Association of non-native Amur honeysuckle (Lonicera maackii, Caprifoliaceae) with other invasive plant species in eastern deciduous forests in southwestern Ohio 1

Authors: Culley, Theresa, and Cameron, Guy N.

Association of non-native Amur honeysuckle (*Lonicera maackii*, Caprifoliaceae) with other invasive plant species in eastern deciduous forests in southwestern Ohio[1]

Theresa Culley[2] and Guy N. Cameron

Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221

Sarah E. Kolbe and Arnold I. Miller

Department of Geological Sciences, University of Cincinnati, Cincinnati, OH 45221

Abstract. Although many invasive plant species negatively impact native plants in natural communities, their relationships with other nonnative plants remain relatively unexplored. In some cases, invasive plant species may be capable of facilitating the invasion of other nonnative species into natural areas, thereby exacerbating their invasive ecosystem effects. We examined whether *Lonicera maackii* (Rupr.) Herder (Amur honeysuckle), a woody shrub from Asia that is rapidly spreading throughout the midwestern USA, is associated with other invasive plant species, compared to locations where *L. maackii* is not yet present. *Lonicera maackii* is known to detrimentally impact native plant communities and to alter soil nutrients and light levels in invaded areas, indicating that it has the potential to act as an invasion facilitator. Using plots with and without *L. maackii* in four study sites across southwestern Ohio, we quantified species richness (*S*), relative abundance (*RA*), proportion of total species (*PR*), and diversity (*H*) of invasive species, compared to native and nonnative species that were not invasive. The presence of *L. maackii* was significantly associated with an increased number, proportion, and diversity of other invasive plant species, but the relative abundance of invasive individuals did not differ between plots with and without *L. maackii*. Presence of *L. maackii* and also distance to roads were explanatory variables that predicted *S, PR, RA,* and *H* for invasive species. Overall, the association of *L. maackii* with other invasive plant species in natural areas indicates the need for continued investigation into the potential role of *L. maackii* as an invasion facilitator in eastern deciduous forests in the midwestern USA.

Key words: Amur honeysuckle, facilitation, invasion meltdown, invasive species

By their very nature, invasive plant species are capable of impacting the natural communities into which they have been introduced. Although many nonnative plant species may never become invasive, other species or genotypes may spread and eventually displace residents of natural areas (Sakai *et al*. 2001). In the worst case, these invaders form extensive monocultures that exclude many or all other plant species. Invasive species often encroach into natural communities by outcompeting native and nonnative species that are not invasive because invaders may grow faster with higher reproductive output and may be better able to compete with resident species for limiting resources such as light or moisture. For example, Van Kleunen *et al*. (2010) used a meta-analysis to determine that invasive plant species possess higher values than noninvasive plants for traits related to physiology, leaf-area and shoot allocation, growth rate, size, and fitness. In another meta-analysis, Vilà *et al*. (2011) found that invasive plants not only reduced fitness and growth of native species and changed community structure by reducing abundance and diversity of native species, but also enhanced overall primary production and soil nutrient pools. It remains unclear whether invasive species drive community changes by directly limiting native species or are less affected by environmental change as compared to native species (Didham *et al*. 2005, MacDougall and Turkington 2005). In general, most studies examining the interaction of invasive and native

species have documented negative effects on the native flora (*e.g.*, Sakai *et al.* 2001, Vilà *et al.* 2011, Jauni and Ramula 2015; but see Rodriguez 2006).

A relatively less studied effect of invasive plants is whether they facilitate the invasion of other nonnative, invasive plants thereby exacerbating their impacts on ecosystem function (Simberloff 2006, Kuebbing *et al.* 2013b, Flory and Bauer 2014). Although land managers must deal with multiple invaders at a given site (Kuebbing *et al.* 2013b), only a handful of studies have examined interactions between two or more invasive species (Tecco *et al.* 2007, Cushman *et al.* 2011, Wundrow *et al.* 2012, Kuebbing *et al.* 2013a, Flory and Bauer 2014). In many cases, interactions among invading plant species are competitive (negative) or neutral (Kuebbing *et al.* 2013b, Kuebbing and Nuñez 2015), but in other situations, facilitation can occur through direct mutualistic interactions (Richardson *et al.* 2000) or indirectly through habitat modification by the initial invader (Simberloff and Van Holle 1999, Flory and Bauer 2014). For example, *Myrica faya* (Aiton) Wilbur is a nonnative, nitrogen-fixing shrub in the Hawaiian Islands that quickly colonizes recent lava flows and changes the soil chemistry of the sites (Vitousek and Walker 1989). This change makes sites inhospitable to native plant species that would have normally colonized the area, and potentially opens the area to colonization by nonnative species that prefer the new conditions. Similarly, the African crystalline ice plant (*Mesembryanthemum crystallinum* L.) is problematic in California because it accumulates salt, which is released into the soil when the plant dies, creating an osmotic environment intolerable to native plants, but conducive to invasion by introduced species (Vivrette and Muller 1977). In the eastern USA, Russian olive (*Elaeagnus angustifolia* L.) is a woody, nitrogen-fixing shrub whose occurrence is associated with subsequent invasions by other nonnative plant species that are better able to utilize the nitrogen-rich soils, compared to native plants (Follstad Shah *et al.* 2010, Gladdis and Sher 2012; but see DeCant 2008). Although reports of positive interactions among nonnatives are relatively rare (18.9% of all reported interactions; Kuebbing and Nuñez 2015), when they do occur, such interactions are three times more frequent when a nitrogen fixer is involved.

The concept of multiple invasive species facilitating the success of other invasive species, resulting in the domination by invasive species in local habitats and subsequent ecosystem effects, is known as invasional meltdown (Simberloff and Van Holle 1999, Simberloff 2006). This concept has often been invoked but may actually be quite rare because mutual facilitation must be documented at the population level and then shown to impact the ecosystem—that is, the relationship must be more than just an association between two or more invaders (Simberloff 2006, Kuebbing *et al.* 2013b, Kuebbing and Nuñez 2015). Facilitation can be direct (*e.g.*, one invader physically excluding herbivores that might otherwise damage other invasive species growing beneath it) or indirect (*e.g.*, suppression of resident native species through competition, allowing other nonnative species to invade; Flory and Bauer 2014). As evident in the examples above, invasion facilitators often modify a component of their abiotic environment permanently (*e.g.*, soil, moisture, or light) so that native species cannot persist and nonnative species have the opportunity to invade, ultimately changing the species composition of the community.

To determine whether a specific invader may be an invasion facilitator, the first step is to confirm that significantly more invasive species are found in areas where the focal invader is present, compared to locations where it has not yet appeared. Although documenting this relationship is important, it does not *per se* confirm that the species of interest is a facilitator, as there could be other reasons why invaders may be associated with one another. For example, propagules from different invasive species could disperse to, and successfully become established in, a highly disturbed site at the same time (*i.e.*, due to propagule pressure), especially if a source of an invasive species is located nearby. However, this type of investigation is key to understanding if subsequent empirical studies of invasion facilitation are warranted (as in Flory and Bauer 2014).

