UNDERSTANDING THE RELATIONSHIP BETWEEN HOUSING AND EXOTIC PLANT INVASIONS

By

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The Return of The Giant Hogweed (executive summary of my PhD)

Turn and run!
Nothing can stop them,
Around every river and canal their power is growing.
Stamp them out!
We must destroy them,
They infiltrate each city with their thick dark warning odour.
They are invincible,
They seem immune to all our herbicidal battering.

Long ago in the russian hills,
A victorian explorer found the regal hogweed by a marsh,
He captured it and brought it home.
Botanical creature stirs, seeking revenge.
Royal beast did not forget.
He came home to london,
And made a present of the hogweed to the royal gardens at kew.

Waste no time!
They are approaching.
Hurry now, we must protect ourselves and find some shelter
Strike by night!
They are defenceless.
They all need the sun to photosensitize their venom.
Still theyre invincible,
Still theyre immune to all our herbicidal battering.

Fashionable country gentlemen had some cultivated wild gardens,
In which they innocently planted the giant hogweed throughout the land.
Botanical creature stirs, seeking revenge.
Royal beast did not forget.
Soon they escaped, spreading their seed,
Preparing for an onslaught, threatening the human race.
The dance of the giant hogweed

Mighty hogweed is avenged.
Human bodies soon will know our anger.
Kill them with your hogweed hairs
Heracleum mantegazziani
Giant hogweed lives

Lyrics Peter Gabriel, Music Tony Banks, Peter Gabriel, Michael Rutherford,
Steve Hackett, Phil Collins
Genesis - Nursery Crime – 1971 - http://www.youtube.com/watch?v=5P3YyIv7dJ0

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Introduction and summary

Biological invasions have fascinated ecologists for many decades, ever since Charles S. Elton published “*The ecology of invasions by animals and plants*” in 1958. In his seminal work, Elton synthesized the knowledge of his time about biological invasions and highlighted three key aspects of the invasion process. First, through the use of maps showing the expansion of particularly successful invaders, Elton stressed the broad scales and fast rates at which biological invasions occur. Second, he described the negative effects of biological invasions on native biodiversity. And third, he postulated the theory that biological invasions are more successful in less biodiverse ecosystems, where more “empty niches” are available.

Today, 50 years after its first edition “*The ecology of invasions by animals and plants*” may be more relevant than ever. The three main points of the book are the main reasons why biological invasions have gained the attention of ecologists and have become a management priority. Because of the wide and fast expansion around the globe biological invasions are considered one of the most detrimental aspects of global change (Dukes and Mooney 1999, Vitousek et al. 1997). Invasive species are one of the main causes of ecosystem degradation and biodiversity loss because exotic species predate and graze on native species, alter fire regimes, nutrient cycling, hydrology, and energy budgets of ecosystems (Mack et al. 2000, Sax and Gaines 2003, Mooney 2005, Theoharides and Dukes 2007). Analysis of the invasion process has been used to test classic hypotheses of ecological theories and species evolution in an attempt to determine the causes of invasion success (Williamson and Fitter 1996, Rejmaneck 2000, Keane and Crawley 2002, Lee 2002, Tilman 1999, 2004).

Plant species, in particular, are very problematic because they have a profound ecological impact when they become invasive. Invasive plants are exotic species that become established in natural areas in large numbers, replacing native vegetation, altering ecosystems, becoming dominant or disruptive and totally changing the ecological properties of the ecosystems (Mehrhoff et al. 2003). Approximately 4,000 species of exotic plants have established free-living populations in the U.S. and over 1,000 are a threat to native biodiversity (Morse et al. 1995, National Parks Service 2006). Classic examples of the scale and impact of plant invasions include the ecological impacts on wetlands (Zedler and Kercher 2004), the fire mediated spread of invasive grasslands in native shrub dominated ecosystems (Brooks et al. 2004) and pine invasions in grasslands in the southern hemisphere (Richardson and Rejmanek 2004).

The magnitude of the invasion problem has stimulated research to develop theories that explain the success of invasions, but some of the main lines of research arrived at contradictory results. The idea of the “vacant niche” proposed by Elton led to the biodiversity hypothesis, proposing that in areas with larger native biodiversity the ecosystem resources are used in a more efficient way thus preventing the establishment of exotic species (Tilman 1999, 2004). However, the biodiversity hypothesis has been challenged by empirical results from field studies that found larger numbers of invasive species in areas with higher native species biodiversity, indicating that both native and exotic species are drawn to the same resources (Stohlgren et al. 1999).

The “enemy release hypothesis” states that exotic species have escaped their natural consumers, predators, or parasites, and the energy that ordinarily would have to be used to battle the “enemy” threat is used to outcompete native species (Keane and Crawley 2002). Disturbances have been found to favor establishment of invasive species (Hobbs and Huenneke 1992), while propagule pressure (i.e. the number of seeds or individuals arriving to a new site) is proportional to the rate of invasion success (Von Holle and Simberloff 2005). And last but not least, certain life history threats make invaders more successful competitors than native species (Baker 1974, Williamson and Fitter 1996, Rejmanek 2000).

Recently, more holistic approaches have attempted to reconcile the different theories explaining species invasion patterns (Davis et al. 2000, Shea and Chesson 2002, Fridley et al. 2007). The new approach basically assumes that an invader will be successful if it has the adequate level of resources available to grow and outcompete native species. Thus, the availability of necessary resources will be a function of less competition from native species, abundant resources, absence of predators, competitors or parasites, or the release of resources after disturbances.

Globally, biological invasions are accelerating, and land managers struggle to control invaders. The need to manage broad scale invasions has resulted in national management plans in several countries, including the U.S. and Australia (Wittenber and Cock 2005). All of these plans highlight the need to detect susceptible areas as targets for monitoring, and to predict the spread and ecological effect of the invasion, as well as effective restoration techniques (e.g., Invasive Species Science Strategy for Department of the Interior Lands in the USGS Central Region (USGS 2000) or the Management Plan of the US National Invasive Species Council (2001)).

Theories of invasion have been very important to define management strategies, but at times it has been difficult to translate the classic theoretical research to effective measures of biological invasion management. For example, controlling invasions by changing patterns of biodiversity is almost impossible. Biological control (developed from the idea of the enemy release hypothesis) has been applied with certain success in some cases, but entails a high risk of negatively impacting native species (Henneman and Memmott 2001, Wittenber and Cock 2005). From a management point of view, there is a continued need for knowledge about aspects of biological invasions that can be effectively addressed by managers.

Despite the differences in theoretical approaches or the scope in the study of biological invasion success, scientists and managers agree on one important point: successful invasion by exotic species is highly related to human activities (Williamson and Fitter 1996, Lonsdale 1999). Humans facilitate invasions by transporting exotic species to new places and by making ecosystems more vulnerable to invasion through habitat disturbances and degradation (Kowarik 1995, Hodkinson and Thompson 1997, Mack et al. 2000, McNeely 2005). Ultimately, human activities determine the availability of resources that invasive species can use to outcompete native species, for example, by causing overgrazing and developing roads, thereby eliminating competition from native species and providing open areas to be invaded.

However, there is still uncertainty about which human activities are the key drivers of plants invasions (Pino et al. 2005). The most important human-related drivers appear to be socioeconomic factors and land use. Richness of exotic plants is correlated to the level of development at a regional scale (Vila and Pujadas 2001) and the real estate gross product (Taylor and Irwin 2004). Land use change also fosters exotic species invasions (Hoobs and Mooney 2005). The predominant human activities related to the dispersion of invasive plants at the landscape scale include changes in disturbance regime (e.g. fire, grazing) (Hobbs and Huenneke 1992), deforestation and forest fragmentation (forest edges are easily invaded by exotic species) (Theoharides and Dukes 2007), and human infrastructure like roads (roads facilitate non-native plant invasions by providing open habitats and propagule dispersal) (Trombulak and Frissell 2000). Human activities transform the landscapes thereby facilitating exotic plant invasions, because landscape configuration can determine the rates of non-native plant dispersion, and render a landscape more easily invaded (With 2002).

The relationship between human activities and invasions of non-native plants provides a unique opportunity for implementing effective management measures. Contrary to other factors considered in theoretical research, human activities can be controlled: roads can be closed, cattle grazing patterns can be modified, and fires can be controlled. The question though, is which human activities are most related to invasions of nonnative plants so that management resources can be targeted?

Housing growth is a global process occurring at a fast rate and developed areas are a land use with strong negative ecological impacts (Antrop 2000, 2004). In the U.S. between 1950 and 2000, the total proportion of urban land area increased from 1% to

2% (Brown et al 2005). U.S. development patterns are becoming increasingly dispersed, a pattern not observed in other large cities outside the U.S. (Schneider and Woodcock 2008). Dispersed development in rural areas in the U.S. is happening at a fast rate, between 1950 and 2000 the area of low density rural housing increased from 5% to 25% of the conterminous U.S. area (Brown et al 2005).

Housing growth in rural areas is mainly the result of an emigration process. People move to rural areas to live closer to natural amenities, particularly forested areas and lakes (Kaplan and Austin 2004, Gonzalez-Abraham et al. 2007). The spread of housing in areas of natural vegetation caused the growth of the Wildland Urban Interface (WUI), i.e., the area where houses meet (Interface WUI) or intermingle (Intermix WUI) with natural vegetation. In the conterminous U.S., WUI covers 718,151 km^2 (9% of total area) and contains 38% of all houses (44.1 million housing units).

Housing development in the U.S. is expected to continue growing at a fast pace. Based on forecasts, urban and suburban densities will expand to 2.2% of the U.S. land area by 2020, and rural development will expand to 14.3% (Theobald et al. 2005). In the north-central U.S., areas with high potential for future residential density growth are spatially clustered on the periphery of metropolitan areas, in smaller urban centers, and in recreational areas thorough the region (Hammer et al. 2004, Lepczyk et al 2007). Given these growth patterns, it is also expected that the WUI will expand over the next two decades (Theobald and Romme 2007).

This raises the question of whether plant invasions are exacerbated by housing development, and especially by development in the WUI. Research at fine scales, mostly conducted in suburban areas and city outskirts, has found a positive relationship between housing and exotic plant invasions. The number of exotic plants increases with the number of houses and decreases with the distance to houses in southern Argentina (Rapoport 1993), central Europe (Zerbe et al. 2003, Wania et al. 2006), Africa (Stadler et al. 2000), North America (Barton et al. 2004, Turner et al. 2005), and New Zealand (Sullivan et al. 2004). Forest patches in urban or near suburban areas usually contain more invasive plant species than forest patches located in more rural areas (Moffatt and McLachlan 2004, Moffatt et al. 2004, Duguay et al. 2007).

What mechanisms explain the relationships between developed areas and plant invasions? First, humans purposefully import large numbers of exotic species to urban areas. A large proportion of the successful plant invaders in the U.S. have been introduced for utilitarian reasons (aesthetic, food, medicine) (Mack and Erneberg 2002) and most of them as landscaping plants (Reichard and White 2001, Mack and Lonsdale 2001). Thanks to active cultivation and protection, cultivated plant populations can grow until they become established (Mack and Erneberg 2002).

Second, disturbances resulting from housing development (e.g., creation of edges, soil exposure, trampling of native vegetation and trails) create microhabitats that are readily invaded by invasive exotic plants (Hobbs and Huenneke 1992, De Candido 2004, Wania et al. 2006). At a fine scale, disturbances are important because many invader plants are adapted to colonize bare soil (Hobbs and Huenneke 1992). And at broad scales, development results in more fragmented and thus vulnerable landscapes. For example, in Seoul (South Korea) exotic plants are concentrated in forest edges near roads and human settlements, and within patches of small size and complex shape (Song et al. 2005).

Given the velocity, expansion and possible ecological consequences of exotic plant invasions and of housing growth, understanding the relationship between these two processes is a priority for ecologists hoping to provide relevant scientific information for successful management plans.

The objective of my dissertation was to analyze the relationship between housing and distribution of exotic invasive plants in forested areas. Ultimately, my goal was to identify key aspects of the influence of housing on plant invasions that can be used for management and to understand the possible consequences of future housing growth.

In chapter one, I examined three basic questions:

- How important is housing - compared to other environmental and human factors – in models explaining exotic invasive plant distribution?
- Which housing patterns are more related to the distribution of invasive exotic plants?
- Which exotic invasive plant types or life history traits are more related to housing?

I used a database compiled at the county level in New England to relate richness of invasive exotic plants with explanatory variables representing patterns of housing growth, environmental and other types of human factors at the regional scale. Housing was as much or more related to richness of exotic invasive plants than environmental or other human factors. Low density residential areas and Interface WUI were more related to richness of invasive exotic plants than Intermix WUI or high density residential areas. Guilds of invasive exotic plants representing different life history traits exhibited similar strength in their relationship with housing. These results showed that at broad scales exotic invasive plants are strongly related to housing, and that the boundary of suburban areas and other cover types, particularly natural vegetation, is a key element to the distribution of exotic invasive plants at a regional scale.

In chapter two I worked at a finer scale to complement the broad scale analysis, and to examine patterns of invasions in more detail. The main questions examined in chapter two were:

- Is the spatial pattern of invasive plants related to the distribution and density of houses at the landscape scale?
- Does the most common main invasive exotic plants relate to housing differently?

In the Baraboo Hills, Wisconsin, I analyzed the relationship between richness and cover of invasive exotic plants and variables describing housing, landscape configuration and environmental variables in 105 field plots. Richness of invasive exotic plants was higher in plots closer to houses and in plots surrounded by higher housing density, while invasive plant cover increased with in plots surrounded by more houses. My results indicate that at the landscape scale distribution of invasive exotic plants is strongly related to rural housing at the same level that forest fragmentation (distance to roads and distance to forest edges), and that invasive plant species with a history of ornamental use are more related to housing.

Both broad-scale and find-scale analyses in chapters one and two confirmed the importance of housing for invasions by exotic plants, but they neglected the temporal dimension. Current patterns of invasive exotic plant distributions may reflect the ecological legacies from past landscape conditions. If that is the case, then we can expect that future patterns of exotic invasive plant distributions will be in part determined by present environmental conditions and current development would cause an ‘invasion debt'. In chapter three I analyzed the ecological legacies of past housing patterns and the relationship with present distributions of invasive exotic plants. In chapter three my main questions were:

- Does the relationship between spatial patterns of invasive exotic plants with housing last longer than the relationship with forest fragmentation?
- Is the relationship with housing in the past stronger for some of the main invasive exotic plants than others?

In the Baraboo Hills, Wisconsin, I mapped the distribution of houses, roads, forest and agriculture in 1938 (based on the detailed information provided by the Wisconsin Land Economic Inventory, Koch 2006), and 2001 (based on aerial photographs and land cover from the 2001 National Land Cover Database) (Homer et al. 2004). The results showed a clear tendency for invasive exotic plants to be more strongly associated with housing in 1938, and with forest fragmentation in 2001. Also, invasive plant species with the longest use as landscaping plants were more associated with housing in 1938. These results have interesting implications, because housing showed a more long lasting effect on invasive exotic plant distribution than forest fragmentation. The five fold increase in housing units in the area between 1938 and 2001 will very likely result in continued invasions by exotic plants even if no more new houses are built.

To assess the generality of my research findings about the relationship of housing and exotic invasive plants, it is necessary to analyze how the process works in different ecological and socioeconomic environments. And it is important to develop new approaches to analyze the distribution of invasive exotic plants and their relationship with housing. In chapter four I examined the spread of an invasive tree in Argentina using satellite imagery. My research questions were:

- What was the pattern of spatial expansion of glossy privet in the study area between 1983 and 2006?
- Is the glossy privet expansion in the area spatially related to urban areas?

In the Sierras de Cordoba, central Argentina, I used Landsat TM images and change detection analysis to map the invasion of the Chinese tree, glossy privet (*Ligustrum lucidum*), between 1983 and 2006 and quantify its relationship with housing distribution. Glossy privet has expanded greatly between 1983 and 2001.

Detailed maps of glossy privet show a clear pattern of invasion moving from urban centers to the surrounding areas. The proportion of glossy privet decreased with distance from the urban area, but this trend weakened as time progressed, suggesting that glossy privet expand far from the urban areas. In general, the results in Cordoba are consistent with my findings for New England and the Baraboo Hills, and highlight the importance of houses as a driver of invasive plant distributions. The successful use of Landsat TM imagery offers promising methodological advances to map glossy privet – and other invading plants – at broad scales. This could be particularly valuable in developing countries, where other monitoring approaches are often too expensive or unavailable.

Conclusions

Housing growth was strongly related to the distribution of exotic invasive plants. At broad and fine scales, I found consistency in the variables more strongly related to the distribution of invasive exotic plants (housing, forest cover and fragmentation). At broad scales (New England) mean annual per capita income and rainfall were also strongly related to invasive exotic plant richness, while at small scales roads and topography (slope and elevation) provided additional explanatory power.

At broad scales, Interface WUI and low-density residential represent the boundary where residential areas meet with other cover types, particularly natural vegetation, and this boundary may be of key importance for the dispersal of invasive exotic plants. At fine scales, the spatial pattern of low density rural housing was strongly related to the distribution of invasive exotic plants. My results suggests that housing at much lower densities than suburban housing density already had a profound effect on the distribution of invasive exotic plants in forested landscapes. Negative ecological effects and the change in landscape pattern due to low density but widespread housing could result in forests particularly susceptible to invasion by exotic plants.

My results support the hypothesis that two processes underlie the relationship of invasive exotic plants and housing, namely propagule pressure and habitat change favoring invasives. The combination of these two processes makes housing development a key determinant of invasive plant species distribution. The positive relationship between richness of exotic invasive plants and distance to the nearest house highlighted the importance of houses as a source of invasive non-native plants.

And the fact that exotic plants with a longer history of landscape use were more strongly and positively related to housing further supported the importance of propagule pressure. The positive association of cover of invasive exotic plants with the number of houses around each plot indicates that the accumulated effect of several houses could result in either increased propagule pressure or a more disturbed forest.

At the landscape scale, housing and roads exhibited longer lasting effects on exotic invasive plant distribution than forest fragmentation. Thus, we can expect future exotic invasive plant invasions as the result of recent development. There was no evidence that regrowing forests on former agricultural lands would limit invasions by decreasing fragmentation because secondary forests in abandoned fields were more easily invaded than continuously forested sites.

In the Sierras Chicas of Cordoba, Argentina, the invasion of glossy privet was strongly spatially related to urban areas. This means that the relationship of invasive exotic plants and housing is consistent across very different biomes and socioeconomic settings. Our time series analysis of glossy privet spread also highlighted the importance of the temporal dimension when studying factors related to invasive plant spread. The use of Landsat TM images resulted in an effective technique to map the spread of an exotic species over several decades that may be applicable to other areas and invasive species as well.

Management recommendations

Our results have important management implications. Housing is expected to continue growing at a high rate and on a global scale. Housing should be considered as a primary factor to take into account when deciding upon management actions, as well as a main focus of research to clarify the role of humans in fostering exotic plant invasions. My management recommendations focus on three areas: monitoring, environmental education, and landscape planning.

Areas undergoing housing growth should be a main target for **invasive species monitoring programs**. Housing development close to or inside of natural areas of special conservation value should be monitored frequently to control potential invaders before they can establish. Spatial models predicting potential invasive species distribution at any scale should consider housing as an important predictive variable. The importance of ecological legacies of housing needs to be considered when designing monitoring plans, setting monitoring priorities in areas of rapid housing growth. New technologies like remote sensing can aid monitoring programs in areas where the invasive plant forms dense stands with a different spectral signature from native plant communities. However, satellite imagery may not be best suited to detect the onset of an invasion.

Home owners should be included in exotic invasive plant management plans via **environmental education**. Environmental education programs can alert home owners to the risk that certain exotic plant species pose when they are used for landscaping, and inform about the benefits of using native species in landscaping. Last but not least, property owners may actively control some invaders or minimize disturbances around their houses, and they can be involved in monitoring programs.

Finally, **landscape planning** should consider the dangers associated with the spread of invasive exotic plants into areas of natural vegetation. Housing developments should be restricted in the vicinity of natural areas of special conservation value, such as forest interior areas or protected areas. Also, housing development could be used as a management tool, for example in the Sierras Chicas of Cordoba housing growth could be directed towards glossy privet invaded areas and away from native forest stands. Potential positive feedbacks between human factors related to exotic invasive plants should be considered in new developments. Housing development is often accompanied by new roads, and both can cause forest fragmentation. Ultimately of course all three factors, houses, roads, and fragmentation, will increase the abundance of invasive exotic plants and landscape planning will have to take cumulative effects into account.

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Chapter 1: Housing is positively associated with invasive exotic plant richness in New England, USA

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 via disturbed habitats, introductions for landscaping around houses, and dispersing 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), altitudinal range and rainfall, and was negatively related to forest area and connectivity.

Life history traits were not strongly related to housing patterns. In New England, as in many other areas in the United States, housing growth is strong in rural areas. We expect the number of invasive exotic plants to increase as a result of future housing growth. Housing development is an important driver of exotic plant invasions and should be considered a primary factor in plans to manage and monitor invasive exotic plant species.

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 5 000 exotic plant species have established free-living populations in the United States, and over 1 000 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 U.S. have resulted in an estimated economic loss of 120 billion dollars per year, out of which exotic plants alone account for 25 billions (Pimentel et al. 2005).

