

Rural housing is related to plant invasions in forests of southern Wisconsin, USA

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Abstract Forests throughout the US are invaded by non-native invasive plants. Rural housing may contribute to non-native plant invasions by introducing plants via landscaping, and by creating habitat conditions favorable for invaders. The objective of this paper was to test the hypothesis that rural housing is a significant factor explaining the distribution of invasive non-native plants in temperate

forests of the Midwestern US. In the Baraboo Hills, Wisconsin, we sampled 105 plots in forest interiors. We recorded richness and abundance of the most common invasive non-native plants and measured rural housing, human-caused landscape fragmentation (e.g. roads and forest edges), forest structure and topography. We used regression analysis to identify the variables more related to the distribution of non-native invasive plants (best subset and hierarchical partitioning analyses for richness and abundance and logistic regression for presence/absence of individual species). Housing variables had the strongest association with richness of non-native invasive plants along with distance to forest edge and elevation, while the number of houses in a 1 km buffer around each plot was the variable most strongly associated with abundance of non-native invasive plants. *Rhamnus cathartica* and *Lonicera* spp. were most strongly associated with rural housing and fragmentation. *Berberis thumbergii* and *Rosa multiflora* were associated with gentle slopes and low elevation, while *Alliaria petiolata* was associated with higher cover of native vegetation and stands with no recent logging history. Housing development inside or adjacent to forests of high conservation value and the use of non-native invasive plants for landscaping should be discouraged.

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Introduction

Non-native plant invasion is considered one of the most detrimental aspects of global change (Vitousek et al. 1996; Theoharides and Dukes 2007), with large negative ecological (Elton 1958; Richardson et al. 2000) and economic consequences (Pimentel et al. 2005). Approximately 5,000 species of exotic plants have established free-living populations in the US and over 1,000 are a threat to the native flora and fauna (Morse et al. 1995; National Parks Service 2005).

The ecological impact of non-native plant invasions is particularly high in the forests of the Eastern and Midwestern US where the most widespread and abundant invasive non-native plants originate from Eurasia and were imported mainly for food and landscaping. In the Midwest, the main invasive species include shrubs like honeysuckle (*Lonicera* spp.), trees such as Norway maple (*Acer platanoides*), and herbs such as garlic mustard (*Alliaria petiolata*) (Cox 1999; Webster et al. 2006) that outcompete and eliminate native vegetation, potentially changing forest succession patterns (Wolfe and Klironomos 2005; Stinson et al. 2007).

Many factors determine invasion patterns, but most biological invasions are facilitated by human activities (Williamson and Fitter 1996; Lonsdale 1999). Human mediated landscape change facilitates invasions by many non-native plant species, because landscape configuration can determine the rates of non-native plant dispersion, and result in a landscape more easily invaded (With 2002). For example, many—but not all—non-native invasive plant species are more common in forest borders and in small forest patches resulting from forest fragmentation (Theoharides and Dukes 2007). Roads facilitate non-native plant invasions by providing open habitats and propagule dispersal corridors (Trombulak and Frissell 2000). In Seoul (South Korea) exotic plants are concentrated in forest edges near roads and human settlements, and within forest patches of small size and complex shape (Song et al. 2005).

It is thus not surprising that non-native invasive plants are associated with housing at the landscape scale in different parts of the world. For example, in the outskirts of a city located in Patagonia (Argentina), the number of non-native plants increase close to the houses at a small scale, and at a landscape scale increase with the number of houses (Rapoport

1993). In Spain, abandoned fields are more rapidly invaded by cacti close to houses because they are used as a landscaping plant (Vila et al. 2003). In New Zealand, the number of non-native plants invading coastal forest patches decreases with the distance to residential areas (Sullivan et al. 2005).

In the US, Honeysuckle (*Lonicera maackii*) presence in woodlots is highest close to towns in Ohio (USA) (Bartuszevige et al. 2006), and multiflora rose (*Rosa multiflora*) and Japanese barberry (*Berberis thunbergii*) are more common in more developed areas (>6 houses/km²) of southern New England (Lundgren et al. 2004). In the state of Colorado (USA) invasive non-native plants are more abundant in areas with ranchettes (small ranches 16 ha in average size) than in non-developed areas, or on large ranches (Lenth et al. 2006).

The relationship between housing and non-native plants has been linked to two processes. First, humans import and grow large numbers of non-native plants for landscaping purposes (Kowarik 1990; Mack and Erneberg 2002) and propagules from non-native plants in yards and parks invade adjacent sites (Sullivan et al. 2005; Wania et al. 2006). Second, disturbances resulting from housing development (e.g. creation of edges, soil exposure, trampling of native vegetation, trails, etc.) create different microhabitats easily colonized by invasive plants (Hobbs and Huenneke 1992; Wania et al. 2006).

