



PROJECT MUSE®

Potential Reinvasion of *Lonicera maackii* after Urban
Riparian Forest Restoration

Kristine N. Hopfensperger, Richard L. Boyce, Devin Schenk

Ecological Restoration, Volume 37, Number 1, March 2019, pp. 25-33 (Article)

Published by University of Wisconsin Press

Ecological Restoration



➔ For additional information about this article

<https://muse.jhu.edu/article/719525>

Potential Reinvasion of *Lonicera maackii* after Urban Riparian Forest Restoration

Kristine N. Hopfensperger, Richard L. Boyce and Devin Schenk

ABSTRACT

The invasive shrub, *Lonicera maackii*, is known to change forest ecosystem communities and functions; however, few have studied the potential for this prolific invader to return after forest restoration. We studied the forest understory, canopy, seed bank, and incoming *L. maackii* seed rain in a riparian urban forest five to nine years after *L. maackii* removal and restoration efforts. We found the restored areas maintained a native canopy, but by nine years post-management efforts, *L. maackii* was becoming more important along multiple transects due to many small individual seedlings. The restored areas had greater herbaceous cover and species richness when compared to the control area (*L. maackii*-dominated). *Lonicera maackii* was not common in the seed bank during the study but was more prevalent in the seed rain of the restored forest with a tree canopy than in the restored open field without a tree canopy. While our results support the premise that removing *L. maackii* returns the community to a more native state, the study also shows that the native state would not last without additional minor intervention. Monitoring beyond ten years post-removal will be key to telling the whole reinvasion story, but management efforts every five to ten years could suffice to keep a restored forest dominated by native species.

Keywords: Amur honeysuckle, invasive species removal, seed bank, seed rain, urban forest community


Restoration Recap

- Removing *L. maackii* from forests is important to return a forest to a native state. However, few studies have examined the potential for reinvasion once *L. maackii* has been removed; of the few studies that exist, they all reported on findings that were less than ten years post-removal.
- We compared the woody canopy, herbaceous understory, seed bank, and seed rain in a restored forest with a native tree canopy, a restored open field without a tree canopy, and a control area (*L. maackii*-dominated) within an urban riparian zone, for five to nine years post-removal and restoration efforts.
- While our results show a short-term return to a native community, approximately ten years post-removal may be a turning point when *L. maackii* begins to dominate again. Our results suggest that the time period between management efforts could extend up to ten years, but longer-term studies are needed to support this speculation.

Invasive plants are known to displace native communities and can drastically change an ecosystem (Ehrenfeld 2003, Vila et al. 2011). Additional stressors in urban settings can cause these community and ecosystem changes to be even more dramatic (Shochat et al. 2010). Because the removal of invasive species can be quite costly and both labor- and time-intensive (Pimentel et al. 2005), this research studied

the reinvasion potential of an invasive plant species after its removal in an urban system to determine the invasion pathways and to better define the management needed to maintain the restored native community.

Lonicera maackii (Amur honeysuckle) is an invasive shrub that dominates many forest understories in the central United States, ultimately changing the forest ecosystems where it resides (Collier et al. 2002, Arthur et al. 2012, Boyce et al. 2012, McEwan et al. 2012). *Lonicera maackii* was introduced from eastern Asia as an ornamental shrub in the late 1800s and was first reported in the wild in southwestern Ohio (Luken and Thieret 1996, Braun 1961)—the region where our field study took place. The bright red fruits of *L. maackii* are distributed by several bird species

 Supplementary materials are freely available online at:
<http://uwpress.wisc.edu/journals/journals/er-supplementary.html>

Ecological Restoration Vol. 37, No. 1, 2019

ISSN 1522-4740 E-ISSN 1543-4079

©2019 by the Board of Regents of the University of Wisconsin System.

(Bartuszevige and Gorchov 2006) and can be dispersed long-distances by *Odocoileus virginianus* (white-tailed deer) (Guiden et al. 2015), and so seed rain is an important component of its propagation. In native forests, *L. maackii* outcompetes native shrubs through a competitive growth pattern, extended leaf phenology, prolific fecundity, and allelopathy (Trisel 1997, Gorchov and Trisel 2003, Dorning and Cipollini 2006, Lieurance and Landsbergen 2013, McNeish and McEwan 2016). This can lead to a changed forest structure with reduced diversity, richness, and cover of native trees and shrubs (White et al. 2014, Shields et al. 2015a) and a nearly nonexistent ground cover community (Hutchinson and Vankat 1997, Collier et al. 2002). A recent review and synthesis of the literature found *L. maackii* to affect multiple ecological scales, including the terrestrial-aquatic interface, thereby impacting forest processes at the watershed scale (McNeish and McEwan 2016).

Stressors to an urban forest, in addition to invasive species, include reduced biodiversity, increased disturbance and light, and air/water pollution (Burton and Samuelson 2008, Duguay et al. 2007, Grimm et al. 2008a & b, Pickett et al. 2011). In urban settings, habitat fragmentation and development increase opportunities for invasive species to thrive (Hobbs 1989, Hobbs and Huenneke 1992) by increasing availability of light through an increase in forest edges, which can also enhance dispersal and distribution (Rose 1997, Renne et al. 2002). In addition, the road network in urban landscapes can serve as a pathway for dispersal (Joly et al. 2011, Gelbard and Belnap 2003, Flory and Clay 2005, 2009), leading to an increase in non-native and invasive plants (Cameron et al. 2015). In fact, others have found greater percent cover of *L. maackii* in urban forests compared to rural landscapes (Borgmann and Rodewald 2005, Trammell and Carreiro 2011, Cameron et al. 2015).

Efforts to remove *L. maackii* are costly, and there is a lack of published studies to support that removal ensures a long-term functioning forest dominated by native species. The most common and successful method to eradicate *L. maackii* is to cut and treat the stems with herbicide (Hartman and McCarthy 2004, Rathfon and Ruble 2007, Schulz et al. 2012). Even with this cut-and-paint treatment, a greater chance of success is achieved by incorporating native plant revegetation efforts, such as seeding, tree and shrub planting, and annual invasive plant control (Kettenring and Adams 2011). These methods of control can range up to \$8,600 per hectare. There have been some studies on the removal of *L. maackii* and the response of the plant community (Runkle et al. 2007, Swab et al. 2008, Cipollini et al. 2009, Shields et al. 2015b, Boyce 2015); however, the studies vary in the years since removal and mostly represent short-term results. Collectively, the short-term studies found conflicting results, where some reported an increase in native species (Runkle et al. 2007, Shields et al. 2015b, Boyce 2015), and some reported no effect from the removal of *L. maackii* (Swab et al. 2008).

