Invasibility of three major non-native invasive shrubs and associated factors in Upper Midwest U.S. forest lands

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ABSTRACT

We used non-native invasive plant data from the US Forest Service's Forest Inventory and Analysis (FIA) program, spatial statistical methods, and the space (cover class)-for-time approach to quantify the invasion potential and success ("invasibility") of three major invasive shrubs (multiflora rose, non-native bush honeysuckles, and common buckthorn) in broadly classified forest-type groups in seven Upper Midwest states. Smoothed maps of presence and cover percent showed a strong clustering pattern for all three invasive shrubs despite their different ranges. The species are clustered around major cities or urban areas (e.g., Chicago, Illinois, and Des Moines, Iowa), indicating the potential role humans played in their invasion and spread on the landscape and throughout the Midwest. Conditional inference tree (ctree) models further quantified the significant factors contributing to the observed regional patterns: for distribution of multiflora rose, percentage of forest cover in the county (measuring human disturbance intensity) and stand density index; for distribution of common buckthorn, distance to major highways. Non-native bush honeysuckles were not associated with any disturbance and site/stand variables except for latitude and longitude. The infested FIA plots by cover class were positively associated in space, signifying a concentric-like spread trend from previously infested sites (hot spots) to surrounding areas. By forest-type groups or as a whole, the three species spread slowly at earlier stages, but recently have increased significantly in presence/ expansion. Oak/hickory and elm/ash/cottonwood forests were more susceptible to the three invasive shrubs compared to other forests. We recommend that resource managers and planners prescribe control and mitigation treatments for non-native invasive plants by forest types and spatial locations close to highways and residences.

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1. Introduction

Non-native invasive plants (NNIPs) have been a part of North American ecological history for as long as human settlement. When NNIPs are introduced, either deliberately or inadvertently, they can employ various competitive characteristics, such as prolific seed production and dispersal, earlier flowering or leaf out, or vegetative expansion, and overwhelm native forest ecosystems that developed over centuries without such competition. The introduction of a species does not necessarily mean it will become established, however. Phenology, seed dispersal, site quality, and other factors influence whether a NNIP can become established. Once established, however, NNIPs can compromise native forest structure, composition, function, and resource productivity (Webster et al., 2006; Boyce et al., 2012).

Previous research suggested that four factors influence invasion success: resource availability, disturbance, propagule pressure, and competitive release (Richardson and Pyšek, 2006). Whether a plant community or habitat is more easily invaded than others depends on how many potential invaders are present and whether the habitat is susceptible to invasion (Lonsdale, 1999; Richardson and Pyšek, 2006). Site productivity is one determinant of invasion success. Richardson and Pyšek (2006) found that resource availability facilitated invasiveness at larger spatial scales. Plant communities with high resource availability are particularly susceptible to invasion (Gelbard and Belnap, 2003). Elton (1958) suggested that high species diversity was important in resisting the establishment of non-native invasive species. He argued that a more diverse assemblage of species meant fewer unoccupied niches that would

provide an opportunity for invaders. Richardson and Pyšek (2006) reported studies that supported Elton's hypothesis, but also found others in which sites with a high species diversity harbor more alien species. They acknowledged Levine and D'Antonio's (1999) conclusion that species richness might be too coarse a factor to explain observed differences in community susceptibility to invasion, given that other factors (disturbance, nutrient availability, climate, and propagule pressure) are frequently covariates.

Disturbance reorders the available resources for plants, reducing it for some and increasing it for others, including invasive species. By upsetting the competitive balance and site occupancy of preceding plant communities, disturbances can make abiotic factors more important than biotic factors in determining the success of plant invasions (Richardson and Bond, 1991; Hood and Naiman, 2000). As the difference between gross resource supply and resource uptake becomes greater, a plant community becomes more vulnerable to invasion. Even temporary variations in resource availability, where they coincide with the arrival of invasive species, can result in successful invasions (Richardson and Pyšek, 2006).

NNIPs have characteristics that exploit the opportunities disturbances provide. Some invading species from the same genus as native species have a better chance of acclimatizing because they share preadaptations to conditions of this new region (Daehler, 2001). Additional research by Daehler (2003) concluded that invasive species have greater phenotypic plasticity than do native species inhabiting the same site, suggesting that common characteristics were less important than the unique ones. In other cases, invaders might benefit by being released from constraints present in their original habitat; others might evolve after their arrival in a new landscape or region (sensu Ellstrand and Schierenbeck, 2000). Unoccupied niches at the ends of the plant performance spectrum could provide opportunities for invasive plants to become established (Crawley et al., 1999). These niches might vary by site, size, or phenology (timing). Regardless, the interaction between invader and invaded is unique (Richardson and Pyšek, 2006) and depends on the context (Daehler, 2003).

Although it is sometimes possible to determine the date an invasive plant first arrived in the country, region, or even a particular site, the actual arrival date for most of the recent invasions is unknown. Estimating the initial arrival date is important, as the likelihood of establishment increases with the time since the original introduction. Where the initial introduction is unknown, scientists use the term "minimum residence time" (MRT). MRT integrates the time of potential establishment opportunity, the size of the supply of seeds or shoots, and (with expanding populations) the area from which the invasive materials originate (Richardson and Pyšek, 2006). Yet, MRT does not always correlate with the rate of spread. Plant invasions do not move continuously across the landscape; both local and long-distance transport can determine the spatial distribution (Pyšek and Hulme, 2005). Based on these analyses, one might conclude that exotic plant invasions spread more rapidly than natural migrations (sensu Richardson and Pyšek, 2006). Given the nature of inadvertent human transport, a significant factor in post-invasion spread rates (Hodkinson and Thompson, 1997), it would be difficult to predict the source and final destination of many invasive species.

Because one cannot always discern the exact starting point (in time and space) for an exotic plant invasion and quantify the finite amount of resources, managers need some indicator of success in managing invasive plant presence in order to best allocate their funds (Moser et al., 2008). One indicator of potential success of restoration efforts is the difference between the current state of an ecosystem and the desired state, perhaps based on historical evidence (Fulé et al., 1997; Moser et al., 2008). Those managers possessing sequential data points have many tools at their disposal to determine the severity and rate of spread of nonnative invasive species (Higgins et al., 1996). Often, however, decisions are made with limited information, perhaps after the initial sighting or after only one survey. Given such a one-time inventory, assumptions must be made about the residence history of the found invasive, which allows a manager to postulate (1) the likelihood of restoration success and the level of investment necessary to eradicate the infestation, and (2) the expected rate of spread and the potential for more damage to the ecosystem (Fan et al., 2013). Although most invasive plant species can be analyzed this way, woody shrub species are particularly suitable subjects for this type of analysis. The above-ground biomass is more obviously cumulative and, barring disturbances that result in top-kill (e.g., fire), is in proportion to total plant biomass.