The relationship between housing development and non-native invasive plants is a concern because housing growth is a global process occurring at a rapid pace (Antrop 2004). In the US, between 1950 and 2000, the total proportion of urban land area increased from 1 to 2%, but the extent of low density housing in rural areas increased from 5 to 25% of the total conterminous US (Brown et al. 2005). Forested areas have been particularly affected (Radeloff et al. 2005) and housing growth near protected areas and on inholdings in National Forests has outpaced the national average (Radeloff et al. 2010).

Rural housing growth results when people from cities emigrate to rural areas, wanting to live closer to natural amenities, particularly forested areas (Kaplan and Austin 2004). Rural housing growth has been strong in the north-central US since 1940, particularly in areas close to natural amenities such as forests and lakes of high conservation value, resulting in habitat loss and fragmentation (Hansen et al. 2005;

Hawbaker et al. 2005, 2006; Gonzalez-Abraham et al. 2007; Lepczyk et al. 2007).

We hypothesize that rural housing facilitates non-native plant invasion at the landscape scale, because houses are sources of propagules for plants used in landscaping, and because disturbances around homes facilitate invasive plant colonization. The rapid spread rates of both non-native plant invasion and rural housing development makes testing this hypothesis a priority, and understanding the relationship between exotic invasive plants and rural housing development will improve our ability to predict the ecological consequences of these processes for natural areas.

The objective of this paper was to assess the importance of rural housing as a factor in non-native plant distributions in forest interiors of the Baraboo Hills, Wisconsin (USA). Specifically, we evaluated the spatial pattern of richness and abundance of invasive non-native plants versus the spatial patterns of houses, topography, forest structure, and human-related forest fragmentation variables. We then compared the association among the most important non-native invasive plants and rural housing, to assess the influence of history of introduction (i.e. landscaping) and life history traits in their relationship with housing.

Methods

Study area

Our study area was located in the Baraboo Hills in southern Wisconsin (89°43'52"W, 43°24'56.6"N) and covers about 22 × 13.4 km (Fig. 1). The maximum elevation is 423 m above sea level. The eastern half of the study area was glaciated and has a more gentle topography (Dott and Attig 2004). The Baraboo Hills contain the largest tract of continuous forest in southern Wisconsin with 889 native vascular plants (70 of which are considered endangered or rare). Most of the area is covered by mixed forest dominated by red and white oaks (*Quercus alba* and *Q. rubra*), accompanied by red and sugar maple (*A. saccharum* and *A. rubrum*) (Lange 1998). Property ownership is mostly in small private parcels in the east side, while the western part includes several large tracts in public ownership and protected areas.

European settlement changed the vegetation through logging and agriculture that peaked in the 1930s, and now most of the area is covered by secondary forests. No major logging has occurred in the last 30 years in protected areas, but some private landowners still actively manage their forests with small clear-cuts. Fire has not been a large disturbance for more than a century, but wind throw events create small forest openings (Mossman and Lange 1982). Invasive plants are becoming a conservation concern particularly in protected areas. The most widespread invaders include garlic mustard (*A. petiolata*), common buckthorn (*Rhamnus cathartica*), honeysuckle, Japanese barberry and multiflora rose (Lange 1998).

Rural housing is extensive in the Baraboo Hills. In the study area, housing density was up to 50 houses/km², but in most of the area the range is 0–7 houses/km². Housing density is higher in the eastern portion of the area (8–30 houses/km²), and decreases towards the West (0–10 houses/km²) where public land and reserves limit development. Housing is concentrated along the major roads, but a large proportion also occurs along secondary roads, particularly in the eastern portion of the study area (Fig. 1).

Sampling design

To capture the effects of rural housing, we used a stratified random design (Elzinga et al. 1998) with three strata (area in brackets) representing forests with (1) no housing (3825 ha), (2) low density (6141 ha), and (3) high density housing (1269 ha). Forest cover information was obtained from the US Geological Survey National Land Cover Data for 1992 (Vogelmann et al. 2001). Forest fragments smaller than 10 ha were excluded from the analysis, because we assumed that plant communities in such small forest patches would largely reflect edge effects, and we wanted to focus in our analysis on forest interiors. We recorded data on 105 plots in the summers of 2006 and 2007 (34 in no housing, 32 in low density housing and 39 in high density housing areas), and placed plots at least 300 m apart to minimize spatial autocorrelation and cover the area more uniformly. All plots were located at least 30 m from a forest edge. The sampling effort was adjusted using power analysis (Sutherland 1996). Plots had a 20-m radius with three interception transects for cover measurements extending from the center outwards at 120° from each other and starting two meters

