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Case Study

Temporal and Spatial Pattern of a Privet (*Ligustrum vulgare*) Invasion

Wanying Zhao, Charles Goebel, and John Cardina*

Privet has escaped from cultivation and is invading natural areas throughout eastern North America. Understanding the pattern of invasion over time could help us develop more efficient management strategies. We studied the invasion history and spatial distribution pattern of privet by mapping age and spatial data for established patches in a 132-ha (326 ac) forested natural area in northeast Ohio. We determined the age of 331 geo-referenced patches by counting annual rings, and mapped them with corresponding land habitat. Age distribution and cumulative number of privet patches over about 40 yr showed three phases of invasion. The initial 19-yr lag phase was characterized as a dispersed spatial pattern (based on nearest neighbor analysis), with patches located mostly at edges of different habitats and open places. In a second phase of about 15 yr, an average of 19 patches were initiated yearly, in a pattern that trended towards clustered. The final phase began around 2007, as the rate of new patch establishment declined, possibly because of saturation of the suitable habitat. Establishment of new patches was not associated with specific habitats. Aggregation of patches with similar ages increased after 1998 and became significantly clustered. Mapping of clusters of old and young patches identified invasion hot spots and barriers. Results affirmed that the best time for invasive control is during the lag phase. By monitoring edge habitats associated with early establishment, managers might detect and control early invaders and delay the onset of the expansion phase.

Nomenclature: Privet, *Ligustrum vulgare* L.

Key words: Age distribution, invasion history, spatial pattern.

Significant financial resources are spent annually to manage invasive plants that have colonized and spread to areas where they interfere with economic activity, transportation, or enjoyment of the outdoors (Pimentel et al. 2005). In natural areas, invasive plants are a particular problem where they displace native species and threaten sensitive habitats that harbor rare or endangered plants. Invasive plants impact not only native plants with which they compete, but also the many organisms of diverse taxa that depend on specific plants as sources of food, habitat, or protection (Rodewald 2011).

Managing invasive plants in forested natural areas is challenging, because by the time a species is recognized as invasive, eradication is difficult (Mack and Foster 2009). Moreover, the probability of detecting an initial colonization, when control would be easy, is unlikely, especially over large areas or variable terrain. Given the limited resources available for invasive plant control, the best that most natural area managers can do is monitor and control invasives in sensitive habitats most vulnerable to invasion. This task, too, is difficult, because modes and pathways of spread into and within a natural area are generally not well understood (Deerling and Vankat 1999; Dietz 2002; Frappier et al. 2003). Thus, insufficient understanding of spread behavior of invasive plants within a landscape context inhibits the development of efficient control or eradication strategies.

Ecological processes underlying the possible displacement of native plant species by invasive species are complex. Factors such as landscape characteristics, competitive interactions, topography, and soil properties, can influence the trajectory and consequence of invasions (Lundgren et al. 2004; Tecco et al. 2007). Landscape features, such as roads and habitat borders can affect

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Management Implications

Invasive plants in natural areas are difficult to detect in early stages when control would be most effective. If managers knew where to expect initial establishment and the pattern of subsequent patch development, control strategies could be targeted more efficiently. In this study, we determined the age distribution and spatial pattern of patches of privet (*Ligustrum vulgare*), a woody invasive plant. We reconstructed the invasion history in a natural area in northeast Ohio where privet has escaped from home landscapes. Since the privet invasion is still in progress, understanding the history and pattern of the current invasion could provide insight into future spread. The oldest privet patch was dated to 1972, but significant increases in patch number did not begin until about 1991. Initial patches appeared mostly in edge habitats, but thereafter the distribution was more random and there was no clear invasion front related to topography or land use. Hot spot analysis suggested that the highly dispersed initial patches, which probably resulted from multiple random dispersals from one or more source populations, could have facilitated further invasion. The rate of new patch formation slowed around 2007, possibly because of saturation of suitable habitat. Results suggest that managers should monitor edge habitats to detect early privet invasion, and that a prolonged lag period provides time for early control efforts before rapid expansion occurs.

invasive plant occurrence, operating as facilitators or barriers. Biological attributes of the invasive species interacting with the landscape result in a particular pattern of invasion that might aid managers in making decisions about how and when to focus monitoring or control efforts (Minor and Gardner 2011). Understanding characteristics of spread of invasive plants at the population and landscape level could reveal the history of plant invasion and allow managers to make predictions about the direction, speed, and consequences of future invasions (Flory and Clay 2006).

