

Regional Patterns of Major Nonnative Invasive Plants and Associated Factors in Upper Midwest Forests

Zhaofei Fan, W. Keith Moser, Mark H. Hansen, and Mark D. Nelson

Abstract: Nonnative invasive plants (IPs) are rapidly spreading into natural ecosystems (e.g., forests and grasslands). Potential threats of IP invasion into natural ecosystems include biodiversity loss, structural and environmental change, habitat degradation, and economic losses. The Upper Midwest of the United States encompasses the states of Illinois, Indiana, Iowa, Michigan, Minnesota, Missouri, and Wisconsin, a region populated with 46 million people. Concerns of IP threats to the productive timberlands in the region have emerged with rapid expansion of urban areas and associated land cover changes caused by increasing human disturbances. Using the strategic inventory data from the 2005–2006 US Department of Agriculture Forest Service Forest Inventory and Analysis program and other data such as forestland cover and transportation coverage/layers, we modeled the regional patterns of IPs by using a combination of nonparametric techniques, including classification and regression tree analysis, kernel density smoothing, and bootstrapping. For the Midwest region, a probability map and historical records of human-related introduction of IPs of interest suggests that invasive shrubs, herbs, and grasses were initially introduced into the central (sparsely forested) areas and then spread north and south (densely forested areas), whereas invasive vines spread primarily from the south into other parts of the region. The probability of IPs in densely forested areas (0.1) was one-fifth of that in sparsely forested areas. Shrubs are the predominant IP threat and are distributed across the vast region with the exception of the northern part. Invasive grasses and herbs are most abundant in the central part of the region, and invasive vines are most common in the southern part. Percent forest cover and road proximity (distance to roads) as indicators of anthropogenic disturbances, were the most significant drivers of IP occurrence/abundance. Site factors, including forest productivity and stand biodiversity, were significantly correlated with the occurrence of vines. *FOR. SCI.* 59(1):38–49.

Keywords: nonnative invasive plant, Forest Inventory Analysis, kernel density smoothing, probability, classification and regression tree, bootstrap

THE UPPER MIDWEST REGION OF THE UNITED STATES, encompassing the states of Illinois, Indiana, Iowa, Michigan, Minnesota, Missouri, and Wisconsin, has historically contained a diversity of different forest types and structures, ranging from closed-canopy forests in the northern Lake States and the Ozark Highlands to open woodland ecosystems in southern Wisconsin to savannas and prairies in Iowa, Illinois, and Indiana. The fertile soils of this region were ideal for farming, and European settlers proceeded to clear forestland for agriculture. In the heavily timbered areas of northern Minnesota, Wisconsin, and Michigan, and in southern Missouri, large-scale commercial harvesting exploited the stands of eastern white pine (*Pinus strobus* L.), shortleaf pine (*Pinus echinata* Mill.), and other species, which resulted in radically altered and fragmented forest landscapes, and the vast savannas and prairies in the central part of the region have been replaced by agricultural lands (Andersen et al. 1996, Soucy et al. 2005).

As in other regions, the combination of clearing land for settlement and timber harvesting created many opportunities for nonnative invasive plants (IPs) to establish in the Midwest. Within forested ecosystems, IPs are defined as

plants that are not indigenous to an ecosystem and have advantageous traits to establish and spread in the new environment, causing deleterious impacts on the structure, composition, and growth of a forest (Webster et al. 2006). These traits include broad climate tolerances, large geographic ranges, prolific seed production, low seed mass, short time to maturity, high growth rates, and the ability to spread clonally (Crawley 1987, Blossey and Notzold 1995, Rejmanek 1995, Vogt-Anderson 1995, Rejmanek and Richardson 1996, Goodwin et al. 1999, Jakobs et al. 2004, Qian and Ricklefs 2006). Native forest ecosystems that developed over centuries are limited in their ability to compete against these invaders. An introduction, however, does not necessarily result in establishment. Whether an IP successfully invades an ecosystem is determined by its competitive advantages or traits over native species including disturbance, competitive release, resource availability, propagule pressure, enemy release, and empty niches (Levine and D'Antonio 1999, Mitchell and Power 2003, Colautti et al. 2004, Jakobs et al. 2004, Gilbert and Lechowicz 2005, Hierro et al. 2005, Richardson and Pyšek 2006, Theoharides and Dukes 2007).

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Disturbance usually increases the availability of resources for plants including invasive species and alters the competitive balance and site occupancy of existing plant communities, rendering abiotic factors more important as determinants of invasion success than biotic factors (Richardson and Bond 1991, Hood and Naiman 2000). Road density provides a salient indication of landscape disturbance (e.g., Gelbard and Belnap 2003, Watkins et al. 2003). When the myriad variations in human transport are considered, it is difficult to predict both sources and destinations of many invasive species (Hodkinson and Thompson 1997). Research to understand the invasion patterns and associated driving factors of a given site or region is still necessary for the management and control of invasive species (Richardson and Pyšek 2006).

The invasion of IPs into an ecosystem or region is a spatial-temporal process that can be classified into four nondiscrete stages: introduction (transport), colonization, establishment, and landscape spread (e.g., Vermeij 1996). For the introduction stage, humans have been the primary dispersers of IPs in many countries and regions either deliberately for food, forage, fuel, lumber, environmental control/restoration, medicinal, and aesthetic purposes, or accidentally through a variety of human activities. Introduction does not necessarily result in colonization. To successfully colonize in the introduced environment, IPs must be able to tolerate abiotic filters (e.g., climate and site condition) and pass through survival- and growth-related biotic processes at the micro/local scale. In addition to the abiotic filters, propagule pressure, often measured by the number of individuals introduced into the new region, has a significant impact on the success of colonization (Williamson 1996, Lockwood et al. 2005). At the establishment stage, biotic filters including competition from other plants or interactions with herbivores, parasites, pathogens, pollinators, and dispersal agents as stated by the enemy release and empty niche theories (e.g., Levine and D'Antonio 1999, Mitchell and Power 2003, Colautti et al. 2004, Jakobs et al. 2004, Gilbert and Lechowicz 2005, Hierro et al. 2005) may be the major barriers to survival, growth, and reproduction for developing self-sustaining, expanding populations at the community scale (Theoharides and Dukes 2007). The spread stage occurs at the landscape or regional scale. Landscape patterns, disturbance regimes, and climatic constraints will largely affect the spread rate and distribution of IPs (With 2002, 2004, Theoharides and Dukes 2007).

Once established, IPs threaten the sustainability of native forest composition, structure, function, and resource productivity (Webster et al. 2006). They also pose significant challenges for decisionmakers attempting to set policy for control and amelioration. There is an underlying need for improved inventory and monitoring methodologies. Information on the invasion process indicates that efforts to control invasive plants should focus on the establishment stage when the invasive population is relatively sparse, and biotic filters may be the major barriers to survival, growth, and reproduction of individuals (Theoharides and Dukes 2007), which introduces further challenges for monitoring and planning efforts because populations are sparse in the establishment phase, and the subsequent expansion and

saturation phases occur rapidly. Once IPs become firmly established (e.g., saturation stage), their control becomes increasingly difficult. The management costs associated with affected forests are often prohibitively expensive, most notably when mechanical and chemical treatments are required. Additional research on the impacts and related science is warranted.