Woody invaders in particular are increasing in importance on a worldwide scale (Richardson and Rejmánek 2011), but they have been relatively understudied compared to herbaceous invaders (Stricker *et al.* 2015). Woody invaders are prevalent in North America, where they can change community structure and ecosystem function by altering abundance, species richness, and

species diversity of native understory herbaceous plants and woody seedlings (Hunter and Mattice 2002, Webster *et al*. 2006). Although introduced species are often thought to be restricted to habitat edges because they are adapted to disturbed soils and high-light environments (Von Holle *et al*. 2003, Harper *et al*. 2005), Martin *et al*. (2009) found that 139 invasive plant species were shade-tolerant, and of these, at least 23 exotic shrubs in the eastern USA were capable of invading forest interiors. However, the impact of these woody species in facilitating the invasion of other nonnative species in edge habitats or forest interiors has been relatively unexplored, even though woody nonnative species are two to four times more likely than native species to experience such interactions (Kuebbing and Nuñez 2015).

An invasive species known to substantially impact natural areas in North America is *Lonicera maackii* (Rupr.) Herder (Amur honeysuckle), a woody shrub from East Asia that is now found extensively in many forested and disturbed sites in the midwestern USA, especially in and around urban areas. This species was introduced to the USA from Asia in 1896 and was first reported in the wild in southwestern Ohio (Braun 1961). Subsequently, *L. maackii* has invaded at least 36 midwestern and eastern states and has spread into Ontario, Canada (BONAP 2014). It was initially planted along roadways to prevent soil erosion and in urban areas as an ornamental shrub because of its fragrant flowers and red berries that attract wildlife (Luken and Thieret 1996). *Lonicera maackii* has now spread to become the most abundant shrub in deciduous forests in southwestern Ohio (Luken 1988; Luken *et al*. 1995, 1997). The extended duration of leaf-retention (mid-March to December) and capacity to withstand freezing temperatures may underlie the negative effects that *L. maackii* has on forest-floor vegetation (McEwan *et al*. 2009). These effects include reduction in growth, survival, and fecundity of annual and perennial herbs (Gould and Gorchov 2000, Miller and Gorchov 2004); lower density and diversity of tree seedlings (Hutchinson and Vankat 1997); lower density and diversity of saplings (Hartman and McCarthy 2008); reduced recruitment of tree seedlings (Cameron *et al*. 2015); lower tree seedling growth and survival (Gorchov and Trisel 2003, Loomis *et al*. 2015); and lower species richness and abundance of native herbs and tree seedlings (Collier *et al*. 2002,

Hartman and McCarthy 2008, Christopher *et al*. 2015). *Lonicera maackii* can also interact with other invaders, with more subdominant nonnative species observed in mixed plots of *L. maackii* and nonnative *Ligustrum sinense* Lour. (Kuebbing *et al*. 2013a), reflecting below-ground differences (Kuebbing *et al*. 2015). Basal area of *L. maackii* also is associated with increased density of soil organic carbon and nitrogen (Kolbe *et al*. 2015) and *L. maackii* litter decomposes at a high rate (Blair and Stowasser 2009), releasing nitrogen into the soil (Schuster and Dukes 2014).

Given that invasive *L. maackii* exerts detrimental effects on the neighboring flora and abiotic environments in its region of spread, our goal was to determine whether *L. maackii* also could facilitate the invasion of other nonnative plant species, especially those that were invasive. Consequently, we sought to determine how *L. maackii* was associated with the occurrence, abundance, and species diversity of other invasive plant species (compared to native species and nonnative, noninvasive plant species) within an urban setting near the epicenter of its invasive range.

Materials and Methods. STUDY SITES. Our study was undertaken in the eastern deciduous forest in and near the Cincinnati metropolitan area in southwestern Ohio (Fig. 1). Four study sites along a west-east gradient included Miami Whitewater Forest (MWW), a 1,732-ha nature and recreational area 40 km west of Cincinnati, owned and managed by Great Parks of Hamilton County; Mount Airy Forest (MAF), a 595-ha stand of deciduous forest in the southwestern corner of Cincinnati, owned and managed by the Cincinnati Park Board; Harris Benedict Nature Preserve (BEN), a 26.2-ha stand of deciduous forest 26 km northeast of the center of Cincinnati in Montgomery, OH, owned and managed by the University of Cincinnati; and East Fork Wildlife Area (EF), a 1,095-ha area of deciduous forest, old fields, and grain crops planted for wildlife food and cover 39 km southeast of Cincinnati, owned and managed by the Division of Wildlife, Ohio Division of Natural Resources. All sites are described further in Cameron *et al*. (2015) and Kolbe *et al*. (2015).

Southwestern Ohio is part of the Western Mesophytic Forest Region with the most important canopy trees being beech (*Fagus grandifolia*
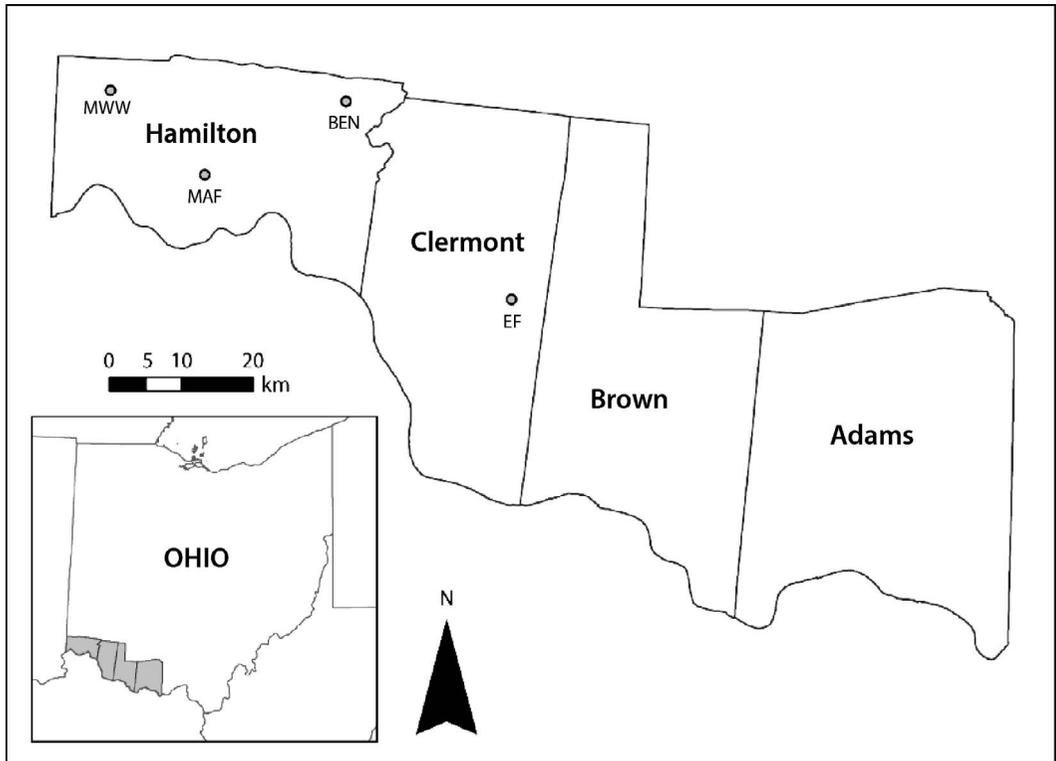
Fɪɢ. 1. Location of study sites in southwestern Ohio. MWF, Miami Whitewater Forest; MAF, Mount Airy Forest; BEN, Benedict Preserve; EF, East Fork Wildlife Area. County names are indicated on the map.

