use, substrate type, and their interaction on daily mortality rates of understory (≤ 5 m) nesting birds in riparian forests in central Ohio, 2001-2002.

Variable	Nest substrate			P-value
	Honeysuckle	Rose	Native	
Nest-placement characteristic				
Nest height (m)	1.90 (0.23)	1.13 (0.08)	2.87 (0.25)	< 0.001
Number of support branches	3.40 (0.19)	2.85 (0.18)	3.52 (0.21)	0.028
Diameter of support branches (cm)	0.89 (0.08)	0.81 (0.05)	1.46 (0.20)	< 0.001
Distance of nest to nearest foliage edge (m)	0.57 (0.09)	0.37 (0.05)	0.47 (0.09)	0.104
Distance of nest from central axis (m)	1.06 (0.20)	0.60 (0.08)	1.24 (0.25)	0.008
Nest-patch characteristic				
Number of small trees (> 8 and < 23 cm dbh)	15.29 (1.65)	16.36 (1.55)	11.78 (1.32)	0.081
Number of medium trees (\geq 23 and < 38 cm dbh)	4.71 (0.90)	4.25 (0.46)	3.83 (0.55)	0.606
Number of large trees (\geq 38 cm dbh)	2.71 (0.44)	2.61 (0.39)	3.04 (0.32)	0.454
Number of snags	1.35 (0.37)	2.43 (0.51)	2.13 (0.39)	0.254
Amount of coarse woody debris	9.94 (1.59)	2.43 (0.51)	11.35 (1.69)	0.745
Canopy cover (%)	85.00 (3.09)	76.43 (3.59)	75.78 (3.99)	0.222
Forb volume (\leq 3 m)	0.53 (0.17)	1.01 (0.17)	0.99 (0.25)	0.174
Exotic shrub volume (\leq 3 m)	2.45 (0.28)	1.61 (0.16)	0.27 (0.12)	< 0.001
Native woody vegetation volume (\leq 3 m)	0.69 (0.08)	1.60 (0.20)	1.43 (0.20)	0.004

TABLE 3.4. Mean (SE) and associated P-values of nest-placement and nest-patch characteristics for Northern Cardinal nests (\leq 5 m) within honeysuckle, rose, and native nest substrates in riparian forests in central Ohio, 2001-2002. Nest-placement (Wilks' Lambda $F_{10,108} = 7.97$, $P = < 0.001$) and nest-patch characteristics differed significantly among nest substrates (Wilks' Lambda $F_{18,114} = 5.65$, $P = < 0.001$).

Variable	Nest substrate			P-value
	Honeysuckle	Rose	Native	
Artificial nest characteristic				
Lateral concealment (%)	20.74 (4.26)	64.26 (5.24)	16.25 (4.39)	< 0.001
Distance of nest to nearest foliage edge (m)	0.50 (0.05)	0.40 (0.04)	0.40 (0.04)	0.280
Distance of nest from central axis (m)	0.04 (0.10)	0.20 (0.05)	0.15 (0.06)	0.013

Table 3.5. Mean (SE) artificial nest characteristics and associated P-values of artificial nests in honeysuckle, rose, and native nest substrates in riparian forests in central Ohio, 2001-2002.

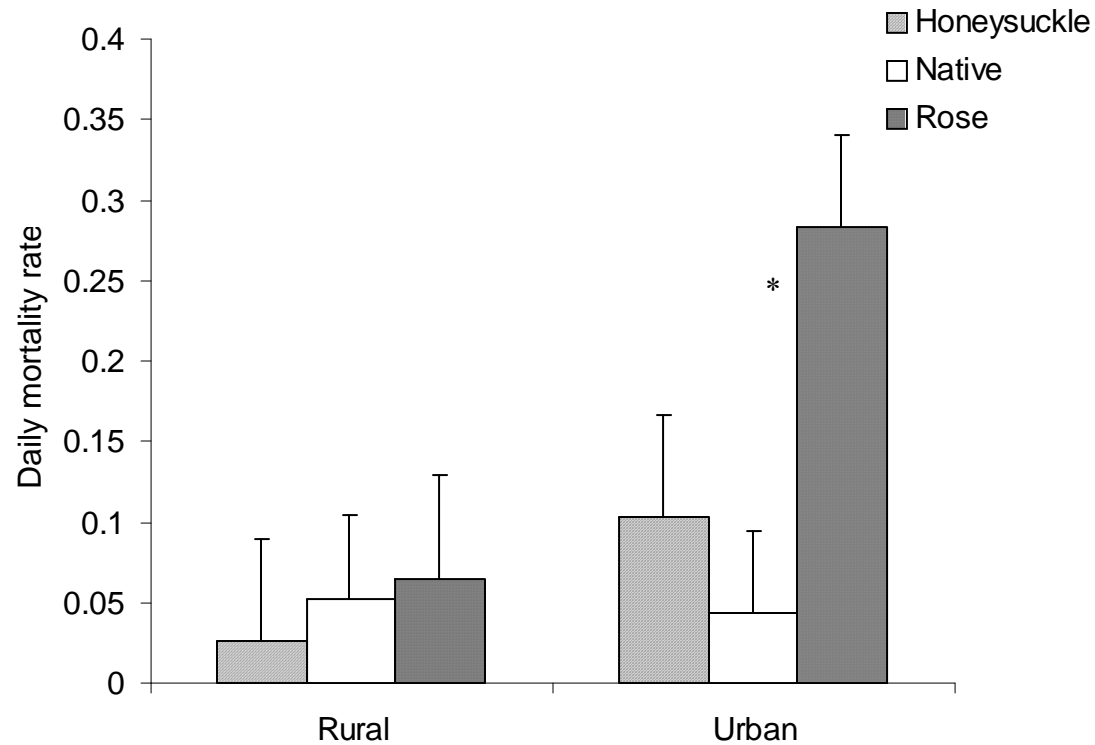


Fig. 3.1. Daily mortality rates for understory (≤ 5 m) nests in honeysuckle, rose, and native nest substrates within rural and urban landscapes ($n = 231$ nests). Land uses were categorized as follows; rural = $< 2\%$ urbanization ($n = 6$), and urban = $> 7\%$ urbanization ($n = 6$) within 1 km of each site. Asterisk indicates significant difference in daily mortality rates among nest substrates within urbanizing landscapes.

