

Housing is positively associated with invasive exotic plant species richness in New England, USA

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Abstract. Understanding the factors related to invasive exotic species distributions at broad spatial scales has important theoretical and management implications, because biological invasions are detrimental to many ecosystem functions and processes. Housing development facilitates invasions by disturbing land cover, introducing nonnative landscaping plants, and facilitating dispersal of propagules along roads. To evaluate relationships between housing and the distribution of invasive exotic plants, we asked (1) how strongly is housing associated with the spatial distribution of invasive exotic plants compared to other anthropogenic and environmental factors; (2) what type of housing pattern is related to the richness of invasive exotic plants; and (3) do invasive plants represent ecological traits associated with specific housing patterns? Using two types of regression analysis (best subset analysis and hierarchical partitioning analysis), we found that invasive exotic plant richness was equally or more strongly related to housing variables than to other human (e.g., mean income and roads) and environmental (e.g., topography and forest cover) variables at the county level across New England. Richness of invasive exotic plants was positively related to area of wildland–urban interface (WUI), low-density residential areas, change in number of housing units between 1940 and 2000, mean income, plant productivity (NDVI), and altitudinal range and rainfall; it was negatively related to forest area and connectivity. Plant life history traits were not strongly related to housing patterns. We expect the number of invasive exotic plants to increase as a result of future housing growth and suggest that housing development be considered a primary factor in plans to manage and monitor invasive exotic plant species.

Key words: *broad-scale; housing; invasive exotic plants; landscape ecology; New England; wildland–urban interface.*

INTRODUCTION

Invasion of exotic species is one of the main factors of ecosystem degradation and biodiversity loss because exotic species alter fire regimes, nutrient cycling, hydrology, and energy budgets of native species (Mack et al. 2000, Sax and Gaines 2003, Mooney 2005, Theoharides and Dukes 2007). Invasive exotic plants are exotic plants that establish themselves in the wild, exhibiting rapid population growth, replacing native vegetation, altering ecosystems, and becoming dominant or disruptive (Mack et al. 2000, Richardson et al. 2000, Mehrhoff et al. 2003). The number of exotic plants in the

U.S. is especially high in the West, the Southwest, along the Gulf coast and New England (Stohlgren et al. 2006). Approximately 5000 exotic plant species have established free-living populations in the United States, and over 1000 have been identified as invasive and a threat to native flora and fauna (Morse et al. 1995, National Parks Service 2006). Biological invasions in the United States have resulted in an estimated economic loss of 120 billion dollars per year, out of which exotic plants alone account for 25 billion dollars (Pimentel et al. 2005).

Several ecological processes play an important role in the success of biological invasions, and plant invasions are closely related to human activities (Williamson and Fitter 1996, Lonsdale 1999, Mack et al. 2000), such as trade, as measured by gross product or importation volume (Mack et al. 2000, Vila and Pujadas 2001, Taylor and Irwin 2004, Hobbs and Mooney 2005). Most aspects of global change (e.g., land use change, introducing new landscaping plants) facilitate exotic plant invasions (Vitousek et al. 1997, Dukes and Mooney 1999, Reichard and White 2001). Since

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biological invasions are among the most harmful consequences of global change (Vitousek et al. 1997, Dukes and Mooney 1999), understanding the factors facilitating invasions of exotic plants at broad scales is a necessary first step to develop successful strategies to control or eradicate exotic plants (Pino et al. 2005).

Human settlement is a land use with high negative ecological impacts, and housing growth is rampant in many parts of the world (Theobald et al. 1997, Antrop 2000, 2004). Housing expansion is particularly fast in the United States. Between 1950 and 2000, the proportion of urban area in the conterminous United States increased from 1% to 2%, and rural low-density housing area increased from 5% to 25% (Brown et al. 2005). Rural growth has been particularly high in areas with natural vegetation, resulting in an increase in the area where natural ecosystems and housing meet, i.e., the wildland–urban interface (WUI; Radeloff et al. 2005). Two distinct housing patterns at this interface are: intermix housing, where housing and wildland vegetation co-occur, and interface housing, where more dense housing is in close proximity to wildland vegetation. While both have grown, intermix developments have grown more and is more commonly associated with rural settings (Hammer et al. 2007, Lepczyk et al. 2007).

Housing development in or near natural areas likely facilitates invasions by exotic plants. At fine scales, there is a positive relationship between exotic plant richness and housing (Rapoport 1993, Sullivan et al. 2004, Wania et al. 2006) explained by two processes. First, humans import exotic plants for landscaping or accidentally introduce them around houses (Kowarik 1990, Mack and Erneberg 2002) and their propagules invade adjacent sites (Reichard and White 2001, Sullivan et al. 2005, Wania et al. 2006). Second, disturbances resulting from housing development (e.g., edges, soil exposure, trails) create favorable microhabitats for exotic plants (Hobbs and Huenneke 1992, De Candido 2004, Wania et al. 2006).

However, few studies have analyzed the relationship of houses and invasive plants at a regional scale. Research in Germany (Deutschewitz et al. 2003) and Spain (Pino et al. 2005) found a positive relationship between the urbanized area and the number of exotic plant species at regional scales. Understanding the broad-scale relationship between housing and invasive exotic plants thus requires additional research on three main questions. First, is housing as important as other human-related and environmental factors in explaining invasive plant distributions? It is unclear whether housing is a more important driver of regional distributions of exotic invasive plants than environmental (e.g., rainfall, topography, productivity) or other human factors (e.g., roads). Second, is richness of invasive exotic plants most strongly related to a particular housing pattern? Knowing the relationship of invasive exotic plants with different patterns of

housing (e.g., urban, suburban, intermix or interface WUI development) could help elucidate the ecological consequences of projected housing growth patterns. And third, are the traits of invasive exotic plants associated with housing patterns? Invasions are most extensive where invasive plant adaptations (e.g., shade tolerance, dispersal mechanisms) match ecosystem conditions (Sher and Hyatt 1999, Kolar and Lodge 2001). However, it is not clear if different plant traits correlate with specific housing patterns. To assess relationships between broad-scale distribution of exotic invasive plant richness and housing, we focused on these three research questions using a broad scale database of invasive exotic plant richness for New England, USA.

