

Effects of site and climate characteristics on forest invasibility by non-native plants in the
Midwest

A THESIS
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF THE UNIVERSITY OF MINNESOTA
BY

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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
MASTER OF SCIENCE

July 2010

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Acknowledgements

I would like to thank my advisor, Dr. Rebecca Montgomery, for helping prepare this thesis. I greatly appreciated her continued support along the way and prompt thesis feedback as I worried countless times about meeting my proposed timeline. I am also grateful that she was a shoulder to lean on when things seemed to go awry. We had a tight deadline that others seemed skeptical about our ability to meet and were able to; thank you for having faith in me and helping to meet the deadline.

I am thankful for the contributions and support of my committee members – Dr. W. Keith Moser from the USDA Forest Service and Dr. Neil Anderson from the Department of Horticulture, the Department of Forest Resources, fellow graduate students, the University of Minnesota’s Statistical Consulting Service, and countless others that I have inadvertently forgotten to acknowledge. I would also like to thank my family for their support and for putting up with me “living” on campus during the countless hours of writing and revising.

Finally I would like to thank the USDA Forest Service’s Forest Inventory and Analysis field crews that spent many laborious hours collecting the data used in this thesis, coworkers for their valuable help, and the USDA Forest Service’s Northern Research Station for their support while taking coursework and completing my degree.

Abstract

Non-native invasive plant (NNIP) species can have significant effects on forest regeneration, structure, biodiversity, and wildlife habitat, costing billions of dollars annually. Understanding how NNIPs in the Midwest may spread in the future requires understanding their response to site and climate characteristics. Current research suggests climate change may influence invasive plant presence and spread. In this study, I modeled the relationship between invasive species presence, site characteristics (e.g. disturbance, live tree volume, city distance, edge distance, physiography, and type of water [e.g. streams] present on plot), and climate (annual average number of days the temperature is $\geq 90^{\circ}\text{F}$ and annual average number of days the temperature is $\leq 32^{\circ}\text{F}$) for five non-native invasive plants (multiflora rose [*Rosa multiflora*], common buckthorn [*Rhamnus cathartica*], non-native bush honeysuckles [*Lonicera* spp.], garlic mustard [*Alliaria petiolata*], and reed canary grass [*Phalaris arundinacea*]) sampled by the USDA Forest Service's Forest Inventory and Analysis program in seven Midwestern states for 2005-2006. Species' response to site and temperature predictors varied due to trait differences such as shade tolerance and moisture affinity. For most species, presence was positively related to biotic disturbance (disease(s) and/or animal(s)) and mesic physiography and negatively related to distance from a city or a nonforest edge. The best predictor for the presence of NNIPs was annual average number of days the temperature is $\leq 32^{\circ}\text{F}$, with all five species presence correlated with the annual average number of days the temperature is $\leq 32^{\circ}\text{F}$. Understanding the effect of site characteristics and climate on NNIP distribution provides insights into important drivers of species presence at a regional scale and allows land managers, scientists, and concerned citizens to predict invasion risk and future ecosystem response.

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INTRODUCTION

Concern over non-native invasive plant (NNIP) species is high and continues to escalate due to increased spread and associated ecological threats posed to natural resources (Ehrenfeld 1997). Invasive species are considered the second greatest threat to biodiversity conservation after habitat loss and fragmentation (With 2002, Yates et al. 2004). Many NNIPs were introduced for their ornamental value (e.g. Japanese barberry [*Berberis thunbergii*], Norway maple [*Acer platanoides*]), wildlife value (e.g. multiflora rose [*Rosa multiflora*], non-native bush honeysuckles [*Lonicera* spp.]), and/or ability to tolerate harsh environments (e.g. autumn olive [*Elaeagnus umbellata*] along roadsides and multiflora rose in agriculture windrows). However, when they escape domestic cultivation, NNIP species invade surrounding ecosystems, threatening native plant communities. In addition to the ecological threat of NNIPs, they also pose a financial threat by increasing inspection and land management costs. Each year companies spend billions of dollars on the increased costs associated with cargo inspection (e.g. ships and airlines) and supplies associated with management of NNIPs (e.g. in agriculture, residential, prairie, and forested areas). The concern over invasive species is high not only in the United States, but worldwide (Ehrenfeld 1997, Dukes and Mooney 1999, Nuzzo 1999, Lundgren et al. 2004, Yates et al. 2004).

Humans facilitate the spread of NNIP species across the landscape by deliberately planting them (e.g. agriculture windbreaks, roadsides/highway corridors, harvest sites, and commercial/homestead landscapes), disturbing and fragmenting the landscape, and dispersing propagules through transportation (e.g. road networks and All Terrain Vehicles). Animals and waterways provide additional sources of spread, dispersing seeds along travel corridors. The spread of NNIPs has deleterious effects on ecosystem structure and function including displacement of native species (Hutchinson and Vankat 1997, Knight et al. 2007, Mascaro and Schnitzer 2007), alteration of soil pH, nutrient cycles, community structure (Ehrenfeld 1997, Nuzzo 1999, Knight et al. 2007, Mascaro and Schnitzer 2007), and diminished aesthetic value (Knight et al. 2007). These effects are interrelated. For example, by changing forest structure NNIP species often displace native species and favor their own regeneration through altered light and nutrient availability (Knight et al. 2007, Mascaro and Schnitzer 2007).

Some ecosystems may be more resilient to establishment of NNIP species (Yates et al. 2004, Weber and Gibson 2007). Research suggests that establishment is greatest when the landscape is more than 20% disturbed, particularly in areas of large or aggregated disturbances, which increase the chance of successful colonization by propagules (With 2004). Invasives are

more likely to occur in areas of more intense land-use, such as pastured and plowed areas (McDonald et al. 2008). In addition, several factors are known to hinder their establishment including low light availability (e.g. late successional [Nuzzo 1999] and/or less intensely harvested forests [McDonald et al. 2008]) and reduced fragmentation (e.g. large tracts [Yates et al. 2004] and/or greater interior:edge ratios [Yates et al. 2004, Webster and Gibson 2007, McDonald et al. 2008]). However, forests that currently seem resistant to invasion may not be able to sustain this resistance as propagule pressure increases (Webster and Gibson 2007). A literature review suggests a multitude of anthropogenic, resource, and climate factors influence the probability that a site will be invaded following propagule arrival.

Dispersal vectors

Humans, animals, waterways, roadways, and storms facilitate dispersal of invasive species. Humans have transported plant species for food and horticultural purposes for thousands of years. Some introduction was intentional (agriculture, apiary, and horticulture use) while other was accidental (e.g. contaminated crop seed, ship ballast water [purple loosestrife [*Lythrum salicaria*]]). Since humans are a major vector for NNIP species, urban (Godefroid and Koedam 2003) and agricultural (McDonald et al. 2008) areas tend to be the most invaded. Several anthropogenic variables are related to NNIP presence (Medley 1996, Hutchinson and Vankat 1997, Lundgren et al. 2004, Bartuszevige et al. 2006, Kalwij et al. 2008). Invasive species presence is positively correlated with level of land development (Medley 1996, Lundgren et al. 2004) and housing density (Kalwij et al. 2008) but is negatively correlated with the distance to the nearest town (Hutchinson and Vankat 1997, Bartuszevige et al. 2006).

Waterways (e.g. rivers, canals), act as additional transport mechanisms for propagules and often span vast distances, some extending across entire countries. Reed canary grass (*Phalaris arundinacea* [Lavoie et al. 2005]), Chinese tallow (*Triadica sebifera* [Gan et al. 2009]), and garlic mustard (*Alliaria petiolata* [Nuzzo 1999]) all rely on waterways for long distance dispersal. In Cuyahoga Valley National Park in Ohio, garlic mustard distribution was found to be negatively correlated with distance to the nearest river (Burls and McClougherty 2008). In addition to natural waterways, man-made structures such as ditches and canals provide means for propagule dispersal, as found with reed canary grass, where drainage ditches provide important dispersal corridors (Lavoie et al. 2005).

Roadways are another method of propagule transport. Vehicle traffic provides a vector for long-distance dispersal of light-weight NNIP seeds along roadways. The risk of ecosystem

invasion increases as NNIP propagules spread across the landscape via local and long-distance dispersal vectors. On average, plant seeds spread up to 1,312 feet per year, but with the help of long-distance dispersal by animals, humans, waterways, and storms, dispersal rates are increased 2-3 times (Moser et al. 2009). In rare long-distance dispersal events, plants are able to spread over 1,000 miles and establish new satellite populations (Cain et al. 2000). Once a propagule arrives at a site, successful establishment and population expansion requires production of sufficient propagules and favorable site conditions, among other variables.

Propagule pressure

Propagule pressure plays a critical role in the spread of invasive species, posing risks to native plant communities. The number of propagules is greater in areas of human activity (e.g. urban, recreation, and agricultural areas) since humans vector NNIPs. Increased propagule pressure is of concern in forested ecosystems because high propagule pressure at forest edges may facilitate establishment in the forest interior (Brothers and Springarn 1992, Godefroid and Koedam 2003). The popularly planted ornamental, Japanese barberry, is an example of a species that began its spread by entering disturbed forest edges and open fields near human development and is now invading the forest interior (New York [Ehrenfeld 1997]). The impacts of this species, along with others capable of establishment in the forest interior (e.g. garlic mustard), must be monitored because of their ability to establish across a wide range of light availability and potentially change the forest composition. NNIPs can alter the forest structure by altering resource conditions (e.g. light, nutrients) which influences the current and future forest community.

Resource availability

NNIPs are generally more likely to invade sites of high resource availability (Funk and Vitousek 2007, Moser et al. 2009). Light is an important resource influencing NNIP establishment, as most NNIPs are shade intolerant (Flory and Clay 2006, McDonald et al. 2008). A change in available light occurs when the stand structure (e.g. basal area, age, and/or canopy cover) is altered. NNIP presence and density have been modeled with respect to several metrics of stand structure (e.g. basal area, age, and canopy cover) and the majority of these studies have found a positive correlation between invasive species presence and/or density and attributes related to increased light availability. Huebner and Tobin (2006) found clearcutting increases invasion risk by 829%, likely due to increased light, nutrient, and moisture availability. However

this may also represent increased invasion from propagules vectored by vehicles, equipment, and roads. Similarly, as stand age (Flory and Clay 2006) and/or basal area (Bartuszevige et al. 2006, Moser et al. 2009) is/are reduced, light availability is increased, thereby increasing NNIP presence.

Another factor related to site resource availability and NNIP establishment is nutrient availability. NNIPs tend to have an affinity for areas of higher nutrient availability (Huebner and Tobin 2006, Moser et al. 2009). Common buckthorn (*Rhamnus cathartica*) is an example of a species that benefits from higher nutrient levels. Though tolerant of a wide range of nutrient availability, common buckthorn prefers disturbed, fertile, calcium-rich, moist, open areas (Knight et al. 2007). These areas of high nutrient availability facilitate NNIP establishment by providing optimal sites for germination. Once invasives germinate on a site, they are often able to out-compete native species due to high growth efficiencies (Funk and Vitousek 2007).

A final factor related to resource availability and invasion by NNIPs is physiographic class. Physiographic class describes the physical geography of a site or region and generally describes moisture availability with respect to the landform, topographic position, and soil (U.S. Department of Agriculture 2007). Physiography limits the survival of common buckthorn since seeds have optimal germination on sites where the seeds are freshly deposited and have not dried out or been immersed for 2 months or longer (Knight et al. 2007). Establishment and growth of most invasive species is favored on mesic (moderate moisture) sites (Huebner and Tobin 2006, Moser et al. 2008) likely due to high growth efficiencies that increase competitive ability compared to native species. Xeric sites (moisture deficient) impede germination and seedling survival whereas hydric sites (over-abundance of water) generally are light-limited from rapid growth of other species (Moser et al. 2008).

Disturbance

Human and natural disturbances have facilitated the vast majority of NNIP invasions (Rejmánek and Richardson 1996). Sources of human disturbance are fragmentation, timber harvesting, and road networks; natural disturbance may occur from storms, waterways, diseases, or animals. Over 90% of the ecosystems east of the Mississippi River, which includes the bulk of the states in this study, are located within 0.66 miles of a road (Flory and Clay 2006). The importance of disturbance for NNIP establishment has been documented by many researchers (With 2002, Godefroid and Koedam 2003, With 2004, Flory and Clay 2006, Huebner and Tobin 2006, Kalwij et al. 2008, McDonald et al. 2008). Examples of species that are associated with

disturbed areas are: common buckthorn (Knight et al. 2007, Mascaro and Schnitzer 2007), Amur honeysuckle (*Lonicera maackii* [Medley 1996]), Chinese tallow (Gan et al. 2009), and garlic mustard (Nuzzo 1999).

Disturbance modifies resource availability. In many cases, disturbance kills plant life, reducing resource use and increasing the supply of water, nutrients, and light (With 2002). NNIP species may have an advantage over native species in disturbed sites since they have higher growth rates (Baruch and Goldstein 1999, Rejmánek 2000, Funk and Vitousek 2007, Knight et al. 2007, Kalwij et al. 2008), higher resource use efficiency (Baruch and Goldstein 1999, Funk and Vitousek 2007, Moser et al. 2008), longer dispersal distances (von der Lippe and Kowarik 2007), and greater seed production (Mason et al. 2008).

Forest edges, associated with fragmentation, provide enhanced opportunities for the establishment of NNIP species since they are characteristically different than interior sites. At the forest edge light availability, anthropogenic influence, temperature, vapor pressure deficit, and nutrient deposition are generally greater than in the forest interior, affecting forest microenvironments up to 164 feet from the edge (Godefroid and Koedam 2003). Propagule pressure is also greater as many birds who ingest the seeds of NNIPs often favor the forest edge over the interior due to increased food and nesting availability (Yates et al. 2004). A number of studies in Ohio have found that as distance to forest edge increases, the establishment of invasive species decreases (Medley 1996, Hutchinson and Vankat 1997, Christen and Matlack 2009). NNIPs generally do not establish in the forest interior and when they do reproduction and growth are generally limited (Hutchinson and Vankat 1997, Yates et al. 2004, Knight et al. 2007, Weber and Gibson 2007). Invasion of forest edges is of concern because the altered stand structure (increased light and resource availability) facilitates NNIPs in areas where there may be significantly greater concentrations of high conservation value species (e.g. ancient and rare species [Godefroid and Koedam 2003]).

Another important indicator of disturbance is the distance to the nearest roadway. Roadways are positively correlated with the presence of NNIP species (Funk and Vitousek 2007). Roadways foster suitable habitat for NNIPs to invade because they are more likely to have exposed mineral soil, greater sunlight, storm water runoff, and vehicle traffic (Flory and Clay 2006, von der Lippe and Kowarik 2007). Similarly, waterways have frequent annual disturbances due to variability in the water level. Disturbance by roadways and waterways promotes invasion by NNIPs such as reed canary grass by providing habitat suitable for establishment (Lavoie et al. 2005). Although NNIP presence is positively correlated with disturbance, it is uncertain whether

invasive plant presence will persist in a forest without continued disturbance, especially if native species that are adapted to low resource environments compete with them (Funk and Vitousek 2007).

Climate

Climate is a key abiotic factor that likely influences invasion probability and spread, as well as limits species ranges to areas similar to their native region. Researchers have noted that a species' native range may be the best predictor for where it is able to invade in its introduced location (Rejmánek and Richardson 1996). A species may be restricted from the north by low summer temperatures causing failure to set seed (Grace 1987, Morin et al. 2007) and/or because of freezing induced xylem embolisms (water flow blockage caused by air bubbles in the vessels and tracheids of plants when air is forced out of sap [Grace 1987]). In contrast, a species may be restricted from the south because of a negative carbon balance (warm temperatures can cause greater respiration than photosynthesis), lack of a required chilling period for germination (Grace 1987), and/or because of a flowering limitation caused by a lack of a chilling period or flowering too early (Morin et al. 2007). Additionally, a species may not currently be limited by climate, but may instead be limited by the location it was introduced and the mean residence time (time since introduction) at a given location.

A key factor for predicting future invasion potential as the climate changes is long-distance dispersal (Leishman et al. 1992, Higgins and Richardson 1999, Zavaleta and Royval 2002). Reconstructed migration rates of species due to past climate change are an order of magnitude slower than will be necessary to keep up with projected climate change because of dispersal limitations (Leishman et al. 1992, Iverson et al. 2004). However, humans may help expedite species migrations.

