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RESEARCH ARTICLE

Edge Effects, Invasion, and the Spatial Pattern of Herb-Layer Biodiversity in an Old-Growth Deciduous Forest Fragment

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ABSTRACT: Habitat loss and fragmentation are major threats to global biodiversity, altering both habitat structure and availability. Small preserves nested within landscapes dominated by human commerce can serve as long-term storehouses of biodiversity, yet they are vulnerable to threats such as exotic plant invasion and disturbance. The Drew Woods State Nature Preserve (DWSNP) in Darke County, Ohio, provided an opportunity to understand the capacity of a small old-growth preserve for maintaining regional floristic biodiversity and assessing ecological threats. A series of six approximately biweekly herbaceous layer samplings were conducted across 32 1-m^2 circular plots within DWSNP, and percent vegetative cover was estimated for each herbaceous species identified. The vascular flora of this 6-ha site was inventoried and used for a Floristic Quality Assessment. Spatial patterns were visualized using ArcGIS software, and linear regression analyses and non-metric multidimensional scaling were used to test for relationships between measures of diversity and cover and environmental variables. A total of 176 species were identified across 124 genera and 67 families, and the majority of species were native (89.2%). Characteristic native herb species included *Jeffersonia diphylla* (twinleaf), *Trillium sessile* (toad trillium), *Allium tricoccum* (wild leek), and *Erythronium americanum* (trout lily), all of which are indicative of high-quality forest. A north–south gradient of species richness was found across all samplings, with the southernmost plots tending to be most species-rich ($P < 0.01$, $r^2 \leq 0.42$). This pattern appeared to be linked with gradients of light and temperature that are likely driven by edge effects. Old-growth forests are known for their resiliency, a trait that was evident in the high-quality flora of DWSNP; however, they are not immune to invasion by exotic species. We discovered a significant, nascent, invasion of *Alliaria petiolata* (garlic mustard), which has the potential to negatively impact the biological integrity of the site if left unchecked. Small forest fragments in agricultural landscapes can act as important reservoirs of biodiversity, but effective preservation and management of these sites requires an understanding of the threats to their ecological integrity as well as environmental drivers of diversity.

Index terms: diversity, edge effects, Floristic Quality Assessment Index, herbaceous layer, old-growth forest

INTRODUCTION

Understanding the factors underlying patterns of biodiversity is a venerable goal in ecology that has taken on increased urgency due to global-scale anthropogenic acceleration of species extinction rates (Rockström et al. 2009; Costello et al. 2013). In the Eastern Deciduous Forest (EDF) of temperate eastern North America, the herbaceous layer is a biodiversity "treasure-house" (*sensu* E.O. Wilson; Ricketts et al. 1999; Gilliam 2007). These species-rich herbaceous communities are variable across both spatial and temporal gradients (Gleason 1926; Braun 1950; Whittaker 1956; Small and McCarthy 2002), and their composition is shaped by an array of local factors, including microtopography, soil fertility, and overstory canopy structure (Bratton 1976; Brewer 1980; Thompson 1980; Croizer and Boerner 1984; Whitney and Foster 1988; Hutchinson et al. 1999; Ford et al. 2000; Gilliam and Roberts 2003; Small and McCarthy 2005; McEwan and Muller 2011; Chapman and McEwan 2013). The herbaceous flora of the EDF includes an array of locally rare species, some of which have low reproductive rates, minimal dispersal distances, and complex dormancies (Bierzychudek 1982; Matlack 1994; Whigham 2004; Albrecht and McCarthy 2006). These "slow plants" are poorly suited to survival in a dynamic anthropogenic landscape (Duffy and Meier 1992; Jules 1998; Matlack 2005; Vellend et al. 2007), and the extinction debt created by land conversion can persist for decades (Vellend et al. 2006).

In landscapes dominated by human commerce, documenting and preserving biodiversity often takes place in fragmented parcels. In large agricultural regions, like the Midwest of North America, habitats are intermingled into a patchwork of farmland and quasi-suburban development. Small patches of habitat in anthropogenic landscapes may play a critical role in maintaining regional biodiversity and landscape utility for a wide range of species (Scherr and McNeely 2008; Edvardsen et al. 2010; Polyakov et al. 2013). Fragmented forest preserves, especially those that are directly adjacent to agricultural lands, may be subjected to edge effects, resulting in altered soil moisture, temperature, light, and wind exposure (Wales 1972; Ranney

1977; Matlack 1993), as well as impacts from herbicide drift and fertilizer runoff (Boutin and Jobin 1998). Invasive species may also be able to penetrate into these habitat fragments (Wilson et al. 2013), with subsequent effects on biodiversity and ecosystem function (Mack et al. 2007; Powell et al. 2011; McEwan et al. 2012).

An old-growth forest parcel located in a matrix of agricultural lands in western Ohio (USA) provided an opportunity to document floristic biodiversity in a high-quality forest fragment and explore the influence of edge effects on herb-layer diversity. This small (~ 6 ha) stand of old-growth forest is nearly square in shape and is surrounded by agricultural fields—a quintessential habitat fragment in an agricultural landscape. The natural hydrology is intact, and the stand typifies the oak-maple swamp forests that dominated this region of North America prior to European settlement. Our objectives were to: (1) document overall floristic biodiversity in the site, including the presence of invasive species; (2) assess floristic diversity relative to spatial position within the parcel; and (3) assess spatial variation of temperature and light in the understory environment.

METHODS

Study Site

The study was performed at Drew Woods State Nature Preserve (DWSNP, 40˚15'N, 84˚39'W) in Darke County, Ohio. This 6-ha forest remnant consists of undrained oak-maple swamp forest (Anderson 1982; Boerner and Kooser 1991; Goins et al. 2013) and is surrounded on the east, west, and south sides by agricultural fields. The north edge is adjacent to a road; however, beyond the road are more agricultural fields. The climate of DWSNP is characterized by warm, humid summers and cold winters, with no distinct dry season. Mean annual precipitation is 95.5 cm, and the mean annual temperature is 10.2 ˚C (National Climatic Data Center 2012). The site has relatively flat topography with soils characterized as Blount silt loam and Glynwood silt loam (Boerner and Kooser 1991).

Data Collection

Thirty-two plots were established by Goins et al. (2013) in 2011 using a systematic sampling approach. Plot center stakes were established approximately 40 m apart according to a digitally created grid. Plots were laid out as equidistant as possible with a few exceptions due to vernal and semi-permanent ponds. The herbaceous layer (all nonwoody species) was sampled biweekly during the spring of 2012 (March 25, April 9, April 21, May 5, May19, and June 3) within 1-m^2 plots centered around each plot stake. The percent vegetation cover for each species was estimated using a modified Domin scale (McCune and Grace 2002): <1%, 1–5%, 6–10%, 11–25%, 36–50%, 51–75%, 76–90%, 91–100%.

Floristic surveys were conducted during 2011 and 2012 to assess total plant diversity at the site. Systematic survey approaches included the previously mentioned herbaceous layer sampling, as well as a woody species inventory conducted by Goins et al. (2013). Additional species were identified while moving between plots and during random walks through DWSNP. Voucher specimens were collected and deposited in the University of Dayton herbarium. Botanical nomenclature follows Jones (2005).