Patterns of invasion history can help us understand the time frame over which invasive plants invade and how they spread through particular types of landscape. Patch expansion rates, dispersal facilitations, and limitations by site conditions can also be revealed (Dietz 2002; Frappier et al. 2003; Lundgren et al. 2004). Several models have been developed to describe the pattern of plant invasion (Crooks 2005; Emry et al. 2011; Higgins and Richardson 1996; Radosevich et al. 2003). Generally, these include a lag phase following initial introduction, a phase of linear expansion, and a phase of saturation once most suitable habitat on a landscape is occupied or unavailable. Invasion history can be reconstructed by studying the spatial and temporal patterns during the invasion period. For example, historical aerial photos (Brown and Carter 1998), age determination (Dietz 2002; Frappier et al. 2003; Wangen and Webster 2006), and density evaluation (Fei et al. 2009; Flory and Clay 2006) have been used for detecting spatial and temporal patterns of invasive plants. Efforts to link spatial and temporal aspects of invasion can provide new perspectives to understand historical processes of invasion by invasive plants on the landscape level. The invasion history over a landscape can be reconstructed based on the spatial locations of individual plants at a relevant temporal scale (Frappier et al. 2003; Wangen and Webster 2006). For example, Dietz (2002) determined the age of five invasive plant species within patches using annual ring analysis, and discovered the directional spread preference and distribution pattern via age spatial structure.

Privet (*Ligustrum vulgare* L.) is a branched, deciduous or semievergreen shrub that was introduced to North America from Europe in the colonial period as hedge plant (Cothran 2003). Privet has escaped from cultivation and is becoming naturalized in eastern North America (USDA-NRCS 2011). Privet was widely planted by homeowners in home landscapes from at least 1920, and by state transportation departments along highways, but has lost favor to other species because of twig blight anthracnose (*Glomerella cingulata*), which causes leaf yellowing (Dirr 2009). Privet can produce more than 10,000 fruits per plant, and fruit number and seed production are not significantly affected by defoliation on flowering branches (Obeso and Grubb 1993). Seed dispersal can be facilitated by berry-eating birds and other animals during winter. Although privet thrives in full sun and along stream banks, it is tolerant of shade and drought, and can grow in almost any kind of soil (Bailey 1922; Gratani and Foti 1998). Consequently, privet frequently invades riparian habitats and forest edges, and can form dense thickets that displace native plant species in natural areas (Weber 2003).

In northeastern Ohio, privet is still found occasionally in home landscapes and has escaped to roadsides and waste areas. It is not considered to have reached the level of infestation of other invasive shrubs, such as several species of *Lonicera*. Since the privet invasion is still in progress, understanding the history and pattern of the current invasion could provide insight into future spread. Our objective was to combine temporal and spatial information to describe the pattern and history of invasion of privet in a natural area, using a geographic information system (GIS) and spatial statistics.

Materials and Methods

Study Sites and Sample Collection. We sampled privet at Wooster Memorial Park (WMP), a 132-ha natural area and public park in Wayne County, Ohio (Figure 1). The predominantly-forested park features streams, steep ravines (up to 70 m [230 ft] deep with 15 to 80% slopes), and rich spring flora (over 580 plant species) including endangered species (e.g. *Carex cephaloidea* (Dewey) Dewey), and threatened species (e.g. *C. sprengelii* Dewey ex Spreng. and *C. retroflexa* Muhl. Ex Willd.). A stream, the Rathburn

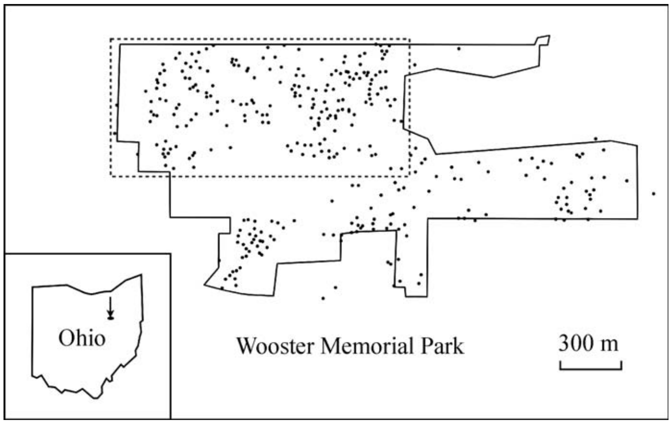

Figure 1. Geographic location of the study site and sampling sites. All privet samples are represented as a dot in the park map. The rectangular region chosen for spatial analysis is indicated by the dashed line.

Run, and associated valley traverse the park from west to east, and several intermittent side streams flow north into the main stream. The park is 8.8 km (5.5 mi) west of the closest urban area. The north side is bordered by mixed land-use, including isolated houses, a small pine plantation, forest, and a persistent stream. The east side merges with a privately-owned forest and a small pasture. South of the park is a mix of farmland, privately owned wooded areas, and a highway. To the west is farmland with mostly grain crops. We drove all surrounding roadways, and visited farmsteads within 4 km of the park, and the closest privet plants were found along a drive about 2 km from the western edge of the park, and one along the highway 4 km to the southeast. The core area of the park is second-growth maple–oak–hickory (*Acer–Quercus–Carya*) forest, with remnants of yellow birch (*Betula alleghaniensis* Britton) and large-toothed aspen (*Populus grandidentata* Michx.) in recently harvested and disturbed areas. Parcels of abandoned farmland in various stages of succession are also common, as the park has acquired additional parcels over time.