Ehrh.), white oak (*Quercus alba* L.), pin oak (*Quercus palustris* Münchh.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum Marshall*), American elm (*Ulmus americana* L.), shellbark hickory (*Carya laciniosa* (Michx. f.) G. Don), and sweet gum (*Liquidambar styraciflua* L.; Braun 1936, 1961). Much of this original deciduous forest was converted to farms and second-growth forest beginning in the first part of the 19th century (Braun 1936), and currently contains second-growth forests dominated by sugar maple (*Acer saccharum*). The major native shrub in these forests is spicebush (*Lindera benzoin* (L.) Blume), which usually occurs as isolated individual shrubs that do not form dense thickets. *Lonicera maackii* has become established at all of our study sites, where it can form a dense midstory canopy with individual shrubs reaching heights ≥ 5 m. Land currently occupied by MAF was cleared and used for dairy and produce farms at the beginning of the 20th century. Starting with land purchases in 1911, the city of Cincinnati initiated replanting and rehabilitation of the forest and planted *L. maackii* for erosion control (Stradling 2011). The preserve

at BEN was originally established in the late 1920s in rural Hamilton County but now is bordered by residences, commercial businesses, and an interstate highway. Originally, half of BEN was native *F. grandifolia-A. saccharum* deciduous forest and half was farmed until the early 1900s. Early in the 19th century, when much of the original forest was logged, EF was home to gristmills, sawmills, gold mines, and tanneries. The MWW consists largely of secondary growth forests that formed after agricultural land obtained by the Great Parks of Cincinnati in the early to mid-1900s was allowed to revert naturally to forest.

Vᴇɢᴇᴛᴀᴛɪᴏɴ Cᴇɴsᴜsɪɴɢ. Sixteen 30 × 30–m plots were established in forests of similar structure at MWW, BEN, and EF in spring 2008 and at MAF in summer 2009. Eight plots were randomly located in areas with *L. maackii* (hereafter referred to as "*L. maackii*–present") and eight plots were randomly placed in areas where there was no history of *L. maackii* presence ("*L. maackii*– absent"). In the latter case, we specifically avoided locations of known *L. maackii* removal. *Lonicera*

maackii–present plots contained an average (± SE) of 59 ± 7 *L. maackii* individuals/plot; these shrubs were typically large, with a maximum of 10.2 stems/plant (mean = 3.4) and a maximum stem diameter of 6.4 cm (mean = 2.2 cm). Even though there was no known history of *L. maackii* presence in the *L. maackii*–absent plots, a few individuals were found in these locations (mean ± SE: 2.5 ± 0.4 individuals/plot) with few stems (maximum stem number = 3.5, mean stem number = 2.1) of small diameter (maximum diameter = 1.6 cm, mean diameter = 1.0 cm). Presence of individual *L. maackii* in the *L. maackii*–absent plots indicated that these plots were susceptible to *L. maackii* invasion. Where possible, plot locations at each site were selected to have similar slope, aspect, local meteorological conditions, bedrock geology, and soil characteristics to minimize floristic variation associated with those characteristics. All plots were located in forested areas with intact canopies. Corners of each plot were permanently marked with rebar topped with a numbered tag, and GPS coordinates were taken for each corner.

Shrubs, vines, and herbaceous vegetation were censused at BEN and EF from July through October 2008, and from September to October 2009 at MWW and MAF. Each plot was divided into four 7.5 × 30–m subplots by three transect lines. For shrubs, we identified each plant to species, counted the number of basal stems/plant, and measured the diameter of the largest basal stem of all plants > 1 m tall whose canopy intersected each transect line. From these data, we calculated the maximum and mean number of *L. maackii* stems/plant and the maximum and mean diameter of the largest *L. maackii* stem/plant for each plot. We then randomly placed a 100-point, 1 × 1–m quadrat in three positions along each transect line for a total of 9 quadrats/plot. Within the boundaries of each quadrat, we identified each herbaceous plant, vine, shrub, or tree seedling to species or morphospecies (in the case of a few nonflowering grasses) and counted the number of points intersected by each taxon. Any plant species present in the quadrat but not occurring on a point was also recorded but abundances of these species were not assessed.

ENVIRONMENTAL MEASURES. From each plot within each study site, we also quantified several abiotic and anthropogenic parameters of the environment, as detailed in Cameron *et al.* (2015). These consisted of elevation, slope, and aspect; soil bulk density, pH, percentage of nitrogen (%N), percentage of carbon (%C), total organic carbon and total nitrogen in the top 15 cm of the soil core; and distances to the nearest road and the nearest major road. Because aspect is a circular variable, we geometrically converted it 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).

STATISTICAL ANALYSES. We classified all identified species (listed in Appendix 1) as native or introduced using the US Department of Agriculture PLANTS database (USDA, NRCS 2015). Introduced species were further classified as invasive or not invasive (in which case, they were then categorized as "nonnative") using the list of invasive species for the state of Ohio (OIPC 2016). For each plot (data summed across the nine quadrats for each of the two categories per site), we calculated the following parameters for each category of native, nonnative, and invasive species: (a) species richness (S), the number of species; (b) proportion (PR), based on total number of species (*e.g.*, number of native species/[native species + nonnative species + invasive species]); (c) relative abundance (RA), based on total points of individuals (*e.g.*, points for native individuals/total points of all individuals); and (d) Shannon-Weiner diversity (H), based on point data. Measures of S and PR included plants present in the quadrats but not occurring on a point. Because the focus of our study was on the effect of honeysuckle on other plant species, we removed *L. maackii* seedlings from the data set prior to the above calculations (but if these data were retained, results were similar with significant effects of *L. maackii*).

To determine if there was a significant effect of presence of *L. maackii* on these parameters, we used a two-way analysis of variance (ANOVA) to examine the fixed effects of *L. maackii* (*L. maackii*–present *vs.* *L. maackii*–absent) and site (BEN, EF, MAF, MWW) and their interaction on S, PR, and H. As necessary, significant site effects were further examined with Tukey tests of multiple comparisons. Although most data met the assumptions of normality and homogeneity of variances, some data had to be transformed prior to analysis; H was $\log_{10}$-transformed for the invasive category, and PR was $\log_{10}$-transformed for the nonnative

category. Relative abundance for all categories exhibited heterogeneous variances regardless of transformation and therefore was analyzed with a generalized linear model with a Gaussian distribution to examine fixed effects of *L. maackii* and locality. In addition, individual one-way ANOVAs were used to determine if *L. maackii*–present and *L. maackii*–absent plots differed in terms of each environmental variable.

We then used a multiple regression analysis with backward elimination to identify the set of environmental/anthropogenic variables that best explained the observed variation in invasive species *S*, *RA*, *PR*, and *H*. This approach first constructed a model of each response variable (*RA, S, PR,* and *H*) based on all explanatory variables in the initial model, and then subsequently removed explanatory variables to achieve the best possible adjusted R^2. To avoid multicollinearity, we removed %N and %C in the top 15 cm of soil as well as total nitrogen because these were all highly correlated with total organic carbon ($r > 0.766$); the latter factor was chosen as it is known to be associated with *L. maackii* (Kolbe *et al.*, 2015). *Lonicera maackii* presence or absence in each plot was recoded as a categorical dummy variable (0 = absent, 1 = present). The initial multiple regression model consisted of the following factors: *L. maackii* presence or absence, maximum number of *L. maackii* stems/plant, maximum *L. maackii* stem diameter, soil bulk density, soil pH, total organic carbon, elevation, slope, aspect (measured as northness and eastness), distance to the nearest road, and distance to the nearest major road. All statistical analyses were conducted in R version 3.2.1 (R Core Team 2015) using the *MASS* package (Venables and Ripley 2002).