METHODS

Study area

We studied the six states of New England (Vermont, Connecticut, New Hampshire, Rhode Island, Maine, and Massachusetts; Fig. 1), because this region has the longest history of plant invasions in the United States (Mehrhoff 2000, Mehrhoff et al. 2003, Farnsworth 2004). In this region, forests are typically invaded by exotic trees and shrubs, while open habitats are more often invaded by herbs and grasses (Von Holle and Motzkin 2007). Invasions started with plants brought for utilitarian reasons by European settlers and with the accidental introduction of agricultural pests in the 17th century (Mehrhoff 2000). Presently, the flora of New England includes 24–45% exotic species (approximately 1000 species) of which 111 are considered invasive (Mack and Erneberg 2002, Mehrhoff et al. 2003). Also, rural housing is widespread in the region: 72% of the area of Connecticut is in WUI, and in New Hampshire 80% of the houses are located in the WUI (Radeloff et al. 2005).

Invasive exotic plants data

We obtained the number of invasive exotic plants for each county in New England from the Invasive Plant Atlas of New England (IPANE; Mehrhoff et al. 2003). The IPANE is based on herbarium records, field records from scientific studies, and field observations from a team of 500 volunteers trained by the IPANE program. The IPANE includes 111 species of invasive plants representing six plant types (shrubs, herbs, grasses/sedges, vines, trees, and aquatic) where invasive plants are defined as exotic species that become established in natural areas, replacing native vegetation, altering ecosystems, and becoming dominant or disruptive (Mehrhoff et al. 2003). The distribution of invasive plants is based on more than 11 000 records, which we considered sufficient to capture presence/absence information at the county level. We used counties as the grain of our analysis because data on the distribution of invasive exotic plants at a finer scale (i.e., townships) are inconsistent. No relationship was found between rich-

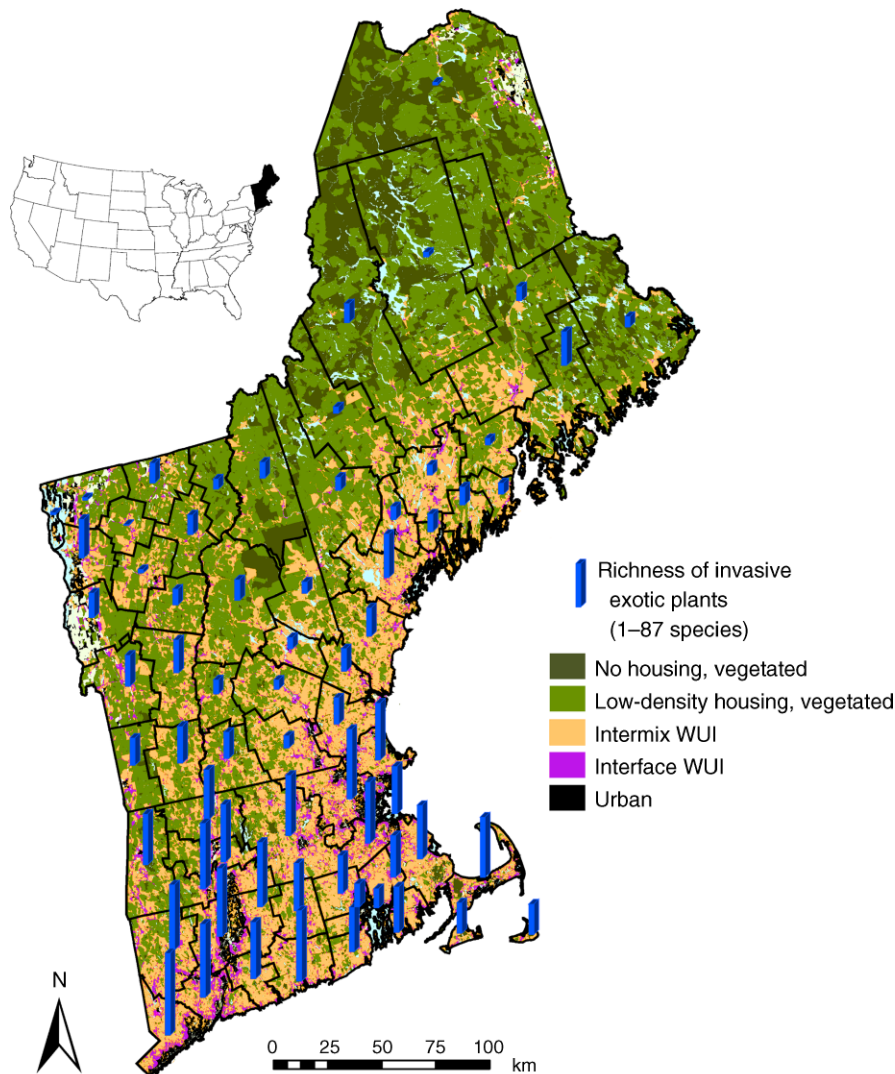


FIG. 1. Distribution of invasive exotic plant richness, housing, and vegetated areas in New England (1 mile = 1.67 km). The two types of WUI (wildland–urban interface, wildland–urban intermix) are defined in *Methods: Human-related and environmental variables*.

ness of invasive exotic plants and county area, so we did not correct for an area effect.

We divided invasive plant species into three groups based on simple life history traits that define species more adapted to live in either open areas or forest interior conditions. Group 1 included shade-intolerant species adapted to live in open habitats (e.g., *Ailanthus altissima* (Miller) Swingle and *Phragmites australis* (Cav.) Trin. ex Steud.). Group 2 included species that are shade tolerant and dispersed by animals, and thus able to colonize forests interiors (e.g., *Rhamnus cathartica* L. and *Berberis thunbergii* DC). Group 3 included shade-tolerant but mechanically dispersed plants (e.g., *Microstegium vimineum* (Trin.) A. Camus and *Alliaria petiolata* (Bieb.) Cavara and Grande), also growing in forests interiors but with lower dispersal abilities than group 2.