Several environmental and biological 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). Human activities such as trade, as measured by gross product or importation volume, are important drivers of biological invasions (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 the distribution of invasive exotic plants (Vitousek et al. 1997, Dukes and Mooney 1999, Reichard and White 2001). Since biological invasions are one of the most harmful consequences of global change (Vitousek et al. 1997, Dukes & Mooney 1999), understanding the factors facilitating invasions of exotic plants at broad scales is a necessary first step to develop successful management strategies (Pino et al. 2005, Lodge et al. 2006).

Housing growth is a land use with high negative ecological impacts, and housing growth is rampant in many parts of the world (Theobald and Hobbs 1997, Antrop 2000, 2004). Housing expansion is particularly fast in the U.S. Between 1950 and 2000, the proportion of urban area in the conterminous U.S. 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 are defined as WUI: 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 WUI has 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 plants richness and housing (Rapoport 1993, Sullivan et al. 2004, Wania et al. 2006) that can be explained by two processes. First, humans import exotic plants for landscaping, and exotic plants are accidentally introduced around houses, and subsidized with fertilizers, water, pest control allowing exotics to establish permanent populations (Kowarick 1990, Mack and Erneberg 2002). Later propagules from exotic plants in yards and parks invade adjacent sites (Mack and Lonsdale 2001, Reichard and White 2001, 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, and trails) create microhabitats that are readily invaded by exotic plants (Hobbs and Huenneke 1992, De Candido 2004, Wania et al. 2006).

However, while fine-scale relationships between housing and plant invasions have been well studied, only few studies have analyzed the same relationship at a regional scale and no such studies have been conducted in the U.S. Research at regional scales 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. However, those analyses included all exotic plant species and not just invasive exotic plants, so is difficult to reach a conclusion about the relationship at large scales between housing and invasive plants that are a threat to native flora and fauna.

Understanding the broad-scale relationship between housing and invasive exotic plants thus requires additional research in three main areas. First, it is unclear if 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). For land managers, it is crucial to know the relative importance of housing, because housing development could potentially be controlled or mitigated, unlike most environmental factors. Second, housing growth occurs in different patterns (e.g. urban, suburban, intermix or interface WUI) and at different rates. Knowing the relationship of invasive exotic plants with different patterns of housing growth could help elucidate the ecological consequences of projected housing growth. And third, plant life history traits (e.g. shade tolerance, dispersal mechanisms) represent different ecological adaptations that may affect their invasion in relation to housing patterns. Invasion is most extensive where invasive plant adaptations 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 three research questions using a broad scale database of invasive exotic plant richness for New England, U.S.:

1) Is housing as important as other human-related and environmental factors in explaining invasive plant distributions? We expected richness of invasive exotic plants to be strongly associated with housing because propagules from exotic plants associated with houses invade adjacent sites, and disturbances associated with development favor the colonization and spread of invasive plants.

2) Is richness of invasive exotic plants more strongly related to intermix and interface WUI than high density residential areas? We expected a stronger relationship with WUI, because the WUI setting facilitates the dispersion of propagules into natural ecosystems.

3) Do natural history traits of invasive exotic plants affect their relationship to housing patterns? We expected the distribution of shade-intolerant, mechanically dispersed invasive exotic plants (representing r-selected plants that are adapted to open areas) to be most strongly associated with the highly modified environment of suburban housing. On the contrary, we expected that shade–tolerant, k-selected exotic invasive plants with large, animal-dispersed seeds (adapted to forests) to be associated with intermix WUI, where housing is more dispersed within forested areas.

Methods

Study area

We studied the six states of New England (Vermont, Connecticut, New Hampshire, Rhode Island, Maine and Massachusetts), because this region has the longest history of plant invasions in the U.S. (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 Europeans 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 1,000 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 richness 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 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 canopy). 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/km^2 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 2002c, 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 (Jenzen 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 they entered the models linearly. We calculated a Pearson’s correlation coefficient matrix for all explanatory variables to measure collinearity. 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, 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 any possible latitudinal effects.

Recent papers have pointed out the limitations of null hypothesis testing and stepwise variable selection (Johnson 1999, Burnham and Anderson 2002, Whittingham et al. 2006). Some alternative approaches are based in information theory (IT)

(Burnham and Anderson 2002) and identify alternative models that describe the data equally well and determine the relative importance of the variables included (Johnson 1999, MacNally 2002, Burnham and Anderson 2002). 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 R2 when the variable is dropped from all of the fitted models (MacNally 2000).

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 $Yi= b_0 + b_1x_i + e_i$, where $e_i = \rho\sum_{j=1}^{n} s_{ij}e_j + u_i$ and $u_i \sim$ ind $N(0, \sigma^2 v_i)$, 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, Vivand 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 (The R Foundation for Statistical Computing 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 rivers were not important variables at the scale of our analysis (Fig. 3).

Is richness of invasive exotic plants more 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).

Do invasive exotic plants traits associate 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 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

Our results suggest that the richness of invasive exotic plants is strongly related to housing variables in New England. Housing was as strong a predictor as other human and environmental variables, but the strength of the relationship varied with housing pattern. Amount of interface WUI, low-density residential area, and change in housing units between 1940 and 2000 were strongly and positively associated with richness of invasive exotic plants, while intermix WUI and high-density residential areas were only weakly associated. Interface WUI and low-density residential represent the boundary where residential areas meet with other cover types, particularly natural vegetation, and we suggest that this boundary is of key importance for the dispersal of invasive exotic plants at broad scales.

Previous studies have highlighted the importance of housing patterns in determining the invasion of exotic plants in forests at finer scales. Around Ottawa, Canada (an area both ecologically and geographically close to New England), forest fragments in urban landscapes have 40% more introduced plant species than fragments located in agricultural or forested landscapes (Duguay et al. 2007), and urban and suburban areas are important foci for the spread of introduced plant species. In Manitoba, Canada, forest patches near suburban areas contain more invasive plants (particularly landscaping shrubs like *Rhamnus cathartica* L.) than forest patches located in more rural areas (Moffatt and McLachlan 2004, Moffatt et al. 2004). In Ohio, USA, forests surrounded by larger urban areas have higher cover of the invasive shrub *Lonicera spp.* (Borgmann and Rodewald 2005), and 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 et al. 2003). It thus appears that housing-related disturbances and propagule pressure make urban-adjacent areas particularly good focal points for exotic plants invasions.

We were surprised by the weak relationship between invasive plant richness and intermix WUI, especially given that low-density residential areas and interface WUI exhibited strong relationships. 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 US (Stohlgren et al. 2006, McKinney 2001, Dark 2004) and fine-scales studies in New England (Von Holle and Motzin 2007). Income was 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 socio-economic activities that favor plant invasions. Wealthy neighborhoods can be associated with more intense landscaping and exotic plant introductions (i.e., “luxury effect”) (Hope et al. 2003), which in turn increases propagule pressure. State-level richness of invasive exotic plants across the U.S. is related to the gross state product, a measure of commercial activity and development that may reflect the import of plants as well as related human disturbances (Taylor and Irwin 2004). 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 a both higher precipitation and higher productivity (i.e., higher 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 U.S. (Stohlgren et al. 2006).

Several studies have shown an association between human population and the richness of invasive exotic plants at large scales (McKinney 2002, Qian and Ricklefs 2006), but it has been suggested that this relationship just reflects the effect of a larger sampling effort in areas with higher human population density (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 showed for richness of exotic plants in the database analyzed by Pautasso and McKinney (2007). And 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. It may be thus 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 found 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 particularly 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 stronger association between shade-tolerant, animal-dispersed invasive exotic plants and Intermix WUI, which represents in our study area housing development in mostly forested areas. On the other hand, shade intolerant and shade tolerant mechanically dispersed (i.e. wind) plants are more likely to colonize open areas such as roadsides (Parendes and Jones 2000).

Our results support suggestion 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 per cent 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 finding suggests that housing favors 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.

Our results have important management implications. In New England, as in the whole U.S., housing is growing particularly in areas with natural amenities, and growth is expected to continue (Theobald 2001). Because invasive plant distributions were strongly related to housing growth between 1940 and 2000, 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).

Large scale management plans have been developed to tackle the invasives problem in the U.S. 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) all agree that preventing the establishment of invasive species and the early detection of new invasion sites are priority objectives. Early detection requires though to conduct risk analysis and to predict which areas are more prone to be invaded or where the impact of invasions would be worst (Lodge et al. 2006). The housing variables analyzed in our study could increase the predictive power of national or regional spatial explicit models detecting natural areas more at risk of being invaded, and to target areas for control and monitoring for invasions in an early stage. Maps of present and future WUI distribution (Radeloff et al. 2005, Theobald and Romme 2007) could be used to forecast the areas of natural vegetation expected to be more at risk of exotic plant invasions in the future.

Land management can also limit the spread of invasive plants from urban areas to natural areas of high conservation value. 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. In already developed areas, educational programs targeted to homeowners and landscaping ordinances can be used to reduce the use of invasive exotic plants for landscaping (Waldner 2008).

To be effective, management at the municipality scale must to be coordinated over large areas, because management in municipality A will not succeed if management is not also done in adjacent municipality B (Waldner 2008). Predictive models and risk analysis can be used to detect at a national scale clusters of municipalities encompassing areas of natural vegetation were management can be coordinate to apply the same ordinances of exotic invasive plants control.

In summary, our results highlight the importance of housing as a factor of invasive exotic plants distribution at broad scales. Housing should be considered as a primary factor to take into account when deciding management actions at large scales and as a main focus of research devoted to clarifying the role of humans in fostering exotic plants invasions.

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Table 1. Explanatory variables used in the analysis. The variables are organized in three groups: housing, other human influence, and environmental.

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 county area (km^2/km^2)	USGS National Land Cover Data, (NationalAtlas.gov)
Housing growth between 1940 and 2000	Change in the number of housing units in 1940 and 2000.	GIS analysis of US Census Bureau data, http://silvis.forest.wisc.edu/
Proportion of Interface WUI	Area of Interface WUI /county area (km^2/km^2)	WUI project. SILVIS Lab home page. http://silvis.forest.wisc.edu/
Proportion of Intermixed WUI	Area of Intermix 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	US Census Bureau
Cropland area	Area of cropland divided by area of county (km^2/km^2)	USGS National Land cover data, taken from the 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 (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 ($)	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, (NationalAtlas.gov)
Forest connectivity	Moving window analysis of forest connectivity, 9x9 window where the amount of forest to forest-boundary is divided by the amount of all forest boundaries. Final map resolution 270m window size, and averaged for the whole county	NationalAtlas.gov Algorithm based on Wade et al. (2003).
Precipitation	Mean annual rainfall (mm)	Oregon Climate Service, PRISM climate digital data (NationalAtlas.gov)
Land cover diversity	Diversity of land cover classes (Shannon index)	GIS analysis on USGS National Land Cover Data (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 (NationaAtlas.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

Figure 1. Distribution of invasive exotic plant richness, housing and vegetated areas in New England.

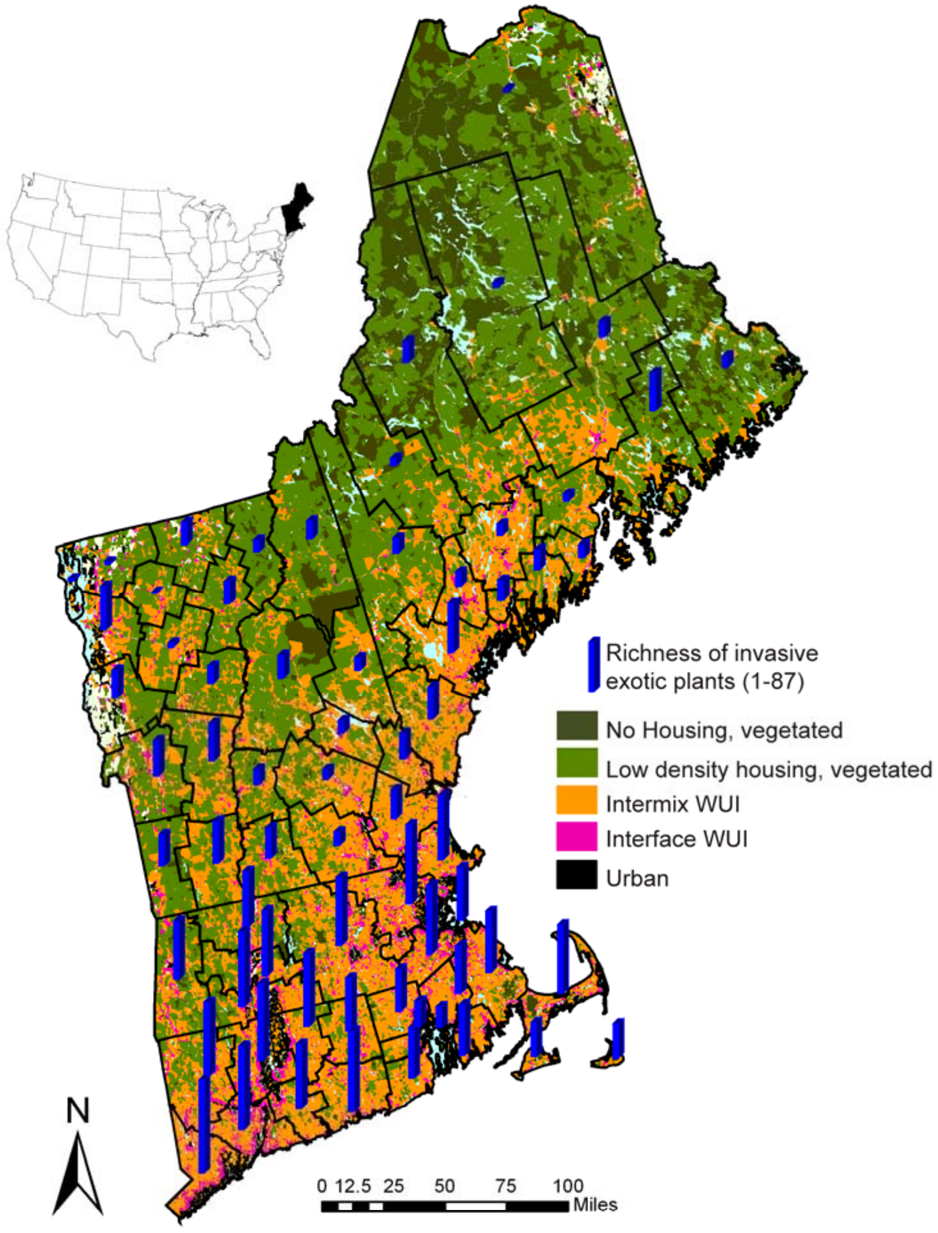
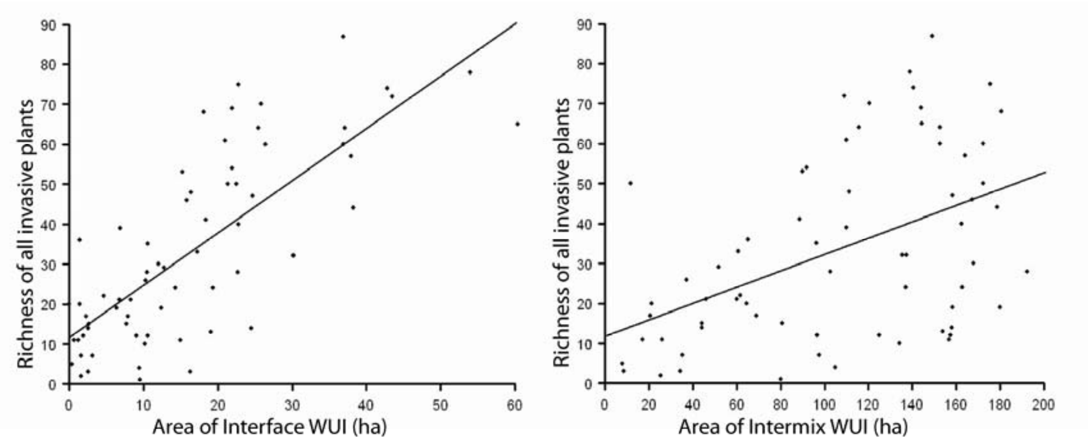
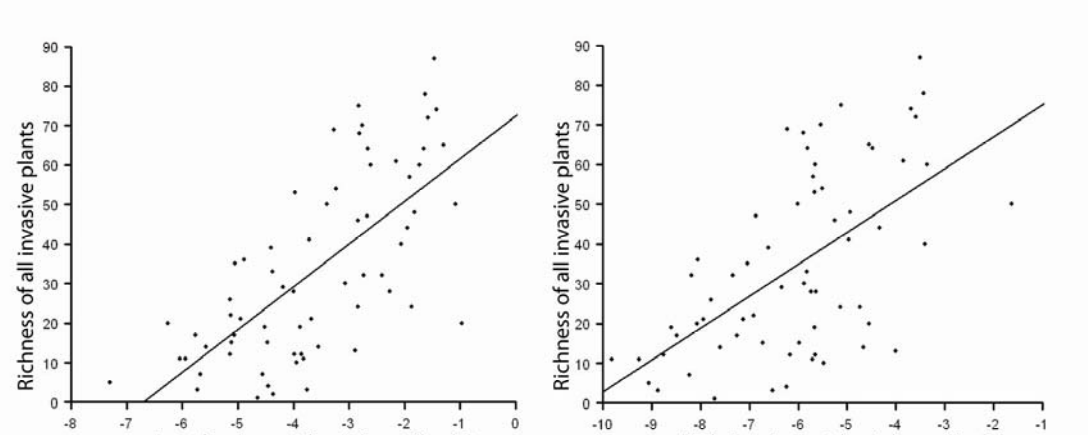


Figure 2. Results of univariate regression analyses between richness of all invasive plant species and housing variables in New England at the county level. In each case, due to the presence of spatial autocorrelation in the residuals of the linear models, both linear and spatial autoregressive Model (SAR) were fitted. * $0.01<p<0.05$, ** $0.001<p<0.01$, *** $p<0.001$. 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: R2=0.46 b=11.045 AIC=575.2, SAR Model: b=8.075 AIC= 547.04).



Linear Model: $R^2 = 0.59$ b=1.3 *** AIC=557.68
SAR Model: b=0.81 *** AIC=541

Linear Model: $R^2 = 0.22$ b=0.2 *** AIC=599.41
SAR Model: b=0.11* AIC=552.74



Linear Model: $R^2 = 0.48$ b=10.82 *** AIC=573.4
SAR Model: b=7.51 *** AIC=547.8

Linear Model: $R^2 = 0.38$ b=0.803 *** AIC=584.1
SAR Model: b=3.22 ** AIC=551.2

Figure 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 R2 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 percent 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 where included only in one analysis each.

