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Source: The Journal of the Torrey Botanical Society, 143(4) : 386-397

Published By: Torrey Botanical Society

URL: <https://doi.org/10.3159/TORREY-D-15-00036.1>

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Relationships between an invasive shrub *Amur honeysuckle* (*Lonicera maackii*, Caprifoliaceae) and environmental factors on recruitment of sugar maple trees (*Acer saccharum*, Aceraceae) in southwestern Ohio^{1,2}

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Abstract. Invasion of deciduous forests by woody shrubs such as *Lonicera maackii* is known to negatively impact the abundance and richness of native herbs, but effects on recruitment of seedlings and saplings of native trees, such as *Acer saccharum*, are less well known. Ultimately, these impacts could alter the species composition of forest trees. Our study was designed to evaluate the impact of *L. maackii* and environmental factors on recruitment of *A. saccharum* seedlings and on the transition of seedlings to saplings and saplings to mature trees. We selected four study sites in southwestern Ohio where we censused *L. maackii* and *A. saccharum* seedlings, saplings, and trees in 16 plots (eight with and eight without *L. maackii*) at each site. We measured *L. maackii* abundance and maximum diameter of the primary stem (an indication of shrub size), edaphic factors (soil density, pH, soil percentage of nitrogen [%N], soil percentage of carbon [%C]), topographic factors (elevation, slope, aspect), biotic factors (overall tree abundance), and human influences (proximity to roadways). Using a generalized linear mixed model with model comparison techniques, we found that in plots with larger *L. maackii*, seedling recruitment was lower, the transition from seedlings to saplings was greater, and the transition from saplings to trees was unaffected. Seedling recruitment increased with increasing soil %C, but decreased with increasing soil %N. Slope was positively associated with a greater transition from seedlings to saplings, and soil density and soil %C negatively affected the transition to trees. The transition to trees was higher with greater tree abundance, and the transition to saplings and trees was greater away from roadways. Overall, these results indicate that environmental factors have positive and negative impacts on recruitment of *A. saccharum*, and large *L. maackii* have both a negative and positive relationship to recruitment. Further studies will be necessary to uncover the mechanisms involved in the negative and positive relationships of *L. maackii* to recruitment of *A. saccharum*.

Key words: seedling recruitment, transition to saplings, transition to trees

¹ We thank M. Bécus, D. Buick, M. Foote, S. Jacob, D. Lentz, J. Wittmer, and J. Zambito for assistance with field work, and the Division of Wildlife, Ohio Department of Natural Resources, for allowing us access to their property. We especially thank those preserve managers who granted us permission to work on their property and assisted with selection of study sites: J. Klein, B. Mason, and J. Mundy, Great Parks of Hamilton County, R. Morgan, East Fork Wildlife Area; L. Parker, Cincinnati Parks. Our research was funded by an Interdisciplinary Research Grant from the University of Cincinnati.

² Supplemental material for this article is online at <http://dx.doi.org/10.3159/TORREY-D-15-00036>.

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doi: 10.3159/TORREY-D-15-00036.1

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Received for publication July 8, 2015, and in revised form December 30, 2015; first published September 8, 2016.

Invasions by woody plants are rapidly increasing on a worldwide scale (Richardson and Rejmánek 2011, Rejmánek 2014). Many of these species were introduced for horticultural purposes and are dispersed primarily by birds (Richardson and Rejmánek 2011). Except for Australia (79 species), North America has the most invasive shrub species (73; Richardson and Rejmánek 2011). In part because of their perennial nature, invasive shrubs can be drivers of community structure and ecosystem change. For example, while they generally decrease overall species diversity (Vilà *et al.* 2011), invasive shrubs may increase aboveground biomass and net primary productivity and also can alter soil nutrient cycling in invaded ecosystems (Lett *et al.* 2004, Ehrenfeld 2010). Invading shrubs can produce a dense vegetation layer near a forest floor that negatively affects growth and survival of seedlings and saplings of native trees and thereby affects recruitment and

relative abundance of tree species in forest canopies (Merriam and Feil 2002, Frappier *et al.* 2003, Fagan and Peart 2004, Webster *et al.* 2006, Richardson and Rejmánek 2011). Using a meta-analysis, Gaertner *et al.* (2014) argued that effective management should concentrate on shrubs that invade forests because they can alter plant community composition as well as ecosystem structure and function through impacts on ecosystem processes that are difficult to reverse, such as soil nutrient cycling.

Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder) is a prolific shrub that was introduced to the USA from East Asia in 1898 and now is prevalent in many eastern and midwestern states as well as some western states and provinces in eastern Canada (USDA, NRCS 2015). Because of its hardiness, *L. maackii* was originally planted in the USA along roadways to prevent soil erosion (Luken and Thieret 1996). It also was commonly sold as an ornamental shrub in the midwestern USA, where it originally was valued for its form, spring flowers, and fruits that attract wildlife. *Lonicera maackii* was first observed invading natural areas around the Cincinnati area over 50 yr ago (Braun 1961) and now is prevalent in the region. Invading *L. maackii* creates a dense midstory stratum that is largely absent from mature forests. This novel vegetative layer, as well as a leaf phenology that extends from mid to late March through late November (McEwan *et al.* 2009, Fridley 2012), can alter light levels within the forest understory. *Lonicera maackii* negatively affects abundance and richness of forest herbs (Gould and Gorchov 2000, Collier *et al.* 2002, Miller and Gorchov 2004), as well as abundance (Hutchinson and Vankat 1997, Hartman and McCarthy 2008) and survival (Gorchov and Trisler 2003, Loomis *et al.* 2015) of seedlings and saplings of the native tree *Acer saccharum* Marshall. *Acer saccharum* also experiences slower growth in the presence of *L. maackii*, presumably because of competition for belowground nutrients (Hartman and McCarthy 2007). Negative effects of *L. maackii* on *A. saccharum* seedlings and other saplings with canopy potential could ultimately alter the species composition of canopy trees and forest regeneration (Collier *et al.* 2002, Hartman and McCarthy 2008).

Seedlings and saplings of *A. saccharum* are especially sensitive to environmental factors that may be altered by *L. maackii* invasion. For example, young *A. saccharum* individuals respond to available light in the forest understory; they are shade-tolerant but their growth increases dramatically when canopy

gaps appear (Hett 1951, Canham 1988, Canham and Burbank 1994, Marks and Gardescu 1998, Kobe 2006). In addition, density and survival of *A. saccharum* seedlings and saplings increase in soils with greater calcium content and higher pH (Kobe *et al.* 1995, Kobe 1996, Juice *et al.* 2006, Bigelow and Canham 2007), and sapling growth increases with nitrogen (N) availability in soil under low light conditions, but not under high light conditions (Finzi and Canham 2000). Presence of *L. maackii* also alters soil nutrient availability, which can affect seedlings and saplings (Arthur *et al.* 2012, McEwan *et al.* 2012, Poulette and Arthur 2012, Trammell *et al.* 2012). Within urban areas, abundance, growth, and survival of sugar maple seedlings decrease with deposition of atmospheric N_x and CO₂ (Eller *et al.* 2011, Talhelm *et al.* 2013). Compaction, increased soil bulk density, and runoff of salt from snow and ice control near roadways also negatively affect seedlings by decreasing root density and restricting roots to upper soil levels (Day and Bassuk 1994, Fay and Shi 2012). Given that *L. maackii* has a propensity to alter soil nutrient levels and hinder light availability for *A. saccharum* seedlings and saplings, this invasive species has the potential to negatively impact tree recruitment.

Our objective was to examine the combined effect of *L. maackii* and environmental variables on regeneration of *A. saccharum* trees. To accomplish this objective, we measured traits of *L. maackii* (abundance, maximum diameter of the primary stem), and environmental factors that could impact regeneration of *A. saccharum*: edaphic variation (soil density, pH, soil %N, soil %C), topographic variation (elevation, slope, aspect), biotic effects (overall tree abundance), and human influences (proximity to roadways). We measured the effect of these variables on recruitment of *A. saccharum* seedlings, on the transition of seedlings to saplings, and on the transition of saplings to mature trees.

Methods and Materials. **STUDY SITES.** Our study was undertaken in tracts of eastern deciduous forest in southwestern Ohio. Woody vegetation in this area is dominated by *A. saccharum*, *Fraxinus americana* L., *Liriodendron tulipifera* L., *Acer negundo* L., *Quercus rubra* L., *Quercus velutina* Lam., and *Quercus muehlenbergii* Engelm with scattered *Prunus serotina* Ehrh., *Ulmus americana* L., *Ulmus serotina* Sarg, and *Celtis occidentalis* L.. Soils in this region are mesic alfisols, most

commonly Typic Hapludalfs and Aquic Fragiudalfs (SSURGO 2011). Four study sites, containing areas with and without *L. maackii*, were selected to represent mature secondary growth forests typical of this region (Fig. 1). Mount Airy Forest (MAF; 39°10'06.11"N, 84°34'09.28"W) is a protected urban forest in Cincinnati. *Lonicera maackii* has been present in this forest since at least 1941, when it was planted to prevent soil erosion (Stradling 2011). Miami Whitewater Forest (MWW; 30°15'42.17"N, 84°44'21.81"W) and Benedict Nature Preserve (BEN; 39°15'50.34"N, 84°21'16.08"W) are located on the suburban to exurban fringes of Cincinnati in areas where honeysuckle was invading by the late 1950s (Braun 1961). East Fork State Park (EF; 39°01'06.81"N, 84°07'48.96"W) is located in a rural setting that has been invaded by honeysuckle within the last three to four decades.

VEGETATION CENSUSES. Within each study site, we established 16 plots (30 × 30 m), with eight plots located in areas containing *L. maackii* and eight plots placed in areas where *L. maackii* was naturally absent (*i.e.*, there was no record of active *L. maackii* removal) or represented by only a few small individuals. Plots were placed in areas with similar slope, elevation, aspect, and vegetation composition. From July through October 2008, we censused trees, shrubs, saplings, and seedlings at BEN and EF, and trees and saplings at MWW. In September and October 2009, we censused seedlings and shrubs at MWW, and trees, shrubs, saplings, and seedlings at MAF.

