

Invasion of an Exotic Shrub into Forested Stands in an Agricultural Matrix

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We investigated the relative importance of stand and landscape characteristics in the invasion of a nonnative shrub, Amur honeysuckle, in 40 woodlots in an agricultural matrix in southwest Ohio. We quantified stand characteristics that could influence invasibility, the intrinsic susceptibility of an area to invasion, including woodlot size, perimeter-to-area ratio, tree basal area, and stand age. At the landscape scale we included factors that potentially influence propagule rain (the contribution of seeds from individuals established outside the focal area), including the land cover and road density in a 1,500-m buffer around each woodlot, as well as the extent to which the perimeter was forested at two points in the past, and latitude (based on an apparent south-to-north invasion in this region). Based on stepwise regression, we determined that honeysuckle cover was determined primarily by landscape parameters, particularly the percent of the buffer comprised of cropland. Woodlots surrounded by more cropland had less honeysuckle cover, which we attribute to paucity of nearby seed sources and/or minimal movement of seed-dispersing animals. From these findings, we argue that impediments to propagule rain are more important in shaping the invasion of this exotic shrub than are characteristics of the woodlots themselves, i.e., community invasibility.

Nomenclature: Amur honeysuckle, *Lonicera maackii* (Rupr.) Herder.

Key words: Community invasibility, invasive plants, land cover, *Lonicera maackii*, propagule pressure.

Two of the key research questions essential to reducing the impact of invasive species (Byers et al. 2002) are: “What limits the spread of nonindigenous species?” and “What determines vulnerability to invasion in particular habitats?” Fundamental to addressing these questions for invasive plant species is assessing the relative importance of site invasibility vs. the landscape context (Brothers and Spingarn 1992; Kuhman et al. 2010).

Invasibility, the intrinsic susceptibility of an area to invasion (Crawley 1987; Lonsdale 1999), has often been linked to pulses of resource availability, typically associated with disturbance (D’Antonio et al. 1999; Davis et al. 2000; Sher and Hyatt 1999). Susceptibility of temperate forest to plant invasion has been shown to correlate with disturbance (Belote et al. 2008), including logging, treefall gaps (Burnham and Lee 2010), and tree mortality due to forest pests (Eschtruth and Battles 2009). Such disturbances increase light availability, which has been shown to benefit invasive shrubs more than natives (Luken et al.

1997). Stand age is expected to be important, with younger stands being more invulnerable than older stands (Flory and Clay 2009; Kuhman et al. 2011). Edge effects are also important, with invasives more prevalent on forest edges than interiors (Brothers and Spingarn 1992); thus, invasibility is negatively correlated with forest patch size.

Landscape features have also been shown to influence invasions (With 2002). Proximity to existing sources of propagules is expected to facilitate invasion, and movement of propagules between invulnerable habitat patches is potentially influenced by connectivity (e.g., corridors) and permeability of the matrix (With 2002). For plants with animal-dispersed seeds, this permeability is influenced by the structure of the landscape (Deckers et al. 2005). If these landscape features have a large influence on the pattern of invasion, this indicates an important role for propagule rain, the extent to which established individuals of a species add offspring to the exotic environment (Lockwood et al. 2009). This is also called “mass effect,” and has been referred to as “propagule pressure” (Eschtruth and Battles 2011; Rouget and Richardson 2003), but the latter term is best defined as a composite measure of the number of individuals released into a region to which they are not native, incorporating both the number of individuals per release or dispersal event, and the number of release/dispersal events (Lockwood et al. 2005).

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Management Implications

Understanding the factors that make forests susceptible to invasion can inform management strategies, including identifying forest stands at greatest risk of invasion and formulating steps that can be taken to minimize invasion risk. We investigated what stand and landscape characteristics best explained the cover of the invasive shrub *Lonicera maackii* (Amur honeysuckle), in a landscape it recently invaded, consisting of woodlots in an agricultural matrix in southwest Ohio. We found that cover of this shrub was best explained by landscape characteristics, rather than by stand characteristics, such as age or basal area. Specifically, the percentage of the 1,500-m buffer around the woodlot that was comprised of cropland, as opposed to pasture, forest, and other land-cover types, was the best predictor of honeysuckle cover. Woodlots surrounded by more cropland had lower cover, which we think indicates more recent colonization. Thus cropland impedes honeysuckle invasion, either by providing a buffer free of seed sources (fruiting shrubs), or a land cover that is unlikely to be crossed by animals dispersing seeds from more distant sources. These findings suggest that woodlots surrounded by cropland, and perhaps by other shrub-free land covers, are at lower risk of invasion by animal-dispersed nonnative plants, and that active management of buffers around forest stands will reduce invasion risk.