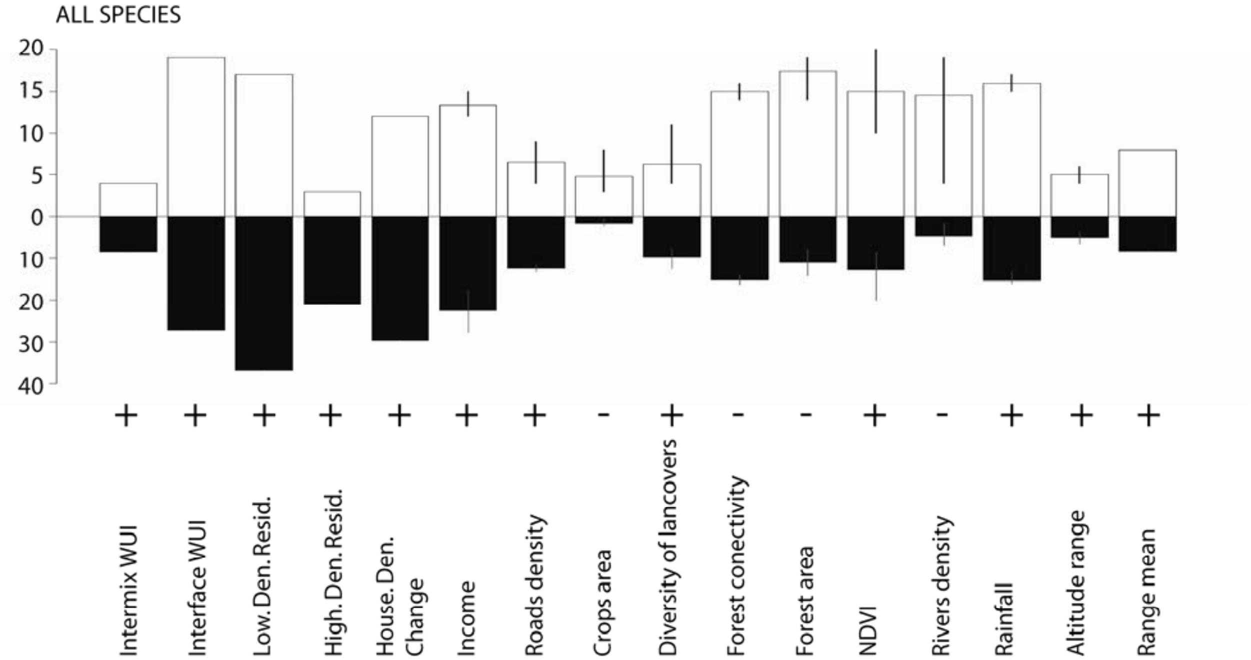
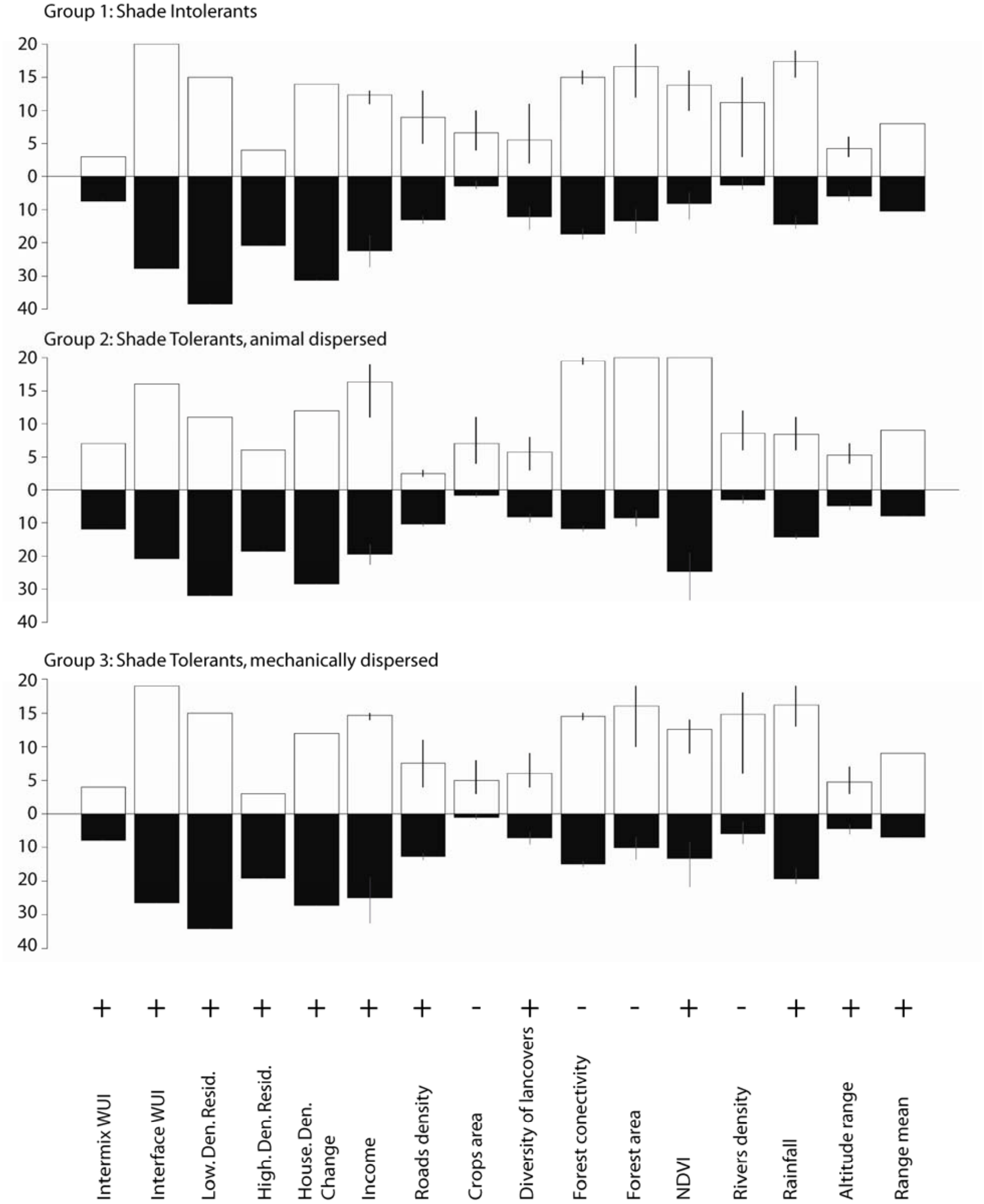


Figure 4. Summary of regression analyses for groups of species representing different life history traits. White bars represent results of best subset analysis (mean, minimum and maximum number of times a variable entered the 20 best models). The range of R2 for the models fitted in the best subsets 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 percent 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 where included only in one analysis each. (Next page)


Group 1: Shade Intolerants
Group 2: Shade Tolerants, animal dispersed
Group 3: Shade Tolerants, mechanically dispersed
20
15
10
5
0
10
20
30
40
+ + + + + + + - + - - + - + + +
Intermix WUI
Interface WUI
Low. Den. Resid.
High. Den. Resid.
House. Den. Change
Income
Roads density
Crops area
Diversity of lancovers
Forest conectivity
Forest area
NDVI
Rivers density
Rainfall
Altitude range
Range mean

Chapter 2: Rural housing is related to plant invasions in forests of southern Wisconsin, USA

Abstract

Forests throughout the US are experiencing the invasion of non-native invasive plants. Rural housing (i.e. low density housing in rural areas) 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 U.S. In the Baraboo Hills, Wisconsin, we sampled 105 plots in forests 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 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 topography, while *Alliaria petiolata* was related to stand condition. Housing development inside or adjacent to forests of high conservation value and the use of non-native invasive plants for landscaping should be discouraged.

Introduction

Non-native plant invasion is considered one of the most detrimental aspects of global change (Vitousek et al. 1996, Theoharides and Dukes 2007). When non-native plants become invasive they establish in large numbers in natural areas, altering profoundly the invaded ecosystem (Elton 1958, Richardson et al. 2000). The economic impacts of non-native plant invasions are substantial; in the U.S. the cost of invasive non-native plants is estimated at $25 billion per year (Pimentel et al. 2005). Approximately 5,000 species of exotic plants have established free-living populations in the U.S. and over 1,000 have been identified as 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 United States. Here the most widespread and abundant invasive non-native plants originate from Eurasia and were imported mainly for food and landscaping, including 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). These non-native plants can outcompete and eliminate native vegetation potentially changing forest succession patterns (Wolfe and Klironomos 2005, Stinson et al. 2007).

Many factors determine invasion patterns, including the ecological condition of the invaded community and propagule pressure, but in general all biological invasions are highly related to human activities (Williamson and Fitter 1996, Lonsdale 1999). Human mediated landscape change facilitates non-native plant invasions, because landscape configuration can determine the rates of non-native plant dispersion, and result in a landscape more easily invaded (With 2002). For example, non-native invasive plants are more common in forest borders and in the typically small forest patches resulting from forest fragmentation (Theoharides and Dukes 2007) and roads facilitate non-native plant invasions by providing open habitats and propagule dispersal corridors (Trombulak and Frissell 2000).

It is thus not surprising that non-native invasive plants are associated with housing at the landscape scale. Honeysuckle (*Lonicera maackii*) presence in woodlots is highest close to towns in Ohio (U.S.) (Bartuszevige et al 2006), and multiflora rose (*Rosa multiflora*) and Japanese barberry (*Berberis thunbergii*) are more common in more developed areas (> 6 houses/km^2) of southern New England (Lundgren et al. 2004). In the state of Colorado (U.S.) invasive non-native plants are more abundant in areas with ranchettes (small ranches 16 ha 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 (Mack and Erneberg 2002, Kowarick 1990) 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 U.S., 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% (Brown et al. 2005), and forested areas were particularly affected (Radeloff et al. 2005). Housing growth has been strong in the north-central U.S. since 1940, and development is common in rural areas close to natural amenities such as forests and lakes, resulting in habitat loss and fragmentation and substantial landscape transformation (Hawbaker and Radeloff 2004, Gonzalez-Abraham et al. 2007, Lepczyck et al. 2007).

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). It often occurs at low densities, can affect an extensive area (Theobald et al. 1997), and often occurs in natural ecosystems with high conservation value (Hansen et al. 2005). However, little is known about the relationship between non-native invasive plants and housing in natural areas undergoing low-density housing development.

We hypothesize that rural housing facilitates non-native plant invasion at the landscape scale, because houses are sources of propagules for species 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, US. Specifically, we evaluated the spatial pattern of richness and abundance of invasive non-native versus the spatial patterns of houses, topography, forest structure, and human-related forest fragmentation variables, and 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 (89º 43’ 52”W, 43º 24’ 56.6”N) and covers about 22 by 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 thirty 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 1979). Invasive plants are becoming a conservation concern particularly in protected areas. The most widespread invaders include garlic mustard (*Alliaria 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/km^2, but in most of the area the range is 0 to 7 houses/km^2. Housing density is higher in the eastern portion of the area (8 to 30 houses/km^2), and decreases towards the West (0 to 10 houses/km^2) 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 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 to focus the 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 et al. 1996). Plots had a 20-m radius with three interception transects for cover measurements extended from the center outwards at 120 degrees from each other and starting two meters 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, acceded 1/2009) and the manual of vascular plants of northeastern United States and adjacent Canada (Gleason and Cronquist 1991).

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). All GIS analyses were performed in ArcGIS 9.1 (ESRI 2005).

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 (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. Aspect can be an important determinant of plant distributions, since south facing slopes are more xeric than north facing ones. 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 in 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 to 25%, 25 to 50%, 50 to 75%, and 75 to 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 with large trees, basal area and variances in tree sizes (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 fitted 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 2001). For each of the two response variables, four models were fitted, 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 methods 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 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 2000). 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 2001). 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 $p \leq 0.05$. 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 fitted, 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.

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. 2). 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 fitted 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 fitted models. Distance to nearest house and road explained less richness variation (between 20 and 30%) and entered 9 models out of 20 fitted. Cover of native vegetation explained substantially less variation of invasive non-native plant richness (11%) and entered the best subsets in just 6 out of 20 fitted models (Fig. 2). 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. 2). 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 fitted 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. 2). 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 nonnative plants also tended to be higher in plots with prior logging.

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 and gentler slope, but also showed a statistically marginal association with the number of houses around each plot. Multiflora rose was only 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).

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.

Prior research on the relationship between housing and invasive exotic plants examined gradients from urban to rural areas (Hansen et al 2005), and forests located inside or in close proximity to suburban areas. Richness and abundance of invasive non-native plants is usually high in suburban forests (Moffatt et al. 2004, Moffatt and McLacchlan 2004, 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 pattern facilitates the dispersal of propagules and results in a habitat more suitable for colonization (With 2002). Rural houses can facilitate dispersal becoming the entry points of propagules to the landscape (i.e. propagules from ornamental plants) (Knops et al. 1995). If housing is widespread, even remote areas of the landscape will receive invasive non-native plant propagules. In forested areas, housing will also result in more fragmentation, thus providing a landscape more suitable for colonization with more forest edges. 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. 1995).

The positive relationship between richness of non-native invasive plants and distance to the nearest house in our study area highlighted the importance of houses as sources of invasive non-native plants. However, abundance of invasive non-native plants was also positively associated with the number of houses around each plot. The combined effect of several houses appears to be a more disturbed forest, where invasive non-native plants could increase in cover and become dominant (Moffatt and McLachlan 2004, Moffatt et al. 2004). Our results suggest that rural housing is facilitating two aspects of invasion of non-native plants: colonization from houses that serve as a source of propagules, and spread (i.e. cover) related to the accumulated effects (i.e., multiple disturbances) of development.

Roads can provide suitable habitat (e.g. bare soil and open areas), changing the conditions in adjacent ecosystems and facilitating invasive plant propagule transportation, thus favoring 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).

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.

The differences in the responses of buckthorn, honeysuckle, Japanese barberry and multiflora rose to our explanatory variables are likely 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 2001) and is not a landscaping plant in our study area, which may explain its lack of association with housing.

Our findings have important management implications. Housing growth rates are high in the U.S. (roughly growing 1.6 % per year), a trend that is likely to continue in the future (Theobald 2001, 2005). Beyond the growth rate, the pattern of 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). For example, 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 dispersal of non-native invasive plants propagules over long periods of time. The list of new plants being imported as ornamentals is growing (Reichard and White 2001), so it is likely the yards of rural houses will continue receiving new, potentially invasive, plants.

Future forest and conservation management plans should address the facilitation of non-native plant invasions by rural housing in three ways. First, areas undergoing rural housing development should be focal targets of non-native plant monitoring. Second, building should be discouraged inside or adjacent to forests of special conservation value. Finally, home owners, developers, landscape architects, and landscaping companies that install and maintain landscapes around homes and in residential common areas should be included in management planning and should be targeted with educational programs aimed at preventing the most harmful non-native plants from being used in landscaping.

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

Latin name	Common name
Alliaria petiolata	garlic mustard
Berberis thunbergii	Japanese barberry
Elaeagnus umbellata	autumn olive
Lonicera sp.	honeysuckle
Rhamnus cathartica	common buckthorn
Rosa multiflora	multiflora rose
Solanum dulcamara	bittersweet nightshade

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	First component obtained from PCA analysis including mean and variance of dbh and basal area, and total basal area per plot

	basal area	
Cover of native vegetation	Describes a gradient from plots with extensive cover of herb or shrubs to plots were 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 3 m
Logging	History of logging	Presence of logging stumps in each plot (present/absent)
Environment		
Aspect	Orientation of the slope were 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 (degrees)	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)

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

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 ***	-0.103 slope 3.69 ·		140.2
Model 2	-0.016 elevation 14.66 ***	-0.10 slope 3.69 ·	0.015 houses around plot 3.69 ·	127.2
garlic mustard				
Model 1	-1.56 logging 8.11 **	0.394 cover natives 5.1*		118.4

* (0.01≤ p ≤0.05) ** (0.001≤ p ≤0.01) *** (p<0.001)

Figure 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.

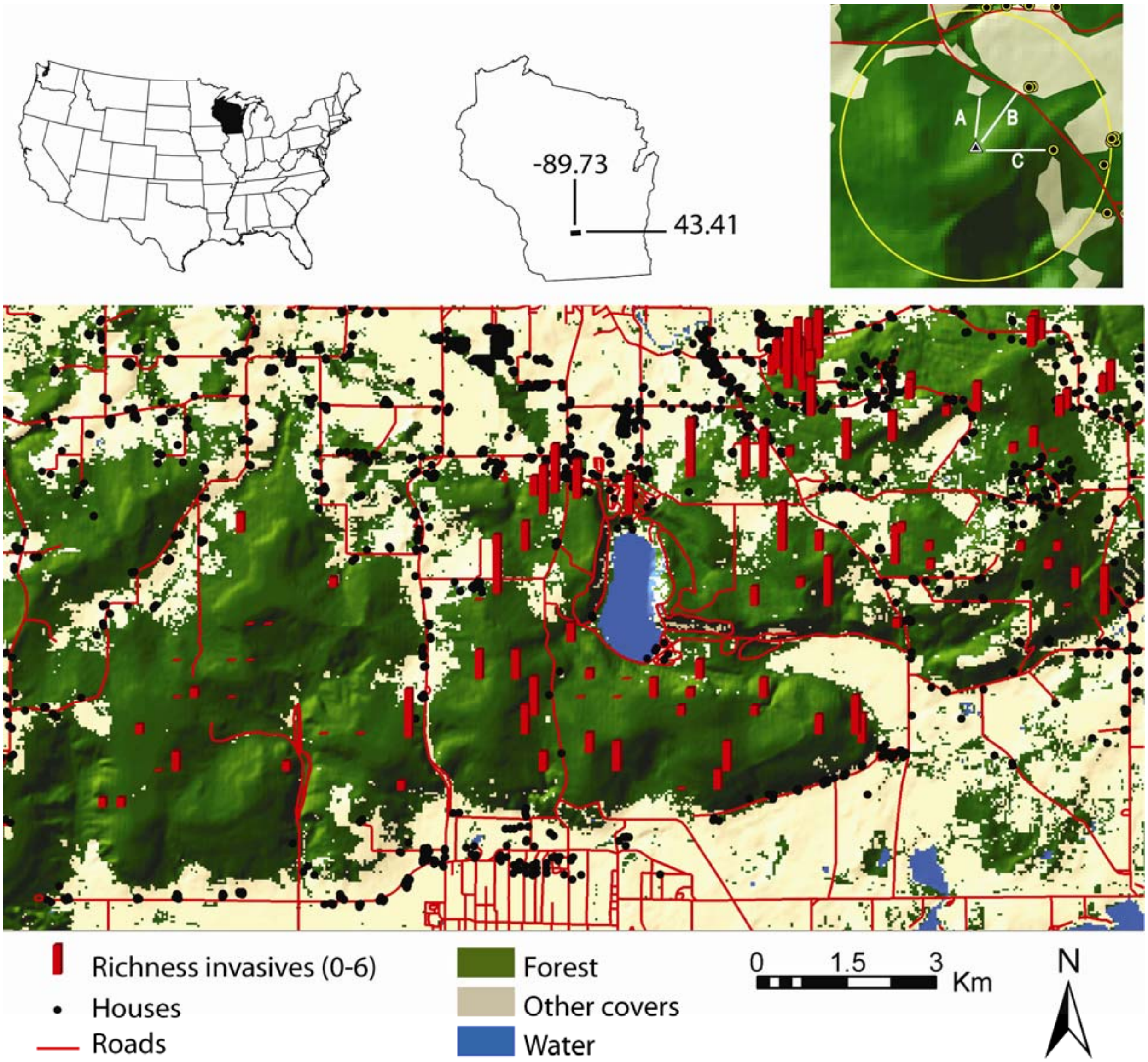
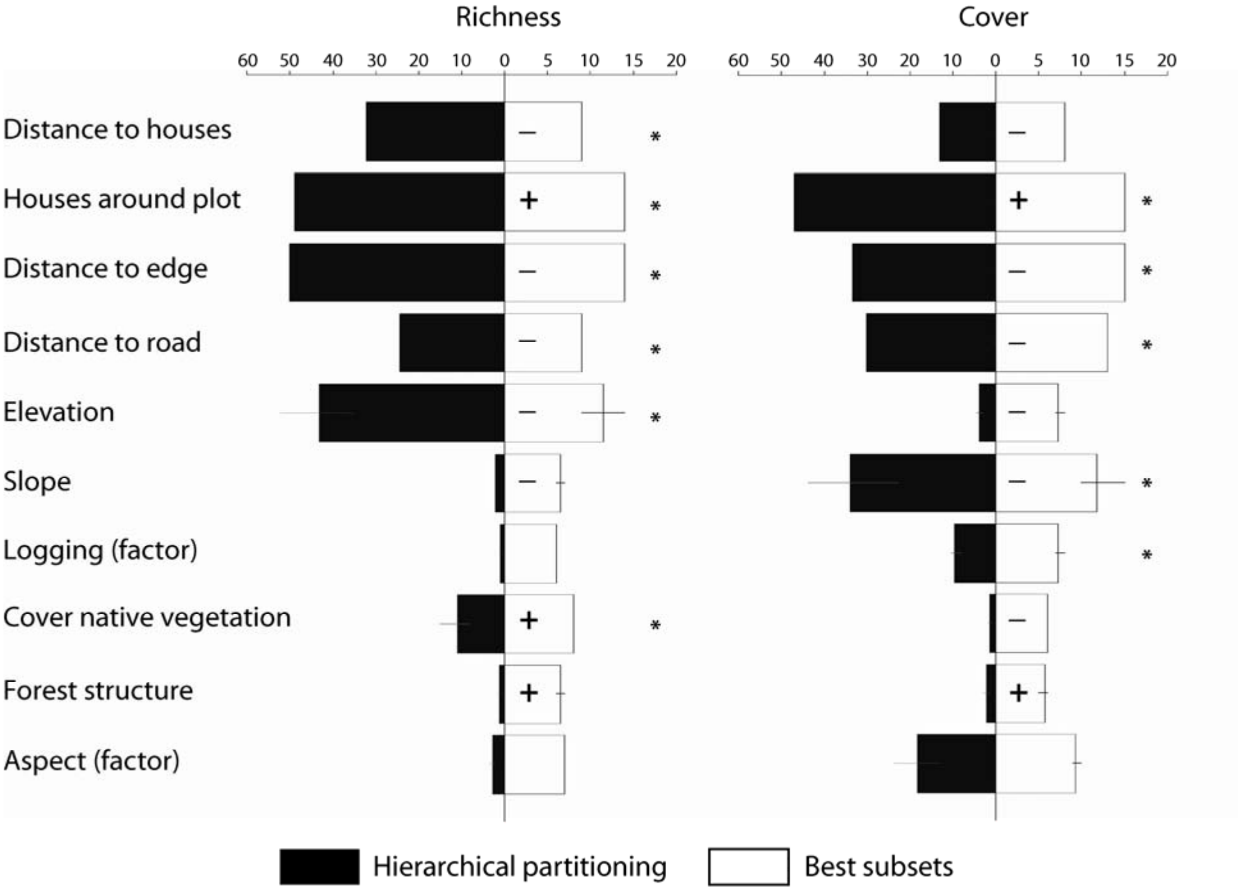


Figure 2. Summary of regression analyses for all richness and cover of invasive non-native plants. White bars represent results of best subset analyses (mean, minimum and maximum number of times a variable entered in 20 models). Black bars represent results of hierarchical partitioning analyses (mean, 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.