Despite the cost and unknown results of *L. maackii* control efforts, there is considerable focus on its management at the federal, state, and local level (Pfennigwerth and Kuebbing 2012). We investigated whether efforts to remove *L. maackii*, in an urban riparian forest, where mechanisms for reinvasion abound, are effective over the long-term. Our objective was to measure understory herbaceous plant and woody communities, the soil seed bank, and the *L. maackii* seed rain, five to nine years after removal efforts ceased, to test the following hypotheses: 1) a native forest canopy may slow re-establishment of *L. maackii*, due to lower light levels and competition, and 2) dominance of *L. maackii* in an urban riparian forest may reduce species richness with a large influx of its seed. Specifically, we predicted that 1) the restored urban riparian area without a tree canopy (field; FL) would have greater *L. maackii* re-establishment than the restored area with a native canopy (forest; RF), and 2) an urban riparian forest dominated by *L. maackii* (control; CF) will have lower species richness and greater seed rain than areas where *L. maackii* has been removed (RF & FL).

Methods

Our study took place in what was originally a narrow (23 to 75 m width), 2.43-ha urban forest, along 900 m of Mook Creek in the northern Kentucky city of Southgate, within the greater Cincinnati, Ohio, metropolitan area (39°03'21" N, 84°28'46" W). The creek is surrounded by two hillsides—to one side is a road with a residential neighborhood, and on the other side is a condominium complex. The stream flow is extremely variable, with high discharge after rain events leading to great erosion and channel modification. Temperature in the region ranges from an average of 4°C in winter to 30.4°C in summer, and it receives an average annual precipitation of 1073 mm (U.S. Climate Data 2015). The riparian forest is less than 40 years old, with a canopy dominated at the time of the study by *Fraxinus americana* (white ash) and *Acer negundo* (box elder). We have previously published the ecosystem function results from this study location (Hopfensperger et al. 2017).

Lonicera maackii has been prevalent in the immediate area since at least the 1960s and dominates the woody understory of the riparian forest with very little herbaceous growth below. Stream restoration efforts began in 2006. Maintenance of invasive species continued for an additional four years with foliar applications of 2% glyphosate (Roundup WeatherMax®, Monsanto) and by hand pulling in the areas that became the restored forest (RF), which had a tree overstory, and the field (FL), which lacked a tree canopy. The RF site was approximately 2.43 ha and included the shrub removal of *L. maackii* and stump application of 20% glyphosate (Roundup WeatherMax®, Monsanto). RF was planted with native shrubs and trees (11 species as bare-root saplings and 12 species as 1-gallon containers)

and seeded with a native woodland mix (18 forb species, 9 grass species, 14 tree species) after *L. maackii* removal. The restored field (FL) area was adjacent to RF. It served as the main access point for heavy machinery and included dramatic reshaping of the hillside and movement of soil as part of the stream restoration effort. The FL site consisted of 1.2 ha of field dominated by invasive plant species that were broadcast sprayed with 2% glyphosate and seeded with native forbs and grasses. Because the field was part of the linear urban riparian forest, part of the restoration was to reforest the area by planting with native shrubs and tree seedlings. In both RF and FL, the tree and shrub plantings were of limited success, but the seeded native forbs and grasses successfully established. We also studied a forest section upstream of FL that had no *L. maackii* removal or restoration efforts (control forest; CF). RF and FL each had two, 20-m transects with five plots randomly placed along each transect, for a total of ten plots per treatment. Because the forest area in CF was very narrow, ten plots were randomly placed along four, 10-m transects. All plots were 1 m² in area (Supplementary Figure 1).

Woody Plant Community

The tree and shrub community was sampled along all study transects in the summers of 2011 (five years after restoration), 2012, and 2015. All woody species found within 2.5 m on each side of the transect (200-m² area sampled per site) were identified and measured for either diameter at stump height (dsh, saplings or shrubs; 25 cm) or diameter at breast height (dbh, trees; 1.37 m). Basal area was calculated for each individual measured in the study. Then, total basal area, density and relative density, dominance and relative dominance, frequency and relative frequency, and importance value were calculated for each species within each transect for every study year. Importance value index was calculated as the sum of relative dominance, relative density, and relative frequency for each species per transect area (Curtis and McIntosh 1950). In June 2011, we measured leaf area index (LAI) in each treatment using an Accupar ceptometer (Decagon, Pullman, WA) to assess the amount of available light both below the canopy and in the open for determining the transmission ratio. Measurements were made under overcast skies.

Herbaceous Plant Community

The herbaceous plant cover and species richness were determined for all 1-m² plots (ten per treatment) during peak biomass of 2011, 2012, 2013, and 2015 (nine years post-restoration). Percent cover of each species within a plot was estimated using a modified Braun-Blanquet (1964) approach with the following categories: trace (1), 0–1% (2), 1–2% (3), 2–5% (4), 5–10% (5), 10–25% (6), 25–50% (7), 50–75% (8), and 75–95% (9). For data analysis, the percent cover reported for each plot was calculated from the sum of category numbers for each species within a plot.

Soil Seed Bank

The seed bank of each plot was sampled with three soil cores, 10-cm long by 3.81-cm in diameter, in March of 2011 and 2013. For each plot, soil cores were homogenized, spread in a thin layer (< 1-cm thick) over vermiculite in bedding trays, and placed in a greenhouse misting room for germination (Poiani and Johnson 1988, Gross 1990). Seedlings emerging from each sample were identified as young as possible and removed from the tray when identified. Seedlings of unknown species were transplanted and allowed to mature for identification. Seed bank abundance was recorded as the number of emerged seedlings per plot. Species richness was recorded as the number of seedling species emerged per plot.

Seed Rain

Lonicera maackii seed rain (i.e. seeds and berries entering the site) was measured in each site using four seed traps per site. To eliminate impacting soil seed bank results, seed trap location did not align with soil seed bank sample plots. A seed trap consisted of a 0.50 × 0.50-m frame made of wood (2 × 4s) and a fine-mesh nylon base, which dried quickly and retained small seeds. The traps were anchored 10 cm above the soil surface. The trap contents were collected every two weeks from October into January in 2011, 2012, and 2013. All honeysuckle seeds and berries were counted after each collection.