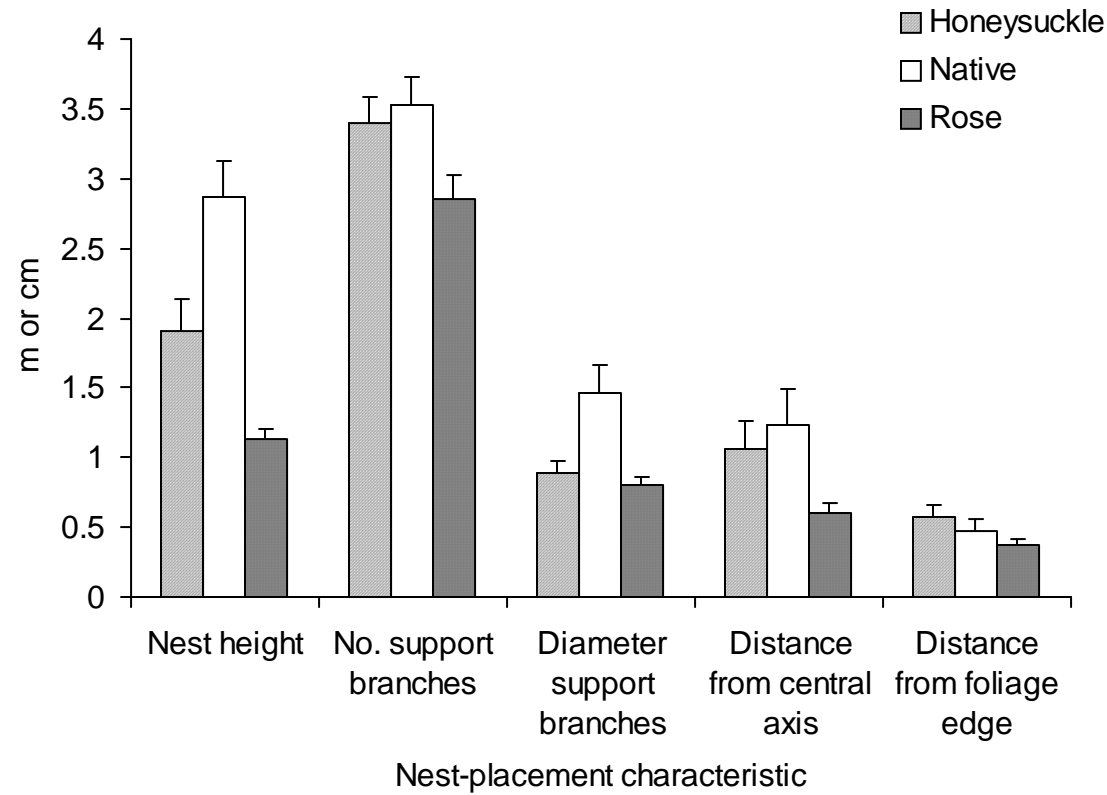


Fig. 3.2. Nest-placement characteristics within each nest substrate for understory (≤ 5 m) Northern Cardinal nests ($n = 68$). Nest placement characteristics differed among nest substrates ($F_{10,108} = 7.97$, $P = <0.001$).

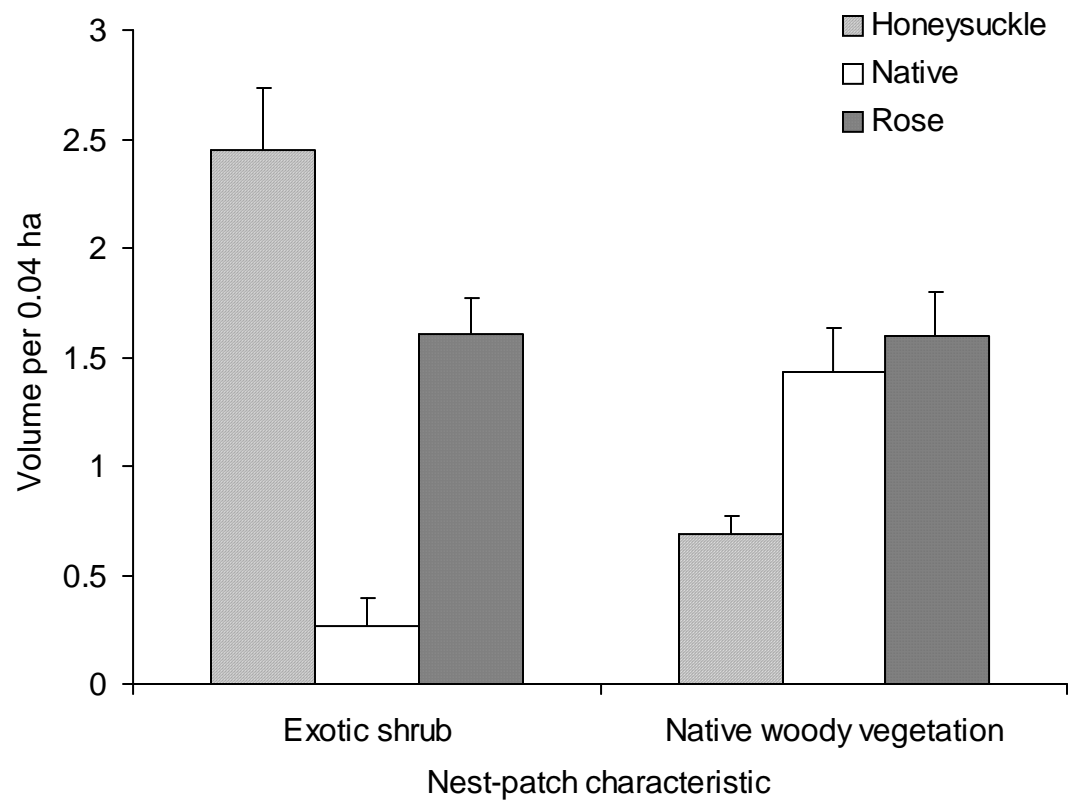


Fig. 3.3. Nest-patch characteristics for understory (≤ 5 m) Northern Cardinal nests ($n = 68$) within 0.04 ha of the center of the nest. Exotic shrub volume ($F_{2,65} = 44.49$, $P = < 0.001$) and native woody vegetation volume ($F_{2,65} = 6.03$, $P = 0.004$) was significantly different among nest substrates. Exotic shrub is volume of exotic shrubs ≤ 3 m in height and native woody vegetation is volume of all native vegetation (trees, shrubs, and vines) ≤ 3 m in height.