Chapter 3: Seventy-year legacies of housing and road patterns are related to non-native plant invasions in the forests of the Baraboo Hills, Wisconsin, USA

Abstract

The ecological legacies of landscape pattern can potentially have a long lasting effect on plant invasions distribution. The objective of this paper was to test the hypothesis that past patterns of human infrastructure (i.e., housing and roads) have a more enduring effect on non-native invasive plant distribution than past forest fragmentation. We recorded richness and cover of the most common invasive non-native plants in 105 plots in forests interiors of the Baraboo Hills, Wisconsin. We summarized forest fragmentation, roads and housing density in 1938 and 2001. Richness and cover of non-native invasive plants were more associated with human infrastructure in 1938 than in 2001. Richness was more related to the number of houses within 1-km of each plot (p= <0.0001, r^2= 0.24) than in 2001 (p= <0.0001, r^2= 0.21). Cover was more strongly related to distance to the closest houses in 1938 (p= <0.0001, r^2= 0.5) than in 2001 (p= ns). On the contrary, forest fragmentation in 2001 was a better predictor of richness and cover of non-native invasive plants than in 1938. *Lonicera spp* (honeysuckle) was more strongly associated with the 1938 landscape (particularly with human infrastructure), and *Rhamnus cathartica* (common buckthorn), *Rosa multiflora* (multiflora rosa), *Berberis thumbergii* (Japanese barberry) weaker (in ranked order).

Human infrastructure (housing and roads) and forest area exhibited 70-year ecological legacies, whereas forest fragmentation effects were more immediate. Land managers need to account for the legacies of past landscapes pattern when fighting invasive species and planning future development.

Introduction

Biological invasions are one of the most important causes of biodiversity loss (Mack et al 2000) and are considered one of the most detrimental aspects of global change (Vitousek et al. 1996, Theoharides and Dukes 2007). Non-native plants can profoundly alter invaded ecosystems (Simberloff 1997) and the cost of plant invasions in the U.S. is estimated at $25 billion per year (Pimentel et al. 2005). Understanding, and potentially predicting, the patterns of biological invasions is thus of great importance for land management and conservation.

Among the factors facilitating non-native plant invasions, human activities are particularly important facilitating invasions by dispersing exotic species to new places, and by making ecosystems more vulnerable through habitat disturbances and degradation (Elton 1958, Mack et al. 2000, Theoharides and Dukes 2007). At a landscape scale, forest fragmentation and infrastructure (roads and housing) render a landscape more easily invaded by non-native plants (Theoharides and Dukes 2007).

Landscape characteristics such as forest fragmentation and human infrastructure are strongly related to the distribution of invasive non-native plants in Eastern U.S forests. Multiflora rose (*Rosa multiflora*), buckthorn (*Rhamnus cathartica*), honeysuckle

(*Lonicera* spp.) and Japanese barberry (*Berberis thumbergi)* are usually associated with roads (Flory 2006, Lundgren et al. 2004, Predick and Turner 2008). Honeysuckle and multiflora rose are frequently associated with forest edges (Ruremonde 1991, Lundgren et al. 2004). Multiflora rose and Japanese barberry are more common in more developed areas (> 6 houses/km^2) of southern New England (Lundgren et al. 2004). In the Baraboo Hills region of Wisconsin (US), low density housing, forests edges and roads are strongly and positively associated with non-native plant invasions in forests interiors (Gavier et al., 2008). The question is how long the factors determining invasions of non-native plants endure, or in other words, whether ecological legacies cause current patterns of invasive plant species to reflect past patterns of human activities.

Legacies of past land use can persist for a long time determining current ecological conditions. Past land uses and disturbances that leave a strong ecological legacy are forestry, agriculture, modification of natural disturbance regimes and overgrazing (Foster et al. 2003). For example, 19th century forest clearing and agricultural expansion strongly influences present forest structure in New England (Foster 1992, Bellemare et al. 2002). Legacies from agriculture in particular are strong determinants of plant invasions, due mainly to the availability of disturbed sites and changes in soil nutrients and biota that facilitate establishment of non-native invasive plants (Milchunas and Lauenroth 1995).

During the 20th century, the U.S. Midwest has undergone a strong process of land use change that also determined changes in the landscape composition and configuration (i.e. forest fragmentation and human infrastructure development). Large-scale land use change occurred since the mid-19th century, first due to logging and agricultural expansion, and later in the form of farm abandonment and forest recovery (Radeloff et al. 1999, Burgi and Turner 2002, Rhemtulla et al. 2007). In addition to initial loss and partial recovery of forest area, Midwestern forests have also become fragmented, with reductions in patch size, increases in forest edges and changes in landcover spatial associations (i.e. urban areas tend to occur near to forests) (Bresee et al. 2004, Martin et al. 2008).

Forest fragmentation is also increasing in the Midwest due to housing growth and road development (Radeloff et al. 2005a, Hawbaker et al. 2006, Gonzalez-Abraham et al. 2007). In the United States, the area of low density housing in rural areas increased from 5% to 25% between 1950 and 2000 (Brown et al. 2005). Housing growth is strong in forested areas (Radeloff et al. 2005b), and widespread in the north-central United States (Hammer et al. 2004, Lepczyck et al. 2007) as people want to live closer to natural amenities (Kaplan and Austin 2004).

Considering the strong relationship between agricultural ecological legacies and non-native plant invasions, we can expect that a history of agricultural abandonment is operating as a strong determinant of plant invasions in the Midwest U.S. However, because of the strong relationship between landscape characteristics and spatial patterns of non-native plant invasions, ecological legacies of landscape configuration are another potential factor in present non-native invasive plant distribution, and these ecological legacies have received little attention previously.

We hypothesized that the ecological legacies of landscape pattern will have a lasting effect on non-native plant invasions, but their effect will depend on the type and spatial dynamics of the landscape characteristic considered (i.e., forest fragmentation vs. human infrastructure). We expected that forest fragmentation (e.g. amount of forest edge, forest patch shape and size) will have a shorter effect on non-native invasive plant distribution, because of their dynamic character in the landscape (i.e. forest regeneration is continually changing forest spatial patterns, so the areas more prone to be invaded are constantly changing). On the other hand, human infrastructure (e.g. housing and roads) will have a more durable effect. The permanent character of human infrastructure in the landscape will result in a long lasting effect determining a surrounding disturbed area and acting as a source of non-native invasive plants propagules for a long time.

Evaluating the importance of past landscape characteristics on the present distribution of non-native invasive plants can have important ecological and management implications. To better forecast the distribution of non-native invasive plants in the future, we need to know which are the key ecological legacies that will determine future patterns of non-native invasive plants. Given how much the landscapes of the Midwest have changed and will likely change in the future, it is important to understand the effects of past landscape pattern on the present condition of non-native plant invasions, and hence the likely effects of current landscape patterns on future patterns of invasive plants.

The objective of this paper was to assess how past landscape pattern and land use are related to current pattern of non-native invasive plants in forests of the midwestern United States. Specifically, we 1) characterized the landscape pattern in Baraboo Hills, Wisconsin (USA) in 1938 and 2001, 2) compared the relationship of non-native plant invasions with forest fragmentation and with human infrastructure (e.g. houses and roads) in 1938 and 2001 to test whether historic or recent forest fragmentation or human infrastructure had greater effects, 3) quantified the effect of past land use (i.e. forested / non forested) on the present distribution of non-native invasive plants, 4) tested the association of the most common non-native invasive plants with landscape pattern in 1938 and 2001 to assess if there was a species specific association with the past landscape characteristics.

Materials and Methods

Study area

Our study area was located in the Baraboo Hills in southern Wisconsin, US (89º 43’ 52”W, 43º 24’ 56.6”N) and covered about 22 by 13.4 km (Fig.1). Hilly topography resulted from the erosion of Precambrian sediments that left a quartzite remnant (maximum elevation: 423 m). The eastern portion of the study area was glaciated and has a more gentle topography (Mossman and Lange 1979, Dott and Attig 2004).

The Baraboo hills contain the largest tract of continuous forest in southern Wisconsin. 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 (*Acer rubrum* and *A. saccharum*) (Lange 1998).

European settlement changed the Baraboo Hills via logging to get wood and agriculture fields. Wood was heavily consumed in limekilns and charcoal production in the late 1800's. Agriculture and cattle grazing peaked in the 1930's but lately agricultural land abandonment (especially pastures) resulted in secondary forest (Lange 1990, Rhemtulla et al. 2007). Logging has ceased in recent decades in protected areas, but most private landowners still actively manage their forests. Fires are rare and actively suppressed. The main natural disturbance is wind throw, which creates small openings (Mossman and Lange 1979, Lange 1990).

Invasive plants are conservation concern particularly in the protected areas. The most widespread invaders include garlic mustard (*Alliaria petiolata*), Common buckthorn and honeysuckle, aggressive invaders particularly in oak forests and woodlands. Japanese barberry and multiflora rose are widespread (Lange 1998, Wisconsin Department of Natural Resources 2008).

Rural housing growth is substantial in the Baraboo Hills, located 60 miles from Madison metropolitan area. Between 2000 and 2005, Sauk County had the third highest house growth rate (16%) of Wisconsin (US Census Bureau 2008). In the study area the range of housing density was 0 to 50 houses/km^2. Housing density was higher in the eastern portion of the Baraboo Hills (typically 8 to 30 houses/km^2) than the western (0 to 10 houses/km^2). Land ownership was diverse in the area. The east side is mostly in small private ownership, while the western part includes several large tracts of public and protected areas (e.g. Devil's Lake state park and Baxter Hollow administrated by The Nature Conservancy).

Maps of the study area in 1938 and 2001

We obtained a detailed map of the Baraboo Hills in 1938 from the Wisconsin Land Economic Inventory (Rhemtulla et al. 2007). The Wisconsin Land Economic Inventory was a state government land survey conducted between 1928 and 1938 at the height of the agricultural period (Koch 2006). Surveyors traversed the landscape at 0.8 km intervals, and drew field maps noting land cover (including species composition, density and diameter for forests), agricultural uses (e.g. pastures, croplands), recent burns, and water with a minimum mapping unit of 0.8 ha, plus all human infrastructure (including buildings and roads). Scanned original maps obtained from the University of Wisconsin Digital Collections were digitized on screen (houses, roads, and land use) with a geopositional error of 20 m or less based on GPS control points. The land use polygons were grouped in five categories (forests, crops, pastures, water and urban) and transformed to a raster format with a 30 m pixel size to match the 2001 landcover data.

We used the 2001 National Land Cover Data (NLCD 2001) to obtain a current landcover map. The NLCD 2001 was created from Landsat images (30 m pixel size) using supervised classification and regression tree algorithms (Homer et al 2004). We grouped the 16 original landcover classes into five (forests, crops, pastures, water and urban).

In 1938 and 2001 maps we eliminated all patches smaller than 1 ha (merged with the largest neighboring patch), and we eliminated fine-scale patterns along patch edges in the 2001 map with a mode filter. As a result, we obtained two comparable maps with the same resolution (minimum patch size) and comparable detail in boundaries shapes. Houses were digitized from aerial photographs taken in the year 2001 at a scale of

1:10,000 or 1:15,000 from the Wisconsin Department of Natural Resources. All GIS analyses were performed in ArcGIS 9.1 (ESRI 2006) and ERDAS IMAGINE 9.0 (Leica Geosystems 2005).

Landscape Change 1938-2001

We estimated the main landscape changes for the whole study area and at the plot level. We calculated a small set of landscape indices for 1938 and 2001 with FRAGSTATS 3.3 (McGarigal et al. 2002) since most landscape indices are strongly correlated (Li and Wu 2004, Martin et al. 2008). We measured the total area in each land use, the number of houses, and for forest the mean patch size, mean distance to the closest forest patch, number of patches and total edge. We also characterized the same changes in the landscape context in a 1 km buffer around our invasive species sampling plots (plot level). We summarize the mean values for all landscape pattern variables calculated at the 1 km buffers for 1938 and 2001. We overlaid the land use maps for 1938 and 2001, and quantified the transition probability among landcovers.

Human infrastructure variables

Housing is a key factor in invasions because houses can be a source of propagules from landscaping plants and human activities related to housing (e.g. vegetation trampling, logging, hunting) can result in an environment more easily invaded (Reichard and White 2001, Wania et al. 2006). Roads can facilitate propagule transportation and determine open areas that facilitate plant invasions (Trombulak and Frissell 2000). We measured the distance from each plot to the closest house and road, and counted the number of houses in a 1-km buffer around each plot.

Forest fragmentation variables

Forest edges have ecological characteristics (e.g. more sunlight, exposure to plant propagules) that make them especially susceptible to plant invasions (Fraver 1994, Cadenasso and Pickett 2001). We measured for each plot the distance to the closest forest edge, and the length of forest edge and the ratio of amount of forest edge/amount of forest within 1 km of each plot. Forests are less prone to be invaded by non-native plants than open areas (Von Holle and Motzin 2007), so we measured the amount of forest within 1 km around each plot.

Land use history

We examined the influence of past land use in the present distribution of non native invasive plants. For each plot we recorded the land use in 1938 represented by four categories: hardwood forests, dense oak-hickory forest, open oak-hickory forest, and open (i.e., agriculture or grassland).

Sampling design

We used a stratified random design (Elzinga et al. 1998) with three strata representing forests with no housing, low density, and high density housing in 2001 to set our field plots (Gavier et al. 2008). Forest fragments smaller than 10 ha were excluded to focus the analysis on forests interiors. We recorded data on 105 plots in the summers of 2006 and 2007 located at least 300 m apart to minimize spatial autocorrelation. All plots were located at least 30 m from a forest edge. The sampling effort was adjusted after a power analysis for each stratum (Sutherland et al. 1996). Plots had a 20-m radius with three line intercept transects for cover measurements extended from the center outwards at 120 degrees from each other and starting two meters from the center, to avoid overlapping measures (Elzinga et al. 1998, Gavier et al. 2008).

Data collected

We examined the six most common invasive non-native plant species in our study area (Invasive Plants Association of Wisconsin 2003, Czarapata 2005), which represented some of the most widespread and problematic invasive plants of eastern U.S. forests (Cox 1999, Webster et al. 2006). The set represents plants with a long history of introduction in the area, all before 1900 (Czarapata 2005) (Table 1). Garlic mustard was not considered because it was first observed in the study area in 1985 (Lange 1998). Richness was measured as the number of the invasive non-native plant species present in the 20-m plot and cover as the length of the intersection of invasive plants projection on the three cover transects (Canfield 1941).

Statistical analysis

We analyzed landscape changes between 1938 and 2001 at the plot level with a paired t-test. We used a semi-variogram analysis to assess if spatial autocorrelation was present in the difference values between the variable values in 1938 and 2001 used in the paired analysis.

Regression analysis was used to measure the association between patterns of plant invasions and landscape variables in 1938 and 2001. Since most landscape variables in both years were correlated above r= 0.6, we used univariate regression instead of multivariate analyses. Several variables (distance to closest house, edge and road; number of houses in a 1 km buffer around each plot) were log transformed to meet assumptions of linear regression. Individual linear regression models were fitted using richness and cover of non-native invasive plants as response variables, and the set of landscape pattern variables (human infrastructure and forest fragmentation) in 1938 and 2001 as explanatory variables. Residual plots were examined to confirm assumptions of linear regression (Chatterjee 2000).

To analyze the relationship between presence of individual non-native invasive plants with landscape pattern in 1938 and 2001, we used univariate logistic regressions (Hosmer and Lemeshow 2000). We analyzed the four most abundant non-native invasive plants (Japanese barberry, honeysuckle, multiflora rose and buckthorn). Logistic models were assessed using a likelihood ratio test and Hosmer and Lemeshow goodness-of-fit test (Hosmer and Lemeshow 2000). The significance of explanatory variables was determined using a likelihood ratio test with $p \leq 0.05$. For each plant species, we fitted models for each explanatory landscape variable in 1938 and 2001.

We assessed if each response variable was more associated with the 1938 or 2001 version of each explanatory variable. We compared the correspondent linear and logistic regressions models for 1938 and 2001 for each explanatory variable to find which year produced the best fit. If both years had a significant association with the response, we fitted models entering both the 1938 and the 2001 version of the explanatory variable. In the first model the 1938 variable was entered first, so we could test if the 2001 variable was explaining a significant portion of the variation in the response after the variance explained by the variable for 1938. A second model was fitted entering the 2001 variable first, so we could test if the 1938 variable was explaining a significant portion of the variation in the response after the variance explained by the variable for 2001.

This approach separated two cases: 1) no variable accounted for more variance after the other was included in the model; we then considered both 1938 and 2001 to be associated with the response at the same level, 2) one variable accounted for significant variation after the other was included in the model, and we considered the variable explaining the extra variance more strongly associated with the response. Spatial autocorrelation of the models' residuals was tested with a semi-variogram analysis (Isaaks and Srivastava 1989).

We used regression analysis to assess the influence of past land use on present non-native plant invasions. Simple linear models were fitted using richness and cover of non-native invasive plants as response variables. Logistic models were fitted using presence of the most common non-native invasive plants. In all cases we used as an explanatory variable a factor representing four land uses: hardwoods forests, dense oak-hickory forest, open oak-hickory forest, open (agriculture or grassland).

We included just the 82 plots located in forested areas in 1938 and 2001 for the regression analysis with landscape pattern variables, because in the plots located in open areas in 1938 the factors related to the invasion of non-native plants are likely to be different than the ones operating in the areas already forested in 1938. All 105 plots were included when landuse in 1938 was the explanatory variable.

Results

Landscape change 1938 – 2001

In the period between 1938 and 2001 the study area experienced considerable housing growth. The number of houses in a 1 km buffer increased five fold but the distance to the closest house did not change substantially. We observed no major changes of the road network, but the distance to the closest road increased because of the abandonment of a few key roads in protected areas (Table 2).

We also observed substantial landcover change in the study area. The forest area increased by 30%, while grasslands and croplands decreased by 23% and 46% respectively. Forested areas in 1938 remained stable, with less than 400 ha transformed to agriculture and grasslands in 2001. Most of the secondary forest growth occurred on abandoned fields, but also on former grasslands. Most grasslands in 1938 were covered by secondary forest by 2001, while most of the 2001 grasslands were crops in 1938 (Fig. 2).

Forest regrowth also reversed forest fragmentation. The number of forest patches decreased as a consequence of patches coalescing; forest patch size increased, and the mean distance between forest patches decreased. Contrary to the entire landscape, the length of forest edge in the 1-km buffers surrounding our plots decreased between 1938 and 2001. The amount of forest in a 1 km buffer increased and consequently the distance to the closest forest edge and the ratio of edge/cover decreased (Table 2, Fig. 3).

Human infrastructure

Richness of non-native invasive plants was strongly and positively associated with the number of houses less than 1 km away from the plot in 1938 and 2001, and the association was stronger with the 1938 version of the variable (Table 3). Similarly, richness of non-native invasive plants was strongly negatively associated with the distance to the closest house and the distance to the closest road both for 1938 and 2001, but the association was stronger with distance to roads in1938.

Cover of non-native invasive plants was strongly and negatively associated with the distance to the closest house in 1938 but was not associated with distance to the closest house in 2001. Cover of non-native invasive plants was also positively associated with the number of houses less than 1 km away from the plot in 1938 and

2001 with about equal r^2 values. Cover of non-native invasive plant was not associated with roads at either time point (Table 3).

Forest fragmentation

Richness of non-native invasive plants was strongly and positively associated with the length of forest edge and the edge to forest ratio within 1 km of the plot both in 1938 and 2001, but in both cases the association was much stronger with the 2001 data. Richness of non-native invasive plants was negatively associated with the amount of forest less than 1 km away from the plot with comparable r^2 values in 1938 and 2001. Richness of non-native invasive plant was negatively associated to distance to the closest edge in 2001, but was not associated to the distance to the closest edge in 1938 (Table 4).

Cover of non-native invasive plants was negatively associated with distance to the closest edge in 2001, but was not associated with distance to the closest edge in 1938. Length of forest edge and edge to forest ratio within 1 km of the plot were not significant for either 1938 or 2001. Cover of non-native invasive plants had an equally strong negative association with amount of forest within 1 km of the plot in 1938 and in 2001 (Table 4).

Effects of past land use

Land use in 1938 was a significant explanatory variable for the cover of non-native invasive plants. Cover of non-native invasive plants was greater in forests that were open areas in 1938 (i.e. crops or grasslands) than in areas that were forested (overall regression with past landcover, $r^2= 0.33$, $p<0.05$). Past land use was not a significant factor associated with richness of non-native invasive plants or presence of the four most common non-native invasives (results not shown).

Presence of non-native invasive plants

The most common invasive plants ranged from stronger to weaker association with the landscape variables in 1938, from honeysuckle (strongest), to buckthorn, multiflora rosa and Japanese barberry (weakest). However, all plant species followed the same trends shown by richness and cover of all non-native invasive plants, where presence of species was more associated with 1938 human infrastructure and 2001 forest fragmentation.

The presence of honeysuckle was more associated with the human infrastructure variables in 1938. It was positively associated with the number of houses in a 1 km buffer around each plot and negatively associated with the distance to the closest road. Honeysuckle was more strongly and negatively associated with the amount of forest within 1 km in 1938 than in 2001, and conversely more strongly and positively associated with the length of forest edge within 1 km in 2001 than in 1938 (Table 5). Buckthorn was also more strongly associated with the human infrastructure variables for 1938, and negatively associated with the distance to the closest house and road.