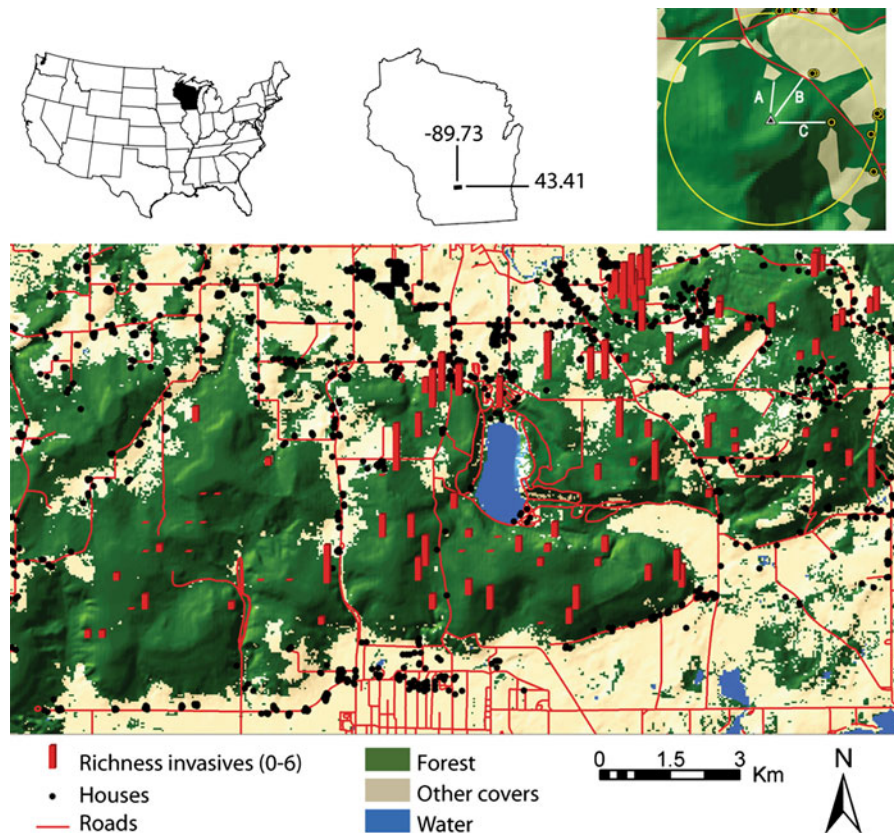


Fig. 1 Location of the study area, richness of non-native invasive plants in the sampling plots, and landscape features of the study area. On top right, detail of the 1 km buffer around

each plot for counting houses. Also shown are examples of variables calculated (A) distance to nearest forest edge, (B) distance to nearest road and (C) distance to nearest house

from the center (Etchberger and Krausman 1997; Elzinga et al. 1998).

Field data collected

We examined seven common invasive non-native plants of southern Wisconsin forests (Invasive Plants Association of Wisconsin 2003; Czarapata 2005), representing some of the most widespread and problematic invasive plants of eastern US forests (Webster et al. 2006) (Table 1). Richness was measured as the number of the seven invasive non-native plant species present in the 20-m plot and abundance as the length of the intersection of invasive plants projections on the three transects (Canfield 1941). Species scientific names follow the ITIS (Interagency Taxonomic Information System at <http://www.itis.gov>, accessed 1/2009) and the manual of vascular plants of northeastern US and adjacent Canada (Gleason and Cronquist 1991).

Table 1 Invasive plants of Baraboo Hills forests included in the analysis

Latin name	Common name
<i>Alliaria petiolata</i>	Garlic mustard
<i>Berberis thunbergii</i>	Japanese barberry
<i>Elaeagnus umbellata</i>	Autumn olive
<i>Lonicera</i> sp.	Honeysuckle
<i>Rhamnus cathartica</i>	Common buckthorn
<i>Rosa multiflora</i>	Multiflora rose
<i>Solanum dulcamara</i>	Bittersweet nightshade

Housing

For each plot we calculated the distance to the nearest house in 2001, and the number of houses within 1-km of each plot. Houses were digitized from aerial photographs (Table 2). Since there was a 5-year