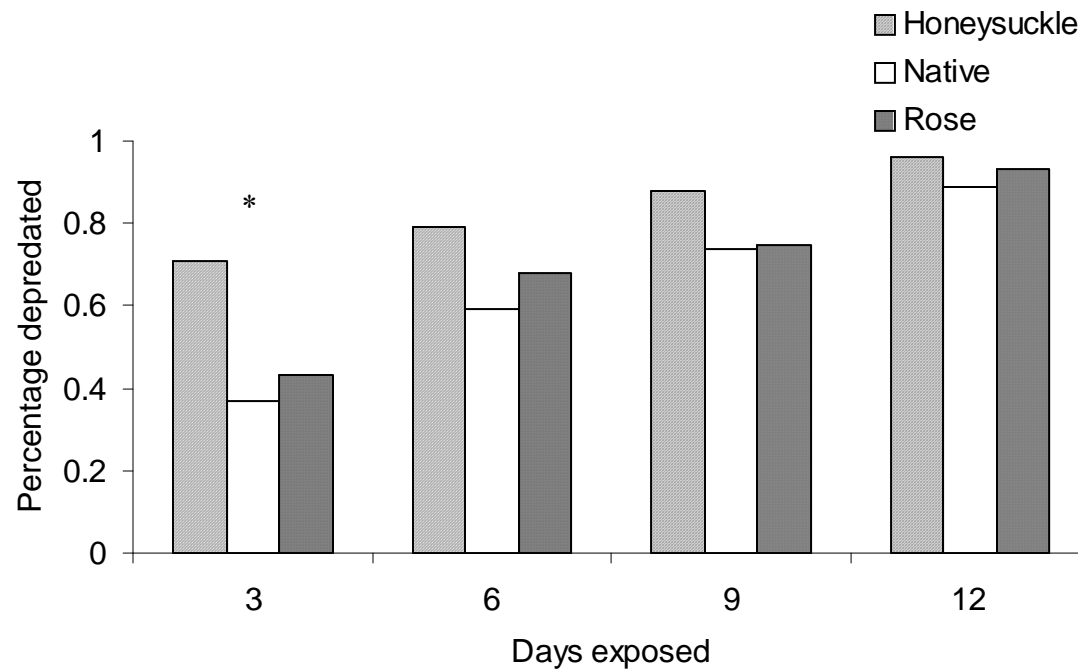


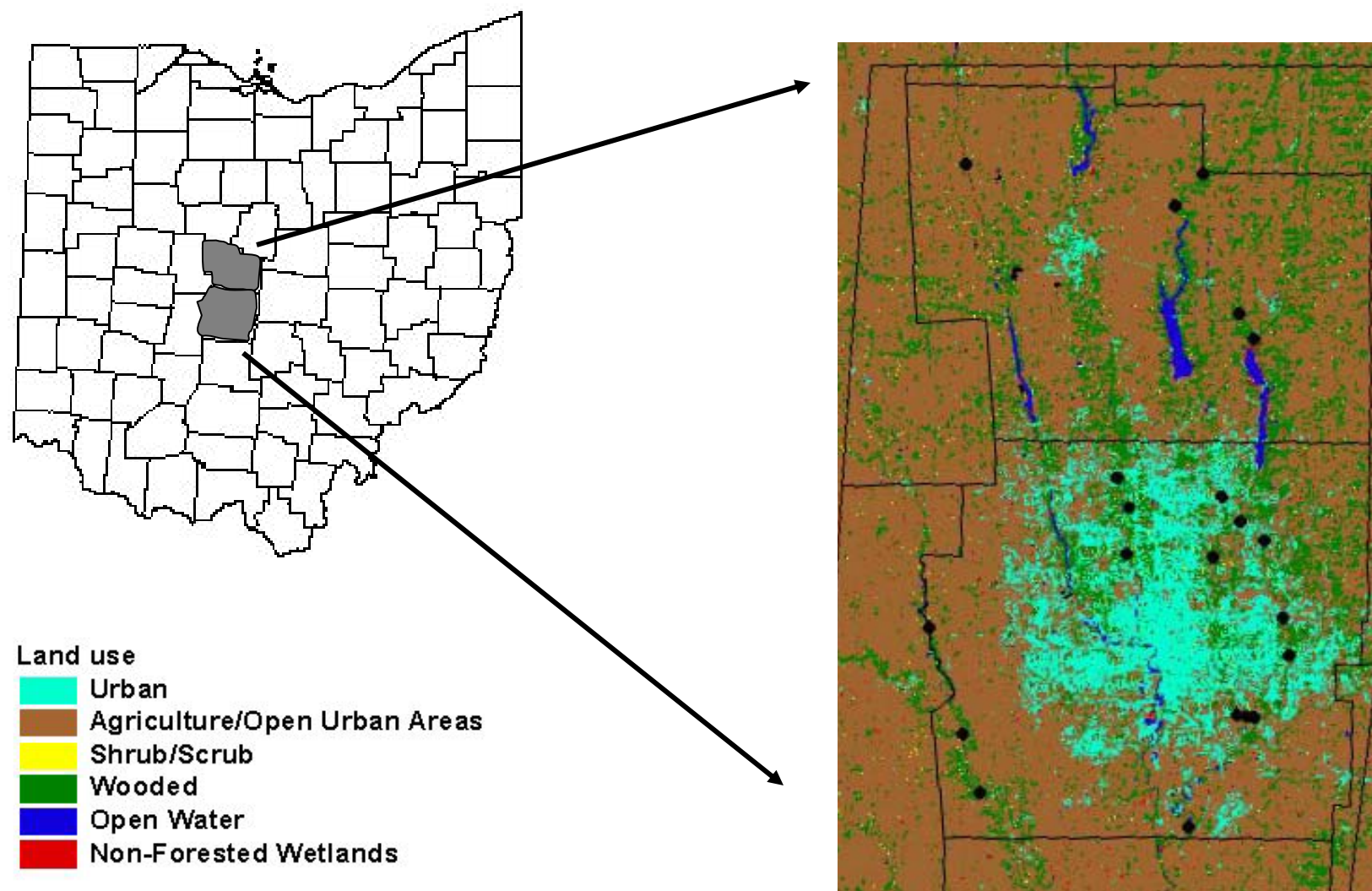
Fig. 3.4. Percentage of depredated artificial nests compared to number of days exposed. Artificial nest experiment began on 18 June 2001 at one rural site and on 30 June 2002 at two rural sites in Delaware County, Ohio, USA. Asterisk indicates significant difference among nest substrates.

APPENDIX A. Scientific and common names of plants frequently encountered within riparian forest sites in central Ohio, USA. Nomenclature follows Braun (1961).

* Indicates exotic species.

Trees	
Scientific name	Common name
<i>Acer negundo</i>	Box Elder
<i>Acer nigrum</i>	Black Maple
<i>Acer rubra</i>	Red Maple
<i>Acer saccharinum</i>	Silverleaf Maple
<i>Acer saccharum</i>	Sugar Maple
<i>Aesculus glabra</i>	Ohio Buckeye
<i>Asimina triloba</i>	Paw Paw
<i>Carya cordiformis</i>	Bitternut Hickory
<i>Carya laciniosa</i>	Big Shellbark Hickory
<i>Carya ovalis</i>	Sweet Pignut
<i>Carya ovata</i>	Shagbark Hickory
<i>Celtis occidentalis</i>	Hackberry
<i>Cercis canadensis</i>	Red Bud
<i>Fagus grandifolia</i>	American Beech
<i>Fraxinus Americana</i>	White Ash
<i>Fraxinus nigra</i>	Black Ash
<i>Fraxinus pensylvanica</i>	Green Ash
<i>Fraxinus quadrangulata</i>	Blue Ash
<i>Gleditsia triacanthos</i>	Honeylocust
<i>Juglans nigra</i>	Black Walnut
<i>Maculara pomifera</i> *	Osage Orange
<i>Platanus occidentalis</i>	Sycamore
<i>Populus deltoides</i>	Cottonwood
<i>Prunus serotina</i>	Black Cherry
<i>Quercus spp.</i>	Oaks

<i>Robina pseudo-acacia</i>	Black Locust
<i>Tilia americana</i>	Basswood
<i>Ulmus americana</i>	American Elm
<i>Xanthoxylum americana</i>	Prickly Ash
<hr/>	
Shrubs	
<hr/>	
Scientific name	Common name
<i>Berberbis thunbergii</i> *	Japanese Barberry
<i>Cornus foemina</i>	Stiff Dogwood
<i>Cornus racemosa</i>	Grey Dogwood
<i>Crataegus</i> spp.	Hawthorn
<i>Elaeagnus umbellata</i> *	Autumn Olive
<i>Euonymus atropurpureus</i>	Burning Bush
<i>Euonymus obvatus</i>	Running Strawberry Bush
<i>Lindera benzoin</i>	Spice Bush
<i>Lonicera maackii</i> *	Amur Honeysuckle
<i>Lonicera morrowii</i> *	Morrow Honeysuckle
<i>Lonicera tatarica</i> *	Tatarian Honeysuckle
<i>Prunus americana</i>	Wild Crab
<i>Rosa eglanteria</i> *	Sweetbrier Rose



Appendix B. Location of riparian forest study sites in Franklin and Delaware counties, Ohio USA

APPENDIX C. Location of vegetation sampling sites in central Ohio, USA.

Site	County	Latitude	Longitude	River
Big Walnut Park	Franklin	39N 56.658'	82W 51.361'	Big Walnut
Casto Park	Franklin	40N 04.966'	82W 55.327'	Alum
Cherrybottom Park	Franklin	40N 03.860'	82W 53.913'	Big Walnut
Darby Public Hunting	Franklin	39N 50.834'	83W 12.168'	Big Darby
Elk Run Park	Franklin	39N 53.835'	82W 53.894'	Big Walnut
Galena	Delaware	40N 12.939'	82W 52.734'	Big Walnut
Gardner Rd.	Franklin	39N 53.695'	83W 13.003'	Big Darby
Innis Park	Franklin	40N 02.129'	82W 56.013'	Alum
Kilbourne	Delaware	40N 19.779'	82W 57.324'	Alum
Lockbourne Park	Franklin	39N 48.638'	82W 58.484'	Big Walnut
North Olentangy	Franklin	40N 06.337'	83W 02.087'	Olentangy
North Galena	Delaware	40N 21.341'	82W 55.324'	Alum
Prairie Oaks	Franklin	39N 59.177'	83W 14.752'	Big Darby
Prindle	Delaware	40N 22.150'	83W 11.100'	Scioto
Smith Farm	Franklin	39N 54.164'	82W 55.020'	Alum
South Galena	Delaware	40N 14.210'	82W 53.675'	Little Walnut
Three Creeks	Franklin	39N 52.901'	82W 54.272'	Blacklick
Whetstone Park	Franklin	40N 02.408'	83W 01.763'	Olentangy
Whitehall Park	Franklin	39N 59.003'	82W 51.863'	Big Walnut
Woodside Green Park	Franklin	40N 02.734'	82W 52.854'	Big Walnut

APPENDIX E. Mean (SE) volume of *Lonicera* and *R. multiflora* and landscape level variables. Mean site width and percent land use covered by urban development, agriculture, and forest within 1 km of 20 riparian forest sites in central Ohio, USA, 2001.