Soil temperature was measured at a soil depth of 10 cm using micro-T Temperature Loggers (model no. DS1921G, NexSens Technology) placed 1 m north of 16 systematically selected plots throughout the stand. Daily high average soil temperatures for the northernmost (n = 5) and southernmost (n = 5) plots were calculated using measurements taken at 4:00 PM. These T-loggers were located within 80 m of the northern or southern forest edge, likely within the depth of edge effect. Two additional T-loggers were attached to the top of 1-m-tall stakes at the center of DWSNP, one on the north side of a large tree and one on the south side to record air temperatures. Average daily high air temperatures were calculated from measurements taken at 4:00 PM by these two suspended T-loggers. To obtain leaf area index measurements, canopy images were taken 1 m above the center of each plot prior to leaf fall in September 2012, using a CID-120 Canopy Imager (CID Bio-Science, Inc.). Plot coordinates were obtained using a Garmin eTrex Legend H GPS unit.

Data Analysis

Relative importance values (RIV) were used to rank species within each sampling date and were calculated as the mean of relative cover and relative frequency values for each species. Minor species had an RIV value of less than one. "True" Shannon diversity (exp(H')), species richness, and total cover (cm^2 m^{-2}) were calculated for each plot.

The Floristic Quality Assessment Index (FQAI) for Ohio (Andreas et al. 2004) was used to assign Coefficient of Conservatism (C of C) values to all species in the DWSNP flora. These values are indicative of relative habitat fidelity, where a low value indicates tolerance of a wide range of habitats, and a high value indicates greater habitat specificity and sensitivity to disturbance. A site-wide FQAI score (I) provided an overall assessment of the site's quality and was calculated using Eqn. 6 provided by Andreas et al. (2004), where CC_i is the Coefficient of Conservatism value for each species and N_{native} is the number of native species within the evaluated community:

$$I = \sum (CC_i)/\sqrt{(N_{native})}$$

In addition, mean C of C values were calculated for each plot, dividing the sum of C of C scores by species richness (including nonnative species).

Distances to western and southern edges were measured in ArcGIS using GPS plot locations and edge polygon data, donated by Darke County Auditor's GIS department. Linear regression was used to test for relationships between herb layer measurements (species richness, Shannon diversity, cover, mean C of C, *Alliaria petiolata* cover) and environmental variables (distance to western and southern edges, leaf area index). Non-metric multidimensional scaling (NMDS) procedure and constrained correspondence analysis (CCA) were used to assess whether patterns of native species composition (based on abundance data collected May 5) were associated with environmental variables ("vegan" and "labdsv" packages in R version 3.0.1). The final NMDS solution contained three axes (stress = 16.8), which provided a substantial reduction in stress over a two-axis solution (stress = 23.4); additional axes beyond three did not improve stress.

RESULTS

Site-wide, we identified a total of 176 vascular plant species across 124 genera belonging to 67 different families. Overall, the majority of these species were dicots, and there were only two species of ferns identified at the site (Table 1). Approximately one-third of the monocot species belonged to the genus *Carex* (sedge, 13 species; Appendix). Characteristic herbaceous species for this site included *Jeffersonia diphylla* (twinleaf), *Trillium sessile* (toad trillium), *Allium tricoccum* (wild leek), and *Erythronium americanum* (trout lily; Table 2), which are indicative of mature, high-quality forest (Andreas et al. 2004). In addition, two rare medicinal species, *Panax quinquefolius* (American ginseng) and *Hydrastis canadensis* (goldenseal) were found at the site (Appendix). Overall, 128 species in Drew Woods had a Coefficient of Conservatism of 3 or higher, indicating a community composed largely of species typically limited to high-quality sites that are relatively stable with little disturbance (see Table 1 in Andreas et al. 2004; Figure 1). In addition, the overall FQAI score for the site (based on the complete flora list) was 51.5, which was on par with other qualitative FQAI scores given by Andreas et al. (2004) for other high-quality sites in Ohio.

Nineteen nonnative species were found in Drew Woods, most of which were cosmopolitan weeds restricted to the perimeter of the site (Appendix). Three woody invasive species, *Ailanthus altissima* (tree-of-heaven), *Lonicera maackii* (amur honeysuckle), and *Rosa multiflora* (multiflora rose), were found at low frequencies within the site. The invasive herb *Alliaria petiolata* (garlic mustard) was the most important species in many of our quantitative surveys (Table 2), and this level of importance, interestingly, was achieved even though the species is relatively constrained within the site. We found that *A. petiolata* was well established on the western boundary of the site and is penetrating the interior of the site; however, its density was quite low across the majority of the plots (Figure 2A).

There were no significant east–west trends in DWSNP, but a north–south gradient of species richness was found consistently throughout all six sampling dates, with the southernmost plots tending to be most species-rich ($P < 0.01$, $r^2 \leq 0.42$). This pattern was most readily obvious on the May 5 sampling during which species richness peaked in the southern portion of the study area, with the northern portion relatively species-poor (Figure 2B, Table 3). Shannon diversity exhibited a statistically significant north–south trend for three of the sampling dates (April 9, April 21, May 5), and all of these relationships were relatively weak ($P < 0.05$, $r^2 \leq 0.18$). Total herbaceous cover and mean C of C did not exhibit any significant spatial patterns within the site (Table 3); however, *Alliaria petiolata* cover was greater near the southern edge of the site ($P = 0.037$, $r^2 = 0.15$). *Alliaria petiolata* cover did not exhibit significant relationships with native species richness ($P = 0.72$), native Shannon diversity ($P = 0.96$), or native cover ($P = 0.50$).

Soil temperature and canopy cover (as measured by leaf area index (LAI)) also varied along a north–south gradient. In general, the southernmost plots experienced slightly higher average daily soil temperatures than the northernmost plots (Figure 3). LAI increased significantly with distance from the southern forest edge ($P < 0.0005$, $r^2 = 0.37$), indicating more open canopy towards the southern edge of the stand. Herb species richness and Shannon diversity on May 5 exhibited inverse linear relationships with LAI, where plots with greater canopy cover tended to have lower species richness and diversity (richness $P = 0.014$, $r^2 = 0.16$; Shannon diversity $P = 0.039$, $r^2 = 0.11$; Table 3). The NMDS ordination reflected these patterns as plots tended to cluster based on their location in either the northern or the southern half of the forest stand (Figure 4). Distance to southern edge was the only significant term in the CCA model ($F = 2.31$, $P = 0.015$), indicating that species composition varies among plots along a north–south gradient (Figure 4).

Table 1. Taxonomic summary of plant species identified in Drew Woods State Nature Preserve, a 6-ha forest remnant in Darke County, Ohio. Percent native species calculated based on native statuses in the Floristic Quality Assessment Index for Ohio (Andreas et al. 2004).