Data Analyses

To determine if there was a difference among the sites (treatments) with the measured response variables, we used repeated-measure analysis of variance (RMANOVA) tests using a mixed model analysis with a compound symmetry covariance structure (SAS v. 9, SAS Institute, Cary, NC 1985). For each RMANOVA, treatment was the independent variable, and the dependent variables included woody species richness, herbaceous cover, herbaceous species richness, seed bank abundance, seed bank species richness, and seed rain abundance. The assumption of homogeneity of variance was checked with Levene's test for all RMANOVAs. A one-way analysis of variance test was used to determine a difference in LAI among the treatments. However, we note that because restoration efforts were applied in single, large areas at our study site, the assumption that treatment effects were independent from spatial locations cannot be made. Basic statistics including mean, minimum, maximum, range, and standard error were calculated for all dependent variables during each sampled year. All variables were checked to verify they met the assumptions of normality. Three variables were log₁₀-transformed: herbaceous cover, seed rain seeds, and seed rain berries. These latter statistical analyses were performed in SPSS (v. 19, IBM SPSS Statistics for Windows, Armonk, NY).

Results

Woody Plant Community

By the end of the study in 2015, nine years after restoration, RF and FL had greater species richness in the woody plant community than CF ($F_{2,15} = 6.34$, $p = 0.001$; Table 1). While most planted seedlings did not survive, we saw woody diversity increase with mostly native volunteers. Two invasive species were found along the RF transects (#1–4) in sampling year 2015 only, *Pyrus calleryana* (Callery pear) and *L. maackii* (Table 1). The invaders found in RF and FL were all small seedlings (dsh < 1.0 cm) unlike the mature individuals found in CF. Species richness did change through the years in the treatments with an increase over time in both RF and FL ($F_{2,15} = 15.1$, $p = 0.001$). The RF canopy remained dominated by *A. negundo*, *Juglans nigra* (black walnut), *Celtis occidentalis* (hackberry), and *Aesculus glabra* (Ohio buckeye). For the duration of our study, FL remained dominated by herbaceous vegetation, but became more diverse with woody seedlings over time. While *L. maackii* was not the most important species in RF during the duration of our study (except for transect 2 in 2015), in 2015 it began to appear with a large importance value in three of the four transects in RF (Table 1). The increase in *L. maackii* importance in 2015 was due to the high number of small (dsh < 0.5 cm) individuals found

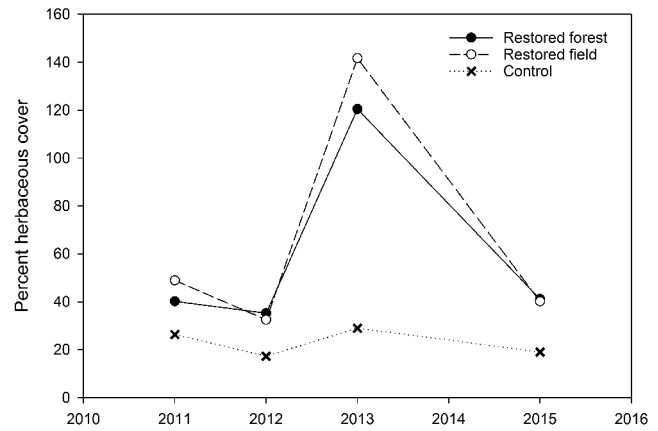


Figure 1. Average percent herbaceous ground cover for each treatment during each year of the study.

along the transects. CF remained dominated by mature *L. maackii* throughout the study, with only small and scattered seedlings of other species and a few mature *Maclura pomifera* (Osage orange) individuals.

Herbaceous Plant Community

The herbaceous plant community in CF, which was dominated by *L. maackii*, had significantly less cover than the RF and FL treatments ($F_{2,81} = 59.1$, $p < 0.0001$; Figure 1), only averaging 17–29% in a sample year. CF also had

Table 1. Woody species richness and species with the highest calculated importance value (IV; most important species) for each transect during each year of woody vegetation sampling. Area sampled for transects 1–4 was 50m², while area for transects 5–8 was 25m².

Transect	Treatment	Year	Species richness	Most Important Species	Importance Value (IV)	<i>Lonicera maackii</i>
1	Restored forest	2011	4	<i>Celtis occidentalis</i>	95.7	not present
1	Restored forest	2012	6	<i>Acer negundo</i>	78.5	not present
1	Restored forest	2015	10	<i>Celtis occidentalis</i>	89.5	<i>L. maackii</i> #2 IV = 72
2	Restored forest	2011	6	<i>Acer negundo</i>	62.0	not present
2	Restored forest	2012	5	<i>Aesculus flava</i>	119.9	not present
2	Restored forest	2015	10	<i>Lonicera maackii</i>	102.2	<i>L. maackii</i> #1
3	Restored field	2011	9	<i>Gleditsia triacanthos</i>	72.3	not present
3	Restored field	2012	2	<i>Maclura pomifera</i>	119.5	not present
3	Restored field	2015	10	<i>Cornus drummondii</i>	83.0	<i>L. maackii</i> #2 IV = 68
4	Restored field	2011	3	<i>Acer negundo</i>	188.4	not present
4	Restored field	2012	0	n/a	n/a	not present
4	Restored field	2015	11	<i>Fraxinus</i> spp.	122.3	<i>L. maackii</i> #4 IV = 67
5	Control	2011	5	<i>Lonicera maackii</i>	171.7	
5	Control	2012	3	<i>Lonicera maackii</i>	217.4	
5	Control	2015	4	<i>Lonicera maackii</i>	143.0	
6	Control	2011	7	<i>Lonicera maackii</i>	152.9	
6	Control	2012	2	<i>Lonicera maackii</i>	217.8	
6	Control	2015	2	<i>Lonicera maackii</i>	179.1	
7	Control	2011	9	<i>Lonicera maackii</i>	157.8	
7	Control	2012	3	<i>Lonicera maackii</i>	202.4	
7	Control	2015	7	<i>Lonicera maackii</i>	127.9	
8	Control	2011	9	<i>Lonicera maackii</i>	133.2	
8	Control	2012	3	<i>Lonicera maackii</i>	138.0	
8	Control	2015	7	<i>Lonicera maackii</i>	163.3	