Site	<i>Lonicera</i>	<i>R. multiflora</i>	Urban (%)	Agriculture (%)	Forest (%)
Big Walnut Park	50.00 (50.00)	2.10 (2.10)	45.78	15.51	36.72
Casto Park	38.20 (20.16)	0.00 (0.00)	47.17	26.71	24.57
Cherrybottom Park	0.00 (0.00)	2.37 (1.26)	31.22	35.38	28.87
Darby Public Hunting	6.40 (6.40)	12.13 (12.13)	0.95	58.27	39.66
Elk Run Park	47.87 (31.06)	20.53 (10.27)	12.64	66.56	17.76
Galena	36.27 (17.88)	18.00 (8.54)	1.23	42.06	42.53
Gardner Rd.	0.00 (0.00)	11.97 (6.03)	1.23	54.01	43.28
Innis Park	0.00 (0.00)	12.53 (6.57)	7.61	39.86	51.09
Kilbourne	0.00 (0.00)	5.97 (5.97)	0.41	62.52	35.54
Lockbourne Park	10.00 (10.00)	0.00 (0.00)	2.68	68.77	24.48
North Olentangy	135.33 (45.71)	0.00 (0.00)	0.14	45.97	53.15
North Galena	0.00 (0.00)	0.00 (0.00)	29.47	22.55	45.04
Prairie Oaks	45.00 (32.33)	11.1 (11.1)	0.98	65.03	29.69
Prindle	0.00 (0.00)	6.00 (4.08)	0.12	83.75	12.92
Smith Farm	6.93 (6.93)	0.00 (0.00)	14.88	71.30	61.02
South Galena	9.43 (5.03)	42.20(16.04)	0.13	50.22	12.01
Three Creeks	82.67 (52.94)	0.00 (0.00)	7.81	73.28	15.36
Whetstone Park	172.73 (62.68)	0.00 (0.00)	30.59	15.17	48.18
Whitehall Park	0.00 (0.00)	0.00 (0.00)	35.42	34.23	49.91
Woodside Green Park	0.00 (0.00)	0.00 (0.00)	17.80	47.68	29.22

APPENDIX F. Location of nest searching sites and years riparian forest sites sampled in central Ohio, USA.

Site	County	Latitude	Longitude	River	Year sampled
Casto Park	Franklin	40N 04.966'	82W 55.327'	Alum	2001-2002
Cherrybottom Park	Franklin	40N 03.860'	82W 53.913'	Big Walnut	2001
Darby Public Hunting	Franklin	39N 50.834'	83W 12.168'	Big Darby	2001-2002
Elk Run Park	Franklin	39N 53.835'	82W 53.894'	Big Walnut	2001, 2002
Galena	Delaware	40N 12.939'	82W 52.734'	Big Walnut	2001-2002
Kilbourne	Delaware	40N 19.779'	82W 57.324'	Alum	2002
North Galena	Delaware	40N 21.341'	82W 55.324'	Alum	2001-2002
Prairie Oaks	Franklin	39N 59.177'	83W 14.752'	Big Darby	2001
Rush Run	Franklin	40N 04.598'	83W 01.862'	Olentangy	2001-2002
South Galena	Delaware	40N 14.210'	82W 53.675'	Little Walnut	2001-2002
Three Creeks	Franklin	39N 52.901'	82W 54.272'	Blacklick	2001-2002
Woodside Green Park	Franklin	40N 02.734'	82W 52.854'	Big Walnut	2001-2002

APPENDIX G. Number of understory (≤ 5 m) nests monitored, number of exposure days, and Mayfield's estimate of daily mortality for nests among each nest substrate at 12 riparian forest sites in central Ohio, USA, 2001-2002.

Site	Substrate	Number of nests	Exposure days	Daily mortality rate
Casto Park	Honeysuckle	11	132.5	0.047
	Rose	6	84.5	0.073
	Native	13	182	0.058
Cherrybottom Park	Honeysuckle	0	NA	NA
	Rose	7	58.5	0.103
	Native	1	25	0.000
Darby Public Hunting	Honeysuckle	1	13	0.077
	Rose	1	30	0.000
	Native	34	605	0.033
Elkrun Park	Honeysuckle	4	25	0.315
	Rose	2	28	0.076
	Native	17	290	0.030
Galena	Honeysuckle	4	79	0.008
	Rose	2	13.5	0.148
	Native	5	113.5	0.027
Kilbourne	Honeysuckle	1	3	0.000
	Rose	6	70	0.057
	Native	4	31.5	0.127
North Galena	Honeysuckle	0	NA	NA
	Rose	0	NA	NA
	Native	28	408	0.046
Prairie Oaks	Honeysuckle	0	NA	NA
	Rose	0	NA	NA
	Native	7	132.5	0.030
Rush Run	Honeysuckle	4	34.5	0.124
	Rose	3	5	0.584
	Native	1	14.5	0.069
South Galena	Honeysuckle	4	102.5	0.018
	Rose	15	186	0.056
	Native	7	105	0.048
Three Creeks	Honeysuckle	9	145.5	0.037
	Rose	0	NA	NA
	Native	22	403.5	0.035
Woodside Green Park	Honeysuckle	0	NA	NA
	Rose	4	42.5	0.580
	Native	8	125.5	0.069

BIBLIOGRAPHY

- Albaugh, G. P., W. H. Mitchell, and J. C. Graham. 1977. Evaluation of glyphosate for multiflora rose control. *Proceedings NE Weed Science Society* **31**:283-291.
- Ambuel, B., and S. A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* **64**:1057-1068.
- Anderson, B. W., A. Higgins, and R. D. Ohmart. 1977. Avian use of saltcedar communities in the lower Colorado River valley. U.S. Dept. Agriculture Forest Service General Technical Report **RM-43**:128-136.
- Andren, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* **73**:794-804.
- Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**:355-366.
- Andren, H. 1995. Effects of landscape composition on predation rates at habitat edges. Pages 225-255 *in* L. Hannon, L. Fahrig, and G. Merriam, editors. *Mosaic landscapes and ecological processes*. Chapman and Hall, New York, New York, USA.
- Angelstam, P. 1986. Predation on ground-nesting birds' nests in relation to predator density and habitat edge. *Oikos* **47**:365-373.
- Askins, R. A. 1995. Hostile landscapes and the decline of migratory songbirds. *Science* **267**:1956-1957.
- Askins, R. A. 2000. *Restoring North America's birds*. Yale University Press, New Haven, Connecticut, USA.
- Askins, R. A., J. F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. *Current Ornithology* **7**:1-57.