Human-related and environmental variables

We used 18 variables to explain county-level richness of invasive exotic plants, capturing the main housing patterns found in New England as well as other human and environmental factors that are known to be associated with invasive exotic plants (McKinney 2002a, Dark 2004, Stohlgren et al. 2006). Explanatory variables were grouped into three categories: housing, other human influence, and environmental (Table 1).

We included five variables to account for housing. The first four variables represented the more common housing patterns found at broad scales in New England: high-density residential (constructed areas with less than 20% of vegetation, e.g., apartment complexes or inner city areas), low-density residential (mixture of constructed and vegetated surfaces, e.g., single-family

TABLE 1. Explanatory variables used in the analysis.

Variable	Comments	Source
Housing		
Proportion of high- and low-density residential areas	Surface of urbanized area (ha). Classified 30-m resolution images, years 1991 to 1993. Classes low-density and high-density residential area were divided by county area (km^2/km^2).	USGS national land cover data (www.NationalAtlas.gov)
Housing growth between 1940 and 2000	Change in the number of housing units in 1940 and 2000.	GIS analysis of U.S. Census Bureau data (http://silvis.forest.wisc.edu/)
Proportion of interface WUI (wildland–urban interface)	Area of interface WUI /county area (km^2/km^2).	WUI project, ILVIS lab home page (http://silvis.forest.wisc.edu/)
Proportion of intermixed WUI	Area of intermixed WUI /county area (km^2/km^2).	WUI project, SILVIS lab home page (http://silvis.forest.wisc.edu/)
Other human influence		
Population density	Number of inhabitants per county in 2000 divided by county area.	U.S. Census Bureau
Cropland area	Area of cropland divided by area of county (km^2/km^2).	USGS national land cover data (www.NationalAtlas.gov)
Transformed land	Sum of cropland, mining land, and urban areas divided by county area (km^2/km^2).	GIS analysis of USGS national land cover data by Vogelmann et al. (2001)
Road density	Length of main roads in a county divided by county area (km/km^2).	The major roads of the United States map layer at a map scale of 1:2 000 000 compiled by the USGS
Mean per capita annual income	Per capita mean annual income by county (US\$).	U.S. Census Bureau
Environmental		
NDVI	Normalized difference vegetation index (NDVI); average value per county, as a surrogate for vegetation productivity.	Derived from NOAA images taken each 2 weeks, and averaged for the year. In this analysis the average of 1990, 1995, 2000, and 2005 was used.
Proportion of forested area	Amount of forested area divided by county area (km^2/km^2)	USGS national land cover data (www.NationalAtlas.gov)
Forest connectivity	Moving window analysis of forest connectivity, 9×9 window where the amount of forest to forest boundary is divided by the amount of all forest boundaries. Final map resolution 270 m window size, and averaged for the whole county.	(www.NationalAtlas.gov) Algorithm based on Wade et al. (2003).
Precipitation	Mean annual rainfall (mm).	Oregon Climate Service, PRISM climate digital data (www.NationalAtlas.gov)
Land cover diversity	Diversity of land cover classes (Shannon index).	GIS analysis on USGS national land cover data (www.NationalAtlas.gov)
Density of main rivers	Total length of main rivers in a county divided by county area (km/km^2).	The main rivers of the United States map layer at a map scale of 1:2 000 000 compiled by the USGS
Temperature	Mean annual temperature.	The Spatial Climate Analysis Service at Oregon State University (www.NationalAtlas.gov)
Mean elevation and elevation range	Mean elevation of each county (m) and elevation range.	USGS GTOPO30 global digital elevation model (DEM), 30-m resolution

Note: The two types of WUI, intermix and interface, are defined in *Methods: Human-related and environmental variables*.

housing units), interface WUI (low- and high-density residential areas in close proximity to natural vegetation), and intermix WUI (sparse housing in areas with dense natural vegetation, often houses under the forest can-

opy). Intermix WUI is defined as census blocks ≥ 6.17 housing units/ km^2 and covered by more than 50% natural vegetation (Radeloff et al. 2005). Interface WUI is defined as census blocks (or portions of blocks)

that have >6.17 housing units/km² and $<50\%$ natural vegetation and are in the proximity (2.4 km) of a large vegetated areas (more than 75% natural vegetation) (Radeloff et al. 2005). The fifth housing variable was housing growth (absolute increase in number of housing units between 1940 and 2000).

A second set of variables represented other human influences related to plant invasions. Road density was included because roads provide suitable habitat for invasive plants and facilitate propagule transport (Trombulak and Frissell 2000). Population density is a good predictor of exotic species richness (McKinney 2002b, 2004, Pautasso and McKinney 2007) and we included it to account for several human effects (e.g., disturbance and spread of propagules due to biking, trekking, hunting, road use, etc.). Total amount of transformed land (agriculture, urban, mines) was included to account for disturbed and open land, and propagule pressure from agriculture weeds. Mean per capita annual income was included because residential areas in wealthy neighborhoods are associated with more intense gardening, and greater plant diversity (Hope et al. 2003).

The third set included environmental variables that determine plant growth, such as average annual temperature and precipitation. Mean elevation and elevation range described topographic variation. We included them because elevation range is related to the diversity of environmental conditions and plant habitats found in an area (Richerson and Lum 1980, Rosenzweig 2002). Land cover diversity is another measure of habitat diversity available for plants and was used in the analysis. NDVI (normalized difference vegetation index) is a remote-sensing index based on red and near-infrared reflection that is an estimate of plant productivity, and was included as an indicator of conditions favoring plant growth (Jensen 1996). We included forest area because forests in New England are less invaded by exotic plants than open areas (Van Holle and Motzkin 2007) and more forested counties have less available area for invasive plants associated with open environments. Forest connectivity was included because higher connectivity is associated with more compact patches, less fragmentation (Wade et al. 2003), and less forest edge, and thus indicates less habitat that is susceptible to exotic plant invasions (Fraver 1994). Length of main rivers was included because riparian areas are more susceptible to plant invasions and act as sources of invasions to adjacent areas (Stohlgren et al. 1998).

