ECOGRAPHY 29: 213–222, 2006

The relative importance of landscape and community features in the invasion of an exotic shrub in a fragmented landscape

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Bartuszevige, A. M., Gorchov, D. L. and Raab, L. 2006. The relative importance of landscape and community features in the invasion of an exotic shrub in a fragmented landscape. – Ecography 29: 213–222.

Although invasive plants are recognized as a major ecological problem, little is known of the relative importance of plant community characteristics versus landscape context in determining invasibility of communities. We determined the relative importance of community and landscape features of 30 woodlots in influencing the invasion of *Lonicera maackii*. We sampled woodlots using the point-quarter method and calculated canopy openness and basal areas and densities of shrub, sapling and tree species, as well as woody species richness. We used aerial photos and ArcView GIS to calculate landscape parameters from the same woodlots using a buffer distance of 1500 m. We used logistic and linear regression analyses to determine the community and landscape factors that best explain *L. maackii* presence and density. We also tested whether woodlot invasion by *L. maackii* begins at woodlot edges.

Presence of *L. maackii* was significantly explained only by distance from the nearest town (logistic regression, $p = 0.017$); woodlots nearer town were more likely to be invaded. Among invaded woodlots, density of *L. maackii* was positively related to the amount of edge in the landscape (partial $R^2 = 0.592$) and negatively related to total tree basal area (partial $R^2 = 0.134$), number of native woody species (partial $R^2 = 0.054$), and sapling shade tolerance index (partial $R^2 = 0.054$). *Lonicera maackii* in woodlot interiors were not younger than those on the perimeters, leading us to reject the edge-first colonization model of invasion.

Our findings reveal that landscape structure is of primary importance and community features of secondary importance in the invasion of *L. maackii*. This shrub is invading from multiple foci (towns) rather than an advancing front. Connectivity in the landscape (i.e. the number of corridors) did not promote invasion. However, edge habitat was important for invasion, probably due to increased propagule pressure. The community features associated with *L. maackii* invasion may be indicators of past disturbance.

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A critical question in the study of plant invasions is what factors determine invasibility of a community. Elton (1958) hypothesized that sites with high species diversity are less invasible than sites with lower species diversity. Some experimental studies have supported this hypothesis (Knops et al. 1999, Dukes 2002, Kennedy et al. 2002) but others have not (Levine 2000, Foster et al. 2002). Comparisons across sites typically find positive, rather than negative, correlations between native species richness and invasive species richness (Wiser et al. 1998, Lonsdale 1999, Stohlgren et al. 1999b, 2003, Brown and Peet 2003). However, Fridley et al. (2004) determined that native and exotic species richness at different scales are similar to a null model

Accepted 12 October 2005

ISSN 0906-7590

which assumes no interactions between native and exotic species. Disturbance is also hypothesized to increase invasibility (Hobbs and Huenneke 1992) with support from manipulative (Gentle and Duggin 1997) and comparative studies (Parker et al. 1993, Anderson 1999, Vujnovic et al. 2002). However, higher disturbance has also been found to be associated with lower invasibility in some manipulative (Smith and Knapp 1999) and non-manipulative studies (Stohlgren et al. 1999a).

In recent years, the importance of landscape structure in influencing biological invasions has received attention (With 2002, Cumming 2003), particularly how the structure of the landscape affects the ability of organisms to colonize suitable sites. Most previous research on the effect of landscape structure focused on the movement of native species, including the degree of connectedness required for organisms of varying dispersal abilities to move through the environment (Wiens et al. 1997, Tischendorf and Fahrig 2000) and the value of corridors for movement of organisms to suitable areas of habitat (Haas 1995, Machtans et al. 1996, Tewksbury et al. 2002, Haddad et al. 2003). Cumming (2003) predicted that more complex habitats have higher rates of invasion, and both the amount of connectivity and the spatial arrangement of corridors affect invasion rate. Wiser et al. (1998) found that distance from a seed source influenced the early stages of the invasion of *Hieracium lepidulum* into forests. Landscape parameters that promote colonization by native species may promote invasion of exotic species as well.

For animal-dispersed plants, the landscape can influence colonization through its effects on disperser movements as well as spatial patterns of suitable habitat for recruitment and reproduction. For example, Johnson and Adkisson (1985) found that blue jay *Cyanocitta cristata* dispersal of seeds between woodlots separated by agricultural fields was enhanced by fencerows, which provide protection from predators. Machtans et al. (1996) provide evidence that adult and juvenile forest birds used buffer strips between clear-cuts to move from one forest fragment to another. Wescott and Graham (2000) concluded that the spatial scale and distribution of the seed shadows of several neotropical bird-dispersed tree species were shaped by interactions between fruit characteristics and bird movements through habitats. Deckers et al. (2005) found that the invasion pattern of *Prunus serotina* in hedgerows in Belgium was strongly related to the movement of seed-dispersing birds through the hedgerows towards roost sites and structurally diverse areas of the hedgerows.