Results. *Lonicera maackii*–present and *L. maackii*–absent plots did not differ in the overall relative abundance of all plants ($F_{[1,56]} = 0.50$, $P = 0.824$) or the total number of species (*S*; $F_{[1,56]} = 0.356$, $P = 0.553$; Fig. 2), although significant differences in both parameters were detected among sites ($F_{[3,56]} = 3.57$, $P = 0.020$ and $F_{[3,56]} = 2.76$, $P = 0.049$, respectively). This was primarily because BEN exhibited a significantly higher number of species compared to EF (Tukey test; $P = 0.033$), while the number of species was statistically similar among all other sites. (Table 1; Fig. 2). In addition, *L. maackii*–present and *L. maackii*–absent plots did not differ in the relative abundance of native ($P = 0.085$), nonnative ($P = 0.085$), or invasive ($P = 0.132$) individuals (Fig. 2). There also were no differences detected ($P > 0.135$) between *L. maackii*–present and *L. maackii*–absent plots in elevation, slope, northness and eastness, soil bulk density, soil pH, %N and %C in the top 15 cm of the soil core, total organic carbon and total nitrogen, or distances to the nearest road and to the nearest major road.

In contrast, *L. maackii*–present plots contained a significantly higher number of invasive species (*S*; mean = 2.16) compared to *L. maackii*–absent plots (mean = 1.41; two-way ANOVA: $P = 0.0004$; Tables 1, 2) with significant differences detected across sites ($P = 0.021$; Table 2; Fig. 2). However, no such differences were found for native or nonnative species richness ($P > 0.357$; Table 1; Fig. 2). Interestingly, *L. maackii* seedlings also were commonly found in *L. maackii*–absent plots (Table 3), even though larger shrubs were absent. A significantly higher proportion of the total species in *L. maackii*–present plots also were invasive (*PR* mean = 14.2%) compared to *L. maackii*–absent plots (*PR* mean = 9.4%; $P = 0.005$; Tables 1, 2). The corresponding proportion of native species was significantly lower in *L. maackii*–present plots (84.8%) than *L. maackii*–absent plots (88.6%; $P = 0.039$; Tables 1, 2), with no difference in the proportion of nonnative species (Fig. 2). *Lonicera maackii*–present plots exhibited significantly greater diversity of invasive species (mean = 0.157) than *L. maackii*–absent plots (mean = 0.041; $P = 0.003$; Tables 1, 2) consistently across all sites (Fig. 2), although there was no difference in the diversity of native or nonnative species ($P < 0.11$; Table 2). The number of points covered by each invasive species varied within each of the four study sites where *L. maackii* was present or absent (Table 3). The MWW site contained the most invasive species primarily because of the high abundance of *Lonicera japonica* Thunb. and *L. maackii*, while BEN and EF had the lowest abundance of invasive species (Fig. 2). Of interest is that MAF had just as many invasive species in *L. maackii*–absent plots as BEN and EF had in *L. maackii*–present plots.

Models from the multiple regression analyses explained 28–41% of the variation in the four measures (*RA, S, PR,* and *H*; Table 4) for invasive species but with different combinations of five to eight of the biotic, anthropogenic, soil, and geographic explanatory variables. Overall, pres-
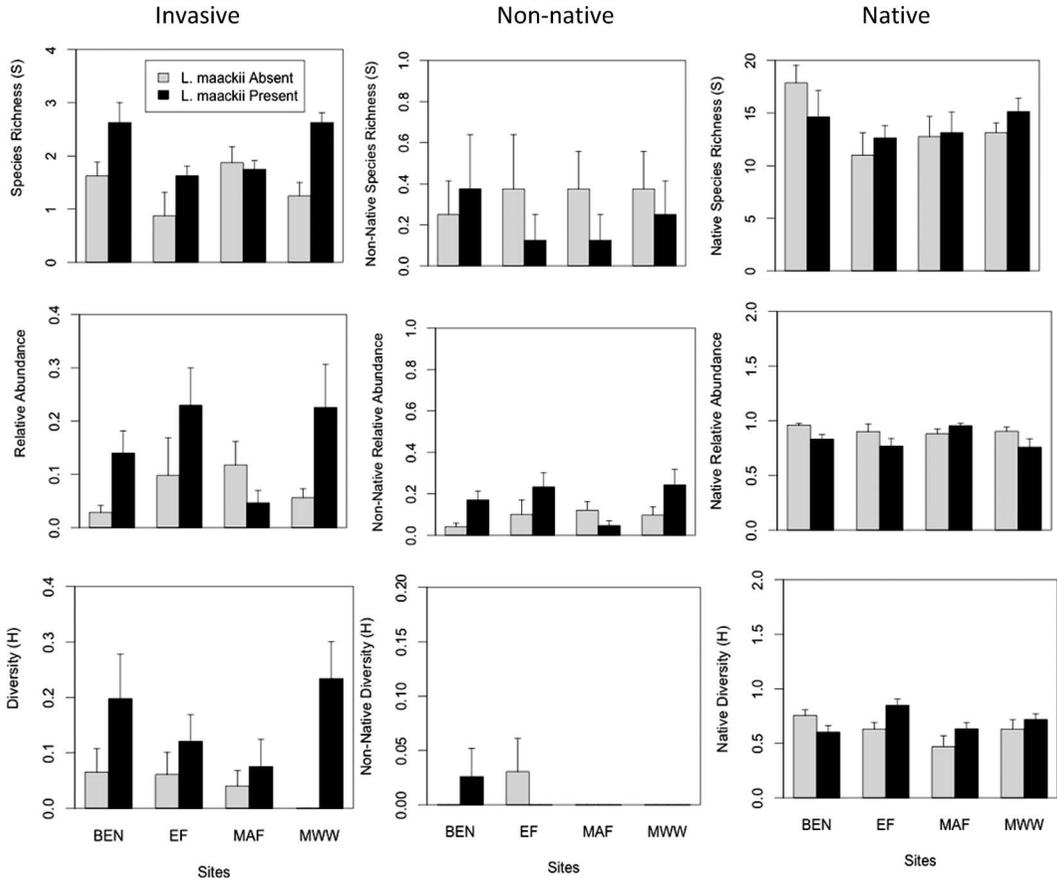
FIG. 2. Mean values for invasive species, nonnative species (introduced taxa but not invasive), and native species (grouped in columns) for species richness (S), relative abundance of points (RA), and diversity (H), as measured in plots where *Lonicera maackii* was absent (light gray bars) or present (black bars) in four different sites in southwestern Ohio: Benedict Preserve (BEN), East Fork Wildlife Area (EF), Mount Airy Forest (MAF), and Miami Whitewater Forest (MWW). The error bars represent the standard error of each mean. Note that the range of the y-axis has been maximized for each panel.

ence of *L. maackii* explained the largest amount of variation for invasive species richness (S) and proportion (PR) of invasive species, and explained the second largest amount of variation for relative abundance (RA) and diversity (H) of invasive species; in the latter two cases, distance to the nearest road explained the largest amount of variation in RA and H. In terms of individual analyses, RA was best explained by a model that incorporated (in descending order of importance) distance to the nearest road, *L. maackii* presence, soil pH, northness, and elevation (all but elevation were significant in improving the model fit; Table 4). These four variables explained a significant amount of total variation ($R^2 = 0.28$). Variation in S was best explained by a model ($R^2 = 0.37$) incorporating *L. maackii* presence, proximity to

the nearest road, distance to the nearest major road, northness, maximum stem diameter of *L. maackii*, slope, maximum number of *L. maackii* stems, and northness (the last three variables did not significantly improve the model; Table 4). Variation in PR was best explained by a model ($R^2 = 0.35$) that incorporated *L. maackii* presence, northness, maximum number of *L. maackii* stems, maximum stem diameter of *L. maackii*, and distance to the nearest major road (Table 4). Similarly, variation in H was best explained by *L. maackii* presence, proximity to the nearest road, eastness, maximum stem diameter, maximum number of *L. maackii* stems, and elevation (Table 4). These six variables explained a substantial proportion of variation ($R^2 = 0.41$).