IPs are found in all the major life forms that comprise forest ecosystems: trees, shrubs, vines, forbs/grasses, herbs, lichens, and mosses. The strategic IP inventory data collected in 2005 and 2006 by the US Department of Agriculture Forest Service Forest Inventory and Analysis (FIA) program recorded 25 commonly found invasive shrubs, vines, herbs, and grasses that may have adverse impacts on the forests in the Midwest. The major objective of this study was to evaluate the current condition of major IP species/groups in the Midwest for regional invasive species monitoring and management efforts. Specifically, this study analyzed two issues: the regional distribution pattern of IPs, in terms of presence and cover mapping, by major life forms; and the probabilistic distribution of IPs by significant contributing factors including disturbance, site and stand factors, and species characteristics that influence the presence and coverage of IPs. This study provides baseline information on IP distribution (presence and abundance) and on the relative importance of contributing factors in the Upper Midwest.

Data and Methods

The FIA program in the North Central Research Station (a predecessor to today's Northern Research Station) began implementing an annual inventory system in 1999. Complete documentation of the plot design and all measurements can be found in USDA Forest Service (2010) and North Central Research Station (2005). The national FIA is conducted in three phases: phase 1—remote sensing for postsampling stratified estimation; phase 2—on-the-ground inventory of tree and forest attributes; and phase 3—more detailed sampling of forest health attributes including ground flora. In lieu of national protocols for monitoring all vegetation on phase 2 samples, some regional FIA programs have implemented exotic invasive plant surveys to address the burgeoning need for this information (Rudis et al. 2006). During the 2005–2006 inventory years, 8,663 FIA phase 2 plots in seven states of the Upper Midwest were assessed for the presence and cover of 25 nonnative invasive plant species (Table 1) (Olson and Cholewa 2005). If one or more of these species was observed, its percent cover was estimated on each subplot and placed into one of seven ordinal categories of abundance (Table 2). All FIA plots were spatially referenced by latitude and longitude and identified by the presence (1) or absence (0) of each species. Because of missing values, 147 FIA plots were deleted, resulting in 8,516 plots included in data analysis and modeling.

Measurements of individual trees and herbaceous species on the plots allowed calculation of percent cover for each IP species as well as associated site variables including mean tree diameter and height, stand or tree species/group basal area, site index (base age 50 years), density (overstory basal

Table 1. Proportion of FIA plots infested by nonnative IPs based on the 2005–2006 survey.

Species name	Presence (%)
Shrubs (7 species)	
Multiflora rose (<i>Rosa multiflora</i> Thunb.)	15.3
Nonnative bush honeysuckle (<i>Lonicera</i> spp.): includes showy fly honeysuckle (<i>Lonicera</i> × <i>bella</i> Zabel [<i>morrowii</i> × <i>tatarica</i>]), Amur honeysuckle (<i>Lonicera maackii</i> [Rupr.] Herder), Morrow’s honeysuckle (<i>Lonicera morrowii</i> A. Gray), and Tatarian honeysuckle (<i>Lonicera tatarica</i> L.)	9.2
Common buckthorn (<i>Rhamnus cathartica</i> L.)	4.8
Autumn olive (<i>Elaeagnus umbellata</i> Thunb.)	2
Japanese barberry (<i>Berberis thunbergii</i> DC.)	1.3
Glossy buckthorn (<i>Frangula alnus</i> Mill.) + European privet (<i>Ligustrum vulgare</i> L.)	0.4
Vines (7 species)	
Japanese honeysuckles (<i>Lonicera japonica</i> Thunb.)	2.6
Kudzu (<i>Pueraria montana</i> [Lour.] Merr.) + Porcelain berry (<i>Ampelopsis brevipedunculata</i> [Maxim.] Trautv.) + Oriental bittersweet (<i>Celastrus orbiculatus</i> Thunb.) + Chinese yam (<i>Dioscorea opposita</i> Thunb.) + Black swallowwort (<i>Cynanchum louiseae</i> Kartsch & Gandhi) + Wintercreeper (<i>Euonymus fortunei</i> [Turcz.] Hand.-Maz.)	0.3
Grasses (3 species)	
Reed canary grass (<i>Phalaris arundinacea</i> L.)	1
Phragmites (<i>Phragmites</i> spp.) + Nepalese browntop (<i>Microstegium vimineum</i> [Trin.] A. Camus)	0.2
Herbs (8 species)	
Garlic mustard (<i>Alliaria petiolata</i> [M. Bieb.] Cavara & Grande)	3.1
Common burdock (<i>Arctium minus</i> Bernh.)	2.3
Leafy spurge (<i>Euphorbia esula</i> L.) + Spotted knapweed (<i>Centaurea stoebe</i> L.) + Dames rocket (<i>Hesperis matronalis</i> L.) + Mile a minute weed (<i>Persicaria perfoliata</i> [L.] H. Gross) + Japanese knotweed (<i>Polygonum cuspidatum</i> Siebold & Zucc.) + Marsh thistle (<i>Cirsium palustre</i> [L.] Scop.)	0.8

area and stand density index) (Reineke 1933, Woodall and Miles 2006), and species diversity (calculated via Shannon’s index [H’]) (Shannon 1948) for species, height, and diameter).

For large scale (landscape/region) variables and human disturbances, we calculated minimum distances, in km, from FIA plots to the nearest road using the methodology detailed in Moser et al. (2009) in each of the following roads classes: interstate highway, state highway, major highway,

Table 2. Cover codes and ranges of percent cover of nonnative IPs used in recording invasive species.

Cover code	Range of percent cover
1	<1, trace
2	1–5
3	6–10
4	11–25
5	26–50
6	51–75
7	76–100

minor highway, and local streets. To evaluate IP presence as a function of forest fragmentation, we estimated fragmentation (percent forest cover) at both the plot level and the county level.

Regional Patterns of IPs

The overall probability for any given IP species being present in the study area was calculated as the number of FIA plots containing the IP species divided by the total number of FIA plots sampled. This provided the relative frequency of each IP species over the study area (Table 1). In the same way, the probability of presence (risk) of an IP species at a spatial location within the study area was computed as the proportion of the FIA plots with the presence value of 1 through a Gaussian kernel density function.