Exotic plants that invade forest patches are generally most prevalent in edge habitat (Brothers and Spingarn 1992). This association of invasives with forest edges is due, at least in part, to environmental conditions, but directed dispersal may also contribute in the case of animal-dispersed plants. Such directed dispersal would shape the invasion pattern. Forest patches might first be colonized at the edge due to seeds dispersed by edge-favoring animals. Once those plants mature and reproduce, their seeds may be taken into the interior of forests by other seed dispersers. This "edge-first colonization model" predicts that the oldest individuals at the edge of a forest patch should be at least one generation older than the oldest individuals in the interior of the patch. Alternatively, if the first dispersers to bring seeds to a patch also penetrate to the interior, then no difference between the ages of edge and interior individuals should be expected. Community and landscape features of woodlots are unlikely to act in isolation in determining a woodlot's invasiveness. In this study we aimed to determine the relative importance of landscape vs community attributes in the invasion of woodlots by *Lonicera maackii* in an agricultural landscape.

Lonicera maackii (Caprifoliaceae) is native to northeast Asia and was introduced to the United States in 1898 as an ornamental (Luken and Thieret 1996). It has since naturalized in 24 states east of the Mississippi River and spread from many metropolitan areas (Trisel and Gorchov 1994). *Lonicera maackii* is an upright shrub capable of growing in many different habitats, including second growth forest and old fields. Its seeds germinate under a variety of light intensities (Luken and Goessling 1995, Luken et al. 1997) and its leaves expand earlier and are retained later than those of native shrubs (Trisel and Gorchov 1994). Individuals begin reproducing at ca 5 yr (Deering and Vankat 1999). Fruits ripen in early autumn but persist into the winter and serve as an abundant but low quality food source for many migrant and resident birds (Ingold and Craycraft 1983, Bartuszevige and Gorchov 2005). Viable seeds of *L. maackii* are dispersed by European starlings *Sturnus vulgaris*, American robins *Turdus migratorius*, hermit thrushes *Catharus guttatus*, cedar waxwings *Bombycilla cedrorum*, and northern mockingbirds *Mimus polyglottus* (Bartuszevige and Gorchov 2005).

Lonicera maackii reduces the survival and fecundity of native annual herbs (Gould and Gorchov 2000) and the growth and fecundity of forest perennials (Miller and Gorchov 2004). Native tree seedlings have reduced survivorship beneath *L. maackii* shrubs (Gorchov and Trisel 2003). Collier et al. (2002) determined that species richness of native herb and tree seedlings was lower under the crowns of *L. maackii*.

Both community and landscape parameters have been implicated in the invasion of woodlots by *L. maackii*. Much of the variation in density of *L. maackii* among woodlots is explained by woodlot characteristics such as canopy cover (Hutchinson and Vankat 1997). But in this same region (southwest Ohio) invasion was more extensive in regions where the woodlots were more connected to one another than where the woodlots

were isolated (Hutchinson and Vankat 1998), leading the authors to hypothesize that connectivity between suitable patches of habitat facilitates invasion.

We tested the relative importance of community and landscape features on invasibility of woodlots by *L. maackii*. We also tested whether *L. maackii* first colonizes woodlots at the edge.

Materials and methods

Study area

To determine the community and landscape features that are associated with *L. maackii* invasion, we studied woodlots in an agricultural matrix at an advancing edge of an *L. maackii* invasion. Woodlots were identified as forest stands surrounded by a matrix of agricultural fields, fallow fields, or lawns, and ranged in size between 0.55 and 33 ha. Woodlots connected by fencerows (defined below) were considered separate woodlots (Fig. 1c). An isolation index (Hokit et al. 1999) was calculated for each woodlot and ranged between 0.23 and 3.74 (smaller values indicate more isolated woodlots). Our operational definition of an invasion edge was an area with patches containing many reproductive plants and other patches of apparently suitable habitat with no *L. maackii* or only a few non-reproductive plants. We identified such an invasion edge in Darke County, Ohio (Fig. 1a, b). This area has numerous woodlots and some old fields in a matrix of agricultural fields interspersed with some urban and suburban areas (Fig. 1c). We located 30 woodlots which were characterized as either: 1) invaded or 2) not-invaded. A not-invaded woodlot was defined operationally as one in which there were no *L. maackii* shrubs at any of the sample points. Woodlots were selected based on cooperation of private landowners.