- Baker, H. G. 1986. Patterns of plant invasions in North America. Pages 44-55 in H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer Verlag, New York, New York, USA. Barbour, M. G., J. H. Burk, and W. D. Pitts. 1987. Terrestrial Plant Ecology. Second Edition. The Benjamin/Cummings Publishing Company, Inc., Menlo Park, California, USA.
- Barber, D. R., and T. E. Martin. 1997. Influence of alternate host densities on Brown-headed Cowbird parasitism rates in Black-capped Vireos. *Condor* **99**:595-604.
- Bayne, E. M., and K. A. Hobson. 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conservation Biology* **11**:1418-1429.
- Bazzaz, F. A. 1986. Life history of colonizing plants: some demographic, genetic, and physiological features. Pages 96-110 in H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.
- Beissinger, S. R., and D. R. Osborne. 1982. Effects of urbanization on avian community organization. *Condor* **84**:75-83.
- Benoit, L. K., and R. A. Askins. 1999. Impacts of the spread of *Phragmites* on the distribution of birds in Connecticut tidal marshes. *Wetlands* **19**:194-208.
- Best, L. B., and D. F. Stauffer. 1980. Factors affecting nesting success in riparian bird communities. *Condor* **82**:149-158.
- Bolger, D. T., T. A. Scott, and J. T. Rotenberry. 1997. Breeding bird abundance in an urbanizing landscape in coastal southern California. *Conservation Biology* **11**:406-421.
- Borgmann, K. L., and A. D. Rodewald. *In review*. Landscape matrix effects on invasion of exotic shrubs in riparian forests. *Biological conservation*.
- Bowman, G. B., and L. D. Harris. 1980. Effect of spatial heterogeneity on ground-nest depredation. *Journal of Wildlife Management* **44**:806-813.
- Braithwaite, R. W., W. M. Lonsdale, and J. A. Estbergs. 1989. Alien vegetation and native biota in tropical Australia: the impact of *Mimosa pigra*. *Biological Conservation* **48**:189-210.
- Braun, E. L. 1916. The physiographic ecology of the Cincinnati region. *Ohio Biological Survey Bulletin* **7**, 2:137.

- Braun, E. L. 1961. The woody plants of Ohio. Ohio State University Press. Columbus, Ohio, USA.
- Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *Bioscience* **33**:31-35.
- Brothers, T. S., and A. Spingarn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Conservation Biology* **6**:91-100.
- Bull, E. L., and J. M. Skovlin. 1982. Relationships between avian fauna and streamside vegetation. Transactions of the North American Wildlife and Natural Resources Conference **47**:496-506.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Byers, J. E., S. Reichard, J. M. Randall, I. M. Parker, C. S. Smith, W. M. Lonsdale, I. A. E. Atkinson, T. R. Seastedt, M. Williamson, E. Chornesky, and D. Hayes. 2002. Directing research to reduce the impacts of nonindigenous species. *Conservation Biology* **16**:630-640.
- Cam, E., J. D. Nichols, J. R. Sauer, J. E. Hines, and C. H. Flather. 2000. Relative species richness and community completeness: birds and urbanization in the mid-Atlantic states. *Ecological Applications* **10**:1196-1210.
- Chase, M. K. 2002. Nest site selection and nest success in a song sparrow population: the significance of spatial variation. *Condor* **104**:103-116.
- Cody, M. L. 1974. Competition and the structure of bird communities. Princeton University Press, Princeton, New Jersey, USA.
- Cody, M. L. 1981. Habitat selection in birds: the roles of vegetation structure, competitors, and productivity. *BioScience* **31**:107-113.
- Collier, M. H., J. L. Vankat, and M. R. Hughes. 2002. Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. *American Midland Naturalist* **147**:60-71.
- Croonquist, M. J., and R. P. Brooks. 1993. Effects of habitat disturbance on bird communities in riparian corridors. *Journal of Soil and Water Conservation* **48**:65-70.
- Cubbedge, A. W., and C. H. Nilon. 1993. Adjacent land use effects on the flood plain forest bird community of Minnesota Valley National Wildlife Refuge. *Natural Areas Journal* **13**:220.

- D'Antonio, C., L. A. Meyerson, and J. Denslow. 2001. Exotic species and conservation. Pages 59-80 in M. E. Soule, and G. H. Orians, editors. Conservation biology: research priorities for the next decade. Island Press, Washington, D.C., USA.
- Davies, K. F., C. Gascon, and C. R. Margules. 2001. Habitat fragmentation: consequences, management, and future research priorities. Pages 81-97 in M. E. Soule, and G. H. Orians, editors. Conservation biology: research priorities for the next decade. Island Press, Washington, D.C., USA.
- Debussche, M., and P. Iseman. 1990. Introduced and cultivated fleshy-fruited plants: consequences of a mutualistic Mediterranean plant bird system. Pages 399-416 in F. diCastri, A. J. Hansen, and M. Debussche, editors. Biological invasions in Europe and the Mediterranean Basin. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Dijak, W. D., and F. R. Thompson. 2000. Landscape and edge effects on the distribution of mammalian predators in Missouri. *Journal of Wildlife Management* **64**:209-216.
- Donovan, T. M., R. H. Lamberson, A. Kimber, F. R. Thompson III, and J. Faaborg. 1995a. Modeling the effects of habitat fragmentation on source and sink demography of neotropical migrant birds. *Conservation Biology* **9**:1396-1407.
- Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995b. Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology* **9**:1380-1395.
- Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* **78**:2064-2075.
- Donovan, T. M., and C. H. Flather. 2002. Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. *Ecological Applications* **12**:364-374.
- Eckardt, N. 1987. Element stewardship abstract, *Rosa multiflora*. Unpublished report for The Nature Conservancy, Arlington, Virginia, USA.
- Ellis, L. M. 1995. Bird use of saltcedar and cottonwood vegetation in the Middle Rio Grande Valley of New Mexico, U.S.A. *Journal of Arid Environments* **30**:339-349.
- Elton, C. 1958. The ecology of invasions by plants and animals. Methuen, London, United Kingdom.

- Emlen, J. T. 1974. An urban bird community in Tucson, Arizona: derivation, structure, regulation. *Condor* **76**:184-197.
- Ewel, J. J., D. J. O'Dowd, J. Bergelson, C. C. Daehler, C. M. D'Antonio, L. D. Gomez, D. R. Gordon, R. J. Hobbs, A. Holt, K. R. Hopper, C. E. Hughes, M. LaHart, R. R. B. Leakey, W. G. Lee, L. L. Loope, D. H. Lorence, S. M. Louda, A. E. Lugo, P. B. McEvoy, D. M. Richardson, and P. M. Vitousek. 1999. Deliberate introductions of species: research needs. *BioScience* **49**:619-630.
- Faaborg, J. F., M. Brittingham, T. Donovan, and J. Blake. 1995. Habitat fragmentation in the temperate zone. Pages 357-380 *in* T. E. Martin and D. Finch, editors. *Ecology and management of Neotropical migratory birds*. Oxford University Press, New York, New York, USA.
- Filliater, T. S., R. Breitwisch, and P. M. Nealen. 1994. Predation on Northern Cardinal nests: does choice of nest site matter? *Condor* **96**:761-768.
- Flather, C. H., and J. R. Sauer. 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. *Ecology* **77**:28-35.
- Forsyth, J. L. 1979. Tills plains. Pages 198-213 *in* M. B. Lafferty, editor. *Ohio's natural heritage*. The Ohio Academy of Sciences, Columbus, Ohio, USA.
- Fowler, J., and L. Cohen. 1990. *Practical statistics for field biology*. Open University Press, Philadelphia, Pennsylvania, USA.
- Fraser, M. W., and T. M. Crowe. 1990. Effects of alien woody plant invasion on the birds of Mountain Fynbos in the Cape of Good Hope Nature Reserve. *South African Journal of Zoology* **25**:97-108.
- Friesen, L. E., P. F. J. Eagles, and R. J. Mackay. 1995. Effects of residential development on forest-dwelling Neotropical migrant songbirds. *Conservation Biology* **9**:1408-1414.
- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* **59**:871-883.
- Gazda, R. J., R. R. Meidinger, I. J. Ball, and J. W. Connelly. 2002. Relationships between Russian olive and duck nest success in southeastern Idaho. *Wildlife Society Bulletin* **30**:337-344.
- Germaine, S. S., S. S. Rosenstock, R. E. Schweinsburg, and W. S. Richardson. 1998. Relationships among breeding birds, habitat, and residential development in greater Tucson, Arizona. *Ecological Applications* **8**:680-691.