Over a large, heterogeneous spatial domain such as the seven Upper Midwest states, the invasion and spread of IPs are typically nonstationary. We used a kernel smoothing technique to map the regional patterns of IPs in terms of probability of presence and percentage of cover across the seven Midwest states. Kernel smoothing (or kernel-based estimators) is a nonparametric “weighted moving averages via the kernel” method used to estimate the true density (probability) of a random variable (Wand and Jones 1995). Given a random sample X_1, \dots, X_n with a continuous, univariate density f , the kernel density estimator at a location of x is

$$\hat{f}(x, h) = \frac{1}{nh} \sum_{i=1}^n K\left(\frac{x - X_i}{h}\right) \quad (1)$$

where K is the kernel function and h is the bandwidth (smoothing parameter). The standardized isotropic Gaussian kernel density was used:

$$K(x) = \prod_{i=1}^n \frac{1}{h\sqrt{2\pi}} e^{-\frac{(x-x_i)^2}{2h^2}} \quad (2)$$

with $n = 2$ for the two-dimension density smoothing.

The selection of the kernel function (i.e., Gaussian kernel or other kernels such as the quadratic kernel) is less important than the selection of the bandwidth (h) in the density (probability) estimation (Hastie and Tibshirani 1990, Schabenberger and Gotway 2005). A larger bandwidth leads to smoother estimates by giving progressively more weight to observations farther away from the spatial location. With smaller bandwidths, only observations close to the spatial location are given significant weight, therefore resulting in a more “ragged” estimate. The basic principle in selecting a bandwidth in kernel density estimation is that the estimated map should capture both the local variation and global trend of the response variable of interest while avoiding “fake” local perturbations from the “noise” embedded in the data. Theoretically, the best bandwidth is the one that minimizes the mean square error through

$$\begin{aligned} \text{MSE}(\hat{f}) &= E[(f(x) - \hat{f}(x;h))^2] \\ &= (E[f(x)] - E[\hat{f}(x;h)])^2 + \text{var}(\hat{f}) \quad (3) \end{aligned}$$

where $f(x)$ and $f(x; h)$ are the real and estimated probabilities of an IP species, respectively. In reality, $f(x)$ is unknown and the MSE is extremely difficult to estimate. To determine the best bandwidth with a continuous variable (x) such as the percentage of cover of IPs, Equation 3 was approximated through

$$m\hat{s}e = \frac{1}{m} \sum_{i=1}^m (O_i - E_i)^2 \quad (4)$$

where O_i and E_i are the observed and expected values of x , respectively. However, with the binary case (presence or absence of an IP species) the optimal bandwidth was estimated using the receiver operating characteristic (ROC) curve analysis (Metz 1978, Zweig and Campbell 1993).

To construct the regional cover and probability of presence maps for each IP species group, the FIA plots were randomly divided into two groups in a ratio of 7:3, with 70% of FIA plots (the construction data set) used to generate the smoothed cover and probability map corresponding to a set of selected bandwidths and the other 30% of FIA plots (the validation dataset) used to validate how well the smoothed cover and probability were estimated by using Equation 4 and through ROC curve analysis, respectively. For each IP species, a set of smoothed cover maps were generated based on the observed cover data from the construction data set by using the kernel smoothing method corresponding to bandwidths = 0.02, 0.04, . . . , 1.0. The smoothed percent cover was compared with the observed percent cover at the same spatial location from the validation data set. The best bandwidth and final cover map (Figure 3) was selected to minimize the MSE in Equation 4.

Similarly, a set of smoothed probability maps was generated based on the observed values (1 if an IP is present, 0 otherwise) from the construction data set by using the kernel-smoothing method corresponding to the same set of bandwidths. Given a possible cutoff value from the range of probability (0–1), each location (cell or pixel) on the smoothed probability map can be classified as presence (the smoothed probability \geq the cutoff value) or absence (the smoothed probability $<$ the cutoff value) of an IP species. In comparison with the validation FIA plots, one of four possible outcomes may be true for the classification result: correctly classified as presence (TP = true presence fraction), falsely classified as presence (FP = falsely presence fraction), correctly classified as absence (TA = true absence fraction), and falsely classified as absence (FA = false absence fraction). As a diagnostic measure of the classification performance, the ROC curve is the true presence rate [sensitivity, TP/(TP + FP)] plotted against the false absence rate [1 – specificity, FA/(TA + FA)] for different cutoff probability values. A classification test with perfect discrimination (no overlap in the two distributions) has a ROC plot that passes through the upper left corner (100% sensitivity and 100% specificity) (Figure 1). Therefore, the closer the ROC plot is to the upper left corner, the higher the overall accuracy of the classification test (Zweig and Campbell 1993). The area under the ROC curve was used to evaluate the classification tests and determine the best band-

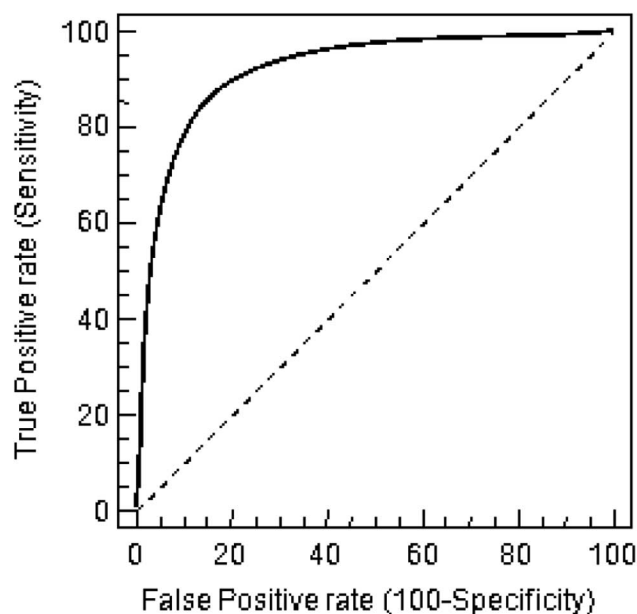


Figure 1. Schematic diagram of a ROC curve. A ROC curve is composed of a series of true positive rate (sensitivity)/false-positive rate (100 – specificity) pairs corresponding to a particular decision threshold. A test with perfect discrimination (no overlap in the two distributions) has a ROC curve that passes through the upper left corner (100% sensitivity, 100% specificity). Therefore, the closer the ROC curve is to the upper left corner, the higher the overall accuracy of the test.¹

width (with the largest area under the ROC curve). For each smoothed probability map, the cutoff probability values of 0.1, 0.2, . . . , 1.0 were used to develop the ROC curve to determine the best bandwidth for the smoothed probability of IPs in the study region.

Identification of Factors Associated with Regional Patterns of IP Species

Classification and regression tree (CART) methods were applied to the 8,516 FIA plots to identify important factors associated with the presence of IP species at the regional scale. The response variable is binary—presence (1) or absence (0) of an IP species in a FIA plot—and the covariates include the aforementioned variables measured or calculated at the plot level and potential landscape and disturbance variables. CART is useful for a variety of scientific questions including classification, prediction, and association (Breiman et al. 1984). CART, a nonparametric statistical technique, recursively partitions a heterogeneous population into a set of relatively homogeneous populations. The target population (usually heterogeneous) in CART is represented by the root node in the tree profile, and a set of more homogeneous subpopulations obtained during the recursive partition process are represented by internal and terminal nodes, respectively. Classification is evaluated based on the relative homogeneity/purity of the terminal nodes. Patterns in the data are thus explicitly and intuitively exhibited by the hierarchical tree structure. CART is composed of two processes: a recursive top-down partitioning process (growing an initial tree) and a bottom-up pruning process (finding the best tree). According to Breiman et al.