Landscape features

To determine landscape features associated with recent *L. maackii* invasion, we analyzed Digital Ortho Quarter Quad (DOQQ) (USGS 1993) images, which are rectified, digitized aerial photographs, using ArcView GIS 3.2. For each woodlot we quantified area, perimeter, area: perimeter ratio, amount of edge in the landscape (the sum of the perimeter of all woody habitat within a 1500 m buffer around each woodlot), number of corridors (fencerows; narrow wooded strips extending from a woodlot and connecting to a second woodlot), and distance to the nearest town.

Our choice of 1500 m as the radius for landscape buffer was based on analysis of data from buffers (Lee et al. 2002, Bender et al. 2003) of distances 250, 500, 1000, 1500, 2000, 2500, and 3000 m from each woodlot perimeter. For each of these buffer distances we calculated total amount of edge habitat. Regressions of *L. maackii* density versus total edge for the seven different buffer distances showed that a 1500 m buffer explained the greatest amount of variation in density (Bartuszevige 2004). Furthermore, this distance is biologically relevant. American robins are major dispersers of *L. maackii* and move distances of this magnitude during the passage time of *L. maackii* seeds (ca 90 min, Bartuszevige and Gorchov 2005). For example, in one 120 min radio tracking session an American robin within a flock of ca 20 others moved a linear distance of ca 1500 m (Bartuszevige 2004).

Community features

In the same woodlots, we quantified community characteristics relating to disturbance history, canopy openness, and woody plant composition, as well as *L. maackii* density, during June and July 2002 and 2003.

To obtain some general information on recent anthropogenic disturbance history of each woodlot, property owners were asked about timber removal for sale, timber removal for personal use (i.e. firewood), grazing history, mowing, and pesticide use within or at the edge of the woodlot in the last 10 yr. Each woodlot was ranked on a scale of 0–5 (0 = no known disturbance, 5 = five of the disturbance types listed above).

For the other community variables, we used a stratified random sampling design in each woodlot. Four equally-spaced transects crossed the woodlot perpendicular to its long axis, as determined from the DOQQ. Each transect was divided into five segments of equal length; one random point from each segment was sampled, for a total of 20 points in each woodlot.

At each point, the point's "gap fraction" (the proportion of the canopy open to the sky) was measured at ca 2 m above the ground using a Li-Cor LAI-2000 Plant Canopy Analyzer (Welles and Cohen 1996). This instrument uses hemispherical optics and a ringed detector to measure diffuse radiation at each sample point. We obtained an initial reading by measuring diffuse radiation at a point near the woodlot, but not under any vegetation. Then at each point along the transect, we obtained a gap fraction reading by dividing the understory reading by the initial reading.

At each point, we used the point quarter method (Krebs 1989) to determine the species, diameter at breast height (dbh), and distance to the point for the nearest tree (dbh > 10 cm), sapling (dbh 2.5–10 cm) and shrub (> 0.5 m tall belonging to a species with a multi-stemmed habit) within each quadrant (total of 80 trees, 80 saplings, and 80 shrubs in each woodlot). We used tree data to calculate each species' basal area and the total stand basal area (Krebs 1989). We divided shrub density