Although studies such as those discussed above document evidence for both propagule rain and invasibility in plant invasions of temperate forests, few studies have allowed an assessment of their relative importance (but see Eschtruth and Battles 2009, 2011; Kuhman et al. 2010; Rouget and Richardson 2003; Von Holle and Simberloff 2005). Our objective was to infer the relative importance of stand invasibility and landscape context in the spread of a nonnative shrub, Amur honeysuckle [*Lonicera maackii* (Rupr.) Herder, Caprifoliaceae] into woodlots in an agricultural landscape, using landscape metrics to make inferences about the importance of propagule rain. Previous studies (Bartuszevige et al. 2006; Hutchinson and Vankat 1997) in two small landscapes in southwest Ohio reached somewhat different conclusions. Hutchinson and Vankat (1997) concluded that both invasibility and propagule rain were important, whereas Bartuszevige et al. (2006) found the latter to be much more important.

The importance of propagule rain was indicated by Hutchinson and Vankat's (1997) finding that proximity to Oxford, Ohio (where horticultural plantings formed a source population) correlated with *L. maackii* cover, and the finding by Bartuszevige et al. (2006) that the only significant predictor of *L. maackii* presence was proximity of the closest town, with stands closer to towns more likely to have *L. maackii* than those farther away. Because these towns might have been locations of horticultural plantings of *L. maackii*, both studies suggest propagules from horticultural plantings may drive invasions. Bartuszevige et al. (2006) also found that among stands that were invaded by *L. maackii*, the best predictor of its density was

the amount of edge in a 1,500-m (4,921-ft) buffer; stands with more forest edge in the buffer had higher densities of *L. maackii*. Such edges could be both seed sources (if they contain fruiting *L. maackii*) and promoters of movement of seed dispersers across largely agricultural landscapes.

Hutchinson and Vankat (1997) also concluded that forest stand invasibility had a major influence on *L. maackii* cover, because that cover correlated negatively with canopy cover and more weakly with stand basal area and sapling shade tolerance index (a measure of the light environment in the recent past). However, Bartuszevige et al. (2006) found only weak negative correlations of *L. maackii* cover with stand basal area, sapling shade tolerance index, and native woody species richness.

In this study we attempt to advance our understanding of the relative importance of stand characteristics vs. landscape parameters in the invasion of *L. maackii* by evaluating a larger geographic area and including new parameters that we expected to be more directly related to invasibility or propagule pressure. We hypothesized that the important driver of invasibility was stand age (Flory and Clay 2009; Kuhman et al. 2011); in our view, predictors such as canopy cover, basal area, and sapling shade tolerance index were negatively correlated with *L. maackii* cover because they were correlated with stand age. Therefore, in this study we directly measured stand (woodlot) age with historical aerial photographs, as well as stand area (Ohlemüller et al. 2006), perimeter-to-area ratio (Moffatt et al. 2004), and stand basal area. Few measures of landscape properties were included in the previous studies: Hutchinson and Vankat (1997) only measured one, and Bartuszevige et al. (2006) only included three. The present study included a more comprehensive set of landscape measures selected because of expected relationships with propagule rain. Two sets of predictors were expected to be associated with proximity of seed sources and permeability of landscape to dispersal agents: (1) the proportional land cover in a 1,500-m buffer around each woodlot and (2) the historical land cover bordering each woodlot. We also included two additional measures expected to correlate with proximity of seed sources: (3) road density in the buffer area (as a measure of the likelihood of local horticultural plantings) and (4) latitude, because there is evidence for a south-to-north invasion in this region (Hutchinson and Vankat 1997).