Division	Families	Genera	Species	% Native Species
Ferns and Fern Allies	2	2	2	100
Monocots	15	21	38	92.1
Dicots	50	101	136	88.2
Total	67	124	176	89.2

DISCUSSION

Habitat loss and fragmentation are among the most important threats to global biodiversity (Fahrig 2003; Mantyka-Pringle et al. 2012), and much attention has been given to assessing the conservation value of remnant forest patches. Drew Woods State Nature Preserve is an important habitat refuge in a landscape largely dominated by agriculture, harboring a number of plant species that have relatively high coefficients of conservatism (scores ranging 5–7) according to the Floristic Quality Assessment Index for Ohio (Andreas et al. 2004). Unfortunately, it is also highly isolated from other forest patches, which

Table 2. Relative importance values (RIV) of herbaceous species sampled across 32 1-m^2 plots located in DWSNP. Values were calculated by averaging together relative cover and relative frequency of each species. Minor species have an RIV < 1 at all sampling dates. All species are rank ordered by RIV on April 21, including minor species.
Minor species: ***Maianthemum racemosum, Elymus hystrix, Solidago ulmifolia, Festuca subverticillata, Carex jamesii, Laportea canadensis, Carex albursina, Cystopteris protrusa, Prenanthes altissima, Galium circaezens, Allium canadense, Carex blanda, Lysimachia ciliata, Solidago caesia, Sonchus arvensis, Tradescantia virginiana, Phytolacca americana, Pilea pumila, Teucrium canadense, Triosteum angustifolium*****.**

	Relative Importance Value					
Species	**March 25**	**April 9**	**April 21**	**May 5**	**May 19**	**June 3**
Alliaria petiolata	15.37	14.31	13.29	15.44	13.96	15.44
Floerkea proserpinacoides	12.83	11.57	10.47	4.07	-	-
Sanicula odorata	5.92	5.58	7.22	8.44	9.89	11.15
Impatiens capensis	6.16	5.76	7	9.58	14.28	16.62
Claytonia virginica	10.02	8.76	6.6	3.46	-	-
Dentaria laciniata	11.29	7.87	6.2	3.32	2.31	-
Galium aparine	4.12	4.46	4.84	5.36	6.38	3.08
Podophyllum peltatum	3.26	5.45	4.58	4.53	4.19	1.12
Trillium sessile	6.23	5.29	4.24	3.57	3.32	3.46
Hydrophyllum macrophyllum	3.84	3.69	3.71	4.22	3.53	2.99
Geranium maculatum	2.38	4.3	3.22	4.12	3.73	2.63
Circaea lutetiana	0.29	1.22	2.9	3.86	4.49	5.16
Polygonatum pubescens	0.29	2.17	2.01	1.97	2.3	2.34
Arisaema triphyllum	-	0.73	1.75	1.89	2.07	2.21
Erythronium americanum	2.38	2.22	1.72	0.61	-	-
Jeffersonia diphylla	0.29	0.87	1.61	3.05	2.7	3.04
Viola pubescens	1.76	1.47	1.54	1.75	2.06	2.22
Phlox divaricata	1.17	0.98	1.39	1.76	1.73	1.84
Cardamine douglassii	2.06	1.68	1.39	0.81	-	-
Symphyotrichum lanceolatum	0.6	0.87	1.25	1.13	1.58	2.66
Polygonum virginianum	-	0.49	1.24	1.56	1.73	1.84
Allium tricoccum	1.49	1.15	1.22	0.61	0.46	0.73
Viola sororia	1.18	1.19	1.18	1.96	2.53	2.96
Geum vernum	1.18	0.94	1.13	1.42	1.95	2.11
Sanguinaria canadensis	0.59	0.98	1.04	1.02	1.15	0.98
Uvularia grandiflora	0.59	0.7	0.98	1.01	1.03	1.12
Oxalis stricta	0.29	0.24	0.62	1.02	1.96	2.09
Lithospermum latifolium	-	-	0.21	0.81	1.27	1.6

limits the dispersal of plants and animals into or out of the stand (Boerner and Kooser 1991). The ecological integrity of such habitat "island" refuges is subject to a number of factors, including edge effects, local species extinctions, and invasive species (Honnay et al. 2005). The long-term value of these forest fragments is unclear in the face of climate change, as the broader range of suitable habitat for many plant species is predicted to shift as global temperature and precipitation patterns change (Walther et al. 2002). Species unable to disperse over long distances face challenges in migrating across dissected landscapes in order to "keep up" with shifting suitable habitats (Pitelka et al. 1997; Neilson et al. 2005).

Edge habitats provide ideal conditions for many shade-intolerant nonnative species, while forest interiors are less easily invaded (Brothers and Spingarn 1992). This phenomenon appears to be true for the majority of the nonnative species found in DWSNP; however, the integrity of the site is being threatened by *Alliaria petiolata*, which has successfully penetrated the southwest