We mapped and collected basal stem samples from 345 privet plants over the entire area of the park. A crew of four people walking about 10 m apart side-to-side surveyed the entire park over a period of 25 d in summer 2010. A patch of privet was defined as a cluster of privet stems at least 10 m from other privet individuals. If a single, isolated privet plant was found to be least 10 m from any other plant, it was designated as a nascent patch. We revisited the park in 2011 to confirm that no patches had been missed. For each patch, the stem with the largest basal diameter, which was assumed to be the oldest in the patch, was selected for sampling. We measured and recorded the diameter of the main stem at 50 cm (19.6 in) height. The main stem was sawed off at the soil level and a 4- to 8-cm long core section of the stem base was obtained for age determination (see below). The remaining stump was marked with paint for possible resampling. Site conditions and surrounding vegetation were recorded for all samples by visual observations and linked to slopes and vegetation maps. All the samples in WMP were geo-referenced, and data entered into ArcGIS version10 for analysis (Environmental Systems Resource Institute, Inc (ESRI), Redlands, CA, 2010). For all analyses, we assume that the age of each sampled plant represents the age of the specific patch, and that all patches present in the park were sampled and mapped.

Age Determination. The cut surfaces of stem core samples were sanded using a belt sander and successively finer sandpaper to obtain a very smooth surface. This surface was scanned to produce a digital image for annual ring analysis (600 dpi). Samples were analyzed using WinDendro (Regent Instrument Inc., Canada) and when necessary determination of annual rings was done manually using the on-screen image. The imaging system was calibrated using 10% of samples to determine that accuracy of age determination was within 1 yr. We successfully determined ages of 331 of the 345 privet samples; missing samples (4%) were caused by damaged or misshapen stems whose ring patterns were unclear. All the age data were combined with GPS coordinate information in an attribute table in ArcGIS v.10.

Maps of Overall Spatial and Age Spatial Distributions. To determine the spatial distribution pattern and habitat preferences of early invasion, we identified the locations of the initial privet colonists. These were defined as those samples with the highest number of annual rings. We overlaid map layers for estimated patch ages, habitats, and an aerial photo of the park (Wayne County Auditor's Office, 2004). Initial site locations were matched to field records of site conditions and surrounding vegetation. Habitats were characterized in terms of vegetation, topography, and land use as described in Table 1. Predominant habitat categories were bottomland forest, hemlock–hardwood forest (on slopes and upland), evergreen (nonhemlock) plantings, old fields, and multi-use areas. Privet was scarcely found in the old fields and multiuse areas. The spatial distribution of privet patches during invasion was described in maps showing the invasion status in four representative years. A map of the distribution pattern by patch age and habitat types was also generated.

Statistical Analysis of Overall Spatial and Age Spatial Distributions. Spatial analyses (nearest neighbor, Moran's I, and hot spot analysis) were performed using spatial statistics tools in ArcGIS v.10 to detect and characterize the overall spatial and age spatial distribution patterns. Because the outer borders of the park are quite

Table 1. Characterization of habitats observed in the survey of Wooster Memorial Park.

Habitat descriptor	Dominant plant species	Number of samples	Area	Description
			ha	
Hemlock–hardwood upland forest	Oak (*Quercus* spp.), Beech (*Fagus* spp.), Black Cherry (*Prunus serotina* Ehrh.), White ash (*Fraxinus americana* L.), Maple (*Acer* spp.), Hemlock (*Tsuga* spp.).	132	40.9	Several areas are immature or pole stage, and invaded by nonnative shrubs.
Hemlock–hardwood slope forest	Oak, Maple, Hemlock, Beech, Yellow birch (*Betula alleghaniensis*), hickory (*Carya* spp.), Aspen (*Populus tremuloides* Michx.).	56	30.7	Located in the Rathburn Run valley and side ravines.
Bottomland forest	Red maple (*Acer rubrum* L.), Sugar maple (*Acer saccharum* L.), Sycamore (*Platanus occidentalis* L.), Black walnut (*Juglans nigra* L.), Basswood (*Tilia* spp.), Elm (*Ulmus* spp.), Green Ash (*Fraxinus pennsylvanica* Marshall), Bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch).	89	29.3	Located in the riparian corridor and wide, forested floodplain.
Evergreen plantings	Pine (*Pinus* spp.)	36	9.5	Native and nonnative, previously planted and gradually being replaced by deciduous trees.
Old field	Perennial grasses and forbs	2	10.7	Had been used for production of corn, hay, and orchard.
Multi-use area	Mowed grass	0	5.7	Areas for entrances, shelters, and parking lot.

irregular, we selected the largest rectangular area of the park (Figure 1) for spatial analyses so that edge irregularity would not affect the estimation of spatial pattern statistics or their significance (Fortin et al. 2006). The rectangular area included 201 samples from different habitats representative of the whole park.