Materials and Methods

Study Species. *Lonicera maackii* is an upright, deciduous shrub introduced to North America in 1898 from northeastern Asia, and marketed for its high flower and fruit production, as well as its ability to prevent erosion (Luken and Thieret 1995). Over the past century it has escaped its horticultural confines and invaded forests and

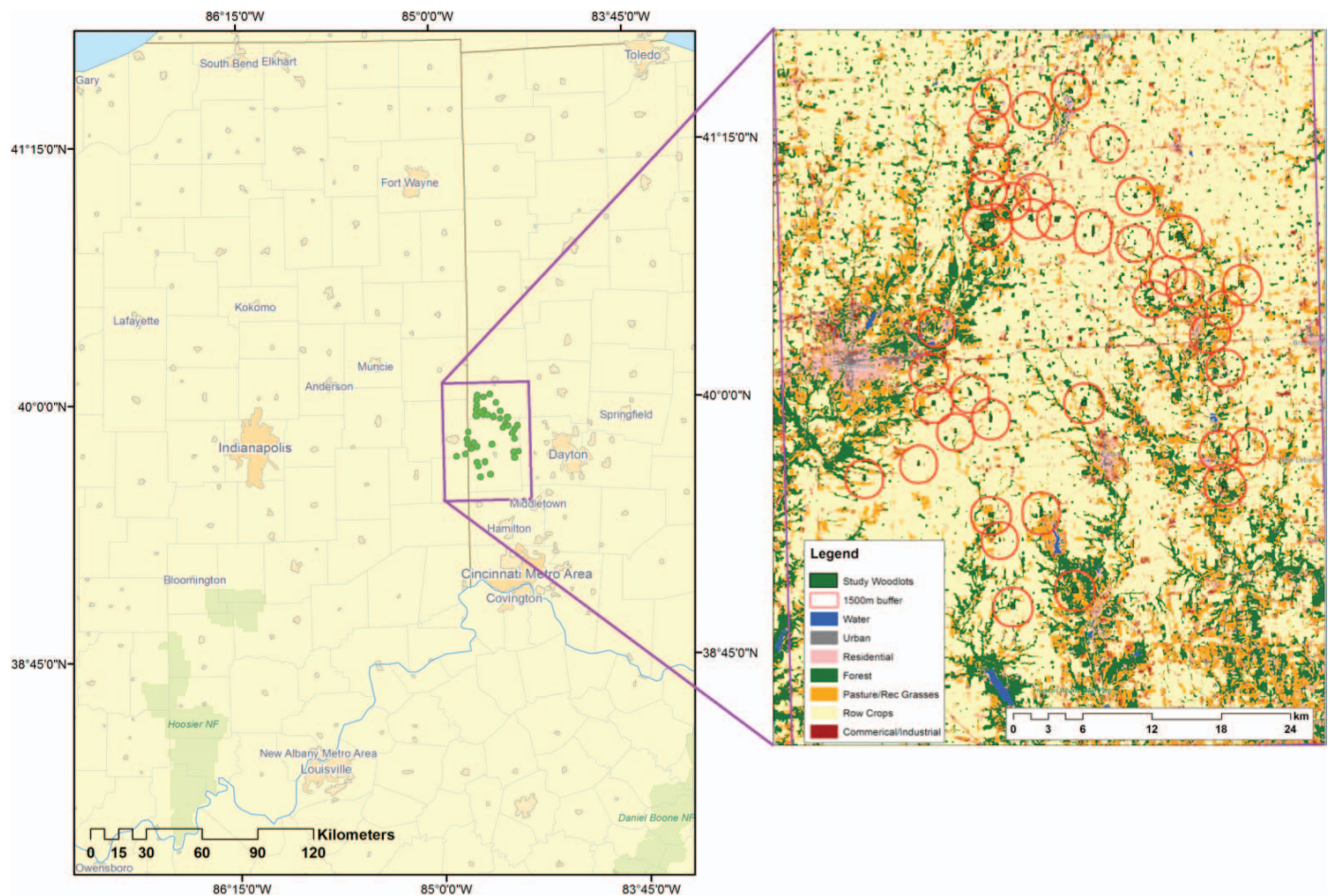


Figure 1. Location of the study woodlots in southwest Ohio (Darke and Preble counties) and adjacent Indiana. Detailed map shows Landsat Thematic Mapper-based land use/land-cover map, and 1,500-m buffer around each study woodlot.