However, the presence of buckthorn was much more strongly associated with forest fragmentation variables in 2001 than in 1938, particularly with edge to forest ratio and the length of forest edges within 1 km in 2001 (Table 5). Multiflora rose and Japanese barberry exhibited a stronger association with 2001 than 1938 variables. The human infrastructure variables were in general terms associated at the same level for 1938 and 2001 for both species, but multiflora rose was more strongly and negatively associated with distance to the closest road in 1938 than in 2001 and Japanese barberry was more strongly and positively associated with the number of houses within 1 km in 2001 than in 1938. The presence of both species was always more strongly associated with forest fragmentation variables in 2001 than in 1938 (Table 5).

Discussion

Our results showed stronger predictive power of 1938 patterns of roads and houses than of 2001 patterns, when correlating them with current patterns of non-native invasive plants. This suggests that the seventy-year ecological legacy of the past landscape characteristics are strongly associated with the current distribution of non-native invasive plants. Landscape variables representing human infrastructure, particularly rural housing, had the longest lasting effect on non-native plant invasions. On the other hand, forest fragmentation showed a more immediate influence. In general terms, landscape pattern was strongly related to non-invasive plant invasions, since most landscape pattern variables both in their 1938 and 2001 versions were significantly correlated to non-native invasive plant richness, cover, and presence (Gavier et al. 2008).

The question is why the effect of human infrastructure lasted longer than that of forest fragmentation. Research in suburban areas has shown an effect of past urban patterns in the distribution of non-native invasive plants. In woodlots of suburban divisions of Clemsom, South Carolina (USA), the presence of *Mahonia bealei* was strongly related to the age of the oldest surrounding house (Allen et al. 2006), while in New Zealand the population in suburban areas in 1945 explained 4.5 times more variation of the distribution of non-native invasive plants than population in 1996 (Sullivan et al. 2004). Since houses and their surrounding landscaping can act as source of propagules, we can expect that houses will determine in part the first pattern of colonization of non-native invasive plants (e.g. the introduction locus). Our results supports the idea of a long lasting effect of houses generating a continuous rain of propagules and a disturbed and invasible environment, since after more than a century since initial introduction, non-native invasive plants are still spatially associated with housing.

Forest pattern has a strong effect determining the spatial distribution of non-native plant invasions in the Baraboo Hills (Gavier et al. 2009). Honeysuckle and multiflora rose are frequently associated with forest edges (Ruremonde 1991, Lundgren et al. 2004). Conversely, continuous forests tend to have fewer non-native invasive plants, since forests are usually more resistant to plant invasions than open areas (Von Holle and Motzin 2007). Why this effect was shorter that the infrastructure effect on invasives?. Since 1938 forest regrowth caused substantial changes in forest pattern and fragmentation of the Baraboo Hills, and as a consequence a shifting of forest edges. Many areas that represented forest edges in 1938 may with time exhibit conditions less suitable for non-native invasive plant colonization, decreasing the association of invasion with these areas and therefore with past patterns of forest fragmentation.

Past land use was a less important predictor than past landscape characteristics, but undoubtedly the legacies of past land use are determining in part the invasion of non-native plants in Baraboo Hills, where non-native invasive plants cover is much more extensive in secondary forest compared to areas that were always forested. Agricultural practices change the concentration and distribution of soil nutrients and biota for several decades after abandonment (Compton et al. 1998, Knops and Tilman 2000) affecting patterns of plant distributions (Fraterrigo et al. 2006) and facilitating plant invasions (Milchunas and Lauenroth 1995). Open areas free of grazing or plowing could have provided suitable conditions for the development of large non-invasive plant individuals that grow better in high levels of light like buckthorn and honeysuckle (Luken et al. 1997).

Buckthorn, honeysuckle, Japanese barberry and multiflora rose share life history traits that make them successful invaders including animal-dispersed seeds (mostly birds), shade tolerance, extended photosynthetic period and extended lifespan (Webster et al. 2006, Yates et al. 2004). Hence, the differences found in their associations with landscape pattern legacies is likely related to their history of introduction and use.

Honeysuckle has been widely used as an ornamental since the last part of the 19th century because of its showy flowers, while buckthorn was introduced to plant hedges (Czarapata 2005, Webster et al. 2006). Japanese barberry and multiflora rose have been used as landscaping plants, but also were planted as cover and food for wildlife, and erosion control (Czarapata 2005). Popularity as a landscaping plant could have distributed honeysuckle widely in association with human uses by 1938.

The changes observed in the landscape between 1938 and 2001 will strongly influence the future distribution of non-native invasive plants in the study area. If the tendency of forest regrowth continues, we can expect a decrease in the level of forest fragmentation and potentially a decrease in the level of non-native plant invasions as a response. But the new forested areas will also be more susceptible to non-native plant invasions, until ecological succession changes the characteristics of the forest (Bailey et al. 1998). The invasion of abandoned fields can be exacerbated by the proximity of houses. In Spain, abandoned fields will be more rapidly invaded by cacti close to houses where they are used as a landscaping plant (Vila et al. 2003). The substantial increase in the number of houses in the Baraboo Hills area will likely also increase non-native invasive plants in the area.

Our results highlight the importance of considering ecological legacies of past landscape characteristics and past land uses when analyzing non-native plant invasion patterns. Understanding these legacies also facilitates better predictions for the future. In the Midwest, present landscape pattern will influence the future spatial distribution of non-native invasive plants at the short and long term. According to our results, we expect that non-native plants will continue to spread because of the effects of present housing patterns, even if no more new houses were built. Housing growth rates have exceeded population growth rates since the 1940s, and both population growth and immigration can be expected to continue in the future, supporting continued housing growth, much of it in the WUI (Hammer et al. 2008). In the Midwest many of the “hot spots” of housing growth are located in rural areas close to forests (Hammer et al. 2004, Lepczyk et al. 2007). This means that ecological legacies and future housing growth will jointly exacerbate non-native plant invasions.

Management plans for non-native invasive plants should also consider the long lasting effects of housing. The list of new plants being imported as ornamentals continues to grow (Reichard and White 2001), and if past trends continue, the yards of rural houses will be planted with new ornamental plant species, some of them potentially invasive. House owners should be included in management plans with educational programs to prevent certain non-native plants from being used in landscaping, and areas undergoing rural housing and agriculture abandonment should be focal targets of plant invasion monitoring.

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Table 1. List of invasive plants of Baraboo Hills forests included in the analysis.

Latin name	Common name
Berberis thunbergii	Japanese barberry
Elaeagnus umbellata	autumn olive
Lonicera sp.	honeysuckle
Rhamnus cathartica	common buckthorn
Rosa multiflora	multiflora rose
Solanum dulcamara	bittersweet nightshade

Table 2. Mean values for landscape pattern variables centered in the sampling plots and results of a paired t-test. Ln indicates variables that were log transformed (natural) to meet assumptions of the test. Variables with an asterisk have been calculated in a 1 km buffer around each plot.

Landscape pattern variables	1938	2001	*t*	*p*
Length of forest edge (km) ln *	5.8	5.02	-2.9	0.0047
Amount of forest (ha) *	201	263	16.6	0.0000
Distance to edge (m) ln	250	473	-8.35	0.0000
Distance to roads (m) ln	567	661	-3.34	0.0012
Distance to houses (m) ln	659	658	2.77	0.0069
Number of houses ln *	5.1	26.9	4.28	0.0000
Ratio edge/forest ln *	0.0036	0.0022	-11.72	0.0000

Table 3. Univariate linear regression results between richness and cover of non-native invasive plants with variables describing human infrastructure in the study area in 1938 and 2001. P-value 38+01 and 01+38 represent the p-value for the variable in 2001 after the variable in 1938 is included in the model and the p-value for the variable in 1938 after the variable in 2001 is already included in the model. Variables with an asterisk have been calculated in a 1 km buffer around each plot.

	1938			2001				
Model	*b*	*p*	r^2	*b*	*p*	r^2	*p* model 01+38	*p* model 38+01
Richness								
Distance to houses	-1.03	<0.0001	0.19	-0.70	<0.0001	0.19	0.0775	0.0538
Number of houses *	0.46	<0.0001	0.24	0.27	<0.0001	0.21	0.0393	0.1986
Distance to roads	-0.81	<0.0001	0.20	-0.63	0.0012	0.11	0.0023	0.1637
Cover								
Distance to houses	-1.18	0.0016	0.50	-0.24	0.1204	0.15		
Number of houses *	0.45	0.0346	0.26	0.15	0.0371	0.26	0.5398	0.6070
Distance to roads	-0.17	0.6204	0.02	-0.23	0.1393	0.14		

Table 4. Univariate linear regression results between richness and cover of non-native invasive plants with variables describing forest fragmentation in the study area in 1938 and 2001. P-value 38+01 and 01+38 represent the p-value for the variable in 2001 after the variable in 1938 is included in the model and the p-value for the variable in 1938 after the variable in 2001 is already included in the model. Variables with an asterisk have been calculated in a 1 km buffer around each plot.

	1938			2001				
Model	*b*	*p*	r^2	*b*	*p*	r^2	*p* model 01+38	*p* model 38+01
Richness								
Distance to edge	-0.26	0.0945	0.03	-0.69	0.0002	0.16		
Edge to forest ratio*	281.4	<0.0001	0.21	441	<0.0001	0.31	0.0003	0.3553
Length of forest edge *	0.15	0.0132	0.07	0.21	<0.0001	0.28	<0.0001	0.07445
Amount of forest *	-1.16	<0.0001	0.29	-1.76	<0.0001	0.28	0.3110	0.1263
Cover								
Distance to edge	-0.0037	0.09826	0.17	-0.2453	0.0498	0.23		
Edge to forest ratio *	149.38	0.0594	0.19	96.993	0.0633	0.21		
Length of forest edge *	0.729	0.8971	0.00	0.415	0.1505	0.13		
Amount of forest *	-1.2597	0.0435	0.24	-1.1086	0.0267	0.29	0.3605	0.8062

Table 5. Logistic regression results between the presence of four common non-native invasive plants and landscape variables for 1938 and 2001. P-value 38+01 represents the p-value for the variable in 2001 after the variable in 1938 is included in the model and 01+38 the p-value for the variable in 1938 after the variable in 2001 is already included in the model. Variables with an asterisk have been calculated in a 1 km buffer around each plot.

Variables	1938			2001			*p* value	*p* value
	b	deviance	p	*b*	deviance	p	38+01	01+38
Lonicera spp.								
Human infrastructure								
Distance to houses	-0.0022	9.48	0.0021	-0.0019	12.54	0.0004	0.0760	0.7719
Number of houses *	0.1750	12.056	0.0005	0.0196	9.56	0.0020	0.2249	0.0464
Distance to roads	-0.0043	23.83	<0.0001	-0.0028	17.91	<0.0001	0.9994	0.0148
Forest fragmentation								
Distance to edge	-0.0037	8.624	0.0033	-0.0024	9.50	0.0020	0.1468	0.2677
Edge to forest ratio *	337.7	10.934	0.0009	438.1	11.32	0.0008	0.3504	0.4866
Length of forest edge *	0.2095	5.197	0.0226	0.2377	12.25	0.0005	0.0077	0.8096
Amount of forest *	-0.1535	16.75	<0.0001	0.1769	10.53	0.0012	0.2359	0.0057
R. cathartica								
Human infrastructure								
Distance to houses	-0.0036	23.76	<0.0001	-0.0021	19.60	<0.0001	0.4374	0.029
Number of houses *	0.28004	20.27	<0.0001	0.0413	21.76	<0.0001	0.0250	0.0584
Distance to roads	-0.0031	20.19	<0.0001	-0.0018	12.98	0.0003	0.4310	0.0051
Forest fragmentation								
Distance to edge	-0.0027	6.46	0.0110	-0.0019	8.19	0.0042	0.1261	0.4362
Edge to forest ratio *	499.5	21.38	<0.0001	825.7	30.89	<0.0001	0.0013	0.3634
Length of forest edge *	0.2351	7.08	0.0077	0.3651	26.92	<0.0001	<0.0001	0.0930
Amount of forest *	-0.1893	25.56	<0.0001	-0.3249	28	<0.0001	<0.0001	0.5413
M. rosa								
Human infrastructure								
Distance to houses	-0.0017	6.31	0.0120	-0.0010	4.37	0.0370	0.9863	0.1618
Number of houses *	0.4031	5.66	0.0173	0.2319	5.27	0.0217	0.5125	0.3634
Distance to roads	-0.0020	8.66	0.0033	-0.0012	5.19	0.0230	0.4907	0.047

Forest fragmentation								
Distance to edge	-0.0016	1.99	0.1583	-0.0019	6.63	0.0100		
Edge to forest ratio *	230.7601	5.42	0.0199	466.213	12.48	0.0004	0.0012	0.064
Length of forest edge *	0.1229	1.85	0.1733	0.2277	11.18	0.0008		
Amount of forest *	-0.1074	8.9	0.0029	-0.2025	13.18	0.0002	0.0276	0.4197
B. thumbergii								
Human infrastructure								
Distance to houses	-0.0013	4.38	0.0364	-0.0010	5.26	0.0218	0.3183	0.7459
Number of houses *	0.1376	8.51	0.0035	0.02302	12.28	0.0005	0.0268	0.2869
Distance to roads	-0.0014	5.05	0.0247	-0.0010	3.97	0.0464	0.9847	0.2986
Forest fragmentation								
Distance to edge	-0.0006	0.37	0.5435	-0.6958	6.27	0.0123		
Edge to forest ratio *	253.9956	6.7	0.0096	439.713	11.61	0.0007	0.0007	0.3141
Length of forest edge *	0.847	0.94	0.3333	2.02	9.55	0.0020		
Amount of forest *	-0.1088	9.62	0.0019	-0.175	10.53	0.0012	0.0012	0.7312

Figure 1. Major land cover types, roads, and houses in the Baraboo Hills in 1938 and 2001.

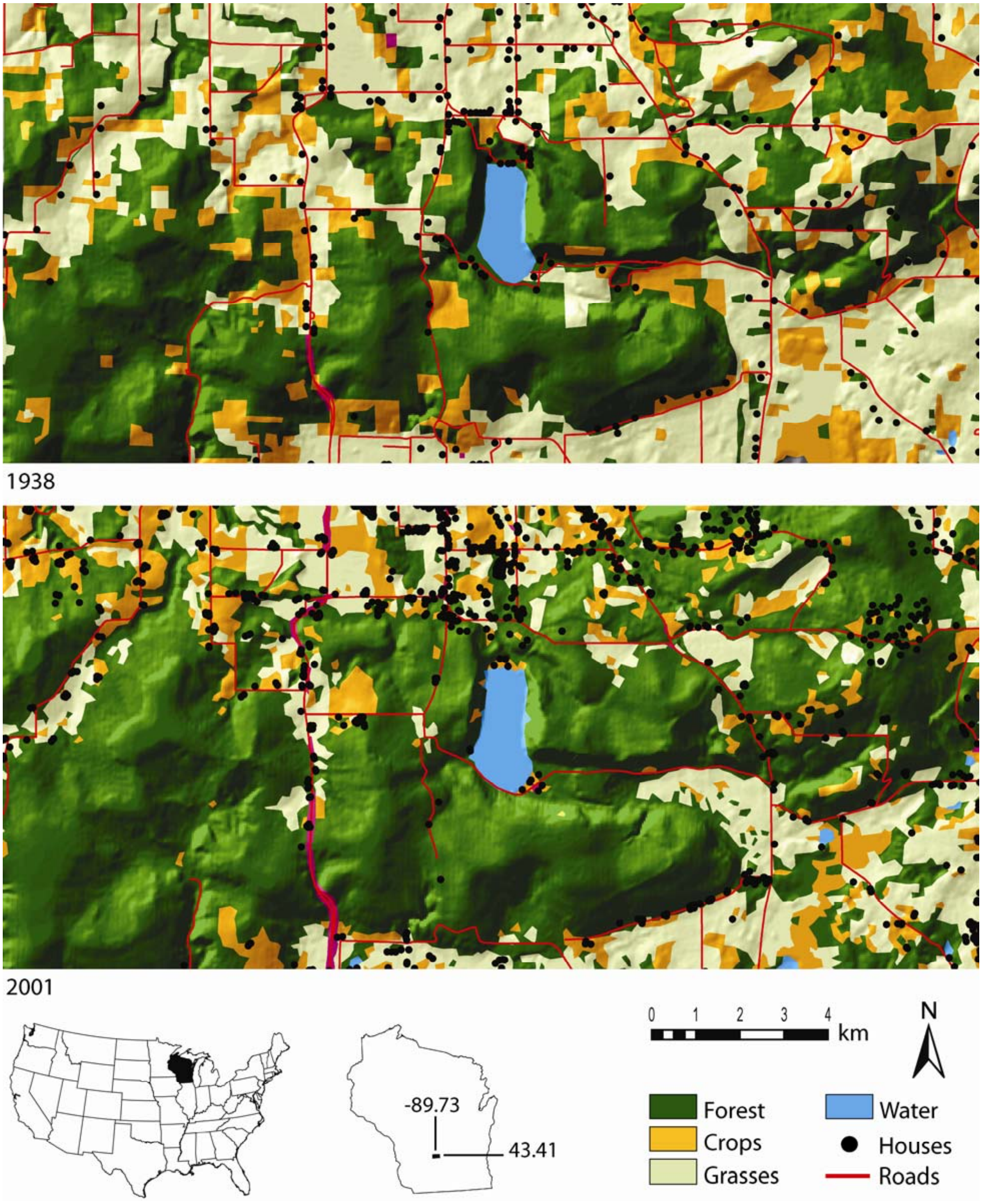


Figure 2. Area of major land cover types in the study area and main trajectories of landcover conversions between 1938 and 2001. Changes smaller than 5% are not shown.

