2017. Proceedings of the Indiana Academy of Science 126(1):55–62

FOREST PLANT COMPOSITION IN PATCHES OF VARYING AGES IN AN INTENSIVELY FARMED LANDSCAPE

Aradhana Joanna Roberts: Heliae Corporation, 578 E. Germann Road, Gilbert, AZ 85297 USA

Jonathon W. Schramm[1]: Merry Lea Environmental Learning Center of Goshen College, P.O. Box 263, Wolf Lake, IN 46796 USA

ABSTRACT. The stability of plant community diversity in post-agricultural forests is an important ecological question throughout the Midwestern United States. Since forests in this region are often islands in a matrix of annual croplands, a better understanding of the persistence of native plant diversity and the potential for incursions of exotic invasive species is crucial for maintaining biodiversity in these landscapes. This study examined plant communities in several post-agricultural forests in northern Indiana that varied by age since agricultural abandonment, and investigated differences in invasive species presence across several canopy layers (canopy, midstory, understory). Vegetation was sampled in circular plots across three distinct forest parcels. In addition to forest age, several other conditions hypothesized to affect plant diversity, such as tree canopy cover, litter depth, underlying soil type, and adjacent land uses, were also measured. Overall herbaceous diversity and integrity, as measured by the Floristic Quality Index (FQI), were relatively high in these forests. Invasive species, e.g., *Alliaria petiolata* and *Rosa multiflora*, were also generally uncommon in these forests, even in areas affected by local disturbances such as deer trails, trash dumps, and canopy gaps, although older plots generally had lower invasive presence than younger ones. This study highlights the importance of maintaining existing older-growth forests in this landscape and avoiding disturbances to the interior of such forests to minimize further expansion of invasive species.

Keywords: plant invasion, land use legacies, edge effects, herbaceous diversity, FQI

INTRODUCTION

A diversity of variables influences the composition of contemporary plant communities and their vulnerability to invasive species. But particularly in landscapes marked by intensive human disturbance, the proximity of native habitats to human-dominated land uses can be a key determinant of both biotic and abiotic conditions in the habitat (Vilà & Ibáñez 2011; With 2002). Further, previous land use often leaves a persistent ecological legacy, even as those portions of the landscape return to a less-disturbed state (Medley & Krisko 2007; Flory & Clay 2009; Kuhman et al. 2010). Our ability to predict areas of natural habitat with high native biodiversity, and contrarily low invasive presence, depends on our understanding of the current and prior arrangement of land uses in an area.

Even in regions with substantial mature forest cover, ongoing agricultural and urban land uses contribute to fragmentation of those habitats, with concomitant increases in edge effects (Gavier-Pizarro et al. 2010; Harper et al. 2005; McDonald & Urban 2006; Tomasetto et al. 2013). A previous study in old-growth forest islands in rural central Indiana found that alien species richness and frequency dropped sharply inward from forest edges, and that forest interiors were relatively free of aliens (Brothers & Spingarn 1992). The primary factors believed to limit invasion were low light and disturbance levels in interiors, combined with limited dispersal of invasive propagules into the interior. In light of the many changes on this landscape since the work of Brothers & Spingarn (including increasing landscape saturation by invasive propagules, higher populations of herbivores, and altered climate regimes), part of the motivation for this study was to ascertain whether their patterns still held in this region. Gignac & Dale (2007) also observed that habitat fragment size and shape affected native and alien plant species richness and abundance in agro-environments, with native abundance highest in larger, less-disturbed patches, and overall richness highest in edges. Invasion processes are also strongly influenced by distur-

[1] *Corresponding author:* Jonathon W. Schramm, 260-799-5869 (phone), 260-799-5875 (fax), jschramm@goshen.edu.

bances, including the passages caused by roads and other transportation routes, such as trails. Increased soil moisture, soil disturbance, nutrient runoff, sun exposure, and temperature along the road edges in the upper Midwest promote plant invasion and growth of exotic species such as *Elaeagnus umbellata* Thunb., *Ligustrum obtusifolium* Siebold & Zucc., and *Lonicera maackii* (Rupr.) Herder (Flory & Clay 2009; Watkins et al. 2003).