successional areas in at least 24 different states, including Ohio (Luken and Thieret 1995; Trisel and Gorcho 1994). *Lonicera maackii* reduces growth and fecundity of forest annuals and perennials (Gould and Gorcho 2000; Miller and Gorcho 2004) and tree seedling recruitment (Gorcho and Trisel 2003; Hartman and McCarthy 2004), with impacts on forest floor diversity and composition (Collier et al. 2002; Hartman and McCarthy 2008; Hutchinson and Vankat 1997). *Lonicera maackii* also reduces nesting success of native birds (Rodewald et al. 2010; Schmidt and Whelan 1999) and survival of larval amphibians (Watling et al. 2011).

Study Area. We investigated woodlots in a landscape in Preble and southern Darke counties, southwest Ohio (Figure 1), that was recently invaded by *L. maackii*. Within this landscape some woodlots have high levels of *L. maackii* and others have not been invaded. The natural vegetation of this area was mostly beech forest (Gordon 1966), but human influence has changed the landscape into an extensive matrix of agricultural fields dotted with

fragmented woodlots, grasslands, pastures, urban, and residential areas. Forty woodlots, ranging in size from 2.3 to 59 ha (5.7 to 146 ac), were included in this study. These were a subset of 70 woodlots censused as part of studies by Johnston et al. (2012) and Wilfong et al. (2009). In order to maximize independence of woodlots, we removed woodlots from this sample that had 1,500-m buffer areas that overlapped extensively with buffers of nearby woodlots. To do this, buffers were displayed with the land-cover map, and buffers that overlapped > 25% based on visual inspection were selected and removed from the geographic information systems (GIS) file. If several buffers were grouped together, we removed the minimum necessary to remove substantial overlap (i.e., if three buffers were located near each other, the buffer located in the middle was removed, allowing the other two to remain). Overlap areas of questionable size (near 25%) were measured to ensure that overlap areas were kept below our threshold. All woodlots had closed canopy and were composed of a mix of broad-leaved deciduous trees; the most common taxa were *Acer saccharum* Marsh (sugar

Table 1. Composite age classes for woodlots based on tree cover in historical aerial photographs.

Age class	Tree cover 1938	Tree cover 1962 to 1963
1	Nonforested	Nonforested
2	Nonforested or partially forested	Partially forested
3	Nonforested or partially forested	Mostly forested
4	Mostly forested	Mostly forested
5	Partially forested	Forested
6	Mostly forested	Forested
7	Forested	Forested

maple), *Fraxinus* spp. (ash), *Ulmus* spp. (elm), *Carya* spp. (hickory), *Prunus serotina* Ehrh. (black cherry), *Juglans nigra* L. (black walnut), and *Quercus* spp. (oak) (Lawlor 2011; Wilfong 2008). In the center of each woodlot we marked a single 100 m by 100 m plot for quantifying *L. maackii* abundance and stand basal area.

***Lonicera maackii* Cover.** We measured the percent cover of *L. maackii* in each plot. For 27 woodlots sampled in 2007 we used four parallel 100-m line transects (Wilfong et al. 2009) and for 13 woodlots sampled in 2010 we used point-intercept sampling along randomly initiated and randomly oriented transects, totaling 400 m (Johnston et al. 2012).

Stand Characteristics. *Area and Perimeter.* The perimeter of each woodlot was digitized using recent (2009) aerial photography. Perimeters and areas were calculated for each woodlot using ArcGIS 10.1 (ESRI 2012). We used this information to calculate the perimeter-to-area ratio for each woodlot as a straightforward measure of woodlot shape complexity. Plots with more compact or simple shapes have less edge per unit area and might be less prone to *L. maackii* invasion.

Basal Area. Stand basal area of trees > 10 cm diameter at breast height (dbh) was determined by point-centered quarter sampling, with 16 points per plot, using equations in Smith and Smith (2001). For plots sampled in 2007, these data were obtained from Wilfong (2008); for plots sampled in 2010, data were from Lawlor (2011).

