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Source: The Journal of the Torrey Botanical Society, 142(3):193-204.

Published By: Torrey Botanical Society

DOI: <http://dx.doi.org/10.3159/TORREY-D-14-00055>

URL: <http://www.bioone.org/doi/full/10.3159/TORREY-D-14-00055>

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Recovery of native plant communities in southwest Ohio after *Lonicera maackii* removal¹

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BOYCE, R. L. (Department of Biological Sciences, Northern Kentucky University, Nunn Drive, Highland Heights, KY 41099). Recovery of native plant communities in southwest Ohio after *Lonicera maackii* removal. *J. Torrey Bot. Soc.* 142: 193–204. 2015.—*Lonicera maackii* (Rupr.) Herder (Amur honeysuckle) is one of the most important invasive plants in the Ohio Valley. Because of its phenology and dense canopy, *L. maackii* can exclude native herbs and interfere with regeneration of woody plants. In 2005, in a county park in southwest Ohio, I established modified Whittaker plots in four stands with a gradient of *L. maackii* cover ranging from 24 yr old to 40 yr old. The *L. maackii* canopies were removed by herbicides in fall 2005. Plant cover was monitored from 2005 to 2013. After 8 yr, there was an increase in species richness and herbaceous cover at all sites. Herbaceous species turnover was generally greater at sites with greater initial *L. maackii* cover. All of the most-common herbaceous species increased or maintained their coverage; most of the species that increased were those that bloom in late spring or summer. The abundances of other invasive species also increased, including *Alliaria petiolata* (M. Bieb.) Cavara & Grande (garlic mustard). However, *A. petiolata* abundance peaked 2–6 yr after *L. maackii* removal, suggesting that this increase, frequently seen after *L. maackii* removal, may be transitory. Previous studies have not shown such a decline after an initial increase in *A. petiolata*, but few studies have extended over this length of time. Ash (*Fraxinus* L.) decline caused by the emerald ash borer may now be affecting the recovery of these stands.

Key words: *Alliaria petiolata*, Amur honeysuckle, garlic mustard, invasive species, restoration ecology.

The spread of invasive plant species is recognized as a major problem for native plant communities, both the in the USA and abroad. Woody invasive plants can have particularly large impacts because they can affect multiple strata of forest communities (Webster *et al.* 2006). Miller (2005) has identified a number of effects that shrubs, in particular, can have on forests. The dense stands they form can reduce biodiversity and hinder forest tree regeneration. Invasive shrubs can destroy habitat for other organisms and disrupt important ecological processes, such as fire frequency and intensity, nitrogen cycling, and altered soil pH. Many invasive

shrubs take advantage of disturbance to become established initially. Many are also prolific seed and fruit producers, and their seed is spread by animals, wind, and water. Seeds often remain viable in the seed bank for many years. Invasive shrubs often reproduce vegetatively, and they can come to dominate a stand *via* the production of root sprouts, stem sprouts, and other forms of vegetative reproduction.

Control efforts, such as clipping, mowing, grazing, herbicides, and biological control, can be effective in at least temporary control of many of these woody species (references cited within Boyce 2009, van Wilgen and Richardson 2014). Nonetheless, invasive plants can change ecosystem function in a variety of ways (Ehrenfeld *et al.* 2001, Ehrenfeld 2003, Webster *et al.* 2006, Rodgers *et al.* 2008), and so, removal of the invasive species may not necessarily result in complete restoration of the preinvasion plant community.

One of the most widespread invasive plants in the Ohio River Valley is *Lonicera maackii* (Rupr.) Herder (Amur honeysuckle). It was introduced from eastern Asia to the USA as an ornamental shrub in the late 19th century (Luken and Thieret 1996). It is now naturalized in at least 33 states and in Ontario, Canada (SEEDN 2014, USDA NRCS 2014). It reduces species richness and the survival and the

¹ This study was funded by the Hamilton County (Ohio) Parks District. Steve Castellano, Mark Miller, Suzanne Truesdell, Lincoln Fugal, Tyler Broering, Alaina Holbrook, and the students of the fall 2007 Northern Kentucky University plant ecology class assisted with field measurements. Richard Durtsche helped age honeysuckle stumps. The manuscript benefitted from reviews by Richard Durtsche, Maggie Whitson, and two anonymous reviewers.

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doi: 10.3159/TORREY-D-14-00055

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Received for publication July 9, 2014, and in revised form December 31, 2014; first published June 17 2015.

growth of both herbaceous and woody species, including even mature trees (Hutchinson and Vankat 1997; Luken *et al.* 1997; Medley 1997; Gould and Gorchoy 2001; Collier *et al.* 2002; Gorchoy and Trisel 2003; Hartman and McCarthy 2004, 2007; Miller and Gorchoy 2004; Runkle *et al.* 2007; McKinney and Goodell 2010; Fridley 2012). These effects have been attributed to its extended, deciduous leaf habit and its dense canopy, as well as to its competition for soil resources (Luken and Thieret 1996, Collier *et al.* 2002, Gorchoy and Trisel 2003). *Lonicera maackii* also has allelopathic effects on herbaceous species (Dorning and Cipollini 2006; Cipollini *et al.* 2008a, b), and Arthur *et al.* (2012) have shown that it affects leaf decomposition rates and soil microbial communities under its canopy.