The major objective of this study was to evaluate the invasibility (invasion potential) and current condition of three important invasive shrubs: multiflora rose (*Rosa multiflora* Thunb. ex Murr.), non-native bush honeysuckles (*Lonicera* spp.; not differentiated by species), and common buckthorn (*Rhamnus cathartica* L.) in Upper Midwest forest lands as a whole, and by major forest communities using spatial statistics and the space-for-time approach. Specifically, we sought to answer the following questions: (1) What is the spatial pattern of the three species in terms of presence probability and cover percentage? (2) Does their invasibility different among major forest communities? (3) What factors are associated with their current spatial patterns? These questions have not been answered at the individual species level and in a spatially explicit way in previous studies. Answering these questions will be critical for monitoring, management and decision making for the control and mitigation of these three common invasive shrubs in the Upper Midwest.

2. Data and methods

For the purposes of this paper, we define non-native invasive plants as those plants that (1) are not indigenous to the ecosystem ("non-native") and (2) have a competitive advantage that causes deleterious impacts on structure, composition, and growth in forested ecosystems ("invasive"). Considering the spatially nonstationary and temporally dynamic characteristics of the invasion and spread of an invasive species, we define invasibility as the susceptibility of a target region or forest community to the colonization and establishment of an invasive species and measure it in this study as the cumulative probability of plots in the US Forest Service's Northern Research Station, Forest Inventory and Analysis (FIA) program corresponding to a given threshold of cover (100 – cover) percentage of an invasive species. The cumulative probability (measuring colonization/occurrence) curve of cover (100 – cover) thresholds (measuring establishment) of an invasive species is a static measure of the invasibility of a region or forest community to an invasive species and the area under the curve can be used to compare the invasibility of different forest communities to an invasive species. During 2005–2006, the FIA program evaluated 8516 plots for presence and cover of any of 25 NNIPs (Olson and Cholewa, 2005; US Forest Service, 2005; Fan et al., 2013) across the 7 states in the Upper Midwest region of the United States. Of the 25 selected NNIPs, multiflora rose, non-native bush honeysuckles, and common buckthorn were the 3 most common invasive shrubs by presence. Multiflora rose had invaded 15.3% of the sampled plots, non-native bush honeysuckles had invaded 9.2%, and common buckthorn had invaded 4.8%; the degree of invasion was measured by percent cover (Fan et al., 2013).

All 8516 FIA plots were spatially referenced by latitude and longitude of the plot center and identified as to presence (1) or absence (0) of an invasive plant species (Moser et al., 2009). The

standard FIA plot consists of four 7.3-m (24.0-foot) radius subplots (each 1/60 ha), on which trees 12.7 cm (5.0 in.) and greater in diameter at breast height (dbh) are measured. If one or more of these species were was found on the site, the percent cover was estimated on each of the four nested subplots and the average was calculated and placed into one of seven ordinal categories (Table 1). The overall probability of presence of a NNIP species in the study area was calculated as the number of FIA plots with a NNIP species divided by the total number of FIA plots sampled, which measures the relative abundance of a NNIP species over the study area. In the same way, the probability of presence (risk) of a NNIP species in any subregion within the study area was computed as the proportion of the FIA plots with the presence value of one (1). Over a large, heterogeneous spatial domain like the seven Midwestern states, the invasion and spread of an invasive species are typically nonstationary. We employed the nonparametric kernel smoothing technique to map the regional invasibility patterns of multiflora rose, non-native bush honeysuckle, and common buckthorn in terms of probability of presence and percentage of cover across the seven states through a Gaussian kernel density function. Kernel smoothing (or kernel-based estimators) is a nonparametric "weighted moving average via the kernel" method to estimate the true density (probability) of a random variable (Wand and Jones, 1994). Given a random sample $X_1,\ldots, X_n$ with a continuous, univariate density f, the kernel density estimator at a location of x is:

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

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

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

with n = 2 for the two-dimension density smoothing. The selection of the bandwidth rather than the kernel density function is the key in density (probability) estimation (Hastie and Tibshirani, 1990; Schabenberger and Gotway, 2005). A cross-validation method was used to select a smoothing bandwidth for the kernel estimation of probability of presence and percentage of cover using the *bw.diggle* function in the R package of *spatstat* (Baddeley and Turner, 2005).

Due to the nature of the 2005–2006 NNIPs survey (i.e., one-time measurement), we employed the space-for-time approach to evaluate the invasion potential of an invasive species in different forest communities and its temporal change. We assumed a NNIP originally invaded the Upper Midwest states from a number of separated locations/regions and then spread to surrounding areas. Both historical records (Czarapata, 2005) and the smoothed probability of presence and percentage of cover maps as characterized by separated hot spots (areas with high probability of presence and percentage of cover) conform to this assumption. We used the cover class (Table 1) as a surrogate for invasion time and classified

Table 1
Cover class and ranges of percent cover of NNIPs used in recording invasive species in FIA plot data and category of infestation condition reclassified for this study.

Cover class	Range of percent cover	Mid-point (%)
I	76–100	87
II	51–75	63
III	26–50	38
IV	11–25	18
V	6–10	8
VI	1–5	3
VII	<1	0.5

Table 2
Number of FIA plots infested by multiflora rose (MR), non-native bush honeysuckles (NNBH), and common buckthorn (CB) and distribution of cover class of NNIPs by invasion phase for spatial-tempo analysis of invasion patterns using the space-for-time approach.

Invasion phase ("time")	NNIP cover (%) greater than	Number of FIA plots infested by			Cover class in Table 1 included
		MR	NNBH	CB	
A (earliest)	75	15	26	15	I
B	50	46	71	43	I + II
C	25	152	145	70	I + II + III
D	10	288	244	130	I + II + III + IV
E	5	495	385	186	I + II + III + IV + V
F	1	960	613	293	I + II + III + IV + V + VI
G (most recent)	0	1310	782	412	I + II + III + IV + V + VI + VII

the invasion phase (from the earliest to the most recent) into one of seven phases (Table 2) based on thresholds corresponding to the midpoints of the cover classes (Table 1).