- Goldblum, D., and S. W. Beatty. 1999. Influence of an old field/forest edge on a northeastern United States deciduous forest understory community. *Journal of the Torrey Botanical Society* **126**:335-343.
- Gould, A. M. A., and D. L. Gorchov. 2000. Effects of the exotic invasive shrub *Lonicera maackii* on survival and fecundity of three species of native annuals. *American Midland Naturalist* **144**:36-50.
- Groom, J. D., and T. C. Grubb Jr. 2002. Bird species associated with riparian woodland in fragmented, temperate-deciduous forest. *Conservation Biology* **16**:832-836.
- Halkin, S. L., and S. U. Linville. 1999. Northern Cardinal (*Cardinalis cardinalis*). Pages 1-32 *In* A. Poole and F. Gill, editors. *The Birds of North America*, Number. 440. The Academy of Natural Sciences, Philadelphia Pennsylvania, and the American Ornithologists' Union, Washington, D.C., USA.
- Haskell, D. G. 1995. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. *Conservation Biology* **9**:1316-1318.
- Heske, E. J. 1995. Mammal abundances on forest-farm edges versus interiors in southern Illinois: is there an edge effect? *Journal of Mammalogy* **76**:562-568.
- Heske, E. J., S. K. Robinson, and J. D. Brawn. 1999. Predator activity and predation on songbird nests on forest-field edges in east-central Illinois. *Landscape Ecology* **14**:345-354.
- Heske, E. J., S. K. Robinson, and J. D. Brawn. 2001. Nest predation and Neotropical migrant songbirds: piecing together the fragments. *Wildlife Society Bulletin* **29**:52-61.
- Hines, J. E., and J. R. Sauer. 1989. Program CONTRAST: a general program for the analysis of several survival or recovery estimates. Technical report **24**. U.S. Fish and Wildlife Service, Laurel, Maryland, USA.
- Hobbs, R. J. 1989. The nature and effects of disturbance relative to invasions. Pages 389-405 *in* J. A. Drake, H.A. Mooney, F. diCasti, R. H. Groves, F. J. Kruger, M. Rejamek, and M. Williamson, editors. *Biological invasions: a global perspective*. Scope 37. John Wiley and Sons, Chichester, United Kingdom.
- Hobbs, R. J. 1991. Disturbance as a precursor to weed invasion in native vegetation. *Plant Protection Quarterly* **6**:99-104
- Hobbs, R. J. 2000. Land-use changes and invasions. Pages 55-64 *in* H. A. Mooney and R. J. Hobbs, editors. *Invasive species in a changing world*. Island Press, Washington, D.C., USA.

- Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* **6**:324-337.
- Hobbs, R. J., and S. E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. *Conservation Biology* **9**:761-770.
- Hohtola, E. 1978. Differential changes in bird community structure with urbanization: a study in Central Finland. *Ornis Scandinavica* **9**:94-100.
- Howell, C. A., S. C. Latta, T. M. Donovan, P. A. Porneluzi, G. R. Parks, and J. Faaborg. 2000. Landscape effects mediate breeding bird abundance in midwestern forests. *Landscape Ecology* **15**:547-562.
- Hunter, W. C., R. D. Ohmart, and B. W. Anderson. 1988. Use of exotic saltcedar (*Tamarix chinensis*) by birds in arid riparian systems. *Condor* **90**:113-123.
- Hutchinson, T. F., and J. L. Vankat. 1997. Invasibility and effects of Amur Honeysuckle in Southwestern Ohio forests. *Conservation Biology* **11**:1117-1124.
- Hutchinson, T. F., and J. L. Vankat. 1998. Landscape structure and spread of the exotic shrub *Lonicera maackii* (Amur honeysuckle) in southwestern Ohio forests. *American Midland Naturalist* **139**:383-390.
- Ingold, J. L., and M. J. Craycraft. 1983. Avian frugivory on honeysuckle (*Lonicera*) in southwestern Ohio in fall. *Ohio Journal of Science* **83**:256-258.
- James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. *Audubon Field Notes* **24**:727-736.
- James, F. C., and N. O. Wamer. 1982. Relationship between temperate forest bird communities and vegetation structure. *Ecology* **63**:159-171.
- Jenkins, M. A., and G. R. Parker. 2000. The response of herbaceous-layer vegetation to anthropogenic disturbance in intermittent stream bottomland forests of southern Indiana, USA. *Plant Ecology* **151**:223-237.
- King, D. I., C. R. Griffin, and R. M. DeGraaf. 1996. Effects of clearcutting on habitat use and reproductive success of the ovenbird in forested landscapes. *Conservation Biology* **10**:1380-1386.
- King, D. I., R. M. DeGraaf, C. R. Griffin, and T. J. Maier. 1999. Do predation rates on artificial nests accurately reflect predation rates on natural bird nests? *Journal of Field Ornithology* **70**:257-262.

- Knopf, F. L., R. R. Johnson, T. Rich, F. B. Samson, and R. C. Szaro. 1988. Conservation of riparian ecosystems in the United States. *Wilson Bulletin* **100**:272-284.
- Laub, K. W. 1979. Changing land use: forests, farms, and wildlife. Pages 272-281 in M.B. Lafferty, editor. *Ohio's natural heritage*. The Ohio Academy of Sciences, Columbus, Ohio, USA.
- Lochmiller, R. L. 1978. Privet as a potential winter food supplement for songbirds. *Bird Banding* **49**:279-280.
- Lonsdale, W. M. 1993. Rates of spread of an invading species *Mimosa pigra* in northern Australia. *Journal of Ecology* **81**:513-521.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**:1522-1536.
- Lowrance, R., R. Todd, J. Fail, Jr., O. Hendrickson, Jr., R. Leonard, and L. Asmussen. 1984. Riparian forests as nutrient filters in agricultural watersheds. *Bioscience* **34**:374-377.
- Luken, J. O. 1988. Population structure and biomass allocation of the naturalized shrub *Lonicera maackii* (Rupr.) maxim. in forest and open habitats. *The American Midland Naturalist* **119**:258-267.
- Luken, J. O. 1997. Management of plant invasions: implicating ecological succession. Pages 133-144 in J. O. Luken and S. W. Thieret, editors. *Assessment and management of plant invasions*. Springer-Verlag, New York, New York, USA.
- Luken, J. O., and D. T. Mattimiro. 1991. Habitat-specific resilience of the invasive shrub Amur honeysuckle (*Lonicera maackii*) during repeated clipping. *Ecological Applications* **1**:104-109.
- Luken, J. O., and N. Goessling. 1995. Seedling distribution and potential persistence of the exotic shrub *Lonicera maackii* in fragmented forests. *American Midland Naturalist* **133**:124-130.
- Luken, J. O., T. C. Tholemeier, L. M. Kuddes, and B. A. Kunkel. 1995. Performance, plasticity, and acclimation of the nonindigenous shrub *Lonicera maackii* (Caprifoliaceae) in contrasting light environments. *Canadian Journal of Botany* **73**:1953-1961.
- Luken, J. O., and J. W. Thieret. 1996. Amur honeysuckle, its fall from grace. *Bioscience* **46**:18-24.

- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* **42**:594-598.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- MacDonald, I. A. W., L. L. Loope, M. B. Usher, and O. Hamann. 1989. Wildlife conservation and the invasion of nature reserves by introduced species: a global perspective. Pages 215-255 *in* J. A. Drake, H. A. Mooney, F. diCastri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. *Biological Invasions: a global perspective*. John Wiley & Sons Ltd., New York, New York, USA.
- Machtans, C. S., M. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. *Conservation Biology* **10**:1366-1379.
- Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-ecosystems* **7**:145-165.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* **10**:689-710.
- Major, R. E., and C. E. Kendal. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis* **138**:298-307.
- Martin, A. C., H. S. Zim and A. L. Nelson. 1951. *American Wildlife and Plants: a Guide to Wildlife Food Habits*. Dover, New York, New York, USA.
- Martin, T. E. 1987. Artificial nest experiments: effects of nest appearance and predator type. *Condor* **89**:925-928.
- Martin, T. E. 1988a. Habitat and area effects on forest bird assemblages: is nest predation an influence? *Ecology*. **69**:74-84.
- Martin, T. E. 1988b. Processes organizing open-nesting bird assemblages: competition or nest predation? *Evolutionary Ecology* **2**:37-50.
- Martin, T. E. 1988c. On the advantage of being different: nest predation and the coexistence of bird species. *Proceedings of the National Academy of Science* **85**:2196-2199.