Table 2 Explanatory variables included in the regression analysis

Variable type and name	Description	Source
Housing		
Distance to houses (m)	Distance from plot center to the closest house	Calculated with ArcGIS after digitizing all houses and building structures from 1/10,000 or 1/15,000 aerial photographs of the Wisconsin Department of Natural Resources
Houses around plot	Number of houses located in a 1 km radius circle (buffer) with center in the sampling plot	Idem
Human caused fragmentation		
Distance to edge (m)	Distance from the plot center to the closest forest edge	Calculated with ArcGIS. Forest edges were obtained after transforming a raster forest cover layer derived from the USGS National Land cover data for 1993 (http://landcover.usgs.gov) to a vector format
Distance to road (m)	Distance from the plot center to the closest road	Calculated with ArcGIS. Roads were obtained from the Census Bureau's TIGER® (Topologically Integrated Geographic Encoding and Referencing) database (http://www.census.gov/geo/www/tiger/)
Forest characteristics		
Forest structure	Describes a gradient of stand structure from large trees, basal area and variances in tree sizes to stands dominated by smaller trees, with less variation in size and basal area	First component obtained from PCA analysis including mean and variance of dbh and basal area, and total basal area per plot
Cover of native vegetation	Describes a gradient from plots with extensive cover of herb or shrubs to plots where litter is the main cover	First component obtained from PCA analysis including cover of native grasses, herbs, shrubs, litter, bare soil, fallen logs, and cover between 1 and 4 m
Logging	History of logging	Presence of logging stumps in each plot (present/absent)
Environment		
Aspect	Orientation of the slope where the plot is located in 8 categories (North–North East–East–South East–South–South West–West–North West)	Calculated with ArcGIS from the 30 m resolution digital elevation model obtained from the USGS national elevation dataset (http://ned.usgs.gov/Ned)
Elevation (m)	Elevation of each plot	Calculated with ArcGIS from the 30 m resolution digital elevation model obtained from the USGS national elevation dataset (http://ned.usgs.gov/Ned)
Slope (°)	Slope of the site where each plot is located	Calculated with ArcGIS from the 30 m resolution digital elevation model obtained from the USGS national elevation dataset (http://ned.usgs.gov/Ned)

difference between the date of the aerial photographs and the field sampling, we overlaid the digitized points for houses on 2005 Quickbird images with a 0.6 m resolution of the study area (available in GoogleEarth™, <http://earth.google.com>), to check if substantial development had occurred. We found only minimal changes in the housing patterns suggesting that there was no bias in our distance measurements. However, because the Quickbird images covered only 70% of our study area, we used the airphotos as a consistent datasource to digitize houses across our study area. All GIS analyses were performed in ArcGIS 9.1 (ESRI 2006).

Human caused forest fragmentation

Forest edges have ecological characteristics (e.g. more sunlight, exposure to non-native invasive plant propagules) that make them especially susceptible to invasion (Fraver 1994). In each 20-m radius plot, we measured the distance from the plot center to the nearest forest edge and the distance to the nearest road, because roads can facilitate propagule transportation and invasive plant establishment (Trombulak and Frissell 2000) (Table 2).

Topography

Elevation, slope, and aspect (the last as a categorical variable) were calculated from the 30-m resolution USGS national elevation dataset. Topography determines plant distributions, since ecological conditions change with elevation and slope. Available soil data, the Soil Survey Geographic database for Sauk County (SSURGO v.2.1, USDA NRCS <http://soils.usda.gov/survey/geography/ssurgo>) was too coarse for our analysis and the main differences in soil type (areas that were glaciated or not) was already captured by elevation, so soil type was not included in the analysis (Table 2).

Forest structure variables

We recorded diameter at breast height (dbh) of all trees >12.7 cm dbh in a nested 15-m diameter circle in each plot. We calculated stem density, and mean and standard deviation of both basal area and dbh. Vertical structure of the forest was divided into three strata: stratum A from 0 to 1 m (for small shrubs and

herbs), stratum B from 1 to 4 m (large shrubs, saplings and small trees), and stratum C above 4 m (forest canopy). Cover was measured for each stratum as the vertical projection of vegetation crowns in the 20-m cover interception transects. Native vegetation was categorized by vegetation type and was not measured to the species level. For stratum A, cover was categorized as shrub, herb, litter, rock, log (fallen logs larger than 15.2 cm in diameter) and bare soil, and measured in the 3 interception lines of each plot. In stratum B, all native vegetation types were recorded in a single measurement. Cover in stratum C was recorded in four categories: 0–25%, 25–50%, 50–75%, and 75–100%. Logging history was recorded as presence of stumps and included as a binary variable (present/not present). We also recorded evidence of fire and deer browsing, but did not include these in the analysis because fire occurred rarely in the last 50 years and deer browsing was ubiquitous (Table 2).

Statistical analysis

We used single and multiple regression analyses to identify the relationships between richness and cover of invasive non-native plants with housing, forest structure, topography, and human related forest fragmentation variables. If necessary, response variables were log transformed to meet linearity assumptions. We calculated a Pearson's correlation matrix for explanatory variables to measure collinearity. The relationships among categorical and continuous variables were tested with ANOVA. Distance to the nearest house in 2001, forests edge, and road, as well as the number of houses in a 1-km buffer around each plot, were all correlated above 0.7 Pearson correlation coefficient. To avoid collinearity problems we included these variables one at a time in each regression analysis.

Since the sets of variables for both forest cover classes and forest structure were strongly correlated, we used principal component analysis (PCA) to reduce the number of variables (McCune and Grace 2002). Stand structure variables were reduced to a principal component (the first) explaining 74% of variance and describing a gradient from stands comprised of large trees with more variation in tree size and basal area (older stands) to stands dominated by smaller trees, with less variation in size and basal

area (younger stands). Forest floor cover variables were reduced to the first principal component explaining 30% of variation describing a gradient from low native vegetation cover and litter-dominated forest floor to areas dominated by shrubs or herbaceous native plants (Table 2).