Stand Age. We obtained aerial photos of the study area to determine the forest cover condition of each woodlot in 1938 (USDA 1938a,b) and 1962 to 1963 (USDA 1962, 1963). Changes in forest conditions between these two time periods and the present day were used to assign a composite age class for each woodlot (Table 1).

Sampled plots were overlaid with natural color 2009 aerial photography of Preble and Darke counties obtained from the National Agriculture Imagery Program (NAIP;

<https://www.fsa.usda.gov/FSA/apfoapp?area=home&subject=prog&topic=nai>). Specific methods of interpretation varied for each set of aerial photographs, depending on photograph availability and format. For instance, some aerial photographs were interpreted from the original hard copy while referencing plot locations on current digital aerial photography on-screen. Others were scanned from their 1 : 20,000 index maps (mosaic of aerial photographs) and georeferenced to match the current aerial photography map coordinates.

For each of the two dates (1938 and 1962 to 1963), the vegetation in each woodlot was classified into one of the following four classes, based on visual inspection of the aerial photography:

1. Nonforested: No trees present; vegetation row crops or open pasture.
2. Partially Forested: Trees cover less than two-thirds of the woodlot; trees sparse with ground layer visible in a large portion of the woodlot.
3. Mostly Forested: Trees cover more than two-thirds of the woodlot; ground layer visible only in small portions.
4. Forested: Trees cover entire woodlot area and little to no ground layer visible.

We used the key in Table 1 to assign age classes to each woodlot. Plots with lower numbers are more recently forested (no trees in 1938 or 1962 to 1963) and higher numbers correspond with plots that have been forested since the 1930s. When censused (2007 to 2010), all plots were “Forested.”

Landscape Parameters. We selected 1,500-m buffers around each woodlot based on the finding by Bartuszevige et al. (2006) that landscape parameters at this scale best correlated with *L. maackii* cover.

Road Density. We used road density as a measure of residential development, enabling us to explore whether residential areas, presumed sites of horticultural plantings, were local propagule sources. We quantified the density of roads (Butler County, Ohio Auditor 2012) within the 1,500-m buffer (ESRI 2012) as the total road length in meters divided by the buffer area in m² (which varied according to woodlot size).

Land Cover in Buffer. A Landsat-derived land-cover map developed for another study in the region (image dates: 2005 to 2007) was used to determine the proportion of different land-cover types within each buffer area. The following land-cover types were distinguished, in order of their average cover in the 40 buffers: crops (74.8%), forest (13.5%), pasture (5.8%), developed (4.2%), recreational grasses (1.5%), and water (0.2%). “Recreational grasses” refers to mowed areas such as lawns and parks.

Classification of Historic Land Cover along Woodlot Perimeter. In addition to historical forest cover for each plot, we also wanted to test the effects of adjacent historical forest cover on current *L. maackii* cover. Each woodlot was digitized two times to represent its perimeter in each of the historic time periods (1938 and 1962 to 1963). We calculated the total perimeter for each woodlot at each date, then measured the extent of each woodlot's perimeter adjacent to each of the four forest categories (forested, mostly forested, partially forested, and nonforested). These distances were divided by the total perimeter to give the proportion of each woodlot's total perimeter adjacent to a given vegetation classification. For the 1938 Preble County photographs, these measurements were made directly from the photos themselves.

Statistical Analyses. To find the model that best explained cover of *L. maackii* among the 40 woodlots, we performed stepwise regression with forward/backward selection and utilizing the Akaike information criterion (AIC), with RCommander in R (www.rcommander.com). Before these regressions, we reduced the list of predictor variables so that none of the retained predictors correlated strongly ($r \geq 0.7$) with other predictors; for correlated pairs of variables, the variable that was more strongly correlated with *L. maackii* cover was retained (Table 2).

The initial regression model had only 37 observations, because three of the woodlots lacked data derived from aerial photographs (stand age and historical woodlot perimeter characteristics). Because the final model from regression retained none of the aerial photo variables, we dropped those variables, and carried out a new stepwise regression using all 40 woodlots.