Despite uncertainty in species dispersal and the climate change models, researchers have attempted to predict changes in the range of both native and invasive species. Model predictions of future climate suggest that plants currently limited by cold may expand their ranges uphill and toward the poles (Dukes and Mooney 1999, McCarty 2001, Zavaleta and Royval 2002, Gen et al. 2009). A climate change model used to predict future species ranges for a sample of harmful, nonindigenous plants and animals indicated 48% of plant and animal species in the United States will likely expand their range due to global warming; however there is still uncertainty surrounding predictions of species response to climate change as 48% of the sampled species do not show clear directional shifts and only 4% are likely to suffer range contractions (Zavaleta and

Royval 2002). It is also predicted climate change will increase the range and severity of Chinese tallow invasion (Gan et al. 2009) and cause range shifts for several native tree species currently restricted to the eastern United States (Iverson et al. 2004). Zavaleta and Royval (2002) suggest climate can reasonably predict the extent of an invasion but note it is important to couple this information with biotic factors to predict the intensity of the invasion.

To date, few studies have predicted range shifts for plant species. Doubled CO₂ concentrations are expected by the end of the next century which will cause an increase in the average minimum winter temperature of 5.40°F and is expected to cause Japanese honeysuckle vine (*Lonicera japonica*) and kudzu (*Pueraria lobata*) to migrate northward up to 249 miles (Sasek and Strain 1990). Increased CO₂ concentrations have also been shown to enhance the success and dominance of exotic annual grasses (Smith et al. 2000). As species shift in distribution from climate change, native species may be replaced by more competitive (e.g. high growth rate and resource use efficiency) NNIP species (McCarty 2001).

An overall model of invasion risk would simplify management of NNIP species; however, it is not practical due to variation among species in traits associated with invasibility (Burls and McLaugherty 2008, Moles et al. 2008). Although dispersal vectors, propagule pressure, resource availability, disturbance, and climate potentially have broad overall effects on patterns of NNIP species across the landscape, species response will undoubtedly vary due to physiological differences such as shade and moisture tolerance. To reduce the impact of invasive plant species in the future, we must determine what site characteristics may influence each of their distributions and analyze how climate change may further alter these distributions. Understanding parameters correlated with forest susceptibility to invasion will help managers determine which areas are best for them to target their resources.

Research objectives

My research contributes to the emerging literature on invasive plants and offers a regional analysis of trends in the presence of NNIPs on Forest Service plots in the Midwest by examining species presence in relation to plot attributes across a seven state area (Figure 1). Few studies have examined multiple NNIPs at such broad, regional scales (Hutchinson and Vankat 1997, Lundgren 2004). The objective of this study was to determine the relationship between several site and climate characteristics and the presence of five non-native invasive plants common on Phase 2 USDA Forest Service Forest Inventory and Analysis plots in seven Midwestern states. The five focal species (multiflora rose, common buckthorn, non-native bush

honeysuckles, garlic mustard, and reed canary grass) are distributed throughout this region. For these species, I examined predictor variables in the following classes: site characteristics (water type, physiographic class, and disturbance), forest structure (sound live tree volume), human presence and related disturbance (city and edge distances), and climate (days the temperature is $\geq 90^{\circ}\text{F}$ and days the temperature is $\leq 32^{\circ}\text{F}$). The examination of these factors helped answer my motivating question: How do site and climate variables influence invasion of forestland by five non-native invasive plants in the Midwest?

The null hypothesis was that none of these factors influence the presence of NNIPs, i.e., NNIPs have an equal probability of occurring on any forested acre in the region. In contrast, the alternative hypothesis was that non-native invasive species presence on forest inventory plots would be positively related to disturbance (biotic [animal(s)/disease(s)] and flooding), water bodies, and mesic physiography, and negatively related to distance from a nonforest edge, distance to the nearest city, and sound volume of all live trees. I also expected cold temperatures to have a greater impact on species distributions than warm temperatures. I hypothesized there would be interactions among variables, especially between city and edge distance; sound wood volume of live trees and edge distance; latitude and city distance; and latitude and edge distance. I expected these relationships to be non-linear since each species response to a variable is dependent on the range tested for the variable, such as species presence at a specific volume for close, medium, and far edge distances. By understanding how these factors correlate with the presence of NNIPs, land managers, scientists, and concerned citizens may be able to predict ecosystem invasion risk in the future. Additionally the knowledge of these factors may help managers mitigate invasive establishment.

METHODS

Study area

This study spans seven states: Minnesota, Iowa, Missouri, Illinois, Wisconsin, Michigan, and Indiana and encompasses a wide variety of ecosystems in the Midwest region. Latitude ranges from approximately 49.3°N at the northern tip of Minnesota to 36.0°N at the southern tip of Missouri and longitude ranges from approximately -82.5°W on the eastern edge of the lower peninsula of Michigan to -97.2°W at the western edge of Minnesota. The temperature extremes shown by National Oceanic and Atmospheric Administration (NOAA) data (<http://hurricane.ncdc.noaa.gov/cgi-bin/climaps/climaps.pl>) range from 180.5-240.4 days $\leq 32^{\circ}\text{F}$ and less than one day $\geq 90^{\circ}\text{F}$ annually at the northern edge of the region to 60.5-90.4 days $\leq 32^{\circ}\text{F}$

and 60.5-90.4 days $\geq 90^{\circ}\text{F}$ annually at the southern edge of this region. This region represents a diverse assemblage of ecosystems, soils, anthropogenic influences, and gradients of temperature (north-south) and precipitation (east-west). Agriculture, human development, and timber harvesting fragment this landscape, facilitating the establishment of NNIP species. All of these factors affect current species distributions. Climate change may further alter these distributions in unknown ways.

Over the past 100 years, the Earth has warmed by 0.54-1.08 $^{\circ}\text{F}$ with the northern hemisphere winter maximum temperatures increasing nearly 5.40 $^{\circ}\text{F}$ and spring maximum temperatures increasing 2.54 $^{\circ}\text{F}$ (McCarthy 2001). Future warming is predicted to be greatest in northern latitudes with an average global warming of 1.80-6.30 $^{\circ}\text{F}$ over the next century (Dukes and Mooney 1999). Changes in global precipitation are less definitive as the models present greater uncertainty. It is predicted that atmospheric warming will interact with other biotic and abiotic drivers to affect future species distributions across the landscape.

DATA

Plot information

The USDA Forest Service Forest Inventory and Analysis plots are sampled on a three-phase sampling scheme: Phase 1 (P1), Phase 2 (P2), and Phase 3 (P3 [U.S. Department of Agriculture 2007]). First, the plots are remotely sensed with satellite imagery and a land use is assigned to each plot (P1). Next, the plots that were determined forested by the P1 interpreter are measured by field crew on a year-round sampling schedule (P2), then a subset of P2 plots (1/16) are more intensively sampled during the summer (P3). In P3, all P2 variables are recorded in addition to crown, down woody material, and forest vegetation variables.

Plots are established on a grid pattern that is a tessellation of hexagons, with one P2 plot per hexagon (5,960 acres). P3 plots are established at one plot per 95,360 acres. Each plot area covers one acre where one-sixth of an acre is sampled by establishing four 24 foot radius subplots. Each year one-fifth of the hexagons are measured, resulting in a complete inventory in five years. For this study, P2 plots sampled over two years (2005-2006) were retrieved from the USDA Forest Service database. This resulted in 8,661 plots spread across seven states, approximately one plot per 23,840 acres. Annual monitoring of plots over time at a regional scale will provide valuable knowledge to researchers and managers by providing better estimates of species distribution, cover, and spread.

Study species

In 2005-2006, each subplot was assessed for the presence and cover category of 25 NNIP species. The 25 species were usually, but not always, the most prominent in the region and were selected based on stakeholder interest, ecological risk, distribution, and seasonal detectability (Moser et al. 2009). Field crew were trained and certified to collect invasive species data. If a field crew member found a specimen and was unsure of its identification, or if the species was not known to be present in the state, a voucher specimen was collected and submitted to St. Paul, Minnesota, USA for positive identification by staff at the USDA Forest Service's Northern Research Station or the University of Minnesota's J.F. Bell Museum of Natural History Herbarium. Since this survey only occurs on forestland, a particular species may be present in an area but may not be detected if it occurs in a nonforest or non-sampled area. For this study, I selected five of the most prominent NNIPs with sufficient geographical range and sample size to test my hypotheses. The plants selected for this study were species from three growth forms: woody, herbaceous, and grass (Table 1).

Data mining

The field data for this study were retrieved from the Forest Inventory and Analysis database via a database query of the 2005-2006 P2 invasive field data using PL/SQL Developer 7.1 (Allround Automations 2007). From the database, I gathered the following plot attributes that were collected in the field: disturbance from disease(s)/animal(s), weather, type of water on the plot, and physiographic class. Additionally, the sound wood volume of live trees was calculated from field data collected on each plot.

Disturbance, water on plot, and physiographic class

Three types of disturbance (disease(s), animal(s), and weather) were surveyed. The three disturbance attributes were binary, recorded as the presence or absence of the disturbance on the plot. Disturbance was scored if there was mortality and/or damage on at least 25% of the trees or 50% of an individual species count (U.S. Department of Agriculture 2007). Disturbances such as grazing, flooding, or browsing were recorded when greater than 25% of the soil surface or understory vegetation were affected (U.S. Department of Agriculture 2007). Evidence of disease included understory and tree damage, inclusive of seedlings and saplings, animal disturbance included evidence of activity and/or damage from beaver, porcupines, deer/ungulate, or domestic

animals/livestock, and weather disturbance included damage from ice, wind, flooding (catastrophic or major [non-periodic]), or drought (U.S. Department of Agriculture 2007). For analysis, disease and animal disturbances were combined into a single variable (biotic disturbance).

Water on the plot was a categorical variable that included whether there was water present and the type of water (Table 2). If more than one water source was encountered, the field crew coded the one that was of greatest impact to the forested portion of the plot. For physiographic class, three broad physiographic categories were used in analyses: xeric, mesic, and hydric. These categories related to water availability within the plot area. Xeric sites were moisture deficient and unable to support vigorous forest growth (e.g. barrens, dry slopes), mesic sites had adequate moisture and growth (e.g. rolling uplands, flatwoods), and hydric sites were excessively wet, limiting growth and species presence (e.g. bogs, beaver ponds [U.S. Department of Agriculture 2007]).

Volume

Sound wood volume of live trees was chosen as a predictor variable over basal area because volume tends to increase over time as the forest ages whereas basal area increases rapidly and then levels off at a relatively young age. This variable was chosen as a surrogate for light availability within the forest. Research on the relationship between live tree volume and NNIPs is limited; however there are data available on basal area, age, and canopy cover, all surrogates of volume.

The sound wood volume of live trees per acre was calculated for trees five inches and greater in diameter at breast height (d.b.h., 4.5 feet above the ground, measured from the high side of the tree), from a one foot stump to a four inch top. This included the sound wood found in growing stock (live trees of high vigor and no serious defect), rough (trees without a current or potential 12 foot log because of roughness or poor form), and rotten (trees where 50% or more of the cull volume is rotten) trees. For the seven states of this study, two sets of volume equations were needed due to differences in forest types and economic/political boundaries (Hahn 1983, Hahn and Hansen 1991).

Geographical Information System

I calculated the distance for each plot to the nearest city > 10,000 people with ArcMap™ ArcGIS 9.1 (ESRI ® 2005). This population size was chosen by looking at the spatial distribution

of cities at various population break points (e.g. 10,000, 15,000, and 40,000 people) and finding a city size represented throughout the region which indicated a moderate level of human development. To obtain distance measurements, all layer geometries were projected into Albers Contiguous Equal Area Conic USGS. Euclidean distance from the plot to the nearest city population center with > 10,000 people was calculated via a spatial join using a city population layer derived from ESRI® Data & Maps 2005 (Environmental Systems Research Institute, Inc. 2005).

A forest/nonforest layer was created from the 2001 National Land Cover Dataset (NLCD; <http://www.mrlc.gov/index.php> [United States Environmental Protection Agency 2001]). The NLCD 2001 data has 30 meter cell spatial resolution and was created by partitioning the U.S. into mapping zones. After downloading the zones that covered the seven states of interest I mosaicked the areas together in ERDAS Imagine 9.3 (ERDAS, Inc. 2008) and recoded the image cover class values into forest and nonforest. To recode the cover classes, I overlaid the mosaicked image atop digital orthoquads and used the swipe tool in ArcMap™ to determine which NLCD classes appeared to meet the Forest Inventory and Analysis (FIA) definition of forestland (a minimum of 120 feet wide, one acre in size, and 10% stocked). I also read the definition of the landcover classification codes given on the NLCD website (<http://www.epa.gov/mrlc/definitions.html#2001>) to help determine if an area qualified as forestland.

NLCD 2001 distinguishes 29 cover classes with only 16 coded in the Midwest (nine classes are coastal only and another four classes apply exclusively to Alaska). Out of the 16 cover classes, five met the qualifications for FIA forestland: deciduous, evergreen, and mixed forest codes (NLCD codes 41, 42, and 43); along with scrub and/or shrub and woody wetlands (NLCD codes 52 and 90). After recoding and collapsing the cover classes, the clump and eliminate commands in ERDAS Imagine 9.3 were used to join the forest and nonforest areas together and eliminate all areas less than 1 acre. I then re-clumped the area using the 8-nearest neighbor method where all touching cells were clumped. The final step involved clipping the NLCD cover to the seven state region of interest which resulted in an image that could be loaded into other geospatial programs.

I next used ArcView to calculate the distance to the nonforest edge. This was calculated by subsetting the forest/nonforest edge and using the Spatial Analyst and Spatial Tools extensions in ArcView. Using the forest/nonforest grid, I transformed the nonforest edge pixels to points.

Then I spatially joined the point layer to the plot location layer to create a distance field where the distance was from the plot center to the center of the nonforest edge pixel.

The following variables were initially used in the analysis and removed in the final models: longitude, distance to the nearest road, stand age, basal area, and patch size. Variables were dropped due to their similarity to other variables and the remaining variables were carefully chosen based on an extensive literature review of factors contributing to invasive spread. After reducing the number of variables in the model, a correlation matrix was evaluated to check for redundancy of the remaining variables. This resulted in a simplified model with fewer variables.

Temperature data

Layer files for the following average annual climate variables were downloaded from NOAA (<http://hurricane.ncdc.noaa.gov/cgi-bin/climaps/climaps.pl>): freeze free period, days the temperature is $\leq 32^{\circ}\text{F}$, extreme maximum temperature, extreme minimum temperature, days the temperature is $\geq 90^{\circ}\text{F}$, and total precipitation. The climate layers were categorical annual averages from 1961 to 1990. After downloading the layer files, I loaded them into ArcMapTM and attributed each plot with the NOAA variables. Some of the climatological layers were dropped from the model (freeze free period, extreme maximum temperature, extreme minimum temperature, and total precipitation) because of the lack of detail due to having large bands that represented little variation in temperature and precipitation over a large area. The most detailed temperature layers from the NOAA downloads were used, which were annual average days the temperature is $\leq 32^{\circ}\text{F}$ and annual average days the temperature is $\geq 90^{\circ}\text{F}$.

DATA ANALYSES

Logistic regression

Logistic regression and a Geographic Information System (GIS) were used to determine factors associated with invasive presence using R Version 2.8.1 (CRAN 2008). Logistic regression was used to model the variables associated with NNIP species since the dependent variable was categorical (species presence or absence). Prior to analysis, normality of each continuous predictor variable was assessed graphically using histograms and appropriate transformations were made. To normalize the distribution of sound volume of all live trees per acre and city distance, a square root transformation was required; a log transformation was used to normalize the distribution of edge distance.

Since fragmentation and urbanization vary across the study region, I explored the role of city and edge distance within more restricted latitudinal ranges. For the regressions, the geographical region for each species was restricted by using GIS to determine the latitude and longitude where ~90% of the plots with each species occurred. This data restriction was performed to ensure that border points were not driving the model as these points may cause false temperature relationships because of the coarse temperature data. For instance if a species was present in the temperature band for 180.5 to 240.4 days of temperature $\leq 32^{\circ}\text{F}$, but only at the southern edge where the days $\leq 32^{\circ}\text{F}$ range from 180.5 to 190.4, then the presence of these plots at the southern edge of the band may skew the temperature analyses. Ideally there would be temperature data for each plot. An additional reason for data restriction is because outliers may confound species relationships with site factors. A similar data restriction method was used by Gan et al. (2009) in their study of Chinese tallow and Moser et al. (2009) in their analysis of NNIPs in the Midwest. After restricting the data, I ran a logistic regression to predict the drivers of species presence within the restricted range.