Each plot was separated into four 7.5 × 30-m subplots by three line transects. We randomly selected two subplots in each plot and counted and identified to species all trees (> 1 m in height and > 12.5 cm diameter at breast height [DBH]) and saplings (> 1 m in height and < 12.5 cm DBH). Along each of the three line transects, we counted any *L. maackii* shrub whose canopy intersected a transect line, and, for each individual shrub, counted the mean number of basal stems/plant, determined the maximum number of stems/plant, and measured the diameter of the largest (primary) basal stem at ground level. Finally, we randomly placed a 1 × 1-m quadrat in three positions along each of the three line transects for a total of 9 quadrats/plot. In each of these quadrats, we counted the number of *A. saccharum* seedlings.

BIOTIC AND ENVIRONMENTAL MEASURES. Biotic measures included total number of trees, total

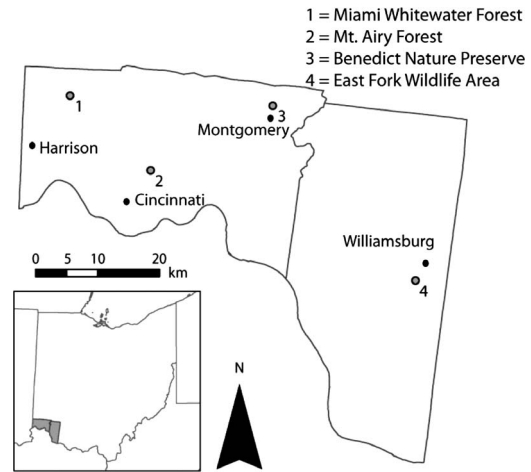


FIG. 1. Location of study sites in southwestern Ohio.

number of *L. maackii* shrubs (number along three 15-m line transects), and maximum diameter (cm) of the primary stem of *L. maackii* shrubs. The mean number of stems/plant and the maximum number of stems/plant were not used in the analyses because they were highly correlated with *L. maackii* abundance or with the diameter of the largest basal stem (Cameron *et al.* 2015).

Environmental measures consisted of edaphic, topographic, and human influence categories. For edaphic factors, we extracted soil cores (AMS soil recovery probe; diameter 2.5 cm; AMS Inc., American Falls, ID) from the center of each plot to depths ranging from 15 to 35 cm, depending on ground penetrability. Cores were enclosed in plastic sleeves with end-caps in the field, immediately transported to the laboratory, and stored at 4 °C. Cores were subdivided into 5-cm increments, and each was sieved to remove coarse material (roots and rocks > 2 mm). Roots and rocks were dried at 70 °C and weighed. For each subsample, we calculated bulk density as (total dry mass – rock mass)/(total volume – rock volume), where rock volume was determined based on mass of the coarse fraction and an assumed coarse-fraction density of 2.7 g/cm³ (following Raciti *et al.* 2011 and Townsend-Small and Czimczik 2010), and total volume was based on the diameter of the core sleeve and the length of the increment (5 cm). After removing the coarse fraction, we homogenized each 5-cm subsample of each core and measured pH on these increments separately using the slurry method (Watson and Brown 1998) with a glass pH meter

(Mettler-Toledo InLab® Expert Pro; Mettler-Toledo LLC, Columbus, OH). We acidified a portion of each subsample to remove inorganic carbon (carbonates); acidified portions were used to determine total soil organic carbon (SOC) concentration and unacidified portions were used to determine total nitrogen (N) concentration. Soil percentage of carbon (%C) and soil percentage of nitrogen (%N) concentrations were determined for each 5-cm subsample by flash-combustion/oxidation using a Thermo CE Elantech Flash EA 1200 elemental analyzer (0.06% C and 0.01% N detection limits; CE Elantech, Inc., Lakewood, NJ). We calculated the density of SOC and N (kg/m) for each subsample as $D = M_j BD(1 - \delta_{2mm})/V$, where D is carbon or nitrogen density, δ_{2mm} is the fraction of material larger than 2 mm diameter, BD is bulk density, M_j is the fraction by mass of SOC or N, and V is the volume of the soil core (Post *et al.* 1982). For the analyses, we computed whole core soil %N and soil %C only from the top 15 cm because these depths were available across all cores. We did not include total SOC or total N in the analyses because these values were highly correlated with soil %N and soil %C (Cameron *et al.* 2015).

We determined topographic variation using ArcGIS 10 (Esri, Redlands, CA) to extract data on elevation (m), slope (% rise), and aspect (based on 360°) for each plot using a 10-m digital elevation model (DEM) available from the US Geological Survey Seamless Server (Gesch 2007). Because aspect is a circular variable, we geometrically converted aspect to measures of “northness” and “eastness,” each of which range from 1 to –1, where 1 describes a slope that faces directly north (or east), and –1 describes a slope that faces directly south (or west; Zar 1999).

Human influence was represented by measuring proximity of plots to roadways. Invasion by *L. maackii* is facilitated by a propensity to disperse along roadside corridors (Flory and Clay 2006). We calculated the distance (km) from each plot centroid to the nearest road and to the nearest major road (primary and secondary highways) using transportation datasets from the 2010 US Census in ArcGIS.