Results and Discussion

Stepwise regression revealed that the simplest model that fit the *L. maackii* cover data had two predictor variables: woodlot area and the percent crops in the 1,500-m buffer around the woodlot (Table 3). As additional variables were added to the model, the fit to the data (AIC) improved only slightly, with the difference in fit between the model and the model of the previous step (δAIC) < 2 for each step (Table 3). Percent crop in the buffer was the first variable included in the stepwise regression, and it had a negative correlation ($r = -0.66$) with *L. maackii* cover; woodlots having more cropland in the buffer had lower *L. maackii* cover (Figure 2). In a univariate regression, percent crop explained 44% of the variation in *L. maackii* cover among the 40 woodlots ($R^2 = 0.44$, $F = 29.85$, $df = 1, 8$, $P = 3.099\text{e}-06$).

The second predictor variable to enter the stepwise regression model, woodlot area, was also negatively correlated with *L. maackii* cover, with larger woodlots having

lower cover of this invasive shrub. However, woodlot area by itself was only weakly correlated ($r = -0.09$) with *L. maackii* cover. Woodlot area was not correlated with percent crop ($r = -0.23$, $P = 0.15$), so these parameters were not confounded.

Three other predictor variables were retained in this stepwise regression model: percent recreational grasses and percent pasture in the 1,500-m buffer, and latitude, but these did not significantly improve model fit.

Landscape parameters were more important than stand characteristics in explaining the abundance of *L. maackii* in woodlots in this agricultural landscape, because both the most important predictor, and four out of the five total predictors, were parameters of the landscape. Similarly, Kuhman et al. (2010) found that invasive plant species richness and total cover in North Carolina watersheds, as well as frequency of several of these invasive species, was best predicted by distance from the closest city (Asheville), although stand characteristics (especially elevation and tree cover) were also important.

Our finding that *L. maackii* cover correlates negatively with percent of cropland in the buffer is consistent with Borgmann and Rodewald (2005), who found invasive honeysuckle *Lonicera* (*L. maackii*, Amur honeysuckle and *L. tatarica* L., Tatarian honeysuckle, pooled) cover in central Ohio riparian forests correlated positively with percent urban land cover in a 1-km buffer. In that study, agricultural land cover was negatively correlated with urban land cover and was therefore not included in statistical analyses. However, its strong negative correlation with urban land suggests that agricultural land in the buffer was negatively correlated with *Lonicera* cover in the forest patches. Similarly, our finding is consistent with the finding by Bartuszevige et al. (2006) that *L. maackii* density in invaded woodlots was best explained by the amount of forest edge in a 1,500-m buffer. Neither Bartuszevige et al. (2006) nor Hutchinson and Vankat (1997) related *L. maackii* cover to land cover in buffers around woodlots.

Lonicera maackii cover in southwest Ohio forests is associated with time since invasion (Hutchinson and Vankat 1997), so we argue that much of the variation in cover reported in this study corresponds to dates of invasion. Higher cover likely is an indication of earlier invasion because forests do not appear to be able to resist this invasive species. Therefore, we interpret the factors that correlate with high *L. maackii* cover to be factors that promote colonization, rather than growth of established populations. Thus the importance of landscape, rather than stand, characteristics in explaining *L. maackii* cover suggests that propagule rain (and impediments to it) are more important than stand susceptibility to invasion.

In this light, the negative effect of cropland in the buffer has two related explanations. First, crops might be the land-cover type that consistently lacks potential sources

Table 2. Correlation coefficients between percent cover of *Lonicera maackii* (Amur honeysuckle) and predictor variables among 40 woodlots in Preble and Darke counties, Ohio, and for the subset of 37 woodlots with aerial photography. Variables that were retained for the stepwise regressions after dropping highly correlated variables are in bold.