Logistic models with the categorical and continuous variables included were run for each species instead of running all species together in a model since each species is characterized by specific traits (e.g. shade and moisture tolerance) that might confound analysis. Even though the categorical output from the regression was not directly analyzed when there were greater than two levels, categorical variables were included because they provide additional information about the species. Categorical data with greater than two levels were instead analyzed from the output of the general linear hypothesis tests in order to differentiate variable effects on species presence. For the logistic models, the null hypothesis tested that the following four independent variables were not associated with invasive presence: biotic disturbance, sound volume of all live trees per acre, distance of the plot to the nearest city $> 10,000$ people, and the distance of the plot from the nonforest edge. For reed canary grass a fifth variable was included in the model, disturbance from weather. This variable was included only for reed canary grass because it was significant ($p < 0.05$) in data exploration using univariate chi-square tests.

In addition to logistic model testing for predictor correlation with species presence, I also determined the volume, city distance, and edge distance beyond which no significant change in species presence could be detected (i.e. an effect of city distance on common buckthorn presence could be detected up to 5.2 miles with no significant difference in presence beyond this distance). This was done for each species where a significant relationship was found between species presence and the continuous variable in the full model ($p < 0.05$). To determine the point where

species presence was affected by the variable, variables were subset and then run in the full model testing for significance. At the point where significance was detected ($p < 0.05$) it was determined that the values less than that number (e.g. 5.2 miles from the nearest city > 10,000 people) caused an effect on species presence whereas greater values did not affect species presence.

To further investigate data relationships, I used hexagon plots to subset the continuous and categorical variables and examine interactions between pairs of variables. Hexagon plots are data visualization tools that depict species presence with respect to two independent continuous or categorical variables (Figure 2). I created hexagon plots for live tree volume versus edge distance and city distance versus edge distance to see how edge distance changed within subset ranges of volume and city distances. Additionally I created hexagon plots for latitude plotted against the following predictors: edge distance, city distance, water on the plot, disturbance, physiography, days the temperature is $\leq 32^\circ\text{F}$, days the temperature is $\geq 90^\circ\text{F}$, and longitude. Hexagon plots for latitude versus longitude and the categorical variables were used to further understand trends between species presence and pairs of variables; these data were not presented in this thesis due to the large number of combinations and breadth of the data. Based on hexagon plots, I visually determined range breaks by choosing ranges where species response to a variable differed from the adjoining ranges. Most plots of species presence for two independent variables resulted in three ranges of data (two break points) though some resulted in four ranges (three break points; Table 3). Logistic regression models were run on data subsets for each variable range to look at variable interactions for each species.

Paired comparisons

For the categorical variables with greater than two levels, general linear hypothesis tests were run on the logistic regression using Tukey multiple comparison of means tests to differentiate the variable effects on species presence. Paired comparisons were run for each species to test the null hypothesis that climate, physiographic, and water type variables (null hypothesis: $\mu_1 = \mu_2 = \mu_x$) did not influence invasive presence.

RESULTS

The Midwest study region spans varying levels of fragmentation, anthropogenic influence, species diversity, and climate providing species with a range of establishment opportunities. Across the Midwest region, multiflora rose was the most common NNIP species

encountered on the 2005-2006 FIA plots, occurring on 15.2% of plots. The next most commonly observed species was non-native bush honeysuckles (9.1% of plots); followed by common buckthorn (4.8%), garlic mustard (3.1%), and reed canary grass (1.0%). Regional maps of the occurrence of these species on the plots are shown in Figures 3 through 7. Overall, 26.4% of the forested plots in this region had at least one of the five invasive species of interest present. At the state level, Iowa had the most plots invaded with 79.7%, followed by Indiana with 72.4%. Minnesota had the lowest percentage invaded (5.9%; Table 4). In the majority of states (four of the seven), the most commonly observed NNIP was multiflora rose, followed by non-native bush honeysuckles and common buckthorn.

Continuous predictor variables

Volume of all live trees per acre

Species showed an inconsistent response to variation in volume, an indicator of overstory density, with only two (multiflora rose and reed canary grass) of the five species having significant relationships between volume and species presence. The sound volume for all live trees ranged from zero to 4,981 cubic feet per acre with an average of 571.7 cubic feet per acre. As sound volume of all live trees increased, the presence of reed canary grass decreased; the opposite was found for multiflora rose where presence increased as volume increased (Table 5). These relationships were non-linear. The probability of finding multiflora rose on a plot increased with sound live tree volume up to 206.2 cubic feet per acre. At volumes > 206.2 cubic feet per acre, multiflora rose presence was unrelated to increasing volume (Table 6). In contrast, the probability of finding reed canary grass present on a plot decreased with increasing volume up to 537.1 cubic feet per acre above which there was no change in the probability of finding reed canary grass.

City distance

Distance of the plot to the center of the nearest city > 10,000 people (city distance) was a significant predictor of the presence of three of the five species modeled. City distance ranged from < 1 to 109.2 miles with an average of 32.5 miles. As the distance from the nearest city increased, the probability of encountering common buckthorn, non-native bush honeysuckles, and garlic mustard decreased (Table 5, Figure 8). Distance to the nearest city was the strongest predictor for common buckthorn with the odds of finding common buckthorn 1.6 times higher for each unit decrease in the square root of city distance. Non-native bush honeysuckles and garlic

mustard also had distance to the nearest city as the most important predictor with odds of finding these species 1.3 times greater for each unit decrease in the square root of city distance.

The probability of finding common buckthorn present on a plot decreased with increasing city distance up to 5.2 miles; city distances > 5.2 miles showed no significant effect on the presence of common buckthorn (Table 6). The same trends were found for non-native bush honeysuckles and garlic mustard with decreasing presence as the distance from the nearest city > 10,000 people increased; the distance effect was significant for these species up to 2.8 and 10.2 miles respectively, after which there was no correlation between city distance and species presence.

Edge distance

Distance of the plot to the nearest nonforest edge (edge distance) was a significant predictor of the presence of four of the species modeled (multiflora rose, common buckthorn, non-native bush honeysuckles, and garlic mustard). Edge distance ranged from 49.9 feet to 91.4 miles with an average of 612.7 feet. As the distance of the plot to the nearest nonforest edge increased, the presence of multiflora rose, common buckthorn, non-native bush honeysuckles, and garlic mustard decreased (Table 5, Figure 9). Reed canary grass also followed this trend, however the trend was not significant (p -value = 0.064). Edge distance was the strongest predictor of occurrence for multiflora rose ($p < 0.0001$) with the odds of finding multiflora rose 1.4 times higher for each unit decrease in the log of the distance from a nonforest edge.

Distance effects were detectable to similar distances for most of the species. The probability of finding multiflora rose present on a plot decreased with increasing distance of the plot to the nearest nonforest edge up to 157.6 feet, with edge distance > 157.6 feet showing no significant effect on the presence of multiflora rose (Table 6). Similar trends were found for common buckthorn, non-native bush honeysuckles, and garlic mustard with decreasing presence as the distance to nonforest edge increased; the distance effect was significant for these species up to 189.0, 110.0, and 914.7 feet respectively, after which there was no correlation between edge distance and species presence.

Interactions

Interactions helped to identify the ranges where variables had the greatest impact on NNIP species presence. The actual range values tested for each appear in Tables 3 and 7; those listed in the following paragraphs are approximate since the variable ranges differed by species.

The interaction data show the relationship between invasive species presence and distance of the plot to the nearest nonforest edge depended on both the distance of the plot to the nearest city > 10,000 people and distance of the plot to the nearest nonforest edge. At a short distance from the city (< 16 miles), the presence of most species decreased as city distance increased and all species showed a decrease in presence as edge distance increased (Table 3). Further away from cities (16 to 40 miles) most species still showed reduced presence as city and edge distance increased, while far from cities (> 40 miles) most species did not show a correlation with edge or city distance. This trend may reflect reduced invasion in the larger, more intact forestland where there are fewer roads, vectors, and propagules because of reduced development.

For sound volume, there was little correlation between invasive species presence, edge distance, and volume at low volume (< 100 cubic feet per acre). Only common buckthorn had a significant relationship, with decreased presence as edge distance increased. At mid-volume range (100 to 500 cubic feet) all five of the invasive species decreased in presence as edge distance increased, but only common buckthorn presence was negatively correlated with volume (as volume increased, presence decreased). At high volumes (> 500 cubic feet) most of the species decreased in presence as the volume and edge distance increased (Table 7), likely because of reduced light levels and propagule pressure.

Latitude

In general, species were most prevalent in the central latitudinal band of their range. At the northern band of the species range, species occurrence decreased with increasing latitude and at the southern band species presence increased with increasing latitude. Latitudinal relationships with species presence were variable at mid-latitude. This overall trend may have occurred because a) species were more abundant in the central part of their range and less abundant at the edges where propagule pressure and residence time (the amount of time the species had been established in an area) were lower and b) climatic limits may have been operating.

In the northern and southern bands, species presence generally decreased as distance to the nearest city increased while in the mid-latitude band city distance generally was not significant (Table 8). In contrast, in the northern and mid-latitude bands species presence generally decreased as edge distance increased, whereas in the southern latitude band species presence tended to be unrelated to distance from an edge. This may suggest that in the northern and southern bands, which have more intact forests, edge is a function of distance to the nearest city > 10,000 people whereas in the central part of the region, edge may not be a function of

distance to the nearest city > 10,000 people due to fragmentation. Only multiflora rose and non-native bush honeysuckles had significant correlations with edge distance in the southern part of their range: presence decreased with increasing edge distance for both species (Table 9).

CATEGORICAL PREDICTOR VARIABLES

Disturbance

Biotic disturbance (from disease(s)/animal(s)) was a significant predictor for three of the five species (multiflora rose, common buckthorn, and garlic mustard); however it was not the strongest predictor for any species. Nevertheless, it was the second most important predictor of multiflora rose presence with the odds of finding multiflora rose 2.6 times greater in areas with biotic disturbance ($p < 0.0001$; Table 5). Garlic mustard presence was also higher where there was biotic disturbance; however common buckthorn presence was lower in areas with biotic disturbance. Reed canary grass was the only species whose presence was related to weather disturbance, the strongest predictor of reed canary grass occurrence, with the odds of occurrence 9.1 times greater in areas disturbed by weather damage.

Water on plot

Water type influenced occurrence of common buckthorn and garlic mustard. Common buckthorn was more likely to be found on plots that contained ditches and/or canals than any other water type category. The odds of finding common buckthorn were 12.3 times greater on plots with ditches and/or canals compared to plots with permanent streams and/or ponds (Table 10). Similarly, the odds of finding garlic mustard were 14.5 times greater on plots with ditches and/or canals than those with permanent streams or ponds. Although the results were not significant ($p = 0.055$), the data suggested reed canary grass, a hydric site species, preferred permanent streams and/or ponds over plots without water. No significant relationships were found between type of water on a plot and the presence of multiflora rose and non-native bush honeysuckles.

Physiography

Most species were more likely to be found on sites with intermediate moisture (e.g. mesic) compared to the extremes (hydric or xeric). For multiflora rose, there was a preference of mesic over hydric and xeric physiography with odds of occurrence 2.6 times greater on mesic than xeric soil (Table 11). Common buckthorn, non-native bush honeysuckles, and garlic mustard

also all showed a preference for mesic over hydric and xeric physiography, with common buckthorn and non-native bush honeysuckles being 2.5 times more likely and garlic mustard 3.5 times more likely to occur on mesic than hydric soil. Additionally, garlic mustard was 24.8 times more likely to occur on mesic than xeric soil. No significant relationships were found between reed canary grass and physiography.

Average annual number of days the temperature is $\geq 90^{\circ}\text{F}$

Average annual number of days the temperature is $\geq 90^{\circ}\text{F}$ was a statistically significant predictor for two of the five species. These analyses, along with the average annual number of days the temperature is $\leq 32^{\circ}\text{F}$, provide important data for determining species range restrictions and potential future range shifts. Multiflora rose occurred in regions that range from 0.5 to 60.4 days of temperature $\geq 90^{\circ}\text{F}$ annually (Zones B-E; Figure 10) and was most likely to occur in temperature band C (Table 12), an area that covers the majority of Iowa, northern and central Illinois, and northwest, central, and southeast Indiana. This temperature band corresponds to an average of 15.5 to 30.4 days of temperature $\geq 90^{\circ}\text{F}$ annually.

Garlic mustard occurred in regions that range from 0.5 to 60.4 days of temperature $\geq 90^{\circ}\text{F}$ annually (Zones B-E) with a preference of zones B and C over D, these preferred zones span the northern and central part of this region whereas zone D is a band in the southern part of this region. Zones B and C cover an area that corresponds to an average of 0.5 to 30.4 days of temperature $\geq 90^{\circ}\text{F}$ annually. In comparison, zone D corresponds to an average of 30.5 to 45.4 days of temperature $\geq 90^{\circ}\text{F}$ annually. Common buckthorn, non-native bush honeysuckles, and reed canary grass did not show a significant relationship with the average annual number of days $\geq 90^{\circ}\text{F}$.

Average annual number of days the temperature is $\leq 32^{\circ}\text{F}$

Average annual number of days the temperature is $\leq 32^{\circ}\text{F}$ was an important predictor of NNIP presence, showing significance for all five of the NNIP species. Multiflora rose occurred in regions that range from 60.5 to 180.4 days of temperature $\leq 32^{\circ}\text{F}$ annually (Zones D-G; Figure 11) with a preference of zone E and F over G (Table 13). Bands E and F span the central and southern part of this region, from central Iowa south on the western edge across to central Michigan south on the eastern edge and correspond to an average of 90.5 to 150.4 days of temperature $\leq 32^{\circ}\text{F}$ annually. Even though the pairwise comparison of zones E to F was not significant at the 0.05 level, there was a trend towards a preference of zone F over zone E ($p =$

0.086). This would mean multiflora rose is most likely to occur in zone F, a band with an average of 120.5 to 150.4 days of temperature $\leq 32^{\circ}\text{F}$ annually and covering an area from central Iowa to northern Missouri at the western edge across to central Michigan to south-central Indiana on the eastern edge.

Common buckthorn occurred in regions that range from 120.5 to 240.4 days of temperature $\leq 32^{\circ}\text{F}$ annually (Zones F-H) with a preference of zones F and G over H ($p < 1 \times 10^{-6}$). The odds of finding common buckthorn in zones F or G over zone H is nearly eight times greater (7.5 and 8.0 times greater, respectively). Zones F and G cover the central part of this region, spanning from central Minnesota to northern Missouri on the western edge and from the southern upper peninsula of Michigan to south-central Indiana on the eastern edge. These preferred temperature bands corresponds with an average of 120.5 to 180.4 days of temperature $\leq 32^{\circ}\text{F}$ annually.

Non-native bush honeysuckles occurred in regions that range from 90.5 to 240.4 days of temperature $\leq 32^{\circ}\text{F}$ annually (Zones E-H) with a preference of zones E, F, and G over H ($p < 0.001$). A preference was also found for zone F over G ($p < 0.001$). Zones E, F, and G cover central Minnesota south on the western edge and the southern upper peninsula of Michigan south on the eastern edge. This area (zones E, F, and G) corresponds to an average of 90.5 to 180.4 days of temperature $\leq 32^{\circ}\text{F}$ annually. Though not significant at the 0.05 level, there is indication of a preference for zone E over G ($p = 0.086$). This would result in a preference for zones E and F over G and H with a preference of G over H. Zones E and F correspond to a region which on the western edge spans from central Iowa south and on the east spans from central Michigan south. This area (zones E and F) corresponds to an average of 90.5 to 150.4 days of temperature $\leq 32^{\circ}\text{F}$ annually.

Garlic mustard occurred in regions that range from 90.5 to 180.4 days of temperature $\leq 32^{\circ}\text{F}$ annually (Zones E-G) with a preference of zones F and G over E. This area extends from central Minnesota to northern Missouri on the western edge and from the southern upper peninsula of Michigan to south-central Indiana on the eastern edge. Temperature bands F and G correspond to an average of 120.5 to 180.4 days of temperature $\leq 32^{\circ}\text{F}$ annually.

Reed canary grass occurred in regions that range from 120.5 to 240.4 days of temperature $\leq 32^{\circ}\text{F}$ annually (Zones F-H) with a preference of zone F over G and the odds of finding reed canary grass 6.5 times greater in zone F than zone G. Zone F spans from central Iowa to northern Missouri on the western edge and on the eastern edge from central Michigan to south-central

Indiana. This temperature band corresponds to an average of 120.5 to 150.4 days of temperature \leq 32°F annually.