Statistical analyses

We used single and multiple linear regression analyses to assess the relationship between the richness of invasive exotic plants and housing, other human-related variables, and environmental variables. Some explanatory variables were log transformed (low- and high-density residential area, housing growth between 1940 and 2000, NDVI, density of roads and rivers) to ensure

that they entered the models linearly. We calculated a Pearson's correlation coefficient matrix for all explanatory variables to measure collinearity. Variables correlated above 0.68 would compete with each other if included together in the regression analyses, and important explanatory variables dropped from the models, particularly housing variables that we wanted to evaluate. Most variables were correlated below 0.65. When the correlation between any two variables was ≥ 0.68 , the explanatory variable which was correlated with the most variables or had a less clear relationship with the response variable was not included in the analysis. For instance, mean temperature, population, and amount of transformed land were correlated with several of the explanatory variables (particularly the other anthropogenic variables) and not used. Elevation range and forest connectivity were correlated with mean elevation and forest area respectively, so we included elevation range and forest connectivity only as a replacement for mean elevation or forest area when the latter two variables had collinearity problems with other variables. Road density was correlated with some housing variables and was excluded from the analyses including low- and high-density residential area and housing growth between 1940 and 2000. Housing variables were correlated with each other above 0.68, and we include them in the analyses one at a time. We tested for the effects of a latitudinal gradient on the relationship between richness of invasive exotic plants and housing by fitting single regression models for richness of invasive exotic plants and housing variables using counties of Massachusetts and Connecticut. We also fitted regression models including latitude and housing as explanatory variables, and in both cases there was still a significant effect of housing on richness of exotic invasive plants. Furthermore, some of the variables included in the analysis (e.g., NDVI and rainfall) were strongly correlated with latitude, so they were accounting for possible latitudinal effects.

Since the focus of our research was to compare the importance of housing variables with environmental and other human variables in determining invasive exotic plant richness, we used two regression-based methods as our main statistical tools: best subset selection and hierarchical partitioning analysis. The two methods complement each other. Best subset selection describes how many times a variable is entered in a set of models, while hierarchical partitioning calculates the amount of variance explained when the variable is entered into a model.

Best subset selection uses the Bayesian information criterion (BIC; Burnham and Anderson 2002) to obtain a subset of models that best explain the response. The approach performs an exhaustive search of all possible models, given a maximum number of predictors allowed, which is specified a priori (Miller 1990). Fitting several models instead of one "best" model highlights variables that are repeatedly chosen in the

best models, and indicates whether they have a consistent effect on the response variable (i.e., negative or positive relationship). We examined only models containing five 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 fitted, and for each model the variable of interest is dropped and the model fitted again. The importance of that variable is calculated as the average change in R^2 when the variable is dropped from all of the fitted models (MacNally 2002).

Neither best subset nor hierarchical partitioning analysis can account for spatial autocorrelation if it is present in a model. Thus, we used stepwise selection analysis to assess the effects of spatial autocorrelation. Using stepwise selection we selected the best models prior to each hierarchical partitioning and best subsets analysis (Venables and Ripley 2002) and analyzed residuals to test model assumptions and eliminate outliers. We used a Moran's I test for detecting the presence of spatial autocorrelation in the residuals of the best models.

When spatial autocorrelation was present in a model's residuals, we fitted a simultaneous autoregressive (SAR) models. A SAR model includes the neighborhood structure of the lattice data into the model's error terms and has the form $Y_i = b_0 + b_1x_i + e_i$, where

$$e_i = \rho \sum_{j=1}^n s_{ij} e_j + u_i$$

and $u_i \sim \text{ind } \mathcal{N}(0, \sigma^2 v_i)$, s_{ij} can be 1 ($i \neq j$, and i and j are neighbors) or 0 ($i = j$, and i and j are not neighbors) representing the neighborhood structure and dependence of i on j and v_i is a weight for the error's variance (Fortin and Dale 2005, Bivand et al. 2008). When comparing the linear models with the equivalent spatial autoregressive models, we found that the values and P values for the estimated slopes of both models were only slightly different, and the sign with which each variable entered the model was consistent in both versions (results not shown). Thus, we concluded that the presence of spatial autocorrelation in the residuals of some of the models did not alter the main findings of the best subset and hierarchical partitioning analyses. All statistical analyses were conducted in R (R Project Development Team 2007).

We repeated the analyses five times each time including a different housing variable, and summarized the mean as well as the minimum and maximum of (1)

the number of times each variable was included in the 20 possible models (best subset analysis) and (2) the percentage of total variation explained by each explanatory variable (hierarchical partitioning analysis).

RESULTS

Is housing as important as other human-related and environmental factors in explaining invasive plant distributions?

Housing variables were strongly and positively related to county level invasive exotic plant richness in New England. In univariate models, all housing variables were significantly and positively related to the richness of invasive exotic plants. The most strongly related variables were amount of interface WUI of low-density residential area and change in housing units between 1940 and 2000. The amount of high-density residential area explained less variance, and amount of intermix WUI had the weakest association with the richness of invasive exotic plants (Fig. 2).

In the multivariate analysis, housing variables were as important as other environmental and human influence variables in determining richness of invasive exotic plants (Fig. 3). Three out of five housing variables were strongly and positively related to invasive exotic plant richness. Amount of interface WUI, low-density residential area, and change of housing units between 1940 and 2000 all showed high values for both the best subset analysis and hierarchical partitioning analysis. Low-density residential areas explained the largest amount of variance of invasive exotic plants richness (37%), followed by change in housing units between 1940 and 2000 (30%) and to a lesser extent amount of interface WUI (27%). All three variables explained more variance in species richness than other human-related or environmental variables (<22% for all; Fig. 3).