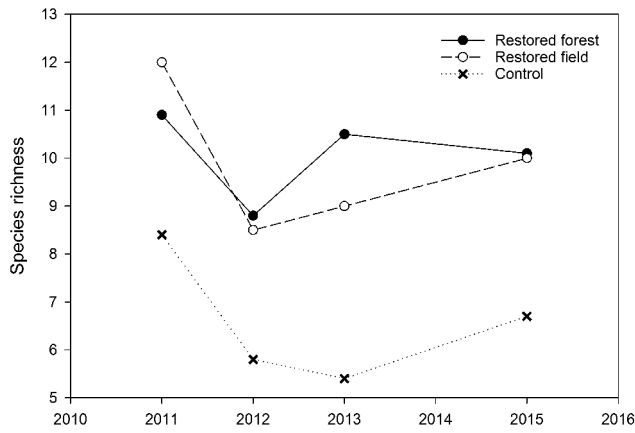


Figure 2. Average species richness in the herbaceous community for each treatment and year of the study.

significantly lower species richness in the herbaceous community when compared to RF and FL, with eight or fewer species present each sample year ($F_{2,81} = 11.9, p < 0.0002$; Figure 2). Not surprisingly, the CF ground cover was dominated by *L. maackii* seedlings, while the RF treatment contained an average of ten species with *Carex jamesii* (James' sedge) and *Geum canadense* (white avens) dominating. RF also averaged ten species, and plots were dominated by *Solidago canadensis* (Canada goldenrod). Species richness and percent cover of the herbaceous community differed throughout the study; however, the number of invasive herbaceous species did not change, the three present being *Alliaria petiolata* (garlic mustard), *L. maackii* seedlings, and small *L. japonica* (Japanese honeysuckle) vines. Herbaceous cover did not increase linearly with time since restoration in RF and FL, but instead peaked in 2013 ($F_{2,81} = 55.7, p < 0.0001$; Figure 1), likely due to greater precipitation that year. In addition, species richness fluctuated among sample years in all treatments, perhaps due to precipitation driving flood events into the riparian area and the resultant seed dispersal and/or altered germination conditions ($F_{2,81} = 7.50, p < 0.001$; Figure 2).

Soil Seed Bank

We identified 51 known species in the seed bank at the study site in 2011 and 40 species in 2013. *Lonicera maackii* was not found in the seed bank of RF and FL in 2011 or 2013 and was found in very low density (~1%) in CF only in 2011. The species composition of the seed bank varied by treatment, with RF dominated by *Juncus tenuis* and *Malva neglecta*, FL dominated by *Ageratina altissima* and *Cyperus strigosus*, and CF dominated by *Agrostis alba* (Figure 3). FL had greater abundance and species richness in the seed bank for both sample years (2011 and 2013) when compared to the RF and CF (Table 2). Seed bank abundance and species richness were greatest in 2011 and decreased during the study period ($F_{1,54} = 23.7, p < 0.0001$ and $F_{1,54} = 70.1, p < 0.0001$, respectively).

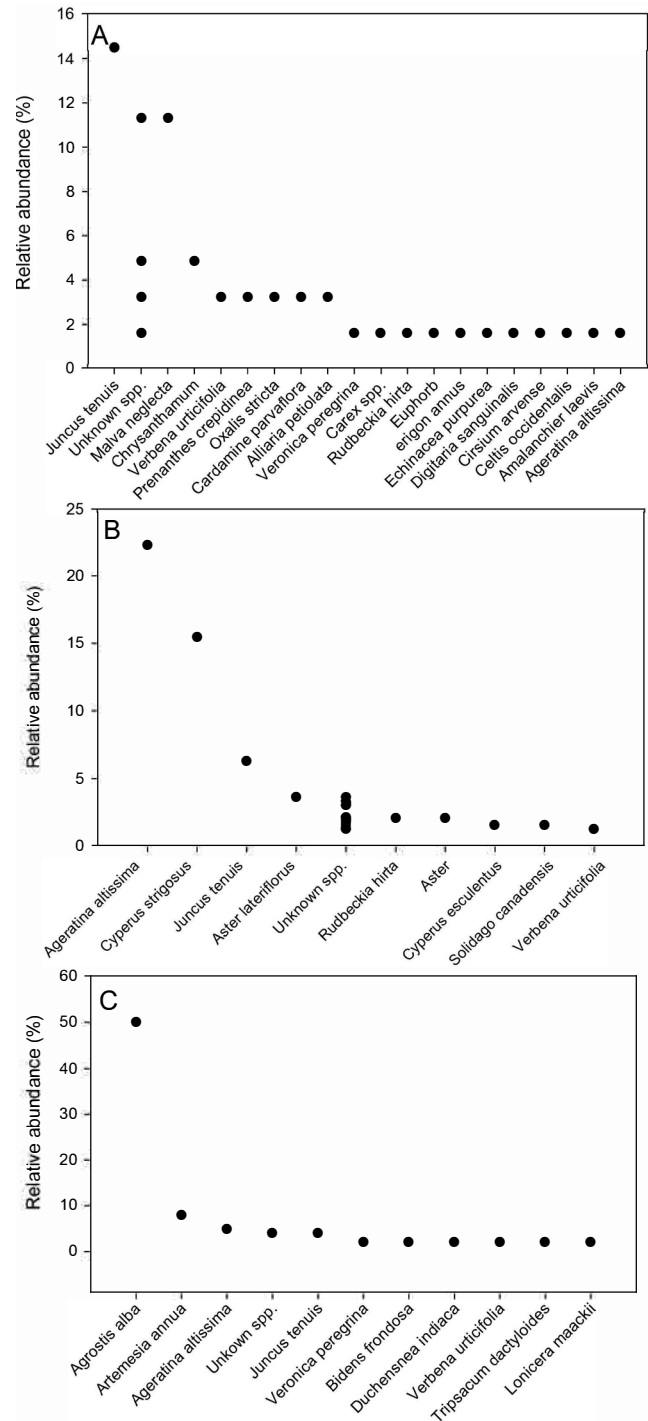


Figure 3. All species with relative abundance > 1% in the seed bank of each treatment in 2011, five years after restoration. Note that *Lonicera maackii*, the invasive species of interest, is only found in low density for the control treatment. Panel A = restored forest (RF), B = restored field (FL), C = control forest (CF).