Lonicera maackii is typically controlled by mechanical or chemical means, or sometimes by a combination (Nyboer 1992, Batcher and Stiles 2000, SE-EPPC 2003, Hartman and McCarthy 2004, McDonnell *et al.* 2005, Moorhead 2005, Williams 2006, Swab *et al.* 2008, Loeb *et al.* 2010, Swearingen *et al.* 2010, Schulz *et al.* 2012). Its extended leaf phenology can be used against it by applying foliar spray in the fall, after other plants have dropped their leaves, thus ensuring that only *L. maackii* is treated (T. Borgman, Hamilton County Parks District, personal communications). Most studies that look at response to the removal of *L. maackii* have been short-term studies, usually 1–3 yr after removal (Luken *et al.* 1997, McDonnell *et al.* 2005, Swab *et al.* 2008). One of the few longer-term studies was carried out by Runkle *et al.* (2007), which showed that recovery of the understory can take at least a year to begin after *L. maackii* removal; however, that study only looked at two time points. A study by Luken *et al.* (1997) also found that *Alliaria petiolata* (M. Bieb.) Cavara & Grande (garlic mustard), another troublesome invasive species, increased its frequency after *L. maackii* removal. Because native species may have difficulty recolonizing a stand from which they have been excluded, removal of older *L. maackii* stands may result in increases in *A. petiolata* with little or no recolonization by native species.

Thus, the objective of this study was to document the changes in plant communities over the medium term—8 yr—after *L. maackii* stands of various coverages were removed. I was particularly interested in the recovery of

native herbs, as well as the colonization by *L. maackii*, *A. petiolata*, and other invasive species.

Materials and Methods. **STUDY SITE.** This project was carried out at Woodland Mound Park (39° 2.3'N, 84° 19.6'W), one of the holdings of the Hamilton County (Ohio) Park District in southwest Ohio. The park is in the southeast corner of the county, overlooking the Ohio River. Elevations in the park range from roughly 150 m to 240 m, and the park covers approximately 400 ha. Much of the park consists of second-growth forest, with a significant cover of *L. maackii* (R.L.B., personal observation).

FIELD METHODS. Four sites were selected in spring 2005 to represent a gradient of *L. maackii* stand cover (Light, Moderate, Heavy, and Very Heavy). *Lonicera maackii* stand ages were not initially known; actual stand age was later estimated by dating the largest stump found in each stand. A modified Whittaker plot (Stohlgren *et al.* 1995) was placed at each site. The modified Whittaker design consisted of a large, 20 m × 50 m (1,000 m²) plot, with the long side aligned with the north to south axis. Subplots were nested within the large plot: 15 m × 20 m (100 m²), 22 m × 5 m (10 m²), and 10 0.5 m × 2 m (1 m²; Fig. 1). All plots were located on south-facing slopes, although one (Moderate) reached the top of the slope and spilled over to the north-facing side. Corners of each 1,000 m² plot were marked with rebar. The *L. maackii* canopy was removed in late fall 2005. Foliar herbicide (glyphosate) was sprayed at all sites, except the moderate site, where *L. maackii* shrubs were cut and glyphosate was painted on the stumps (T. Borgman, Hamilton County Parks District, personal communication). The lower halves of the Heavy and Very Heavy sites missed complete treatments. Although the 1-m² and 10-m² subplots were subsequently hand-cleared at the Heavy site, *L. maackii* cover was left over one 10-m² and four 1-m² subplots at the Very Heavy site.

Each site was visited weekly from late March into May, every 2 wk through mid-summer, and then monthly into the fall in 2005, 2006, 2007, 2009, 2011, and 2013. Herbaceous coverage (percentage) for each species was estimated on the 10 1-m² subplots, using a 0.5-m × 2-m frame marked into 0.1-m

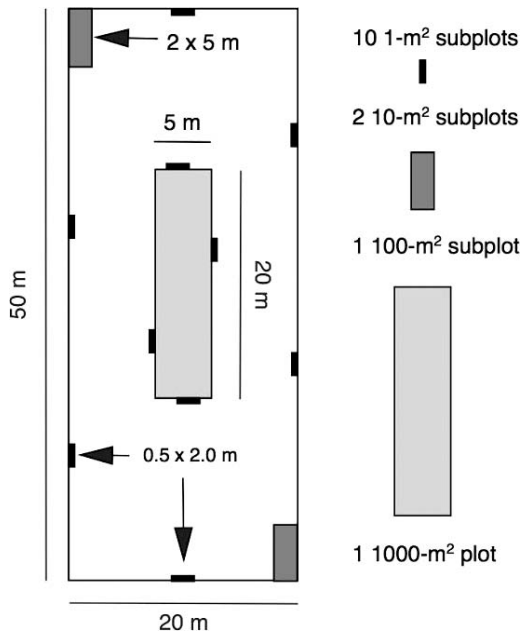


FIG. 1. Layout for modified Whittaker plots used in this study. Plots were laid out on south-facing slopes with tops oriented toward the north. Diagram modified from Stohlgren *et al.* (1995).

increments; the maximum coverage of each species was the one reported for each year. Shrub coverage (percentage) was measured on the two 10-m² subplots in 2005 only, before *L. maackii* removal. Individual shrub canopy areas were estimated by assuming they had elliptical shapes; thus, the longest diameter was measured as the major axis of an ellipse, and the minor axis was measured at right angles to the major axis. Areas for canopies that extended beyond the subplot boundaries were calculated as truncated ellipses. Because shrub canopies overlapped, total shrub coverage could exceed 100%. Tree basal areas (square meters per hectare) were estimated by measuring diameter at breast height in 2005, 2007, 2011, and 2013 on the 100-m² subplots. Species presence, as well as evidence of flowering or fruiting, was noted on plots and subplots (1 m² to 1,000 m²). Species names follow Jones (2005).