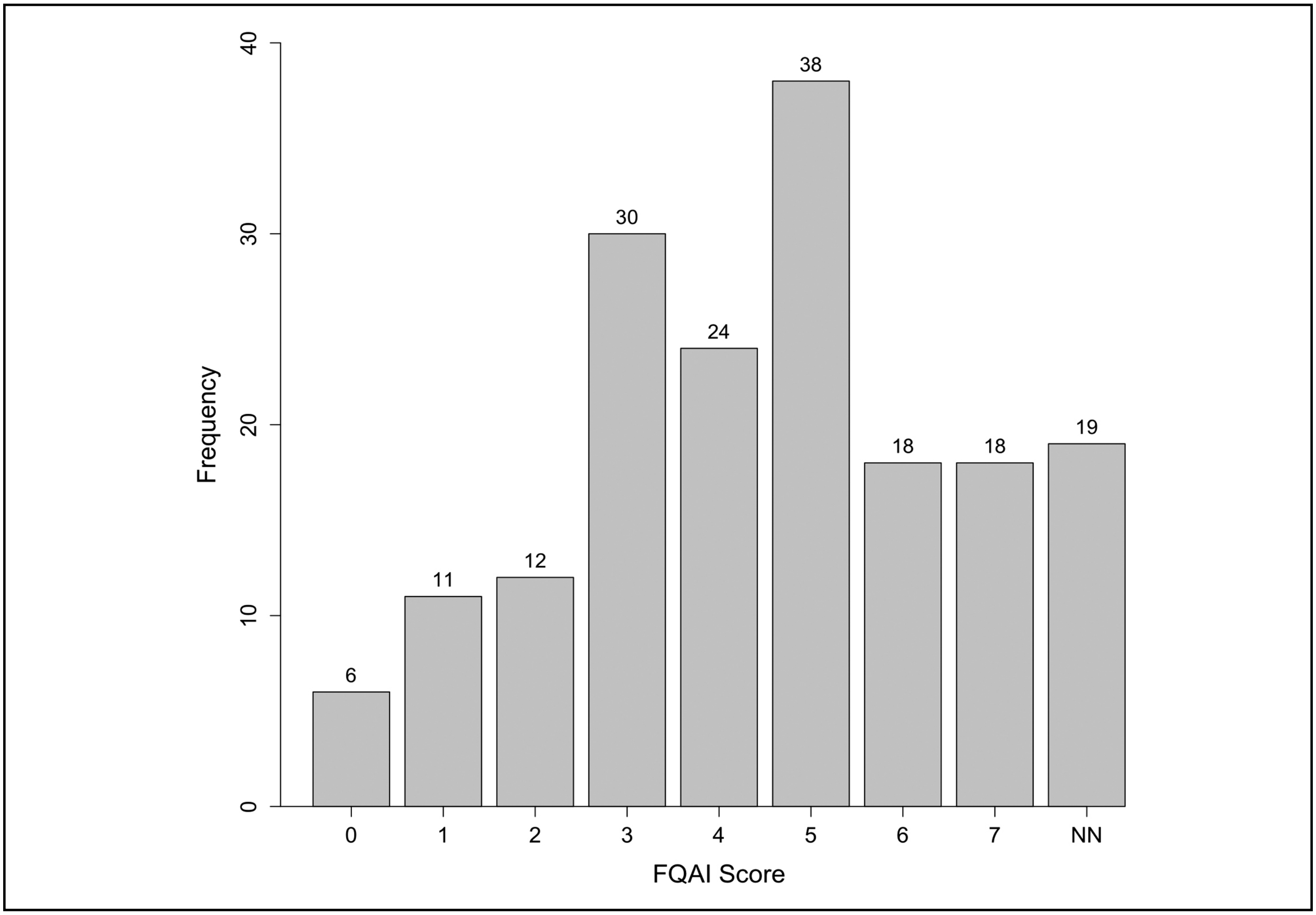

Figure 1. Frequencies of Coefficient of Conservatism scores of all plant species within DWSNP, according to the Ohio Floristic Quality Assessment Index (Andreas et al. 2004). The bar labeled "NN" represents nonnative species.

quadrant of the site. One important finding of our work was that although *A. petiolata* is relatively constrained spatially (Figure 2A), it is still the most abundant plant in Drew Woods based on cover. The local density of *A. petiolata* in invaded areas is vastly greater than what is attained by native species, and if left unchecked, this invasion could have negative consequences for the native species present in the site. Even though *A. petiolata* did not have any statistically significant negative impacts on herb-layer diversity in DWSNP at the time of this study, its ability to form monocultures and suppress the growth of native herbs (Stinson et al. 2007) is cause for concern.

Environmental gradients occurring perpendicular to the edge of a forest remnant may influence the spatial patterns of biotic communities. Such gradients usually include increased wind exposure, increased solar radiation, decreased moisture, and higher temperatures closer to the forest edge (Ranney 1977; Laurance et al. 1997). Nightly atmospheric re-radiation of heat also contributes to the temperature gradient seen across forest edges adjacent to open areas, such as roads or agricultural fields (Murcia 1995). In the northern hemisphere, these gradients tend to be more evident along south-facing forest edges than north-facing ones (Wales 1972; Palik and Murphy 1990), a phenomenon that was observed in Drew Woods. Boerner and Kooser (1991) estimated that approximately 42% of DWSNP consisted of edge, assuming a 30-m edge effect. Over time, closure of the side canopy along an edge has a dampening effect on these edge-related gradients (Matlack 1993), a process that has been present in DWSNP for decades. Still, we were able to detect some edge-driven variations in temperature and light, and we hypothesize that these microclimatic trends are still influencing patterns of herb-layer diversity in DWSNP.

Forest remnants act as important reservoirs of genetic diversity, but the isolated nature of these stands may contribute to a loss of allelic richness and heterozygosity as a result of bottlenecking and/or inbreeding (Young et al. 1996; Honnay et al. 2005). Genetic diversity among herb species within DWSNP may be impacted by such isolation, as we witnessed a number of native plants with morphological anomalies (e.g. 4-, 5-, and 6-leaved *Trillium sessile*, 6-petaled *Claytonia virginica* (spring beauty), 3-leaved *Podophyllum peltatum* (mayapple)). It was beyond the scope of

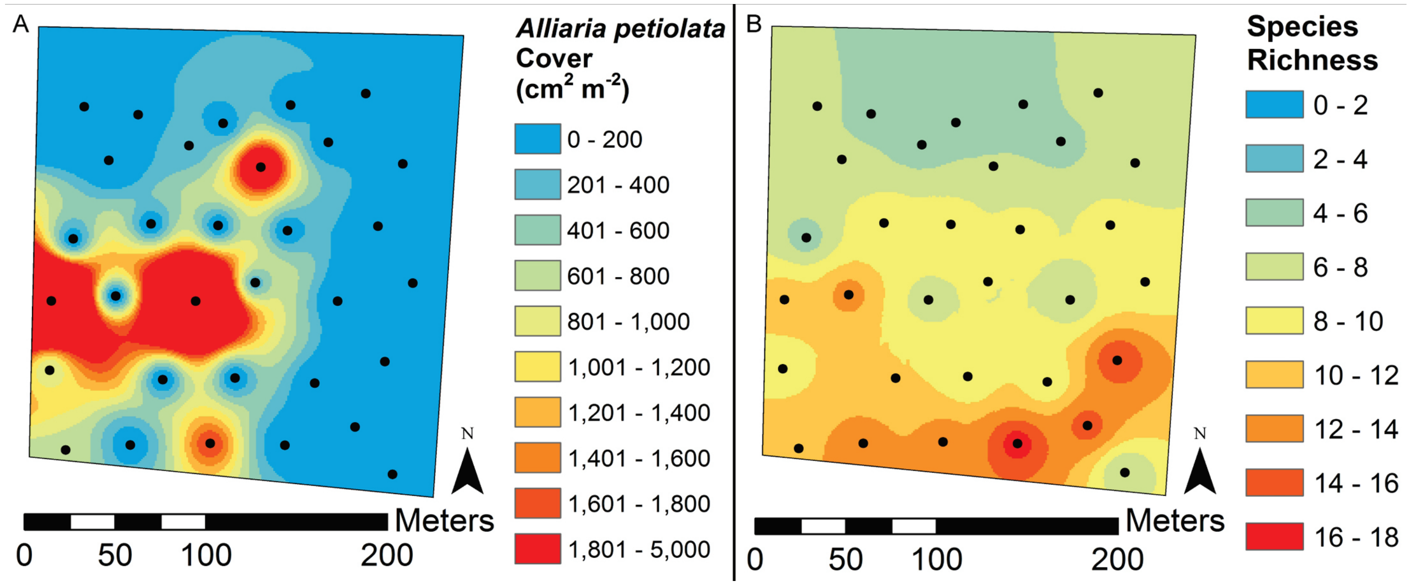

Figure 2. Inverse distance weighted interpolations of (A) *Alliaria petiolata* cover (cm^2 m^{-2}), and (B) herbaceous species richness sampled across 32 1-m^2 plots in DWSNP on May 5, 2012. Species richness displayed a significant north–south trend across all 6 sampling dates (P < 0.01, $r^2 \leq 0.42$); this pattern was strongest on May 5.

this project to pursue the genetic basis or fitness consequences of these morphologies; however, in our experience with floristic surveys (McEwan et al. 2005; Chapman et al. 2012), the concentration of anomalies in DWSNP was unusual.

In summary, the flora of DWSNP indicates that this old-growth remnant is an important storehouse of biodiversity in the agriculture-dominated landscape of western Ohio. The assemblage of plant species found there is typical of minimally impacted oak-maple swamp forest, but whether the site will retain its value as a high-quality representative of the region's historically natural flora is uncertain. Goins et al. (2013) described an ongoing shift in overstory composition from *Quercus* (oak) and *Carya* (hickory) to *Acer* (maple), which, coupled with the impending loss of *Fraxinus* (ash) due to the emerald ash borer (Poland and McCullough 2006), may influence future herb-layer composition at the site. In addition, *Alliaria petiolata* poses a significant threat to the site's floristic biodiversity if left unmanaged. Small preserves surrounded by areas of heavy human use can provide storehouses of biodiversity that serve as both genetic reservoirs and examples of desired endpoints for forest restoration and management; however, continued monitoring and discrete management interventions are likely needed to maintain ecological integrity of such sites.