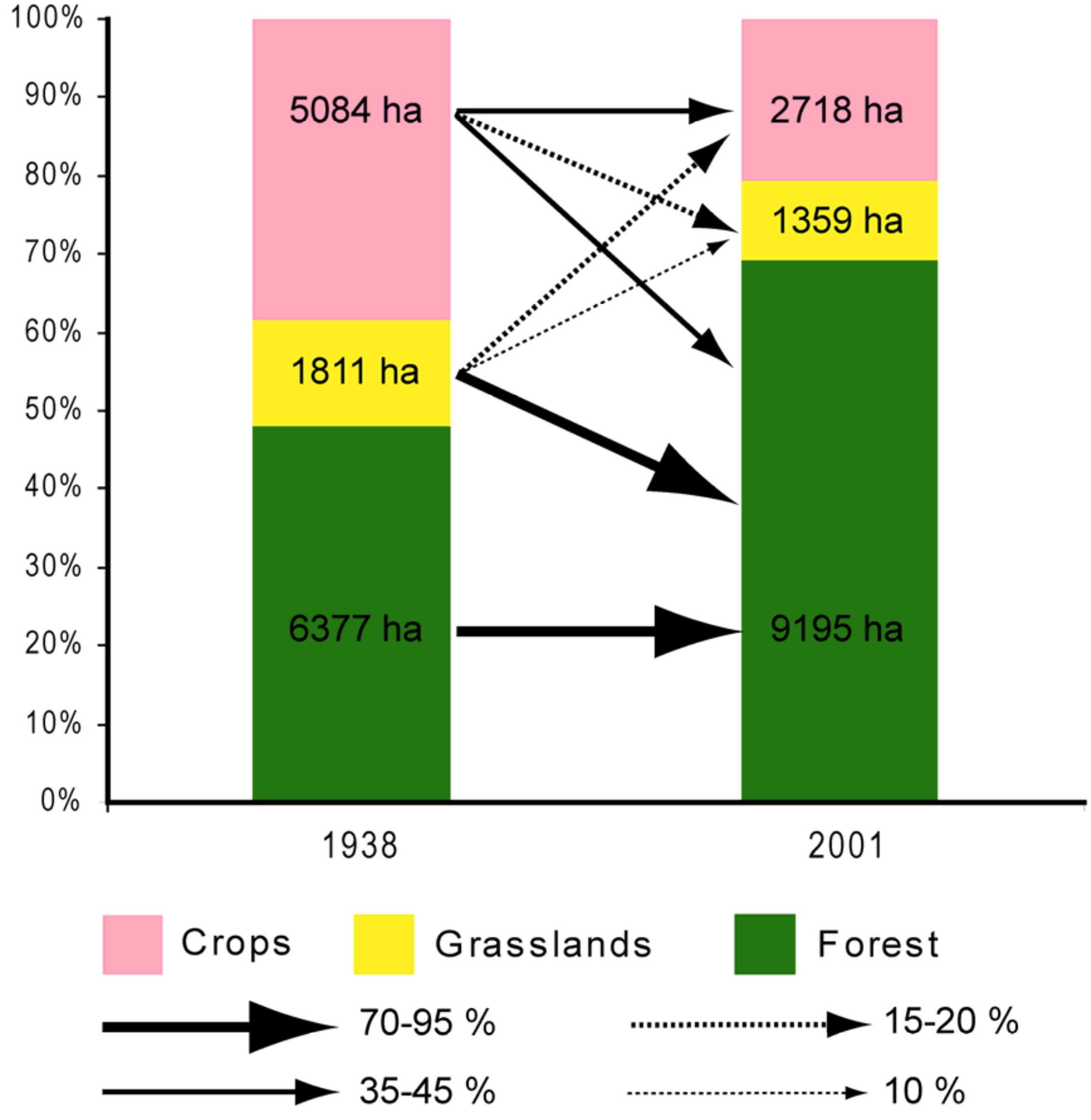
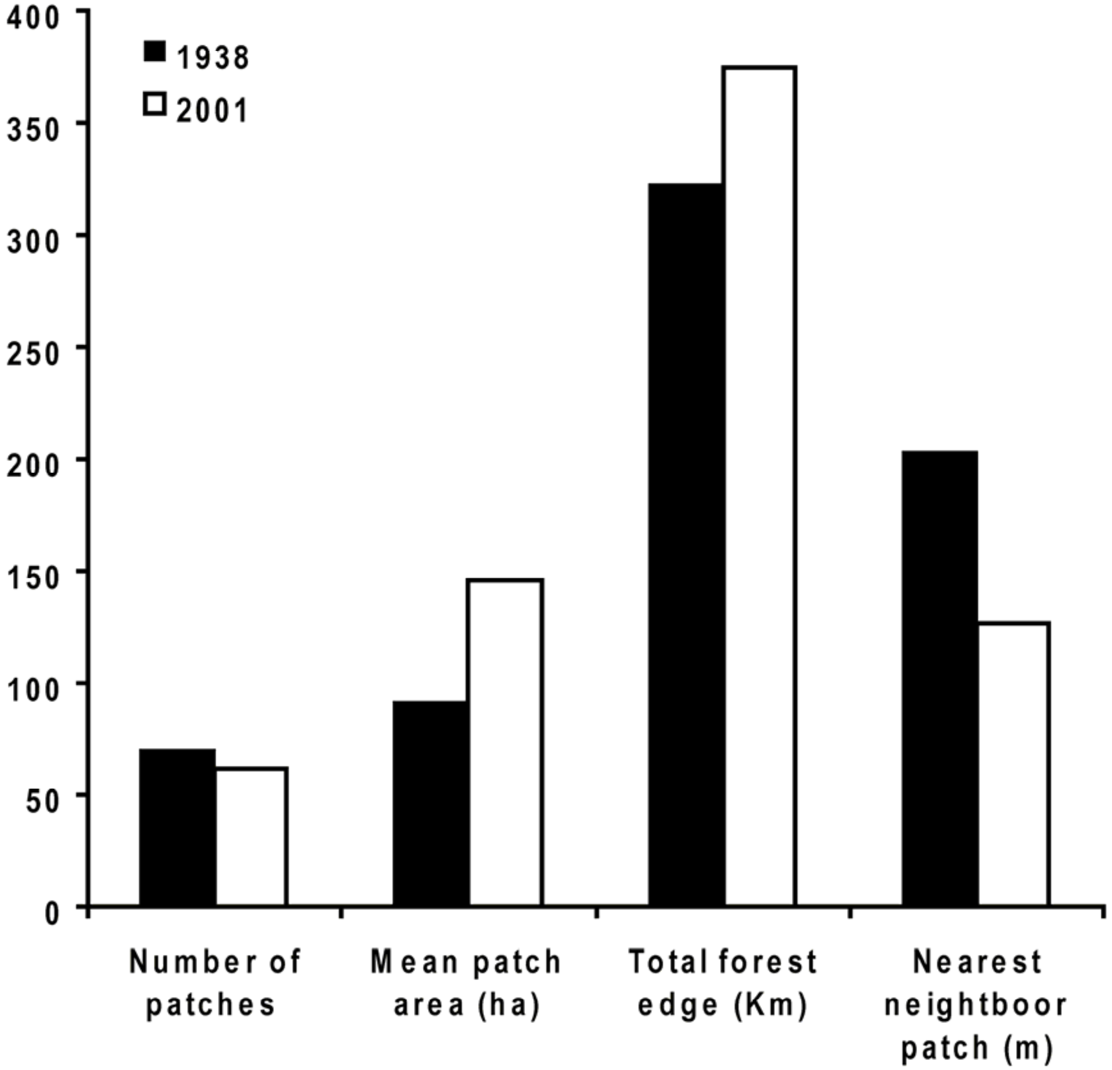


Figure 3. Changes in forest fragmentation between 1938 and 2001. Standard deviations for mean patch size are 405 for 1938 and 1050 for 2001.



Chapter 4: Invasion of an exotic tree (*Ligustrum lucidum*) between 1983 and 2006 and its relationship with urban areas

Abstract

In central Argentina, the Chinese tree glossy privet (*Ligustrum lucidum*) is used as a landscaping tree in urban areas. Glossy privet is also a successful invader replacing native forests, forming dense stands, and thus a major conservation concern. Mapping the spread of biological invasions is a necessary first step toward understanding the factors determining invasion patterns. Satellite images have been used successfully to map invasive plants forming homogeneous stands. The objectives of this paper were to 1) develop a map of glossy privet expansion between 1983 and 2006 using a time series of Landsat TM/ETM+ images, and 2) analyze the spatial pattern of glossy privet stands with regard to urban extent. Using six summer Landsat TM images (1983, 1987, 1992, 1997, 2001, 2006) the expansion of glossy privet was analyzed using Support Vector Machines, a non-parametric classifier. We measured the area of glossy privet in a series of 200 m buffers around urban areas, and we calculated an index of spatial association between glossy privet stands and urban areas, and compared it with the distribution of the index obtained from 1000 random maps. Glossy privet in the study area spreads rapidly. Between 1983 and 2006 glossy privet area increased from 50 to 2,500 ha. The largest proportion of glossy privet dominated area was located within 600 m of urban areas, and analysis of our index of spatial

association suggested that glossy privet stands were spatially related to urban areas ($p < 0.05$) highlighting that landscaping was the likely introduction cause. However, the rate of expansion accelerated substantially after 1992 and new glossy privet dominated stands tends to be located away from urban areas suggesting that glossy privet is now self-sustaining. Expected urban growth in the area could result in increased levels of invasion. Management plans should limit development close to native forests and educational plans should explain the risk of invasion associated with the use of glossy privet for landscaping.

Introduction

Biological invasions are one of the main aspects of global change, negatively affecting ecosystem functioning and biodiversity (Vitousek et al. 1996, Theoharides and Dukes 2007). Non-native, invasive plants can have particularly strong effects on natural ecosystems, changing the dominant vegetation type (e.g., shrubland to grassland conversions), affecting soil properties, altering biogeochemical cycles, changing patterns of herbivory and affecting disturbance regimes (Mack et al. 2000, Brooks et al. 2004). Invading trees may result in the most substantial negative ecosystem impacts (Richardson et al. 1994). For example, pine invasion in the southern hemisphere have reduced the structural diversity, changed vegetation patterns and altered nutrient cycle of grasslands and shrublands (Richardson 1998, Zalba and Villamil 2002).

Many factors determine invasion success and patterns, but most biological invasions are connected to human activities (Williamson and Fitter 1996, Lonsdale

1999). One of the potential factors related to the distribution of invasive non-native plants is the expansion of urban areas which is occurring at increasing rates in many parts of the world (Antrop 2000, 2004). Non-native plants in residential areas can invade adjacent natural areas (Sullivan et al. 2005, Wania et al. 2006) and housing development creates habitat that can easily be invaded (e.g. creation of forest edges, soil exposure, etc; Hobbs and Huenneke 1992, De Candido 2004, Wania et al. 2006). As a result, rural housing, suburban areas, and urbanization results in the invasion of adjacent forests by non-native plants originally planted for landscaping (Moffatt et al. 2004, Duguay et al. 2007, Gavier et al. 2009 a, b).

In an increasingly globalized world, the frequency and spatial scale of biological invasions are growing rapidly, and thus, there is a growing need for monitoring the spread, and forecasting future distributions of non-native plants invasions (Vitousek et al. 1996, Meyerson and Mooney 2007). Detailed maps of invasive species spread provide the baseline data needed for defining the factors associated with their successful invasion (Elton 1958, Mack et al. 2000) and are a necessary first step for successful management action.

Remote sensing is a very promising tool to map invasive non-native plants at broad scales. The availability of long-term satellite images archives permits mapping non-native invasive plants spread retrospectively (Rejmanek and Pitcairn 2002, Cohen and Goward 2004, Wulder et al. 2008). However, most studies used high-resolution or hyper-spectral imagery covering a relatively small area and analyzed only a single point in time or a short time (Akasheh et al. 2008, Hestir et al. 2008). The limitation of such approaches in a management context is their high cost, limiting it’s the use of remote sensing for long-term assessments of invasive plants spread particularly in developing countries (Hunt et al. 2003, Lass et al. 2005, Noujdina 2008, Asner et al. 2008).

The Landsat program has been extensively used for ecosystem monitoring (Goward and Masek 2001, Cohen and Goward 2004) and the 35-years record of Landsat imagery provides a rich dataset to map the invasion of trees at the landscape scale. Also, Landsat TM images are now available at no cost (Woodcock et al. 2008). Landsat TM images are limited by a 30-m resolution which makes it impossible to map individual trees and difficult to distinguish tree species (Foody et al. 2005). However, Landsat TM/ETM+ images have been successfully used to map invasions for single points in time for invading plants that form homogeneous patches larger than 0.5 ha and have a spectral signature distinct from the surrounding vegetation (Peterson 2005, Bradley and Mustard 2006). However, we are not aware of any study that used a time series of Landsat images to map the spread of an invasive tree.

Digital change detection can map changes in vegetation composition, and is thus a powerful tool to mapping the spread of invasive trees. Composite analysis is a type of change detection where all images are combined into one multitemporal dataset and change classes are directly classified (Coppin and Bauer 1994). Composite analysis allows inclusion of more than two points at a time, while accounting for inaccuracies associated with comparing two images classified independently (Coppin et al. 2004, Pu et al. 2008).

Landcover change classes obtained from multitemporal datasets are often characterized by complex class distributions (multi-modal, non-normal). Non-parametric classifiers such as decision trees, neural networks, or support vector machines (SVM) are, consequently, better suited for change classifications than parametric classification techniques (e.g. maximum likelihood) (Foody and Mathur 2004). Moreover, SVM have successfully been applied to analysis of land-cover changes using Landsat TM images (Nemmour and Chibani 2006, Kuemmerle et al. 2008, 2009).

In Argentina, non-native trees entail high ecological and economic costs (Grau and Aragón 2000, Zalba and Villamil 2002, Chaneton et al. 2004). One of the most widespread invasive trees in central Argentina is the glossy privet (*Ligustrum lucidum* W. T. Aiton), native from China and imported as an ornamental (Ribichich and Protomastro 1998, Montaldo 1993, Montaldo 2000). Glossy privet grows fast under both shaded and full sun conditions, reaching heights of up to 15 m. Dispersal occurs through abundant bird dispersed seeds and vegetative propagation (Aragón and Morales 2003, Aragón and Groom 2003).

Glossy privet is particularly widespread in the Sierras Chicas of Cordoba Province (central Argentina), where it was introduced around 1900 as an ornamental plant (Rio and Achaval 1904) and has become a very successful invader of forested sites resulting in dense stands, where most native vegetation is eliminated (Grau and Aragón 2000, Gavier and Bucher 2004, Hoyos et al. 2009). The Sierras Chicas of Cordoba have also experienced widespread landscape change since 1970, characterized by forest loss, increased forest fragmentation, and urban growth (Gavier and Bucher 2004). Glossy privet has been widely used as a landscaping tree, and privet expansion may thus be connected to the region’s urban growth. While earlier work has shown the potential for mapping glossy privet from Landsat TM/ETM+ images (Gavier and Bucher 2004, Hoyos et al. 2009), no study so far assessed privet expansion using a time series of images and the relationship between privet expansion and urban growth remains largely hypothetical.

The objective of this paper was to map the spread of glossy privet stands in an area representative of the Sierras de Cordoba (Argentina) between 1983 and 2006, to analyze the rates and spatial patterns of privet invasions, and to assess the relationship between privet expansion and urban development. We hypothesized that glossy privet dominated stands are spatially related to the distribution of urban areas, because urban areas act as a source of propagules and have associated disturbances (e.g. clearing of properties) that facilitate the invasion of glossy privet.

Methods

Study area

The study area encompasses 380 km^2 on the eastern slope of the Sierras Chicas of Córdoba, Argentina (-31º 17.4´S; 64º 30´W). Altitude ranges from 450 m on the eastern plain to 1350 m on the plateau (Sierras Chicas) in the western part. Climate is temperate semi-arid with a monsoonal rain regime, average annual rainfall of 949 mm and mean annual temperature of 18.9 ºC (Capitanelli 1979a,b, Gavier and Bucher 2004). Natural vegetation consists of four vegetation zones: Llanura (plains < 750 m, dominated by *Aspidosperma quebracho-blanco*, *Prosopis* spp. and *Acacia* spp. forests), Serrano forest (sierras between 1200 and 700 m and dominated by *Lithraea molleoides* and *Fagara coco* forest), shrubland (between 1100 and 1000 m) and grassland (usually > 1000 m) (Luti et al. 1979, Zak and Cabido 2002, Gavier and Bucher 2004) (Fig. 1).

Main land uses, including cattle grazing, open mining, and extensive logging, have substantially altered natural vegetation communities. Current deforestation rates are high (2.8 % per year) with increasing fragmentation and the remaining forests are under pressure from grazing, selective logging, fire, and non-native invasive plants. Urban areas have grown rapidly (from 577 to 2,653 ha from 1970 to 1997) particularly in forested valleys as people moved closer to natural amenities (Zak and Cabido 2002, Gavier and Bucher 2004) (Fig. 1).

Glossy privet is widespread, occupying 1,783 ha in 2001 (17% of the forested area) and forming sometimes stands larger than 150 ha (Gavier and Bucher 2004, Hoyos 2007). Relative crown cover of glossy privet in heavily invaded stands can exceed 80%, and regeneration of native trees is practically absent. Glossy privet is also distributed outside the heavily invaded stands, as isolated individuals mixed with native trees (Hoyos 2007).

Datasets

To map the glossy privet invasion we used six Landsat TM and ETM images (scene path 229 / row 82) from 1983 (December 8th), 1987 (February 4th), 1992 (January 17th), 1997 (November 14th), 2001 (January 1st) and 2006 (March 12th) obtained from the United States Geological Survey Earth Resources Observation and Science Data Center (USGS EROS) (http://edc.usgs.gov) (1983, 1987, 1992, 2001, 2006), and the National Argentine Commission of Spatial Activities (CONAE, www.conae.gov.ar) (1997). All images were taken during summer or late spring after the onset of the rainy season when vegetation was in full vigor. Images were almost cloudless; the remaining few clouds were masked. Images were orthorectified and georeferenced with an RMS error <1 pixel (approximately 25 m) using 1:15,000 topographic maps from the Geographic Military Institute of Argentina, 30 control points and 10 km of roads recorded with a GPS unit (geopositional error <10 m). The six multispectral bands of the six images were combined into a single multitemporal stack with 36 bands that was a subset of the extent of the study area. A hillshade image based in the sun position parameters of the 2006 Landsat image was included in the stack to account for shading caused by topography.

Change detection analysis

We identified eight different classes from the multitemporal image stack. One class represented the distribution of glossy privet in 1983 (‘Privet 1983’); five classes represented glossy privet expansion (‘Expansion 1983 – 1987’, ‘Exp. 1987 – 1992’, ‘Exp. 1992 – 1997’, ‘Exp. 1997 – 2001’, ‘Exp. 2001 – 2006’); one class represented native forest dominated areas (‘Permanent forest’); and one class represented all other cover types (‘Other’, i.e., grasslands, shrubs, urban, cropland, water, and changes among these classes).

Training areas for the eight different classes mapped were digitized on the raw Landsat TM/ETM+ images using ArcGIS 9.2 (ESRI 2006). ‘Privet 1983’ and ‘Permanent forest’ training areas were digitized based on field visits in October 2007, The size of privet trees indicated if they were present in 1983 already (see below). To facilitate the interpretation of Landsat TM images, we calculated the Normalized Difference Vegetation Index (NDVI) and the brightness, greenness, and wetness components of the Tasseled Cap Transformation (Crist and Cicone 1984) for each image. Glossy privet-dominated stands differ substantially in structural and physical characteristics compared to native forest stands. Privet canopies are more dense and close, resulting in higher absorption in the visible domain and higher reflection in the near-infrared domain and thus a higher NDVI (Hoyos 2007) (Fig. 2). The spectral signatures of all privet polygons were double-checked against areas identified as privet sites in the field in 2007 using ERDAS Imagine 9.0 (Leica Geosystems 2003). Once training polygons were digitized, a random sample of 400 locations (pixels) for each class was selected from the polygons. For the first two classes (‘Privet 1983’ and ‘Expansion 1987 - 1992’), relatively few training polygons could be located and we therefore used all available pixels (150 and 250, respectively).

The training sites were used to parameterize a Support Vector machine (SVM) classifier. SVM is a non-parametric approach that separates classes by fitting a hyperplane between two classes based on training samples. The basic idea of SVM is to define a hyperplane that separate points corresponding to two different classes that are projected on a multidimensional space (Huang et al. 2002, Foody and Mathur 2004). The hyperplane that best discriminates two classes maximizes the distance between the hyperplane and the closest training samples (the support vectors) (Burges 1998, Pal and Mather 2005). SVM use only training samples characterizing class boundaries, thus potentially requiring only a relatively small number of training samples (Foody and Mathur 2004). When classes are linearly not separable, a kernel function transforms training data into a higher dimensional space where a separating linear hyperplane can be fitted (Huang et al. 2002, Pal and Mather 2005). This allows SVM to handle complex class distributions and makes SVM well suited for classifications in a multitemporal feature space (Kuemmerle et al. 2008). A limitation of SVM is that it was designed for binary classifications, but in land cover classification usually more than two classes are mapped. We used a one-against-all strategy, where one individual class is classified at a time, and all the other classes are grouped into a single class also included in the classification. When a pixel is classified in two or more classes, a confidence criterion (dependent on the distance of a pixel to the hyperplane) is calculated and the pixel is labeled to the class with maximum confidence criteria (Vapnik 1995, Kuemmerle et al. 2008).

We used a Gaussian kernel function, which requires setting a parameter γ to control the kernel width, and a parameter C to determine the magnitude of penalty given to misclassified training samples. C is a regularization parameter that considers the distance that the misclassified training sample is away from the correspondent hyperplane (Foody and Mathur, 2004). To apply the SVM to classify satellite images we set the two parameters for the kernel function γ and C systematically testing a wide range of γ and C combinations and compared them based on cross-validation errors (Janz et al. 2007).

Once optimal parameters were found for all binary problems, we used the resulting SVM to classify the multitemporal stack of the six Landsat TM images and to derive a map of glossy privet expansion. The SVM parameterization and classification were performed with the software imageSVM (Janz et al. 2007, www.hu-geomatics.de). To obtain a final map of glossy privet expansion all patches smaller than 4 pixels (using a 4-neighbor rule) were eliminated by merging them into the largest neighboring patch, to eliminate small artifacts of the classification.

Field data and classification accuracy

Two set s of data were used to validate our glossy privet map. First, we measured diameter at breast height (DBH) of all glossy privet trees larger than 10 cm and of all native trees in a stratified sample of 46 plots of 100 m2 in October and November of 2007. In a 20-m radius circle, we also cored the three largest glossy privet individuals to estimate tree age (Elzinga et al. 1998, Avery and Burkhart 2002). The sampling plots were distributed based on a preliminary glossy privet map derived from the 1983, 1997 and 2001 Landsat images (Hays et al. 1981, Elzinga et al. 1998). Tree cores were sanded and growth rings counted using a magnifying glass in eighty cores where reliable counting was possible. Growth ring counts were used to fit a simple linear regression to relate DBH and tree age. Second, an extra set of 138 sample plots of 100 m2 recorded in 2002 in areas of glossy privet and native forest stands (Hoyos 2007) was used to quantify the accuracy of our final classification of glossy privet distribution.

Relationship of privet expansion and urban areas

We used two approaches to analyze the spatial relationship between glossy privet stands and urban areas: measuring the area of glossy privet at different distances from urban areas and neutral model simulation. We calculated the area of glossy privet dominated stands in multiple rings of 200 m width around urban areas. The proportion of the total glossy privet area located in each interval was compared with the proportion of the total study area contained in that ring, as an index of the expected glossy privet distribution under randomness (e.g. proportional to the available area in each buffer). We analyzed the distribution of glossy privet stands in 200 m width interval at different distances from the urban areas in 1983, and 2006 and for the expansion of glossy privet stands between 2001 and 2006.

Neutral landscape models have been used in landscape ecology to simulate landscape configurations in the absence of a factor that structures the landscape (With and King 1997, Turner et al. 2001). We used the landscape simulation program SIMMAP 2.0 (Saura and Martinez-Millan 2000) to simulate 1,000 random maps that were neutral regarding the spatial configuration of glossy privet. SIMMAP requires setting three parameters: (1) the number of land cover classes, (2) the proportion of each class, and (3) the degree of percolation (*p*) controlling the level of aggregation of each class. Small values of *p* result in relatively dispersed patterns (i.e. many, small, and fragmented patches), while large values of *p* result in clumped patterns. We considered four land-cover classes (glossy privet, native forest, urban areas, and other) using class proportions from 2006. To estimate *p*, we calculated the fractal dimension (McGarigal et al. 2001), a commonly used landscape fragmentation index, for simulated and real (2006 in our case) landscapes. We varied the *p* until the fractal dimension of the glossy privet class in simulated and real landscape was comparable (fractal dimension around 1.4). Using these parameters, we simulated 1,000 landscapes where the spatial association of classes was kept random (i.e., our simulated landscapes were neutral regarding spatial association of glossy privet stands and urban areas).