Predictor variable	Description	Correlation coefficient, <i>r</i>	
		<i>N</i> = 37	<i>N</i> = 40
Stand characteristics			
BA	tree basal area (m² ha⁻¹)	0.164	0.165
AREA	woodlot area (m²)	-0.083	-0.094
Peri:Area	Perimeter:area ratio m m ⁻²	0.064	0.069
Tree38	tree cover in 1938 aerial photograph	-0.380	
Tree62	tree cover in 1962 to 1963 aerial photograph	-0.367	
Age_Class	(see Table I)	-0.401	
Land cover in 1,500-m buffer			
Percent_Crops		-0.693	-0.663
Percent_Developed		0.445	0.412
Percent_Forest		0.616	0.599
Percent_Pasture		0.678	0.623
Percent_Rec_Grass		-0.019	0.042
Percent_Water		0.356	0.332
Other landscape parameters			
Road_Density	roads (m km⁻²) in 1,500-m buffer	0.268	0.239
Ycoord	Latitude (UTM, meters)	-0.274	-0.264
Woodlot perimeter in historical aerial photographs			
TP38	total perimeter 1938	-0.090	
TP62	total perimeter 1962/63	0.084	
PMF38	proportion mostly forested in 1938	-0.068	
PMF62	proportion mostly forested in 1962 to 1963	0.061	
PNF38	proportion nonforested in 1938	-0.166	
PNF62	proportion nonforested in 1962 to 1963	0.098	
PPF38	proportion partially forested in 1938	0.238	
PPF62	proportion partially forested in 1962 to 1963	-0.120	
PTF38	proportion forested in 1938	-0.026	
PTF62	proportion forested in 1962 to 1963	-0.038	

of *L. maackii* seeds, due to annual tilling. *Lonicera maackii* shrubs can establish and fruit in forests, pastures, and developed areas, providing seeds that animals can disperse into focal woodlots. Secondly, animals that disperse *L. maackii* seeds might avoid crossing cropland during the late fall and winter, when these seeds are dispersed, while foraging in other land-cover types. For example, Bartuszevige and Gorchoy (2006) showed that robins move mostly along forest edges when dispersing *L. maackii* seeds. Nixon et al. (1991) showed that in an Illinois agricultural landscape, white-tailed deer (which also disperse viable *L. maackii* seeds; Castellano and Gorchoy 2013) preferentially spent time during winter months in forest and forage crops, and tended to avoid row crops.

Our findings suggest that, at least in this rural landscape, residential planting of *L. maackii* is not an important driver

of invasion, as proposed by Bartuszevige et al. (2006), based on their finding that distance to the closest town to be the best predictor of *L. maackii* presence. Although we did find *L. maackii* cover to be positively correlated with road density within a 1,500-m buffer (Table 2), road density was not selected in the stepwise regression. We think that correlation was spurious, due to the negative correlation we found between road density and percent crop in the buffer ($r = -0.34$). When one factors in the land cover of the buffer, proximity to towns probably does not shape the *L. maackii* invasion.

The only woodlot characteristic that correlated with *L. maackii* abundance was woodlot area. A similar relationship was apparent with perimeter-to-area ratio ($r = 0.07$). However, this ratio was strongly correlated with woodlot area, and did not vary as much among the 40 woodlots, so

Table 3. Stepwise regression model for cover of *Lonicera maackii* (Amur honeysuckle) in 40 woodlots in an agricultural matrix. In each step of the model, using Akaike information criterion (AIC), one independent variable is added to the model. δ AIC is the difference in fit between the model and the model of the previous step. Models that improve AIC by > 2 are considered to better fit the data.

Step	Independent variable	AIC	δ AIC
	none (intercept only)	242.23	—
1	Percent crop in 1,500-m buffer	221.05	21.18
2	Woodlot area	218.09	2.96
3	Percent recreational grass in 1,500-m buffer	216.51	1.58
4	Percent pasture in 1,500-m buffer	215.40	1.11
5	Latitude	215.01	0.39

it was not included in the stepwise regression model. The negative relationship between cover of this invasive shrub and woodlot area parallels the finding by Ohlemüller et al. (2006) that smaller forest fragments in New Zealand have more invasive plant species. Similarly, the positive correlation between *L. maackii* cover and perimeter-to-area ratio is analogous to the findings of Moffatt et al. (2004) for an urban–rural gradient in Canada, where more urban forests had lower area:perimeter ratios and higher proportions of exotic plant species. Neither area nor perimeter-to-area ratio significantly explained *L. maackii* density in Bartuszevige et al. (2006), perhaps due to confounding effects with other variables.