To further validate the synchronological order between an invasion phase and all subsequent cover classes – that is A-II, A-III, A-IV, A-V, A-VI, A-VII; B-III, B-IV, B-V, B-VI, B-VII; C-IV, C-V, C-VI, C-VII; D-V, D-VI, D-VII; E-VI, E-VII; F-VII – the L-cross function from the *spatstat* package of R (Baddeley and Turner, 2005) was used. The cross-type L-function, a transformed cross-type K-function, was used to measure the spatial association of two event types (here, an invasion phase and a subsequent cover class). The decreasing order (e.g., A-II > A-III > A-IV > A-V > A-VI > V-VII) of the L-cross function curves (values) between an invasion phase and all subsequent cover classes (less than the threshold) demonstrated the synchronological order of the invasion phases and the appropriateness of the space (cover)-for-time approach (using cover class as a surrogate for invasion/residence time). Given this evidence that invasive species spread from FIA plots with high cover class to those with low cover class, we then computed the cumulative probability of presence by the threshold of invasion phases for different forest type-groups and the whole region. The cumulative probability of presence (measuring the abundance of NNIPs) was plotted against 100 minus the threshold of the invasion phase (measuring the "time" since a NNIP invaded a site or region) by NNIP and forest-type group to generate an invasion curve. These curves were used to evaluate a NNIP's invasibility in different forest-type groups. For instance, a forest-type group with its invasion curve on top of that of another forest-type group is more susceptible to being invaded. A permutation test was conducted to test the statistical significance of the cumulative probabilities (invasion curves) among different forest-type groups.

Finally, the conditional inference tree (ctree) model from the R package *party* (Hothorn et al., 2015) was employed to evaluate the effect of geographical, stand/site, and disturbance factors on the spatial distribution patterns of cover classes. These variables are the latitude, longitude, and forest community/cover types of each infested FIA plot, tree density, mean tree diameter and height, stand or tree species/group basal area, site index, slope, aspect and species diversity computed or measured based on site/plot level data to reflect stand or site conditions, and minimum distances from FIA plots to the nearest road in each of five road classes (Interstate highway, state highway, major highway, minor highway, and local streets), and forest fragmentation (percent forest cover) at both the county level and plot level as surrogates of human disturbances. These variables and their calculation are described in Moser et al. (2009) and Fan et al. (2013). All statistical analyses and simulations including graphical analyses were conducted under the R statistical environment (R Development Core Team, 2014).
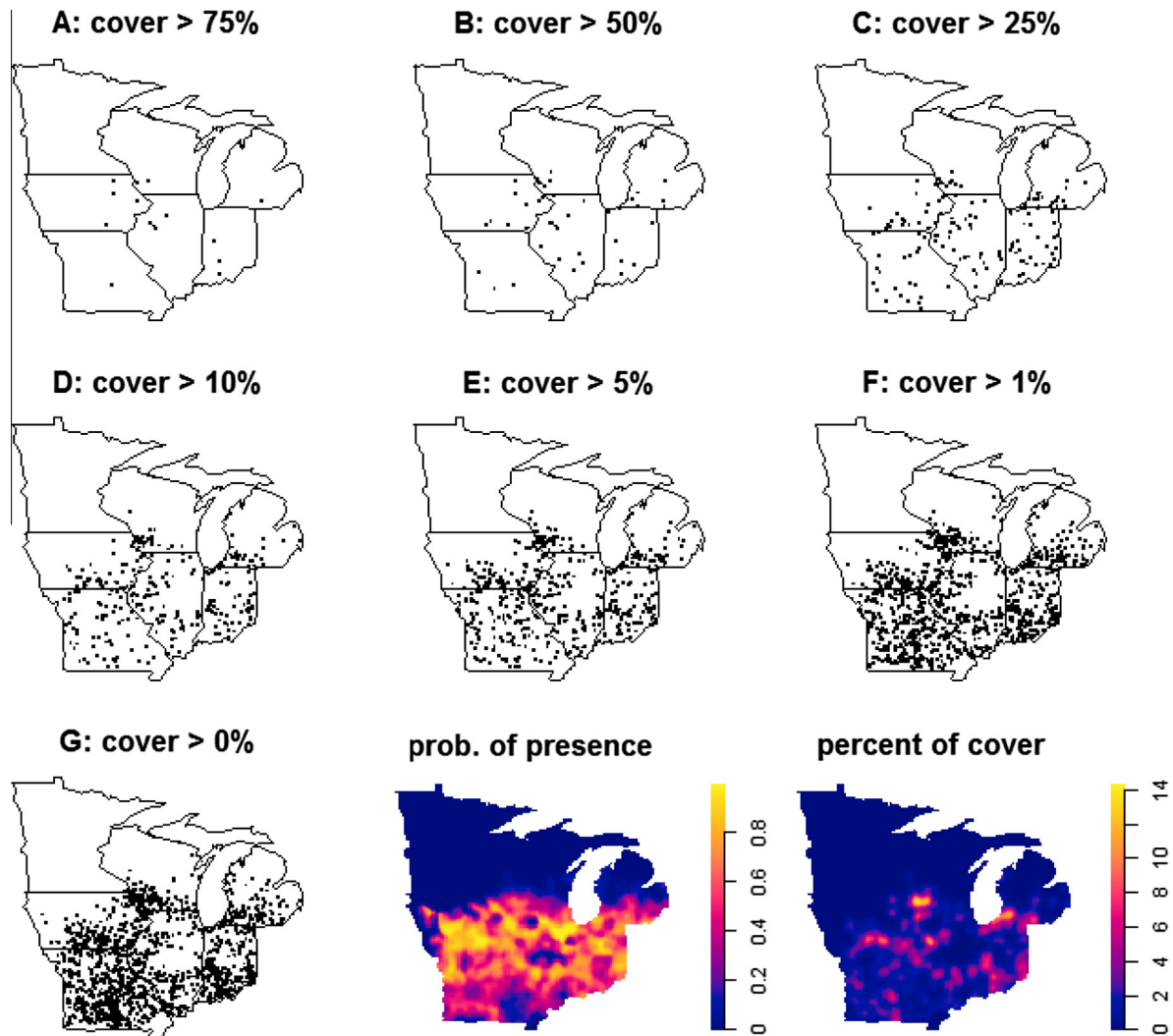
Fig. 1. Spatial distribution of FIA plots infested by multiflora rose by invasion phase A through G (varying thresholds of cover class) and the smoothed probability and cover rate of infested FIA plots during 2005–2006, the inventory period.

3. Results

The smoothed maps of both presence probability and cover percentage indicated different regional patterns among the three invasive shrubs. Multiflora rose was distributed largely in the central and southern states in the region (Iowa, Missouri, Illinois, and Indiana), whereas common buckthorn was found mainly in the northern states (Minnesota, Wisconsin, and Michigan). Non-native bush honeysuckles were widespread in most states (Figs. 1–3). There was great spatial variation in presence probability and cover percentage. Hot spots of greater probability and cover surrounded major cities and urban areas such as Chicago, Illinois, and Des Moines, Iowa.