Multiple linear regression models were fit using all explanatory variables (housing, forest structure, environmental and human related variables), while richness and invasive non-native plant abundance were the response variables. Stepwise selection was used to eliminate non-significant variables (Chatterjee et al. 2000). For each of the two response variables, four models were fit, each one allowing one of the four correlated variables (distance to the nearest house in 2001, the nearest edge, the nearest road, and the number of houses within 1-km of each plot) as a candidate in the selection. Each of these four variables was modeled one at a time together with the other explanatory variables. When non-natives species richness was the response variable, all 105 plots were included in the analysis, but for cover of non-native plants we included only those plots where cover was >0 in the interception transects ($n = 35$). Spatial autocorrelation of the model residuals was tested with a semi-variogram analysis (Isaaks and Srivastava 1989).

Stepwise selection has limitations in that it identifies one best model (among several that could explain the responses equally well) and it does not provide information about the amount of variance explained by each variable (Whittingham et al. 2006). To overcome this limitation, we used best subsets and hierarchical partitioning analysis to assess the importance of variables included in the models.

The best subsets method uses the Bayesian Information Criterion (BIC) to obtain a subset of models that best explain the response. The approach performs an exhaustive search of all possible models, and the maximum number of predictors allowed is specified a priori (Miller 1990). Fitting several models instead of one “best” model highlights which variables are repeatedly chosen in the best models, and whether they have a consistent effect on the response variable (i.e., negative or positive coefficient). We analyzed only models with 3 predictor variables, and considered the 20 best models obtained in each analysis of a set of candidate variables. We then counted the number of times that each variable was included in

the 20 best models as a measure of their relative importance.

Hierarchical partitioning analysis calculates the amount of variance of the response variable explained by the variable of interest when all other variables are included in the model. In hierarchical partitioning analysis, all possible models based on different combinations of the original variables are fit, and for each model the variable of interest is dropped and the model fit again. The importance of that variable is calculated as the average change in R^2 when the variable is dropped from all of the fit models (MacNally 2002). For each response variable, we performed best subsets and hierarchical partitioning analysis four times, including distance to the nearest house in 2001, the nearest edge, the nearest road, and the number of houses in a 1-km buffer one at a time in the set of explanatory variables.

To analyze the distribution of individual non-native invasive plants, we used stepwise logistic regression (Chatterjee et al. 2000). Logistic models were assessed using a likelihood ratio test and Hosmer and Lemeshow goodness-of-fit test (Hosmer et al. 1997). The significance of independent variables was determined using a likelihood ratio test with $P \leq 0.05$ considered statistically significant. We analyzed the five most frequent non-native invasive plants (garlic mustard, Japanese barberry, honeysuckle, multiflora rose and buckthorn). For each plant species, four multivariate models were fit, including distance to the nearest house in 2001, the nearest edge, the nearest road, and the number of houses in a 1-km buffer around each plot one at a time.

Results

Invasive non-native plants were widespread in the study area. Eighty-six plots (81%) contained at least one invasive non-native plant. Buckthorn was the most widespread species, present in 57 plots (52%), followed by Japanese barberry in 42 (40%), honeysuckle in 38 (36%), multiflora rose in 36 (34%) and garlic mustard in 30 (29%). Autumn olive and bittersweet nightshade were present in less than 15 plots each. Most plots showed low cover of non-native invasive plants. Only 10% of the 105 plots had non-native invasive cover higher than 5%, and only 6% of the plots had non-native invasive cover higher

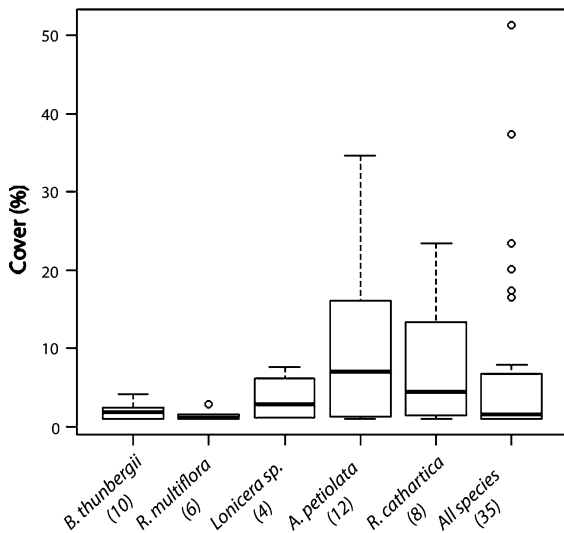


Fig. 2 Cover of non-native invasive plants at the plot level for the five most frequent species separately and for all species together. The *black line* inside each box is the median, the upper and lower sides of the boxes are the 0.75 and 0.25 quantiles, and the extreme of the lines represent the range of the data. Outliers are denoted with a *circle*. Shown in *brackets* is the number of plots where that species was present on the intersection transects

than 15%. In the two most invaded plots cover was 51 and 37%. Cover varied among species. Japanese barberry, honeysuckle and multiflora rose had generally low cover in the plots, usually as scattered individuals of variable size. On the other hand, garlic mustard and buckthorn exhibited higher cover, usually creating dense groups of individuals and in some cases completely dominating the plots (34 and 23% cover in the two most invaded plots, respectively) (Fig. 2).