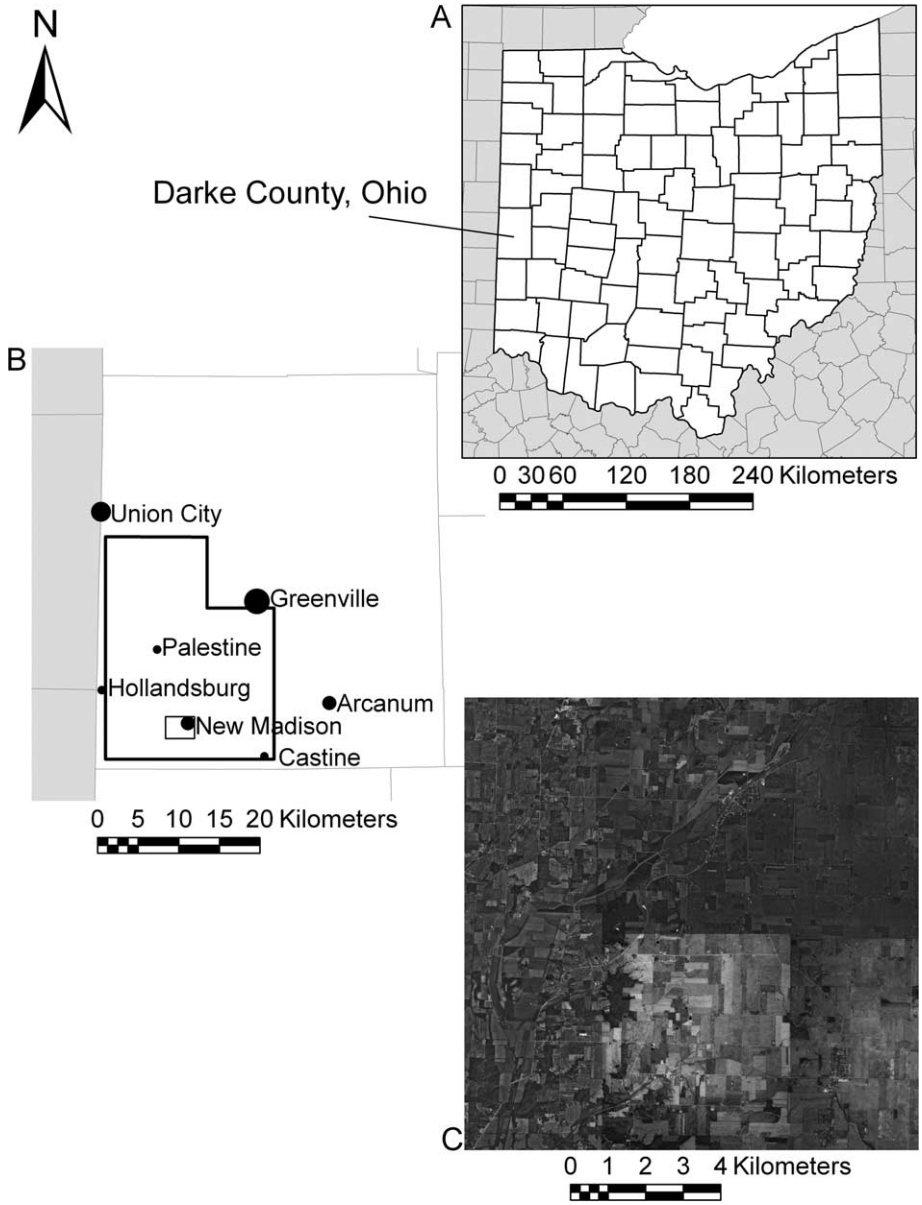

Fig. 1. A) Map of Ohio (white area) and location of Darke County, Ohio. B) Darke County, Ohio and the location of the towns that were nearest to the studied woodlots. Relative size of the dot represents the relative population of the town. The large polygon is the study area including the 30 woodlots. The smaller polygon is the area represented in (C). C) Aerial photo composite of a portion of our study area. Note that the area is a matrix of agriculture with woodlots and small towns.

into *L. maackii* density and non-*L. maackii* shrub density. Non-*L. maackii* shrub density included both native and exotic shrubs. We also counted the number of native woody species sampled in each woodlot.

We calculated importance values (IV, calculated from relative basal area, relative density, and relative frequency) for each species in the sapling layer. We calculated the shade tolerance index for each woodlot by multiplying sapling IVs by the shade tolerance value (Burns and Honkala 1990) of each species which ranged from 1 (very intolerant) to 5 (very tolerant). The shade tolerance index provides an indirect measure of the understory conditions in the recent past. A woodlot with a high shade tolerance index indicates that in the past the canopy of the woodlot was continuous and thus excluded the growth of shade-intolerant tree seedlings into the sapling layer (Hutchinson and Vankat 1997).

Statistical analysis

We used stepwise logistic regression analysis to determine which community or landscape features explained the presence of *L. maackii* in the 30 woodlots. For those 20 woodlots where *L. maackii* was present, we determined which landscape or community features explained the density of *L. maackii* using stepwise multiple linear regression. For all regression models (logistic and linear) we used $p = 0.15$ for a variable to enter or leave the model. In the linear multiple regression model, we log transformed *L. maackii* density because of the presence of two woodlots with very high *L. maackii* densities. Analyses on non-transformed data with and without the outliers yielded similar results.