Amount of interface WUI, low-density residential area, and change of housing units between 1940 and 2000 entered most of the models fitted in the best subset analysis (19, 17, and 14 times, respectively). However, some of the other human-related and environmental variables (median income, forest area and connectivity, NDVI, and rainfall) were included in the best model subsets (on average 14 to 18 times). Rivers entered the models equally often as housing variables, but explained substantially less variance of invasive exotic plant richness (Fig. 3).

Considering the results of both hierarchical partitioning and best subset analyses, invasive exotic plant richness was explained by a positive association with interface WUI, low-density residential area and change of housing units between 1940 and 2000, median income, NDVI, rainfall, and a negative association with forest area and degree of connectivity. Road density was positively related to invasive exotic plant richness, but less so than other variables. Area of agricultural land, diversity of land cover, topography and density of main

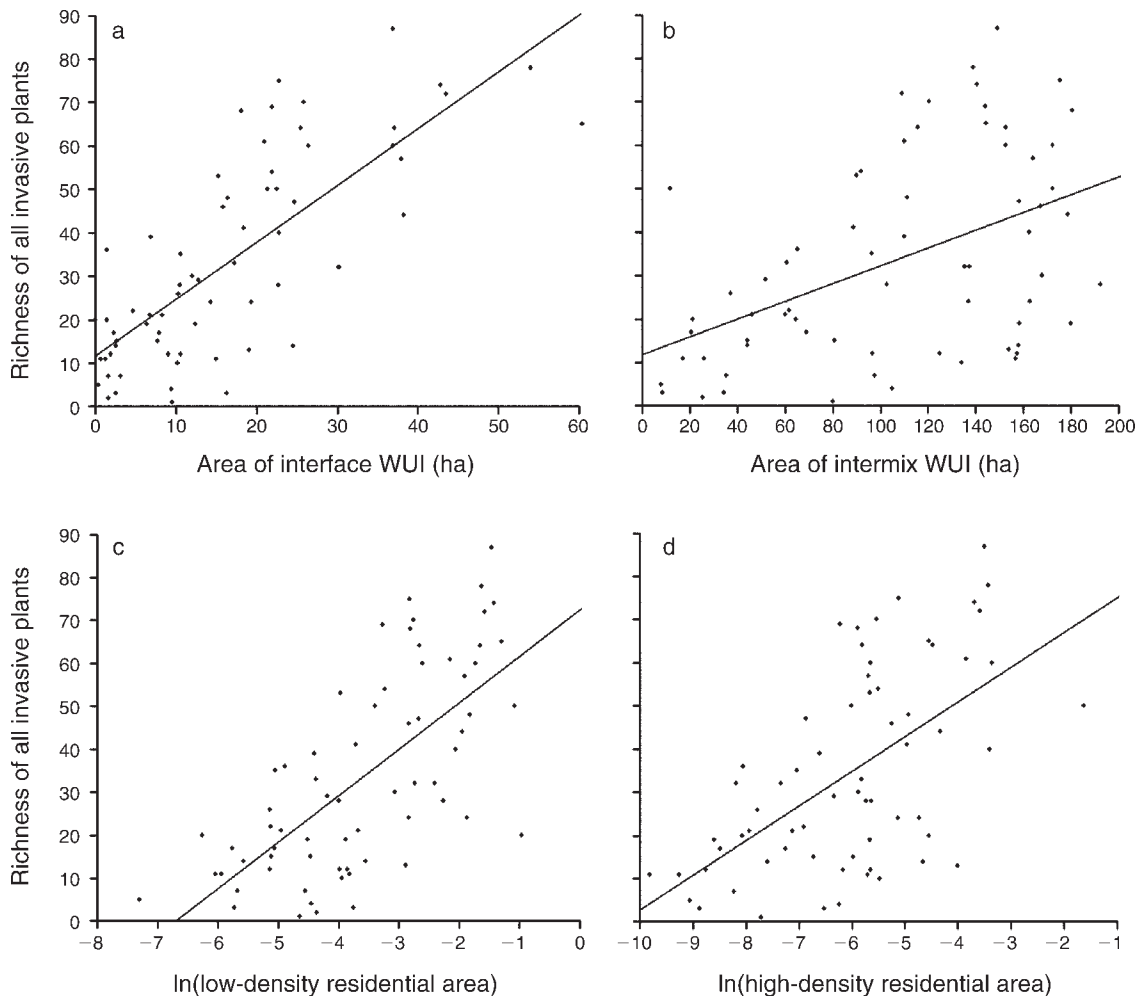


FIG. 2. Results of univariate regression analyses between richness of all invasive plant species and housing variables in New England at the county level. In each case, due to the presence of spatial autocorrelation in the residuals of the linear models, both linear and spatial autoregressive models (SAR) were fitted. Results are as follows. (a) Linear model, $R^2=0.59$, $b=1.3^{***}$, AIC = 557.68; SAR model, $b=0.81^{***}$, AIC = 541. (b) Linear model, $R^2=0.22$, $b=0.2^{***}$, AIC = 599.41; SAR model, $b=0.11^*$, AIC = 552.74. (c) Linear model, $R^2=0.48$, $b=10.82^{***}$, AIC = 573.4; SAR model, $b=7.51^{***}$, AIC = 547.8. (d) Linear model, $R^2=0.38$, $b=0.803^{***}$, AIC = 584.1; SAR model, $b=3.22^{**}$, AIC = 551.2. The model of the relationship between richness of all invasive plant species and change of house units between 1940 and 2000 is not included in the figure (linear model, $R^2=0.46$, $b=11.045$, AIC = 575.2; SAR model, $b=8.075$, AIC = 547.04). Variables are: b , slope of the regression; AIC, the Akaike information criterion.

* $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$.

rivers were not important variables at the scale of our analysis (Fig. 3).

Is richness of invasive exotic plants most strongly related to a particular housing pattern?