DISCUSSION

Invasive species impose ecological and financial costs to forests by impacting health, productivity, diversity, and aesthetic value. Understanding factors responsible for forest invasion is important since one-third of the earth's land surface is forested and these forested areas support much of the world's biological diversity and are important to the livelihood of many people (Chornesky et al. 2005). Most studies have examined single species at small, local scales; uncertainty about whether these studies can be generalized over larger regions hinders invasive species management efforts. The large dataset of field observations compiled here offered many advantages such as the ability to reveal trends in NNIP presence that may not be detected by small-scale studies (Gan et al. 2009). In general, many of the predictors found in prior, local studies were also significant at the regional scale (e.g. biotic disturbance, edge distance) but some differences were found (e.g. sound live tree volume, weather disturbance). This regional analysis using a large, robust, empirical dataset thus contributes to elucidating general patterns associated with forest invasion and provides tools for land managers and concerned individuals to predict areas of increased invasion potential in this region.

Approximately one-quarter of the plots in this Midwest, USA study region had one or more of the five NNIP species (multiflora rose, common buckthorn, non-native bush honeysuckles, garlic mustard, and reed canary grass) present. Overall, no single model emerged that could predict whether a plot was invaded, instead a unique set of predictors was associated with each species. Although no general overall model arose, the results highlight the importance of anthropogenic influence, propagule pressure, disturbance, and climate. Key factors influencing whether a site was invaded by NNIPs were the distance from a sample plot to a non-forest edge, the distance from sample plot to a city, mesic physiography, and biotic disturbance. The temperature analysis suggested that the species were more restricted by cold temperatures than warm temperatures, a trend also found in other studies (e.g. Saxe et al. 2001, Gan et al. 2009).

Anthropogenic influence and means of propagule dispersal

Humans have facilitated the spread and establishment of NNIPs by fragmenting the landscape and dispersing propagules through horticultural planting and contaminated agriculture seed. From 1950 to 2000 urban areas increased by 1% within the conterminous USA while rural

low-density housing increased 20% (Gavier et al. 2008), causing fragmentation and anthropogenic effects in less developed areas. Such development is likely to continue increasing in these rural areas (Gavier et al. 2008). There is a strong connection between anthropogenic influence, propagule pressure, and the presence of NNIP species (Brothers and Spingarn 1992, Hutchinson and Vankat 1997, Lundgren et al. 2004, Bartuszevige et al. 2006, Mascaro and Schnitzer 2007). Species establishment is initially controlled by propagule pressure and mean residence time and later influenced by biological traits (Pyšek et al. 2009).

Cities are a major source of propagule pressure as invasive plants are often planted in urban areas for horticultural interest (e.g. common buckthorn, non-native bush honeysuckles). The effect of cities varied with latitude. I found that city distance was a significant predictor in the northern and southern latitudinal bands but not in the central band, likely because in the center of a species' geographic range forestland may be saturated by high propagule pressure and the species may have been present in the area for a longer time frame. The northern and southern latitudinal bands have likely not been fully exploited by the species as these areas have a lower mean residence time, reduced densities, and thus reduced propagule pressure. However, temperature effects may also play a role (see discussion below).

Across the region, the influence of cities varies because as city distance increases the distance from the source populations increases; this may also be linked to the patchiness of the landscape. The probability of exotic species occurrence is lower in highly fragmented forestland isolated by agriculture or lacking connectivity (Hutchinson and Vankat 1998, Bartuszevige et al. 2006). Isolated forested areas lack the propagule pressure found in urban forests, potentially due to the inability of some propagules to cross large spans of agriculture land. However, propagule dispersal in agricultural areas may be assisted by artificially created ditches and canals that disperse seeds across the landscape, creating satellite populations and resulting in new areas of infestation and spread. In general, waterways serve as corridors for human and wildlife travel, both potential propagule vectors (Burls and McClaugherty 2008).

Disturbance and resource availability

After transport to an area, disturbance and resource availability are important predictors of NNIP occurrence as a suitable site must be present for establishment. Disturbance alters light and soil resource availability through disruption of existing vegetation and for a brief time period ecosystems are particularly vulnerable to invasive establishment (With 2002, Lavergne and Molofsky 2004). Several studies have looked at the implications of various disturbances (e.g.

human, wind, fire, and flooding) on the presence of NNIPs (e.g. Nuzzo 1999, With 2002, Lavergne and Molofsky 2004). Disturbance typically facilitates NNIP presence since many invasive species are early successional with fast growth rates and long seed viability (MacDougall et al. 2006). Disturbed areas offer opportunities for invasive establishment due to increased light, water, and nutrient availability as a result of reduced cover and resource uptake by the forest vegetation. In this study, I looked at the following metrics of disturbance and resource availability: existence of biotic and weather disturbance, distance to a forest edge, sound live tree volume, and physiography. Distance of a plot to a non-forest edge, distance to the nearest city > 10,000 people, biotic disturbance, and mesic physiography were important predictors for the presence of most of the species studied, while sound volume of all live trees and weather disturbance were only significant predictors for two species and one species, respectively.

Edge distance was the continuous variable with the highest predictive power, significant for four of the five species. All four species were more common close to forest edges. Forest edges are important because they alter the microclimate (e.g. higher temperature, vapor pressure deficit, and light availability). These alterations can extend more than 150 feet from the forest edge with most edge species growing within 20 feet of the forest edge (Matlack 1994). Exposure (e.g. south-facing edge) also influences the depth of edge effect: microclimate differences penetrate further into the forest interior leading to changes in composition deeper on south-facing edges (164 ft) than on north-facing edges (98 ft; Fraver 1994). These distances, from selectively harvested forests, may be slightly greater than would be expected in undisturbed forests in the eastern and central United States (Fraver 1994). In the Midwest, I found edge effects detectable to similar distances (< 190 feet) for multiflora rose, common buckthorn, and non-native bush honeysuckles, suggesting that microclimate alteration may be one of the mechanisms underlying the significant effect of edge distance on the presence of the NNIPs. Understanding the distance these species generally penetrate into forestland can help managers make more informed decisions to protect the forest interior from invasives, especially in fragmented landscapes.

Biotic disturbance caused by disease and animal damage plays an important role in facilitating invasion since disturbance reduces vegetation providing enhanced resource opportunities. I found common buckthorn declined with increasing biotic disturbance whereas multiflora rose and non-native bush honeysuckles increased with biotic disturbance. Cattle were the major animal disturbance agent on the plots (81.4% of 408 plots with biotic disturbance). This may help to explain the negative relationship between common buckthorn and biotic disturbance

since common buckthorn is less common in the heavily farmed areas of Iowa, northern Illinois, and northern Indiana where cattle disturbance is greater whereas multiflora rose and non-native bush honeysuckles are more common in these areas. Reed canary grass was the only species to show a relationship with weather damage, emphasizing the importance of flooding in its establishment since this was the most coded disturbance for this category (66.5% of 161 plots with weather disturbance). Biotic and weather disturbances were only coded on a plot if the disturbance occurred in the last five years; thus, their importance for NNIP establishment may have been underestimated because disturbances that occurred more than five years ago may have left legacies that were not recorded.

Sound volume of all live trees, a potential indicator of past disturbance, is lower in younger and disturbed stands. Moreover, these low volume stands generally have higher light and soil resource availability. I found sound live tree volume was a significant predictor for multiflora rose and reed canary grass and that the presence of most species was reduced at high volume. However, the low correlation between sound live tree volume and species presence may indicate that my assumptions about the relationship between light availability and volume were too simplistic. A possible explanation for the lack of correlation is because different trees provide different canopy coverage (e.g. black walnut has lower canopy coverage than red oak [Hutchinson and Vankat 1997]).

The last resource availability indicator modeled in this study was physiography. Four of the five species preferred mesic physiography, consistent with other research that suggests NNIPs prefer sites of greater soil resource availability (Nuzzo 1999, Moser et al. 2009). Areas with limited resource availability often restrict invasive species since many flower mid-summer when moisture is minimal, differing from native species that are often adapted to limited resources and flower early or are tolerant of low moisture (MacDougall et al. 2006). However, the low number of plots that occurred on hydric and xeric soils may limit inference. This skewed distribution of physiography was due to the focus on forestland: nonforest areas too wet or too dry to support tree growth were not surveyed. Had this study covered both forest and nonforest areas, other physiographic trends may have emerged.

Determining the predictors of NNIP presence increases our understanding of forest attributes that relate to their presence, however we must be cautious because correlation does not necessarily mean causation. For example, although NNIPs were more common in areas with high resource availability (mesic forests, close to edges), these also coincide with areas historically chosen by settlers as desired locations for agriculture or homesteads (Moser et al. 2009). Despite

some potential hidden correlates in the data, the findings presented in this study will help managers determine variables influential to the presence of the five NNIPs studied within this region.

Climate

Climate is an important determinant of native species range limits (Grace 1987, Saxe et al. 2001); however, the role of climate in determining invasive species distributions is poorly understood (Dukes and Mooney 1999). Limitations to species ranges can be directly related to temperature, where northern range limits are related to mortality induced by xylem embolisms and/or the inability to undergo full fruit ripening or flowering, and southern range limits are set by a negative carbon balance, lack of a chilling period required for germination, inability to flower, and/or frost injury due to flowering too early (Grace 1987, Saxe et al. 2001, Morin et al. 2007). Limits can also be indirect via reduced growth rates that place a species at a competitive disadvantage near range margins (Grace 1987, Iverson et al. 2004). The legacy of recent introduction and current migration may obscure the signal of climate on invasive species ranges. However, there is evidence that a species' ability to invade in its introduced location generally coincides with its native latitudinal range (Rejmánek and Richardson 1996). There is also evidence of limits to invasive species distributions related to minimum temperatures (e.g. itchgrass [*Rottboellia cochinchinensis*] [Dukes and Mooney 1999], Chinese tallow [Gan et al. 2009], multiflora rose, and common buckthorn [Moser et al. 2009]). In fact, a regional study by Gan et al. (2009), using six NOAA climate layers, found minimum temperature was the most restraining factor of species range for Chinese tallow.

For the five species studied, research suggests there are climatic limitations to their presence. Average annual number of days $\geq 90^{\circ}\text{F}$ was a significant predictor for the presence of multiflora rose and garlic mustard. Garlic mustard was associated with cooler climates (< 30 days $\geq 90^{\circ}\text{F}$), whereas multiflora rose was most common at sites that ranged from 16 to 45 days $\geq 90^{\circ}\text{F}$. Maps of species distributions revealed a noticeable cutoff in multiflora rose and garlic mustard presence north of 44°N latitude and a noticeable cutoff of common buckthorn presence south of 42°N latitude (Figures 3, 4, and 6, Moser et al. 2009).

Average annual number of days $\leq 32^{\circ}\text{F}$ was a significant predictor for all five species. The study region ranged from 61 to 240 days $\leq 32^{\circ}\text{F}$ with all species more common on sites with 121 to 180 days below freezing. Analysis within the preferred range of these species indicated that presence was greatest in the central latitudinal band of the region of occurrence. Since

latitude can be considered a surrogate for climate, fewer invaded plots at the northern and southern latitudes may be due to climate limitations. Alternatively, these latitudinal trends may be related to legacies of introduction: where species are more abundant in the central part of their range and less abundant at the edges because propagule pressure is lower and species generally have a lower mean residence time.

With the prediction of doubled CO₂ concentrations by the end of the century and corresponding increases in temperature (approximately + 5.40°F), ranges of all study species may shift northward (Sasek and Strain 1990). Though there is considerable uncertainty surrounding such predictions. Climate change will likely affect not only temperature and nutrient availability, but also the frequency and severity of extreme events such as storms, fire, drought, seasonal patterns of precipitation, and disturbance regimes, as well as species interactions such as herbivory and competition (Saxe et al. 2001). With increased disturbance levels, NNIPs will likely be favored (Dukes and Mooney 1999), although cold-adapted species may lose their competitive advantage if they are unable to adapt fast enough to environmental change. Moreover, long-distance dispersal, mechanisms of transport, and the ability of a species to migrate with climate change are also important factors to consider when predicting future invasive spread. The effect of climate change on indirect influences of NNIP spread, such as animal dispersal and competition with native species is unknown (Zavaleta and Royval 2002). Animal ranges are predicted to shift and since they are important dispersers of plant seeds these shifts may have important implications. Climate change may also shift native plant species ranges; if species shift ranges at variable rates, disassembly of ecological communities may occur (Chornesky et al. 2005), making them more susceptible to invasion. For example, migration of native species may create niche opportunities for NNIP establishment (Dukes and Mooney 1999).

Species-specific trends

Since each species had a unique suite of variables that predicted their presence, the following paragraphs address each species individually.

Multiflora rose

Multiflora rose is a thorny shrub native to eastern Asia (e.g. China, Korea, and Japan). While generally considered shade intolerant, it can establish in the forest interior when propagule pressure is high (Weber and Gibson 2007), though vigor is generally reduced (Brothers and Springarn 1992, Yates et al. 2004, Weber and Gibson 2007). Multiflora rose was the most

frequently encountered NNIP in this study area. It is a successful invader throughout the Midwest partially due to its introduction in both urban and rural settings for ornamental, wildlife, and living fence uses. Many state conservation departments distributed cuttings of multiflora rose to landowners into the late 1960s (Moser et al. 2008). Its dispersal by animals is of conflicting importance as some researchers suggest animals are important vectors of this species (Brothers and Springarn 1992) while others suggest animals have little effect on propagule spread and suggest the primary factor responsible for the spread of multiflora rose is vegetative propagation (Christen and Matlack 2009).

The key predictors of multiflora rose presence were biotic disturbance, edge distance, sound live tree volume, physiographic class, average annual number of days $\geq 90^{\circ}\text{F}$, and average annual number of days $\leq 32^{\circ}\text{F}$. Multiflora rose was more likely to be found in warmer parts of the study region, near forest edges, on sites with evidence of biotic disturbance, in open forests (e.g. low sound volume), and on mesic sites. These patterns suggest resource availability, especially light, is an important influence on multiflora rose presence. My results corroborate prior studies that found multiflora rose benefits from soil disturbance and increased light (McDonald et al. 2008, Christen and Matlack 2009) and that growth is restricted in areas with low (Christen and Matlack 2009) and high water tables (Moser et al. 2008). Edge distance was the strongest predictor of multiflora rose presence with detection of edge effect up to 158 feet, consistent with data collected by Brothers and Springarn (1992), where presence of multiflora rose showed a significant negative relationship with distance from edge and a large decrease in presence at 164 feet.

Common buckthorn

Common buckthorn is an animal dispersed, shade tolerant, woody shrub species planted for ornamental use as a hedge or landscape material. It is capable of establishing in forest interiors, though germination and species vigor may be reduced because highest dominance is thought to occur when colonizing high light, nonforest environments (Knight et al. 2007, Mascaro and Schnitzer 2007). Common buckthorn leafs out early and is able to photosynthesize before much of the rest of the forest vegetation, a phenological advantage. Presence is greatest along the prairie tension zone from central Minnesota to southeast Wisconsin, an area of high development with roadways, fragmentation, and agricultural ditches and canals. Common buckthorn is currently limited in distribution by spring and fall frost damage and establishes in areas where it utilizes the full growing season through maximizing carbon fixation and proper timing of

hardening/dehardening (Saxe et al. 2001, Knight et al. 2007). A chilling period is required for germination with seedling survival reduced by deep litter layers, dry or water-logged soils, and desiccation in hot, dry summers (Knight et al. 2007, Kurylo et al. 2007, McCay and McCay 2009), all factors which may impact the northern and southern limits of this species following climate change.

Common buckthorn presence was highest along ditches and canals, on mesic sites, near cities and edges, and in areas with biotic disturbance. Higher presence near forest edges and cities is indicative of where common buckthorn has traditionally been planted; suggesting propagule pressure from urban areas is an important factor for understanding its distribution (see also Gavier et al. 2008). Common buckthorn preferred ditches and canals, sources of moisture and propagule dispersal; these areas often have small strips of uncultivated land along them that provide cover and habitat for seed vectors such as birds and mammals. Although common buckthorn may ultimately be limited by cold in the north, it was generally more common in the cooler parts of the study region (average annual number of days $\leq 32^{\circ}\text{F}$ from 121 to 180).

Non-native bush honeysuckles

Non-native bush honeysuckles are shade intolerant shrub species planted near cities for ornamental use as hedges or focal points in gardens. When they escape from cultivation, dense thickets are formed that shade native species (Bartuszevige et al. 2006). They have high seed production and are often used for nesting by birds, which act as important seed vectors.