Table 2. Average seed bank abundance ($F_{2,54} = 33.4$, $p < 0.001$) and seed bank species richness ($F_{2,54} = 10.4$, $p < 0.001$) for 2011–2013 were greater in the restored field than in the restored forest and control area of the study.

Treatment	Seed bank abundance \pm SE	Seed bank richness \pm SE
Restored forest (RF)	3.10 \pm 0.51	3.75 \pm 0.78
Restored field (FL)	9.95 \pm 1.35	19.0 \pm 4.65
Control forest (CF)	2.40 \pm 0.87	2.90 \pm 1.09

Seed Rain

The amount of incoming *L. maackii* seeds and berries (i.e., seed rain) differed among the treatments. CF had the greatest number of *L. maackii* seeds and berries, but interestingly RF had greater incoming *L. maackii* seed than FL ($F_{2,27} = 46.4$, $p < 0.0001$). CF plots averaged 14 seeds ($57/\text{m}^2$, $5.7 \times 10^5/\text{ha}$) and 20 berries per plot ($81/\text{m}^2$, $8.1 \times 10^5/\text{ha}$), while RF plots averaged four seeds ($16/\text{m}^2$, $1.6 \times 10^5/\text{ha}$) and 0.1 berries per plot ($0.6/\text{m}^2$, $6 \times 10^3/\text{ha}$) and FL only averaged one seed ($4/\text{m}^2$, $4 \times 10^4/\text{ha}$) and 0.05 berries per plot ($0.2/\text{m}^2$, $2 \times 10^3/\text{ha}$). Interestingly, we found more berries than seeds only in CF plots. The number of incoming seeds and berries did not change from year to year (respectively, $F_{2,27} = 2.19$, $p = 0.13$; $F_{2,27} = 0.18$, $p = 0.68$). The forest understory cover in CF was dominated by *L. maackii*, which is consistent with the greater seed rain in that treatment. In addition, the two forested areas had greater LAI (CF = 3.4 ± 1.3 and RF = 4.0 ± 1.5) than the restored area with no canopy (FL = 0.5 ± 0.4) ($F_{2,27} = 25.5$; $p < 0.0001$). Overall, we found the mean differences between the two restored sites (RF and FL) and CF were quite large. Therefore, our findings based on treatments were unlikely to be seriously affected by spatial autocorrelation effects that may have occurred because of the assumption of independence violation between treatment and location. Furthermore, it would be difficult to design an experiment of this sort where treatment could be separated from spatial effects.

Discussion

Nine years after removing invasive *L. maackii* from an urban riparian forest, the plant community is dominated by natives, but the invasive shrub has returned, and its abundance may be on the rise. For the first several years after *L. maackii* was eradicated from the site, native woody and herbaceous plant species richness increased in RF and FL compared to richness in the CF site dominated by *L. maackii*. In addition, native species dominated the seed bank, and the *L. maackii* seed rain entering RF and FL was substantially less than in CF. However, by nine years after removal, *L. maackii* was present with a moderate importance value in three of four transects in RF and FL combined and had the greatest importance value of all

woody species in the fourth (Table 1). This finding supports the recommendation that monitoring and maintenance of restored sites and reinvasion research studies needs to extend a minimum of ten years post-removal efforts.

Current literature on the impacts of *L. maackii* eradication to the forest community range from one to nine years post-removal, i.e., short-term studies (ours included). When examined collectively, the results generally demonstrate success in creating a native community by removing *L. maackii*. Very short-term studies, one to three years post-removal, found an increase in native woody seedlings when *L. maackii* was removed (Hartman and McCarthy 2004, Shields et al. 2015b). Studies that were seven to eight years post-removal found increases in both native cover and species richness in the communities where *L. maackii* was removed (Runkle et al. 2007, Boyce 2015). If our study terminated in year 7 or 8, we too would have reported an increase in herbaceous cover and species richness (Figures 1–2). Even in year 9, we saw that increase; however, it was not until year 9 that we observed *L. maackii* present and re-invading or becoming a more important species within the community (Table 1). Boyce (2015) suggested that variability in native species richness and cover can occur due to the time it takes for species to respond to *L. maackii* removal, while Hartman and McCarthy (2004) stress the importance of microenvironmental conditions. We suggest that dispersal and the site conditions that influence dispersal may also be important in driving the rate of community change post-removal of *L. maackii*. For example, we found *L. maackii* in RF to have greater importance values; it even became the most important species along one transect in year 9, when compared to the FL treatment. *Lonicera maackii* was present in FL in year 9, but the lower importance values may represent a lag effect; the existing canopy in RF may have allowed for easier dispersal and faster re-establishment of *L. maackii* than in FL. An alternative reason for the lag effect in FL could be the greater herbaceous cover between 2012 and 2015 slowed *L. maackii* seedling establishment.

Annual dispersal of *L. maackii* is important for the species, as it lacks a persistent seed bank (Luken and Matimiro 1991, Luken and Goessling 1995). We did not find *L. maackii* seeds in the soil seed bank of RF and FL, and we found very few seeds in our CF samples (Figure 3). *Lonicera maackii* seeds do not have well-developed dormancy mechanisms that would allow them to persist in the seed bank, and they exhibit a minimal delay between dispersal and germination (Luken and Goessling 1995). These seed characteristics of *L. maackii* are common and are similar to the life history of other forest species; furthermore, forest seed banks frequently have lower seed density and species richness than seed banks in other habitats (Hopfensperger 2007). In fact, we found FL to have greater species richness than both the RF and CF sites (Table 2). In addition, it is typical for a normally short-lived seed bank

to be degraded after an invasive species has occupied the site long enough (Collier et al. 2002).