Nearest neighbor analysis was performed using the Average Nearest Neighbor function in ArcGIS to evaluate the degree of clustering of privet patches in the park. Statistical significance in the nearest neighbor analysis indicates that patches are more likely to be either spatially close (clustered pattern) or evenly dispersed across an area (dispersed pattern) than would be expected only by chance (Peacock et al. 2008). We created data layers, which included accumulated sample points from the beginning of the invasion, for each year from 1990 (the year with 12 initial patches) and performed nearest neighbor analysis on each of the data layers.

To compute the degree of correlation between patch age and spatial distances during the invasion process, spatial autocorrelation coefficients of age values for each year were computed using Moran's I. Moran's I is a method to evaluate whether patches of similar value (in this case, age) tend to be close to each other (clustered pattern), randomly distributed (random pattern), or evenly dispersed (dispersed pattern) (Mueller-Warrant et al. 2008). Using Moran's I, we evaluated the degree of clustering of patches with similar ages. Analysis was performed with accumulated samples, for each year starting in 1994 when there were sufficient samples to accurately calculate the Z score.

Hot spot analysis was performed using the Getis-Ord Gi* statistic (Ord and Getis 1995) to detect and locate the old and young age clusters in the park. The Getis-Ord Gi* hot spot analysis can provide information on where the features with similarly high or low values spatially cluster in the study area.

For all three analyses, the Z score was used to measure the significance with a 90% confidence level. The nonsignificant zone of Z scores is between -1.65 and 1.65, indicating a random pattern. The higher the Z score, the more intense is the clustering for Moran's I, and the more dispersed for nearest neighbor analysis.

Habitat Relation to Age and Growth Rate. To investigate effects of forest type on growth rate of privet, we calculated the average growth rates of samples located in four different habitats (hemlock–hardwood upland forest, bottomland forest, hemlock–hardwood slope forest, and evergreen forest). Growth rate (average increase in stem diam yr^{-1}) of privet was calculated by dividing the stem diameter (cm) by age (number of rings, i.e. yr) for all the samples for which age could be determined. In addition, we compared ages of samples among these four different habitats. To assign samples to habitats, we overlaid the habitat category

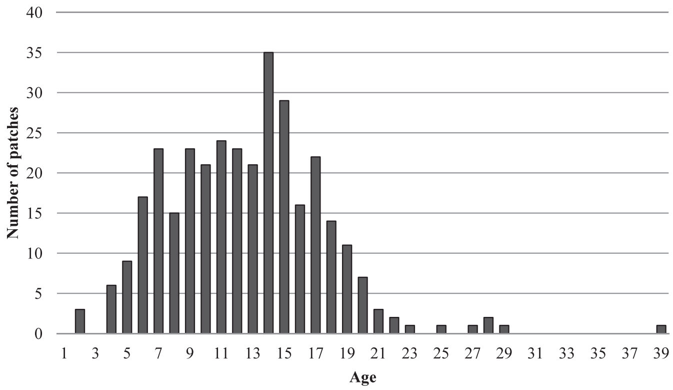

Figure 2. Age distribution (number of privet patches by patch age) of the 331 privet samples obtained at Wooster Memorial Park.

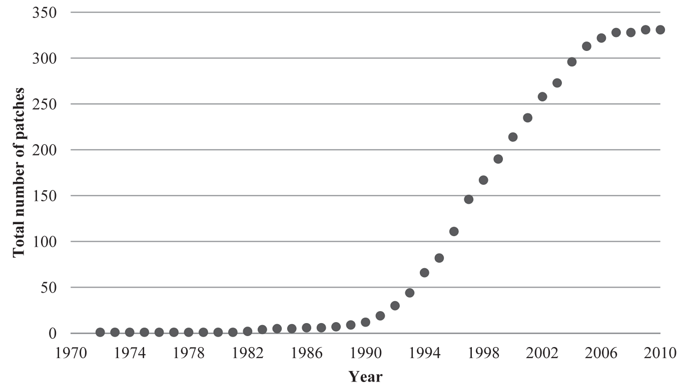

Figure 3. Cumulative number of privet patches in Wooster Memorial Park from 1972 to 2010.

map with a map of sample points. All the samples outside the park or at the edge of two habitats, where it is difficult to assign the samples, were excluded, resulting in 310 samples that were successfully categorized to habitats. We used the general linear model in Minitab (Minitab, Inc., State College, PA) to analyze effects of habitat on growth rate and age. We conducted a regression analysis of growth rate in relation to age for all the samples using GS+ version 5 (Gamma Design Software Inc., Plainwell, MI) to evaluate whether growth rate was associated with time of invasion.

Results and Discussion

Invasion History. The frequency distribution of privet patches by age followed a Gaussian distribution, with a long right tail, indicating low frequencies of the oldest aged patches (Figure 2). Age distribution was continuous from the 4-yr-old to 23-yr-old patches. There were no patches of 3-, 24-, 26-, or 30- to 38-yr old. The oldest patch was represented by an individual plant that had 39 rings, suggesting that the invasion of privet into this park started about 40 yr ago.