Richness of invasive exotic plants showed a strong association with specific housing patterns (Fig. 3). Interface WUI explained 27% of variance and entered 19 of 20 best subset models, but contrary to our expectations, area of intermix WUI explained just 8% of variance and entered only four out of 20 best subset models. As expected, amount of high-density residential area was weakly related to richness of invasive exotic plants (it explained 21% of variance, but entered only three best subset models). On the other hand, low-

density residential area explained 35% of the variance of invasive exotic plant richness and entered 17 of the best subset models. In general terms, richness of invasive exotic plants was most strongly related to the housing variables representing the boundary between development and wildlands (i.e. low-density residential areas and interface WUI; Fig. 3).

Are the traits of invasive exotic plants traits associated with housing patterns?

The richness of plant types largely followed the pattern that we found for total invasive exotic plant richness in their relationship to housing and other human and environmental variables. All three groups of plant traits were positively associated with the change in

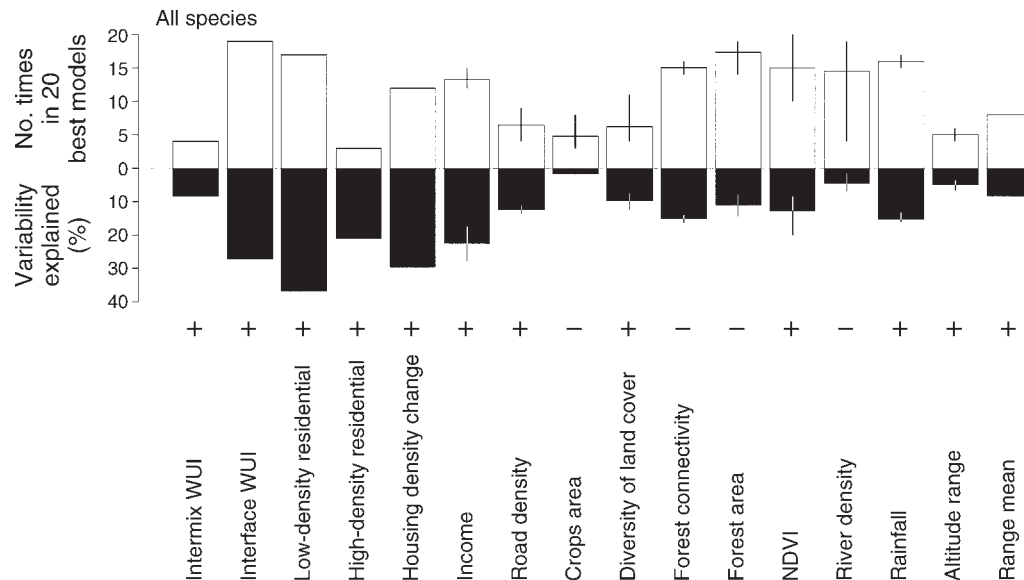


FIG. 3. Summary of regression analyses for all invasive plant species. White bars represent results of best subset analysis (mean, minimum, and maximum number of times a variable entered the 20 best models). The range of R^2 for the models fitted in the best subset analysis is 0.57–0.71. Black bars represent results of hierarchical partitioning analysis (mean, minimum, and maximum percentage of the variability explained by each variable when all variables are included in the model). Housing variables and elevation range do not have range bars because they were included only in one analysis each. The “+” and “–” symbols represent the nature of the relationship between the explanatory variables represented in the bars and the response variable richness of invasive exotic plants. A “+” represents a positive or direct relationship (increase of explanatory increase of response), and a “–” represents a negative or inverse relationship (increase of the explanatory, decrease in the response). NDVI is the normalized difference vegetation index.

housing units between 1940 and 2000, the amount of interface WUI and low-density residential area, income, NDVI, and rainfall, and negatively related to forest amount and degree of connectivity. Road density and elevation range were positively related but to a much lesser extent (Fig. 4). However, one difference among plant groups was that shade-tolerant animal dispersed plants (group 2) were more strongly related to intermix WUI and less strongly related to road density than shade-tolerant mechanically dispersed and shade-intolerant plants (groups 3 and 1; Fig. 4).

DISCUSSION

We found that housing was a major factor in determining the richness of exotic invasive plants at regional scales in New England. Our results suggest that the two processes that explain the relationship of invasive exotic plants and housing at fine scales (propagule pressure and suitable habitat; Hobbs and Huenneke 1992, Wania et al. 2006) also operate at broad scales, and that their combination makes housing development a key determinant of exotic invasive plant species patterns.

The extent to which exotic invasive species disturb ecosystems has stimulated research to develop theories that explain successful invasions based on environmental conditions, including biodiversity and disturbance levels (Stohlgren et al. 1999, Tilman 1999, 2004). However, our results show that besides environmental

conditions, human activities and particularly housing will shape the large scale patterns of invasions. This finding is important, because housing is expected to grow in rural areas of the United States, which indicates the effect of housing will be an increasingly influential variable behind future regional patterns of invasive exotic plants distributions (Theobald and Romme 2007).

However, housing certainly interacts with other factors that determine exotic plant invasions. The distribution of exotic plants in New England was also correlated with environmentally favorable conditions for plant growth (e.g., high NDVI), so we can expect that in any region housing will be a major determinant of exotic plants invasions as long as environmental conditions are not limiting their growth. Also, housing in forested regions will result in more fragmentation and creation of forest edges, amplifying the ecological effect of housing. Indeed, in New England, the boundary between suburban areas and natural vegetation (represented by Interface WUI) was strongly associated with the distribution of exotic invasive plants at regional scales.