Since the remaining forest fragments in agricultural landscapes are likely under high invasion pressure, it is crucial that efficient methods for identifying and controlling invasions in these habitats be developed. This study was designed to provide a limited snapshot of current herbaceous diversity and invasion extent in mixed-hardwood forests of the agricultural upper Midwest. Specifically, we questioned whether the abundance of invasive plant species varied significantly with the age of the forest fragments, and how it was related to other patterns of plant diversity and environmental variables.

METHODS

Study location.—The study was conducted at the Merry Lea Environmental Learning Center (MLELC), in Wolf Lake, Indiana (approx. 41.3180° N, 85.5140° W), in the summer of 2013 (June – July). MLELC is an area consisting of diverse ecosystems and landscapes, including prairies, forests, marshes, wetland, and savanna. This high landscape heterogeneity means that many of the habitats have high perimeter: area ratios, although the natural habitat patches are still generally much larger than in the surrounding agricultural landscape. The 481 ha preserve is not only a host for much of the region's biodiversity but also incorporates many ongoing restoration projects, including recreation of wetland habitats by altering hydrology and reestablishing prairies through controlled burning. The landscape bears numerous prominent features that are remnants of the last glaciation, including eskers, kames, and kettle ponds.

Plot selection and structure.—Sampled plots were in three forests within MLELC, designated Thomas, Wysong, and Byer after the original landowners (Fig. 1). These forests were chosen to represent as much of the range of upland forest types present on the MELEC property as possible. Each one has complete canopy cover, but the tree species richness varies across the three forests, as does the specific land use history. None are primary, old-growth forest, although Byer (formerly managed woodlot) has been closed canopy since at least the 1930's (decade of the earliest aerial photographs of the region), while Thomas and Wysong (formerly pastures and crop fields; Fig. 2) were released from agriculture 50–60 years ago.

Each circular plot was 78.5 m^2 in area (5 m radii) and 50 m from neighboring plots (measured from center-to-center). To assure sampling covered the breadth of sub-habitats present in each forest, plots were laid out along transects radiating out from the approximate center of the forest, as spokes from a hub. The factors assessed for each plot are detailed in Table 1. In addition to field data, each plot's coordinates were collected using GPS, and geographic information systems (ArcMap, ESRI) were then used to calculate distances to the nearest non-forested land cover, as well as plot slope, plot aspect (both from the State of Indiana Geographic Information Office), and USDA-SSURGO (Soil Survey Geographic Database) soil series.

Thomas: This woodlot was relatively open in the understory (Fig. 2A) with housing, old fields, and active farm land surrounding the edges. Dominant tree species in these plots included *Acer saccharum* Marshall, *Ulmus americana* L., *Quercus alba* L., *Q. velutina* Lam., *Q. rubra* L. and *Ostrya virginiana* (Mill.) K. Koch. Shrubs were generally sparse in this woodlot but included scattered populations of *Xanthoxylum americanum* Mill. and the invasive species *Eleagnus umbellata* and *Lonicera maackii*. The range of litter depth in Thomas was 1.8 mm to 34 mm (mean 16.6 mm). The average canopy cover was 94%.

Wysong: The edges and some of the interior featured dense thickets of shrubs, including natives such as *X. americanum, Rubus occidentalis* L., *Lindera benzoin* L., and occasional clusters of invasives including *Rosa multiflora* Thunb., and *E. umbellata*. The tree community was quite diverse, but dominant species included *Q. alba, Ulmus rubra* Muhl., *Juglans nigra* L., *A. saccharum*, and *Crataegus* spp. (Fig. 2B). Along one of the transect lines the distance between plots was larger due to interspersed vernal pools that were not sampled because of their dramatically different hydrology and edaphic conditions. The range of litter depth