Table 1. Mean values ± SE across plots ($n = 8$) within each site for each measured variable (*RA*, *S*, *PR*, and *H*). Data presented are based upon number of points measured for each taxon (see Materials and Methods). Sites in southwestern Ohio included Benedict Preserve (BEN), East Fork Wildlife Area (EF), Mount Airy Forest (MAF), and Miami Whitewater Forest (MWW).

Variable	*Lonicera maackii* present					*Lonicera maackii* absent				
	All sites	BEN	EF	MAF	MWW	All sites	BEN	EF	MAF	MWW
Relative abundance (*RA*)										
Total	98.72 ± 18.08	61.50 ± 36.69	60.00 ± 9.70	81.50 ± 26.66	191.88 ± 44.07	104.00 ± 17.45	54.00 ± 12.98	97.88 ± 28.14	134.88 ± 33.84	129.25 ± 51.95
Invasive	0.16 ± 0.03	0.14 ± 0.04	0.23 ± 0.07	0.05 ± 0.02	0.22 ± 0.08	0.08 ± 0.02	0.03 ± 0.01	0.10 ± 0.07	0.12 ± 0.04	0.06 ± 0.02
Native	0.83 ± 0.03	0.83 ± 0.04	0.77 ± 0.07	0.95 ± 0.02	0.76 ± 0.08	0.91 ± 0.02	0.96 ± 0.02	0.90 ± 0.07	0.88 ± 0.04	0.90 ± 0.04
Nonnative	0.17 ± 0.03	0.17 ± 0.04	0.23 ± 0.07	0.05 ± 0.02	0.24 ± 0.08	0.09 ± 0.02	0.04 ± 0.02	0.10 ± 0.07	0.12 ± 0.04	0.10 ± 0.04
Species richness (*S*)										
Total	16.25 ± 0.99	17.62 ± 2.88	14.38 ± 1.18	15.00 ± 1.99	18.00 ± 1.50	15.44 ± 1.01	19.75 ± 1.81	12.25 ± 2.29	15.00 ± 2.11	14.75 ± 0.86
Invasive	2.16 ± 0.14	2.62 ± 0.38	1.62 ± 0.18	1.75 ± 0.16	2.62 ± 0.18	1.41 ± 0.17	1.62 ± 0.26	0.88 ± 0.44	1.88 ± 0.30	1.25 ± 0.25
Native	13.88 ± 0.88	14.62 ± 2.52	12.62 ± 1.15	13.12 ± 1.97	15.12 ± 1.29	13.69 ± 0.94	17.88 ± 1.67	11.00 ± 2.11	12.75 ± 1.92	13.12 ± 0.93
Nonnative	0.22 ± 0.09	0.38 ± 0.26	0.12 ± 0.12	0.12 ± 0.12	0.25 ± 0.16	0.34 ± 0.10	0.25 ± 0.16	0.38 ± 0.26	0.38 ± 0.18	0.38 ± 0.18
Proportion (*PR*)										
Invasive	14.22 ± 1.07	16.72 ± 2.81	11.88 ± 1.68	13.40 ± 2.60	14.88 ± 1.06	9.39 ± 1.26	8.15 ± 0.92	7.15 ± 3.80	13.52 ± 2.44	8.72 ± 1.86
Native	84.79 ± 1.00	81.91 ± 2.34	87.43 ± 1.77	85.81 ± 2.38	84.01 ± 1.00	88.58 ± 1.50	90.49 ± 1.23	90.72 ± 4.41	84.30 ± 2.83	88.82 ± 2.65
Nonnative	0.99 ± 0.37	1.37 ± 0.90	0.69 ± 0.69	0.78 ± 0.78	1.10 ± 0.73	2.03 ± 0.57	1.36 ± 0.89	2.13 ± 1.39	2.18 ± 1.19	2.46 ± 1.20
Shannon-Weiner diversity (*H*)										
Total	0.759 ± 0.030	0.725 ± 0.056	0.873 ± 0.052	0.670 ± 0.060	0.768 ± 0.053	0.679 ± 0.039	0.794 ± 0.061	0.682 ± 0.055	0.552 ± 0.089	0.688 ± 0.087
Invasive	0.157 ± 0.032	0.198 ± 0.080	0.120 ± 0.048	0.075 ± 0.049	0.234 ± 0.067	0.042 ± 0.016	0.065 ± 0.043	0.061 ± 0.040	0.040 ± 0.028	0 ± 0
Native	0.700 ± 0.032	0.602 ± 0.060	0.848 ± 0.058	0.633 ± 0.058	0.718 ± 0.051	0.621 ± 0.041	0.756 ± 0.052	0.631 ± 0.060	0.468 ± 0.101	0.631 ± 0.086
Nonnative	0.006 ± 0.006	0.026 ± 0.026	0 ± 0	0 ± 0	0 ± 0	0.008 ± 0.008	0 ± 0	0.030 ± 0.030	0 ± 0	0 ± 0

Table 2. The effect of *Lonicera maackii* (HS) and study site (site) on native, nonnative, and invasive categories of species in terms of relative abundance (*RA*; based on number of points for each taxon, see Materials and Methods) using a generalized linear model (GLM), and on species richness (*S*), proportion (*PR*; based on number of points for each taxon), and Shannon-Weiner diversity (*H*) using a two-way ANOVA. In the case of the GLM for *RA*, there were no significant differences across individual sites or pairs of interactions (indicated by "ns"). For the two-way ANOVA for *S*, *PR*, *H*, and *E*, the d.f. for HS, site, and HS × site are 1, 3, and 56 respectively. Significant effects appear in bold.

| | | Native | | Introduced | | | | Total | |
| | | | | Nonnative | | Invasive | | | |
Measure	Effects	F or t	P	F or t	P	F or t	P	F or t	P
RA	HS	1.753	0.085	1.753	0.085	1.530	0.132	0.050	0.824
	Site	—	ns	—	ns	—	ns	**3.570**	**0.020**
	HS × site	—	ns	—	ns	—	ns	1.221	0.310
S	HS	0.022	0.881	0.862	0.357	**13.903**	**0.0004**	0.356	0.553
	Site	2.300	0.087	0.072	0.975	**3.508**	**0.021**	**2.786**	**0.049**
	HS × sSite	0.916	0.439	0.431	0.732	2.510	0.068	0.762	0.520
PR	HS	**4.459**	**0.039**	1.351	0.250	**8.652**	**0.005**	—	—
	Site	0.898	0.448	0.174	0.913	1.037	0.383	—	—
	HS × site	1.356	0.266	0.196	0.898	1.243	0.303	—	—
H	HS	2.688	0.107	0.013	0.909	**9.340**	**0.003**	2.937	0.092
	Site	2.722	0.053	0.671	0.573	0.467	0.707	2.567	0.063
	HS × site	**2.904**	**0.043**	1.329	0.274	1.941	0.133	1.374	0.260