Previous studies have highlighted the importance of urban and suburban housing in determining the invasion of exotic plants in forests at finer scales. Around Ottawa, Canada, forest fragments in or near urban landscapes have 40% more introduced plant species than fragments located in agricultural or forested

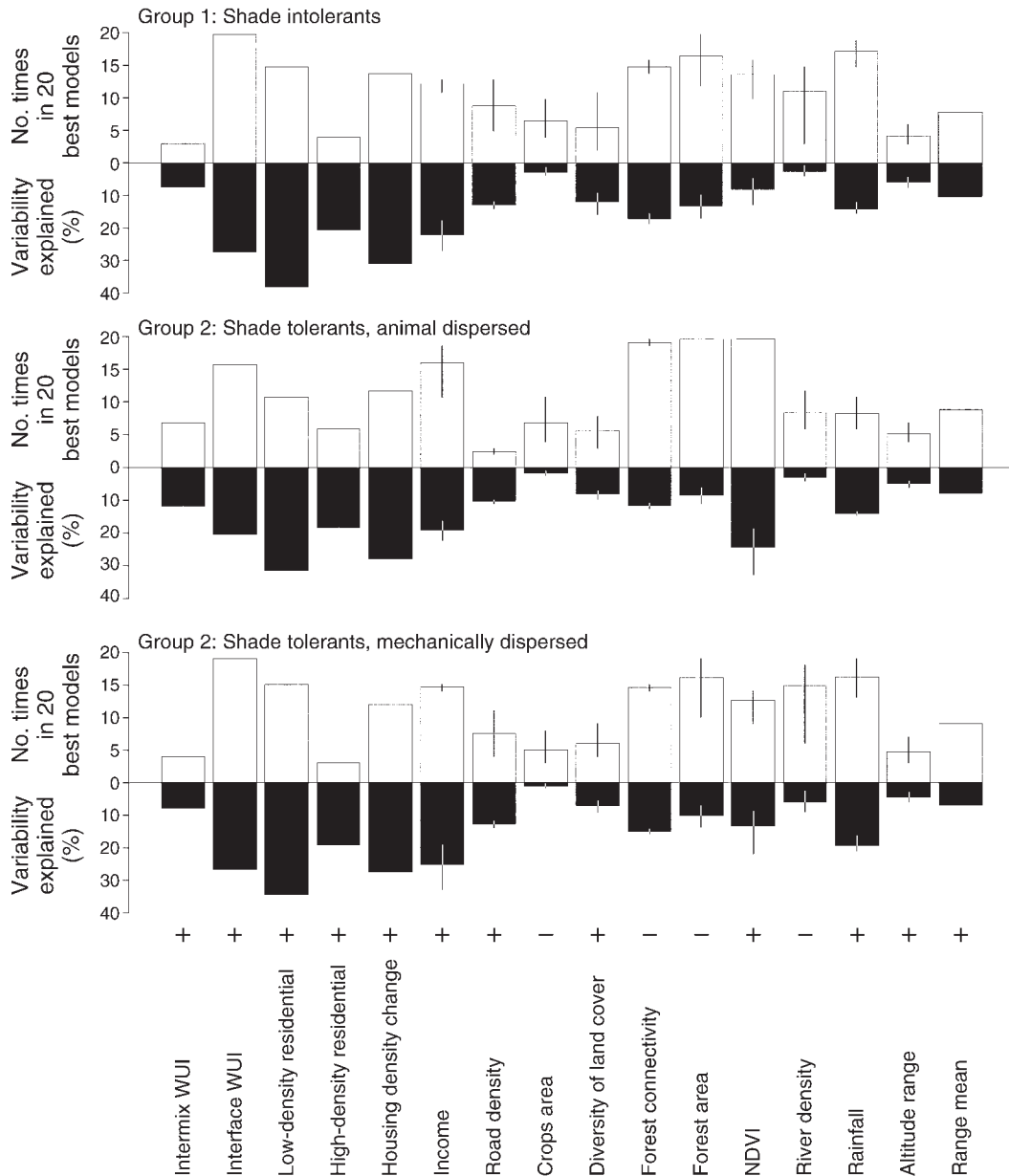


FIG. 4. Summary of regression analyses for groups of species representing different life history traits. White bars represent results of best subset analysis (mean, minimum, and maximum number of times a variable entered the 20 best models). The range of R^2 for the models fitted in the best subsets analysis is 0.54–0.70 (group 1), 0.63–0.73 (group 2), and 0.45–0.59 (group 3). Black bars represent results of hierarchical partitioning analysis (mean, minimum, and maximum percentage of the variability explained by each variable when all variables are included in the model). Housing variables and elevation range do not have range bars because they were included only in one analysis each. Plus (+) and minus (–) symbols have same meaning as in Fig. 3.

landscapes, and urban and suburban areas are important foci for the spread of introduced plant species (Moffatt and McLachlan 2004, Moffatt et al. 2004, Duguay et al. 2007). In West Virginia, USA, two invasive exotic plants (*Lonicera tatarica* L. and *Ailanthus altissima*) are correlated with urban land use at the county level (Huebner 2003). We were thus surprised by the weak relationship between invasive plant richness and intermix WUI, especially given that

low-density residential areas and interface WUI exhibited strong a relationship. A possible explanation is that intermix WUI areas may have been developed relatively recently, and a time lag may obscure a relationship between intermix WUI and exotic plants invasions. For example, in New Zealand, current invasive exotic plant richness is more strongly correlated with suburban population density in 1945 than with present density (Sullivan et al. 2004).

Several other human and environmental variables contributed to the richness of invasive exotic plants in New England, supporting the results of other broad-scale studies in the United States (McKinney 2001, Dark 2004, Stohlgren et al. 2006) and fine-scale studies in New England (Von Holle and Motzin 2007). Income was positively related to invasive exotic plant richness while road density and area of agriculture did not play a major role at the scale of our analysis. Income may function as a proxy measure of socioeconomic activities that favor plant invasions. Wealthy neighborhoods can be associated with more intense landscaping and exotic plant introductions (i.e., the “luxury effect”; Hope et al. 2003), which in turn increases propagule pressure. Road density is strongly related to the presence of invasive exotic plants at fine scales (Trombulak and Frissell 2000, Harrison et al. 2002, Gelbard and Belnap 2003), but contradictory results have been found at broad scales (Dark 2004, Von Holle and Motzin 2007). Other studies at fine scales show a weak relationship between agricultural area and the presence of invasive exotic plants (Moffatt and McLachlan 2004, Moffatt et al. 2004, Duguay et al. 2007).