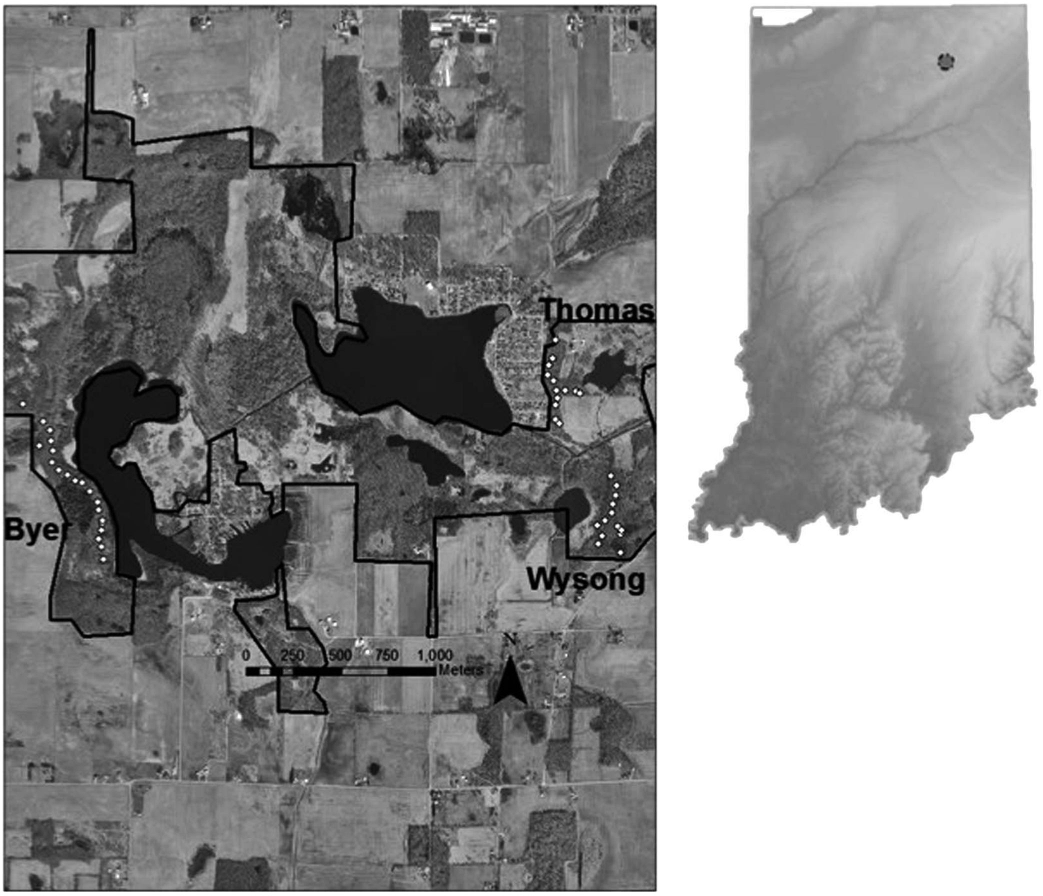

Figure 1.—Aerial photograph of the Merry Lea Environmental Learning Center (MLELC; border shown with solid dark line), with the Thomas, Wysong, and Byer woodlots labeled. Plot locations in each woodlot are denoted by gray dots. Highlighted dot on the Indiana map indicates the location of MLELC in Noble County. (Source data from the Indiana Geological Survey, Spatial Data Portal, at: http://gis.iu.edu/downloadData/index.php)

in Wysong was 2.2 mm to 34 mm (mean 9.9 mm). The average canopy cover was 95%.

Byer: This woodland surmounts a gravelly esker, with more mesic forest communities on either side of this drier upland. It has many deer trails and a great diversity of plot settings; for example, dense populations of *Prunus serotina* Ehrh. could be found away from the esker but *U. rubra* was well represented throughout. Important tree species in this woodlot included *A. saccharum, Celtis occidentalis* L.*, Fraxinus americana* L.*, J. nigra, O. virginiana, P. serotina*, and *U. rubra*. Significant shrub species included *L. benzoin, R. occidentalis*, and *R. multiflora*, as well as saplings of many of the above tree species. The majority of these plots were located along a narrow section of the woodland with frequent canopy gaps due to fallen oak and elm trees. In addition, patches of marshy soil and accompanying fern cover were present within or adjacent to several plots. The range of litter depth in Byer was 10.8 mm to 27.4 mm and the average was 17.3 mm. The average canopy cover was 96%.

Statistical analysis.—Data were analyzed using PC-ORD (v5.1) and R (v3.0.2). PC-ORD was used to run non-metric multidimensional scaling (NMS) ordination of the understory community data (autopilot mode with Sorensen distance measure; 50 runs with real data, and 50 with randomized; maximum iterations set at 200; stability criterion over last

Figure 2.—Typical plot structure of Thomas (A) and Wysong (B). Note the relatively open understory in the former as compared to the latter. Both forests are on former agricultural land (pastures) within a half-mile of each other.