(1984), three basic elements are necessary to grow the initial tree: the selection of the splits, a rule to stop splits, and a rule for assigning a terminal node to a class. To select the best split, CART exhaustively searches the pool of all candidate splits based on certain measures of node impurity. For a binary case as is in this study, two measures to quantify the node impurity are

$$I(t) = 2 * P(y = 1|X) * \{1 - P(y = 1|X)\} \quad (5)$$

and

$$I(t) = p(y = 1|X) * \log\{P(y = 1|X)\} + (1 - P(y = 1|X)) * \log\{1 - P(y = 1|X)\} \quad (6)$$

where $P(y = 1|X)$ is the proportion of cases where $y = 1$ given X and X represents the vector of explanatory variables. The best split was then defined to maximize

$$\Delta I(s,t) = I(t) - W_L I(t_L) + W_R I(t_R) \quad (7)$$

where $I(t)$, $I(t_L)$, and $I(t_R)$ are the impurities of the parent node t and its left and right child nodes (t_L and t_R) corresponding to a split. W_L and W_R are the weights for $I(t_L)$ and $I(t_R)$, most commonly represented by the proportion of subjects sent from node t to its left and right child nodes t_L and t_R . Given the node impurity and best split measures, CART will do a recursive split. If there are no stopping rules for the recursive split process, a fully grown tree will finally be obtained that is characterized by either only one subject in its terminal nodes or all subjects in the terminal nodes with identical values for the explanatory variables. A fully grown tree more often than not is too complex to be useful and too large to be interpreted easily. Moreover, late splits are often dubious because of small sample sizes and can subsequently jeopardize the efficiency and generalization of a fully grown tree. Because the purpose of this study was to identify potential factors related to the regional trend of IPs,

CART splits were subjectively stopped when the number of FIA plots in a node was less than 400. The resultant CART model was bootstrapped 200 times to calculate the relative risk (the ratio of presence probabilities of an IP in the right and left node) and confidence intervals for quantifying the importance of each split and the associated driving factors.

All computations and simulations were conducted under the R statistical environment (R Development Core Team 2011). Two statistical packages, rpart and spatstat, were used for CART analysis and kernel smoothing, respectively (Therneau and Atkinson 1997, Baddeley and Turner 2005).

Results

Based on the 8,516 FIA plots in the seven Midwest states, the overall presence probability of all 25 IP species is 26.5%. Each of the IP species was classified as either shrub, herb, vine, or grass based on their life form and had overall presence probabilities of 23.7% (2,012 plots), 5.5% (471 plots), 2.8 (238 plots), and 1.2 (102 plots), respectively. Compared with other life forms, invasive shrub species were the most prevalent, with multiflora rose (15.3%), nonnative bush honeysuckle (9.2%), and common buckthorn (4.8%) as the top three shrub species in presence probability. All IPs in the other life forms (e.g., herb, vine, and grass) combined had an approximately 10% presence probability, and 14 of the 18 nonshrub species were very rare (probability <0.1%) (Table 1).

All of the life forms had similar cover class distribution with the cover class of from 1 to 5% being most abundant, followed by the trace cover class (<1%). The proportion of FIA plots decreased with cover class (Figure 2). The ratio of FIA plots among cover classes <0.01% (lightly infested), 1–50% (moderately infested), and >50% (severely infested) was approximately 20:70:10 for shrubs, 27:65:8 for

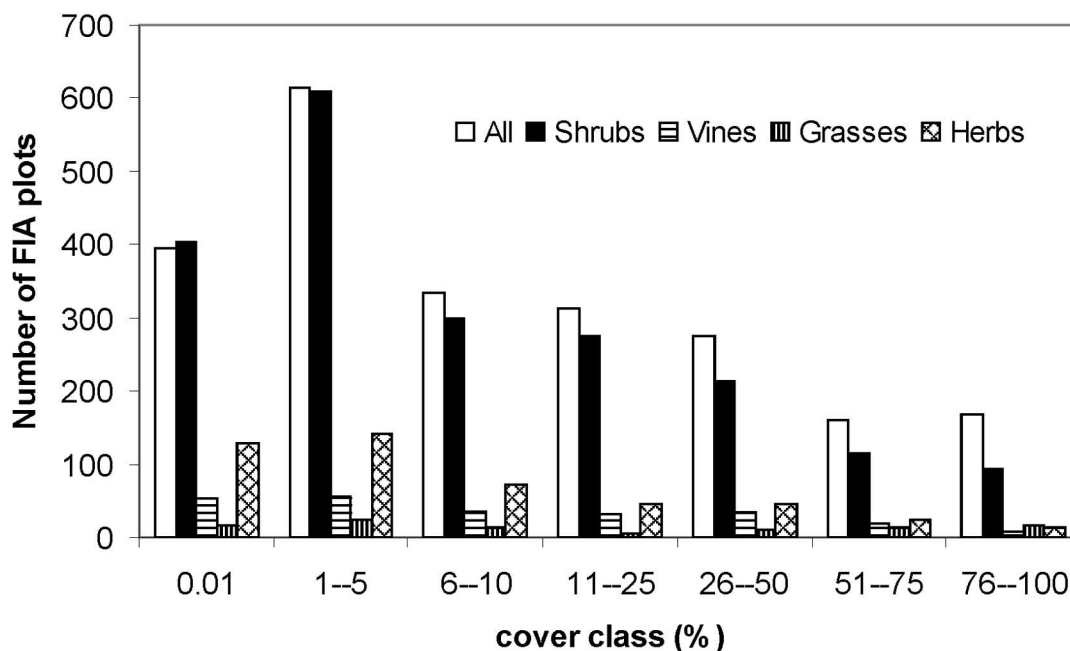


Figure 2. The number of FIA plots in each cover class (%) infested by IP species, by life form.

herbs, 22:66:12 for vines, and 17:55:28 for grasses, respectively. Severely infested plots (cover >50%) comprised only 10% of all infested FIA plots for shrubs, herbs, and vines; however, up to 28% of plots infested with invasive grasses were severely infested (Figure 2).

With the exception of herbs and vines, there were strong positive associations ($P < 0.0001$) between the distributions of other life forms (e.g., shrubs and herbs, shrubs and grasses, shrubs and vines, herbs and grasses, and vines and grasses) based on the χ^2 test using a 2×2 contingency table. This means that plots infested by one life form will probably be infested by another life form. In the Upper Midwest, invasive shrubs, herbs, and grasses are mainly distributed in the central part surrounding Chicago and other major cities/urban areas such as Des Moines, Iowa, whereas vines are mainly distributed in the southern part (Figure 3). The probability and cover maps for shrubs, grasses, and herbs might suggest that IPs were first introduced into the central part of the region, whereas the vines were from the south (Figure 3).