DATA ANALYSIS. We computed rates of recruitment of *A. saccharum* seedlings by trees as ($\log_{10}$ [number of seedlings/number of trees]), transition from seedlings to saplings as ($\log_{10}$ [number of saplings/number of seedlings]), and transition from saplings to trees as ($\log_{10}$ [number of trees/number

of saplings]). In some cases, a value for recruitment of seedlings or transitions to saplings and trees could not be computed for a particular plot because of an absence of seedlings, saplings, or trees. To account for instances of an empty cell, we added 0.5 to all of the data used in the analysis of recruitment or transitions between life stages. We used a general linear model to determine that there was a significant effect of study site on recruitment of seedlings ($F = 10.5$; $P < 0.01_{3,47}$), transition from seedlings to saplings ($F = 17.0$, $P < 0.01_{3,54}$), and transition of saplings to trees ($F = 3.5$, $P = 0.02_{3,54}$). Accordingly, site was included as a random effect in the following analyses.

We used a generalized linear mixed model and model comparison techniques to identify the variables that were significantly related to seedling recruitment or transitions to saplings or trees. We first identified potentially important variables by comparing the full model containing all potential variables and including the random effect (site) to a model with the variable of interest removed (e.g., soil bulk density). If there was no difference between these models as determined by a likelihood ratio test, we concluded, for instance, that soil bulk density, was not a significant factor. This process was repeated for each independent variable to produce a set of variables for the final model. This final model was used to assess the significance of each variable in a similar way as above, but here the comparison was between the final model and a model with that term of interest removed.

Because we were interested in comparing models with different fixed effects, these comparisons were made using maximum likelihood estimates (Crawley 2013). Full and final models were compared with likelihood ratio tests based on a χ^2 statistic. The χ^2 value reflects the deviance explained by each variable and the parameter estimates reflect the relationship between a particular fixed effect and seedling recruitment or transitions to saplings and trees.

We tested all data for model assumptions. We tested for equality of variance using the Fligner-Killeen test and for normality using the Shapiro-Wilk test. After fitting, all models were inspected for patterning in residuals, leverage, and outliers. We checked for correlations among variables and eliminated some edaphic and biotic variables that were highly correlated (see Biotic and Environmental Measures, above). All statistical analyses

Table 1. Recruitment of *Acer saccharum* seedlings by *A. saccharum* trees and transition from seedlings to saplings and saplings to trees (reported as mean $\pm$ SE log₁₀ number recruited) for each study site and plot type in southwestern Ohio. Study sites: BEN = Benedict Nature Preserve, EF = East Fork Wildlife Area, MAF = Mount Airy Forest, MWW = Miami Whitewater Forest (locations in Fig. 1). Plot types: No LM = *Lonicera maackii* absent; LM = *L. maackii* present.

Study site	Plot type	Number of seedlings recruited/tree	Number of saplings recruited/seedling	Number of trees recruited/sapling
BEN	No LM	0.156 $\pm$ 0.020	0.305 $\pm$ 0.082	0.029 $\pm$ 0.005
	LM	0.041 $\pm$ 0.032	0.682 $\pm$ 0.196	0.078 $\pm$ 0.008
EF	No LM	-0.173 $\pm$ 0.032	2.360 $\pm$ 0.641	-0.011 $\pm$ 0.008
	LM	0.014 $\pm$ 0.034	0.934 $\pm$ 0.383	0.325 $\pm$ 0.011
MAF	No LM	0.156 $\pm$ 0.035	0.046 $\pm$ 0.015	0.112 $\pm$ 0.010
	LM	0.112 $\pm$ 0.032	0.106 $\pm$ 0.128	0.147 $\pm$ 0.010
MWW	No LM	0.207 $\pm$ 0.032	0.108 $\pm$ 0.016	0.061 $\pm$ 0.014
	LM	0.288 $\pm$ 0.030	0.321 $\pm$ 0.206	0.088 $\pm$ 0.014

were performed using R (version 3.0.2, R Development Core Team 2013).

Results. Recruitment of *A. saccharum* seedlings and the transition from seedlings to saplings and saplings to trees varied by study site and plot type (Table 1). For example, the number of seedlings recruited/tree was higher in plots without *L. maackii* than with the invasive shrub at BEN (0.16 vs. 0.04), and MAF (0.16 vs. 0.1), but was higher in plots with *L. maackii* for EF (-0.17 vs. 0.01) and MWW (0.29 vs. 0.21). By contrast, the number of saplings recruited from seedlings and the number of trees recruited from saplings were higher in plots with *L. maackii* for all study sites except for EF where the number of saplings recruited/seedling was higher in plots without *L. maackii* (see Table 1).

Variation in values of biotic and environmental variables also differed by study site and presence/absence of *L. maackii* (see Table 2). Particularly striking in these data are the higher pH, soil %C, and soil %N at MAF and the steeper slope at MAF and in plots without *L. maackii* at MWW. In addition, distance to the nearest roads was higher at MWW and distance to major roads was higher at MWW and EF than at the other study sites. As would be expected, abundance and size (maximum diameter of the primary stem) of *L. maackii* was much less in those plots categorized as free of *L. maackii*. Raw data for these variables organized by study site, plot, and presence/absence of *L. maackii* are available as Supplemental Material (Table S1).