Dispersal mechanisms employed by *L. maackii* include a combination of neighboring spread and long-distance dispersal (McNutt 2010, Gorchov et al. 2014, Barriball et al. 2015). In general, *L. maackii* can re-establish in a restored site or colonize a new location through both local expansion and long-distance dispersal mediated by animals (Bartuszevige and Gorchov 2006, Barriball et al. 2015). Multiple bird species, especially those that prefer woodlot edges, and white-tailed deer are the dominant animals that disperse *L. maackii* seeds (Bartuszevige and Gorchov 2006, Castellano and Gorchov 2013, Guiden et al. 2015). Birds have been found to disperse viable *L. maackii* seeds in wooded corridors and edges after seed consumption and gut passage (Ingold and Craycraft 1983, Bartuszevige and Gorchov 2006). Therefore, locations where *L. maackii* has been removed that have an existing forest canopy may be more at risk for reinvasion than open areas without a tree canopy. While we found this to be true—by year 9, *L. maackii* held greater importance in the RF community than in the FL community—it may be only temporary until succession leads the open area into a shrub and early forest stage. Gorchov et al. (2014) found that this external recruitment is integral in *L. maackii* population establishment until around years 8 or 9, when the original colonists begin to reproduce and internal recruitment dominates. At the point when colonists become mature, *L. maackii* exhibits a clustered dispersal pattern with seedlings around mature individuals (Shields et al. 2014), which we clearly observed in our control treatment (data not shown). In addition, the CF treatment had more berries (likely falling directly from the parent plants) than seeds in the seed rain traps, while the RF and FL treatments had more seeds and fewer berries in the traps, suggesting dispersal of seed by birds into the areas.

While our findings represent only one urban restoration site, we have learned two new and potentially important lessons for managers of *L. maackii* removal sites. To prove most useful, these lessons should be further tested at multiple restoration locations and for even longer study durations (e.g., 15–20 years). The first lesson was that the removal method should be employed for multiple years (instead of only one year) to completely eradicate the existing *L. maackii* population (Loeb et al. 2010). During the first year, a native herbaceous seed mix should be applied to the removal area, along with planting native trees and shrubs to inhibit swift *L. maackii* re-establishment (Kettenring and Adams 2011). At this time, the seed bank should not be of concern and is not likely to contribute to *L. maackii* re-establishment. An existing tree canopy can help to slow *L. maackii* re-establishment, as the seedlings prefer 100% sunlight (Luken et al. 1997, Cipollini et al. 2009). However, as our seed rain data shows, one can expect avian dispersal of *L. maackii* into the site, especially

if there are nearby *L. maackii* patches (Bartuszevige and Gorchov 2006). In addition, if the site is near or connected via corridors to *L. maackii* patches, then dispersal by white-tailed deer should also be expected (Castellano and Gorchov 2013, Guiden et al. 2015).

The second lesson was that approximately ten years post-*L. maackii* removal may be a turning point for *L. maackii* to begin dominating the study area again. However, longer-term studies, such as those that extend to 15, 20, and 25 years post-removal effort, are needed to support and confirm this notion. How the continued invasion of *L. maackii* proceeds in these restored areas will be especially interesting. Because of light availability and competing canopy cover, we hypothesize that *L. maackii* shrubs will grow and gain importance at different rates in RF compared to FL. With longer studies, we may learn how much long-term management will be essential for a restored *L. maackii* site to remain free from its re-establishment. Our study already suggests that maintenance may not need to be extensive. Gorchov et al. (2014) recommended searching for and removing colonists as infrequently as once every three years due to the lack of reproduction in the youngest age class. However, at our study site *L. maackii* instead began to have greater importance values in some RF transects only after nine years post-removal (Table 1); therefore, managers could minimize costs by performing maintenance eradication as infrequently as every ten years.

In conclusion, we found the RF and FL areas to have greater species richness in both the herbaceous and woody plant communities when compared to the CF site dominated by *L. maackii*. We found *L. maackii* seed rain to be greatest in CF, and RF received more seed than FL. In addition, the seed bank was not found to be a concern for re-establishment of *L. maackii*. Most interestingly, by year 9 we began to see *L. maackii* gaining dominance in RF and becoming established in FL. Future research efforts must expand to include additional years post-removal to determine the fate of these restored systems, and future management of *L. maackii* sites would benefit by periodic elimination of *L. maackii* colonists to ensure a forest dominated by native species.

Acknowledgments

We thank the Northern Kentucky University Center for Environmental Restoration (formerly the Center for Applied Ecology) for funding the project and for helping with the seed rain trap deployment. Undergraduate students that were integral to data collection and analyses include Ellen Albrecht, James Brown, Renee Kirtman, Sarah Stryffeler, and Alicia Weber.

Literature Cited

Arthur, M.A., S.R. Bray, C.R. Kuchle and R.W. McEwan. 2012. The influence of the invasive shrub, *Lonicera maackii*, on leaf decomposition and microbial community dynamics. *Plant Ecology* 213:1571–1582.