At the regional scale, county forest cover percent, as an indicator of human disturbances/influence, was the most significant driver of IP occurrence. For all IP species, the relative risk of percent forest cover at the county level in the densely forested region versus sparsely forested region reached up to 5.19 (Figure 4; Table 3). Other IP determinants included distance to national roads and major state roads, slope, stand condition, biodiversity, and basal area of softwood and oaks. For instance, the presence probability of IPs in densely forested regions (northern and southern parts, county forest percent >47%) was as low as 9.8%, compared with the high probability of 51.2% in sparsely forested areas (the central part) (Figures 3 and 4A).

Discussion

Since the mid-19th century, thousands of nonnative species have been introduced, intentionally or accidentally, into virtually all US ecosystems. Approximately 15% of these species are harmful and have been suggested to have significant negative impacts to nearly half of the endangered native species listed under the Endangered Species Act and to some degree threaten the integrity and health of most of our natural and managed ecosystems (Office of Technology Assessment 1993, Wilcove et al. 1998). The cost of monitoring, preventing, and controlling invasive plants alone is approximately \$13 billion per year (Westbrooks 1998). The nation's forestlands are particularly susceptible with estimated losses of \$2.1 billion per year due to lost forest production alone (Pimental et al. 2001).

The invasion and spread of nonnative invasive species into natural and managed ecosystems (e.g., forests) are spatiotemporal processes that involve multiple factors and causes. In addition to the specific characteristics (traits) of IPs, including the number of propagules they produce, the susceptibility of natural and managed ecosystems to invasion is affected by numerous factors involving climate, disturbance regimes, competitive abilities of the resident species, and the presence (or absence) of herbivores, pathogens, and mutualistic species that significantly contribute to

the extent and condition of the invading organisms (e.g., Crawley 1987, D'Antonio 1993, Lonsdale 1999). Many hypotheses, including natural enemy release (e.g., Elton 1958, Mitchell and Power 2003, Jakobs et al. 2004, Hierro et al. 2005), empty niche (e.g., Elton 1958, Levine and D'Antonio 1999, Gilbert and Lechowicz 2005, Hierro et al. 2005), propagule pressure (e.g., Williamson 1996, Lonsdale 1999), disturbance (e.g., Gelbard and Belnap 2003), novel weapons (e.g., Callaway and Aschehoug 2000), and species richness (e.g., Levine and D'Antonio 1999) have been proposed to explain the invasion and spread of IPs. However, inconsistency, or even conflict, still exists between reported results and proposed hypotheses. Davis et al. (2000) attempted to use the term "fluctuating resource availability" to integrate these hypotheses and resolve the inconsistencies. To date, however, there is no general theory to explain the multitude of invasion patterns that have been observed.

At large scales (e.g., region), the distribution of invasive species is believed to be nonstationary and varies dramatically in space and by ecosystems. To combat invasions effectively, identification of regional invasion patterns and associated ecological and socioeconomic factors that foster the establishment and spread of IPs is relevant to being able to distinguish between those factors that influence colonization and establishment (presence/incidence in a region) and those that affect spread (abundance/cover in a region). Regional species inventories such as FIA provide useful information to identify large-scale patterns of IP presence and to test alternative hypotheses explaining the observed patterns.

With the nonstationary nature of large-scale distributions of IPs, we used the nonparametric statistical methods (e.g., CART and kernel smoothing) in our data analyses and modeling. To explore the patterns of IPs in the Midwest region, we subjectively required that the terminal node size of CART should not be less than 400 plots. In this way, the CART models only included drivers that play important roles at large spatial scales (including a number of counties). The bootstrap confidence intervals for these variables were all significant, indicating that the identified variables were useful in detecting hot spots/areas of IPs. Even though other drivers such as stand biodiversity and condition might be important at smaller, more local scales, they were not included in the CART models because of the stopping rule of CART splits (i.e., number of FIA plots in the terminal nodes >400). These variables may, in fact, influence small-scale IP occurrence and to an extent may be related to cover class changes.

Percent forest coverage at the county level and distance to state and federal roads were considered indicators of forest fragmentation and intensities of human land use changes. These factors appeared in all CART models, suggesting that human disturbances are common contributors to the occurrence of most, if not all, IP species. This conforms to the historical records showing that most IPs were introduced by humans, either intentionally or by accident (Czarapata 2005). For the past two centuries, the central area of the Midwest region has experienced dramatic land use changes, characterized by forest cover being replaced by