Recruitment of *A. saccharum* seedlings by *A. saccharum* trees was explained by soil bulk density, soil %N, soil %C, and maximum diameter of the primary stem of *L. maackii*. These variables were included in the final model, although soil bulk density did not contribute to the significance of the final model (Table 3). Inspection of the parameter estimates showed that seedling recruitment increased with increasing soil %C, but decreased with increasing soil %N. Additionally, seedling recruitment decreased with larger maximum diameter of the primary *L. maackii* stem.

The transition of *A. saccharum* seedlings to saplings was explained by topography (slope), biotic factors (overall tree abundance and maximum diameter of the primary stem of *L. maackii*), and human influence (distance to the nearest major road). These factors were included in the final model and all were significant except overall tree abundance (Table 4). The transition of seedlings to saplings increased with steeper slope, larger diameter of the primary *L. maackii* stem, and greater distance to the nearest road.

The transition of *A. saccharum* saplings to trees was explained by edaphic factors (soil bulk density, soil %N, soil %C), biotic factors (overall tree abundance), and human influence (distance to the nearest road). All contributed significantly to the final model except soil %N (Table 5). The transition from saplings to trees decreased with an increase in soil bulk density and percent soil %C. This transition also increased with an increase in overall tree abundance and with a greater distance to the nearest road.

Table 2. Values (mean $\pm$ SE) for biotic and environmental variables organized by study site and plots (with and without *Lonicera maackii*). Abundance of *L. maackii* measured as number of shrubs intersecting three 15-m transects in each 30 $\times$ 30-m plot at each study site; abundance of trees measured as total number of trees in two 15 $\times$ 30-m subplots in each 30 $\times$ 30-m plot at each study site. See Methods for more details on these variables. Study sites: BEN = Benedict Nature Preserve, EF = East Fork Wildlife Area, MAF = Mount Airy Forest, MWV = Miami Whitewater Forest (locations in Fig. 1). Plot types: No LM = *Lonicera maackii* absent; LM = *L. maackii* present.

Variable	BEN		EF		MAF		MWV	
	No LM	LM	No LM	LM	No LM	LM	No LM	LM
Soil density (g/cm ³)	1.15 $\pm$ 0.04	1.15 $\pm$ 0.04	1.21 $\pm$ 0.03	1.20 $\pm$ 0.03	1.15 $\pm$ 0.03	1.20 $\pm$ 0.03	1.45 $\pm$ 0.05	1.21 $\pm$ 0.03
pH	5.67 $\pm$ 0.20	5.39 $\pm$ 0.17	5.10 $\pm$ 0.18	5.06 $\pm$ 0.14	5.80 $\pm$ 0.30	6.70 $\pm$ 0.15	5.17 $\pm$ 0.24	5.35 $\pm$ 0.18
Soil %N	0.18 $\pm$ 0.02	0.17 $\pm$ 0.02	0.17 $\pm$ 0.02	0.18 $\pm$ 0.02	0.22 $\pm$ 0.03	0.31 $\pm$ 0.02	0.21 $\pm$ 0.03	0.18 $\pm$ 0.02
Soil %C	1.71 $\pm$ 0.15	1.46 $\pm$ 0.16	1.47 $\pm$ 0.14	1.53 $\pm$ 0.18	2.41 $\pm$ 0.29	3.22 $\pm$ 0.22	1.86 $\pm$ 0.28	1.42 $\pm$ 0.16
Elevation (m)	251.2 $\pm$ 1.30	257.1 $\pm$ 0.43	253.9 $\pm$ 3.14	260.0 $\pm$ 1.21	254.1 $\pm$ 3.22	245.6 $\pm$ 3.92	241.0 $\pm$ 2.83	242.2 $\pm$ 3.02
Slope (% rise)	2.71 $\pm$ 0.64	2.86 $\pm$ 0.81	4.75 $\pm$ 2.03	4.39 $\pm$ 1.00	14.60 $\pm$ 1.46	17.0 $\pm$ 1.00	11.36 $\pm$ 1.44	6.05 $\pm$ 1.00
Eastness	-0.24 $\pm$ 0.18	-0.22 $\pm$ 0.28	-0.58 $\pm$ 0.24	-0.43 $\pm$ 0.27	-0.15 $\pm$ 0.25	-0.38 $\pm$ 0.26	-0.84 $\pm$ 0.09	-0.21 $\pm$ 0.29
Northness	-0.61 $\pm$ 0.22	-0.12 $\pm$ 0.23	0.39 $\pm$ 0.13	0.27 $\pm$ 0.18	0.69 $\pm$ 0.11	0.21 $\pm$ 0.22	0.19 $\pm$ 0.17	-0.32 $\pm$ 0.20
Distance of nearest road (km)	0.26 $\pm$ 0.01	0.18 $\pm$ 0.02	0.32 $\pm$ 0.08	0.27 $\pm$ 0.06	0.11 $\pm$ 0.03	0.20 $\pm$ 0.05	0.70 $\pm$ 0.02	0.55 $\pm$ 0.06
Distance of nearest major road (km)	0.27 $\pm$ 0.01	0.24 $\pm$ 0.02	3.05 $\pm$ 0.21	3.14 $\pm$ 0.16	0.63 $\pm$ 0.12	0.91 $\pm$ 0.20	2.49 $\pm$ 0.02	2.39 $\pm$ 0.02
Maximum stem diameter (cm)	0.74 $\pm$ 0.11	5.48 $\pm$ 0.91	2.81 $\pm$ 1.20	7.34 $\pm$ 2.02	1.75 $\pm$ 0.85	7.83 $\pm$ 0.89	0.38 $\pm$ 0.13	5.38 $\pm$ 1.08
Abundance of <i>L. maackii</i>	4.38 $\pm$ 0.63	33.63 $\pm$ 3.44	3.00 $\pm$ 1.18	31.75 $\pm$ 7.45	1.00 $\pm$ 0.38	85.63 $\pm$ 12.87	1.25 $\pm$ 0.59	85.13 $\pm$ 15.33
Abundance of trees	12.00 $\pm$ 1.39	11.86 $\pm$ 1.22	14.38 $\pm$ 1.76	16.5 $\pm$ 1.95	13.88 $\pm$ 1.37	14.25 $\pm$ 1.71	16.00 $\pm$ 1.36	13.38 $\pm$ 1.66