- Barriball, K., E.J. McNutt, D.L. Gorchov and O.J. Rocha. 2015. Inferring invasion patterns of *Lonicera maackii* (Rupr) Herder (Caprifoliaceae) from the genetic structure of 41 naturalized populations in a recently invaded area. *Biological Invasions* 17:2387–2402.
- Bartuszevige, A.M. and D.L. Gorchov. 2006. Avian seed dispersal of an invasive shrub. *Biological Invasions* 8:1013–1022.
- Borgmann, K.L. and A.D. Rodewald. 2005. Forest restoration in urbanizing landscapes: interactions between land uses and exotic shrubs. *Restoration Ecology* 13:334–340.
- Boyce, R.L., R.D. Durtsche and S.L. Fugal. 2012. Impact of the invasive shrub *Lonicera maackii* on stand transpiration and ecosystem hydrology in a wetland forest. *Biological Invasions* 14: 671–680.
- Boyce, R.L. 2015. Recovery of native plant communities in southwest Ohio after *Lonicera maackii* removal. *Journal of the Torrey Botanical Society* 142:193–204.
- Braun, E.L. 1961. The woody plants of Ohio. Columbus, OH: Ohio State University Press.
- Braun-Blanquet, J. 1964. *Pflanzensoziologie*. Berlin, Germany: Springer-Verlag.
- Burton, M.L. and L.J. Samuelson. 2008. Influence of urbanization on riparian forest diversity and structure in the Georgia Piedmont, US. *Plant Ecology* 195:99–115.
- Cameron, G.N., T.M. Culley, S.E. Kolbe, A.I. Miller and S.F. Matter. 2015. Effects of urbanization on herbaceous forest vegetation: the relative impacts of soil, geography, forest composition, human access, and an invasive shrub. *Urban Ecosystems* 18:1051–1069.
- Castellano, S.M. and D.L. Gorchov. 2013. White-tailed deer (*Odocoileus virginianus*) disperse seeds of the invasive shrub, Amur honeysuckle (*Lonicera maackii*). *Natural Areas Journal* 33:78–80.
- Cipollini, K., E. Ames and D. Cipollini. 2009. Amur honeysuckle (*Lonicera maackii*) management method impacts restoration of understory plants in the presence of white-tailed deer (*Odocoileus virginiana*). *Invasive Plant Science and Management* 2:45–54.
- Collier, M.H., J.L. Vankat and M.R. Hughes. 2002. Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. *American Midland Naturalist* 147:60–71.
- Curtis, J.T. and R.P. McIntosh. 1950. The interrelations of certain analytic and synthetic phytosociological characters. *Ecology* 31:434–455.
- Dorning, M. and D. Cipollini. 2006. Leaf and root extracts of the invasive shrub, *Lonicera maackii*, inhibit seed germination of three herbs with no autotoxic effects. *Plant Ecology* 184:287–296.
- Duguay, S., F. Eigenbrod and L. Fahrig. 2007. Effects of surrounding urbanization on non-native flora in small forest patches. *Landscape Ecology* 22:589–599.
- Ehrenfeld, J.G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6:503–523.
- Flory, S.L. and K. Clay. 2005. Invasive shrub distribution varies with distance to roads and stand age in eastern deciduous forests in Indiana, USA. *Plant Ecology* 184:131–141.
- Flory, S.L. and K. Clay. 2009. Effects of roads and forest successional age on experimental plant invasions. *Biological Conservation* 142:2531–2537.
- Gayek, A. 2000. Effect of habitat variation on rate and success of colonization of two invasive shrubs, *Lonicera maackii* and *Ligustrum vulgare*, in a forested glen. MS thesis. Ohio State University.
- Gelbard, J.L. and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology* 17:420–432.
- Gorchov, D.L. and D.E. Trisel. 2003. Competitive effects of the invasive shrub, *Lonicera maackii* (rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. *Plant Ecology* 166:13–24.
- Gorchov, D.L., S.M. Castellano and D.A. Noe. 2014. Long-distance dispersal and diffusion in the invasion of *Lonicera maackii*. *Invasive Plant Science and Management* 7:464–472.
- Gould, A.M.A. and D.L. Gorchov. 2000. Effects of the exotic invasive shrub *Lonicera maackii* on the survival and fecundity of three species of native annuals. *American Midland Naturalist* 144:36–50.
- Grimm, N.B., S.H. Faeth, N.E. Golubiewsk, C.L. Redman, J. Wu, X. Bai and J.M. Briggs. 2008a. Global change and the ecology of cities. *Science* 319:756–760.
- Grimm, N.B., D.R. Foster, P.M. Groffman, J.M. Grove, C.S. Hopkinson, K.J. Nadelhofer, et al. 2008b. The changing landscape: ecosystem responses to urbanization and pollution across climate and societal gradients. *Frontiers in Ecology and the Environment* 6:264–272.
- Gross, K.L. 1990. A comparison of methods for estimating seed numbers in the soil. *Journal of Ecology* 78:1079–1093.
- Guiden, P., D.L. Gorchov, C. Nielsen and E. Schaubert. 2015. Seed dispersal of an invasive shrub, Amur honeysuckle (*Lonicera maackii*), by white-tailed deer in a fragmented agricultural-forest matrix. *Plant Ecology* 216:939–950.
- Hartman, K.M. and B.C. McCarthy. 2004. Restoration of a forest understory after the removal of an invasive shrub, Amur honeysuckle (*Lonicera maackii*). *Restoration Ecology* 12:154–165.
- Hidayati, S.N., J.M. Baskin and C.C. Baskin. 2000. Dormancy-breaking and germination requirements of seeds of four *Lonicera* species (Caprifoliaceae) with underdeveloped spatulate embryos. *Seed Science Research* 10:459–469.
- Hobbs, R.J. 1989. The nature and effects of disturbance relative to invasions. Pages 389–405 in J.A. Drake, H.A. Mooney, F. diCastri, R.H. Groves, F.J. Kruger, M. Rejmanek and M. Williamson (eds), *Biological Invasions: A Global Perspective*. Scope 37. Chichester, UK: John Wiley and Sons.
- Hobbs, R.J. and L.F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6:324–337.
- Hopfensperger, K.N. 2007. A review of similarity between seed bank and standing vegetation across ecosystems. *Oikos* 116:1438–1448.
- Hopfensperger, K.N., R.L. Boyce and D. Schenk. 2017. Removing invasive *Lonicera maackii* and seeding native plants alters riparian ecosystem function. *Ecological Restoration* 35:320–327.
- Hutchinson, T.F. and J.L. Vankat. 1997. Invasibility and effects of Amur honeysuckle in southwestern Ohio forests. *Conservation Biology* 11:1117–1124.
- Ingold, J.L. and M.J. Craycraft. 1983. Avian frugivory on honeysuckle (*Lonicera*) in southwestern Ohio in fall. *Ohio Journal of Science* 83:256–258.
- Joly, M., P. Bertrand, R.V. Gbangou, M.C. White, J. Dubé and C. Lavoie. 2011. Paving the way for invasive species: road type and the spread of common ragweed (*Ambrosia artemisiifolia*). *Environmental Management* 48:514–522.
- Kettenring, K.M. and C.R. Adams. 2011. Lessons learned from invasive plant control experiments: a systemic review and meta-analysis. *Journal of Applied Ecology* 48:970–979.
- Lieurance, D. and K. Landsbergen. 2013. The influence of light habitat on the physiology, biomass allocation, and fecundity of the invasive shrub Amur honeysuckle (*Lonicera maackii*, Caprifoliaceae). *The Journal of the Torrey Botanical Society* 143:415–426.