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Table 3. Results of linear regression testing for relationships between herbaceous layer measures and environmental variables across 32 sampling plots (1 m^2 each) within Drew Woods State Nature Preserve. All response variables represent data collected on 5 May 2012.

Response Variable	Distance to Southern Edge		Distance to Western Edge		Leaf Area Index (LAI)	
	r^2	P	r^2	P	r^2	P
Species Richness	**0.42**	**0.000033**	-0.033	0.92	**0.16**	**0.014**
Shannon Diversity	**0.18**	**0.0099**	0.048	0.12	**0.11**	**0.039**
Total Cover	-0.023	0.59	0.0084	0.27	-0.028	0.69
Plot Mean C of C	0.02	0.21	-0.016	0.48	-0.0015	0.34
Alliaria petiolata cover	**0.15**	**0.037**	-0.023	0.59	-0.026	0.64

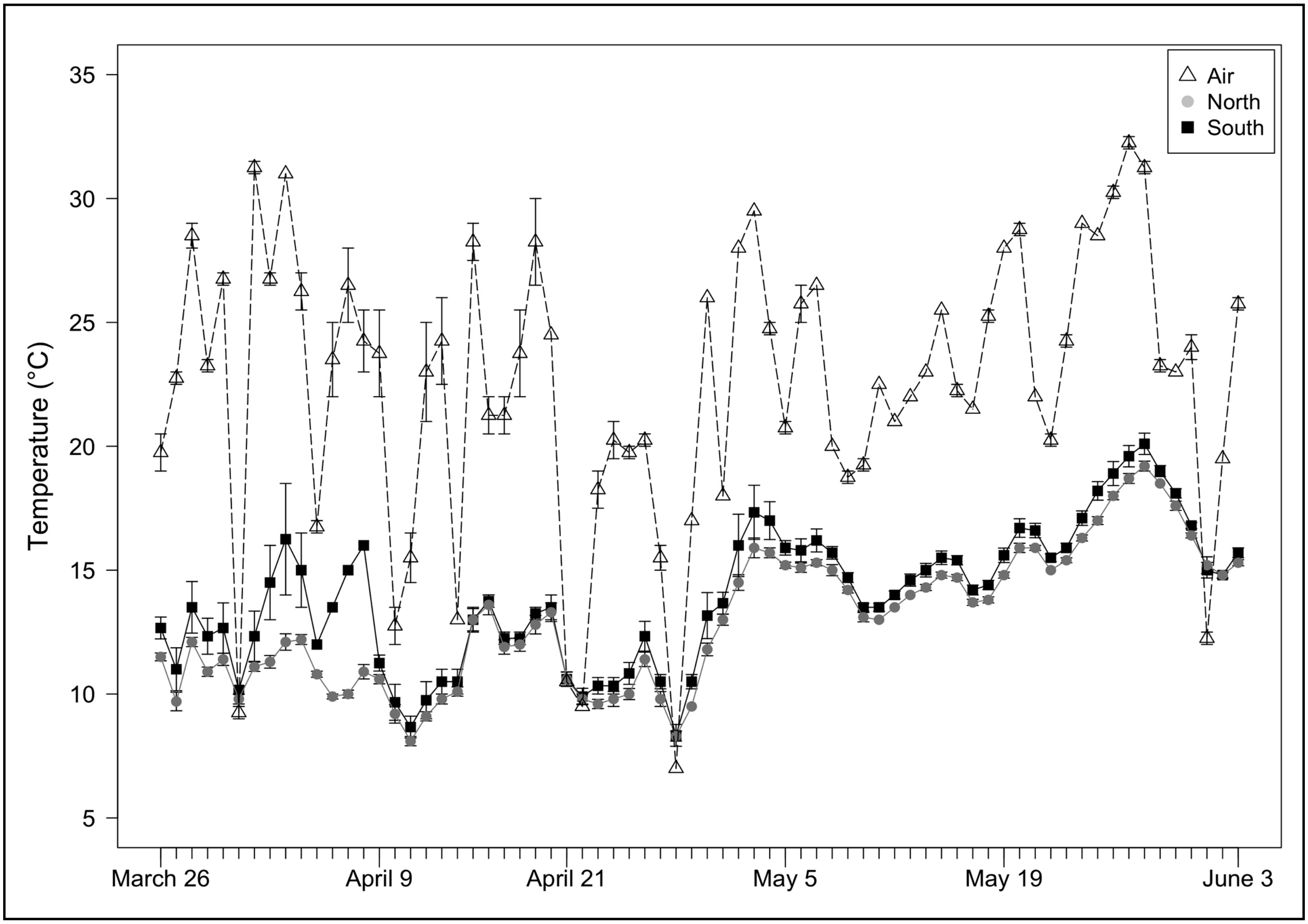

Figure 3. Mean daily high soil temperatures (4:00 PM) recorded by micro-T temperature loggers buried 10 cm deep near northern (n = 5) and southern (n = 5) plots in DWSNP. Air temperatures were recorded by micro-T loggers suspended 1 m above ground (n = 2). Erratic data between March 26 and May 4 were omitted, as some loggers were dug up by animals between sampling dates. Error bars represent ± standard error (SE).

Julia Chapman was concluding her Master of Science in Biology degree at the University of Dayton at the time of this study. Since then, she has been teaching introductory biology lab courses at UD and has continued her involvement in forest ecology research as a research technician in the McEwan lab.

Amy Myers was an undergraduate student at the University of Dayton at the time of this study. Since completing her dual Bachelor of Science degrees in Biology and Education in May 2013, she has been teaching at Piqua High School in Piqua, Ohio.

Albert Burky is a Professor in the Department of Biology at the University of Dayton. His research focuses on the ecology of both temperate and tropical crustaceans, fish, clams, and snails. Some of his previous work on freshwater clams was conducted in vernal ponds at Drew Woods.

Ryan McEwan is an Assistant Professor in the Department of Biology at the University of Dayton. His research focuses on long-term forest dynamics, ecological impacts of invasion, and biodiversity and ecosystem function relationships.

LITERATURE CITED

Albrecht, M.A., and B.C. McCarthy. 2006. Seed germination and dormancy in the medicinal woodland herbs *Collinsonia canadensis* L. (Lamiaceae) and *Dioscorea villosa* L. (Dioscoreaceae). Flora 201:24-31.

Anderson, D.M. 1982. Plant communities of Ohio: a preliminary classification and description. Ohio Department of Natural Resources, Division of Natural Areas and Preserves, Columbus, OH.

Andreas, B.K., J.J. Mack, and J.S. McCormac. 2004. Floristic Quality Assessment Index (FQAI) for vascular plants and mosses for the State of Ohio. Ohio Environmental Protection Agency, Division of Surface Water, Wetland Ecology Group, Columbus, OH.

Bierzychudek, P. 1982. Life histories and demography of shade-tolerant temperate forest herbs: a review. New Phytologist 90:757-776.