10 iterations set to 0.00001). R was used to run stepwise multiple linear regressions (functions ‘lm’ and ‘step’) to better describe which of the numerous plot level variables most influenced the richness and abundance of non-native species in the plots. R was also used to generate one-way ANOVAs (function ‘aov’) to compare means for biotic and environmental variables between the three woodlots ($\alpha < 0.05$), with Tukey’s pairwise test used post-hoc to identify significantly different forests.

The floristic quality index (FQI) value was calculated for each plot using the formula below, which was developed by Swink & Wilhelm (1979, 1994), and subsequently modified for use in Indiana (Rothrock 2004). This index weights the species present in a community by the relative coefficient of conservatism (CC) of each species, where lower values are assigned to more wide-ranging, disturbance-tolerant species and higher

Table 1.—Measurements, observations, and spatial data collected for each plot.

Data category	Variables measured or calculated
Overstory (Trees)	- species identification - diameter at breast height (DBH; all individuals > 2 m tall)
Midstory (Shrubs and Saplings)	- species identification - measured stem count and area covered by each individual (m^2) - sapling trees shorter than 2 m were recorded in this layer
Understory (Herbs and Seedlings)	- species identification (including tree and shrub seedlings) - % cover for each species in four randomly-distributed 1 m^2 quadrats per plot, one quadrat per quarter-section of the circle (cover classes: one small plant [0.01], several small plants [0.05], 0.25-0.75, 0.75-1.25, 1.25-5, 5-10, 10-15, 15-20, 20-30, 30-50, 50-90, and > 90%) - floristic quality index value (FQI) calculated for each plot (see text)
Environmental Variables	- % canopy cover (mean of concave spherical densiometer readings at 5 locations in plot: center and 1 m from center on each of four cardinal direction bearings) - mean leaf litter depth-to-duff, cm (measured at same five locations) - presence/absence of natural (deer trails, windthrown trees) and anthropogenic (foot trails, farm trash dumps) disturbances within the plot borders
Geospatial Data	- distance of each plot center to forest edge in 2012 (using orthophotography) and in 1938 (Byer only; using georectified aerial photography; Thomas and Wysong have regenerated since 1938) - underlying SSURGO soil series (then simplified to two main series – muck and loam) and permeability class (high, medium, and low) - mean slope of plot (%) and plot aspect (azimuth categorized into appropriate cardinal direction [e.g., $315 \leq x < 45 = N$, $45 \leq x < 135 = E$, etc.]; both calculated based on $5 \times 5'$ digital elevation models from the State of Indiana)

Table 2.—Summary of the species richness, densities (cover), and selected physical characteristics of plots in this study. All numerical values are means of plots in that category (standard error values follow in parentheses); qualitative values are the most common value for that variable in that woodlot. Variables with a significant difference in means among the three forests are bold-faced, with the *p*-value of their one-way ANOVA test indicated.

Woodlot	Thomas ($n = 13$)	Wysong ($n = 13$)	Byer ($n = 18$)	Overall ($n = 44$)
Species Richness				
Trees	3.9 (1.1)	2.4 (0.7)	3.0 (0.7)	**3.1 (0.2) $p = 0.011$**
Shrubs	1.6 (0.4)	3.1 (0.9)	2.9 (0.7)	**2.6 (0.3) $p = 0.039$**
Herbs	10.8 (3.0)	12.7 (3.5)	13.2 (3.1)	12.3 (0.7)
Invasive	0.8 (0.2)	1.2 (0.3)	1.2 (0.3)	1.1 (0.1)
Species Densities				
Shrub Cover (m^2)	4.1 (1.1)	11.7 (3.2)	3.8 (0.9)	**6.2 (1.0) $p < 0.001$**
Herbs (% cover)	30.7 (8.5)	45.3(12.6)	50.8 (12.0)	43.2 (4.2)
Invasive Herbs (% cover)	2.1 (0.6)	7.4 (2.0)	3.6 (0.8)	4.3 (1.7)
Physical Characteristics				
Primary Soil Type	Loam	Loam	Loam	Loam
Soil Permeability	High	High	Medium	High
Mean Litter Depth (mm)	13.8 (3.8)	9.8 (2.7)	17.3 (4.1)	14.1 (1.3)
Mean Canopy Cover (%)	94 (1.1)	95 (1.5)	96 (0.4)	95.4 (0.6)

coefficients (up to 10) to more disturbance-sensitive species. Together with the overall richness of native species in the community, this index differentiates communities based not just on richness, but also the likelihood that the species present represent the native suite for such habitats. The FQI values were then used in the regression analyses with R. The formula below describes calculation of the standard FQI value, where CC_i is the CC value for every species in the sample and $N_{\text{native species}}$ is the richness of native species found in the sample.