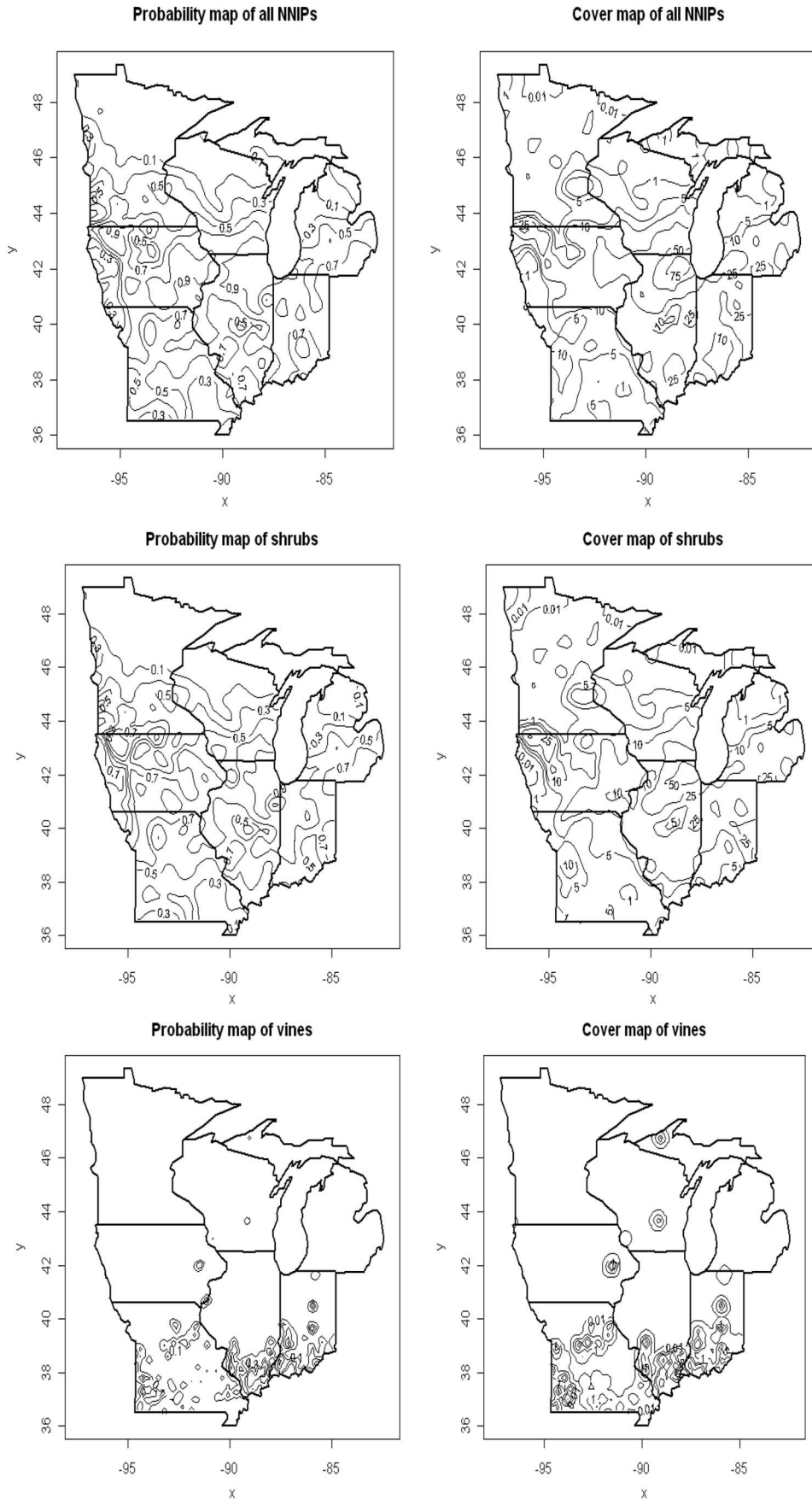


Figure 3. Regional probability and cover map of nonnative invasive plant (NNIP) species by life form in the Midwest states, USA. The contour line shows the probability of 0.1, 0.3, 0.5, 0.7, and 0.9 and cover class of 0.01, 5, 10, 25, 50, and 75% of NNIPs.

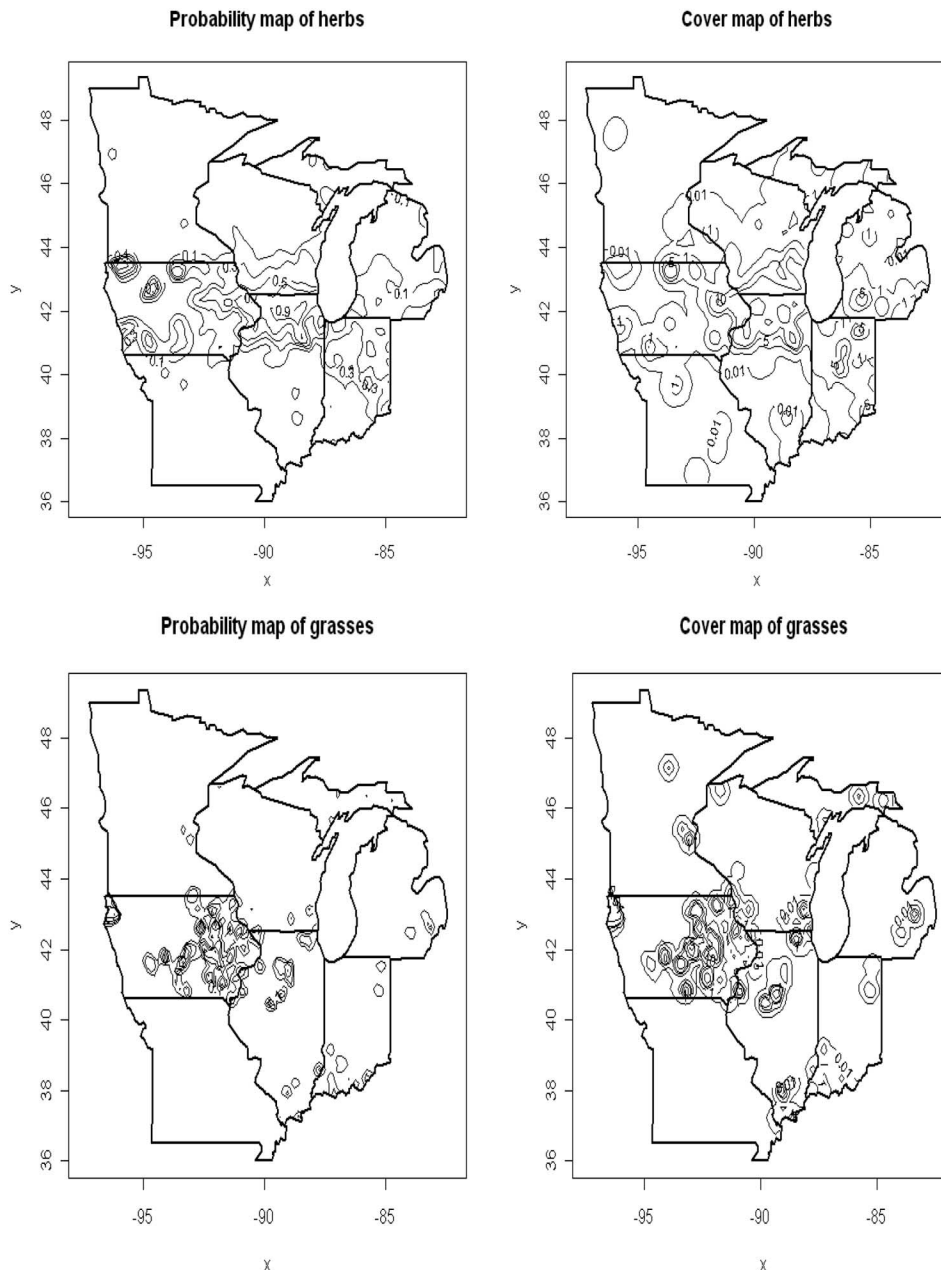


Figure 3. Continued.

cropland, fields, pastures, and urban areas. With the exception of vines, the probability of IP species in sparsely forested areas (i.e., the central portion of the region) was 5–9 times higher than that in the densely forested southern and northern parts. Hot spots (probability >80%) for shrubs, herbs, and grasses were mainly located in the central portion and tended to expand both south and north (Table 3; Figure 3). Vine species, however, were most abundant in the southern portion of the region. As shown by Fan et al. 2009, invasive vine species generally originated in the southeastern states and are expanding to the north.