Discussion. In southwestern Ohio where *L. maackii* first began to spread over 50 yr ago (Braun 1961), we found that plots with *L. maackii* exhibited a significantly lower proportion of native plant species, compared to where *L. maackii* was absent. This finding is consistent with the ability of *L. maackii* to reduce the growth, survival, and fecundity of annual and perennial herbs (Gould and Gorchov 2000, Miller and Gorchov 2004), to be associated with lower abundance of herbs and tree seedlings (Collier *et al.* 2002, Hartman and McCarthy 2008, Christopher *et al.* 2014), and to decrease recruitment of native *Acer saccharum* tree seedlings (Loomis *et al.* 2015, Cameron *et al.* in press). We also found that presence of this invasive shrub was significantly associated with an increased number and proportion of invasive plant species, as well as increased diversity of these species. In contrast, the relative abundance of invasive taxa did not differ in plots with and without *L. maackii*, possibly reflecting variation across plots and sites (Tables 1, 3). Furthermore, plots with and without *L. maackii* did not differ in any measured environmental parameters, further

Table 3. The number of points covered by each invasive species within each of the four study sites in southwestern Ohio where *Lonicera maackii* was present or absent. Values are cumulative for eight plots (as measured by 72 1 × 1–m quadrats for each plot) at each study site for *L. maackii*–present and *L. maackii*–absent categories, respectively. Study sites consisted of Benedict Nature Preserve (BEN), East Fork Wildlife Area (EF), Mount Airy Forest (MAF), and Miami Whitewater Forest (MWW). Values for *L. maackii*, consisting of seedlings, are presented in the table but were excluded from the data set used for the statistical analysis.

| | *L. maackii* present | | | | *L. maackii* absent | | | |
Invasive species	BEN	EF	MAF	MWW	BEN	EF	MAF	MWW
Alliaria petiolata (garlic mustard)	9	8	14	12	9	0	62	44
Celastrus orbiculatus (Asian bittersweet)	0	0	6	0	0	0	13	0
Euonymus fortunei (wintercreeper)	1	0	2	0	0	0	0	0
Ligustrum sp. (privet)	0	0	0	2	2	0	0	0
Lonicera japonica (Japanese honeysuckle)	12	86	0	305	0	25	1	0
Lonicera maackii (Amur honeysuckle)	108	27	202	334	31	5	49	3
Pyrus calleryana (Callery pear)	4	1	0	0	0	0	0	0
Rosa multiflora (multiflora rose)	3	23	0	23	0	4	0	0
Vinca minor (small periwinkle)	0	0	0	0	0	1	0	0
Total	137	145	224	676	42	35	125	47

Table 4. Results of separate multiple regression models with backwards elimination used to identify the set of variables that best explain the observed per plot variation in relative abundance (*RA*; based on total number of points for each taxon, see Materials and Methods), species richness (*S*), proportion (*PR*; based on total number of species), and Shannon-Weiner diversity (*H*) of invasive plant species. Shown for each parameter is the multiple R^2 of the model and the associated *P* value as well as each regression coefficient and its significance (*$P < 0.1$, **$P < 0.05$, ***$P < 0.001$) for the individual explanatory variables. The sign of the each regression coefficient indicates the relationship with the invasive species measure (*RA*, *S*, *PR*, and *H*). Biotic variables consist of *L. maackii* presence or absence (honeysuckle, HS), maximum number of *L. maackii* stems, maximum stem diameter of *L. maackii*; anthropogenic variables are the distance to the nearest road and the distance to the nearest major road; soil variables consist of soil bulk density, pH, and total organic carbon (TOC); geographic and topographic variables are elevation, slope, eastness and northness (*i.e.*, aspect).

Invasive species measure	Model R^2, P	Biotic variables			Anthropogenic variables		Soil variables			Geographic/topographic variables			
		L. maackii	Max no. of HS stems	Max HS stem diam.	Distance nearest road	Distance major road	Bul density	pH	TOC	Elevation	Slope	East	North
RA	0.280, 0.001	0.109**	—	—	−0.167*	—	—	—	—	−0.003	—	—	0.055*
S	0.365, 0.0004	1.342***	−0.025	−0.063*	1.093*	−0.339***	—	—	—	—	−0.029	—	0.339***
PR	0.353, < 0.0001	11.715***	−0.549**	−0.525**	—	−1.607**	—	—	—	—	—	—	2.230*
H	0.408, < 0.0001	0.128**	0.007*	−0.013*	0.192**	—	—	−0.099***	—	0.004**	—	0.066**	—

suggesting that the observed increases in invasive species number, proportion, and diversity were primarily related to the presence of *L. maackii*. This overall effect was exclusive to invasive nonnative plants because there were no similar associations of *L. maackii* with nonnative species that were not invasive. Two of the invasive species (*Pyrus calleryana* Decne. and *Euonymus fortunei* [Turcz.] Hand.-Maz.) were observed only in plots with *L. maackii* (albeit at very low counts; Table 3), and the other six invasive species (*Alliaria petiolata* [M.Bieb.] Cavara & Grande, *Celastrus orbiculatus* Thunb., *Ligustrum* sp., *L. japonica*, *Rosa multiflora* Thunb., and *Vinca minor* L.) were observed in plots with and without *L. maackii* (Table 3). The influence of *L. maackii* on the invasive plant community also was reinforced by the multiple regression analysis in which *L. maackii* presence was consistently identified as the first or second major explanatory variable for variation in *S*, *PR*, *RA*, and *H* (Table 4).

These results confirm an association between *L. maackii* and other invasive plant species in the study sites that we examined, and represent a first step in determining whether *L. maackii* is an invasion facilitator. Future investigations are necessary to determine whether *L. maackii* coincidentally occurs with these other invasive species or facilitates the subsequent appearance of other invaders that may be detrimental to the ecosystem (*i.e.*, invasion meltdown; Simberloff 2006). In our forest tracts, we found that both *L. maackii*–present and *L. maackii*–absent plots were susceptible to invasion by seedlings of *L. maackii* (Table 2); there were substantially more *L. maackii* seedlings in plots with large *L. maackii* shrubs. In addition, we found that environmental/anthropogenic characteristics were similar between *L. maackii*–present and *L. maackii*–absent plots. These findings indicate that there is no intrinsic reason why invasive plants were less common in *L. maackii*–absent plots and strengthens the argument that facilitation by *L. maackii* accounted for the increased presence of invasive plants in *L. maackii*–present plots. This conclusion could be strengthened by additional studies. For example, it is well known that forest stands in Ohio are susceptible to invasion by *L. maackii*, and absence of *L. maackii* in some areas of these forests likely reflects a lack of propagule pressure (Bartuszevige *et al*. 2006, Gorchov *et al*. 2014). Verification of facilitation of invasive plants by *L. maackii* could be obtained by long-term

monitoring of sites not currently invaded by *L. maackii*, but with *L. maackii* in relatively close proximity to ensure adequate propagule pressure. Similar verification could be obtained by examining sites with a known temporal history of invasion, or through careful factorial experiments involving *L. maackii* and other native and introduced plant species (*e.g.*, Flory and Bauer 2014, Stricker *et al*. 2015).