Richness of invasive exotic plants in our study area was also related to sparser and more fragmented forest cover, higher plant productivity, higher rainfall, and greater elevation range. Forested areas have fewer invasive plants, because low light conditions can prevent many invaders from establishing (Von Holle and Motzin 2007). Consequently, forest fragmentation increases the extent of forest borders, which facilitates invasive exotic plant establishment (Fraver 1994, Cadenasso and Pickett 2001). In our study, counties with both relatively high precipitation and high productivity (i.e., NDVI) represented good growing conditions for plants, potentially leading to greater richness of invasive exotic plants, as has been shown in California (Dark 2004) and across the conterminous United States (Stohlgren et al. 2006).

Several studies have shown an association between human population density and invasive exotic plant richness at large scales (McKinney 2002a, Qian and Ricklefs 2006), but this relationship may only reflect the effect of a larger sampling effort in areas with larger human populations (i.e., the “botanist effect”; Moerman and Estabrook 2006). However, studies that detrended invasive species data to account for the number of herbariums in each county also show a positive relationship between human population density and the richness of exotic invasive plants (Pautasso and McKinney 2007). In our case, the distribution of exotic invasive plant richness of the database that we used followed the same trend manifested for exotic plant species richness in the database analyzed by Pautasso and McKinney (2007). In examining invasive species richness, we chose a robust indicator, which is less sensitive to differences in the sampling effort than, for example, invasive species abundance. We suggest thus

that the associations between housing and invasive species richness presented here is not simply an artifact caused by the botanist effect.

Contrary to our expectation, plant traits did not relate substantially to housing pattern. The grain of our analysis could in part explain this result. Because we worked with presence/absence data, a county may be an area large enough for all groups of plants to find available habitat and be present, even if the differences in abundance among plant types are substantial. Thus, it may be necessary to analyze data on exotic invasive plant cover in addition to species richness. For example, Pysek and Hulme (2005) suggest that a lack of correlation between life history traits and rate of dispersal at broad scales for invasive exotic plants could be a result of variations in the fine scale success of the invaders.

However, the subtle differences in the relationship of plant groups representing different life history traits with intermix WUI and road density may indicate that traits do influence how invasive exotic plants interact with human and environmental variables at broad scales. Shade-tolerant, animal-dispersed plants like *Rhamnus cathartica* L. and *Lonicera* spp. are better adapted for dispersal into and colonization of forest interiors than shade-tolerant, mechanically dispersed plants and shade-intolerant plants (most of which are also mechanically dispersed) (Webster et al. 2006, Von Holle and Motzin 2007). This differential adaptation could explain the comparatively strong association between shade-tolerant, animal-dispersed invasive exotic plants and intermix WUI, which is represented in our study area by housing developments in mostly forested areas.

Our results suggest that the two processes that explain the relationship of invasive exotic plants and housing at fine scales (propagule pressure and suitable habitat) also operate at broad scales, and that the combination makes housing development a key determinant of invasive plant species patterns. Housing-related landscaping can make propagules of ornamental plants available to adjacent areas (Sullivan et al. 2005, Wania et al. 2006) and housing-related disturbances can make the environment more easily invaded (Hobbs and Huenneke 1992).

Approximately 60% of the invasive exotic plants in New England have been introduced as ornamentals (Mehrhoff et al. 2003), but the proportion of ornamental plants differed among the three groups of plant traits. Fifty percent of the shade-tolerant plants were introduced as ornamental plants, while 85% of animal- and mechanically dispersed shade-tolerant plants were introduced ornamentals. However, the relationship with most housing variables was consistent, independent of the proportion of ornamental plants in each group. This suggests that housing causes an increase in ornamental plant invasions as well as invasions by non-ornamental accidentally introduced plants that depend on the

disturbances and human activities (e.g., transportation) related to housing.

We expect the number of invasive exotic plants to increase with future housing growth, further exacerbating the ecological problems that invasive plants pose (Farnsworth 2004). The same process is happening in several parts of the world, for example in central Argentina (Gavier and Bucher 2004). But our findings suggest several ways this expected increase could be reduced. Our results could be used in predictive models to identify and target areas likely to be invaded. In these areas, control measures are necessary if they are already invaded, and monitoring programs need to be in place if no invasion has yet occurred to detect invasions at an early stage. Such early detection is a key element of many large scale management plans aimed at preventing invasive species establishment like the 2008–2012 National Invasive Species Management Plan (National Invasive Species Council 2008), the Invasive Species Science Strategy for Department Of The Interior lands in the USGS central region (U.S. Geological Survey's Invasive Species Working Group 2000), and the Invasive Species Program (U.S. Geological Survey 2004). Similarly, maps of present and future WUI distribution (Radeloff et al. 2005, Theobald and Romme 2007) could be used to forecast at large scales the areas of natural vegetation expected to be more at risk of exotic plant invasions in the future.

Ultimately though, management of future plant invasions may need to go beyond being able to predict areas at risk to active invasion prevention, by requiring changes in existing and future housing developments. 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). Reducing the number of invasives in gardens and other landscaped areas can remove important propagule sources and thereby slow the rates of invasions. However, our results show that the disturbance associated with housing development also fosters invasions. The latter suggests that land use planning may need to take the potential spread of invasive plants from urban areas to natural areas of high conservation value into consideration, and direct development to places with a lower invasion risk. Municipalities have tools (e.g., construction permitting process, public-private partnerships) that can be used to direct housing growth away from areas of natural vegetation of special conservation interest (Waldner 2008).

To be effective, management must be designed and implemented at regional scales. For example, invasive species management in municipality A will not succeed if management is not also conducted in adjacent municipality B (Waldner 2008). Invasive plant management plans will need to be coordinated across administrative jurisdictions, including municipalities and states, in

order to be successful. Grass-roots organizations, including Cooperative Weed and Pest Management Areas throughout the United States, are showing some success towards this goal. Nonetheless, progress is often hampered by a lack of national or even global, standardized invasive plant best management practices that can be applied at the landscape scale (Mehrhoff et al. 2003).

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