The distance of FIA plots to state and federal roads, a variable linearly measuring forest fragmentation caused by road expansion (Riitters et al. 2004), was the second most common variable associated with IP probability. Studies using satellite imagery to model forest fragmentation across the conterminous United States have indicated that forest

fragmentation is pervasive and extensive in the region, with three-fourths of all forest found in or near the edges of larger, heavily fragmented regional forests (Vogelman et al. 2001, Riitters and Wickham 2003). Most of the large interior forests remaining in the Midwest states are publicly owned and mainly distributed across the southern and northern parts of this region. Forest fragmentation caused by roads is of special interest because roads can alter habitats and water drainage patterns, disrupt wildlife movement, and facilitate the introduction of exotic plant species (Gelbard and Belnap 2003). The relative risk of IP infestation in all splits (S4 and S6 in model A, S4 in model B, S2 and S3 in model C, S3 in model D, and S4 and S6 in model E of Figure 4) induced by the nearest distance to national and state roads indicated that forests near roads were, on average, 3–6 times more prone to being infested by IPs (Table 3). Federal and major state highways are strong pathways

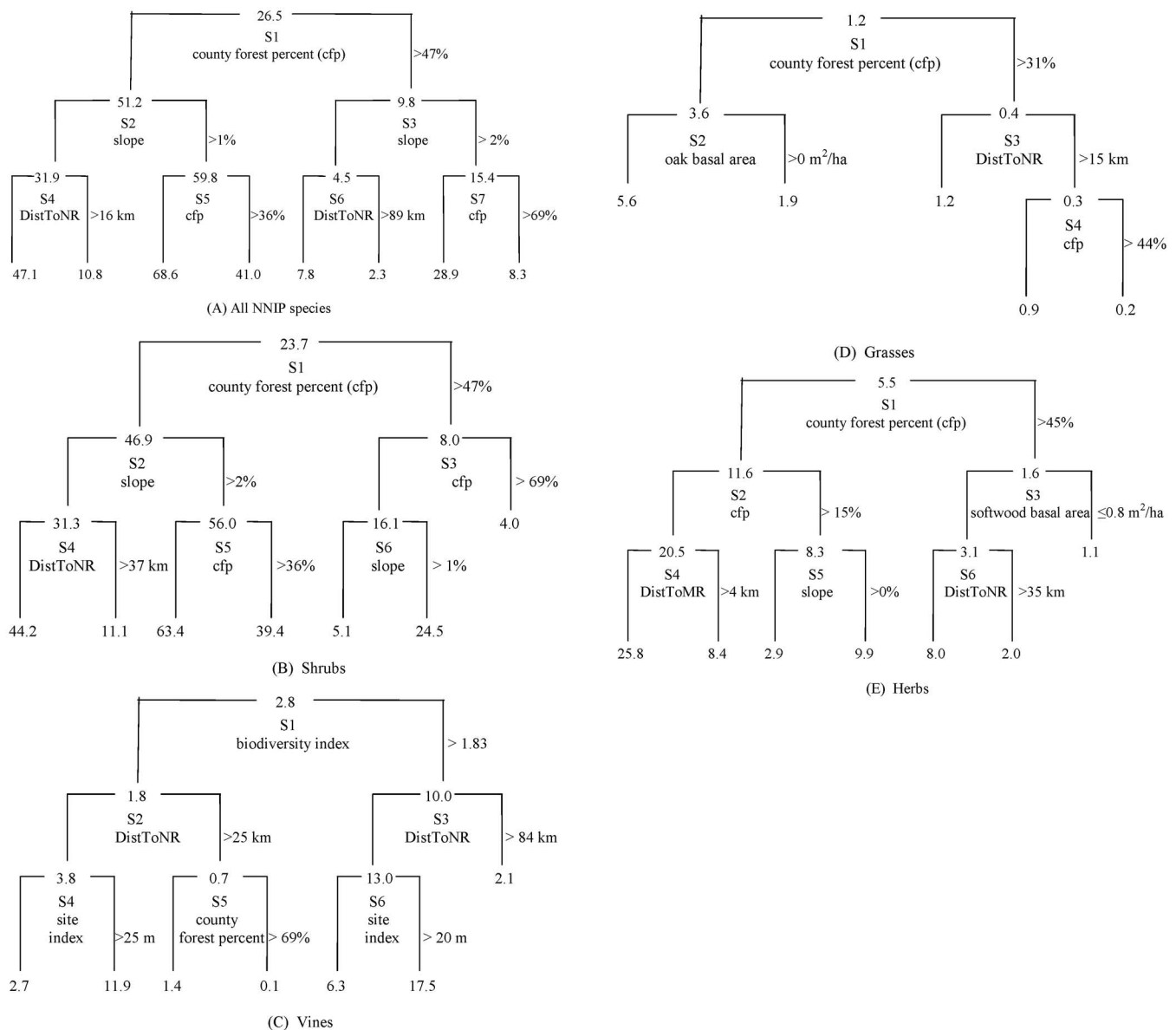


Figure 4. Regional NNIP species distribution by associated factors in the Midwest states: A.) all NNIP species; B.) shrubs; C.) vines; D.) grasses; E.) herbs. The number at each node represents the probability of NNIPs. CART splits are represented using S1 through S7 and associated variables. The cutoff value for each variable is given on the right of each split in the tree. DistToMR, the nearest distance from a FIA plot to major state freeway; DistToNR, the nearest distance from a FIA plot to the interstate freeway; biodiversity index, Shannon's biodiversity index; site index (m), base age of 50 years.

for IP spread compared with local or minor roads because they are involved in major movement or flow of materials including IPs (Mack 2004). A study in Utah found that the activities of expanding roads in interior forest areas (road construction, maintenance, and vehicle traffic) were correlated with increased cover and richness of nonnative species and decreased richness of native species (Gelbard and Belnap 2003). An inverse relationship commonly exists between distance to road and prevalence of exotic species (e.g., Watkins et al. 2003), although the influence is most pronounced close to the road. Forman and Alexander (1998) could not document many cases in which species spread more than 1 km from a road. For these reasons, this study assumed that distance to the nearest road is a surrogate of human activity, rather than a direct conduit for invasive exotics.

Percent forest coverage at the county level, distance to major highways, and slope are interrelated and combined provide a measure of the intensity of human disturbance and the multitudes of regional transport vectors and pathways for invasive plant dispersal. Therefore, they generally serve as strong indicators of regional occurrence (propagule pressure) of invasive plants, particularly shrubs, in the Midwest (Figure 4B and E). In sparsely forested areas (cfp < 45%), FIA plots with slope > 1% had higher probability of being infested by shrubs. As shown in Figure 4B, for instance, slope is the most important determinant of invasive shrubs in sparsely forested areas, with higher probability (56%) on sites with slope > 2% compared with the probability of 31.3% on flat sites with slope < 2%. The high occurrence of shrubs such as multiflora rose and nonnative bush honeysuckle in areas with high slope is related to past land use

Table 3. RR of associated split factors in the CART models and change of IP presence probability.