Table 3. The final model for recruitment of *Acer saccharum* seedlings by trees contained all of the individual factors identified as significant by model comparison techniques. This final model was used to assess the significance of each variable by comparison to a model with that term removed using likelihood-ratio tests. The χ^2 value reflects the deviance explained by each variable. Sign of the parameter estimate indicates the relationship between a particular fixed effect and seedling recruitment. Degrees of freedom = 1 for all model comparisons except for the final model vs. the null model where d.f. = 4. For the random effects, site: variance = 0.0861, SD = 0.2909; residual: variance = 0.11065; SD = 0.3326. * = $P < 0.05$.

Fixed effects	Estimate	SE	<i>t</i>	χ^2	<i>P</i>
(Intercept)	−0.46190	0.68939	−0.670		
Final model vs. null				18.02	< 0.01*
Soil bulk density	0.55227	0.53700	1.028	1.05	0.31
Soil %N	−2.84971	1.21833	−2.339	5.20	0.02*
Soil %C	0.31208	0.13880	2.248	4.67	0.03*
Maximum diameter of primary <i>Lonicera maackii</i> stem	−0.15849	0.04271	−3.710	12.18	< 0.01*

Discussion. The biotic effects on seedling recruitment and transition to saplings and trees included *L. maackii* presence and overall tree abundance (Tables 3–5). The presence of larger *L. maackii* (measured as maximum diameter of the primary stem) was associated with lower recruitment of *A. saccharum* seedlings (Table 2). This relationship between *L. maackii* and *A. saccharum* corroborates other studies from southwestern Ohio that found negative effects of this introduced shrub on abundance of *A. saccharum* seedlings (Hutchinson and Vankat 1997, Hartman and McCarthy 2008) and on survival of *A. saccharum* seedlings (Gorchov and Trisel 2003, Loomis *et al.* 2015). There are several possible reasons for this effect. One is that the dense shrub layer created by large *L. maackii* decreases the amount of light reaching the forest floor (Luken *et al.* 1997, McKinney and Goodell 2010). Although *A. saccharum* seedlings are shade-tolerant, the further reduction in available light attributable to *L. maackii* could adversely affect seedling growth and survival (Trammell and Carreiro 2011). Additionally, increased shade

at the forest floor coupled with reduced abundance of forest-floor herbs in areas invaded by *L. maackii* (Christopher *et al.* 2014) could alter temperature and soil moisture, which could in turn affect seedling survival (Hutchinson and Vankat 1997). Additionally belowground processes attributable to the presence of *L. maackii* also could affect survival of *A. saccharum* seedlings. For example, extracts from *L. maackii* leaves, fruits, and roots contain allelochemicals that inhibit germination of native herbs (Dorning and Cipollini 2006, McEwan *et al.* 2010), and *L. maackii* also alters availability of soil nutrients (Arthur *et al.* 2012, McEwan *et al.* 2012, Poulette and Arthur 2012, Trammell *et al.* 2012). These processes may be exacerbated by the shallow roots of *L. maackii*, which are concentrated in the upper 15 cm of soil. These shallow roots have been implicated in belowground competition with herbs (Gorchov and Trisel 2003), but also could adversely affect *A. saccharum* seedlings and possibly even mature *A. saccharum* trees (Hartman and McCarthy 2007).

Table 4. The final model for the transition from *Acer saccharum* seedlings to saplings contained those individual factors identified as significant by model comparison techniques. This final model was used to assess the significance of each variable by comparison to a model with that term removed using likelihood-ratio tests. The χ^2 value reflects the deviance explained by each variable. Sign of the parameter estimate indicates the relationship between a particular fixed effect and seedling recruitment. Degrees of freedom = 1 for all model comparisons except for the final model versus the null model where df = 4. For the random effects, site: variance = 0.1098, SD = 0.3314; residual: variance = 0.1326; SD = 0.3641. * = $P < 0.05$.