Richness of invasive non-native plants

Distance to the nearest house in 2001, distance to nearest edge and road, and elevation were negatively associated with richness of invasive non-native plants. Number of houses within 1-km of each plot and cover of native vegetation were positively associated with invasive plant richness (Fig. 3). No spatial autocorrelation was present in the residuals. Both hierarchical partitioning and best subsets analyses provided consistent results. Number of houses in the 1 km buffer around each plot and distance to nearest edge explained the largest amount of variance (almost

50%) and were part of the best subset models in 14 out of 20 models. Elevation explained 43% of richness of invasive non-native plant variation and was part of the best subset models in 11 out of 20 models. Distance to nearest house and road explained less richness variation (between 20 and 30%) and entered 9 models out of 20. Cover of native vegetation explained substantially less variation in invasive non-native plant richness (11%) and entered the best subsets in just 6 out of 20 models (Fig. 3). In summary, in order of degree of association, richness of invasive non-native plants was greater in plots surrounded by more houses, closer to forest edges, at lower elevations, and closer to houses and roads. It also tended to increase in plots with greater cover of native plants.

Abundance of invasive non-native plants

Abundance of invasive non-native plants was positively associated with number of houses within 1-km of each plot and negatively associated with distance to nearest edge and road, and slope. Logging was also associated with cover of invasive non-native plants; we found greater amounts of cover of invasive non-native plants in plots with evidence of past logging. The variables associated with invasive non-native plant cover were selected ($P \leq 0.05$) in the reduced linear model after stepwise selection when included in the analysis (Fig. 3). Results for hierarchical partitioning and best subsets analysis were also consistent for cover of invasive non-native plants. Number of houses within 1-km of each plot and distance to nearest edge were the variables that explained the largest amount of variability in cover (47 and 33%, respectively) and entered the best subsets in 15 out of 20 models. Slope and distance to nearest road also explained a substantial amount of variation (33 and 29%, respectively) and entered the best subsets in 14 and 13 models, respectively. Logging history explained less than 10% of the invasive species cover and entered the best subset just an average of 7 out of 20 models. Distance to nearest road and elevation were weakly associated with cover of invasive non-native plants (Fig. 3). In summary, cover of invasive non-native plants was greater in plots surrounded by a large number of houses, closer to forest edges and roads, and on gentle slopes. Abundance of the non-native plants also tended to be higher in plots with prior logging.

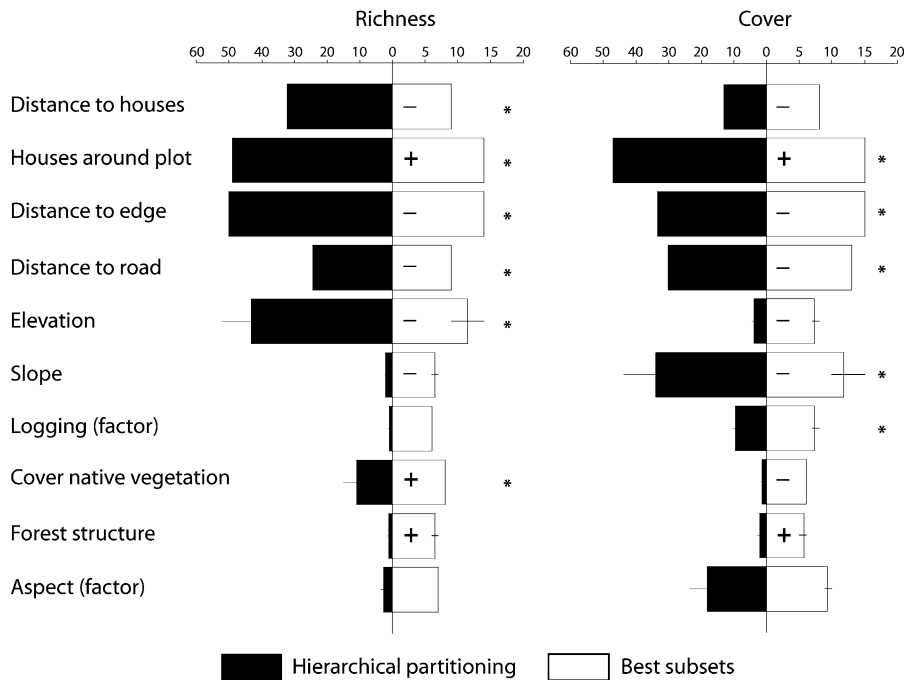


Fig. 3 Summary of regression analyses for all richness and cover of invasive non-native plants. *White bars* represent results of best subset analyses (mean, minimum and maximum number of times a variable entered in 20 models). *Black bars* represent results of hierarchical partitioning analyses (mean, minimum and maximum percent of the variability explained by