- Loeb, R.E., J. Germeraad, T. Treece, D. Wakefield and S. Ward. 2010. Effects of 1-year vs. annual treatment of Amur honeysuckle (*Lonicera maackii*) in forests. *Invasive Plant Science Management* 3:334–339.
- Loomis, J.D., G.N. Cameron and G.W. Uetz. 2014. Impact of the invasive shrub *Lonicera maackii* on shrub-dwelling *Araneae* in a deciduous forest in eastern North America. *American Midland Naturalist* 171:204–218.
- Luken, J.O. 1988. Population structure and biomass allocation of the naturalized shrub *Lonicera maackii* (Rupr.) Maxim. in forest and open habitats. *American Midland Naturalist* 119:258–267.
- Luken, J.O. and N. Goessling. 1995. Seedling distribution and potential persistence of the exotic shrub *Lonicera maackii* in fragmented forests. *American Midland Naturalist* 133:124–130.
- Luken, J.O. and D.T. Mattimiro. 1991. Habitat-specific resilience of the invasive shrub Amur honeysuckle (*Lonicera maackii*) during repeated clipping. *Ecological Applications* 1:104–109.
- Luken, J.O. and J.W. Thieret. 1996. Amur honeysuckle, it's fall from grace. *Bioscience* 46:18–24.
- Luken, J.O., L.M. Kuddes and T.C. Tholmeier. 1997. Response of understory species to gap formation and soil disturbance in *Lonicera maackii* thickets. *Restoration Ecology* 5:229–235.
- McEwan, R.W., M.A. Arthur and S.E. Alverson. 2012. Throughfall chemistry and soil nutrient effects of the invasive shrub *Lonicera maackii* in deciduous forests. *American Midland Naturalist* 168:43–55.
- McNeish, R.E. and R.W. McEwan. 2016. A review on the invasion ecology of Amur honeysuckle (*Lonicera maackii*, Caprifoliaceae) a case study of ecological impacts at multiple scales. *The Journal of the Torrey Botanical Society* 143:367–385.
- McNeish, R.E., E.M. Moore, M.E. Benbow and R.W. McEwan. 2015. Removal of the invasive shrub, *Lonicera maackii*, from riparian forests influences headwater stream biota and ecosystem function. *River Research Applications* 31:1131–1139.
- McNutt, E.J. 2010. Inferring invasion patterns of *Lonicera maackii* in southwestern Ohio from the genetic structure of established populations. MS thesis, Kent State University.
- Pfennigwerth, A.A. and S.E. Kuebbing. 2012. Direct costs associated with invasive non-native plants in Tennessee. *Wildland Weeds* 15:4–6.
- Pickett, S.T.A., M.I. Cadenasso, J.M. Grove, C.G. Boone, P.M. Groffman, E. Irwin, et al. 2011. Urban ecological systems: scientific foundations and a decade of progress. *Journal of Environmental Management* 92:331–362.
- Pimentel, D., R. Zuniga and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52:273–288.
- Poiani, K.A. and W.C. Johnson 1988. Evaluation of the emergence method in estimating seed bank composition of prairie wetlands. *Aquatic Botany* 32:91–97.
- Rathfon, R. and K. Ruble. 2007. Herbicide treatments for controlling invasive Bush honeysuckle in a mature hardwood forest in West-Central Indiana. Pages 187–197 in D.S. Buckley and W.K. Clatterbuck (eds.), *Proceedings of the 15th Central Hardwood Forest Conference*; February 27–March 1, 2006, Knoxville, TN. General Technical Report SRS101. Asheville, NC: Southern Research Station, US Department of Agriculture, Forest Service.
- Renne, I.J., W.C. Barrow Jr., L.A. Johnson Randall and W.C. Bridges Jr. 2002. Generalized avian dispersal syndrome contributes to Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasiveness. *Diversity and Distributions* 8:285–295.
- Rose, S. 1997. Influence of suburban edges on invasion of *Pittosporum undulatum* into the bushland of northern Sydney, Australia. *Australian Journal of Ecology* 22:89–99.
- Runkle, J.R., A. Disalvo, Y. Graham-Gibson and M. Dorning. 2007. Vegetation release 8 years after removal of *Lonicera maackii* in west-central Ohio. *Ohio Journal of Science* 107:125–129.
- Schulz, K.E., J. Wright and S. Ashbaker. 2012. Comparison of invasive shrub honeysuckle eradication tactics for amateurs: stump treatment versus regrowth spraying of *Lonicera maackii*. *Restoration Ecology* 20:788–793.
- Shields, J.M., M.A. Jenkins, P.A. Zollner and M.R. Saunders. 2014. Effects of Amur honeysuckle invasion and removal on white-footed mice. *Journal of Wildlife Management* 78:867–880.
- Shields, J.M., M.A. Jenkins, M.R. Saunders, K.D. Gibson, P.A. Zollner and J.B. Dunning, Jr. 2015a. Influence of intensity and duration of invasion by Amur honeysuckle (*Lonicera maackii*) on mixed hardwood forests of Indiana. *Invasive Plant Science Management* 8:44–56.
- Shields, J.M., M.R. Saunders, K.D. Gibson, P.A. Zollner, J.B. Dunning, Jr. and M.A. Jenkins. 2015b. Short-term response of native flora to the removal of non-native shrubs in mixed-hardwood forests of Indiana, USA. *Forests* 6:1878–1896.
- Shochat, E., S.B. Lerman, J.M. Anderies, P.S. Warren, S.H. Faeth and C.H. Nilon. 2010. Invasion, competition, and biodiversity loss in urban ecosystems. *Bioscience* 60:199–208.
- Swab, R.M., L. Zhang and W.J. Mitsch. 2008. Effect of hydrologic restoration and *Lonicera maackii* removal on herbaceous understory vegetation in a bottomland hardwood forest. *Restoration Ecology* 16:453–463.
- Trammel, T.L.E. and M.M. Carreiro. 2011. Vegetation composition and structure of woody plant communities along urban interstate corridors in Louisville, KY, U.S.A. *Urban Ecosystems* 14:501–524.
- Trisel, D.E. 1997. The invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae) factors leading to its success and its effect on native species. PhD dissertation, Miami University.
- Vila, M., J.L. Espinar, M. Hejda, P.E. Hulme, V. Joaróšik, J.L. Maron, et al. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14:702–708.
- White, R.J., M.M. Carrerio and W.C. Zipperer. 2014. Woody plant communities along urban, suburban, and rural streams in Louisville, Kentucky, USA. *Urban Ecosystems* 17:1061–1094.

Kristine N. Hopfensperger (corresponding author):
 Department of Biological Sciences, Northern Kentucky University,
 1 Nunn Drive, Highland Heights, KY 41099,
 hopfenspek1@nku.edu.

Richard L. Boyce, Department of Biological Sciences,
 Northern Kentucky University, Highland Heights, KY.

Devin Schenk, The Nature Conservancy, Ohio Chapter,
 Dublin, OH.

Copyright of Ecological Restoration is the property of University of Wisconsin Press and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.