Oringinally, data on 20 different variables were collected on each woodlot. Variables were thinned using a correlation matrix and biological knowledge of the system to prevent problems with collinearity and to increase the power of the analysis. The following ten variables were used in both the multiple logistic regression and multiple stepwise linear regression. We chose these variables because they were not significantly correlated with one another, are not redundant and they provided a sufficient description of the community and landscape characteristics of the woodlots. These variables were: number of native woody species (range: 12–35), gap fraction (3.1–4.9), shade tolerance index (230.9–468.0), basal area of trees (10.3–35.7 m^2 ha^{-1}), density of shrubs other than *L. maackii* (26.8–2247.5 shrubs ha^{-1}), disturbance (0–3), area:perimeter (17.7–109.9), total edge in buffer (9766.9–69462.7 m), number of corridors (0–3), and distance to the nearest town (1417–7699 m). These data met all assumptions for normality, heteroscedasticity and collinearity.

Due to potential non-independence of spatial variation in the landscape variables, another regression analysis was carried out. The variables that best explained the variation in *L. maackii* density in the final stepwise linear regression model were used in a spatial covariance model using a SAS PROC MIXED model (Anon. 1999) that adjusted for potentially correlated observations due to linear geographical proximity. The results from this test did not significantly improve the fit of the model, indicating that linear spatial dependence was not important. Therefore results from only the linear least squares models are reported.

Pattern of *L. maackii* invasion into woodlots

We selected a subset of 15 of the 20 woodlots with *L. maackii* for investigating whether invasion began at the edge. To determine the ages of the oldest perimeter and interior *L. maackii* in each woodlot, we first selected the four largest perimeter and four largest interior shrubs based on stem diameter, during June and July 2003. We located the perimeter shrubs by walking the perimeter of the woodlot and inspecting all shrubs within 5 m of the edge of the woodlot. We located the interior *L. maackii* shrubs by walking straight line transects 20 m apart and marking large shrubs. The interior transects were started 20 m into the interior of the woodlot to avoid marking perimeter shrubs. For each of the largest four interior and four edge shrubs, we aged the largest two stems and the largest two roots (based on the assumption that the largest stems and roots were the oldest Luken (1988)). We cut stems 2 cm above the burl using a pull stroke pruning saw or pruning shears. We cut roots 2 cm below the burl using a hatchet. We dried these burls with proximal segments of stems and roots for at least 24 h then cross-sectioned using a miter saw. We stained cross sections with lignin pink or rubbed with white chalk to accentuate the annual rings (Jozsa 1988). For each plant, the highest annual ring count (root or stem) was used as the plant's age. For each woodlot, the oldest edge and interior aged plants were used to test whether edge plants were older using a one-tailed paired t-test.

Results

Landscape and community analysis

Twenty of the 30 woodlots had been invaded by *L. maackii* (range 2–3201 shrubs ha^{-1}). Stepwise logistic regression revealed that distance to the nearest town was the only significant predictor for presence of *L. maackii* in woodlots ($\chi^2 = 6.36$, DF = 1, $p = 0.017$). Woodlots invaded by *L. maackii* were closer to a town (mean ± SD = 3.1 ± 1.3 km) than those not invaded (mean ± SD = 4.8 ± 2.1 km, Fig. 2).

For the 20 invaded woodlots, stepwise linear regression revealed that *L. maackii* density was significantly explained by the following variables (in order of importance): total edge in the buffer, basal area of trees, number of native woody species (trees, saplings, and shrubs), and sapling shade tolerance index (Table 1).

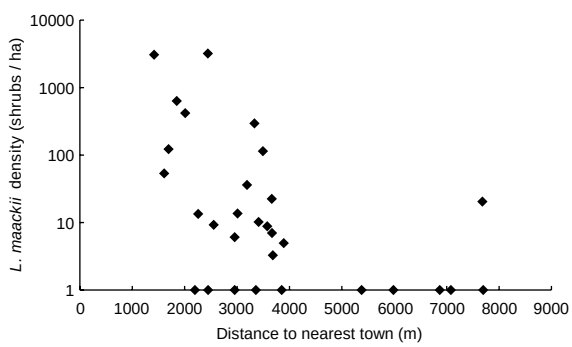

Fig. 2. Scatter plot of *L. maackii* density (log scale) versus the distance from nearest town for 30 woodlots.

Table 1. Results from stepwise multiple regression analysis of log-transformed *L. maackii* density in 20 woodlots. Sign in parentheses before the variable indicates the relationship of the variable with *L. maackii* density.

Variable	Partial R^2	Model R^2	F	p
(+)Total edge within buffer	0.592	0.592	26.25	<0.0001
(−)Tree basal area	0.134	0.727	8.36	0.01
(−)# Native woody species	0.054	0.781	3.95	0.06
(−)Shade tolerance index	0.054	0.834	4.84	0.04

These four variables explained much of the variation ($R^2 = 0.83$, adjusted $R^2 = 0.79$, Table 1). Density was significantly positively associated with total edge (Fig. 3); and significantly negatively associated with basal area, native species, and shade tolerance index.