Positive spatial correlation (clustering) occurs among all infested FIA plots (Figs. 1–3), but the strength of spatial correlation as measured by the L-cross function decreases with the difference between an invasion phase (Table 2, Figs. 1–3) and a selected subsequent cover class (Table 1) (Fig. 4). The observed changes (decreasing trend) in spatial correlation indicated that it is appropriate to use the space (cover class)-for-time approach to compare the invasibility of the invasive shrubs among different forest communities from the regional scale. Fig. 5 shows the change in cumulative probability of infested FIA plots versus 100 – percent cover the invasion phase ("time", from G to A) of the three shrubs in

the entire region and by forest community. Overall, oak/hickory,[1] elm/ash/cottonwood, and maple/beech/birch forest-type groups were more severely invaded by the invasive shrubs than were white/red/jack pine, spruce/fir, and aspen/birch forest-type groups. A post hoc multiple comparisons test based on the permutation test further showed that the oak/hickory forest-type group is significantly more severely infested by multiflora rose compared to other forest communities, and the oak/hickory and elm/ash/cottonwood forest-type groups are more susceptible to invasion by non-native bush honeysuckles and common buckthorn than are other forest-type groups. Oak/hickory and elm/ash/cottonwood forests are the two Upper Midwest forest communities that are most susceptible to the three invasive shrubs.

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[1] The forest type groups are based on FIA classifications U.S. Forest Service (2015). Particular numerical algorithms are used to assign a stand to a forest type, which represent the most prominent of the species in each category, but by no means all of the species that could be present. Forest types are then grouped into forest type groups, the broad level of classification used here. The following scientific names for genus and occasionally species can be used to as approximations of the species composition: Oak/hickory – Quercus spp./Carya spp.; elm/ash/cottonwood – Ulmus spp./Fraxinus spp./Populus deltoides; maple/beech/birch – Acer spp./Fagus Grandifolia/Betula spp.; white/red/jack pine – Pinus strobus/P. resinosa/P. banksiana; spruce/fir – Picea spp./Abies spp.; aspen/birch – Populus spp./Betula spp.
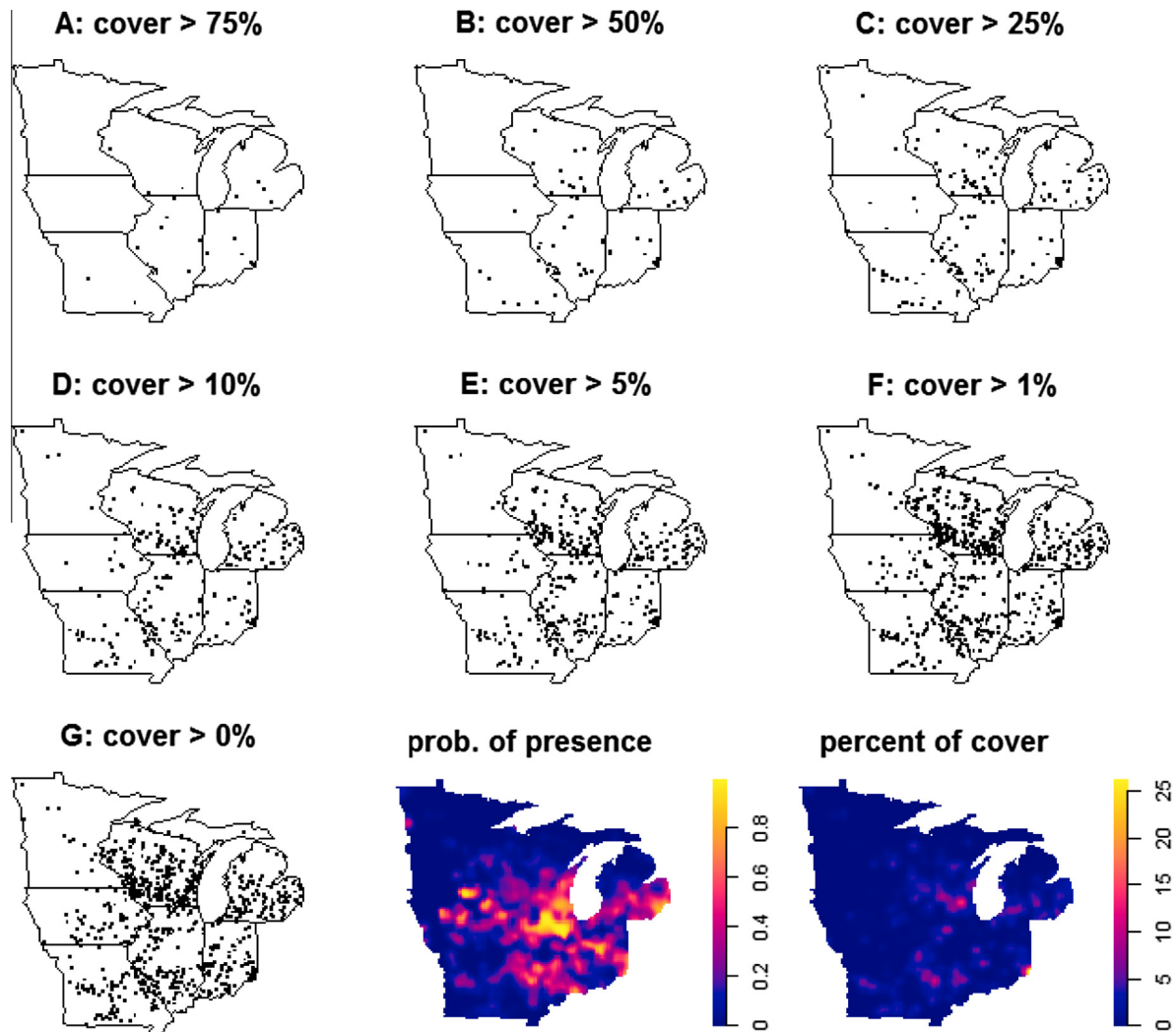
Fig. 2. Spatial distribution of FIA plots infested by non-native bush honeysuckles by invasion phase A through G (varying thresholds of cover class) and the smoothed probability and cover rate of infested FIA plots during 2005–2006, the inventory period.

The conditional inference tree (ctree) models showed that the spatial distribution of infested FIA plots by multiflora rose is primarily determined by county forest percentage (cpcf) and stand density index (sdi5) (Fig. 6A). Nearly 70% (920 out of 1320) of infested FIA plots (Node 2) were in counties with forest cover ⩽39%. Within counties with forest cover >39%, stand density index (sdi5) appears to be a driving factor with 92% (368 out of 400) of infested plots falling in stands with sdi5 ⩽198.42 (Node 5). Further examinations of the number of infested FIA plots and the cover class distribution within each terminal node found that there were relatively more infested FIA plots, including those with higher proportions of moderate and high cover classes (26–50%, 51–75%, 76–100%) in counties with low forest covers, suggesting that multiflora rose invaded these areas in earlier times.