In this study, the presence of non-native bush honeysuckles was greatest near cities and edges and on mesic sites throughout the Midwest. The increased presence of non-native bush honeysuckles near cities is indicative of where they have traditionally been planted; suggesting the importance of propagule pressure from urban areas in their distribution. This trend was found across all latitudinal bands tested, with a city distance effect detectable up to 2.8 miles. This same tendency was found at a local scale in southwest Ohio, USA where Amur honeysuckle cover was generally $> 50\%$ in stands ≤ 3.1 miles from the city and cover declined with increased city distance (Hutchinson and Vankat 1997) as well as near Madison, Wisconsin, USA (Gavier et al. 2008). The presence of non-native bush honeysuckles was also associated with mesic physiography. Frequent co-occurrence with common buckthorn, known to thrive on moist, unsaturated sites (Knight et al. 2007), suggests that non-native bush honeysuckles have an affinity for mesic sites.

Garlic mustard

Garlic mustard is an herbaceous biennial which is often planted near homesteads for culinary purposes. It is shade tolerant with a low photosynthetic rate at high irradiance and a high photosynthetic rate under low irradiance in comparison with sun- and shade-adapted species (Dhillion and Anderson 1999). This physiological trait may impede establishment of garlic mustard in high light environments and explain why garlic mustard is able to inhabit the forest interior (Brothers and Springarn 1992, Fraver 1994). It spreads only through seed dispersal, with humans and waterways identified as the primary long-distance dispersal agents (Nuzzo 1999, Burls and McClougherty 2008). The small, sticky, light-weight seeds are short-lived with highest germination in floodplains and reduced germination in drier environments (Burls and McClougherty 2008, Moser et al. 2008).

Garlic mustard occurred most frequently in the central part of the study region, near cities and edges, on mesic sites (strong disfavor of xeric sites), and disturbed areas (biotic disturbance and along ditches and canals). Ditches and canals facilitate seed dispersal and spread into the forest interior. Along these corridors, seeds are also vectored by animals and humans. Waterways, biotic disturbances, and edge distance offer proxies of light and resource availability and provide microhabitats in which garlic mustard can establish satellite populations and spread (Nuzzo 1999, Burls and McClougherty 2008, Moser et al. 2008). This species is still spreading throughout the Midwest and establishment along edges may be a predecessor to more extensive forest invasion (Dhillion and Anderson 1999, Weber and Gibson 2007). Garlic mustard is able to tolerate a wide range of light availability found within forests (Burls and McClougherty 2008, Moser et al. 2008) as was found in this study where edge effect was detectable much further into the forest for garlic mustard (914.7 feet) than the other species. The spread of this species threatens the mycorrhizal community; garlic mustard is capable of disrupting the mutually beneficial relationship and may cause forests to undergo species changes by reducing the competitive ability of species (Weber and Gibson 2007). Future monitoring of garlic mustard is necessary as this species may pose a risk to ecosystem composition, function, and health.

Reed canary grass

Reed canary grass is a shade intolerant species with transcontinental distribution. Although it is native to North America, non-native genotypes have been introduced for agriculture and erosion control and have crossed with the native genotypes to create more

aggressive clones (Lindig-Cisneros and Zedler 2002, Lavergne and Molofsky 2004, Lavoie et al. 2005). Reed canary grass is able to grow in wet or dry areas and is still widely planted in rural and urban environments for forage, erosion control, and soil contaminant extraction (Lavergne and Molofsky 2004), where it can form dense monocultures and displace native species.

Reed canary grass was more likely to be found in areas of low volume and disturbed by weather, suggesting a preference for disturbed, open areas (Lavergne and Molofsky 2004). Light is a key predictor of successful germination and disturbance facilitates reed canary grass establishment by creating optimal germination conditions (Lindig-Cisneros and Zedler 2002, Lavergne and Molofsky 2004). Climate change also may affect reed canary grass as optimal growth typically occurs under cool, moist conditions (Lavergne and Molofsky 2004). Tuck et al. (2006) studied the distribution of reed canary grass in Europe and found it was most common from 35°N to 44°N latitude, consistent with its distribution in the American Midwest (Figure 7). They predict climate change will cause reed canary grass to decrease in coverage from 35°N to 44°N latitude and increase from 45°N to 71°N latitude, an area in the Midwest spanning from central Minnesota across to the northern Lower Peninsula of Michigan northward.

CONCLUSION AND FUTURE RESEARCH DIRECTIONS

Understanding factors that influence NNIP species presence is important as invasive plants are one of the greatest risks to ecosystems, causing substantial impact by displacing native species and altering wildlife habitat. NNIPs are also a concern in forest management because they can reduce tree regeneration, kill trees (e.g. Japanese honeysuckle, kudzu), and are costly to control. Across the Midwest study region, NNIP presence was generally greater closer to cities, at forest edges, on mesic sites, and was strongly influenced by the annual number of days the temperature was $\leq 32^{\circ}\text{F}$, suggesting climate change may facilitate northward migration of these species. For a number of predictors, relationships differed across latitude suggesting patterns of establishment were influenced by climate and mean residence time. However, since species differed in the relative importance of the predictors, management at a species level may be necessary.

This study also offers general recommendations to help focus management efforts by suggesting factors influential to the spread of these NNIPs so managers can monitor habitat at the perimeter of the spread zone. Forests close to cities, with significant edge, and on mesic sites should be target areas for monitoring and eradication. Efforts should be made to educate the

public and especially forestland owners about invasive species to help mitigate the impact of these species.

With climate change, there is added concern about the ability of species to expand their ranges northward. Future remeasurement data will make valuable contributions to our knowledge of range expansion as the climate changes as well as help determine predictors important for NNIP spread. Currently long-term regional monitoring data is not available for NNIPs, creating a gap in our knowledge. This knowledge gap is important to fill to better understand ecosystem invasion by NNIPs. Long-term monitoring offers the benefits of determining factors of establishment and spread and potentially helping to separate out some of the anthropogenic effects. Coupling long-term monitoring with large-scale studies provides an added benefit of being able to view regional progressions.

For this study, I analyzed trends for areas that met the qualifying forestland definition (one acre) and used a very generalized climate layer, reducing predictive power. In the future, regional studies should analyze fragmentation (forest connectivity), exposure (aspect), nonforest areas, and climate change, using a detailed climate dataset to obtain better predictions of potential species range shifts. Continued invasive research is necessary as there are still many unanswered questions, especially regarding the response of NNIP species to climate change.

Table 1. List of non-native invasive plant species of interest. Data for these species were gathered from Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006.

Species	Growth form	Date and reason for introduction	Origin
<i>Rosa multiflora</i> (multiflora rose)	woody	late 1700s, ornamental	Asia
<i>Rhamnus cathartica</i> (common buckthorn)	woody	early 1800s, ornamental	Eurasia
<i>Lonicera</i> spp. (non-native bush honeysuckles)	woody	1897 (<i>Lonicera maackii</i> [Amur honeysuckle]), ornamental	Asia
<i>Alliaria petiolata</i> (garlic mustard)	herbaceous	1868, culinary, restoration	Eurasia
<i>Phalaris arundinacea</i> (reed canary grass)	grass	shortly after 1850, forage, restoration	Native, Europe

Table 2. Categories of water on plot for Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006. The codes are listed in a hierarchy from permanent streams and ponds having the greatest impact to temporary water having the lowest impact. Adapted from Forest Inventory and Analysis National Core Field Guide, U.S. Department of Agriculture, 2007.

Water on plot categories and numeric code	Description
none (0)	no water sources within the accessible forest land
permanent streams or ponds (1)	too small to qualify as noncensus water (noncensus water is 1.0 to 4.5 acres in size and 30 to 200 feet in width)
permanent water (2)	deep swamps, bogs, marshes without standing trees and less than 1.0 acre in size, or forested swamps, bogs, or marshes classified as accessible forest land with standing trees (no acreage limit)
ditch and/or canal (3)	human made channels to move water and are too small to qualify as noncensus water
temporary water (4)	three codes were combined into one code for temporary water (the three codes combined were: temporary streams, flood zones, and other temporary water)

Table 3. The effect of distance to the nearest city > 10,000 people on distance to the nonforest edge for individual non-native invasive plant species of interest on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006. When significant, edge distance and city distance were always negatively related to presence of NNIPs. In other words, as distance from edge or city increases, NNIPs presence decreases.

Species	City distance class†	Predictor	
		Edge distance††	City distance†
<i>Rosa multiflora</i> (multiflora rose)	Overall	***	NS
	< 16	***	NS
	16-49	***	**
	> 49	NS	NS
<i>Rhamnus cathartica</i> (common buckthorn)	Overall	***	***
	< 3.24	NS	.
	< 9	***	***
	9-49	***	***
	> 49	*	NS
<i>Lonicera</i> spp. (non-native bush honeysuckles)	Overall	***	***
	< 1.96	NS	***
	< 16	***	***
	16-49	***	***
	> 49	*	NS
<i>Alliaria petiolata</i> (garlic mustard)	Overall	**	***
	< 6.76	NS	.
	< 16	**	***
	16-33.64	NS	.
	> 33.64	NS	NS

(.)Significance at the 0.1 level, *significance at the 0.05 level, **significance at the 0.01 level, ***significance at the 0.001 level

†City distance is the distance, in miles, from the plot to the nearest city > 10,000 people.

††Edge distance is the log of the distance from the plot, in feet, to the nearest nonforest edge.

Table 3 (continued). The effect of distance to the nearest city > 10,000 people on distance to the nonforest edge for individual non-native invasive plant species of interest on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006. When significant, edge distance and city distance were always negatively related to presence of NNIPs. In other words, as distance from edge or city increases, NNIPs presence decreases.

Species	City distance class†	Predictor	
		Edge distance††	City distance†
<i>Phalaris arundinacea</i> (reed canary grass)	Overall	***	.
	< 9	*	NS
	9-42.25	***	NS
	> 42.25	.	NS

(.)Significance at the 0.1 level, *significance at the 0.05 level, **significance at the 0.01 level, ***significance at the 0.001 level

†City distance is the distance, in miles, from the plot to the nearest city > 10,000 people.

††Edge distance is the log of the distance from the plot, in feet, to the nearest nonforest edge.

Table 4. Percentage of sample plots with one or more individuals of multiflora rose, common buckthorn, non-native bush honeysuckles, garlic mustard, or reed canary grass present by state and percentage of plots invaded by the most common invasive species for the state. Sample plots were drawn from the 2005-2006 Phase 2 Forest Inventory and Analysis invasive species dataset for the Midwest region.

Percentage of plots with one or more invasive species present		Most commonly observed invasive species by state and percentage of plots the species occurs on	
Iowa	79.70%	<i>Rosa multiflora</i> (multiflora rose)	59.40%
Indiana	72.40%	<i>Rosa multiflora</i> (multiflora rose)	59.70%
Illinois	70.20%	<i>Rosa multiflora</i> (multiflora rose)	52.10%
Missouri	42.00%	<i>Rosa multiflora</i> (multiflora rose)	36.20%
Wisconsin	21.40%	<i>Lonicera</i> spp. (non-native bush honeysuckles)	11.70%
Michigan	19.50%	<i>Lonicera</i> spp. (non-native bush honeysuckles)	8.10%
Minnesota	5.90%	<i>Rhamnus cathartica</i> (common buckthorn)	5.10%

Table 5. The effect of explanatory variables on individual non-native invasive plant species presence on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006.

Species	volume†			city distance††			edge distance†††		
	<i>estimate</i>	<i>p (> z)</i>	<i>odds ratio</i>	<i>estimate</i>	<i>p (> z)</i>	<i>odds ratio</i>	<i>estimate</i>	<i>p (> z)</i>	<i>odds ratio</i>
<i>Rosa multiflora</i> (multiflora rose)	0.0174	0.0017**	1.0176	0.0353	0.3089	1.0359	-0.3325	2.77e-11***	0.7171
<i>Rhamnus cathartica</i> (common buckthorn)	-0.0071	0.3010	0.9929	-0.4557	< 2e-16***	0.6340	-0.3452	7.84e-06***	0.7081
<i>Lonicera</i> spp. (non-native bush honeysuckles)	0.0026	0.614	1.0026	-0.248	3.29e-14***	0.7804	-0.341228	1.96e-10***	0.7109
<i>Alliaria petiolata</i> (garlic mustard)	-0.0040	0.6781	0.9960	-0.278	4.88e-06***	0.7573	-0.2037	0.0367*	0.8157
<i>Phalaris arundinacea</i> (reed canary grass)	-0.0485	0.0056**	0.9527	-0.0158	0.8711	0.9843	-0.3633	0.0644(.)	0.6954

(.)Significance at the 0.1 level, *significance at the 0.05 level, **significance at the 0.01 level, ***significance at the 0.001 level

†Volume is the square root of all sound live tree volume in cubic feet per acre.

††City distance is the square root of the distance, in miles, from the plot to the nearest city > 10,000 people.

†††Edge distance is the log of the distance from the plot, in feet, to the nearest nonforest edge.

Table 5 (continued). The effect of explanatory variables on individual non-native invasive plant species presence on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006.

Species	disturbance (biotic)			disturbance (weather)		
	<i>estimate</i>	<i>p</i> (> z)	<i>odds ratio</i>	<i>estimate</i>	<i>p</i> (> z)	<i>odds ratio</i>
<i>Rosa multiflora</i> (multiflora rose)	0.9492	4.83e-11***	2.5836			
<i>Rhamnus cathartica</i> (common buckthorn)	-1.365	0.00178**	0.2554			
<i>Lonicera</i> spp. (non-native bush honeysuckles)	0.1916	0.2572	1.2112			
<i>Alliaria petiolata</i> (garlic mustard)	0.6082	0.0210*	1.8371			
<i>Phalaris arundinacea</i> (reed canary grass)	0.1193	0.7626	1.1267	2.2022	8.04e-06***	9.0449

(.)Significance at the 0.1 level, *significance at the 0.05 level, **significance at the 0.01 level, ***significance at the 0.001 level

-Blank predictor variables indicate no significant relationship was found between the variable and the invasive plant in the chi-square test (e.g. multiflora rose x disturbance [weather]).

†Volume is the square root of all sound live tree volume in cubic feet per acre.

††City distance is the square root of the distance, in miles, from the plot to the nearest city > 10,000 people.

†††Edge distance is the log of the distance from the plot, in feet, to the nearest nonforest edge.

Table 6. Maximum value that a variable caused an effect on individual non-native invasive plant species presence, after which no significant effect on species presence was found. Data was collected on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006.

Species	volume†	city distance††	edge distance†††
<i>Rosa multiflora</i> (multiflora rose)	206.23		157.57
<i>Rhamnus cathartica</i> (common buckthorn)		5.20	189.00
<i>Lonicera</i> spp. (non-native bush honeysuckles)		2.83	110.00
<i>Alliaria petiolata</i> (garlic mustard)		10.16	914.67
<i>Phalaris arundinacea</i> (reed canary grass)	537.09		

-Blank predictor variables indicate no significant relationship was found between the variable and the invasive plant in the full logistic regression (e.g. common buckthorn x volume).

†Volume is in cubic feet per acre for all sound live tree volume.

††City distance is in miles from the plot to the nearest city > 10,000 people.

†††Edge distance is in feet from the plot to the nearest nonforest edge.

Table 7. The effect of volume and edge distance on individual non-native invasive plant species presence on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006. When significant, relationships are shown as + (positive) or – (negative).

Species	Volume Class†	Predictor	
		Edge distance††	Volume‡
<i>Rosa multiflora</i> (multiflora rose)	Overall	(-)***	NS
	< 36	NS	NS
	< 100	NS	(+)*
	100-576	(-)***	NS
	> 576	(-)***	(-)**
<i>Rhamnus cathartica</i> (common buckthorn)	Overall	(-)***	(-)***
	< 100	(-)**	NS
	100-625	(-)***	(-)***
	> 625	(-)***	(-)***
<i>Lonicera</i> spp. (non-native bush honeysuckles)	Overall	(-)***	(-)***
	< 100	NS	(+)***
	100-625	(-)***	NS
	> 625	(-)***	(-)***
<i>Alliaria petiolata</i> (garlic mustard)	Overall	(-)*	NS
	< 121	NS	(+).
	121-400	(-)**	NS
	> 400	NS	(-).
<i>Phalaris arundinacea</i> (reed canary grass)	Overall	(-)**	(-)***
	< 196	NS	NS
	196-400	(-)**	NS
	> 400	(-)**	NS

(.)Significance at the 0.1 level, *significance at the 0.05 level, **significance at the 0.01 level, ***significance at the 0.001 level

†Volume is the sound live tree volume in cubic feet per acre.

††Edge distance is the log of the distance from the plot, in feet, to the nearest nonforest edge.