Tree and shrub seedling densities (≤ 1 m tall) were also determined in each 1-m² subplot in October 2007, 2011, and 2013. Tree canopy cover was estimated at each site in 2009, 2011, and 2013. A spherical densiometer (Forestry Suppliers, Jackson, MS) was used over all

10, 1-m² plots; it was held at waist height (~ 1.3 m), and readings from the four cardinal directions at each plot were averaged.

STATISTICAL ANALYSIS. Unless otherwise specified, statistical analyses were carried out in SPSS 21.0 (IBM, Armonk, NY). Initial herbaceous coverages were compared with a one-way ANOVA on arcsine-transformed measurements, followed by a Ryan's test. Trends for herbaceous species with $\geq 5\%$ average cover in at least 1 yr in 1-m² plots were examined with Spearman rank correlations between cover and time (year).

For each year and site, the Shannon index H' was calculated, using natural logarithms, for the herbaceous species collected on the 10, 1-m² plots. For comparisons of the H' from different years and sites, 95% confidence intervals were calculated. Using a procedure similar to Pla (2004), a vector of consecutive integers was created in the statistical program R (R Development Core Team 2014), where the number of each integer was proportional to the mean coverage of each species, multiplied by 100. The vector was then randomly sampled with replacement until a vector equal in length to the original was obtained, where the quantity of each integer was proportional to the mean coverage of each species. The procedure binning in the package 'sm' was used to extract the number of times each integer appeared into another vector with a length equal to the number of species. This last vector was then used to calculate H' . The process was repeated 10,000 times. Bias-corrected, accelerated, bootstrap, 95% confidence intervals were then calculated using the procedure of Dixon (2001); details are provided in the Appendix.

Nonmetric multidimensional scaling (NMDS) ordination, with Bray-Curtis distances, was performed on herbaceous species diversity in the 1-m² subplots, using the procedure 'labds'v' in R software. The geometric distance that each site traveled in ordination space from 2005 to 2013 was also calculated. Site variables, including species richness and herbaceous cover, were compared against site-year scores on each of the NMDS axes using Spearman rank correlation.

Repeated-measures, univariate ANOVAs were used to analyze changes in seedling densities of *L. maackii* and trees among different sites over time. Because seedling

Table 1. Initial percentage of cover of the herbaceous and shrub strata and tree basal area at four Woodland Mound Park honeysuckle sites, as well as *Lonicera maackii* stand age, before removal of *L. maackii* in fall 2005.

Factor	Light	Moderate	Heavy	Very Heavy
Herbs (% cover)†	50.4 (16.0) a	32.1 (31.3) ab	12.8 (7.2) b	17.2 (9.1) b
Shrubs (% cover)	45	122	153	221
Trees (m ² ha ⁻¹)	37.0	32.6	12.6	37.6
<i>L. maackii</i> stand age (yr)	35	24	33	40

† Standard deviations are given for herbs only ($N = 10$). Different letters indicate significantly different herbaceous means (one-way ANOVA followed by Ryan's test, $P \leq 0.05$).

densities were counts, and some 1-m² plots had values of 0, y values were transformed to $y' = \sqrt{y + 0.5}$ before analysis (Zar 2010). The Greenhouse-Geisser ϵ , which is considered conservative, was used to correct for lack of sphericity, resulting in noninteger degrees of freedom in the ANOVA (von Ende 2001). The post hoc Ryan's test was used to find site

differences if site was a significant factor and there were not interactions between site and time. An analysis of covariance (ANCOVA) was used to analyze changes in the total number of invasive species over time at each site, with square-root-transformed data and site as a covariate. A repeated-measures ANOVA was used to analyze mean number of invasive species at the 1-m² level, using the procedures described above.

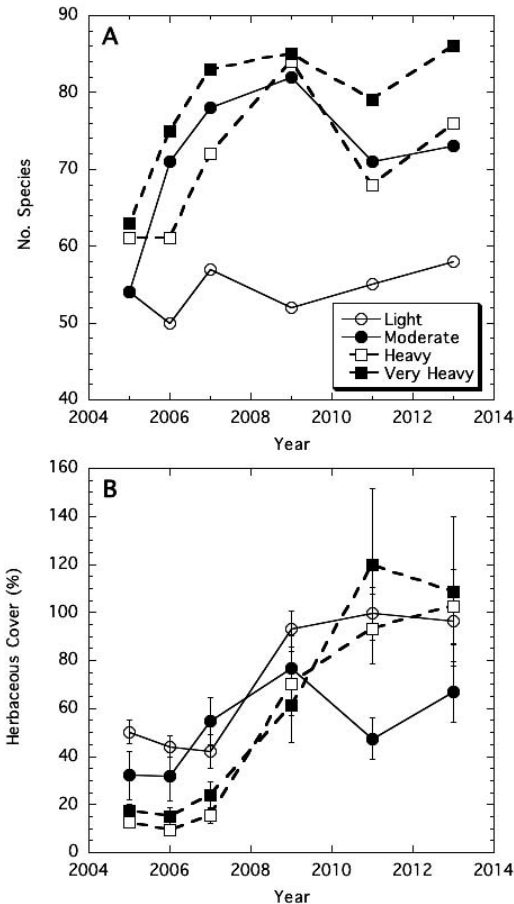


FIG. 2. (A) Total species richness at each site (1,000-m² plot) by year. (B) Mean herbaceous cover in 1-m² plots at each site by year (means \pm 1 SE, $N = 10$).