No geographical or stand/site variable except for latitude and longitude was found to be related to the spatial distribution of non-native bush honeysuckles (Fig. 6B). The node size (the number of infested plots) and cover class distribution within each node indicate that bush honeysuckles (88%, or 691 out of 788 plots) are concentrated in the southwestern portion of the study area with latitude ⩽44.8° and longitude ⩽−83.2°. The distribution of common buckthorn is significantly associated with distance to major highways (mdist2) (Fig. 6C). Plots with greater percent cover

were mostly found in areas near major highways (Node 2), and percent cover of common buckthorn in the infested FIA plots decreased between areas near highways and those farther away (Nodes 4 and 5).

4. Discussion

This study examined patterns of distribution of three major nonnative invasive plant species in the Upper Midwest of the United States and their relationships with selected forest and site characteristics. We found that plots with a higher probability of NNIP presence and greater percent cover were located near major cities, such as Chicago, Illinois and Des Moines, Iowa; such urban areas are characterized by frequent, large-scale human disturbances (e.g., commercial and residential development, road building, and other land cover conversion activities that simultaneously disrupt the previous ecological equilibrium and introduce new, exotic species), one of the most significant factors for predicting invasive species' spread across a landscape or region. In some portions of the region, plots had even higher rates of NNIP presence. Indiana, Illinois, and Iowa were the states with the highest overall proportion of plots with invasive species; Minnesota had the fewest. Our data revealed a strong latitudinal pattern, especially
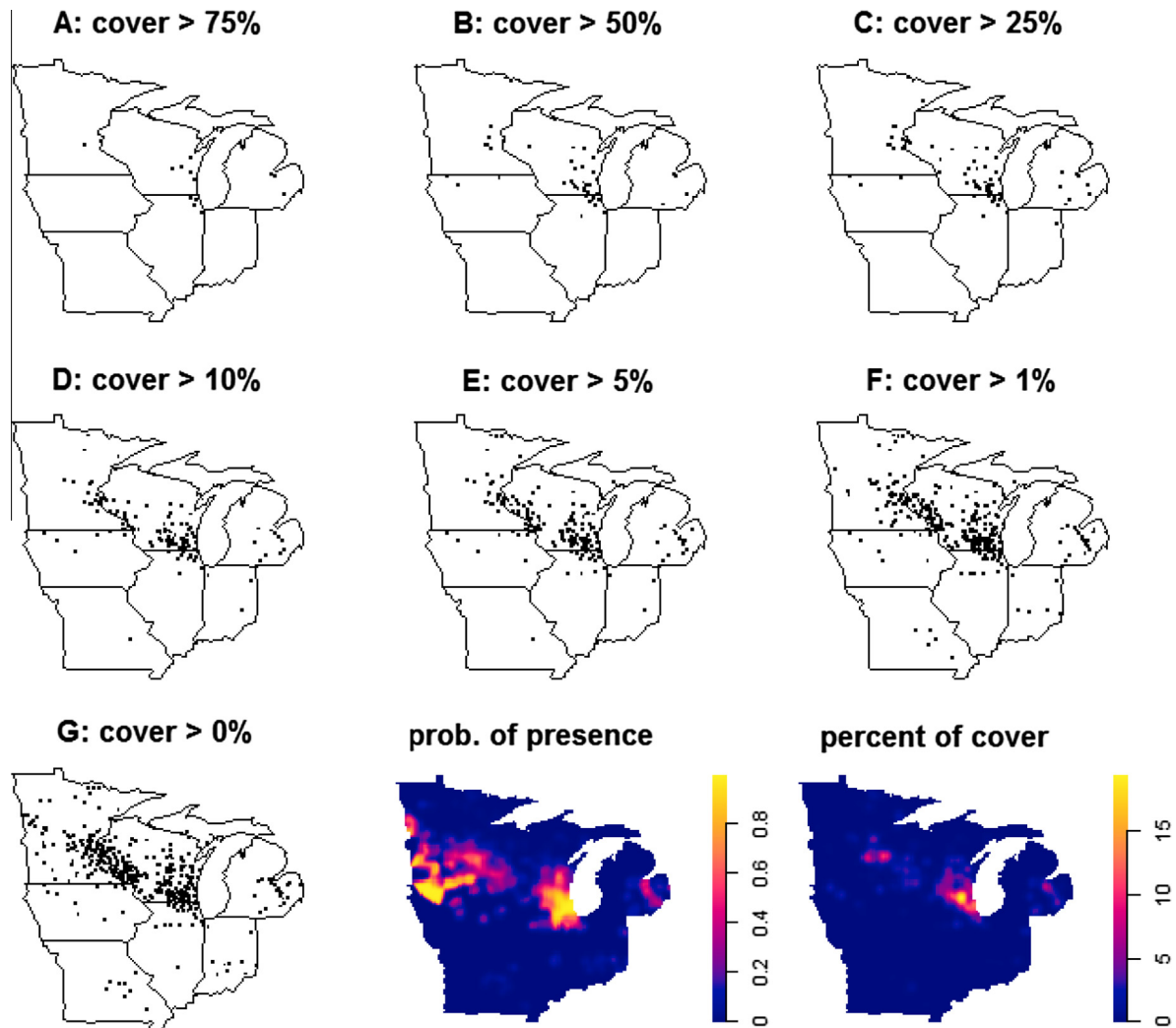
Fig. 3. Spatial distribution of FIA plots infested by common buckthorn by invasion phase A through G (varying thresholds of cover class) and the smoothed probability and cover rate of infested FIA plots during 2005–2006, the inventory period.

for woody invasive species (Moser et al., 2009). Common buckthorn was conspicuous in Wisconsin and Minnesota, whereas multiflora rose was more prominent in Missouri, Illinois, and Indiana (Figs. 1–3).

Sub-boreal forest types had lower percentages of NNIP presence. Accordingly, we observed lower occurrences in Minnesota, Wisconsin, and Michigan compared to the states in the southern portion of the region. Early successional forest types, which are more often influenced by natural disturbances in the center of the region, appear to have a higher percentage of plots with NNIP. But it was difficult to separate any relationship from the sampling effect, as these early successional forest types were often the most predominant on the landscape (Figs. 1–3).