Boerner, R.E.J., and J.G. Kooser. 1991. Vegetation of Drew Woods, an old-growth forest remnant in western Ohio, and issues of preservation. Natural Areas Journal 11:48-54.

Boutin, C., and B. Jobin. 1998. Intensity of agricultural practices and effects on ad-

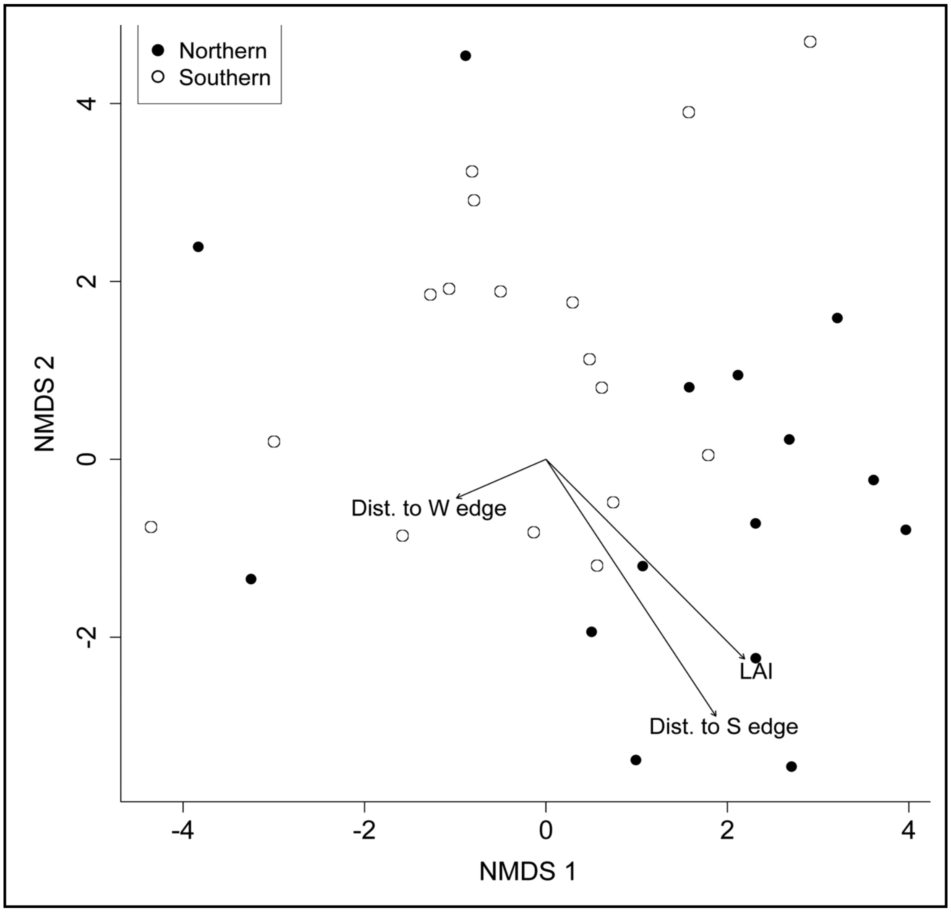

Figure 4. NMDS ordination plot based on native herbaceous species abundances sampled on May 5, 2012. This solution had three axes, but only axes 1 and 2 are shown here. Plot symbols are coded based on plot location in either the northern (solid black) or southern (open) half of DWSNP. Three environmental vectors are overlaid: distance to western edge (Dist. to W edge), distance to southern edge (Dist. to S edge), and leaf area index (LAI); however, only distance to southern edge was significant in the CCA model (F = 2.31, P = 0.015).

jacent habitats. Ecological Applications 8:544-557.

Bratton, S.P. 1976. Resource division in an understory herb community: responses to temporal and microtopographic gradients. American Naturalist 110:679-693.

Braun, E.L. 1950. Deciduous Forests of Eastern North America. Blakiston, Philadelphia, PA.

Brewer, R. 1980. A half-century of changes in the herb layer of a climax deciduous forest in Michigan. Journal of Ecology 68:823-832.

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

Chapman, J.I., and R.W. McEwan. 2013. Spatiotemporal dynamics of α and β diversity across topographic gradients in the herbaceous layer of an old-growth deciduous forest. Oikos 122:1679-1686.

Chapman, J.I., K.L. Perry, and R.W. McEwan. 2012. Changing flora of an old-growth mesophytic forest: undetected taxa and the first appearance of invasive species. Journal of the Torrey Botanical Society 139:206-210.

Costello, M.J., R.M. May, and N.E. Stork. 2013. Can we name the Earth's species before they go extinct? Science 339:413-416.

Crozier, C.R., and R.E.J. Boerner. 1984. Correlations of understory herb distribution with microhabitats under different tree species in a mixed mesophytic forest. Oecologia 62:337-343.

Duffy, C.D., and A.J. Meier. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? Conservation Biology 6:196-201.

Edvardsen, A., R. Halvorsen, A. Norderhaug, O. Pedersen, and K. Rydgren. 2010. Habitat specificity of patches in modern agricultural landscapes. Landscape Ecology 25:1071-1083.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487-515.

Ford, M.F., R.H. Odom, P.E. Hale, and B.R. Chapman. 2000. Stand-age, stand characteristics, and landform effects on understory herbaceous communities in southern Appalacian cove-hardwoods. Biological Conservation 93:237-246.

Gilliam, F.S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience 57:845-852.

Gilliam, F.S., and M.R. Roberts. 2003. Interactions between the herbaceous layer and overstory canopy of eastern forests. Pp. 163–176 *in* F.S. Gilliam and M.R. Roberts, eds., The Herbaceous Layer in Forests of Eastern North America. Oxford University Press, Oxford, UK.

Gleason, H.A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53:1-20.

Goins, S.M., J.I. Chapman, and R.W. McEwan. 2013. Composition shifts, disturbance and canopy-accession strategy in an old-growth forest of southwestern Ohio. Natural Areas Journal 33:384-394.

Honnay, O., H. Jacquemyn, B. Bossuyt, and M. Hermy. 2005. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. New Phytologist 166:723-736.

Hutchinson, T.F., R.E.J. Boerner, L.R. Iverson, S. Sutherland, and E.K. Sutherland. 1999. Landscape patterns of understory composition and richness across a moisture and nitrogen mineralization gradient in Ohio (U.S.A.) *Quercus* forests. Plant Ecology 144:177-189.

Jones, R.L. 2005. Plant Life of Kentucky. University of Kentucky Press, Lexington.

Jules, E.S. 1998. Habitat fragmentation and demographic change for a common plant: Trillium in old-growth forest. Ecology 79:1645-1656.

Laurance, W.F., R.O. Bierregaard, C. Gascon, R.K. Didham, A.P. Smith, A.J. Lynam, V.M. Viana, T.E. Lovejoy, K.E. Sieving, J.W. Sites, M. Andersen, M.D. Tocher, E.A. Kramer, C. Restrepo, and C. Mortiz. 1997. Tropical forest fragmentation: synthesis of a diverse and dynamic discipline. Pp. 502–514 *in* W.F. Laurance and R.O. Bierregaard, Jr., eds., Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, Chicago.