each variable when all variables are included in the model from four analyses). Housing variables, distances to roads and edges do not have range bars because they were included only in one analysis each. A *sign* indicates the direction of the relationship and an *asterisk* indicates variables that entered at least one out of the four models obtained by stepwise selection

Distribution of individual invasive non-native plants species

The five most abundant invasive non-native plants showed differences in their association with housing, human, and environmental variables. Buckthorn and honeysuckle showed the same pattern of associations with the explanatory variables and were the two species most associated with housing and fragmentation. Japanese barberry and multiflora rose showed a different pattern in that their presence was more closely associated with topography than housing. Garlic mustard was the species most closely associated with stand condition and logging history (Table 3).

For buckthorn presence, distance to the nearest house in 2001, number of houses within 1-km of each plot, and distance to nearest edge and nearest road entered the best model when included in the analysis along with elevation. Distance to nearest house and number of houses around the plot were the two most important predictors of buckthorn presence according

to their deviance, and overall, buckthorn was the species most related to housing patterns (Table 3).

Honeysuckle was associated more strongly with distance to nearest road and forest edge than housing variables, and it was also positively associated with south facing slopes and lower elevations. Thus, both buckthorn and honeysuckle tended to occur close to houses, roads and forest edges, and at lower elevations. Buckthorn also occurred in plots surrounded by a larger number of houses while honeysuckle showed a stronger positive association with south facing slopes (Table 3).

Japanese barberry was primarily associated with lower elevation. Multiflora rose was negatively associated with elevation. Both Japanese barberry and multiflora rose occurred at lower elevations, but Japanese barberry also occurred on gentler slopes and less often in plots surrounded by a large number of houses. Garlic mustard tended to occur in plots that had not been logged in recent decades and that had more cover of native shrubs and herbs (Table 3).

Table 3 Logistic regression models fit by stepwise selection to explain presence of individual invasive non-native plants in Baraboo Hills, Wisconsin (USA)

Species	Variables included in each model			AIC		
Multiflora rose						
Model 1	–0.02	Elevation	17.9***	121		
Buckthorn						
Model 1	–0.002	distance to houses	19.32***	–0.009 elevation 7.63**	123.8	
Model 2	0.044	houses around plot	18.47***	–0.003 elevation 7.63**	124.6	
Model 3	–0.003	distance to edge	16.76***	–0.008 elevation 7.63**	126.4	
Model 4	–0.002	distance to roads	12.17***	–0.008 elevation 7.63**	131.1	
Honeysuckle						
Model 1	–0.002	distance to houses	9.24**	–0.009 elevation 7.05**	0.65 aspect 8.34*	124.8
Model 2	–0.012	elevation	7.05**			134.4
Model 3	–0.003	distance to edge	10.42**	–0.008 elevation 7.05**	0.65 aspect 8.29*	123.6
Model 4	–0.003	distance to roads	15.74***	–0.005 elevation 7.05**	0.69 aspect 8.81*	117.8
Japanese barberry						
Model 1	–0.022	elevation	14.66***			140.2
Garlic mustard						
Model 1	–1.56	logging	8.11**	0.394 cover natives	5.1*	118.4

Four models were fit for each species (entering housing and human fragmentation variables one at a time), and if all reduced models included the same variable only one model is shown. For each variable, sign and estimated slope, deviance and *P*-value are shown * ($0.01 \leq P \leq 0.05$); ** ($0.001 \leq P \leq 0.01$); *** ($P < 0.001$)

Discussion

Rural housing was strongly associated with the distribution of invasive non-native plants in forests in our study area. Non-native invasive plant richness was associated with both the distance to the nearest house and the number of houses around each plot, while cover was strongly associated with the number of houses around each plot. Rural housing and fragmentation variables showed in general a stronger association with the distribution of invasive non-native plants than did topography and forest structure variables.

Changes in landscape pattern and invasions:
the rural housing factor

Prior research examining gradients from urban to rural areas (Hansen et al. 2005) shows higher richness and abundance of invasive non-native plants in suburban areas (Moffatt and McLachlan 2004; Moffatt et al. 2004; Song et al. 2005; Duguay et al. 2007). Our results suggests that housing at much lower densities than suburban areas also has a

profound effect on the distribution of invasive non-native plants in a forested landscape.