A plot of cumulative patch number with time showed three phases of the privet invasion over 40 yr (Figure 3). Following the initial invasion around 1972, there was a 19-yr (1972 to 1990) lag phase during which 12 new patches or individuals became established. A rapid increase in patch number began around 1991 and continued to 2006 (expansion phase). The average annual increase in patches was approximately 19 yr^{-1}, with a maximum of 35 yr^{-1}, which occurred in 1994. During the expansion phase, a total of 310 patches or individuals became established, which is about 94% of all the patches we identified. The rate of new patch establishment decelerated suddenly beginning around 2007 and leveled off (saturation phase).

We examined the locations of the initial patches to determine if there was a pattern of landscape characteristics associated with initial establishment. Patches that arose during the lag phase were overlain with the habitat layer, and an aerial photo, with reference to the sample sites. The only consistent pattern was that colonization by the oldest aged patches (21- to 39-yr old) was generally associated with edge habitats, where two or more kinds of habitats intersected (Table 2). The oldest sampled patch was at the edge of the woods, adjacent to a farm field. Forest edges are often early sites for invasion of exotic plant species into forests because they serve as a transition zone from open habitat to the forest interior, and provide cover, nesting sites, and food that attract birds and small mammals that can disperse seeds and other propagules of invasives (Gates 1991; Yates et al. 2004). Other initial colonization sites were open, full-sun habitats, possibly because of the preference of privet for light and higher survival at open sites (Dirr 2009). Although there are reports that privet prefers bottomland habitats (Olson and Cholewa 2009; Weber 2003; Webster et al. 2006), most of the oldest patches were located in upland forest sites, and only two of the initial patches were found in the bottomland (Table 2).

The 19-yr lag phase (Figure 3) for privet represents the initial arrival into the park and a period of establishment before significant spread began. Because of their long juvenile (prereproductive) period, woody perennial invasive species usually have a long lag phase, during which expansion is delayed (Petit et al. 2004). Wangen and Webster (2006) reported an approximate 27-yr lag phase for the invasion of *Acer platanoides* L. after its first establishment on an 1100-ha island. Deerling and Vankat (1999) examined the population structure of *Lonicera maackii* (Rupr.) Herder in a natural area in southwest Ohio, and concluded that the number of initial colonizers was very small and remained so for 10 yr before significant increases began. They attributed the lag period to various factors limiting seed production, and assumed that subsequent population growth came from seeds produced by the initial invaders rather than from secondary invasion events. The spatial pattern of the privet invasion in our

Table 2. Location of the 12 oldest privet patches identified in Wooster Memorial Park during the lag phase (1971 to 1990). Hyphenated terms represent the edge area of two or three different but adjoining habitats.

Patch age	Location
Years	
39	Farmland–upland forest
29	Trail–stream–slope forest
28	Farmland–upland forest
28	Upland–slope forest
27	Grassland–evergreen forest
25	Upland forest
23	Upland forest
22	Upland–slope forest
22	Bottomland forest
21	Farmland–upland forest
21	Stream–bottomland forest
21	Upland forest

study suggests multiple invasion events as the source of those oldest patches and preliminary genetic evidence confirms this (Zhao 2012). Crooks (2005) suggested that the lag phase is characteristic of populations with exponential increase patterns, which is probably the case in this study, rather than a prolonged lag indicative or more complex dynamics.

Controlling invasives during lag phase can help stop further spread through propagule dispersal (Emry et al. 2011). Identifying favorable habitats for initial patches can assist in early detection of plants such as privet during the lag phase before the population undergoes rapid expansion. However, because populations are small during this phase, they can be difficult to detect. For species like privet, which are probably initially introduced to natural areas by bird-dispersed seeds, scouting edge habitats is probably the most effective way to detect early invasion. The duration of the lag phase for privet in WMP was about 20 yr, and simulations of invasive plant control strategies suggest that persistent scouting and removal would have been required to prevent rapid population expansion (Moody and Mack 1988). The use of weed maps could have helped managers follow existing patches over time, but scouting of the entire site would have been required to detect new or previously undetected patches, as suggested by Emry et al. (2011).

Understanding reasons for the change from lag phase to the log increase phase might help us predict the rapid expansion of privet after 1990 (Figure 3). We examined historical weather information and maps of the area over time to see if changes in environmental conditions or land use might explain the timing of this transition. We found no evidence of significant change; the only anomaly was that 1990 was a year of unusually high rainfall (42% above normal), but this was followed by a relatively dry year (22% below normal), so we think short term weather is unlikely to have been a cause of the change. Results from simulation studies suggest that this is simply the inherent pattern of exponential populations rather than a change in the habitat or the species (Crooks 2005; Emry et al. 2011).