Fixed effects	Estimate	SE	<i>t</i>	χ^2	<i>P</i>
(Intercept)	−0.63348	0.58499	−1.083		
Final model vs. null				24.30	< 0.01*
Slope	0.04636	0.01440	3.220	9.30	< 0.01*
Distance to nearest major road	0.54143	0.16251	3.332	10.32	< 0.01*
Maximum diameter of primary <i>Lonicera maackii</i> stem	0.12361	0.04952	2.496	6.42	0.01*
Overall tree abundance	−0.02650	0.01431	−1.852	3.59	0.06

Table 5. The final model for the transition from *Acer saccharum* saplings to mature trees contained those individual factors identified as significant by model comparison techniques. This final model was used to assess the significance of each variable by comparison to a model with that term removed using likelihood-ratio tests. The χ^2 value reflects the deviance explained by each variable. Sign of the parameter estimate indicates the relationship between a particular fixed effect and seedling recruitment. Degrees of freedom = 1 for all model comparisons except for the final model versus the null model where df = 4. For random effects, site: variance = 0.1098, SD = 0.3314; residual: variance = 0.1326; SD = 0.3641. * = $P < 0.05$.

Fixed effects	Estimate	SE	<i>t</i>	χ^2	<i>P</i>
(Intercept)	0.97247	0.72761	1.338		
Final model vs. null				29.23	< 0.01*
Soil bulk density	−1.30496	0.54310	−2.408	5.90	0.02*
Soil %N	2.36028	1.26775	1.862	3.52	0.06
Soil %C	−0.43035	0.14848	−2.898	7.98	< 0.01*
Distance to nearest road	1.01308	0.36554	2.771	7.96	< 0.01*
Overall tree abundance	0.05595	0.01308	4.227	17.39	< 0.01*

Contrary to the lower recruitment of seedlings in forests with greater diameter of the primary stem of *L. maackii*, these forests had more seedlings transitioning into saplings. This may be explained by the protection afforded by larger *L. maackii* shrubs from deer herbivory, which is a major cause of mortality of young saplings (Rooney and Waller 2003). Supporting this possibility, Cipollini *et al.* (2009) suggested that even dead *L. maackii* shrubs left standing after herbicide treatment by managers may protect understory plants, such as older *A. saccharum* seedlings, from deer grazing. Inversely, growth of *A. saccharum* seedlings was reduced by deer browsing when *L. maackii* was removed (Gorchov and Trisel 2003). It is possible that young saplings could suffer the same fate growing away from *L. maackii*.

In contrast to seedling recruitment, the transition from *A. saccharum* saplings to trees was not impacted by the presence of large *L. maackii* (Table 5). In contrast, Fagan and Peart (2004) found that another invasive shrub, *Frangula alnus* Mill, decreased growth and survival of *A. saccharum* saplings. Like *L. maackii*, *F. alnus* has shallow roots that may compete with *A. saccharum* saplings for nutrients or water. Both species reduce available light to the forest floor and are capable of altering soil temperature or moisture. The different outcomes may result from differences in allelopathy. While we are unaware of any evidence that *F. alnus* produces allelochemicals, *A. saccharum* saplings may be large enough or have deep enough roots to be relatively immune to effects of *L. maackii* allelochemicals, which would explain the lack of decrease in survival in the presence of large *L. maackii*. It also is possible that *A. saccharum* saplings eventually are tall

enough to avoid or minimize any effects of shading by *L. maackii*. Because height of *L. maackii* shrubs can exceed 4 m, *A. saccharum* saplings would have to be quite tall to avoid shading effects. Furthermore, sapling growth is very slow under dense forest conditions, suggesting that *A. saccharum* saplings would only be able to overtop *L. maackii* when their growth rapidly increases in forest canopy gaps (Canham 1985, 1988; Gasser *et al.* 2010).

Factors other than presence of *L. maackii* also were also associated with *A. saccharum* recruitment. For example, there was a strong positive relationship between overall tree abundance and the transition of *A. saccharum* saplings to trees. One reason saplings occur in areas with abundant tree cover is that they are protected from environmental forces such as high winds. Because of their narrow trunk diameter, *A. saccharum* saplings naturally have low stability (King 1986). The advantage to saplings growing in a forest understory is that they are protected from wind-throw because wind speeds under forest canopies are much less than in open areas (Baldocchi and Meyers 1988). When growing in areas with high overall tree abundance, saplings increase in girth with deposition of heavy dense wood, which increases their stability (Lei and Lechowicz 1990).

Edaphic and topographic factors also affected recruitment of *A. saccharum* seedlings as well as the transitions to saplings and trees (Tables 3–5). Increased soil bulk density was negatively related to the transition from saplings to trees. Compaction of soil decreases tree establishment and growth, reduces root density, confines roots to upper soil layers, and reduces soil aeration and hence shoot and root growth (Voorhees *et al.* 1975, McCon-

naughay and Bazzaz 1991, Day and Bassuk 1994, Brady and Weil 2002). These effects would be expected to reduce sapling growth and survival, thus inhibiting their transition to trees.

The transition from *A. saccharum* seedlings to saplings was higher on steeper slopes (Table 4). Steeper slopes may be more favorable for seedling growth because soils are drier, and more runoff results in less litter accumulation providing open spaces for seedling growth. Additionally, substrate slippage and concomitant loss of vegetation on steeper slopes also provides open sites for seedling growth. Growth of both seedlings and saplings also is greatest in canopy gaps (Hett 1951, Canham 1988, Canham and Burbank 1994, Marks and Gardescu 1998, Kobe 2006). In the Cincinnati area, soil slippage on steep slopes often leads to landslides, which can contribute to the formation of canopy gaps. As such, the enhanced transition from seedlings to saplings may reflect the occurrence of more canopy gaps at our study sites with the steepest average slopes (MAF, MWW) compared to those with much less slope (EF, BEN; Table 2).