Results. PREREMOVAL. In 2005, before *L. maackii* cover was removed, herbaceous cover was less at sites with greater shrub cover, with almost all shrubs being *L. maackii* (Table 1). Tree basal area was quite similar at all sites, except for the Heavy site, which showed signs of recent canopy disturbance. Although tree canopy cover measurements were not available until 2009, initial canopy cover did not appear to differ greatly among sites (R.L.B., personal observation). Dominant species included *Acer saccharum* L. (sugar maple), *Carya cordiformis* (Wangenh.) K. Koch (bitternut hickory), *Fraxinus americana* L. (white ash), *Juglans nigra* L. (black walnut), and *Quercus muehlenbergii* Engelm. (chinquapin oak). *Lonicera maackii* stand age (24–40 yr) generally was positively related to shrub cover (45–221%); however, the stand at the Light site was older than expected, based on its relatively low *L. maackii* cover. Total species richness values in 2005 were similar at all sites (55–65), although the sites with heavier shrub cover contained more species (Fig. 2A), perhaps because of fine-scale site differences.

POSTREMOVAL—ALL SPECIES. The Light site maintained roughly the same amount of species (50–55) in the 1,000-m² plot across the study period (Fig. 2A). The other sites appeared to reach a maximum of ~80 species in 2009, declined in 2011, and then started increasing again in 2013.

Table 2. Shannon diversity index (H') for the herbaceous stratum at each site in 2005, 2006, 2007, 2009, 2011, and 2013.†,‡

Year	Light	Moderate	Heavy	Very Heavy
2005	1.970 b 1.944, 1.992	1.723 a 1.667, 1.771	2.012 bc 1.946, 2.062	1.800 a 1.741, 1.849
2006	2.040 c 2.013, 2.063	1.681 a 1.614, 1.731	2.149 c 2.056, 2.207	1.799 a 1.729, 1.855
2007	1.959 b 1.930, 1.985	2.136 b 2.090, 2.173	1.903 b 1.834, 1.956	2.296 b 2.239, 2.337
2009	1.625 a 1.596, 1.650	2.667 c 2.622, 2.675	1.752 a 1.706, 1.766	2.734 d 2.707, 2.755
2011	2.249 d 2.226, 2.269	2.914 d 2.881, 2.939	2.057 b 2.026, 2.083	2.711 d 2.687, 2.730
2013	2.441 d 2.421, 2.458	2.815 d 2.794, 2.838	2.033 b 2.006, 2.056	2.429 c 2.403, 2.452

† Bootstrapped 95% confidence intervals (95% described in the text) are given below values of H' .
‡ Different letters show that 95% confidence intervals do not overlap.

POSTREMOVAL—HERBACEOUS SPECIES. A number of measures indicated that herbaceous species responded positively to the removal of *L. maackii*. Mean percentage of cover increased at all sites over the study period (Fig. 2B), with the Heavy and Very Heavy sites showing the greatest absolute increase. Shannon diversity (H') was generally greater in 2013 than it was in 2005, although the

change was not monotonic (Table 2). The distance that sites traveled in NMDS ordination space from 2005 to 2013 increased from the Light through Moderate to the Heavy and Very Heavy Sites, with the latter two quite similar (Fig. 3). The first two NMDS axes were strongly correlated with species richness and total herbaceous cover. Similar results were obtained using principal components analysis and detrended correspondence analysis (data not shown).

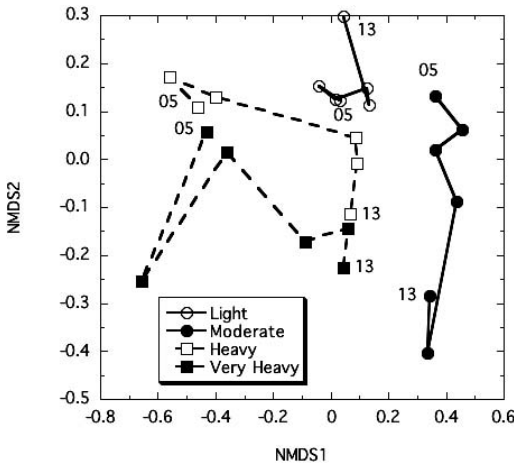


FIG. 3. Nonmetric multidimensional scaling ordination for the four sites, based on herbaceous species cover in the 1-m² subplots across the 2005–13 period, showing the first two axes. Initial position in 2005 is indicated by “05,” whereas final position is shown by “13.” First axis is correlated with species richness (Spearman $r = 0.592$; $P = 0.0023$) and cover (Spearman $r = -0.502$; $P = 0.0135$); second axis is correlated with species richness (Spearman $r = -0.642$; $P = 0.0007$). Distance in ordination space at each site moved from 2005 to 2013: Light = 0.18, Moderate = 0.42, Heavy = 0.58, and Very Heavy = 0.55.

Herbaceous species with more than 5% coverage in any year of the study are shown in Table 3. All of these species either increased or maintained cover relative to 2005, while none decreased. Species that increased in at least two sites included *Ageratina altissima* (L.) R. M. King & H. E. Rob. (white snakeroot), *A. petiolata*, *Carex willdenowii* Schkuhr ex Willd. (Willdenow’s sedge), and *Delphinium tricorne* Michx. (dwarf larkspur); of these, only *A. petiolata* is an invasive species.