$$FQI = \frac{\sum(CC_i)}{\sqrt{N_{\text{native species}}}}$$

RESULTS

General forest descriptions.—In general the plots were similar across all three forests in terms of structural variables such as soil series and permeability, litter layer thickness, and canopy coverage (Table 2). Herbaceous species richness and overall cover were also similar across all plots, although the species composition varied from plot to plot. On average, plots in these forests contained about 12 total species in their mid-summer herbaceous layers, with one of those being a non-native invasive species (from among four principal species: *Alliaria petiolata* (M. Bieb.) Cavara & Grande, *Euonymus alatus* (Thunb.) Siebold, *Rosa multiflora*, and *E. umbellata*). Similarly, herbaceous plants covered 43% of the forest floor in these plots, with invasives comprising one-tenth of that total coverage. The three forests, however, did have differences between them in terms of the woody plants (Table 2). Thomas had significantly higher richness of tree species and significantly lower shrub species richness per plot. In terms of total shrub cover, though, Wysong had substantially more shrubs than either Thomas or Byer (Table 2).

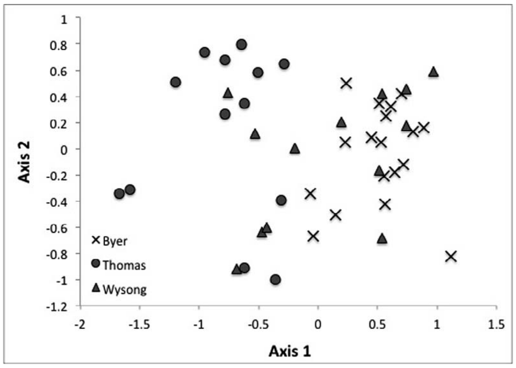

Figure 3.—NMS ordination results for three woodlots in Noble County, Indiana. For clarity, only two dimensions of the ordination are depicted, although a three-dimensional solution was more parsimonious. Plots from different woodlots are depicted with different symbols.

Table 3.—Correlations of key environmental variables to the three axes from the most parsimonious NMS solution.

	Axis 1		Axis 2		Axis 3	
	r	r^2	r	r^2	r	r^2
Canopy Density	0.405	0.164	0.128	0.016	0.09	0.008
Litter Depth	-0.075	0.006	0.162	0.026	0.195	0.038
Disturbance Presence	-0.172	0.029	-0.318	0.101	-0.175	0.031
Distance-to-Edge	0.404	0.163	-0.036	0.001	-0.295	00.087
Adjacent Land Use	0.431	0.186	0.362	0.131	0.014	0.000
Soil Category	-0.126	0.016	0.320	0.103	-0.280	0.078

Invasion characteristics by plot.—Invasion was also related to plot-scale disturbance factors such as deer trails, fallen trees, and farm trash dumps. There was an inverse relationship between the herb and shrub layers in such plots. In plots with higher shrub abundance, whether native or not, there was less herbaceous cover overall. Invasion also seemed to vary with soil type; muck soils were observed to have more total herb abundance and richness but loam soils had higher invasion. In our plots greater herbaceous species richness and cover of invasive herbs occurred on plots with loamy soils of medium-high permeability.

Composition in relation to environmental variables.—The ordination graph (Fig. 3) illustrates the relative dissimilarities between the different plots according to the understory species present. NMS analysis illustrated the dissimilarity between Thomas and Byer woodlots, and the high variability of the plots in Wysong. Mean final stress for a two-dimensional solution was 24.706 (28.03 in the Monte Carlo test), for a 3-dimensional solution was 17.476 (18.97 in Monte Carlo) and 14.011 for a 4-dimensional solution (14.5 in Monte Carlo). Axis 1 explained 31.8% of the variation, Axis 2 12.0%, and Axis 3 an additional 16.0%, meaning the three-dimensional solution accounted for 60% (r^2 = 0.598) of the total variation. The environmental factors correlated to the plot ordination axes include canopy cover, litter depth, present distance from edge, and adjacent land use type (Table 3).