Pattern of *L. maackii* invasion into woodlots

Based on the oldest individual *L. maackii* shrubs, woodlots in this area were colonized 3–20 yr ago (mean ± SD: 11.2 ± 4.2). Contrary to our predictions, the oldest perimeter shrubs were not significantly older than the oldest interior shrubs ($t = 1.74$, $DF = 14$, $p > 0.05$). In fact, the oldest perimeter *L. maackii* tended to be younger than the oldest interior plant in the same woodlot (mean ± SD: 9.9 ± 3.6 and 12.5 ± 4.4 yr, respectively). The oldest edge shrub was older than the oldest interior shrub in only three of the 15 woodlots and one generation (5 yr) older in only two woodlots (Fig. 4).

Discussion

Our finding that the presence of *L. maackii* in a woodlot was best explained by distance to the nearest town supports the hypothesis that landscape features are more important than community factors in determining *L. maackii* invasion. In fact, none of the community variables were significant in the logistic regression model of *L. maackii* presence. The greater likelihood of *L. maackii* in woodlots closer to town suggests that *L. maackii* is not moving as an advancing front from the south but rather is moving out from multiple loci (Moody and Mack 1988), in this case towns where presumably this shrub was intentionally planted. Hutchinson and Vankat (1997) also found an inverse relationship between *L. maackii* cover and distance from town across 93 woodlots. Others have also found a relationship between invasive plants and proximity to human habitats or density. For example, Barton et al. (2004) found greater density of invasive plants closer to a New England town and concluded that there is a relationship between horticulture and invasion.

The invasion of *L. maackii* from multiple loci rather than an advancing front has important implications for management. Specifically, eradication of small loci that have escaped from larger populations is crucial to controlling the spread of an exotic species invading in this manner (Moody and Mack 1988).

Our results indicate that landscape features explained most of the variation of *L. maackii* abundance. The variable that explained the greatest variation in *L. maackii* density was total amount of edge in the landscape. Our finding that the number of corridors was

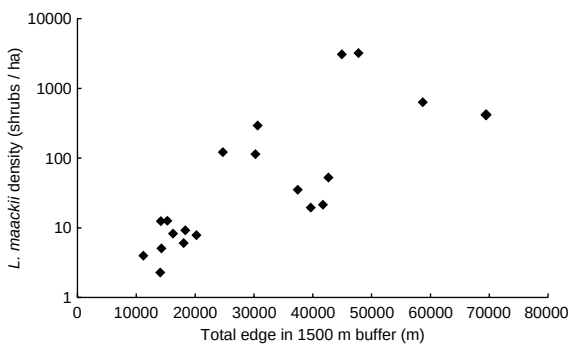

Fig. 3. Scatter plot of *L. maackii* density (log scale) versus total edge in the 1500 m buffer for the 20 woodlots invaded by *L. maackii*.

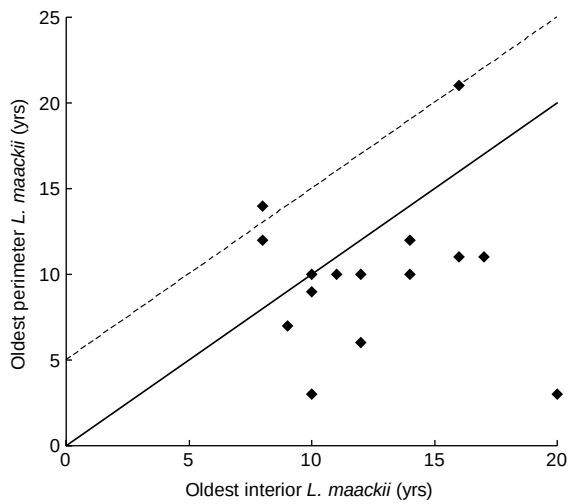

Fig. 4. Age of the oldest perimeter *L. maackii* individual versus age of oldest interior *L. maackii* individual in 15 woodlots. The solid line represents the null hypothesis that perimeter plants are the same age as interior plants. The dashed line represents the prediction from the edge-first colonization model in which the oldest perimeter *L. maackii* are one generation (5 yr) older than the oldest interior *L. maackii*.