- Martin, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455-473 in J. M. Hagan III and D. W. Johnston, editors. *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Institution Press, Washington, D.C., USA.
- Martin, T. E. 1993a. Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist* **141**:897-913.
- Martin, T. E. 1993b. Nest predation and nest sites: new perspectives on old patterns. *BioScience* **43**:523-532.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* **65**:101-127.
- Martin, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* **79**:656-670.
- Martin, T. E., and D. M. Finch, editors. 1995. *Ecology and management of Neotropical migratory birds*. Oxford University Press, New York, New York, USA.
- Martin, T. E., and J. R. Karr. 1986. Patch utilization by migrating birds: resource oriented? *Ornis Scandinavica* **17**:165-174.
- Martin, T. E., and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the hermit thrush. *Condor* **90**:51-57.
- Martin, T. E., C. Paine, C. J. Conway, and W. M. Hochachka. 1997. BBIRD field protocol. Montana Cooperative Wildlife Resource Unit, Missoula, Montana, USA.
- Marzluff, J. M., F. R. Gehlbach, and D. A. Manuwal. 1998. Urban environments: influences on avifauna and challenges for the avian conservationist. Pages 283-299 in J. M. Marzluff and R. Sallabanks, editors. *Avian conservation research and management*. Island Press, Washington, D.C., USA.
- Marzluff, J. M., and K. Ewing. 2001. Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. *Restoration Ecology* **9**:280-292.
- Marzluff, J. M., R. Bowman, and R. Donnelly, editors. 2001a. *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston, Massachusetts, USA.

- Marzluff, J. M., R. Bowman, and R. Donnelly. 2001*b*. A historical perspective on urban bird research: trends, terms, and approaches. Pages 1-17 *in* J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Boston, Massachusetts, USA.
- Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the Eastern United States. *Biological Conservation* **66**:185-194.
- Matlack, G. R. 1994*a*. Vegetation dynamics of the forest edge – trends in space and successional time. *Journal of Ecology* **82**:113-123.
- Matlack, G. R. 1994*b*. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* **75**:1491-1502.
- Matthiae, P. E., and F. Stearns. 1981. Mammals in forest islands in southeastern Wisconsin. Pages 55-66 *in* R. L. Burgess and D. M. Sharpe, editors. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, New York, USA.
- Maurer, B. A., and R. C. Whitmore. 1981. Foraging of five bird species in two forests with different vegetation structure. *Wilson Bulletin* **93**:478-490.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* **73**:255-261.
- McDonnell, M. J. and E. W. Stiles. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* **56**:109-116.
- McDonnell, M. J., and S. T. A. Pickett. 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology* **71**:1232-1237.
- Meents, J. K., B. W. Anderson, and R. D. Ohmart. 1984. Sensitivity of riparian birds to habitat loss. Pages 619-625 *in* R. E. Warner and K. M. Hendrix, editors, California riparian systems: ecology, conservation and productive management. University of California Press, Berkeley, California, USA.
- Mensing, D. M., S. M. Galatowitsch, and J. R. Tester. 1998. Anthropogenic effects on the biodiversity of riparian wetlands of a northern temperate landscape. *Journal of Environmental Management* **53**:349-377.
- Miller, J. R., and P. Cale. 2000. Behavioral mechanisms and habitat use by birds in a fragmented agricultural landscape. *Ecological Applications* **10**:1732-1748.

- Mills, G. S., J. B. Dunning, Jr., and J. M. Bates. 1989. Effects of urbanization on breeding bird community structure in southwestern desert habitats. *Condor* **91**:416-428.
- Mills, G. S., J. B. Dunning, Jr., and J. M. Bates. 1991. The relationship between breeding bird density and vegetation volume. *Wilson Bulletin* **103**:468-479.
- Misenhelter, M. D., and J. T. Rotenberry. 2000. Choices and consequences of habitat occupancy and nest site selection in sage sparrows. *Ecology* **81**:2892-2901.
- Mooney, H. A. 1999. A global strategy for dealing with alien invasive species. Pages 407-418 in O. T. Sandland, P. J. Schie, and A. Viken, editors. *Invasive species and biodiversity management*. Kluwer Academic Publishers, Netherlands.
- Moran, M. A. 1984. Influence of adjacent land use on understory vegetation of New York forests. *Urban Ecology* **8**:329-340.
- Morrow, J. L., J. H. Howard, S. A. Smith, and D. K. Poppel. 2001. Habitat selection and habitat use by the box turtle (*Clemmys muhlenbergii*) in Maryland. *Journal of Herpetology* **35**:545-552.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* **10**:58-62.
- Naiman, R. J., and H. Decamps. 1997. The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics* **28**:621-658.
- Naiman, R. J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* **3**:209-212.
- Neill, W. M. 1983. The tamarisk invasion of desert riparian areas. *Education Bulletin* 83-84, Desert Protective Council, Spring Valley, California, USA.
- Nilsson, C., G. Grelsson, M. Johansson, and U. Sperens. 1989. Patterns of plant species richness along riverbanks. *Ecology* **70**:77-84.
- Noble, I. R. 1989. Attributes of invaders and the invading process: terrestrial and vascular plants. Pages 301-313 in J. A. Drake, H. A. Mooney, F. diCastri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. *Biological Invasions: a global perspective*. John Wiley & Sons Ltd., New York, New York, USA.
- Novak, S. J., and R. N. Mack. 1995. Allozyme diversity in the apomictic vine *Bryonia alba*: potential consequences of multiple introductions. *American Journal of Botany* **82**:1153-1162.

- O'Connell, T. J., L.E. Jackson, and R. P. Brooks. 2000. Bird guilds as indicators of ecological condition in the Central Appalachians. *Ecological Applications* **10**:1706-1721.
- Oehler, J. D., and J. A. Litvaitis. 1996. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. *Canadian Journal of Zoology* **74**:2070-2079.
- Opdam, P., G. Rijsdijk, and F. Hustings. 1985. Bird communities in small woods in an agricultural landscape: effects of area and isolation. *Biological Conservation* **34**:333-352.
- Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology* **8**:17-26.
- Peterjohn, W. T., and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. *Ecology* **65**:1466-1475.
- Peterman, R. M. 1990. Statistical power analysis can improve fisheries research and management. *Canadian Journal of Fisheries and Aquatic Sciences* **47**:2-15.
- Planty-Tabacchi, A., E. Tabacchi, R. J. Naiman, C. Deferrari, and H. Decamps. 1996. Invasibility of species-rich communities in riparian zones. *Conservation Biology* **10**:598-607.
- Pysek, P., and K. Prach. 1993. Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. *Journal of Biogeography* **20**:413-420.
- Pysek, P., V. Jarosik, and T. Kucera. 2002. Patterns of invasion in temperate nature reserves. *Biological Conservation* **104**:13-24.
- Ranney, J. W., M. C. Bruner, and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67-95 *in* R. L. Burgess and D. M. Sharpe, editors. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- Rappole, J. H., and M. V. McDonald. 1994. Cause and effect in population declines of migratory birds. *Auk* **111**:334-345.
- Ratti, J. T., and K. P. Reese. 1988. Preliminary test of the ecological trap hypothesis. *Journal of Wildlife Management* **52**:484-491.
- Rehder, A. 1927. *Manual of cultivated trees and shrubs hardy in North America*. MacMillan, New York, New York, USA.