Richness of the understory was correlated with several variables that influenced the abiotic conditions of the forest floor, as seen in the multiple regression model results (Table 4). The richness of invasive species alone was not strongly connected to the environmental variables measured in this study, except that it increased with increasing overall herbaceous richness and decreased with increasing presence of more ecologically 'conservative' native species (i.e., FQI). Not surprisingly, the cover of invasive species was positively related to the richness of invasives present (where one species was found more typically were), although their abundance also increased on loamy soils and decreased where a rich shrub community was present.

DISCUSSION

This study, although limited in scope, underlines the crucial importance of forest longevity on limiting the spread of non-native invasive species, even though numerous other variables can

Table 4.—Summary of forward-selected linear regression models examining the relationships between invasive species richness and abundance and a suite of environmental variables collected at the plot level. Estimated coefficients of each relationship are shown, with significant relationships in **bold** (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Overall model results: Invasive richness (F = 8.137 on 5 and 37 df (p = 0.00003), final AIC of -56.96 vs null model AIC of -18.35); Invasive abundance (F = 5.877 on 5 and 37 df (p = 0.00043), final AIC of 112.5 vs null model AIC of 127.61).

Variable	Invasive richness	Invasive abundance
(Intercept)	0.4303	2.9861
Invasive Richness		**2.6701*** **
Shrub Spp. Richness	-0.1003	**-0.8035***
Muck Soils		1.5040
Loam Soils		**3.0702***
Tree Spp. Richness		-0.7359
Invasive Abundance	0.0364	
FQAI	**-0.1371****	
Herb Richness	**0.1583*****	
Slope	-0.0150	

likewise affect the composition of forest plant communities. Although invasive species, such as *A. petiolata* and *R. multiflora*, were observed in many of the plots in this study, in very few of those plots were invasive species common, even those species that have been present on the surrounding landscape for decades (Brothers & Spingarn 1992). This same pattern held across relatively large variations in the structure (mid- and understory cover) and richness of the plant community, with the particular species composition being less important than the age and structural development of the surrounding forest (Table 4). Surprisingly, local disturbances of any type tended to correlate to lower cover of invasives in the understory, with many of these also associated with higher understory FQI values. This hints that local (plot-level/microsite) disturbance may be important in promoting diversity and even limiting invasion in these forests, by creating reservoirs of plant propagules necessary to maintain landscape (beta) diversity and support community resistance to invasion (Hobbs & Huenneke 1992; Holle 2013).

Although invasive species were sparse in many of the plots, the type of plots that they were preferentially found in was telling, namely those with recent (i.e., 50–60 years before present) agricultural activity (often loamy soil sites), and adjacent to ongoing agricultural disturbances. Although these factors were not all statistically significant in our study, they align with other studies that identified recent soil disturbance, elevated soil nutrient levels (especially nitrogen), and propagule dispersal through wildlife such as birds as vital for the spread of invasive species (Flinn & Vellend 2005; Knight et al. 2009; Medley & Krisko 2007). They also are often brighter, warmer, and drier than older, more structurally complex forests in the region, and thus may be preferred habitats for many of the common invasive species in the area, which are well-adapted for droughty, disturbed, higher-light conditions (Brothers & Spingarn 1992; McDonald et al. 2008).

These findings have several useful implications for management regimes regarding invasive plants in this region. Concentrating invasive species management in forests with recent agricultural histories, rich soils, and close to agricultural land will more clearly reduce the population densities of many invasive plants. By contrast native-dominated forest interiors will likely continue to support that diversity, provided canopies remain largely intact outside of natural tree fall or careful selective logging. Another corollary is that awareness and careful monitoring of existing disturbed areas in forest interiors is an important way to prevent incipient invasions from becoming larger ones.

ACKNOWLEDGMENTS

This work would not have been possible without the support of the MLELC and Goshen College, especially the Maple Scholars program and the 2013 cohort. Special thanks to Bill Minter at Merry Lea for assistance with the historical land cover imagery. In addition, we thank the work of three anonymous reviewers, whose comments and suggestions made this a much clearer manuscript.

LITERATURE CITED

Brothers, T.S. & A. Spingarn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conservation Biology 6:91–100.