Mack, R.N., B. Von Holle, and L. Meyerson. 2007. Assessing the impacts of invasive alien species across multiple spatial scales: the need to work globally and locally. Frontiers in Ecology and the Environment 5:217-220.

Mantyka-Pringle, C.S., T.G. Martin, and J.R.

Rhodes. 2012. Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. Global Change Biology 18:1239-1252.

Matlack, G.R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation 66:185-194.

Matlack, G.R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. Ecology 75:1491-1502.

Matlack, G.R. 2005. Slow plants in a fast forest: local dispersal as a predictor of species frequencies in a dynamic landscape. Journal of Ecology 93:50-59.

McCune, B., and J.B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR.

McEwan, R.W., M.A. Arthur, and S.S. Alverson. 2012. Throughfall chemistry and soil nutrient effects of deciduous forest invasion by the exotic shrub *Lonicera maackii*. American Midland Naturalist 168:43-55.

McEwan, R.W., and R.N. Muller. 2011. Dynamics, diversity, and resource gradient relationships in the herbaceous layer of an old-growth Appalachian forest. Plant Ecology 212:1179-1191.

McEwan, R.W., R.N. Muller, R.D. Paratley, and C.L. Riccardi. 2005. The vascular flora of an old-growth mixed mesophytic forest in southeastern Kentucky. Journal of the Torrey Botanical Society 132:618-627.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution 2:58-62.

National Climatic Data Center. 2012. Climate Data Online. Annual Summaries: Greenville Water Plant, OH. <http://www.ncdc.noaa.gov/cdo-web/datasets/ANNUAL/stations/COOP:333375/detail>.

Neilson, R.P., L.F. Pitelka, A.M. Solomon, R. Nathan, G.F. Midgley, J.M.V. Fragoso, H. Lischke, and K. Thompson. 2005. Forecasting regional to global plant migration in response to climate change. BioScience 55:749-759.

Palik, B.J., and P.G. Murphy. 1990. Disturbance verses edge effects in sugar-maple/beech forest fragments. Forest Ecology and Management 32:187-202.

Pitelka, L.F., J. Ash, S. Berry, R.H. Bradshow, L. Brukaken, and J.S. Clark. 1997. Plant migration and climate change. American Scientist 85:464-473.

Poland, T.M., and D.G. McCullough. 2006. Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. Journal of Forestry 104:118-124.

Polyakov, M., A.D. Rowles, J.Q. Radford, A.F. Bennett, G. Park, A. Roberts, and D. Pannell. 2013. Using habitat extent and composition to predict the occurrence of woodland birds in fragmented landscapes. Landscape Ecology 28:329-341.

Powell, K.I., J.M. Chase, and T.M. Knight. 2011. A synthesis of plant invasion effects on biodiversity across spatial scales. American Journal of Botany 98:539-548.

Ranney, J.W. 1977. Forest island edges – their structure, development, and importance to regional forest ecosystem dynamics. EDFB/IBP–77/1, Environmental Sciences Division Publication No. 1609, Oak Ridge National Laboratory, Oak Ridge, TN.

Ricketts, T.H., E. Dinerstein, D.M. Olson, and C. Loucks. 1999. Who's where in North America. BioScience 49:369-381.

Rockström, J., W. Steffen, K. Noone, Å. Persson, F.S. Chapin, III, E. Lambin, T.M. Lenton, M. Scheffer, C. Folke, H. Schellnhuber, B. Nykvist, C.A. De Wit, T. Hughes, S. van der Leeuw, H. Rodhe, S. Sörlin, P.K. Snyder, R. Costanza, U. Svedin, M. Falkenmark, L. Karlberg, R.W. Corell, V.J. Fabry, J. Hansen, B.H. Walker, D. Liverman, K. Richardson, C. Crutzen, and J. Foley. 2009. A safe operating space for humanity. Nature 461:472-475.

Scherr, S.J., and J.A. McNeely. 2008. Biodiversity conservation and agricultural sustainability: towards a new paradigm of "ecoagriculture" landscapes. Philosophical Transactions of the Royal Society B 363:477-94.

Small, C.J., and B.C. McCarthy. 2002. Spatial and temporal variation in the response of understory vegetation to disturbance in a central Appalachian oak forest. Journal of the Torrey Botanical Society 129:136-153.

Small, C.J., and B.C. McCarthy. 2005. Relationship of understory diversity to soil nitrogen, topographic variation, and stand age in an eastern oak forest, USA. Forest Ecology and Management 217:229-243.

Stinson, K., S. Kaufman, L. Durbin, and F. Lowenstein. 2007. Impacts of garlic mustard invasion on a forest understory community. Northeastern Naturalist 14:73-88.

Thompson, J.N. 1980. Treefalls and colonization patterns of temperate forest herbs. American Midland Naturalist 104:176-184.

Vellend, M., K. Verheyen, K.M. Flinn, H. Jacquemyn, A. Kolb, H.V. Calster, G. Peterken, B.J. Graae, J. Bellemare, O. Honnay, J. Brunet, M. Wulf, F. Gerhardt, and M. Hermy. 2007. Homogenization of forest plant communities and weakening of species-environment relationships via agricultural land-use. Journal of Ecology 95:565-573.

Vellend, M., K. Verheyen, H. Jacquemyn, A. Kolb, H.V. Calster, G. Peterken, and M. Hermy. 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. Ecology 87:542-548.

Wales, B.A. 1972. Vegetation analysis of north and south edges in a mature oak-hickory forest. Ecological Monographs 42:451-471.

Walther, G-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T.J.C. Beebee, J-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389-395.

Whigham, D.F. 2004. Ecology of woodland herbs in temperate deciduous forests. Annual Review of Ecology, Evolution, and Systematics 35:583-621.

Whitney, G.G., and D.R. Foster. 1988. Overstorey composition and age as determinants of the understory flora of woods of central New England. Journal of Ecology 76:867-876.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26:1-80.

Wilson, H.N., M.A. Arthur, A. Schörgendorfer, R.D. Paratley, B.D. Leen, and R.W. McEwan. 2013. Site characteristics as predictors of *Lonicera maackii* in second-growth forests of central Kentucky, USA. Natural Areas Journal 33:189-198.

Young, A., T. Boyle, and T. Brown. 1996. The population genetic consequences of habitat fragmentation for plants. Trends in Ecology and Evolution 11:413-418.

Appendix. Vascular flora of Drew Woods State Nature Preserve, Darke County, Ohio, USA.

FERNS AND FERN ALLIES

Dryopteridaceae
Cystopteris protrusa (Weath.) Blasdell

Ophioglossaceae
Botrychium virginianum (L.) Sw.

ANGIOSPERMS – DICOTS

Aceraceae
Acer negundo L.
Acer rubrum L.
Acer saccharinum L.
Acer saccharum Marshall

Anacardiaceae
Toxicodendron radicans (L.) Kuntze

Apiaceae
**Conium maculatum* L.
**Daucus carota* L.
Osmorhiza claytonii (Michx.) C.B.Clarke
Osmorhiza longistylus (Torr.) DC
Sanicula odorata (Raf.) Pryer & Phillippe

Apocynaceae
Apocynum cannabinum L.

Araliaceae
Panax quinquefolius L.