The sudden deceleration in patch initiation after 2006 (Figure 3) may have resulted from saturation of favorable habitats, leading to decreased probability of establishment. In addition, adjacent patches could have merged to form larger patches, so that at some point, new colonists located in or adjacent to old patches cannot be distinguished. The saturation phase in this study, when the rate of new patch formation declined, is possibly due in part to our inability to distinguish new patch establishment. In other words, a seed germinating after being carried at least 10 m by biotic or abiotic forces would have resulted in a new patch, whereas a seed germinating after falling beneath the same mother plant would not. The absolute density of privet could have increased after year 2006, but the geographical extent of clearly discernible new patch development in WMP slowed at this point. Work by Wangen and Webster (2006) suggests that invasions can have multiple lag phases, so what we are interpreting as a leveling off of patch establishment could also be a second lag phase that is part of a prolonged expansion phase that would be detected in the future.

Spatial Distribution Pattern Over Time. To better understand the invasion process from a landscape perspective, we compared spatial distribution maps of privet patches in each year during the invasion; four representative maps are shown (Figure 4). Privet patches established during the lag phase (Figure 4a) were highly dispersed across the park. Secondary patches in the early expansion phase (Figure 4b) were also dispersed and were not associated with specific locations or habitats. This suggests multiple invasion events from outside the park or widespread dispersal within the park from the early colonizing plants, which could have reproduced by seeds about 5 yr after initial establishment (Dirr 2009). Although a large number of new patches formed during the expansion phase (Figure 4b, c), there was no obvious cluster of patches associated with habitats or even previously established patches.

To characterize the spatial pattern statistically, we performed nearest neighbor analysis using coordinates of all the sample data by year beginning in 1990, when there were 12 initial patches present (Figure 5). The Z score values larger than 1.65 suggest significant dispersion of privet patches before 1994, with an anomalous dip in the trend in 1991 during the early invasion. Over time, the decreasing Z scores indicated that the spatial pattern

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Figure 4. Spatial distribution of privet patches in four representative yr: a. Yr 1990 shows the end of the lag phase; b. Yr 1996 shows the early expansion phase; c. Yr 2001 shows the late expansion phase; and d. Yr 2010 shows all the patches sampled. Gray dots indicate new patches, i.e. those not present in the previous map.

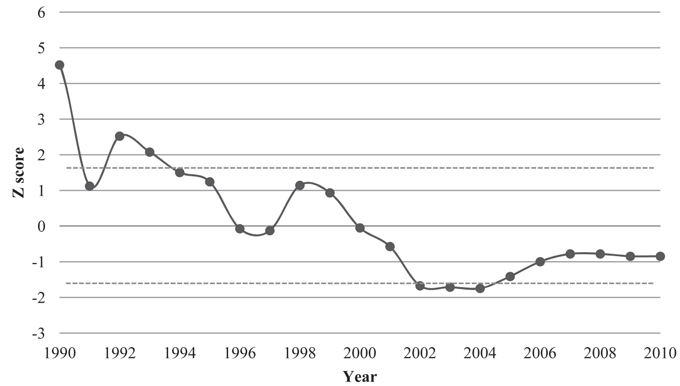

Figure 5. Clustering status during invasion based on nearest neighbor analysis. The extent of spatial clustering each yr is represented by a normal standardized score (Z score values), which indicates the intensity of clustering. The nonsignificant area between the two dashed lines (-1.65 to 1.65) indicates a random pattern of spatial clustering. Positive significance ($Z > 1.65$) indicates a dispersed pattern and negative significance ($Z < -1.65$) indicates a clustered pattern.

became generally less dispersed, suggesting greater clustering as seeds were spread locally. A clustered pattern was observed from 2002 to 2004; however, putative patches were distributed randomly in the study area during most years of the invasion, which follows the pattern seen in Figure 4. This is consistent with findings by Moody and Mack (1988) that plant invasions generally expand from multiple nascent foci rather than expanding from the edge of a single patch. These results suggest a large geographic extent of patch establishment during the entire invasion process. The initial patches, which were highly dispersed across the park, may have been the source of some of the subsequent patch development, thereby contributing to the spatial pattern at the later stages of invasion. The initial patches were likely isolated foci that facilitated local recruitment in the later part of the expansion phase and the saturation phase, which supplemented a probable steady continued introduction from outside the park. New patches originating from propagules sources outside the landscape or from populations established within it, are generally easily overlooked in invasive management, although they play important roles as sources of reproductive propagules in invasion expansion (Ghersa et al. 2000; Radosevich et al. 2003).

Age Spatial Distribution. Privet patches of different age were spatially mixed across the landscape (Figure 6). These findings support our conclusion that there was no invasion front or a consistent direction of movement of the invasion in the park, which might have been the case if there was one primary means of dispersal (Crooks 2005). Furthermore, there was no correlation between patch age and growth rate (data not shown).