Landscape pattern influences many ecological processes, including species dispersal and colonization (Turner 1989). Non-native plants can become invaders when landscape patterns facilitate their dispersal and provide abundant disturbed and thus easily colonized habitat (With 2002). Rural houses can act as entry points of propagules to the landscape (i.e., propagules from ornamental plants) (Knops et al. 1995). In forested areas, housing also causes fragmentation, thus providing a landscape more suitable for colonization. Honeysuckle and multiflora rose are frequently found in forest gaps and edges, as well as less isolated forest patches (van Ruremonde and Kalkhoven 1991; Luken et al. 1997).

Housing, roads, and forest edges are correlated in their origin, spatial distribution and ecological consequences (e.g., forest fragmentation and open areas). Rural housing is thus a process that will favor plant invasion both directly (i.e., the specific housing effect) and indirectly as a determinant of roads and forest edge creation. In conclusion, most of the landscape transformations associated with rural

housing will likely result in more non-native plant invasions.

Invasion factors and associated processes

The positive relationship between richness of non-native invasive plants and distance to the nearest house in our study supports the role of houses as sources of invasive non-native plants. Most species considered in the study have a long history of landscaping use (Invasive Plants Association of Wisconsin 2003; Czarapata 2005). For example, large individuals of multiflora rose, honeysuckle and Japanese barberry were observed in house's yards during field trips (G. Gavier-Pizarro, Pers. Obs.).

However, the abundance of invasive non-native plants was also positively associated with the number of houses around each plot, which could be related to the accumulation of human related vegetation and soil disturbances in areas with higher house densities (Theobald et al. 1997; Wania et al. 2006).

Roads can provide suitable habitat (e.g. bare soil and open areas) for non-native plants adapted to disturbance, and facilitate plant propagule dispersal resulting in non-native plants invasions (Trombulak and Frissell 2000). Multiflora rose, buckthorn, honeysuckle and Japanese barberry are usually associated with roads (Lundgren et al. 2004; Predick and Turner 2008). The association of non-native invasive plants with low elevation areas and gentle slopes may result from a concentration of human disturbances in flat areas and bottom valleys. However, more xeric conditions on hill tops could be less favorable to those non-native invasive plants better adapted to humid conditions, like buckthorn (Archibold et al. 1997). The concentration of nutrients in the soil can determine also the heterogeneity of vegetation at small scales (Fraterrigo et al. 2006). Availability of this information would help to explain the differences at small scales found among proximate plots, however, no nutrient data was available in our study area, and we did not collect soil data in our field work due to logistical constraints.

Life history traits or history of use?

The differences in the responses of buckthorn, honeysuckle, Japanese barberry and multiflora rose to our explanatory variables may be due to their

history of introduction and use, because they share life history traits that make them successful invaders including animal dispersed seeds (mostly birds), extended photosynthetic period, and longevity (Webster et al. 2006). Buckthorn and honeysuckle have been introduced mainly as landscaping plants and were more related to rural housing and fragmentation in the landscape (Webster et al. 2006). Japanese barberry and multiflora rose have been used as landscaping plants but also as wildlife cover and food and erosion control (Czarapata 2005), and were more strongly related to topographic variables than to rural housing or fragmentation. Garlic mustard is not bird dispersed but has a short generation time (biennial herb) that can facilitate a rapid spread (Meekins and McCarthy 2000) and is not a landscaping plant in our study area, which may explain its lack of association with distance to the nearest house.

Future invasion scenarios and management recommendations

Our findings have important management implications. Housing growth rates are high in the US (roughly growing 1.6% per year), a trend that is likely to continue in the future (Theobald 2001, 2005). The pattern of housing growth, especially the concentration of housing growth “hot spots” in rural areas rich in natural amenities, is cause for concern (Hammer et al. 2004; Lepczyk et al. 2007). In our study area housing occurs often close to protected areas, a common pattern for many regions (Gude et al. 2007; Wittemyer et al. 2008). The pervasive and persistent character of housing is likely to result in widespread non-native plant dispersal over long periods of time. The list of new plants being imported as ornamentals is growing (Reichard and White 2001), making it likely that the yards of rural houses will be planted with potentially invasive new plants.

However, land managers can limit the magnitude and the impact of expected future invasions. First, areas undergoing development should be a focal point of monitoring programs to detect invasions and control them at an early stage (strategy suggested in the 2008–2012 National Invasive Species Management Plan, National Invasive Species Council 2008). Second, in already developed areas, educational programs targeted towards homeowners and lawn-care and landscaping companies, as well as landscaping

ordinances could reduce the use of invasive exotic plants for landscaping (Waldner 2008). Finally, housing development should be discouraged near or in forests of high conservation value (Radeloff et al. 2010). Development should be directed towards places with lower invasion risk (Waldner 2008), and our results may provide further justification for such efforts.

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