Table 8. The effect of latitude on city distance for individual non-native invasive plant species presence on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006. When significant, variable relationships are shown as + (positive) or – (negative).

Species	Latitude Class †	Predictor	
		Latitude †	City distance ††
<i>Rosa multiflora</i> (multiflora rose)	Overall	NS	(-)*
	< 38.1	NS	(+)***
	38.1-40.1	(+)***	NS
	40.1-42.1	NS	NS
	> 42.1	(-)***	(+)***
<i>Rhamnus cathartica</i> (common buckthorn)	Overall	(-)***	(+)***
	< 43.3	(+)***	(-)***
	43.3-45.8	(-)***	(-)***
	> 45.8	(-)***	(-)***
<i>Lonicera</i> spp. (non-native bush honeysuckles)	Overall	(-)***	(-)***
	< 39.9	(+)***	(-)*
	39.9-43.9	(+)*	(-)***
	> 43.9	(-)***	(-)***
<i>Alliaria petiolata</i> (garlic mustard)	Overall	(+)**	(-)***
	< 40.5	NS	(-)**
	40.5-42.5	(+)***	NS
	> 42.5	(-)***	(-)*
<i>Phalaris arundinacea</i> (reed canary grass)	Overall	(-)***	NS
	< 42.2	(+)**	NS
	42.2-44.2	(-)***	NS
	> 44.2	NS	(-)*

*Significance at the 0.05 level, **significance at the 0.01 level, ***significance at the 0.001 level

†Latitude is in degrees north.

††City distance is square root of the distance, in miles, from the plot to the nearest city > 10,000 people.

Table 9. The effect of latitude on edge distance for individual non-native invasive plant species presence on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006. When significant, variable relationships are shown as + (positive) or – (negative).

Species	Latitude Class†	Predictor	
		Latitude‡	Edge distance††
<i>Rosa multiflora</i> (multiflora rose)	Overall	(-)*	(-)**
	< 39.0	(-)**	(-)**
	39.0-40.1	(-).	(-)**
	40.1-41.9	NS	NS
	> 41.9	(-)**	(-)**
<i>Rhamnus cathartica</i> (common buckthorn)	Overall	(-)**	(-)**
	< 43.0	(+)**	NS
	43.0-45.8	(-)**	(-)**
	> 45.8	(-)*	(-)**
<i>Lonicera</i> spp. (non-native bush honeysuckles)	Overall	(-)**	(-)**
	< 39.8	(+)**	(-)*
	39.8-42.4	(+)**	(-)*
	> 42.4	(-)**	(-)**
<i>Alliaria petiolata</i> (garlic mustard)	Overall	(+)*	(-)*
	< 41.2	(+)*	NS
	41.2-43.0	NS	NS
	> 43.0	(-)**	NS
<i>Phalaris arundinacea</i> (reed canary grass)	Overall	(-)**	(-)**
	< 41.7	(+)*	NS
	41.7-42.8	(-).	(-)*
	> 42.8	(-)**	(-).

(.)Significance at the 0.1 level, *significance at the 0.05 level, **significance at the 0.01 level, ***significance at the 0.001 level

†Latitude is in degrees north.

††Edge distance is the log of the distance from the plot, in feet, to the nearest nonforest edge.

Table 10. The effect of water on plot on individual species observed on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006.

water category†	<i>Rosa multiflora</i> (multiflora rose)			<i>Rhamnus cathartica</i> (common buckthorn)			<i>Lonicera</i> spp. (non-native bush honeysuckles)		
	<i>Estimate</i>	<i>p</i> (> z)	<i>odds ratio</i>	<i>estimate</i>	<i>p</i> (> z)	<i>odds ratio</i>	<i>estimate</i>	<i>p</i> (> z)	<i>odds ratio</i>
1-0	0.2995	0.5020	1.3492	-1.0208	0.1254	0.3603	-0.0027	1.0000	0.9973
2-0	-0.0433	1.0000	0.9576	-0.4957	0.4620	0.6091	-0.0425	1.0000	0.9584
3-0	0.6675	0.8190	1.9494	1.4902	0.1086	4.4380	0.1532	0.9990	1.1656
4-0	0.0300	0.9990	1.0305	-0.3234	0.6369	0.7237	-0.0574	0.9910	0.9442
2-1	-0.3428	0.8030	0.7098	0.5251	0.8418	1.6906	-0.0398	1.0000	0.9610
3-1	0.3681	0.9790	1.4450	2.5110	0.0076**	12.3172	0.1559	0.9990	1.1687
4-1	-0.2695	0.6890	0.7638	0.6974	0.5871	2.0085	-0.0547	0.9990	0.9467
3-2	0.7108	0.8230	2.0356	1.9858	0.0258*	7.2849	0.1957	0.9970	1.2162
4-2	0.0733	0.9990	1.0761	0.1723	0.9895	1.1880	-0.0149	1.0000	0.9852
4-3	-0.6376	0.8480	0.5286	-1.8135	0.0434*	0.1631	-0.2106	0.9960	0.8101

(.)Significance at the 0.1 level, *significance at the 0.05 level, **significance at the 0.01 level, ***significance at the 0.001 level

†Water on plot categories are given in Table 2.

Table 10 (continued). The effect of water on plot on individual species observed on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006.

water category†	<i>Alliaria petiolata</i> (garlic mustard)			<i>Phalaris arundinacea</i> (reed canary grass)		
	<i>estimate</i>	<i>p</i> (> z)	<i>odds ratio</i>	<i>estimate</i>	<i>p</i> (> z)	<i>odds ratio</i>
1-0	-1.0252	0.1197	0.3587	1.1199	0.0545(.)	3.0645
2-0	-0.3495	0.9497	0.7051	0.4572	0.9518	1.5796
3-0	1.6498	0.1684	5.2058	1.8153	0.4604	6.1429
4-0	0.0518	0.9990	1.0531	0.2061	0.9802	1.2289
2-1	0.6757	0.8198	1.9655	-0.6627	0.8895	0.5155
3-1	2.6750	0.0158*	14.5119	0.6954	0.9736	2.0045
4-1	1.0770	0.1305	2.9357	-0.9139	0.3583	0.4010
3-2	1.9992	0.1472	7.3834	1.3581	0.7992	3.8888
4-2	0.4012	0.9322	1.4936	-0.2512	0.9964	0.7779
4-3	-1.5980	0.2180	0.2023	-1.6093	0.6202	0.2000

(.)Significance at the 0.1 level, *significance at the 0.05 level, **significance at the 0.01 level, ***significance at the 0.001 level

†Water on plot categories are given in Table 2.

Table 11. The effect of physiographic class on individual non-native invasive plant species presence on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006.

Species	physiographic class	estimate	<i>p</i> (> z)	odds ratio
<i>Rosa multiflora</i> (multiflora rose)	Mesic-Hydric	0.8885	0.0053**	2.4315
	Xeric-Hydric	-0.0698	0.9715	0.9326
	Xeric-Mesic	-0.9583	< 0.001***	0.3835
<i>Rhamnus cathartica</i> (common buckthorn)	Mesic-Hydric	0.9175	0.0044**	2.5030
	Xeric-Hydric	-0.1062	0.96408	0.8992
	Xeric-Mesic	-1.0237	0.0034**	0.3593
<i>Lonicera</i> spp. (non-native bush honeysuckles)	Mesic-Hydric	0.9043	< 0.001***	2.4702
	Xeric-Hydric	0.5137	0.1289	1.6715
	Xeric-Mesic	-0.3906	0.0233*	0.6767
<i>Alliaria petiolata</i> (garlic mustard)	Mesic-Hydric	1.2694	0.0447*	3.5587
	Xeric-Hydric	-1.9413	0.1894	0.1435
	Xeric-Mesic	-3.2107	0.0039**	0.0403
<i>Phalaris arundinacea</i> (reed canary grass)	Mesic-Hydric	0.746	0.566	2.1085
	Xeric-Hydric	-15.4945	1	1.87e-07
	Xeric-Mesic	-16.2406	1	8.85e-08

*Significance at the 0.05 level, **significance at the 0.01 level, ***significance at the 0.001 level

Table 12. The effect of average annual number of days the temperature is $\geq 90^\circ\text{F}$ on individual non-native invasive plant species presence on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006.

temperature category†	<i>Rosa multiflora</i> (multiflora rose)			<i>Rhamnus cathartica</i> (common buckthorn)			<i>Lonicera</i> spp. (non-native bush honeysuckles)		
	<i>estimate</i>	<i>p</i> (> z)	<i>odds ratio</i>	<i>estimate</i>	<i>p</i> (> z)	<i>odds ratio</i>	<i>estimate</i>	<i>p</i> (> z)	<i>odds ratio</i>
B-A				11.0895	1.0000	65,479	12.7025	1.0000	328,568
C-A				11.1172	1.0000	67,319	12.7515	1.0000	345,069
D-A				-3.9665	1.0000	0.0189	12.3313	1.0000	226,681
E-A							12.2130	1.0000	201,390
C-B	0.5621	<0.001***	1.7544	0.0276	1.0000	1.0280	0.0490	0.9960	1.0502
D-B	0.1763	0.7507	1.1928	-15.0561	1.0000	2.89e-07	-0.3713	0.3082	0.6899
E-B	-0.3017	0.4642	0.7396				-0.4895	0.3507	0.6129
D-C	-0.3858	0.0243*	0.6799	-15.0837	1.0000	2.81e-07	-0.4203	0.0719(.)	0.6568
E-C	-0.8638	<0.001***	0.4216				-0.5385	0.1821	0.5836
E-D	-0.4780	0.0040**	0.6200				-0.1183	0.9859	0.8885

(.)Significance at the 0.1 level, *significance at the 0.05 level, **significance at the 0.01 level, ***significance at the 0.001 level

†Categories for average annual number of days $\geq 90^\circ\text{F}$ are given in Figure 10.

-Blank temperature categories indicate the species did not occur within the category.

Table 12 (continued). The effect of average annual number of days the temperature is $\geq 90^\circ\text{F}$ on individual non-native invasive plant species presence on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006.

temperature category†	<i>Alliaria petiolata</i> (garlic mustard)			<i>Phalaris arundinacea</i> (reed canary grass)		
	<i>estimate</i>	<i>p</i> ($> z $)	<i>odds ratio</i>	<i>estimate</i>	<i>p</i> ($> z $)	<i>odds ratio</i>
B-A						
C-A						
D-A						
E-A						
C-B	0.3044	0.3106	1.3558	0.1966	0.8280	1.2173
D-B	-2.1736	0.0135*	0.1138	-18.6643	1.0000	7.8379e-09
E-B	-11.9510	1.0000	6.4528e-06			
D-C	-2.4780	0.0027**	0.0839	-18.8609	1.0000	6.4390e-09
E-C	-12.2554	1.0000	4.7594e-06			
E-D	-9.7774	1.0000	0.0001			

(.)Significance at the 0.1 level, *significance at the 0.05 level, **significance at the 0.01 level, ***significance at the 0.001 level

†Categories for average annual number of days the temperature is $\geq 90^\circ\text{F}$ are given in Figure 10.

-Blank temperature categories indicate the species did not occur within the category.

Table 13. The effect of average annual number of days the temperature is $\leq 32^{\circ}\text{F}$ on individual non-native invasive plant species presence on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006.

temperature category†	<i>Rosa multiflora</i> (multiflora rose)			<i>Rhamnus cathartica</i> (common buckthorn)			<i>Lonicera</i> spp. (non-native bush honeysuckles)		
	estimate	p (> z)	odds ratio	estimate	p (> z)	odds ratio	estimate	p (> z)	odds ratio
E-D	0.6504	0.4585	1.9163						
F-D	0.9448	0.1690	2.5723						
G-D	-0.1745	0.9832	0.8399						
F-E	0.2945	0.0864(.)	1.3425				0.1271	0.8397	1.1355
G-E	-0.8249	<0.001***	0.4383				-0.4633	0.0861(.)	0.6292
G-F	-1.1194	<0.001***	0.3265	0.0551	0.97	1.0567	-0.5904	<0.001***	0.5541
H-F				-2.0182	<1e-06***	0.1329	-1.6984	<0.001***	0.1830
H-G				-2.0730	<1e-06***	0.1258	-1.1080	<0.001***	0.3302
H-E							-1.5713	<0.001***	0.2078

(.)Significance at the 0.1 level, *significance at the 0.05 level, **significance at the 0.01 level, ***significance at the 0.001 level

†Categories for average annual number of days the temperature is $\leq 32^{\circ}\text{F}$ are given in Figure 11.

-Blank temperature categories indicate the species did not occur within the category.

Table 13 (continued). The effect of average annual number of days the temperature is $\leq 32^\circ\text{F}$ on individual non-native invasive plant species presence on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006.

temperature category†	<i>Alliaria petiolata</i> (garlic mustard)			<i>Phalaris arundinacea</i> (reed canary grass)		
	<i>estimate</i>	<i>p</i> ($> z $)	<i>odds ratio</i>	<i>estimate</i>	<i>p</i> ($> z $)	<i>odds ratio</i>
E-D						
F-D						
G-D						
F-E	1.4305	0.0001***	4.1808			
G-E	1.0889	0.0178*	2.9710			
G-F	-0.3416	0.1938	0.7106	-1.8710	1.30e-06***	0.1540
H-F				-17.6010	1.0000	2.27e-08
H-G				-15.7300	1.0000	1.47e-07
H-E						

(.)Significance at the 0.1 level, *significance at the 0.05 level, **significance at the 0.01 level, ***significance at the 0.001 level

†Categories for average annual number of days the temperature is $\leq 32^\circ\text{F}$ are given in Figure 11.

-Blank temperature categories indicate the species did not occur within the category.

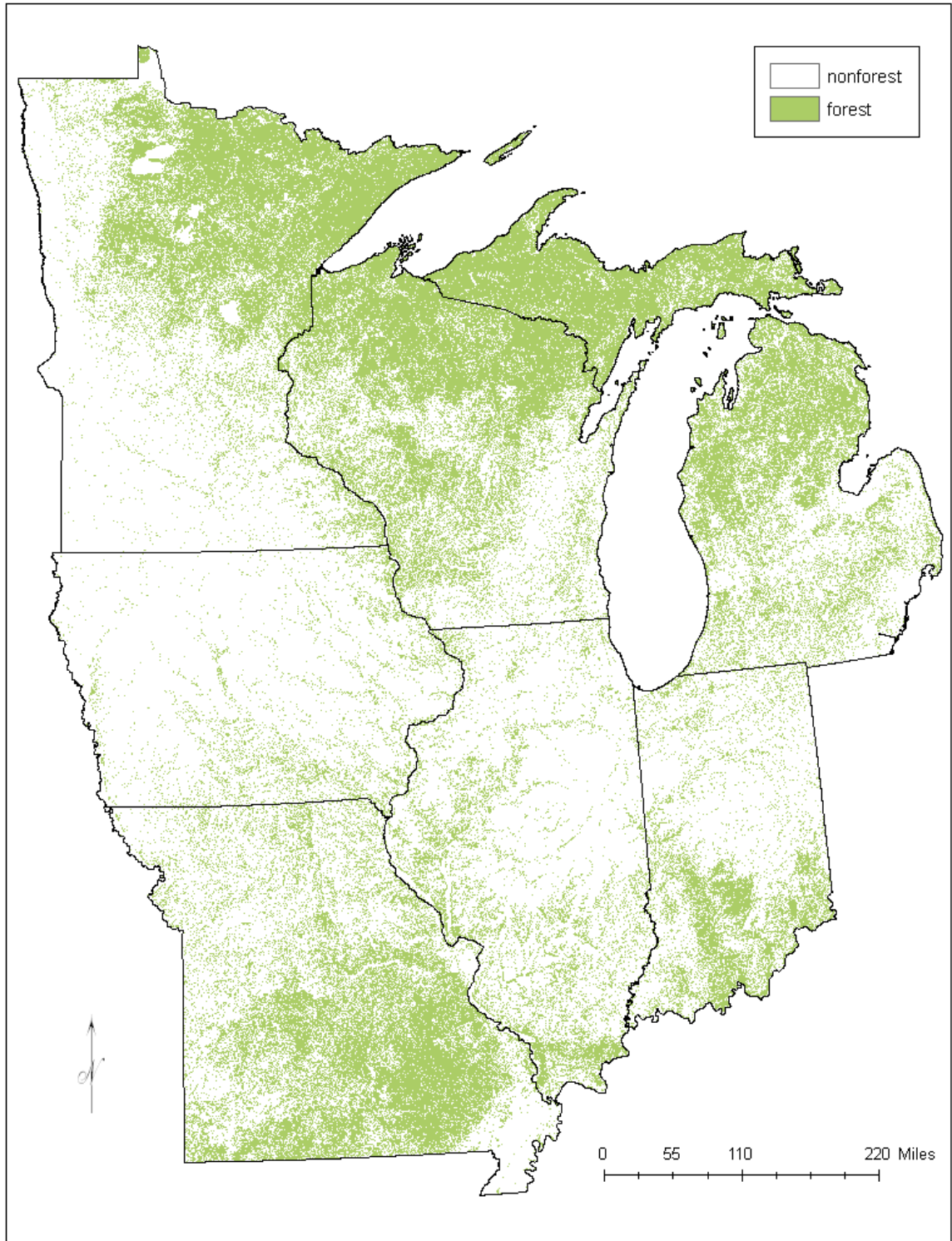


Figure 1. Map of study region showing forest and nonforest areas. Forest/nonforest source: 2001 National Land Cover Dataset (NLCD; <http://www.mrlc.gov/index.php> [United States Environmental Protection Agency 2001]).