The possibility of positive interactions (*i.e.*, facilitation) between *L. maackii* and other invasive species is consistent with what is already known about this woody shrub. As reviewed by Kuebbing and Nuñez (2015), positive interactions among nonnative species are most prevalent in woody species (such as *L. maackii*) and in taxa able to increase the nitrogen content of the surrounding soil (such as *L. maackii*, which increases soil nitrogen and carbon concentration in areas of heavy infestation; Kolbe *et al*. 2015). In addition, Kuebbing *et al*. (2013a) examined the ability of *L. maackii* to interact with another nonnative invader, *Ligustrum sinense*, and found that plots with both invaders contained twice as many subdominant invasive plant species as plots with only a single nonnative species. In their study, invasive species richness was similar in plots with and without *L. maackii*, which differed from our results (Table 1; Fig. 2A), although it is unclear whether Kuebbing *et al*. (2013a) distinguished between nonnative species that were invasive and those that were not invasive, as we did. Mean species richness in plots containing *L. maackii* was slightly lower in the Kuebbing *et al*. (2013a) study ($S = 2.00$) than in our investigation ($S = 2.16$; Table 1), which may reflect different sampling strategies or location/ invasion age (Tennessee *vs*. Ohio) of the two studies. However, several of the invasive species associated with *L. maackii* in Kuebbing *et al*. (2013a) were the same as those in our investigation (Table 3), including *Celastrus orbiculatus*, *Lonicera japonica*, and *Vinca minor*.

Although the exact reason for the association of *L. maackii* with other nonnative invaders remains unknown, it most likely involves a combination of different mechanisms. In the first place, these results are consistent with what is already known about the biology of *L. maackii* and its effect on other organisms. For example, the branching structure of large *L. maackii* shrubs creates physical barriers, shielding understory plants from browsing by large herbivores, such as white-tailed deer (*Odocoileus virginianus*; Gorchov and Trisel 2003, Cipollini *et al*. 2009), one of the major herbivores in southwestern Ohio, but also a seed disperser of *L. maackii* (Castellano and Gorchov 2013). In addition, the allelopathic nature of *L. maackii* (McEwan *et al*. 2010, Bauer *et al*. 2012, Cipollini *et al*. 2012) also means that only those herbs and tree seedlings able to persist in this environment will survive under the shrub. It remains to be seen whether nonnative species are more likely to persist in this allelopathic soil, compared to native plant species. Similarly, the ability of *L. maackii* to increase soil nitrogen and carbon (Kolbe *et al*. 2015) and thereby alter nutrient availability on the forest floor (McEwan *et al*. 2012) may indirectly facilitate other invaders that can persist in this modified soil environment and outcompete native species that are not adapted to the new soil conditions. For example, the nonnative shrubs *Rhamnus davurica* Pall. and *Ligustrum sinense* grow better in soils conditioned by *L. maackii* (Kuebbing *et al*. 2015). Finally, the fact that *L. maackii* can dramatically change the light regime of local natural areas because of its extended leaf phenology (Miller and Gorchov 2004) and dense midstory canopy may create unfavorable abiotic conditions under which some native species may not be able to persist. For example, spring ephemerals whose reproduction is impacted by light levels may not do well under a dense midstory canopy; this includes herbs that depend on high light levels to attract pollinators in early spring for seed production or *Viola* species that rely on light to switch between chasmogamous and cleistogamous floral production (Culley 2002). Soil conditioning and less light at the forest floor in areas invaded by *L. maackii* may have an adverse effect on two of the invasive species. Asian bittersweet (*Celastrus orbiculatus*) and garlic mustard (*Alliaria petiolate*) were more abundant in *L. maackii*–absent plots (Table 3), perhaps suggesting that alteration in the microclimate by *L. maackii* yielded unsuitable conditions for these two invasive species.

In addition to these biological traits of *L. maackii*, it also is possible that an association between *L. maackii* and other invasive plant species may reflect similar propagule pressure in response to landscape attributes (*e.g.*, percentage of urban land cover in the surrounding area, amount of forest edge), local site conditions, or community features (*e.g.*, degree of disturbance

[tree falls, hiking trails, etc.], forest age). Landscape structure typically is of primary importance in explaining patterns of spread of *L. maackii* (Borgmann and Rodewald 2005, Bartuszevige *et al*. 2006, Gorchov *et al*. 2014). For example, cover of *L. maackii* in forested areas in southwestern Ohio is lowest in areas with more cropland—presumably because of a paucity of nearby seed sources and minimal movement of animal seed vectors (Gorchov *et al*. 2014). In contrast, urban areas may experience higher propagule pressure from nonnative species given the large number of ornamental plants in this landscape. If a natural location near urban areas experiences a disturbance, dispersal of propagules from nonnative plants in urban areas into forest communities may increase. This also may result in the concurrent dispersal of multiple nonnative species (including *L. maackii*) into a given site (*i.e.*, the "passenger model" of MacDougall and Turkington 2005). However, in our study we minimized site disturbances by restricting plot areas to relatively undisturbed areas within the interior forest (*i.e.*, no tree gaps, forest edges, or roadsides), where the only obvious difference was the presence or absence of *L. maackii*.

Environmental factors also may explain the relationship between *L. maackii* and other invasive plant species. For example, proximity to roads within the landscape may promote invasions by nonnative species and also may aid dispersal of *L. maackii* (Flory and Clay 2006). In the current study, distance to the nearest road or nearest major road were major explanatory factors in each of the four multiple regression models (Table 4), and these indictors of urbanization were sometimes identified as even more important than *L. maackii* presence (for *RA* and *H*; Table 4). Distance to nearest major roadways was negatively related to both richness and proportional representation of invasive species (*i.e.*, higher *S* and *PR* near major roads); in addition, *RA* was negatively related to distance to nearest roadways (*i.e.*, more invasive species closer to nearest roadways). Both of these associations likely reflect the role of these roadways in southwestern Ohio as major dispersal corridors for *L. maackii* and other invasive plants (Flory and Clay 2006). In contrast, species richness and diversity of invasive species were greater at distances away from nearby roadways. This could reflect differences in dispersal distances among invasive species, with those species with

longer dispersal distances occurring more often at distances away from roadways. This result also could reflect differences in landscape features whereby habitats at some distance from nearby roadways were more conducive to germination of propagules from some invasive plants, perhaps because these habitats contained mature *L. maackii* and germination was facilitated by presence of this shrub. At this point, however, it is not possible to discern whether invasive species were more abundant closer to a road because they arrived concurrently with *L. maackii* of if they were only able to invade after *L. maackii* had become established. In either of these cases, their successful dispersal may have been facilitated by *L. maackii*.

Overall, these relationships are not surprising because *L. maackii* invasions often are associated with urban areas (Huebner 2003, Bartuszevige *et al*. 2006), abundance of *L. maackii* decreases with distance from roadways (Flory and Clay 2006), and nearby roadways may serve as pathways of introduction for invasive species. In fact, *L. maackii* often dominates the understory of all but the least urbanized sites in regions where it occurs (Pennington *et al*. 2010); percentage of cover of *L. maackii* is positively associated with the proportion of urban land cover (Borgmann and Rodewald 2005; but see Gorchov *et al*. 2014) and presence of this invader is associated with distance from the nearest town (Bartuszevige *et al*. 2006). In general, richness of invasive plant species is related to the area of wildland-urban interfaces (Gavier-Pizarro *et al*. 2010), and urban and suburban areas often are foci for the spread of exotic plant species (Duguay *et al*. 2007). These effects are related primarily to fragmentation of native habitats with the concomitant creation of edge effects (Harper *et al*. 2005, Walter *et al*. 2009), and are most dramatic in the midwestern USA where $< 15\%$ of native forests occur in blocks (3.4 km^2) without housing (Radeloff *et al*. 2005). In addition, several invasive plants in and around urban areas, such as *L. maackii* and *Pyrus calleryana* (Culley and Hardiman 2007), also have a history of past or current ornamental use within the urban landscape. These species can spread into large parks within the urban matrix and then into other surrounding natural sites, with consequent effects on resident plant communities. For example, both plant species diversity and native plant density increase and abundance of nonnative species decreases

along urban-rural gradients (Porter *et al*. 2001, Moffatt *et al*. 2004).