Grasses were particularly prominent in the fragmented forest landscapes in the center of the study area. Agricultural or urban sites appeared to be the biomes most susceptible to invasive species encroachment, supporting Richardson and Pyšek's (2006) hypothesis. The fact that we had no earlier data meant that we were examining only those that were successful in establishing themselves on forested plots, not those species that failed to become established in the region. Thus our examination of particular plant relationships to a specific site or disturbance pattern was probably skewed (Moser et al., 2009). Although we could not conclusively tie the presence of NNIPs to particular forest-type groups,

disturbance most likely played a role in the life history strategy of both overstory tree species and understory invasive plants. The principal forest types in the southern portion of the region – oaks – are mid-shade tolerants and generally depend upon some form of disturbance to maintain their position in most their range (Johnson et al., 2011).

The invasibility of forests in the Upper Midwest will increase in the future as habitat becomes increasingly fragmented as shown by the skyrocketing increase in the slope of the cumulative probability curves (Fig. 5). The average forest size in the region is already small, owing to private forest ownership (Shifley et al., 2014). Projected increases in population levels are expected to further increase fragmentation. Other factors could also act to decrease forest coverage. Oak decline, invasive insects, and climate change are all factors that may contribute to the spread of multiflora rose, common buckthorn, honeysuckles, and other NNIPs (Moser et al., 2006; Shifley and Moser, 2016). Oak/hickory forests are the most heavily affected forest-type group in the region and if trees (or forests) are lost through sudden oak death or defoliating insects, invasive plants are likely to fill the gaps left behind. Additionally, as temperatures increase, oak/hickory forests may encroach on, and displace, aspen forests, allowing invasive plants to move farther northward.
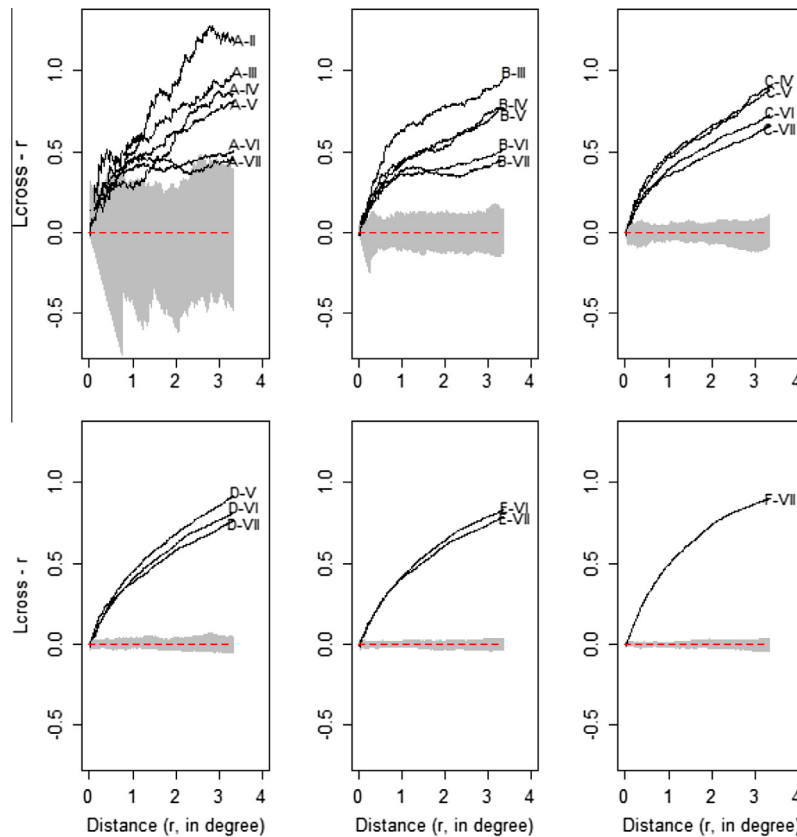
Fig. 4. Spatial association as indicated by the L-cross function between FIA plots infested by multiflora rose in an invasion phase (A through F in Table 2 and Fig. 1) with subsequent cover classes (II through VII in Table 1). The decreasing, synchrological order of the L-cross function between infested FIA plots in an invasion phase (higher cover classes) with its subsequent (lower) cover classes indicates that FIA plots with higher cover class were generally infested earlier than those with lower cover classes.

We were not able to evaluate the interval between the start of an invasion and the typical phase of exponential increase. Our inability to determine the contribution of site and stand factors to invasibility is probably due to the NNIP patterns that we observe today are largely due to summary effects of introductions and prevailing conditions and processes from 50 to 100 years or more ago. Given the limitations of our data (one-time measurement), we tried to integrate spatial statistics and the space (cover)-for-time approach to examine and compare the difference in invasibility among forest-type groups without considering site and stand factors. Strong spatial correlation/association between infested FIA plots and the decreasing synchronological order as shown by the L-cross curves (Fig. 4) between an invasion phase (higher cover classes) and subsequent (lower) cover classes are the key assumptions when using the space (cover)-for-time approach. This approach uses cover class to represent invasion or residence time to calculate regional or forest type level invasibility. This conclusion suggests an ecological momentum, where the quantity of established invasive species will increase going forward even when no additional introductions occur (Kowarik, 1995; Richardson and Pyšek, 2006; Moser et al., 2009).

Disturbance is the principal influence in invasive species establishment and growth. All variables with a significant influence on the presence of NNIPs are derivatives of human habitation and transport: the percentage of total county area in forest (negative) (Fig. 6A) and distance to highways (positive) (Fig. 6C). Even the forest-type groups with the highest NNIP presence are those closest to human population centers: oak/hickory, elm/ash/cottonwood, and maple/beech/birch. Although

latitude and longitude were the geographic variables found to influence NNIP presence (Fig. 6B), we found almost no evidence of an ecological influence. The only exception was multiflora rose's susceptibility to embolism at temperatures less than −20 °F (−29 °C). This result suggests that the apparent latitude/longitude influence could be an artifact of the narrow distribution of the seven-state study area. Perhaps examining a wider range of states, running from, for example, the Great Plains to the Atlantic Ocean and from the Gulf of Mexico to Canada, might provide evidence of latitude/longitude (i.e., climatic) influence.

The findings of the present study expand on those of Fan et al. (2013), who found that areas in the Upper Midwest near roads and with low forest cover percentage had greater presence of invasive shrubs as a group. Multiflora rose was widely planted in the Upper Midwest as highway dividers and living fences, and has since spread throughout the region. We found that where multiflora rose occurred in forested areas, it was in less dense stands (Fig. 6A), which allow for greater light availability and increased area for invasive spread. Honeysuckle species were also most prevalent in the southern portion of the region (Fig. 2), where more-open conditions are available and little competition for sunlight and precipitation is found. Common buckthorn outgrows most competing species in open conditions, probably owing to its early leaf emergence and later senescence compared to other species (Knight et al., 2007).