We developed and calculated an association index to measure the spatial association of glossy privet and urban areas in real and simulated landscapes. This index counts co-occurrences of glossy privet and urban areas pixels using a 4-neighbor rule. From the 1,000 random simulations we calculated a distribution function for the association index under randomness and we obtained rejection values for a two tailed test with a p=0.05 (values for accumulated frequency for *p*=0.025 and *p*=0.0975). We then compared the value of the association index for the real landscape with the distribution generated from the 1,000 random landscapes. If the value of the index of association for the real landscape was larger than the value for the upper rejection zone under a random spatial association, we concluded that glossy privet stands and urban areas were more associated than expected by chance.

Results

Expansion of glossy privet stands

Between 1983 and 2006, glossy privet-dominated stands expanded in the study area from 50 to more than 2,500 ha (Table 1). In 2006, glossy privet stands represented more than 20% of the total forests. The expansion of glossy privet was relatively slow between 1983 and 1992 (326 ha, 36.2 ha per year), but invasion rates increased rapidly between 1992 and 2006 (2,125 ha, 152 ha per year) (Table 1).

In 1983, most glossy-privet dominated areas were contained in a few small stands located in the urban areas of Rio Ceballos and Salsipuedes, as well as a few hectares of glossy privet stands south of Rio Ceballos located between urban areas and native forest stands. Between 1983 and 1987 glossy privet expanded particularly in native forests located on the slopes west of the town of Rio Ceballos, following a south-west direction along a river located west of Rio Ceballos and in a few stands west of the town of Salsipuedes. Between 1987 and 1992 a few new glossy privet dominated stands appeared in the area between Rio Ceballos and Sasipuedes, and also as an expansion of the glossy privet stands on the slopes west of Rio Ceballos (Fig. 3).

The rapid expansion of glossy privet after 1992 had two well defined patterns. Between 1992 and 2001 there was again a large expansion of glossy privet dominated stands between Rio Ceballos and Salsipuedes, and the stands located west of Rio Ceballos. However, another large increase of glossy privet area occurred around the town of Unquillo in the southern part of the study area. Between 2001 and 2006 the expansion of glossy privet dominated areas occurred mainly in the area located south of Salsipuedes, but also in the narrow valleys dominated by native forests in the north of the study area (Fig. 3).

Classification accuracy and stand age

The SVM classification of glossy privet expansion classified accurately the rapid spread of glossy privet during our study period (Fig. 4). Our 2006 classification had a high degree of accuracy particularly for glossy privet (95.5 %) (Table 2). The total accuracy for the 2006 map was 86 %. The overall Kappa index was 0.76, 0.89 for glossy privet, 0.62 for native forests and 0.78 for all other cover types.

The mean age for the whole sample of cored trees was 26.02, with a maximum of 50 and a minimum of 10. A linear model of the relationship between DBH and tree age showed moderate predictive power (r^2= 0.63, Tree age = 4.11 + 0.9267 DBH, Fig. 5). According to our model, the oldest individual glossy privet recorded is 62 years old (with a dbh of 63 cm). This individual is located in a small patch of very large glossy privets planted in a small riparian park in the town of Salsipuedes and classified as privet invaded stand in 1983 in the satellite classification.

Both the dbh and the number of tree growth rings counted decreased as the satellite classification-derived date of invasion increased (Fig. 6). However, DBH showed an inconsistent pattern with the time of invasion. Mean DBH was largest in 1983 and decreased substantially in the plots invaded by glossy privet between 1983 and 1987, but remained stable from 1987 to 2001 (Fig. 6). On the other hand, tree age showed a more consistent relationship with the time of glossy privet expansion (Fig. 6).

Spatial relationship between glossy privet stands and urban area

We found a strong spatial association between glossy privet stands and urban areas. The amount of glossy privet dominated area decreased with distance from urban area in 1983, 2006, and the expansion between 2001 and 2006 (Fig. 7). For 1983, 2006 and the period 2001-2006, the proportion of total glossy privet dominated area located < 600 meters from urban areas was substantially larger than the proportion of the study area represented by the buffer area, but the proportion of glossy privet area located between 600 and 1200 m from urban areas was proportional to the available area (Fig. 7).

In addition to the general pattern of more glossy privet close to urban areas, there was a change in the distribution of glossy privet proportions around urban areas between 1983 and 2006. In 1983, a large proportion of total glossy privet dominated areas (82%) was located < 600 m away from urban areas. In 2006 the proportion of total glossy privet dominated area located < 600 m from urban areas had decreased (52%), but a substantial proportion of glossy privet area was located > 600 m from urban areas. In other words, the distribution of privet between 2001 and 2006 showed a tendency of glossy privet expansion outwards from urban areas (Fig. 7).

There was a significant spatial association between glossy privet stands and urban areas. The value of pixel neighborhoods between glossy privet stands and urban areas (3826) was significantly larger than expected by chance ($p < 0.05$). The 2006 landscape structure was not neutral in regards to the spatial relationship between glossy privet stands and urban areas, and glossy privet stands tended to appear close to urban areas (Fig. 8).

Discussion

Glossy privet has spread rapidly in our study area. Glossy privet was only present in a few small stands in urban areas in 1983 but expanded their distribution to become one of the main vegetation types, accounting for more than 20% of the forested area in 2006. The spread of glossy privet was relatively slow until 1992. After 1992 there was a substantial increase in the rate of native forests conversion to glossy privet stands, reaching a maximum rate in the period 2001-2006. This trend indicates that the glossy privet invasion is likely going to continue at a fast pace. For example, after 1992 the rate of glossy privet expansion in certain areas (e.g. between the towns of Río Ceballos and Salsipuedes) was close to the 76 m per year found for *Mimosa pigra* in northern Australia, a woody weed that invades wetlands (Lonsdale 1993).

The rapid expansion of glossy privet stands in the study area can be explained by the presence of forest stands where glossy privet is mixed with native trees. The five year time span used in the multitemporal analysis is not enough to allow for the establishment and growth of a new glossy privet stand. Rather, the fast expansion of glossy privet is the result of a change in the dominating tree species in forests stands during the last stages of invasion, when glossy privet grows taller than native species and dominates the canopy cover (Hoyos et al. 2009). A similar pattern shown by *Ailanthus altissima* results in fast ecosystems conversion to invasive trees dominated stands (Knapp and Canham 2000).

Glossy privet age estimates obtained from tree cores confirmed the temporal expansion of invaded areas obtained from the multitemporal Landsat data. Individual treess recorded in glossy privet stands already invaded in 1983 were large (up to 63 cm dbh) with an estimated age of 62 years. This means that the oldest trees in the study area were approximately 37 years old in 1983, and thus tall enough to be detected in the 1983 Landsat TM image. However, differences in tree ages among the more recently invaded area were small, although there was clear tendency of younger trees in the more recently invaded stands.

The natural variability in structure and composition of native forest could explain the small differences in glossy privet ages found in more recent invaded areas. Native forest in the Sierras Chicas can be very heterogeneous, presenting different heights, stems densities, cover and species composition depending of ecological conditions of the site (i.e., soils and topography) or degree of disturbances (e.g. overgrazing and logging) (Zak and Cabido 2002). Glossy privet invasion is slower where native forests are tall and dense (Aragon and Morales 2003). As a consequence, glossy privet trees of the same age will be dominant in some stands but still part of the understory in others.

The strong spatial relationship between urban areas and glossy privet stands could be explained by two processes. First, urban areas can act as a source of propagules invading adjacent areas. Forests surrounding urban and suburban areas often have large numbers of non-native invasive plants. For example in Canada, forest fragments in urban landscapes around Ottawa and in Manitoba contain more non-native invasive plants that fragments in agricultural landscapes (Moffatt and McLachlan 2004, Moffatt et al. 2004, Duguay et al. 2007). The location and distance of urban areas as seed sources is a determining factor in glossy privet colonization (Grau and Aragón 2000). In the study area the oldest glossy privets were located in urban recreational areas, concordant with its use as an ornamental plant starting around 1900 (Rio and Achaval 1904). This pattern of early invasions starting from old plants in urban parks is similar to sites in Australia and New Zealand (Adamson 1977).

Second, disturbances related to urban development often results in open areas and bare soils that favor the establishment and spread of exotic invasive plants (Davis et al. 2000, Theoharides and Dukes 2007). In the Sierras Chicas of Cordoba, urban development has resulted in substantial logging of native forests and created areas of bare soil. Much of the forests invaded between 1987 and 1992 were logged in the 1950s and 1960s in preparation for urban development that never materialized (Gavier and Bucher 2004). The homogeneous population structure of the glossy privet stands in this area can be explained by the rapid invasion after logging. Soil disturbance favors the establishment of glossy privet, eliminates the competition of other plants and increases the availability of nutrients and water (Buchanan 1989), and glossy privet is common in secondary forests that originated in abandoned citrus plantations (Aragón 2000). Again, similar patterns have been found elsewhere. For example, deforestation of large areas in Puerto Rico resulted in rapid expansion of invasive exotic trees (Lugo 2004).

Changes in landscape pattern due to human activities can also facilitate plant invasions, because landscape configuration can determine the rates of non-native plants dispersal (With 2002). Human activities in the Sierras Chicas of Córdoba resulted in a landscape that facilitates the glossy privet invasions, because urban growth and rural sprawl cause deforestation and fragmentation of native forest and an increase in forest edges that are easily invaded (Gavier and Bucher 2004, Theoharides and Dukes 2007, Gavier Pizarro et al. 2009 a, b). The fast spread of glossy privet in the Sierra Chicas of Córdoba is thus likely the result of complex interactions between landscape pattern, including location of urban areas vs. forests most vulnerable to invasion, and the ecology of dispersers (i.e., birds) (Hastings et al. 2005).

Landsat TM images produced excellent results for mapping glossy privet invasion. The 95.5% detection accuracy for glossy privet stands is comparable to the 97% accuracy obtained for mapping invasive grasses with a hyperspectral sensor (Lass et al. 2005) and superior to the 65 to 74% accuracy found for mapping gramineae invading pastures with Landsat TM images (Bradley and Mustard 2006). However, Landsat TM images had limitations for mapping glossy privet because the spatial and spectral resolution of the Landsat TM sensor was not capable of detecting mixed stands of glossy privet and native forests.

The change detection analysis and support vector machine classification were very useful to map the expansion of glossy privet dominated areas, i.e., very homogeneous stands where glossy privet accounts for more than 80% of canopy cover (Hoyos et al. 2009). However, glossy privet was also widely distributed as isolated trees forming mixed communities with native trees (Aragón and Morales 2003, Hoyos et al. 2009). The mixed stands and low-density privet sites were very difficult to detect with the Landsat TM images with a spatial resolution of 30 m. In our study area, substantial portions of the areas classified as native forest may represent mixed stands and different stages of glossy privet invasion. Our results are thus conservative, and field research may reveal even higher amounts of glossy privet than what is reported here.

Our findings have important management implications. Urban growth in the area is rampant and expected to continue (Gavier and Bucher 2004). The expansion of urban areas will exacerbate glossy privet invasions into native forest that are already stressed by logging and fragmentation (Zak and Cabido 2002, Gavier and Bucher 2004). The consequences of glossy privet expansion in the study area can be profound in terms of biodiversity loss and ecosystem change. In glossy privet dominated stands, most of the native species of trees and shrubs are eliminated (Lichstein et al. 2004), forest vertical and horizontal structure is greatly reduced, and with it the plant diversity decreases, and microhabitat for animals change (Dascanio et al. 1994, Hoyos et al. 2009).

Conservation plans for the area should consider the importance of keeping the urban areas apart from natural forest of high ecological value to avoid glossy privet invasions. Environmental education and communication with landscaping firms, developers and homeowners could help prevent glossy privet’s use as an ornamental plant in new urban developments, particularly in the countryside. At the same time, continued monitoring of glossy privet expansion is crucial. The SVM-based method we developed here and the availability of free Landsat TM imagery provides managers and scientist with a powerful toolset to assess the spatial distribution and expansion of glossy privet at a regional scale, and to ultimately better understand the factors that determine large-scale glossy privet invasions in Argentina and elsewhere.

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Table 1. Expansion of glossy privet dominated stands in 5 years time steps between 1983 and 2006.

Year	Glossy privet stands area (ha)	Privet expansion (ha)	Percent growth of glossy privet area
1983	50		
1987	293	243	486
1992	376	83	28
1997	1075	699	186
2001	1783	708	66
2006	2501	718	40
Forest in 2006	9440		
Other classes in 2006	26048		

Table 2. Confusion matrix for the classification of glossy privet stands, native forest classes and other land cover in 2006. Rows indicates the number of control points for each land cover recorded in the 2006 classification that corresponds to each cover types according to field observations.

		Field control points		
		Glossy privet	Native forest	Other
Satellite Classified	Glossy privet	85 (95.5%)	4 (4.6%)	0
	Native forest	10 (20.8%)	34 (70.8%)	4 (8.3%)
	Other	6 (17%)	0	28 (82.3%)

Figure 1. Study area in Córdoba province, Argentina, north of the city of Córdoba.

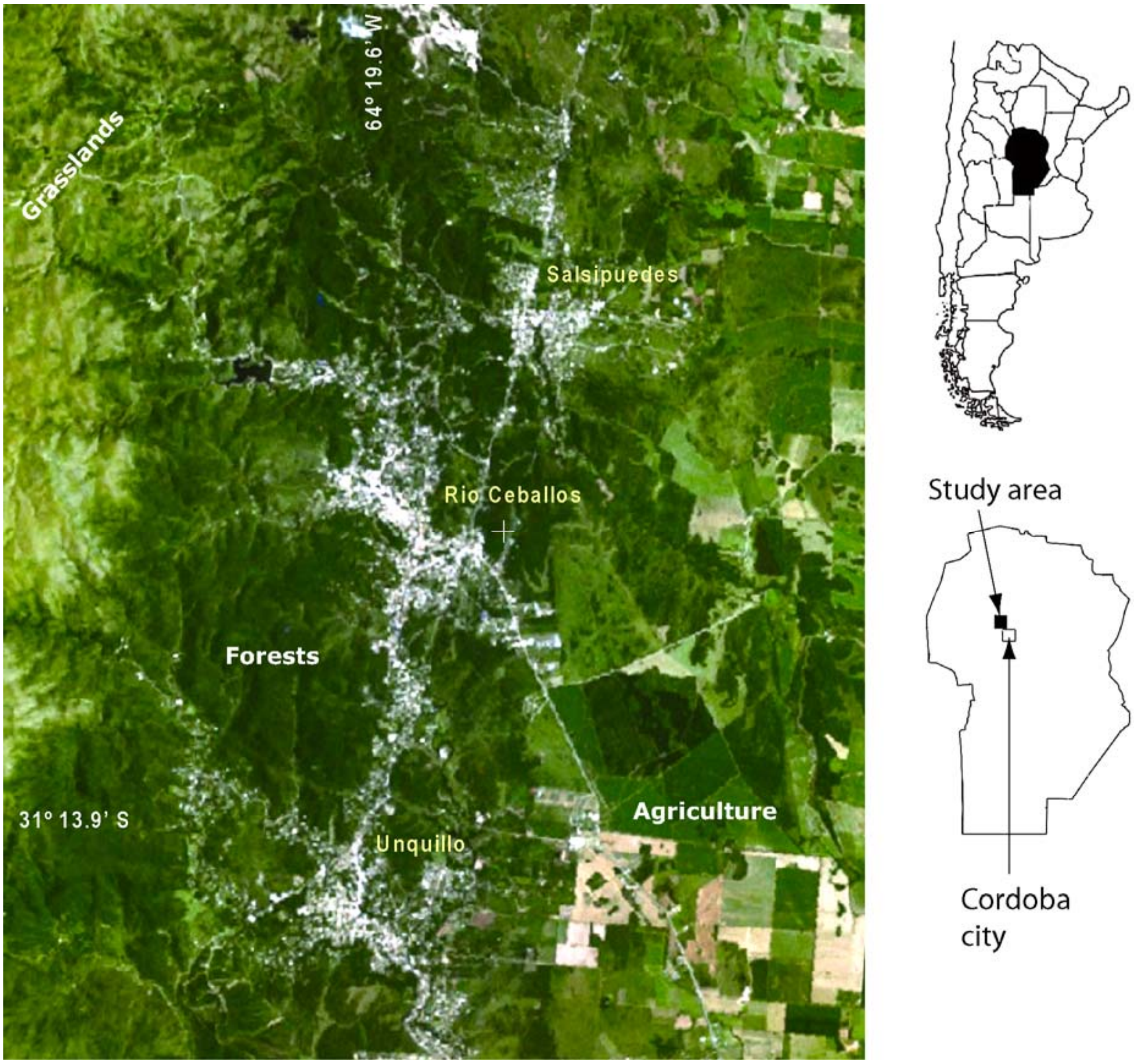


Figure 2. Examples of differences in glossy privet and native forest canopy and detection with Landsat TM images. A) Differences in color and density of glossy privet and native forest canopies on the ground. B) Values in bands 2, 3 and 4 from a Landsat TM image of 2006 for a random sample of 100 pixels of glassy privet stands and native forest of the sierras and the plains. Values in band 4 (near infrared) is substantially higher for glossy privet stands than for native forests. C) Color composite of bands 4 (blue), 3 (red) and 2 (green) in 1997. Bright red areas indicate higher values of band 4 (near infrared). D) NDVI, dark green areas indicates more dense photosynthetic active tissue.

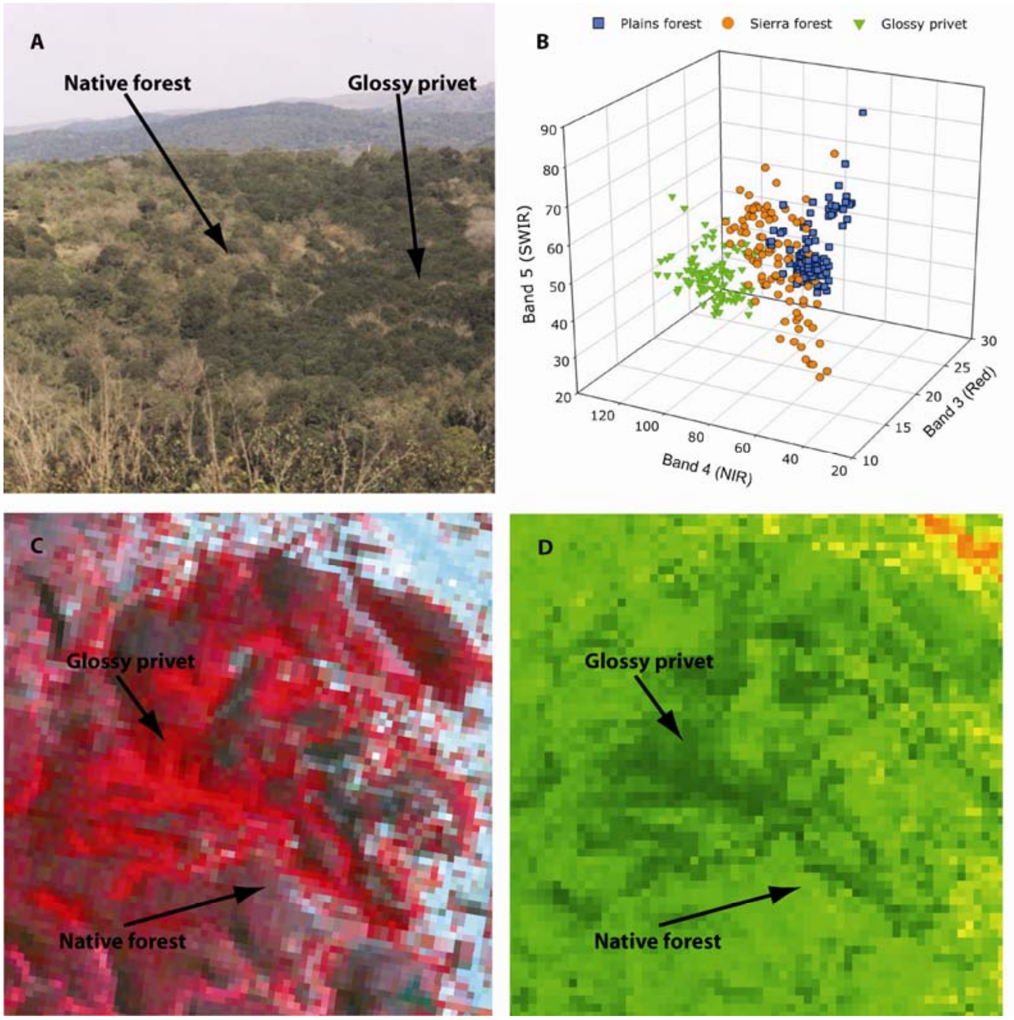


Figure 3. The expansion of glossy privet dominated stands in the study area between 1983 and 2006.