POSTREMOVAL—TREE CANOPY COVER AND WOODY PLANT SEEDLINGS. The percentage of tree canopy cover, which was collected over all 10 1-m² plots, was fairly constant at most sites from 2009 to 2011 (90–95%); however, there were large declines at the Heavy and Very Heavy sites in 2013 (85–90%; data not shown). In 2007, the greatest *L. maackii* seedling densities were at the Very Heavy site, whereas the lowest were at the Light site (Fig. 4A). A repeated-measures ANOVA found that there was significant site \times year interaction ($F_{4,45, 53,45} = 4.008$, $P = 0.005$), indicating that *L. maackii* seedling densities changed differently at each site from 2007 to 2013. In

Table 3. Herbaceous species with $\geq 5\%$ average coverage in at least 1 yr from 1-m² plots in 2005, 2006, 2007, 2009, 2011, and 2013.

Site	Species†	Flowering period	Mean % coverage‡						Change direction§	
			2005	2006	2007	2009	2011	2013		
Light	<i>Ageratina altissima</i> (L.) R.M. King & H. Rob.	July–October	0.1	0.2	0.3	0.5	4.0	20.3	↑	
	<i>Alliaria petiolata</i> (M. Bieb.) Cavara & Grande*	May–June	13.7	8.3	15.5	52.9	29.2	6.8	→	
	<i>Carex jamesii</i> Schwein.	May–June	—	—	—	2.2	1.2	6.4	↑	
	<i>Carex willdenowii</i> Schkuhr ex Willd.	May–June	—	—	0.2	0.4	0.3	5.4	↑	
	<i>Chaerophyllum procumbens</i> (L.) Crantz	April–May	10.4	9.7	2.1	5.0	3.5	3.9	→	
	<i>Delphinium tricorne</i> Michx.	April–May	9.0	8.9	9.0	7.3	12.0	7.6	→	
	<i>Floerkea proserpinacoides</i> Willd.	April–May	2.6	2.6	6.0	8.0	17.6	17.4	↑	
	<i>Galium aparine</i> L.	April–June	6.9	7.1	3.9	7.3	11.9	4.0	→	
	<i>Stellaria media</i> (L.) Vill.*	March–November	0.9	0.9	0.3	0.9	5.0	11.4	→	
	Moderate	<i>Ageratina altissima</i> (L.) R.M. King & H. Rob.	July–October	—	—	—	2.2	5.5	9.6	↑
<i>Alliaria petiolata</i> (M. Bieb.) Cavara & Grande*		May–June	18.8	19.5	25.6	18.2	6.8	8.3	→	
<i>Carex willdenowii</i> Schkuhr ex Willd.		May–June	0.6	0.2	2.4	8.5	2.3	4.4	→	
<i>Festuca subverticillata</i> (Pers.) Alexeev		April–July	0.03	0.2	3.9	12.5	0.5	6.1	→	
<i>Galium aparine</i> L.		April–June	1.5	1.9	0.9	6.6	1.3	0.6	→	
<i>Geum vernum</i> (Raf.) Torr. & A. Gray		April–May	0.3	0.5	0.2	1.2	1.1	6.2	→	
<i>Stellaria media</i> (L.) Vill.*		March–November	0.8	0.4	6.9	1.3	1.5	0.3	→	
<i>Viola cucullata</i> Aiton		April–May	1.1	3.0	4.2	5.4	5.6	6.4	↑	
Heavy		<i>Ageratina altissima</i> (L.) R.M. King & H. Rob.	July–October	—	—	—	1.2	3.6	24.9	↑
		<i>Alliaria petiolata</i> (M. Bieb.) Cavara & Grande*	May–June	0.1	0.1	2.8	31.1	38.0	33.1	↑
	<i>Chaerophyllum procumbens</i> (L.) Crantz	April–May	1.2	0.8	0.1	14.4	16.7	1.2	→	
	<i>Delphinium tricorne</i> Michx.	April–May	2.7	2.8	5.5	12.0	12.9	14.0	↑	
	<i>Geum vernum</i> (Raf.) Torr. & A. Gray	April–May	0.1	0.3	0.1	0.2	2.2	11.8	→	
	Very Heavy	<i>Polygonatum biflorum</i> (Walter) Elliott	May–June	—	2.6	4.0	2.7	4.0	6.2	↑
		<i>Ageratina altissima</i> (L.) R.M. King & H. Rob.	July–August	0.5	0.2	1.1	15.3	19.1	33.0	↑
		<i>Alliaria petiolata</i> (M. Bieb.) Cavara & Grande*	May–June	—	—	0.1	6.5	29.0	18.8	↑
		<i>Carex willdenowii</i> Schkuhr ex Willd.	May–June	—	—	0.1	0.6	0.6	6.7	↑
		<i>Delphinium tricorne</i> Michx.	April–May	6.3	6.3	7.1	7.5	12.2	13.1	↑

Table 3. Continued.

Site	Species†	Flowering period	Mean % coverage‡					Change direction§	
			2005	2006	2007	2009	2011		2013
	<i>Geum vernum</i> (Raf.) Torr. & A. Gray	April–May	—	0.1	1.7	2.1	3.0	7.5	↑
	<i>Hackelia virginiana</i> (L.) I.M. Johnst.	July– September	—	—	—	6.1	8.9	—	→
	<i>Polygonatum biflorum</i> (Walter) Elliott	May–June	5.5	4.2	6.1	5.2	6.3	4.6	→

† Invasive species are marked with an asterisk.