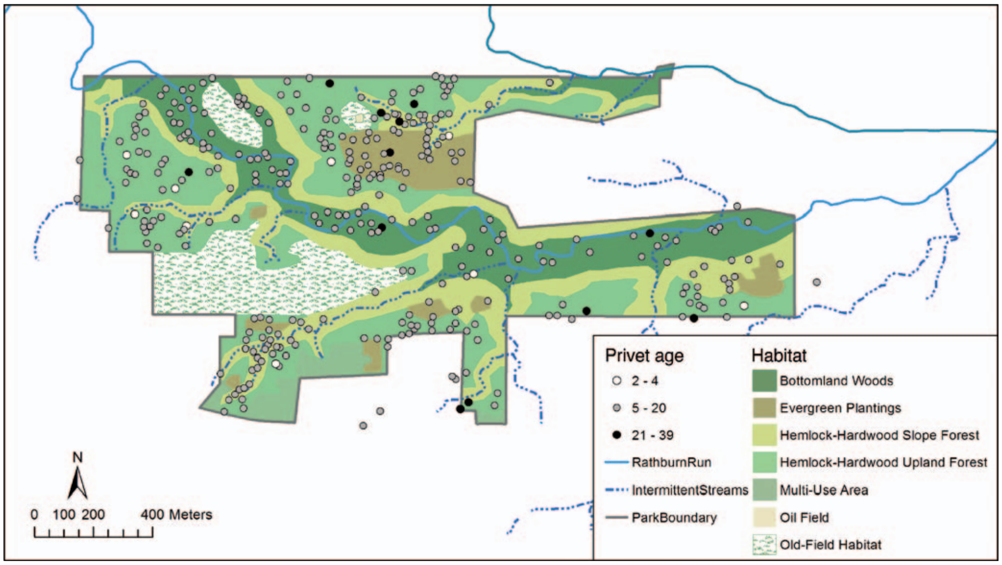

Figure 6. Age spatial distribution of privet samples across the park landscape. The colors representing different age classes are indicated in the legend. The twelve initial patches are in black. The age class division interval and class number were generated according to the three phases of invasion (lag, expansion, saturation). The map also shows habitats, rivers, and park boundary.

We used Moran's I to evaluate spatial autocorrelation over time based on age and geographic locations of privet patches. We observed a trend toward spatial clustering starting around 1999 (Figure 7), with significant clustering of patches after 2002. This spatial clustering trend started in the late part of the expansion phase, which may indicate the formation of juvenile (prereproductive) privet clusters.

Using Getis-Ord Gi* hot spot analysis, two old- and two young-patch clusters were identified (Figure 8). The larger cluster of older patches in the northeastern portion of the park was in a younger regrowth forest. Because of relatively high light availability, this might have been a more suitable habitat for initial establishment of invasive plants compared to older woods (Flory and Clay 2006). The larger cluster of young privet patches in the southwest part of the park was in upland forest that was partially isolated by farmland to the west and grassland to the south. The eastern and northern sides of this area were bordered by hemlock-dominated slopes (15 to 50% slope) leading to less disturbed bottomland forest. Therefore, although some old patches—including an initial patch—were found in this area, the generally low number of older privet plants might have been caused by the separation of the site by the farmland, grassland, and hemlock-slope forest. It is also possible that a great number of well-established invasive plant species in this area (mostly *Rosa multiflora* Thunb. and *Lonicera* spp.) prevented privet establishment at this site by occupying the understory of the woods.

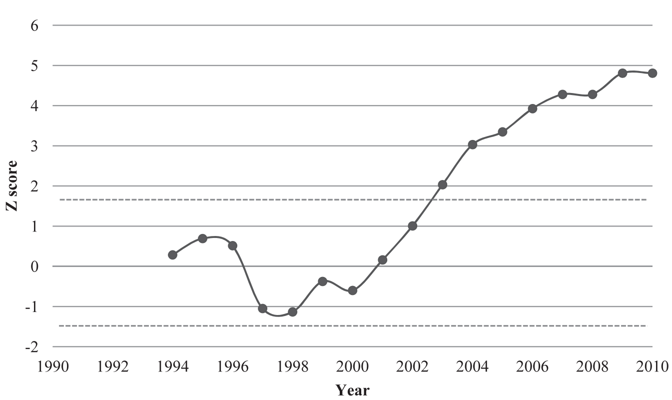

Figure 7. Age spatial autocorrelation each yr based on global Moran's I. The extent of clustering of similar age samples is indicated by a Z-score value. A minimum of 30 samples starting from 1994 were required to obtain an accurate estimation. The nonsignificant area (-1.65 to 1.65) between the dashed lines indicates a random pattern of age spatial correlation. A clustered pattern is measured by a Z-score over 1.65, while a dispersed pattern is represented by Z-scores less than -1.65.