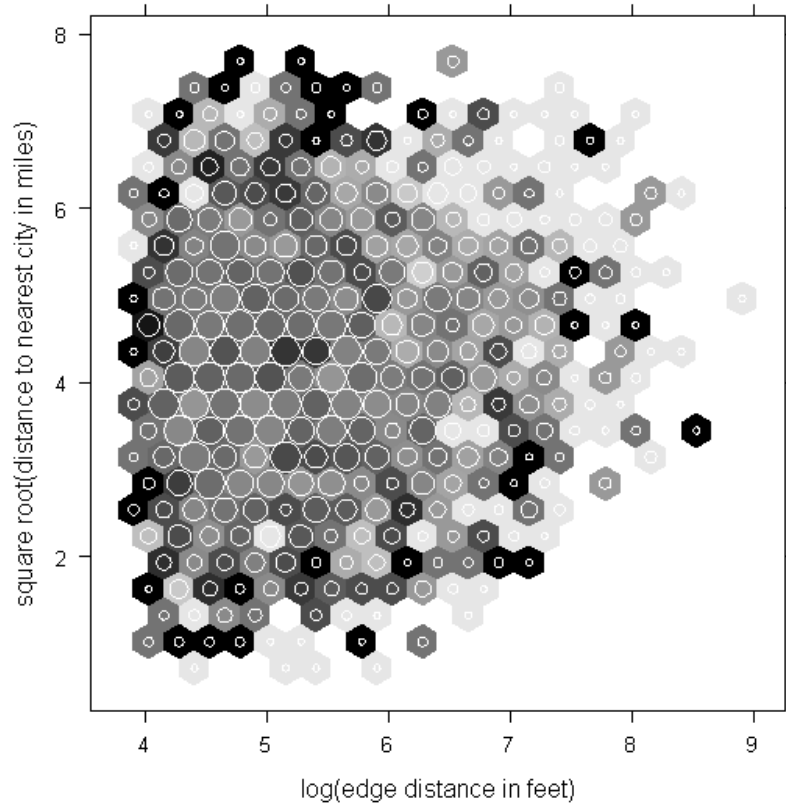


Figure 2. Hexagon plot of *Rosa multiflora* (multiflora rose) presence with respect to distance of the plot to the nearest city for different distances to forest edge. Species presence is indicated by hexagons with the darkest colors relating to the highest presence of *Rosa multiflora* and the lightest colors relating to the absence of the species on plots. Circles within the hexagons represent the number of plots established for a given combination of city and edge distance, with smaller circles indicating fewer plots and larger circles indicating a greater number of plots. Data are from 2005-2006 Phase 2 Forest Inventory and Analysis plots in the Midwest.

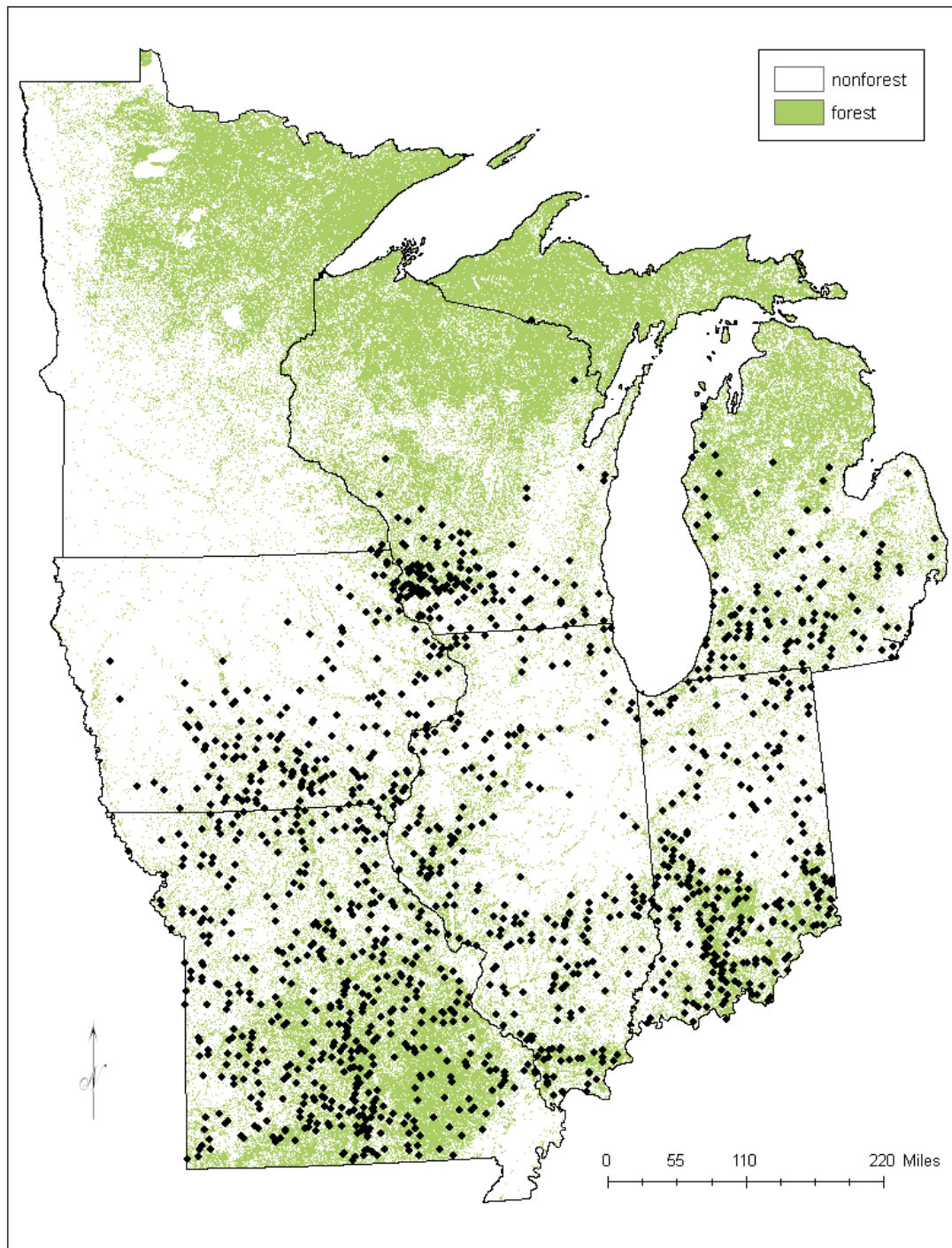


Figure 3. *Rosa multiflora* (multiflora rose) presence on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006. Depicted plot locations are approximate. Forest/nonforest source: 2001 National Land Cover Dataset (NLCD; <http://www.mrlc.gov/index.php> [United States Environmental Protection Agency 2001]).

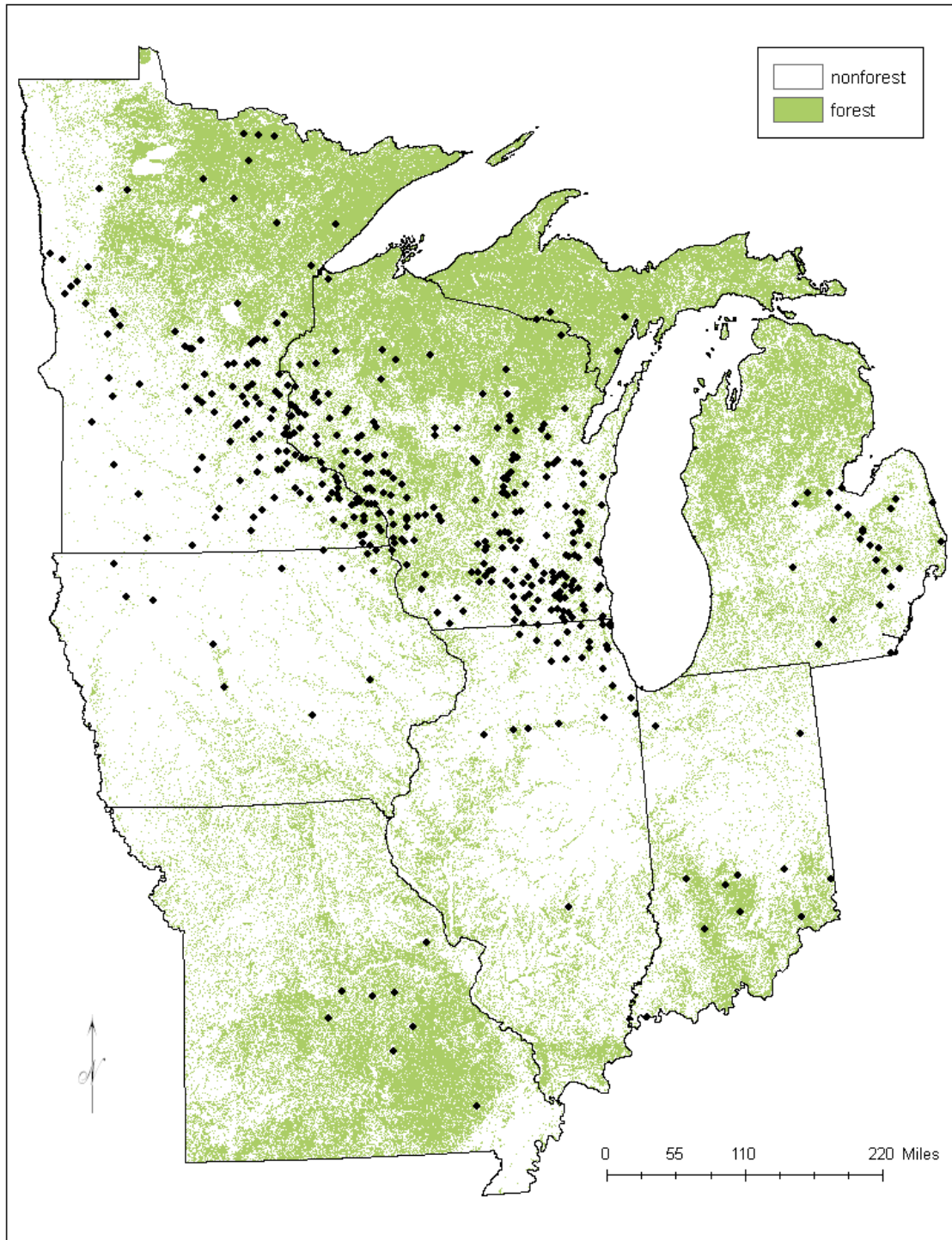


Figure 4. *Rhamnus cathartica* (common buckthorn) presence on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006. Depicted plot locations are approximate. Forest/nonforest source: 2001 National Land Cover Dataset (NLCD; <http://www.mrlc.gov/index.php> [United States Environmental Protection Agency 2001]).

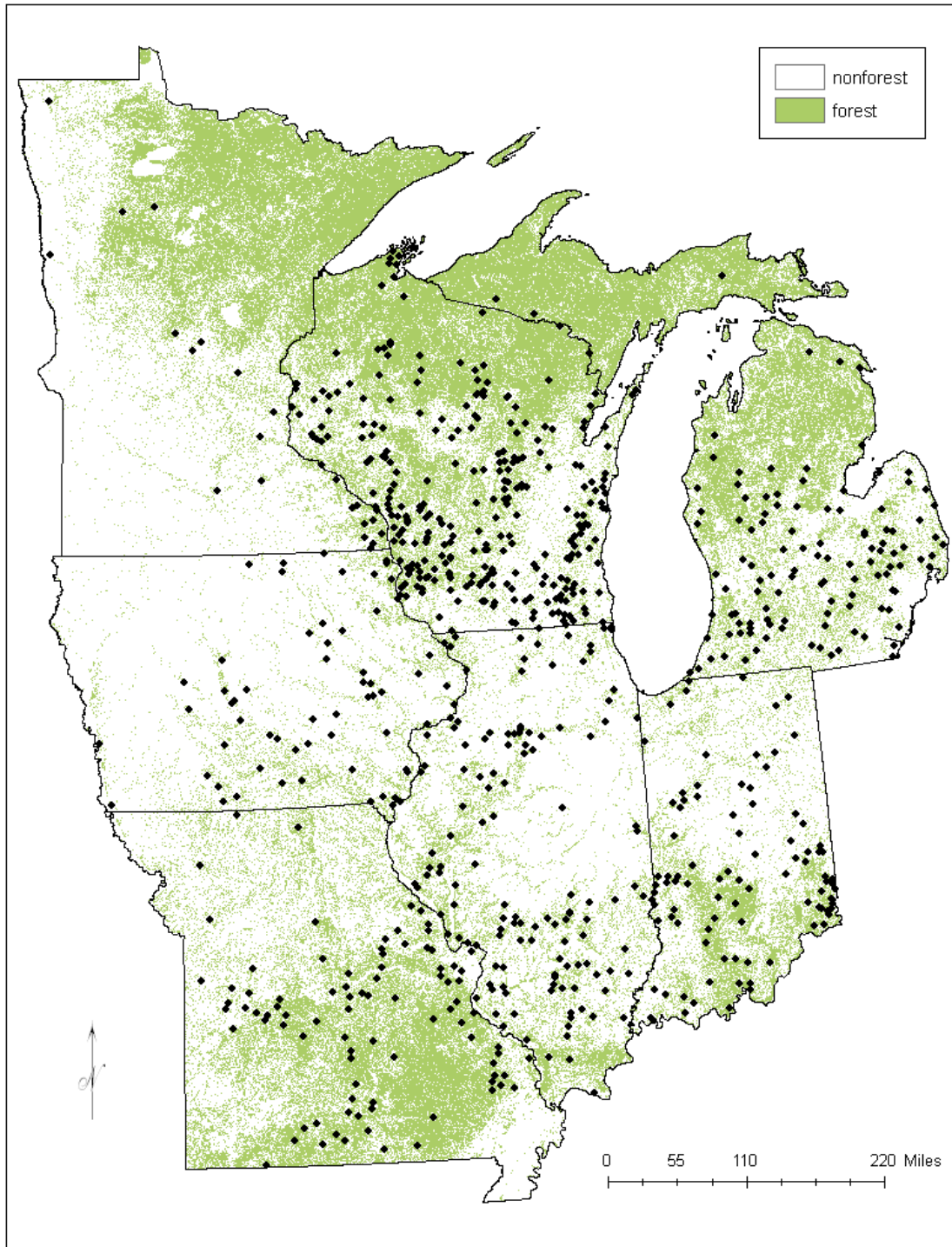


Figure 5. *Lonicera* spp. (non-native bush honeysuckles) presence on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006. Depicted plot locations are approximate. Forest/nonforest source: 2001 National Land Cover Dataset (NLCD; <http://www.mrlc.gov/index.php> [United States Environmental Protection Agency 2001]).