‡ Absence of species indicated by a dash (—). Flowering times are taken from Jones (2005).

§ Arrows indicate direction of change in species cover over time as indicated by Spearman rank correlations ($P \leq 0.05$).

contrast, tree seedling densities increased at all sites from 2007 to 2013 ($F_{1,80, 64.86} = 10.131$, $P < 0.001$), with the highest densities at the Light site and the lowest at the Very Heavy

site (Fig. 4B). A post hoc Ryan’s test found that the Light and Very Heavy sites had the highest and lowest tree densities, respectively, whereas the other two sites did not differ significantly from these two sites. The most common species found among the tree seedlings were *Celtis occidentalis* L. (common hackberry) and *Prunus serotina* C. Mohr (black cherry; data not shown). *Cercis canadensis* L. (eastern redbud) and *Fraxinus* spp. became abundant in 2011 and 2013, respectively. Other common species included *Acer negundo* L. (boxelder), *Acer saccharum* L. (sugar maple), *Carya* L. spp. (hickory), and *Ulmus rubra* Muhl. (slippery elm).

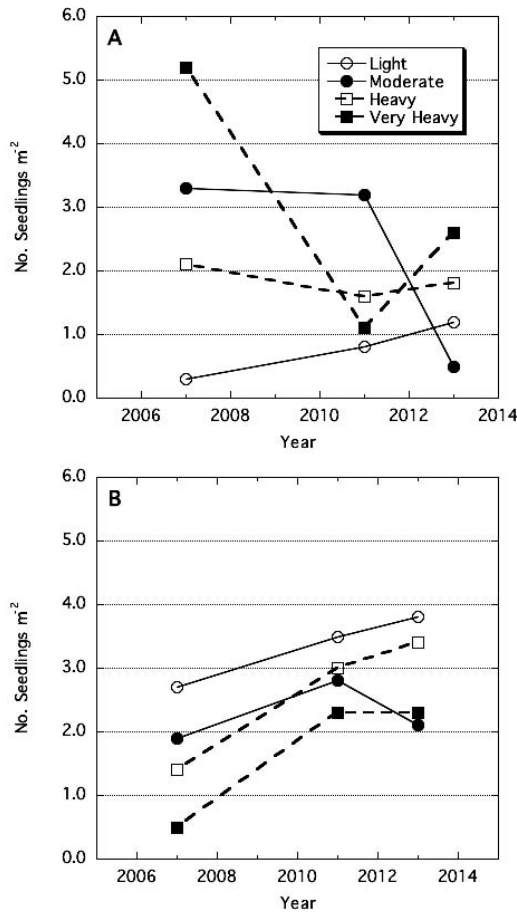


FIG. 4. (A) *Lonicera maackii* and (B) tree seedling density over time, estimated from 1-m² subplots ($N = 10$).

INVASIVE SPECIES TRENDS. At the 1,000-m² scale, an ANCOVA test showed an overall increase over time in the number of invasive species ($F_{5, 17} = 7.133$, $P = 0.001$; Fig. 5A). The mean number of invasive species at the 1-m² level also increased significantly at all sites, as indicated by a repeated-measures ANOVA ($F_{2,76, 99.21} = 17.934$, $P < 0.001$; Fig. 5B). The fraction of herbaceous cover at 1-m² represented by invasive species also initially increased at all sites but the Moderate site (Fig. 5C); however, the invasive fraction then decreased at all sites, so that it was 15–40% in 2013. Initial invasive cover fraction was quite high at the Moderate site but fell to the lowest of all sites in 2013. The most important invasive species was *A. petiolata* (Fig. 6). *Alliaria petiolata* was initially present at the Light and Moderate sites but absent at the Heavy and Very Heavy sites. Herbaceous cover of this species initially increased at all sites but then declined, with the Heavy and Very Heavy sites reaching peaks later than the Light and Moderate sites. Because *A. petiolata* accounted for most of the invasive herbaceous