Split	Probability of IP (%)	No. plots	RR (95% CI)
All IP species			
S1	26.5	8,516	5.19 (4.64–5.82)
S2	51.2	3,438	1.87 (1.61–2.18)
S3	9.8	5,078	3.45 (2.78–4.29)
S4	31.9	1,062	4.36 (3.10–6.11)
S5	59.8	2,376	1.67 (1.40–1.99)
S6	4.5	2,579	3.39 (2.26–5.07)
S7	15.4	2,499	3.49 (2.78–4.39)
Shrubs			
S1	23.7	8,516	5.87 (5.20–6.63)
S2	46.9	3,438	1.79 (1.54–2.07)
S3	8.0	5,078	4.07 (3.28–5.05)
S4	31.3	1,273	3.97 (3.90–5.43)
S5	56.0	2,156	1.61 (1.33–1.94)
S6	16.1	1,686	4.84 (3.37–6.95)
Vines			
S1	2.8	8,516	5.67 (4.35–7.39)
S2	1.8	7,460	5.77 (3.86–8.61)
S4	3.8	2,622	3.94 (2.59–5.99)
S5	0.7	4,838	12.50 (3.80–41.08)
S6	13.0	771	2.76 (1.65–4.62)
Grasses			
S1	1.2	8,516	8.57 (5.50–13.34)
S2	3.6	2,085	3.00 (1.80–5.00)
S3	0.4	6,431	4.42 (1.95–9.12)
S4	0.3	5,530	4.98 (1.86–13.30)
Herbs			
S1	5.5	8,516	7.08 (5.57–8.99)
S2	11.6	3,328	2.46 (1.98–3.06)
S3	1.6	5,188	2.86 (1.86–4.40)
S4	20.5	898	3.07 (1.93–4.88)
S5	8.3	2,430	3.44 (2.05–5.79)
S6	3.1	1,367	4.01 (2.17–7.40)

RR, relative risk; CI, confidence interval.

history. Both species were originally introduced to the United States from Asia in the mid to late 1800s for ornamental purposes and were widely planted from the 1930s to 1960s in the eastern United States for erosion control, as wildlife food sources and cover, and as living fences (Czarapata 2005). Experimental plantings were conducted in Missouri and Illinois in the late 1960s. Dispersal of these species, the two most prevalent invasive shrubs in the Midwest, was accomplished through both human activities and wildlife (seed dispersal after consumption of fruits). These two IP shrubs have become serious invaders of forests, agricultural lands, and pastures throughout the Midwest.

The observed regional patterns of invasive shrubs were mainly related to disturbance (percent forest coverage at the county level and distance to roads) and site (slope) factors. However, stand factors such as site index and species richness (e.g., biodiversity index) were also shown to be important to other life forms, particularly vines (Figure 4). In the Midwest, invasive vines were mainly composed of Japanese honeysuckle, which was originally introduced to the United States from Asia in the 1800s as a horticultural ground cover and is currently distributed primarily in the southeastern and central-eastern states (Smith 1998). The probability map, for instance, indicates that the species is mainly distributed in southern Illinois, Indiana, and Mis-

souri in the Midwest. Japanese honeysuckle is tolerant of a wide variety of soil conditions and is especially aggressive in disturbed bottomlands and floodplains. The CART model indicates that the prevalence of Japanese honeysuckle is positively related to stand biodiversity and condition. It typically invades forest canopy openings by means of seeds dispersed by birds. Our result suggests that site quality is an important factor influencing the success of Japanese honeysuckle invasion compared with that of other life forms (Figure 4C). Gelbard and Belnap (2003) found that plant communities with high-resource availability (i.e., deep, silty, or otherwise fertile soils) were particularly susceptible to disturbance and invasion, noting that disturbance, when combined with superior site conditions, maximized the vulnerability of a plant community to invasive species. Richardson and Pyšek (2006) also postulated that resource availability was a facilitator of invasiveness at larger spatial scales. Much has been made of the role of diversity in defending against nonnative invasive species (Elton 1958). However, Huston and DeAngelis (1994) pointed out that species-rich communities occur in habitats with high heterogeneity in terms of climate, soil, and topography and that invasive species are more likely to gain a foothold on such sites than in less heterogeneous habitats.

Climate influences other site factors, in addition to acting as an independent causal factor in its own right. IPs often successfully establish in habitats with climates similar to those of their native ecosystems (Richardson and Pyšek 2006). However, many IPs have broad climatic tolerances and large geographic ranges (e.g., Rejmanek 1995, Goodwin et al. 1999, Qian and Ricklefs 2006). Climate may affect the invasion pathway and potential impacts on recipient ecosystems (Hellmann et al. 2008). The distribution pattern of Japanese honeysuckle in the Midwest states is, to some extent, related to climate conditions.

Given the nature of FIA data, our analyses were limited to exploring associations between observed patterns of IPs and a set of surrogates that reflect disturbances and resource availability as related to socioeconomic activities as well as ecological factors. On-site studies to test specific hypotheses or to reveal other factors and/or the cause-effect relationships for longer periods of time will be needed to help prevent and control the spread of invasive species in the region.

Conclusion

Regionally, the IPs that we studied have invaded vast areas of midwestern forests with the exception of those in the northern portions of Minnesota, Michigan, and Wisconsin. More than one-quarter of the FIA plots were observed to contain at least one of the IP species. Major IP threats come primarily from nonnative shrubs including multiflora rose, nonnative bush honeysuckle, and common buckthorn. Nearly one-quarter (23.7%) of FIA plots from the southern border to the central region of the northern states were infested by these shrubs. Only 5.5 and 1.2% of FIA plots were infested by nonnative herbaceous species and grasses, respectively, predominantly concentrated in the central

region. Nonnative vines occurred in only 2.8% of FIA plots and were mainly distributed in the south.

Among those plots containing IP shrubs, vines, and herbs, approximately 10% had severe infestations (cover >50%), whereas 28% of plots with IP grasses were severely infested. Spatially, most regions had less than 10% IP cover although the presence probability of IPs was more than 0.5 in the central area. Compared with shrubs and herbs, vines and grasses were locally abundant and clustered in numerous separate areas. Overall, the CART models indicate that IP presence is largely a function of human disturbance (e.g., deforestation, urbanization, and land use change), site factors, and stand characteristics. Further monitoring of invasive species should focus on the northern and southern portions of the region, particularly in forests in close proximity to major transportation corridors (e.g., roads/highways) or in those areas that have experienced significant land use changes such as housing construction and urbanization. In the central area of the region where IPs are already widely distributed, IP cover changes and associated contributing factors should be closely followed to monitor the rate of spread. Such monitoring information will support establishment priorities for IP control and management.

Another interpretation of these results might be that deforestation, urbanization, and land use change processes that have occurred in the region have greatly increased the invasion of IPs, either intentionally or by accident. That IP species, particularly shrubs, are less prevalent on flat sites is probably related to the fact that these species were intentionally planted on high-slope sites for controlling erosion or that these species were more readily eradicated on flatter sites. There could also be some micro-scale meteorological or climatic factors (e.g., lack of sunlight if under a canopy, a “pooling” of water after precipitation events, etc.) that prevent IPs from growing on flat sites. Subsequent research would be needed to confirm this.

Endnote

1. From MedCalc. ROC curve analysis in MedCalc. Available online at www.medcalc.be/manual/roc.php; last accessed Jan. 25, 2012.

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