- Reichard, S. H., L. Chalker-Scott, and S. Buchanan. 2001. Interactions among non-native plants and birds. Pages 179-223 in J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Boston, Massachusetts, USA.
- Reijnen, R., R. Foppen, C. T. Braak, and J. Thissen. 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to proximity of main roads. *Journal of Applied Ecology* **32**:187-202.
- Rejmanek, M. 1989. Invasibility of plant communities. Pages 369-388 in J. A. Drake, F. diCastri, R. Groves, F. Kruger, H. A. Mooney, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. Scope 37. John Wiley and Sons, Chichester, United Kingdom.
- Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? *Ecology* **77**:1655-1661.
- Renne, I. J., W. C. Barrow Jr., L. A. Johnson Randall, and W. C. Bridgers Jr. 2002. Generalized avian dispersal syndrome contributes to Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasiveness. *Biodiversity Research* **8**:285-295.
- Rey, P. J. 1995. Spatio-temporal variation in fruit and frugivorous bird abundance in olive orchards. *Ecology* **76**:1625-1635.
- Richardson, D. M., N. Allsopp, C. M. D'Antonio, S. J. Milton, and M. Rejmanek. 2000. Plant invasions – the role of mutualisms. *Biological Review* **75**:65-93.
- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* **9**:1-48.
- Robinson, S. K. 1996. Threats to breeding neotropical migratory birds in the Midwest. Pages 1-21 in F. R. Thompson, III, editor. Management of midwestern landscapes for the conservation of neotropical migratory birds. U.S. For. Serv. Gen. Tech. Rep. NC-187. North Central For. Exp. Sta., St. Paul, MN, USA.
- Robinson, S. K., and R. T. Holmes. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. *Auk* **101**:672-684.
- Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* **267**:1987-1990.
- Rodewald, A. D. 2002. Nest predation in forested regions: landscape and edge effects. *Journal of Wildlife Management* **66**:634-640.

- Rodewald, A. D., and R. H. Yahner. 2001a. Influence of landscape composition on avian community structure and associated mechanisms. *Ecology* **82**:3493-3504.
- Rodewald, A. D., and R. H. Yahner. 2001b. Avian nesting success in forested landscapes: influence of landscape composition, stand and nest-patch microhabitat, and biotic interactions. *Auk* **118**:1018-1028.
- Rotenberry, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics? *Oecologia* **67**:213-217.
- Rotenberry, J. T. 1998. Avian conservation research needs in western shrublands: exotic invaders and the alteration of ecosystem processes. Pages 261-272 in J.M. Marzluff and R. Sallabanks, editors. *Avian conservation research and management*. Island Press, Washington, D.C., USA.
- Rottenborn, S. C. 1997. The impacts of urbanization on riparian bird communities in central California. Ph.D. dissertation, Stanford University, Stanford, California, USA.
- Rottenborn, S. C. 1999. Predicting the impacts of urbanization on riparian bird communities. *Biological Conservation* **88**:289-299.
- Rudnick, T. C., and M. L. Hunter. 1993. Avian nest predation in clearcuts, forests, and edges in a forest-dominated landscape. *Journal of Wildlife Management* **57**:358-364.
- Ruesink, A. 1998. Links between land use and *Lonicera*: patterns of honeysuckle invasion in a post-agricultural landscape. M.S. Thesis. University of Vermont, Burlington, Vermont.
- Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. *Ecological Applications* **9**:135-151.
- Sallabanks, R. 1993. Fruiting plant attractiveness to avian seed dispersers: native vs. invasive *Crataegus* in western Oregon. *Madrono* **40**:108-116.
- Sanders, R. E., editor. 2001. A guide to Ohio's streams. Streams Committee, Ohio Chapter of the American Fisheries Society, Columbus, Ohio, USA.
- SAS Institute. 1990. SASSTAT user's guide. SAS Institute, Cary, North Carolina, USA.
- Schery, R. 1977. The curious double life of *Rosa multiflora*. *Horticulture* **55**:56-61.
- Schmidt, K. A. 1998. The consequences of partially directed search effort. *Evolutionary Ecology* **12**:263-277.

- Schmidt, K. A. 1999. Foraging theory as a conceptual framework for studying nest predation. *Oikos* **85**:151-160.
- Schmidt, K. A., and C. J. Whelan. 1998. Predator-mediated interactions between and within guilds of nesting songbirds: experimental and observational evidence. *American Naturalist* **152**:393-402.
- Schmidt, K. A., and C. J. Whelan. 1999a. Effects of exotic *Lonicera* and *Rhamnus* on songbird nest predation. *Conservation Biology* **13**:1502-1506.
- Schmidt, K. A., and C. J. Whelan. 1999b. Nest predation on woodland songbirds: when is nest predation density dependent? *Oikos* **87**:65-74.
- Schmiegelow, F. K. A., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology* **78**:1914-1932.
- Schmitz, D. C., D. Simberloff, R. H. Hofstetter, W. Haller, and D. Sutton. 1997. The ecological impacts of nonindigenous plants. Pages 39-61 in D. Simberloff, D. C. Schmitz, and T. C. Brown, editors. *Strangers in paradise*. Island Press, Washington, D. C., USA.
- Siepielski, A. M., A. D. Rodewald, and R. H. Yahner. 2001. Nest site selection and nesting success of the red-eyed vireo in central Pennsylvania. *Wilson Bulletin* **113**:302-307.
- Sieving, K. E., and M. F. Willson. 1998. Nest predation and avian species diversity in Northwestern forest understory. *Ecology* **79**:2391-2402.
- Southwood, T. R. E. 1961. The number of species of insect associated with various trees. *Journal of Animal Ecology* **30**:1-8.
- Timmins, S. M., P. A. Williams. 1991. Weed numbers in New Zealand's forest and scrub reserves. *New Zealand Journal of Ecology* **15**:153-162.
- Trisel, D. E., and D. L. Gorchov. 1994. Regional distribution, ecological impact, and leaf phenology of the invasive shrub, *Lonicera maackii*. *Bulletin of the Ecological Society of American* **75**:231.
- Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* **14**:18-30.
- Trzcinski, M. K., L. Fahrig, and G. Merriam. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications* **9**:586-593.

- USGS EROS Data Center. 2000. MRLC regional land cover characterization project land cover data for Ohio early 1900s (version 2000-03). Multi-resolution land characteristics consortium. National Land Cover Data Program.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* **47**:893-901.
- Vitousek, P. M. 1986. Biological invasions and ecosystem properties: can species make a difference? Pages 163-176 *in* H. A. Mooney, and J. A. Drake, editors. *Ecology of biological invasions of North America and Hawaii*. Springer-Verlag, New York, New York, USA.
- Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* **57**:7-13.
- Vitousek, P. M., C. M. D'Antonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997. Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* **21**:1-16.
- Whelan, C. J. 2001. Foliage structure influences foraging of insectivorous forest birds: an experimental study. *Ecology* **82**:219-231.
- Whelan, C. J., M. L. Dilger, D. Robson, N. Hallyn, and S. Dilger. 1994. Effects of olfactory cues on artificial-nest experiments. *Auk* **111**:945-952.
- Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 167-190 *in* R. L. Burgess and D. M. Sharpe, editors. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- White, D. W., and E. W. Stiles. 1992. Bird dispersal of fruits of species introduced into eastern North America. *Canadian Journal of Botany* **70**:1689-1696.
- Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* **66**:1211-1214.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, E. Losos. 1998. Quantifying threats to imperiled species in the United States. *Bioscience* **48**:607-615.
- Willson, M. F. 1974. Avian community organization and habitat structure. *Ecology* **55**:1017-1029.
- With, K. A. 2002. The landscape ecology of invasive spread. *Conservation Biology* **16**:1192-1203.

- Woods, K. D. 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four New England forests. *American Midland Naturalist* **130**:62-74.
- Wyman, D. 1949. Shrubs and vines for American gardens. Macmillan Company, New York, New York, USA.
- Yahner, R. H. 1996. Habitat fragmentation and habitat loss. *Wildlife Society Bulletin* **24**:592.
- Yahner, R. H., and A. L. Wright. 1985. Depredation on artificial ground nests: effects of edge and plot age. *Journal of Wildlife Management* **49**:508-513.
- Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution* **16**:454-459.