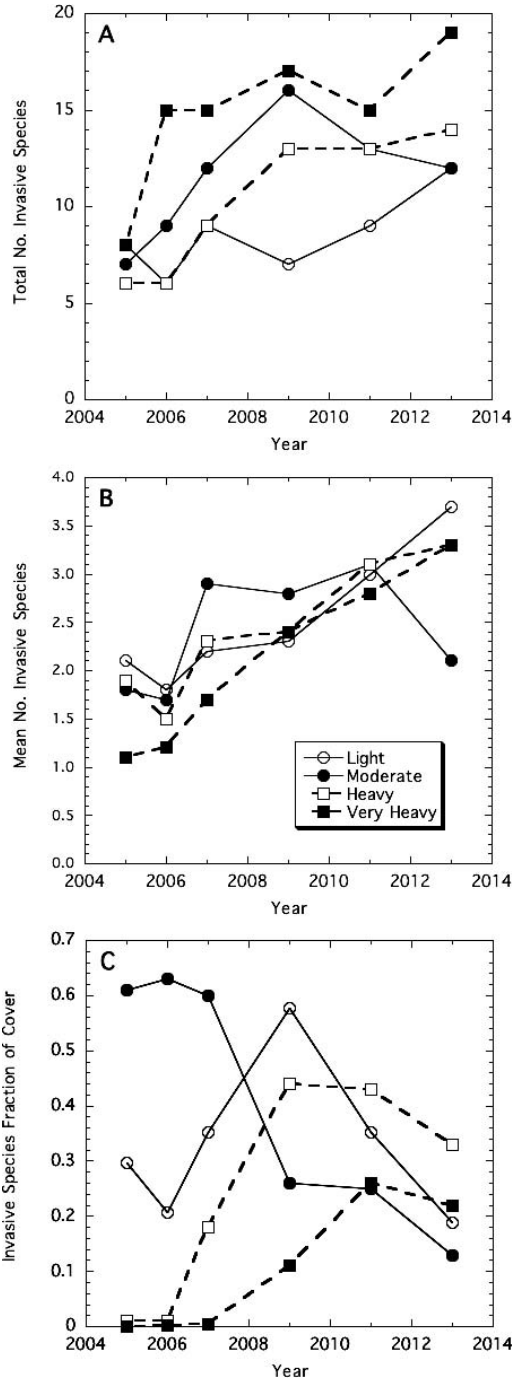


FIG. 5. (A) Total number of invasive species at each site (1,000-m² plot) by year. (B) Mean number of invasive species average across 1-m² plots at each site by year (*N* = 10). (C) Fraction of herbaceous cover represented by invasive species in the 1-m² plots at each site by year (*N* = 10).

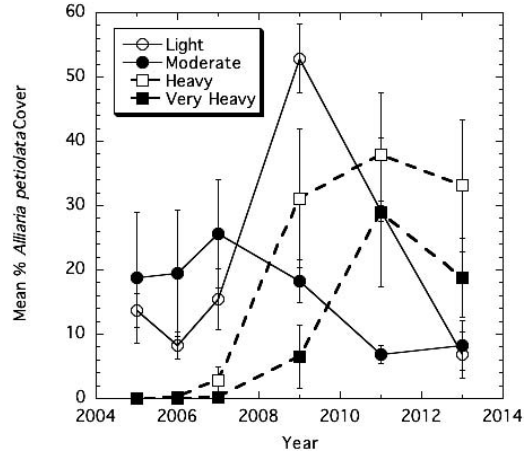


FIG. 6. Mean percentage of *Alliaria petiolata* cover for the 2005–13 period, determined from 1-m² subplots (means ± 1 SE; *N* = 10).

cover, total invasive cover was very similar to that of this species (data not shown).

Discussion. Total species richness at each site followed a similar trajectory for the Moderate, Heavy, and Very Heavy sites, increasing from 55–65 species in 2005 to 80–85 in 2009, followed by a decline in 2013 (Fig. 2A). All sites, including Light, increased in 2013. However, although species richness increased in the first year for the Moderate and Very Heavy sites, it did not do so at the other two sites. This may explain the contradictory findings of previous short-term studies in upland forests, with some studies finding an increase in species richness the year after *L. maackii* removal (e.g., McDonnell *et al.* 2005, Luken *et al.* 2007), whereas other studies did not (e.g., Swab *et al.* 2008). The time that species take to respond to *L. maackii* removal may be highly dependent on other site factors. Longer-term studies, such as those by Luken *et al.* (2007) and Runkle *et al.* (2008), support the idea that species richness will eventually increase, as seen in this study for all but the Light site. Herbaceous cover increased at all sites (Fig. 2B), whereas all except the Heavy site had significantly greater values of *H'* in 2013 vs. 2005 (Table 2). Runkle *et al.* (2007) found that herbaceous cover declined in both the control and *L. maackii* removal sites, but the cover was greater in the removal sites 8 yr after removal, so the current study may be in partial agreement with that study.

Species with more than 5% cover in any year increased or maintained coverage over the 2005–13 period (Table 3); some of these species were not initially present at the sites. *Ageratina altissima* and *Alliaria petiolata* were among the most prominent, as seen in previous studies (Luken *et al.* 1997, Runkle *et al.* 2007), although *A. petiolata* decreased at all sites after reaching a peak in 2–6 yr (Fig. 6). Most of the increasing species flowered in May or later (Table 2). However, flowering time may be less important than leaf phenology. Many species that flower in May or later retain leaves into the fall, whereas early bloomers are often spring ephemerals with leaves that die back by summer. *Lonicera maackii* generally leafs out completely by April in this area (McEwan *et al.* 2009, Boyce *et al.* 2012), and so we would expect both spring ephemerals and later bloomers to be affected. It may be, however, that *L. maackii* removal has a proportionally greater positive effect on understory herbs with summer-green foliage; more research is required to determine whether that is true.

The overall change in herbaceous species composition and cover was mainly related to initial *L. maackii* cover because sites with greater initial *L. maackii* cover tended to experience the greatest movement in NMDS ordination space over time (Fig. 3). This was caused by the appearance of new species and the increase in abundance of both new and initially present species, as indicated in Table 3. Thus, changes in the environment caused by *L. maackii* removal had profound effects on the herbaceous stratum at these sites.