not an important predictor in determining either the presence of *L. maackii* or its density, is evidence against Hutchinson and Vankat's (1998) hypothesis that connectivity of woodlots is important in the spread of *L. maackii*. However, for our woodlots, the number of corridors was correlated with total edge ($r = 0.63$), and the univariate regression of *L. maackii* density on the number of corridors was significant ($R^2 = 0.15$, $p = 0.03$, $N = 30$). Thus it is difficult to tease apart the role of edge habitat vs. connectivity with our data. The importance of corridors to conservation has been debated (Beier and Noss 1998, Haddad et al. 2000). Few manipulative experiments have been done, due largely to the difficulty of manipulating large landscapes. However, studies by Tewksury et al. (2002) and Haddad et al. (2003) found that corridors were important in aiding animal and plant movements from one habitat to another.

Our finding that woodlots in landscapes with more edge have greater *L. maackii* density could be explained by greater propagule pressure. Because *L. maackii* grows very well at the edges of woodlots (Medley 1997, Luken et al. 1997), a landscape with more edge provides more propagules for invasion into the woodlots. Propagule pressure has also been hypothesized to be important in other plant invasions. Bergelson et al. (1993) found that faster invasion of *Senecio vulgaris* where suitable habitat was clumped and attributed this to the greater seed bank that accumulated in these areas. Rouget and Richardson (2003) modeled the importance of propagule pressure and a variety of environmental parameters on invasion of three tree species and determined that propagule pressure was the single most important factor. Levine (2000) showed that propagule pressure could explain the positive correlation between species diversity and invasibility in *Carex nudata* tussocks in California. In experiments of plant community invasibility, however, the role of propagule pressure can be dependent on the diversity of the community being invaded (Tilman 1997, Foster 2001).

Another mechanism by which edge habitat can promote invasion is via suitable habitat it provides. Higgins and Richardson's (1999) model predicted that spread rates of invasives decreased in landscapes with habitat loss and they hypothesize that habitat loss reduces the probability of successful migration across a fragmented landscape. In our study total edge was highly negatively correlated ($r = -0.84$) with the isolation index of Hokit et al. (1999). Since the univariate regression of *L. maackii* on total edge had a higher R^2 than its regression on isolation, we used only the former measure in our multivariate models.

Since total edge is such a strong predictor of density of *L. maackii* in woodlots, we would expect that woodlots are first invaded at the edge and then the invasion moves to the interior of the woodlot (edge-first colonization). Our results show that this was not the case: perimeter *L. maackii* were not older than interior *L. maackii*. However, it is possible that woodlots have expanded in recent years, so shrubs we considered as "interior" were formally "edge" shrubs. In that case, the edge-first colonization model might apply, but we would be unable to detect that pattern without information on past woodlot boundaries. However, this is unlikely as property owners indicated that none of the woodlots had changed size or shape in at least the last 10 yr and in many cases for several decades.

Others have documented a phenomenon of edge trees and shrubs, both native and exotic, creating a wall of vegetation that is impenetrable to seeds of other species (Brothers and Spingarn 1992, Cadenasso and Pickett 2001). However, Cadenasso and Pickett (2001) studied the movement of wind-dispersed seeds across thinned and unthinned forest edges. For species dispersed by birds or mammals, where the behavior of the dispersal agent is critical, a wall of vegetation may not inhibit dispersal. Of the known avian dispersers of *L. maackii*, all are capable of traveling through the forest foraging for food in the winter. The movements of these birds between the edge and the interior of woodlots may explain why there is not an edge-first invasion pattern for *L. maackii*. However, this model may apply to invasive plant species dispersed by other animals or by abiotic means.

Our finding that three community variables contributed to explaining the density of *L. maackii* in invaded woodlots indicates that community characteristics do contribute to invasibility. Tree basal area was the second variable entered into the multiple regression model; woodlots with a greater basal area had less *L. maackii* density. Hutchinson and Vankat (1997) similarly found basal area was a significant predictor of *L. maackii* density across 93 woodlots. Presence of the invasive *Rubus fruticosus* was negatively associated with basal area in eucalyptus forests in Australia (Lindenmayer and McCarthy 2001).

Our finding that woodlots with more native woody species had lower *L. maackii* density provides indirect evidence for Elton's (1958) hypothesis that habitats with greater species diversity are more resistant to invasion. In our study, we sampled the same number of points throughout all of our woodlots and therefore may have missed some species, particularly in the larger woodlots. However, we found no correlation between woodlot area and number of native woody species ($r = 0.26$). Woodlot species diversity may affect presence of *L. maackii* at different life stages. For example, as seedlings *L. maackii* will also compete for resources with understory herbaceous plant species, so research on the effects of herbaceous plant diversity on *L. maackii* establishment and growth is needed. Some explicit tests of Elton's hypothesis have found that habitats with high species richness are better able to resist invasion by non-native species

(Tilman 1997, Knops et al. 1999, Naeem et al. 2000, Kennedy et al. 2002). However, the results of these studies may be due to other features of communities related to richness, such as competition and functional diversity (Wardle 2001).