Age and Growth Rate in Four Different Habitats. Growth rates were examined for privet stem sections by age and within different habitats to determine if conditions for growth varied with time or place of establishment. There was a slightly negative but nonsignificant relationship between growth rate and time of privet establishment (data not shown). When comparing age and growth rate among four habitats, we found that privet in the bottomland forest had higher growth rates than privet in the upland forest (Figure 9). There was no significant difference in the average age of privet among the four habitats (data not shown). These results suggest that, although light was more

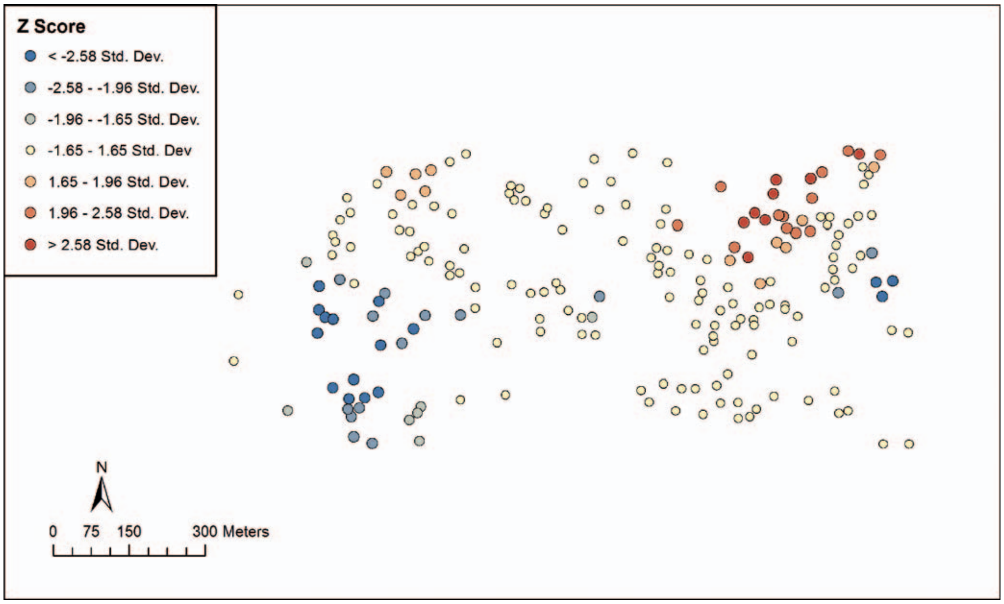

Figure 8. Map of clustering intensity of younger and older patches generated according to Getis-Ord Gi* statistic, indicating old- and young-age clusters in 2010. The local Gi* statistic is represented by a Z score. The Z score values indicate the intensity of the clustering. Blue points are younger privet patches (average age = 9 yr) that are significantly clustered. Red points represent plants in older patches (average age = 15 yr) that are also significantly clustered; yellow points are not significantly clustered. The color gradient corresponding to the Z scores indicates the intensity of clustering.

limited in the bottomland forest, privet was favored at these sites by greater water availability. However, early or late establishment of privet did not appear to be significantly affected by habitats. The clustering of age spatial pattern from the Moran's I and hot spot analysis suggested some preference of locations for early and late establishment, but clustering was not associated with habitats. More information on landscape features is needed to further understand their associations with early or late establishment.

There was no clear invasion front of privet in this park, and no pattern of patch establishment outward in a regular fashion from initial patches. The complex landscape environment provided varying habitat conditions, which may have influenced within-park movement, as well as germination, growth, and survival (Tecco et al. 2007). The mosaic of environmentally-driven factors may have greatly increased the nonlinearity of the invasion pattern. In addition, the highly dispersed initial satellite patches, which probably resulted from multiple random dispersions by animals from various source populations, could have functioned as source patches facilitating the invasion pattern that we observed. Mapping of clusters of younger and older patches provided evidence of a possible invasion center and invasion barrier, both of which could be significant for privet management. Further analysis is required to determine if the large cluster of older patches found in one area of the park area acted as a hot spot of invasion for the entire park.

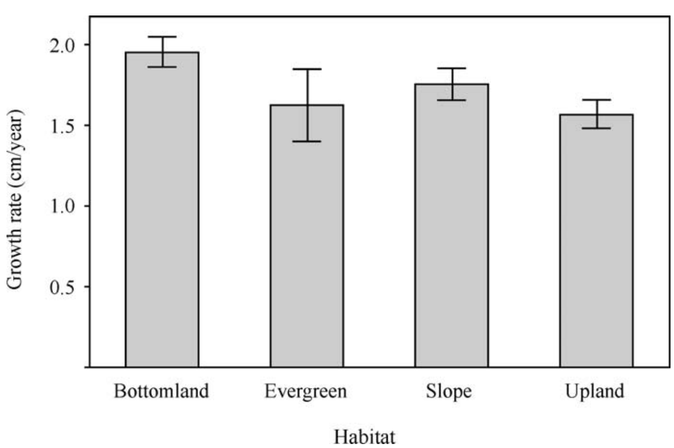

Figure 9. The growth rate of privet in four habitats; bars represent standard errors.

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