Open and fragmented landscapes tend to present conditions suitable for the establishment and proliferation of NNIPs (Fan et al., 2013), but not all open landscapes are the result of human activity. Some open areas in the Upper Midwest are part of the
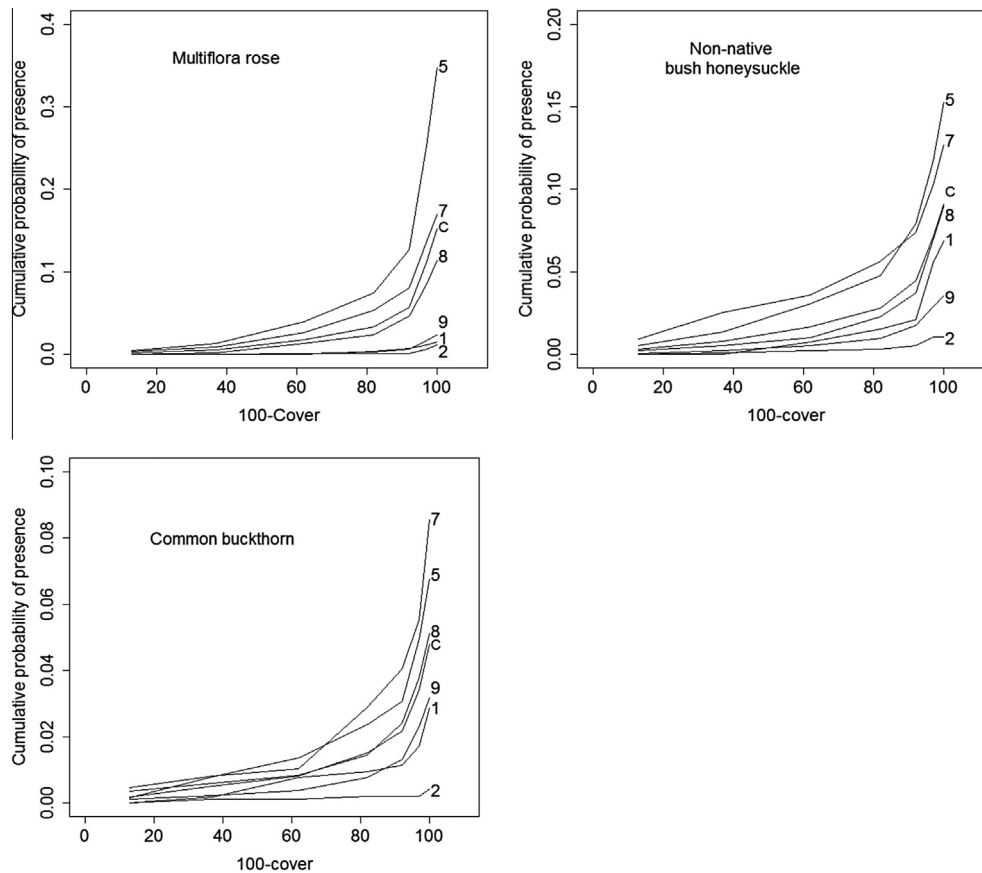
Fig. 5. Cumulative probability of infested FIA plots versus 100 – percent cover of an invasive species in a plot, measuring the invasibility of different forest communities to an invasive species in the Upper Midwest states. 1 – white/red/jack pine; 2 – spruce/fir; 5 – oak/hickory; 7 – elm/ash/cottonwood; 8 – maple/beech/birch; 9 – aspen/birch; C – the seven-state region.

prairie ecoregion. NNIP species may be able to exploit competitive advantages in open conditions to gain a foothold in the region. Schulz and Moser (2012) found that the prairie ecological division exhibited the second greatest mean coverage of invasive plants in the northern United States. The prairie region is composed of open grasslands and is a major flyway for migratory birds; birds are commonly linked to the spread of NNIPs (Moser et al., 2009).

Metrics of disturbance and fragmentation, such as the percent of total county land area in forest cover, the distance to the nearest road, or the forest intactness index, were significantly related to NNIP presence and coverage (Moser et al., 2009). There was no significant connection between the presence of NNIPs and FIA treatment or disturbance codes and other measures such as the ratio of tree removals to current volume. Disturbances that led to an invasive plant's presence probably occurred several decades ago (sensu Hulme, 2003; Richardson and Pyšek, 2006). Patterns of fragmentation and landscape-level forest proportions may better capture the cumulative effect of past disturbances than more site-specific variables (Moser et al., 2009).

Although some of our results may be extrapolated to other species or regions, a posteriori analysis of invasive species at one point in time is usually not sufficient to evaluate trends in regeneration, expansion, or growth (Rejmánek, 1989). The FIA database tracks disturbance and management activities, but only since the last inventory. Subsequent inventories will be necessary to verify any trends that may be related to anthropogenic activity or other disturbances.

Given the history of biotic and anthropogenic disturbances and forest types whose shade tolerance results in less than full occupancy of understory growing space, we expected to find multiple relationships between NNIPs and forest and site characteristics. Considering disturbance, we noted that multiflora rose significantly benefitted from lower overstory basal areas, but this relationship did not apply to other species. Another disturbance metric, distance to the nearest road, showed a significant negative relationship with the presence of non-native bush honeysuckles and reed canary grass (Moser et al., 2009).