Birds consistently reintroduce *L. maackii* seeds after removal (Bartuszevige and Gorchoff 2006). There were differences in the density of *L. maackii* seedlings in 2007, but trends from 2007 to 2013 were mixed (Fig. 4A). Overall, seedling densities appeared to remain at relatively low levels at all sites, especially when compared with previous studies (Luken *et al.* 1997, McDonnell *et al.* 2005, Loeb *et al.* 2010). This may be due in part to the emergence of honeysuckle leaf blight (Boyce *et al.* 2014), which was observed at all sites in 2013. Tree seedlings, on the other hand, showed a steady increase from 2007 to 2013 (Fig. 4B). The densities of tree seedlings were lower than those found by some studies (McDonnell *et al.* 2005, Loeb *et al.* 2010), although they were similar to the most common tree species that was found by Luken *et al.*

(1997)—*Acer negundo*—3 yr after *L. maackii* removal. Thus, the removal of *L. maackii* appears to benefit both herbs and trees without immediate recolonization by *L. maackii*.

Invasive species also increased their numbers after *L. maackii* removal, at both the fine and large scales (Fig. 5); this was also reported by Luken *et al.* (1997). Even the Light site saw increased numbers of invasive species. The most abundant of these invasive species was *A. petiolata* (Table 3). However, this species appeared to decline after reaching a peak 2–6 yr after *L. maackii* removal (Fig. 6). This decline was unexpected. Although older *A. petiolata* populations become less competitive and their increase in abundance slows (Lankau *et al.* 2009), this is the first study, to my knowledge, to show a decline after initial invasion. Perhaps infection by powdery mildew (*Erysiphe cruciferarum* Opiz ex. L. Junell), which has been seen in the area and has been shown to decrease *A. petiolata* growth, reproduction, and competitive ability (Enright and Cipollini 2007, Cipollini and Enright 2009), is responsible. This decline is especially important because initial increases can be discouraging to managers when *L. maackii* is first removed. In this study, the initial increase of *A. petiolata* did not appear to have hindered recolonization of these sites by either herbaceous species or trees. Eventual levels of coverage by *A. petiolata* are unknown, although it appears to be about 5–10%. However, major canopy openings, such as that caused by ash decline, may lead to increases in abundance, similar to that seen after *L. maackii* removal. In addition, it is unclear how other invasive species will respond and how those species may hinder the regeneration of native species.

The emerald ash borer (*Agrilus planipennis* Fairmaire) appeared in the region in 2011, and *Fraxinus* spp. decline at Woodland Mound was quite apparent by 2013. *Fraxinus americana* basal area declined at all sites where the species was in the tree stratum, and tree canopy cover also declined (data not shown). This may be responsible for the increase in species richness at all sites from 2011 to 2013 (Fig. 2A), as well as the increase in *L. maackii* seedlings at three out of four sites across the same period (Fig. 4A). Thus, the loss of an important overstory tree may greatly modify the subsequent course of recovery from *L. maackii* removal of these stands.

Conclusions. Removal of the *L. maackii* shrub canopy caused herbaceous species to respond positively during the following 8 yr, in species richness, percentage of coverage, and diversity as measured by H' . The most common herbaceous species either increased or maintained their coverage at all sites. Although tree seedling density increased at all sites, *L. maackii* seedling response was mixed. Other invasive species abundances increased, including *Alliaria petiolata*. However, all sites showed a peak in *A. petiolata* coverage 2–6 yr after *L. maackii* removal, suggesting that the increase may be transitory. The plant communities also appeared to respond to the decline in ash, which may alter how these communities recover from *L. maackii* removal.

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APPENDIX

This contains R code used to calculate 95% bootstrapped confidence intervals around calculated values of H' , the Shannon diversity index, using sample cover data.

```
#This calculates 95% confidence
intervals around for a value of H'
(Shannon diversity index).
```

```
library(sm)

#function for calculating H'
shannon.coeff <- function(h) {
  sum.h <- sum(h)
  p <- h/sum.h
  log.p <- log(p)
```

```

    p.log.p <- p*log.p
    -sum(p.log.p)
  }
#set up vectors a and boot.out with
nothing in them
a<-c()
boot.out <-c()

#set up a vector raw with percent cover
values from a site
raw <- c(4.025, 29.200, 1.350, 1.200,
3.650, 0.300, 3.475, 11.950, 0.050,
0.300, 0.500, 17.600, 11.900, 0.500,
0.100, 3.500, 0.800, 0.650, 0.200,
5.000, 1.850, 1.100, 0.300, 0.025)

#calculate estimated Shannon Index
shannon.coeff(raw)

#fill vector a with integers, with # of
each integer proportional to values in
vector raw (Pla 2004). If % cover
values are used, use raw[i]*100, as
given below. If using proportions,
then change to raw[i]*10,000.
for(i in 1:length(raw)) {
  a <- append(a, rep(i, times=round
    (raw[i]*100)))
}

#B=No. replications in bootstrap
sample. 10,000 takes a while but gives
consistent results.
B <- 10000

#Fill boot.out with bootstrapped
values
for (k in 1:B){
  aperm.bin <- binning(sample(a,
length(a), replace = T),
breaks=seq(0,length(raw),by=1))
  boot.out[k] <-shannon.coeff(aperm.
bin$x.freq)
}

#report mean & SD from bootstrap
estimates, and do histogram
mean(boot.out)
sd(boot.out)
boot.out <- sort(boot.out)
hist(boot.out)

#Calculate bias-corrected 95% CIs,
following Dixon (2001)
z <- qnorm(rank(boot.out)[round
(B/2)]/B);z

p.l <- pnorm(2*z-1.96); p.l
p.u <- pnorm(2*z+1.96); p.u

boot.out[round(p.l*B)]
boot.out[round(p.u*B)]

```