Flinn, K.M. & M. Vellend. 2005. Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and the Environment 3:243–250.

Flory, S.L. & K. Clay. 2009. Effects of roads and forest successional age on experimental plant invasions. Biological Conservation 142:2531–2537.

Gavier-Pizarro, G., V. Radeloff, S. Stewart, C. Huebner & N. Keuler. 2010. Rural housing is related to plant invasions in forests of southern Wisconsin, USA. Landscape Ecology 25:1505–1518. http://doi.org/10.1007/s10980-010-9516-8.

Gignac, L.D. & M.R. Dale. 2007. Effects of size, shape, and edge on vegetation in remnants of the upland boreal mixed-wood forest in agro-environments of Alberta, Canada. Botany 85:273–284.

Harper, K.A., S.E. Macdonald, P.J. Burton, J. Chen, K.D. Brosofske, S.C. Saunders, E.S. Euskirchen, D. Roberts, M.S. Jaiteh & P.-A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology 19:768–782. http://doi.org/10.1111/j.1523-1739.2005.00045.x.

Hobbs, R.J. & L.F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6:324–337. http://doi.org/10.1046/j.1523-1739.1992.06030324.x.

Holle, B.V. 2013. Environmental stress alters native-nonnative relationships at the community scale. Biological Invasions 15:417–427. http://doi.org/10.1007/s10530-012-0297-7.

Knight, T.M., J.L. Dunn, L.A. Smith, J. Davis & S. Kalisz. 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. Natural Areas Journal 29:110–116. http://doi.org/10.3375/043.029.0202.

Kuhman, T., S. Pearson & M. Turner. 2010. Effects of land-use history and the contemporary landscape on non-native plant invasion at local and regional scales in the forest-dominated southern Appalachians. Landscape Ecology 25:1433–1445. http://doi.org/10.1007/s10980-010-9500-3.

McDonald, R.I., G. Motzkin & D.R. Foster. 2008. Assessing the influence of historical factors, contemporary processes, and environmental conditions on the distribution of invasive species. The Journal of the Torrey Botanical Society 135:260–271. http://doi.org/10.3159/08-RA-012.1.

McDonald, R. & D. Urban. 2006. Edge effects on species composition and exotic species abundance in the North Carolina piedmont. Biological Invasions 8:1049–1060. http://doi.org/10.1007/s10530-005-5227-5.

Medley, K.E. & B. Krisko. 2007. Physical site conditions and land use history as factors influencing the conservation of regrowth forests in a southwest Ohio nature reserve. Natural Areas Journal 27:31–40. http://doi.org/10.3375/0885-8608(2007)27[31:PSCALU]2.0.CO;2.

Rothrock, P. 2004. Floristic Quality Assessment in Indiana: the Concept, Use and Development of Coefficients of Conservatism. Final Report for ARN A305-4-53, EPA Wetland Program Development Grant CD975586-01. Taylor University, Upland, IN. 96 pp. At: http://www.lrl.usace.army.mil/Portals/64/docs/regulatory/FloristicAssessment_IND.pdf.

Swink, F. & G.S. Wilhelm. 1979. Plants of the Chicago Region (3rd ed.). Morton Arboretum, Lisle, Illinois. 922 pp.

Swink, F. & G.S. Wilhelm. 1994. Plants of the Chicago Region (4th ed.). Indiana Academy of Science, Indianapolis, Indiana. 936 pp.

Tomasetto, F., R.P. Duncan & P.E. Hulme. 2013. Environmental gradients shift the direction of the relationship between native and alien plant species richness. Diversity and Distributions 19:49–59. http://doi.org/10.1111/j.1472-4642.2012.00939.x.

Vilà, M. & I. Ibáñez. 2011. Plant invasions in the landscape. Landscape Ecology 26:461–472. http://doi.org/10.1007/s10980-011-9585-3.

Watkins, R.Z., J. Chen, J. Pickens & K.D. Brosofske. 2003. Effects of forest roads on understory plants in a managed hardwood landscape. Conservation Biology 17:411–419. http://doi.org/10.1046/j.1523-1739.2003.01285.x.

With, K.A. 2002. The landscape ecology of invasive spread. Conservation Biology 16:1192–1203. http://doi.org/10.1046/j.1523-1739.2002.01064.x.

Manuscript received 28 April 2015, revised 7 April 2017.