In our study, soil %N negatively affected seedling recruitment (Table 3). This result corroborates the findings of studies that experimentally augmented soil %N to simulate increased atmospheric N deposition and reported a decrease in abundance and survival of *A. saccharum* seedlings with increased soil %N (Eller *et al.* 2011, Patterson *et al.* 2012, Talhelm *et al.* 2013; but see Zaccherio and Finzi 2007 who reported the opposite effect). Talhelm *et al.* (2013) suggested that this negative effect could be explained by increased production of potential alleopathic phenol compounds caused by higher soil %N (Hane *et al.* 2003, Smemo *et al.* 2007). The negative effect also could be caused by an increased accumulation of litter resulting from a negative effect of increased N on activity of microbial decomposers which retarded tree seedling germination and growth (Patterson *et al.* 2012).

Soil %C positively affected seedling recruitment, but negatively affected the transition from saplings to trees (Tables 3, 5). The lifespan of fine roots in *A. saccharum* saplings is adversely affected by a decrease in C:N in roots, which likely impacts nutrient uptake, plant growth rate, and ultimately plant longevity (McCormack *et al.* 2012). Decreased growth and survival of saplings would negatively affect the transition to mature

trees, and could explain our finding of a negative impact of soil %C on this transition. Similarly, changes to the C:N ratio also could affect the recruitment of seedlings and *L. maackii* may play a role in this process. Kolbe *et al.* (2015) found that soil %N and soil %C increased with size (basal area) of *L. maackii* at MAF, our study site with the longest history of invasion by *L. maackii*. This likely was related to the much higher decomposition rate of *L. maackii* litter compared to litter from native species (Arthur *et al.* 2012; Trammell *et al.* 2012), as well as alterations to the microbial decomposer communities by *L. maackii* (Arthur *et al.* 2012, Kuebbing *et al.* 2014). Increases in soil %N occur in response to enhanced organic matter input to soils, which contains N and can stimulate biological N fixation by providing microbes with more carbohydrates (Knops *et al.* 2002, Luo *et al.* 2006). Such changes to the C:N ratio by *L. maackii* could explain the positive impact of C on recruitment of seedlings. Further study is needed to fully understand whether changes in soil %C and the C:N ratio have a differential effect on seedlings and saplings, and to understand the role that *L. maackii* might play in these processes.

The impact of human influence was manifested by proximity to roadways; greater distances from nearest roadways and nearest major roadways positively affected the transition to saplings and trees (Tables 4, 5). This largely is attributable to edge effects of roadways, which may permeate into adjacent forest by as much as 1 km (Gascon *et al.* 2000). Examples of edge effects include drier, more compacted, and more acidic soils near roadways; road edges also collect residue of salt runoff used to control snow and ice and therefore contain high concentrations of lead, copper, N, calcium, magnesium, and potassium (Saunders *et al.* 2002, Pouyat *et al.* 2008, Pickett *et al.* 2011). Slower water movement through compacted soils slows leaching of salts used in snow control and contributes to the overall adverse effects upon seedlings and saplings, further hindering the transition to the next life stage (Day and Bassuk 1994). In addition, roadways are conduits for dispersal of *L. maackii* (Flory and Clay 2006) resulting in high densities of this shrub near roadways and into the adjacent habitat edge. Because survival of *A. saccharum* seedlings is adversely affected by *L. maackii* (Gorchov and Trisel 2003, Loomis *et al.* 2015), their recruitment

and transition to saplings should be higher away from roadways.

Our results demonstrate a complex pattern of the impact of *L. maackii* on recruitment of *A. saccharum* coupled with impacts of edaphic, biotic, and human factors. The negative effect of *L. maackii* on recruitment of seedlings contrasts with a positive effect of this invasive shrub on the transition of *A. saccharum* seedlings to saplings and with no effect on the transition from saplings to trees. In spite of such differences in effects among life stages, the negative effect of *L. maackii* combined with the negative effects of soil %N on seedling recruitment could have long-term impacts on the overall abundance of *A. saccharum* in eastern deciduous forests because seedlings are the genesis of a future forest. This effect may be exacerbated because *L. maackii* also can increase concentrations of soil %N and soil %C. Although the transition from seedlings and saplings is affected by *L. maackii* as well as by edaphic (slope) and human (roadways) factors, the transition from saplings to trees is only affected by edaphic (soil density, soil %C), other biotic (tree abundance), and human (roadways) factors. To uncover the reasons for these findings, experimental studies are needed to elucidate the mechanisms involved in the negative impact of *L. maackii* on seedling recruitment and the positive impact of *L. maackii* on the transition to *A. saccharum* saplings. Future investigations also could be designed to elucidate the mechanisms whereby soil %C and soil %N affect recruitment of seedlings and whether this impact results from an increase in soil %C and soil %N (and likely alteration of the C:N ratio) caused by the presence of *L. maackii*.

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