Although many invasions by *L. maackii* in the midwestern USA are triggered by major environmental disturbances, this species also is able to encroach into intact, natural areas over time, eventually becoming in itself a biotic disturbance that can dramatically impact the remainder of the natural community. *Lonicera maackii* is known to negatively impact the flora in areas of invasion (*e.g.*, Hutchinson and Vankat 1997, Gould and Gorchov 2000, Collier *et al*. 2002, Gorchov and Trisel 2003, Miller and Gorchov 2004, Hartman and McCarthy 2008, Christopher *et al*. 2014, Cameron *et al*. 2015) as well as alter ecosystem processes such as litter decomposition (Trammell *et al*. 2012; Kuebbing *et al*. 2014) and soil nutrient availability (Arthur *et al*. 2012, McEwan *et al*. 2012, Kolbe *et al*. 2015). Our study is the first to demonstrate that invasion of *L. maackii* into natural areas also is associated with an increased occurrence of other invasive plant species, indicating the need for continued investigation into the potential role of *L. maackii* as an invasion facilitator in eastern deciduous forests in the USA.

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Appendix

List of plant species recorded across plots in the presence or absence of invasive *Lonicera maackii* (Amur honeysuckle) within four sites in southwestern Ohio. Species are classified as invasive, nonnative (not invasive), or native.

Scientific name	Common name	Habit
Invasive		
Alliaria petiolata	Garlic mustard	Herb
Lonicera japonica	Japanese honeysuckle	Herb
Celastrus orbiculatus	Asian bittersweet	Vine
Euonymus fortunei	Wintercreeper	Vine
Ligustrum sp.	Privet	Shrub
Pyrus calleryana	Callery pear	Tree
Rosa multiflora	Multiflora rose	Shrub
Vinca minor	Small periwinkle	Herb
Nonnative		
Cyperus esculentus L.	Yellow nutsedge	Herb
Euonymus alatus (Thunb.) Siebold	Burning bush	Shrub
Glechoma hederacea L.	Ground ivy	Herb
Melissa officinalis L.	Lemon balm	Herb
Polygonum L. sp.	Lady's thumb	Herb
Aphanes arvensis L.	Field parsley	Herb
Pastinaca L. sp.	Field parsnip	Herb
Native		
Acalypha rhomboidea Raf.	Three-seeded mercury	Herb
Acer negundo L.	Box elder	Tree
Acer saccharum	Sugar maple	Tree
Achillea L. sp.	Yarrow	Herb
Alisma L. sp.	Water plantain	Herb
Allium burdickii (Hanes) A.G. Jones	Narrowleaf wild leek	Herb
Allium L. sp.	Wild onion	Herb
Amphicarpaea bracteata (L.) Fernald	American hogpeanut	Herb
Asarum canadense L.	Canadian ginger	Herb
Asimina triloba (L.) Dunal	Common paw paw	Tree
Asplenium platyneuron (L.) Britton, Sterns & Poggenb.	Ebony spleenwort	Herb
Aster L. sp.	Aster	Herb
Botrchyium dissectum var. *dissectum* Spreng.	Dissected grapefern	Herb
Botrychium Sw. sp.	Grapefern	Herb
Carex L. sp.	Sedge	Herb
Carpinus caroliniana Walter	Hornbeam, ironwood	Tree
Carya cordiformis (Wangenh.) K. Koch	Bitternut hickory	Tree
Carya Nutt. sp.	Hickory	Tree
Celtis tenuifolia Nutt.	Hackberry	Tree
Cercis canadensis L.	Eastern redbud	Tree
Circaea lutetiana L.	Enchanter's nightshade	Herb
Clitoria mariana L.	Atlantic pigeonwings	Herb
Commelina L. sp.	Dayflower	Herb
Conyza Less. sp.	Horseweed	Herb
Cryptotaenia canadensis (L.) DC.	Canadian honewort	Herb
Elymus hystrix L.	Eastern bottlebrush grass	Herb
Eupatorium rugosum (Houtt.)	White snakeroot	Herb
Eupatorium serotinum Michx.	Late-flowering thoroughwort	Herb
Fagus grandifolia	American beech	Tree
Fragaria L. sp.	Strawberry	Herb
Fraxinus quadrangulata Michx.	Blue ash	Tree
Fraxinus L. sp.	Ash	Tree
Galium asprellum Michx.	5-Leaf galium, bedstraw	Herb
Galium circaezans Michx.	4-Leaf galium, bedstraw	Herb
Galium concinnum Torr. & A. Gray	Small galium, tiny bedstraw	Herb
Galium triflorum Michx.	6-Leaf galium, bedstraw	Herb
Geum L. spp.	Avens	Herb
Gillenia stipulata (Muhl. ex Willd.) Baill.	American ipecac	Herb
Hackelia Opiz sp.	Stickseed	Herb

Appendix

Continued.

Scientific name	Common name	Habit
Hydrastis canadensis L.	Goldenseal	Herb
Hydrocotyle L. sp.	Marsh pennywort	Herb
Leersia oryzoides (L.) Sw.	Rice cut grass	Herb
Lindera benzoin	Spicebush	Shrub
Linum L. sp.	Flax	Herb
Luzula DC. sp.	Woodrush	Herb
Maianthemum racemosum (L.) Link	False solomon's seal	Herb
Nyssa silvatica Marshall	Black gum	Tree
Osmorhiza Raf. *sp.*	Sweet cicely	Herb
Oxalis stricta L.	Common yellow oxalis	Herb
Parthenocisus quinequefolia (L.) Planch.	Virginia creeper	Vine
Phytolacca americana L.	Pokeberry	Herb
Pilea pumila (L.) A. Gray	Clearweed	Herb
Polygonatum biflorum (Walter) Elliott	Solomon's seal	Herb
Polygonum L. sp.	Polygonum	Herb
Polygonum virginianum L.	Virginia knotweed	Herb
Polystichum acrostichoides (Michx.) Schott	Christmas fern	Herb
Prunus serotina Ehrh.	Black cherry	Tree
Pyrola americana Sweet	American wintergreen	Herb
Quercus muehlenbergii Engelm.	Chinquapin oak	Tree
Quercus rubra L.	Red oak	Tree
Rubus L. sp.	Blackberry	Herb
Sanicula canadensis L.	Canadian black snakeroot	Herb
Sassafras albidum (Nutt.) Nees	Sassafras	Tree
Smilax glauca Walter	Cat greenbriar	Vine
Solidago juncea Aiton	Early goldenrod	Herb
Taraxacum officinale F.H. Wigg.	Common dandelion	Herb
Toxidendron radicans (L.) Kuntze	Poison ivy	Vine
Tradescantia L. sp.	Spiderwort	Herb
Ulmus americana L.	American elm	Tree
Viburnum acerifolium L.	Maple leaf viburnum	Tree
Viburnum L. sp.	Viburnum	Tree
Viola L. sp.	Violet	Herb
Vitis L. sp.	Grape	Herb
Unknown	Daisy	Herb
Unknown	Grass	Herb
Unknown	Orchid	Herb