The percentage of total land area in a county that is forest provided a good indicator of historical disturbance. This measure displayed a significant negative relationship with NNIP abundance. These results are hardly surprising; invasive species are known to flourish on sites with more available resources (Richardson and Pyšek, 2006). The challenge is to separate human from ecological influences. Our results may well reflect the heavily-disturbed nature of the Midwest's second- and third-generation forests, which either re-established following the abandonment of agricultural land or were influenced by adjacent property that was heavily disturbed (Moser et al., 2009). The characteristics of the landscape that affected NNIP presence may also be related to settlers' choice of homestead. Our measures of disturbance (lower basal area and high road density and the resulting fragmentation) could reflect as much the enduring influence of historical human disturbance the facilitated the establishment as the microsite attributes that allowed them to thrive.
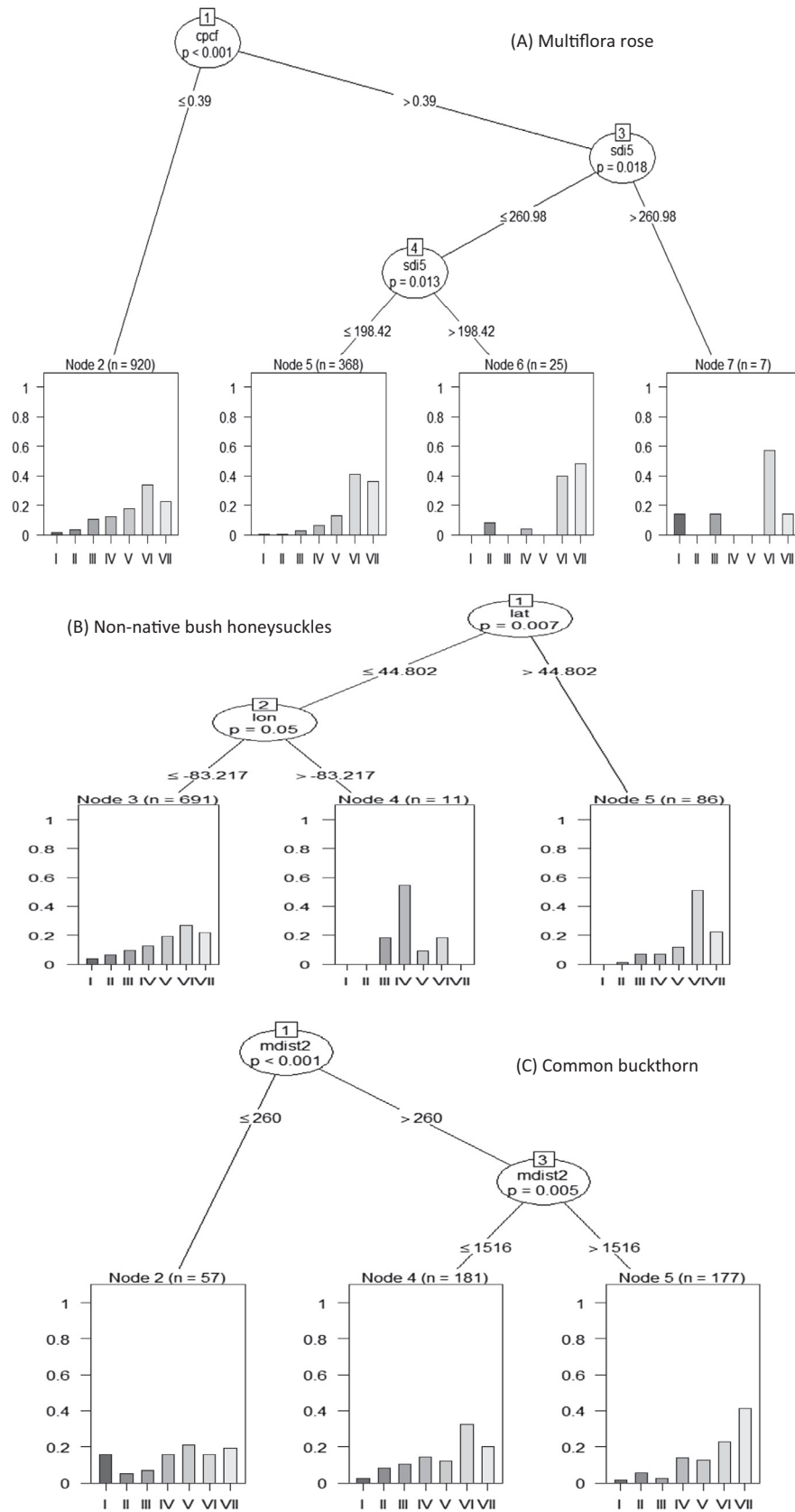
Fig. 6. Factors associated with the distribution of cover class of (A) multiflora rose, (B) non-native bush honeysuckles, and (C) common buckthorn on FIA plots surveyed in the Upper Midwest states during 2005–2006. The bar from left to right in a terminal node represents the probability of FIA plots with an invasive species in cover class I (76–100%), II (51–75%), III (26–50%), IV (11–25%), V (6–10%), VI (1–5%) and VII (<1%), respectively.

5. Conclusions

Several ecoregions come together in the Upper Midwest of the United States, including woodland ecosystems in southern Wisconsin, savannas and prairies in Illinois, Indiana, and Iowa, and forests in the north (Michigan, Wisconsin, and Minnesota) and south (Missouri) (Moser et al., 2009). The combination of land clearing, wildfires, and timber harvesting in this region have created a fragmented landscape that presents many opportunities for the establishment of non-native invasive plants. According to the 2005–2006 FIA data from the US Forest Service's Northern Research Station (NRS) Forest Inventory and Analysis (FIA) program, at least 25 NNIPs have been found to varying degrees in the Midwestern forest lands. Multiflora rose, non-native bush honeysuckles, and common buckthorn are three primary invasive shrubs that may have caused adverse effects on native forest ecosystems. A number of hot spots located near metropolises and other urban areas have been identified based on the smoothed cover maps, while the smoothed maps of probability of presence reveal their current spatial range. The cover and presence maps provide baseline information for regional-scale planning and management to control and mitigate the spread of these three shrubs in the future.

Oak/hickory and elm/ash/cottonwood forests are among the most susceptible habitats to the three invasive shrubs based on the species' prevalence and rate of spread. These forests have also been heavily affected by both natural and human disturbances over the last century. The relationship between probability of presence and cover (Fig. 5) and the distribution of infested FIA plots by cover class (Figs. 1–3) indicates a significant recent trend of the expansion of the three invasive shrubs in space and by forest community. The *ctree* model revealed that county-level forest percent and distance to road (measures of human disturbances or geographical region) are closely associated with their expansion at a regional scale. Even though rapid changes in land use and land cover largely contribute to this expansion as large-scale factors associated with their spread, the mechanisms of spread at local scales (e.g., county, landscape, or stand) should be further evaluated for adaptive resource management. Due to the heterogeneous nature of the distribution of invasive species, local models will be helpful. More data at the stand and landscape level will need to be collected for future studies to investigate NNIP spread pathways and mechanisms and to quantify the rate of spread under alternative management regimes and natural disturbances. This study may help to shed light for future local studies, such as the identification of forest community and site location and their relationships with invasive species presence, variables collected or measured, and interaction of site-specific data with FIA data.

Once NNIP species are established, they are difficult to eradicate. They are resistant to natural pathogens and have few biological controls (Knight et al., 2007). Direct control remains the only option. Prescribed fire is commonly used to control many invasive species, but it is unlikely to be effective against multiflora rose, honeysuckles, and common buckthorn. These three shrubs are able to evade fire through seed banking and increase post-fire (Huebner, 2006), potentially due to decreased competition from less fire-tolerant species. Honeysuckles, particularly, can act as fire ladders and cause crown fires. These issues are important considering the low motivation for active management of Northern U.S. forests, a situation that must be addressed in order to coordinate a regional effort to control NNIPs in the future (Shifley et al., 2014).

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