In our system the greater abundance of *L. maackii* in smaller woodlots is likely due to proximity of the forest edge, where *L. maackii* grows quickly, reaches large sizes and densities, and fruits prolifically. Because our study plots were in the center of each woodlot, these were more distant from the edge in larger woodlots, and thus avoided higher cover areas closer to the edge. By measuring cover in the centers of woodlots, rather than over the entire woodlot, we likely overestimated any negative correlation between woodlot size and whole-woodlot *L. maackii* cover.

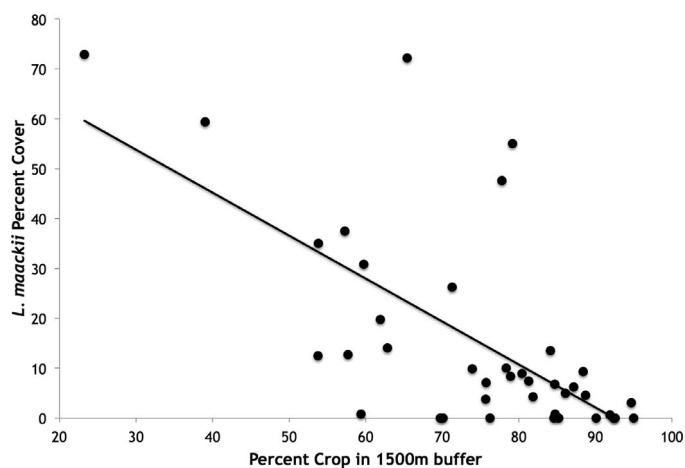


Figure 2. Regression of Amur honeysuckle cover in woodlot vs. percent of cropland in 1,500-m buffer around the woodlot for 40 woodlots in southwest Ohio and adjacent Indiana.

The true relationship between area and whole-woodlot *L. maackii* cover was likely even weaker than that reported here ($r = -0.09$).

Our hypothesis that stand age was important in this invasion was not supported. *Lonicera maackii* was one of three invasive shrubs in Flory and Clay's (2009) study that showed several effects of stand age, including a significant interaction of age and origin (native vs. exotic) on seedling height, such that the growth of seedlings in young vs. mature forest was greater for exotic than native species. However, Flory and Clay (2009) did not report results for the individual invasive species. Although we found *L. maackii* cover to correlate with stand age as expected ($r = -0.40$), with younger stands tending to have higher *L. maackii* cover, this predictor dropped out in stepwise regression models. There were similar correlations between current *L. maackii* cover and forest cover in 1938 ($r = -0.38$) and 1962 ($r = -0.37$), with lower forest cover at each of these earlier dates tending to correlate with higher *L. maackii* cover in 2007 to 2010. These findings suggest that stands of all ages are susceptible to invasion by *L. maackii*. If this is true, the correlation between *L. maackii* abundance and sapling shade tolerance index reported by Hutchinson and Vankat (1997) and Bartuszevige et al. (2006) requires an alternative explanation. We propose that localized disturbance (e.g., logging or windthrow), which promotes seedling establishment of shade-intolerant trees, also promotes *L. maackii* colonization in those woodlots. We cannot evaluate the role of localized disturbance in our study because we did not measure parameters associated with past disturbance.

The importance of propagule pressure in this invasion could be tested by investigating the proximity of stands to older (previously established) *L. maackii* populations. However, in this study we did not age the shrubs in each stand, nor census surrounding areas for older shrubs. Although our inference that in this invasion propagule rain is more important than stand characteristics is tentative, our finding contributes to an emerging general pattern for temperate forests. An experimental test by Von Holle and Simberloff (2005) found that invasion was more attributable to propagule pressure (the number of introduced

plants) than to factors associated with site invasibility, including flooding regime and density and species richness of resident plants. An observational study (Eschtruth and Battles 2011) found that propagule pressure (number of germinating seeds) better predicted the extent of invasion of three exotic species than did a direct measure of invasibility (establishment and survival). Evaluations of direct measures of propagule rain and stand invasibility in additional systems are needed to assess this generalization.

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