Our finding that *L. maackii* density had a negative relationship with sapling shade tolerance index is similar to that of Hutchinson and Vankat (1997). A low shade tolerance index indicates that the canopy of the woodlot was open in the recent past, permitting growth of shade intolerant species. Low shade tolerance index thus suggests past disturbance and canopy openness.

The hypothesis that high light promotes invasion has considerable support (Brothers and Spingarn 1992, Hutchinson and Vankat 1997, Sanford et al. 2003). Our study adds indirect support to this hypothesis. Two of the three community variables entered into our final model are associated with past or present light environments (shade tolerance index and stand basal area, respectively). However, we argue that light availability may not be the primary factor influencing *L. maackii* density in southwest Ohio. Our most direct measure of light, gap fraction, was positively correlated with stand basal area ($r = 0.49$), and was not significant as a univariate predictor of *L. maackii* density. This suggests that there are other characteristics of high basal area stands that prevent *L. maackii* invasion. Basal area is correlated with stand age, and older forests may have more leaf litter than younger forests (Facelli and Carson 1991). Studies have shown that increased leaf litter inhibits germination and establishments of seedlings (Xiong and Nillson 1999); increased leaf litter may also inhibit establishment of invasive species. Older forests may also have a more mature soil microbial flora that prevents establishment of exotic species not adapted to the native soil flora. The effects of soil microflora on native and exotic species have been found to be complicated (Klironomos 2003, Callaway et al. 2004). For example, positive effects of native soil microflora on exotic plant species are explained by the release from enemies hypothesis (Klironomos 2002, Reinhart et al. 2003).

The negative relationship between basal area and *L. maackii* density may be more a reflection of disturbance history (e.g. selective logging) than current environmental conditions. Although our measure of disturbance was not a significant predictor of *L. maackii* density, it was a coarse measure. We scored only anthropogenic disturbances and treated these equally in our analyses. Furthermore, we did not quantify extent or intensity of these disturbances. It is likely that our stands with lower basal area or shade tolerance index experienced more extensive or intensive disturbances. Such disturbances could facilitate invasion via altered competitive interactions between plants (Minchinton and Bertness 2003), increased nutrients (Davis et al. 2000, Thompson et al. 2001, e.g. waste from grazers or slash from timber harvest), exposure of bare soil (Hrenko et al. 2004), or increased light levels (Greenberg et al. 2001). Disturbances might also promote invasion via effects on dispersal agents. Gaps may have attracted frugivorous birds and served as foci for defecated seeds (Hoppes 1988). The role of disturbance in the invasion of *L. maackii* requires further investigation.

Conclusions

Invasion of *L. maackii* involves stratified dispersal (cf. "stratified diffusion" Hengeveld 1989); long-distance dispersal to towns, presumably as horticultural plants, and shorter distance seed dispersal by birds to woodlots and other suitable patches of habitat. At this second level, landscape features are more important than community features in determining presence and density of *L. maackii*. However, community parameters also influenced density. It is important to recognize the importance of the interaction between both community and landscape features to better understand the pattern and intensity of invasion. In addition, invasions may not always begin at the edge of an area of suitable habitat. Vertebrate-dispersed plants may be able to penetrate the edge of the habitat and begin their invasion from the interior, making early detection difficult.

Acknowledgements – We thank Kristy Combs, Eric Donaldson, Rikki Hrenko, and Lauren Saunders for their assistance in the field. John Bailer, Mike Hughes, and Bob Noble provided statistical advice. We thank the property owners of the woodlots used and the Miami Univ. Ecology Research Center and Ryan Stander for use of the miter saw. Rob Blair, Tom Crist, Jim Hickey, M. Henry Stevens, Rebecca Brown and Andrew Liebold provided valuable comments on earlier drafts. This research was funded by U.S. Dept of Agriculture National Research Initiatives Biology of Invasive and Weedy Plant Program (# CG00717 to D.L.G.), Miami Univ. Botany Dept Academic Challenge, Miami Univ. Undergraduate Summer Scholars Program, and the Garden Club of Ohio.

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Subject Editor: Andrew Liebhold.