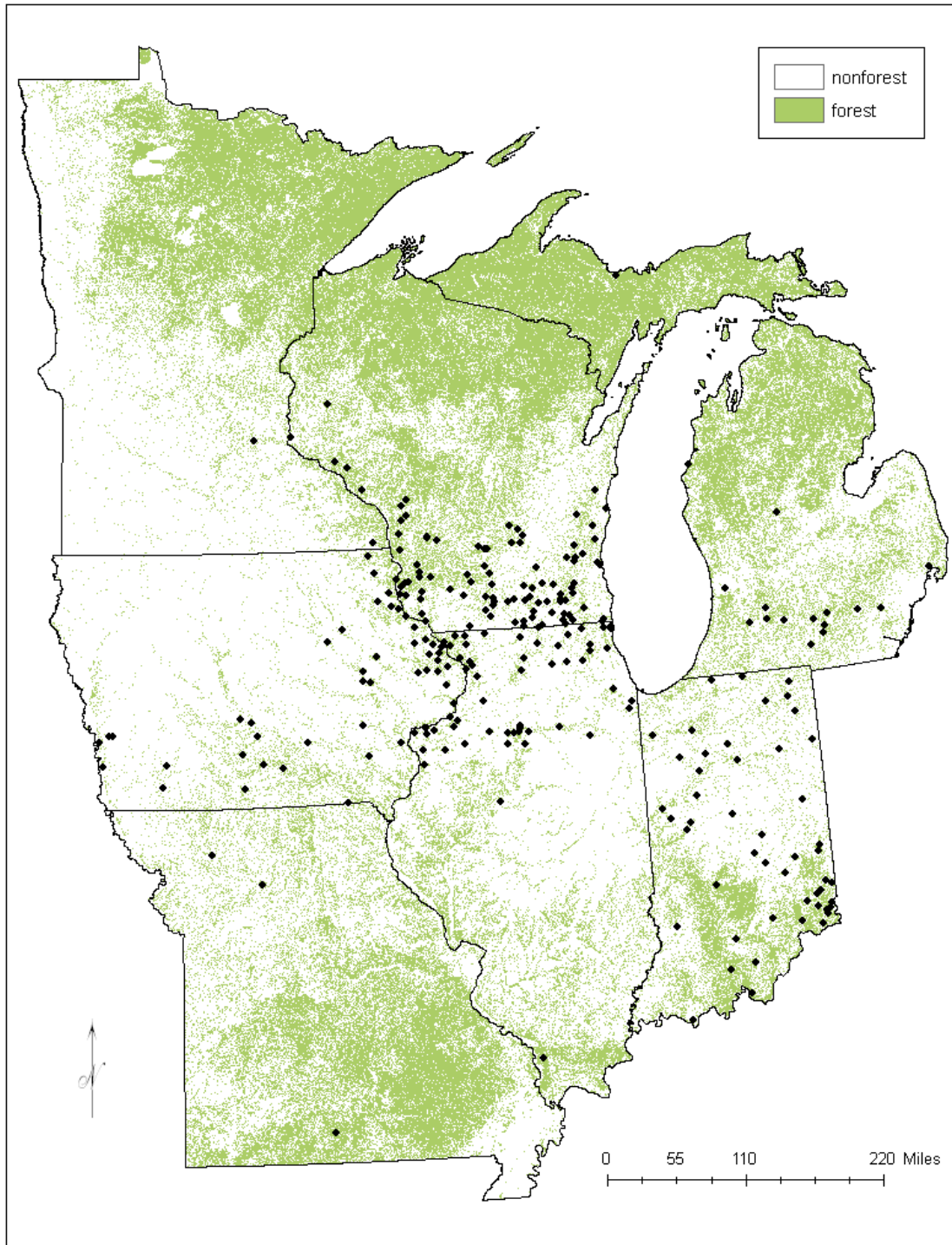


Figure 6. *Alliaria petiolata* (garlic mustard) presence on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006. Depicted plot locations are approximate. Forest/nonforest source: 2001 National Land Cover Dataset (NLCD; <http://www.mrlc.gov/index.php> [United States Environmental Protection Agency 2001]).

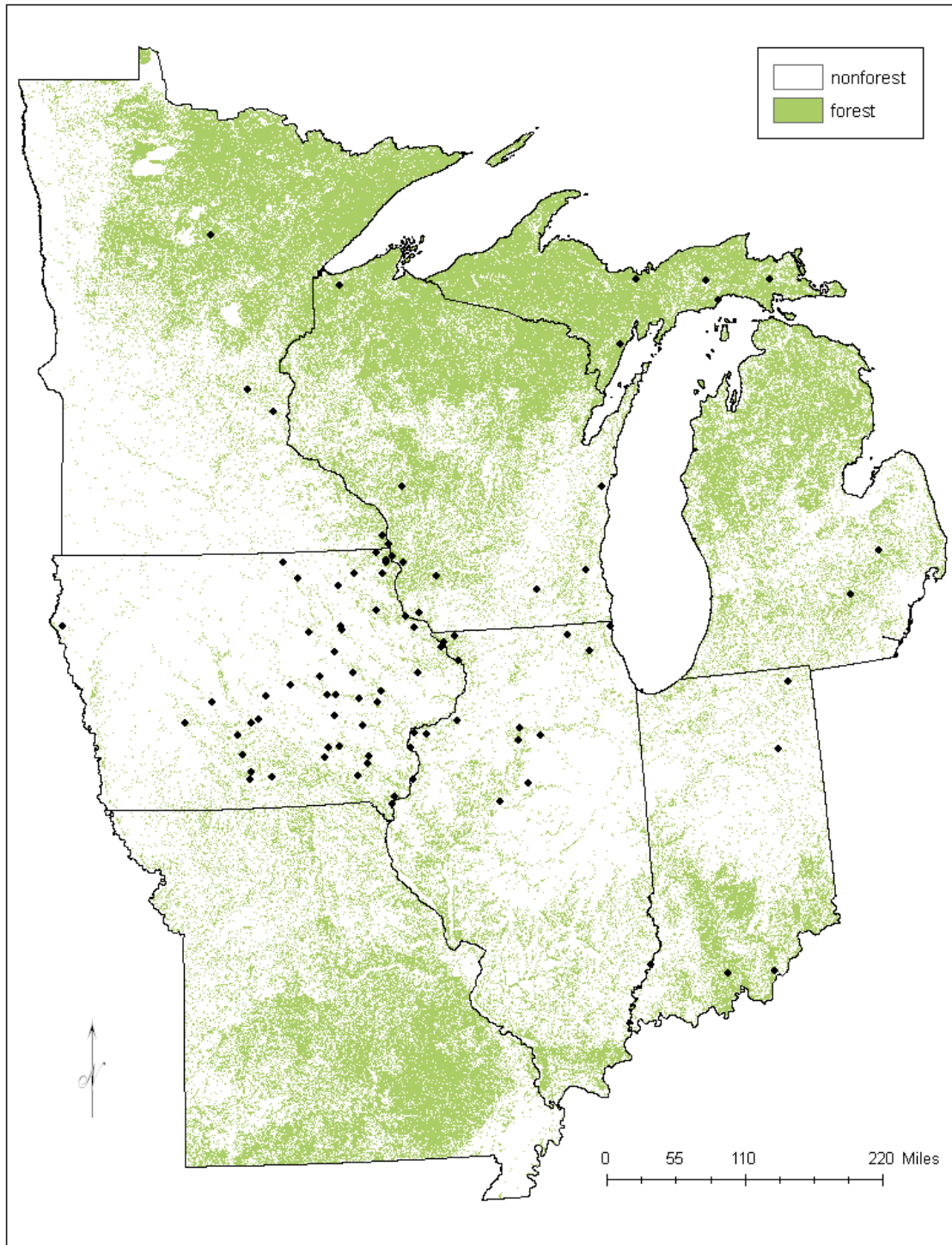


Figure 7. *Phalaris arundinacea* (reed canary grass) presence on Phase 2 Forest Inventory and Analysis plots in the Midwest, 2005-2006. Depicted plot locations are approximate. Forest/nonforest source: 2001 National Land Cover Dataset (NLCD; <http://www.mrlc.gov/index.php> [United States Environmental Protection Agency 2001]).

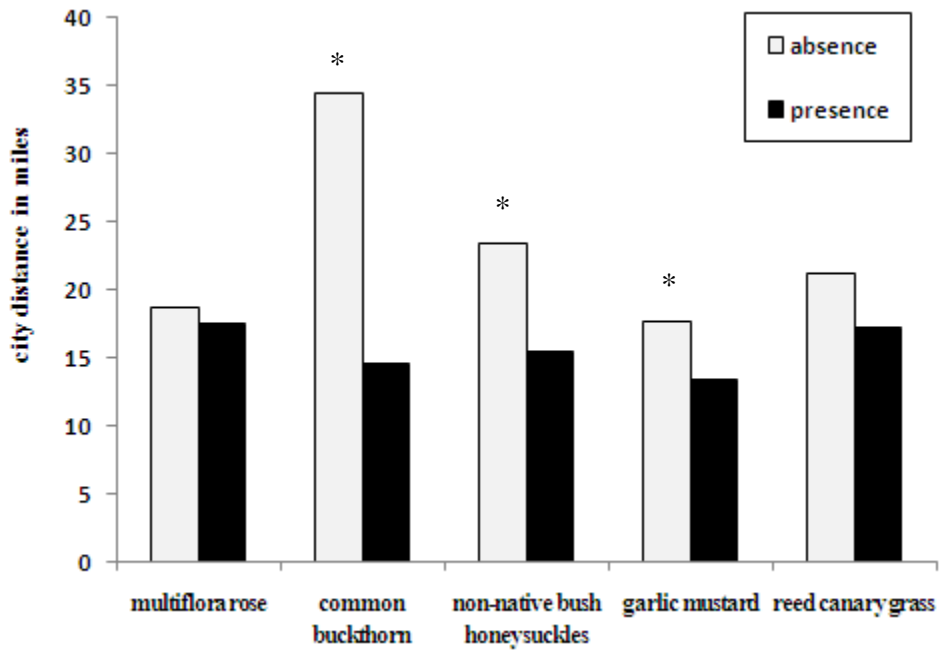


Figure 8. Mean distance (in miles) from the plot to the nearest city > 10,000 people on 2005-2006 Phase 2 Forest Inventory and Analysis plots where the five non-native invasive plants were absent versus present.

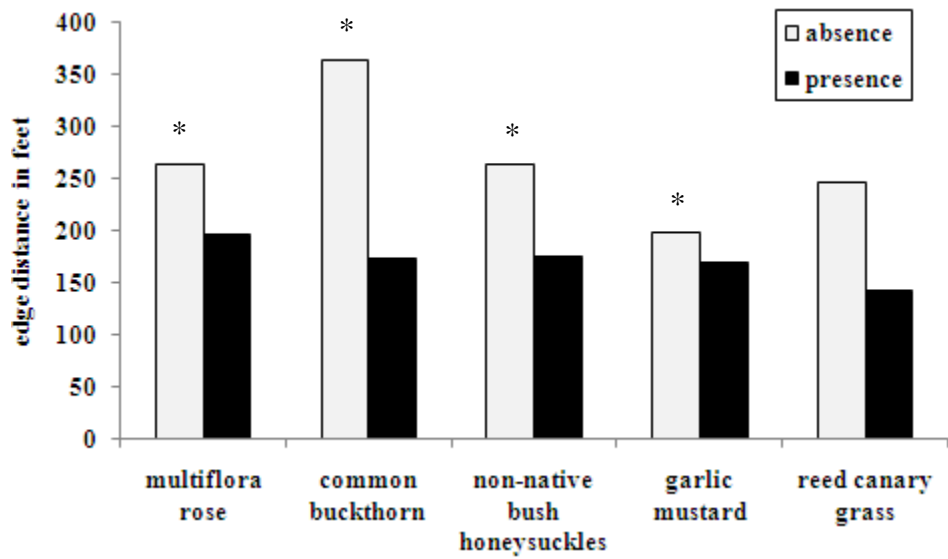


Figure 9. Mean distance (in feet) from the plot to the nearest nonforest edge on 2005-2006 Phase 2 Forest Inventory and Analysis plots where the five non-native invasive plants were absent versus present.

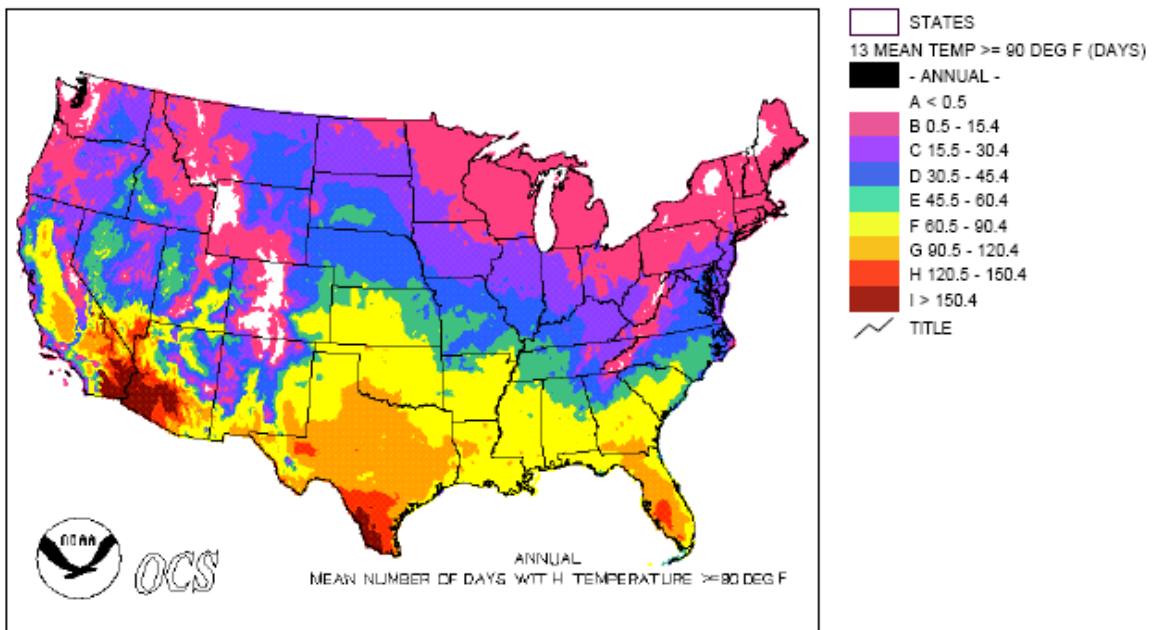


Figure 10. Mean number of days with temperature $\geq 90^{\circ}\text{F}$ annually. Source: National Oceanic and Atmospheric Administration (NOAA; <http://hurricane.ncdc.noaa.gov/cgi-bin/climaps/climaps.pl>).

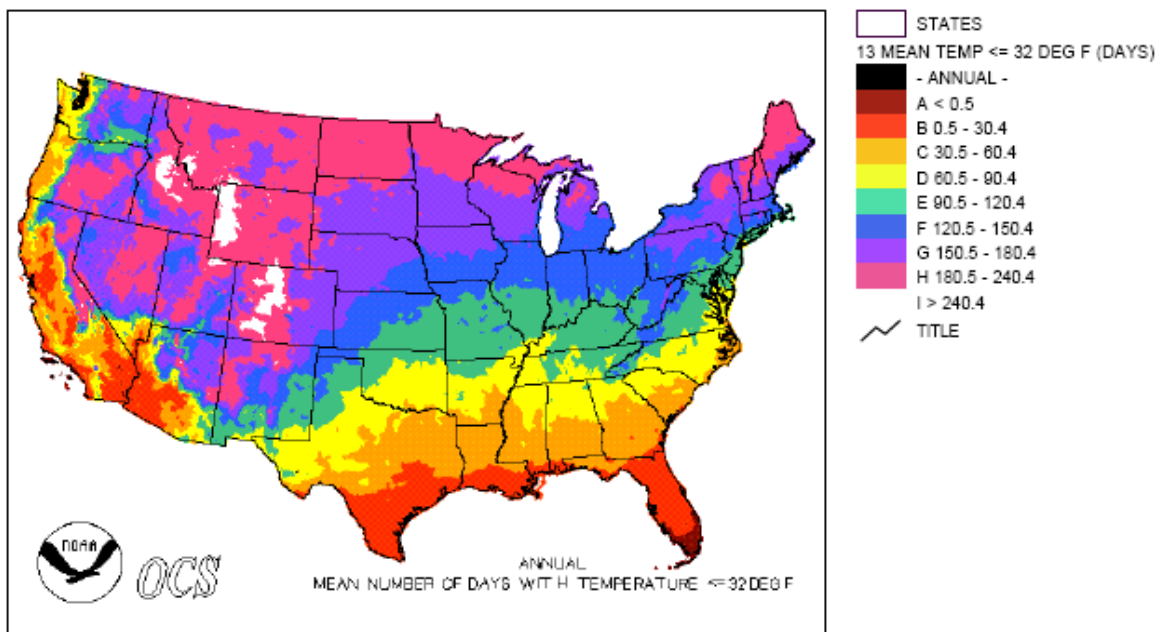


Figure 11. Mean number of days with temperature $\leq 32^{\circ}\text{F}$ annually. Source: National Oceanic and Atmospheric Administration (NOAA; <http://hurricane.ncdc.noaa.gov/cgi-bin/climaps/climaps.pl>).

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