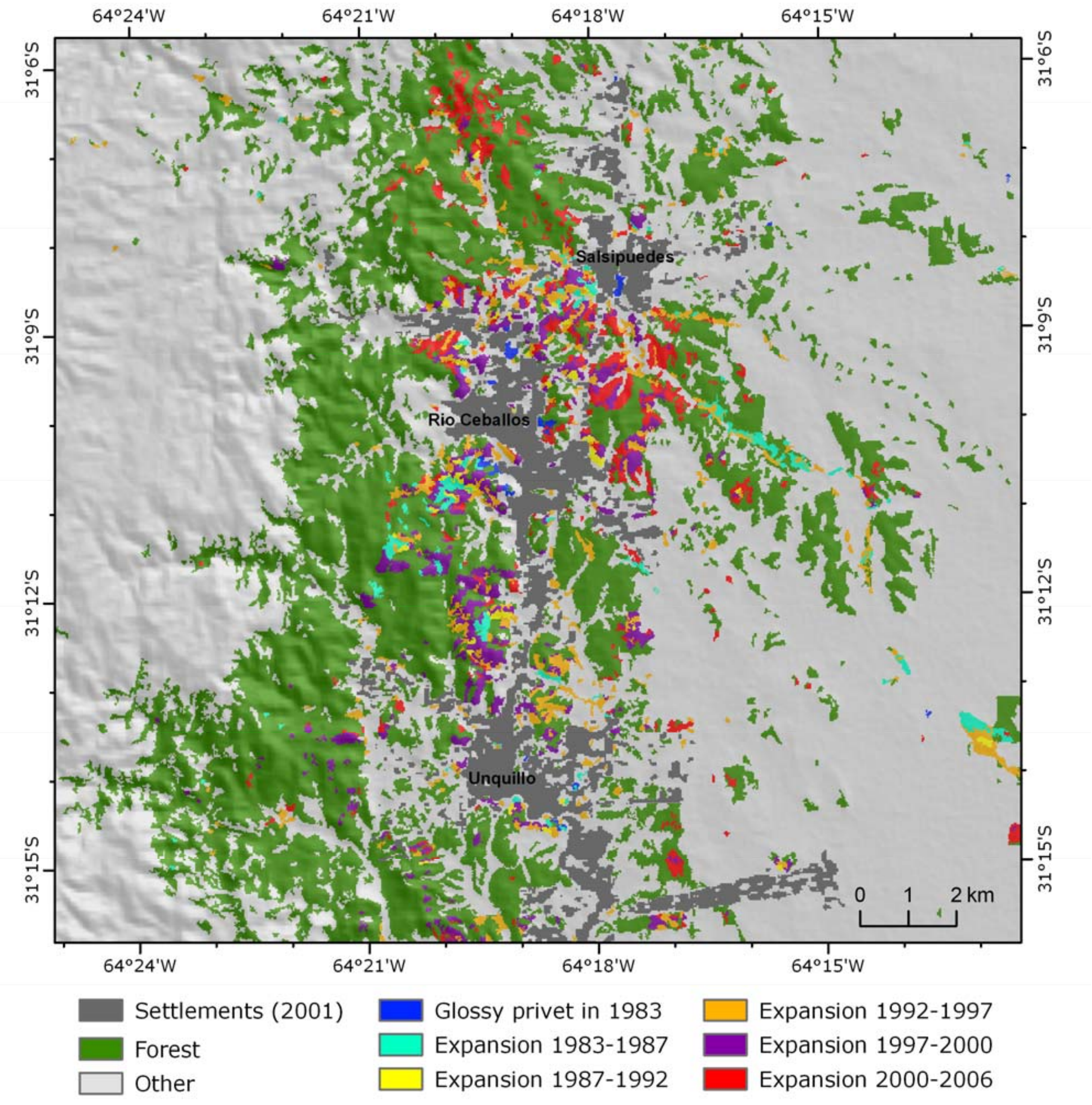


Figure 4. Example of expansion of glossy privet dominated stands and results of the change detection with Landsat TM dividing the time frame in three periods. Color composite images in the left column, and superimposed classification results in the right column.

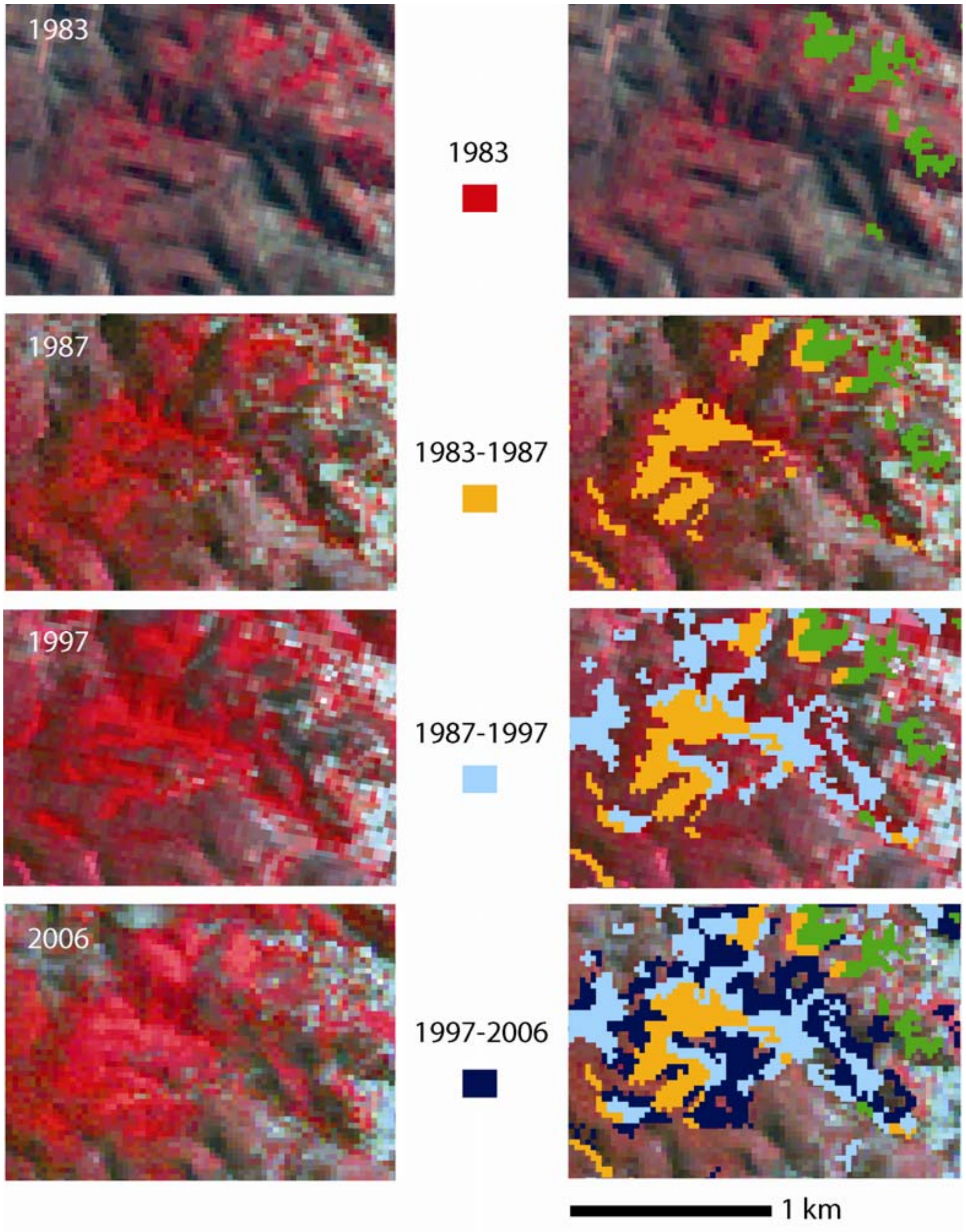


Figure 5. Relationship of tree age and diameter at breast height for 79 glossy privet cored in the study area in November 2007.

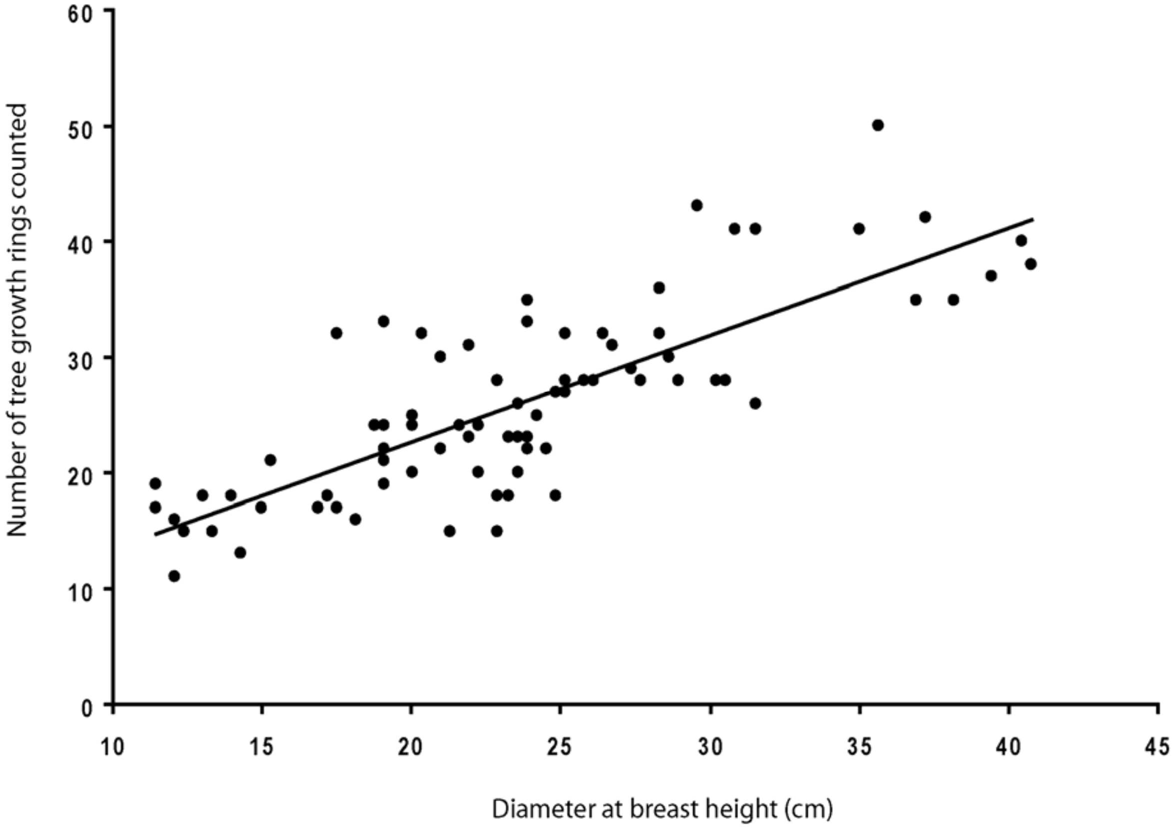


Figure 6. Variation in diameter at breast height (mean dbh) and number of tree growth rings counted (oldest tree) in each time period of glossy privet invasion. The black line inside each box is the median, the upper and lower sides of the boxes are the 0.75 and 0.25 quantiles, and the extreme of the lines represent the range of the data. Outliers are denoted with a circle.

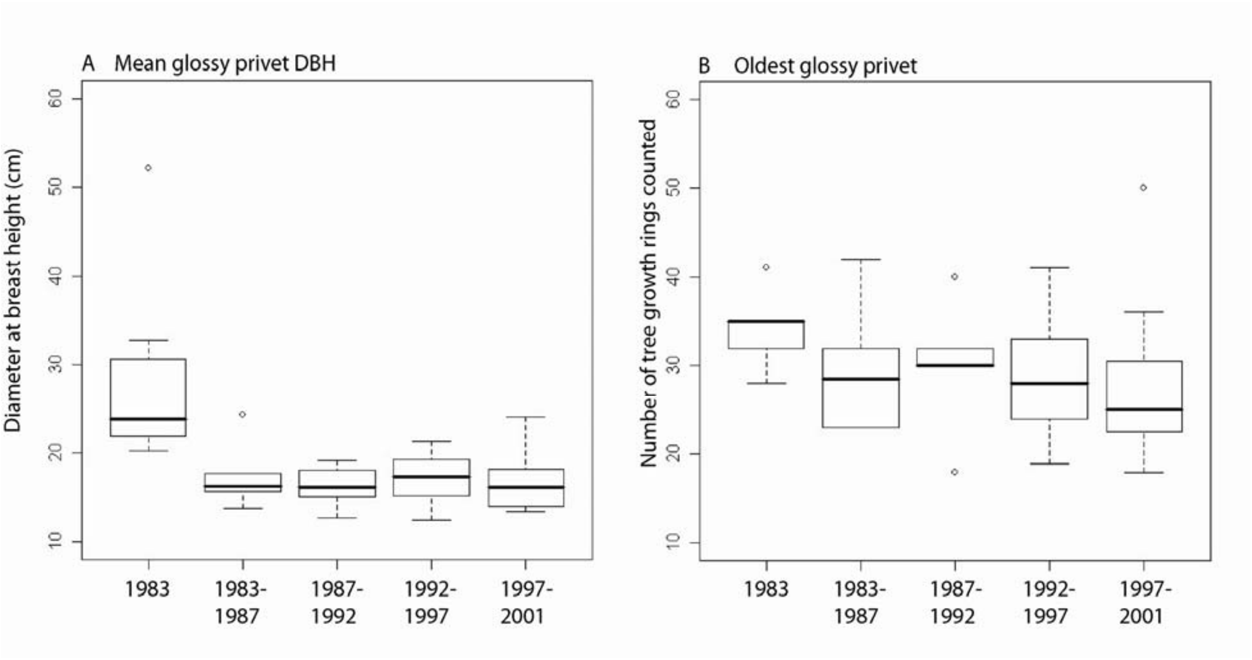


Figure 7. The proportion of glossy privet dominated stands at different distances from urban areas 1983, 2006 and for stands newly invaded from 2001 to 2006. White bars indicate the proportion of the total study area contained in each 200 m buffer, as an index of the expected distribution of glossy privet under randomness (proportional to the available area). (Next page).

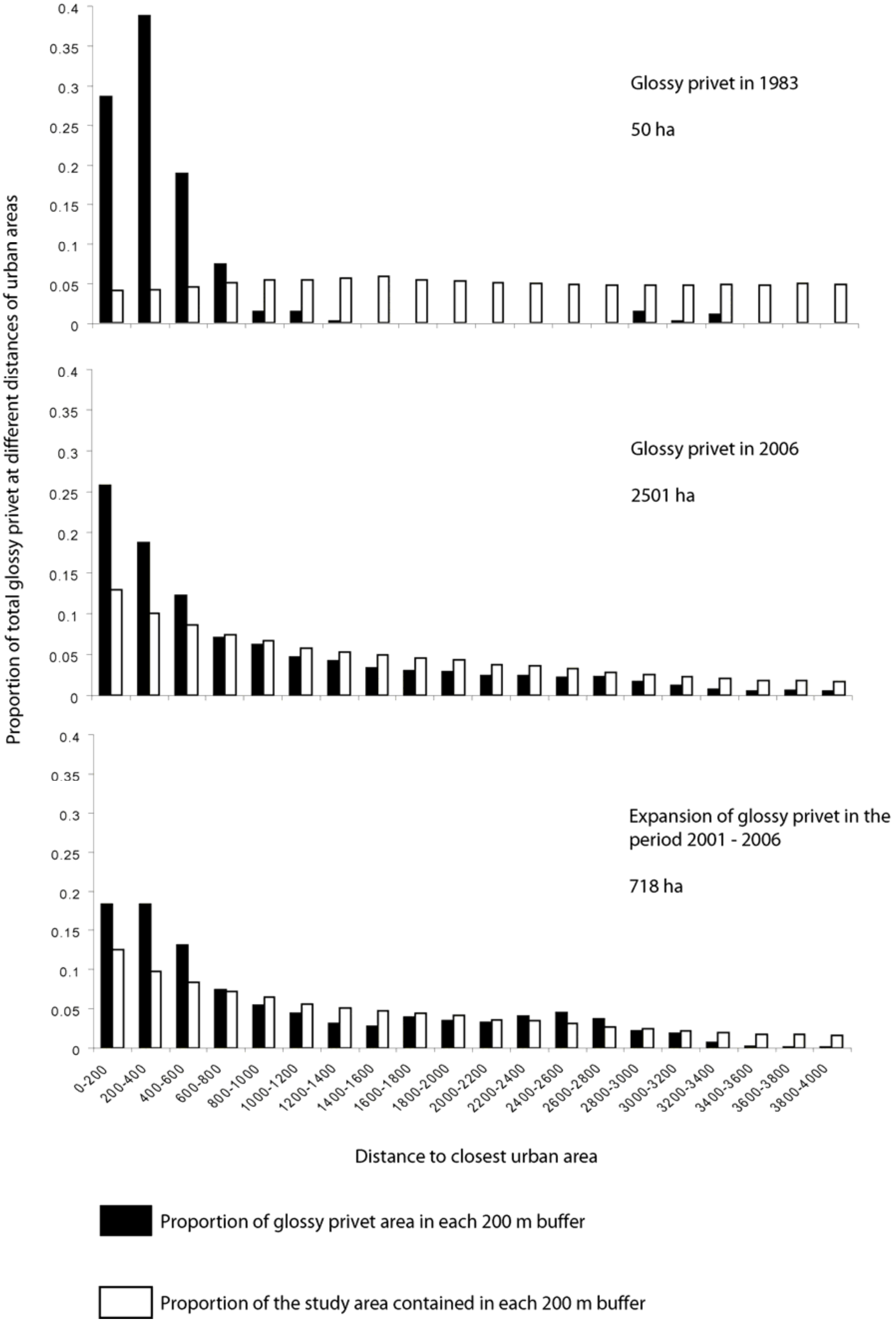
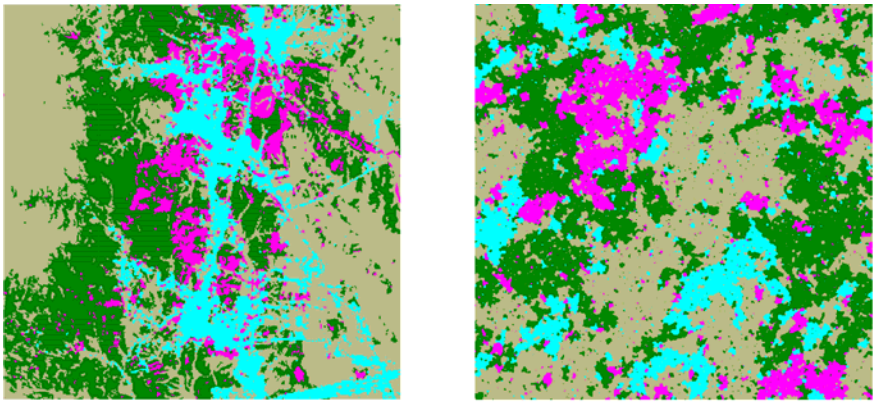
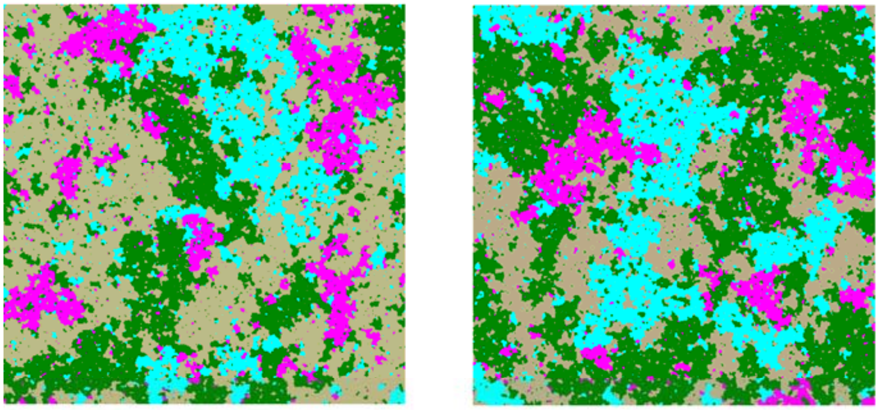

Glossy privet in 1983
50 ha
Glossy privet in 2006
2501 ha
Expansion of glossy privet in the period 2001 - 2006
718 ha
Proportion of total glossy privet at different distances of urban areas
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0-200
200-400
400-600
600-800
800-1000
1000-1200
1200-1400
1400-1600
1600-1800
1800-2000
2000-2200
2200-2400
2400-2600
2600-2800
2800-3000
3000-3200
3200-3400
3400-3600
3600-3800
3800-4000
Distance to closest urban area
Proportion of glossy privet area in each 200 m buffer
Proportion of the study area contained in each 200 m buffer

Figure 8. The actual landscape in 2006 and three examples of the 1,000 random maps that simulated landscape pattern. The frequency distribution function for an association index between urban areas and glossy privet stands is shown with the p=0.025 and p=0.975 rejection values for a p=0.05 test for a value belonging to that distribution. The association index value for the real landscape is shown in red.



Study area landscape 2006

Simulation 1



Simulation 2

Simulation n