Aristolochiaceae
Aristolochia serpentaria L.

Asteraceae
Ambrosia artemisiifolia L.
Ambrosia trifida L.
**Arctium minus* Bernh.
Bidens discoidea (Torr. & A.Gray) Britton
**Chrysanthemum leucanthemum* L.
**Cichorum intybus* L.
Erigeron annuus (L.) Pers.
Eupatorium purpureum L.
Eurybia divaricata (L.) G.L.Nesom
***Packera glabella* (Poir.) C.Jeffrey
Prenanthes altissima L.
Solidago caesia (L.)
Solidago ulmifolia Muhl.
***Sonchus arvensis* L.
Symphyotrichum lanceolatum (Willd.) G.L. Nesom

Balsaminaceae
Impatiens capensis Meerb.

Berberidaceae
Caulophyllum thalictroides (L.) Michx.
Jeffersonia diphylla (L.) Pers.
Podophyllum peltatum L.

Betulaceae
Carpinus caroliniana Walter
Corylus americana Walter
Ostrya virginiana (Mill.) K.Koch

Bignoniaceae
Campsis radicans (L.) Seem. ex Bureau
***Catalpa speciosa* Warder ex Engelm.

Boraginaceae
Lithospermum latifolium Michx.

Brassicaceae
**Alliaria petiolata* (M. Bieb) Cavara & Grande
Cardamine douglassii (Torr.) Britton
Dentaria laciniata Muhl. ex Willd.

Campanulaceae
Campanulastrum americanum (L.) Small.
Lobelia siphilitica L.

Caprifoliaceae
**Lonicera maackii* (Rupr.) Maxim.
Sambucus canadensis L.
Triosteum angustifolium L.
Viburnum acerifolium L.

Continued

Appendix. (*Continued*)

Viburnum dentatum L.
Viburnum prunifolium L.

Caryophyllaceae
**Dianthus armeria* L.
Silene virginica L.

Celastraceae
Celastrus scandens L.
Euonymus obovatus Nutt.

Cornaceae
Cornus drummondii C.A.Mey
Cornus florida L.

Fabaceae
Cercis canadensis L.
Gleditsia triacanthos L.
Gymnocladus dioicus (L.) K.Koch
Robinia pseudoacacia L.

Fagaceae
Fagus grandifolia Ehrh.
Quercus alba L.
Quercus bicolor Willd.
Quercus coccinea Münchh.
Quercus macrocarpa Michx.
Quercus muehlenbergii Engelm.
†*Quercus palustris* Münchh.
Quercus rubra L.
Quercus stellata Wangenh.

Geraniaceae
Geranium maculatum L.

Grossulariaceae
Ribes cynosbati L.

Hippocastanaceae
Aesculus flava Ait.
Aesculus glabra Willd.

Hydrophyllaceae
Hydrophyllum macrophyllum Nutt.
Hydrophyllum virginianum L.

Juglandaceae
Carya cordiformis (Wangenh.) K.Koch
Carya glabra (Mill.) Sweet
Carya laciniosa (F.Michx.) Loudon
Carya ovata (Mill.) K.Koch
Carya tomentosa (Poir.) Nutt.
†*Juglans cinerea* L.
Juglans nigra L.

Lamiaceae
**Lamium purpureum* L.
Lycopus americanus Muhl.
Teucrium canadense L.

Limnanthaceae
Floerkea proserpinacoides Willd.

Menispermaceae
Menispermum canadense L.

Moraceae
Morus rubra L.

Oleaceae
Fraxinus americana L.
Fraxinus nigra Marshall
Fraxinus pennsylvanica Marshall
Fraxinus quadrangulata Michx.

Onagraceae
Circaea lutetiana (L.) Asch. & Magnus

Orobanchaceae
Conopholis americana (L.) Wallr.

Oxalidaceae
Oxalis stricta L.

Continued

Appendix. (*Continued*)

Papaveraceae
Sanguinaria canadensis L.

Phytolaccaceae
Phytolacca americana L.

Polemoniaceae
Phlox divaricata L.
Polemonium reptans L.

Polygonaceae
**Polygonum convolvulus* L.
Polygonum virginianum L.
**Rumex crispus* L.

Portulacaceae
Claytonia virginica L.

Primulaceae
Lysimachia ciliata L.

Ranunculaceae
Anemonella thalictroides (L.) Spach.
Cimicifuga racemosa (L.) Nutt.
Hydrastis canadensis L.

Rosaceae
Agrimonia pubescens Wallr.
Amelanchier arborea (F.Michx.) Fernald
Crataegus mollis (Torr. & A.Gray) Scheele
Crataegus punctata Jacq.
Geum vernum (Raf.) Torr. & A.Gray
Potentilla simplex Michx.
†*Prunus serotina* Ehrh.
Prunus virginiana L.
Rosa carolina L.
**Rosa multiflora* Thunb.
Rubus allegheniensis Porter.
Rubus occidentalis L.

Rubiaceae
Cephalanthus occidentalis L.
Galium aparine L.
Galium circaezans Michx.
Galium concinnum Torr. & A.Gray

Rutaceae
Zanthoxylum americanum Mill.

Salicaceae
Populus deltoides W.Bartram ex Marshall

Simaroubaceae
**Ailanthus altissima* (Mill.) Swingle

Tiliaceae
†*Tilia americana* L.

Ulmaceae
†*Celtis occidentalis* L.
Ulmus americana L.
Ulmus rubra Muhl.

Urticaceae
Boehmeria cylindrica
Laportea canadensis (L.) Wedd.
Pilea pumila (L.) A.Gray

Vitaceae
Parthenocissus quinquefolia (L.) Planch.
Vitis vulpina L.

Violaceae
Viola pubescens Aiton
Viola sororia Willd.

ANGIOSPERMS – MONOCOTS

Alliaceae
Allium canadense L.
Allium tricoccum Sol.

Araceae
Arisaema dracontium (L.) Schott.
Arisaema triphyllum (L.) Schott.

Commelinaceae
Tradescantia virginiana L.

Continued

Appendix. (*Continued*)

Convallariaceae
Maianthemum racemosum (L.) Link.
Polygonatum pubescens (Willd.) Pursh.

Cyperaceae
Carex albursina Sheld.
Carex amphibola Steud.
Carex blanda Dewey
Carex cephalophora Muhl. ex Willd.
Carex cristatella Britton.
Carex gracilescens Steud.
Carex grayi J.Carey
Carex hyalinolepis Steud.
Carex jamesii Schwein.
Carex muskingumensis Schwein.
Carex rosea Schkuhr ex Willd.
Carex shortiana Dewey
Carex vulpinoidea Michx.

Dioscoreaceae
Dioscorea villosa L.

Hemerocallidaceae
**Hemerocallus fulva* (L.) L.

Hyacinthaceae
Camassia scilloides (Raf.) Cory

Juncaceae
Jucus tenuis Willd.

Lemnaceae
Lemna minor L.

Liliaceae
Erythronium albidum Nutt.
Erythronium americanum Ker Gawl

Poaceae
**Bromus inermis* Leyss.
Cinna arundinacea L.
Elymus hystrix L.
Elymus virginicus L.
Festuca subverticillata (Pers.) E.B.Alexeev.

Smilacaceae
Smilax herbacea L.
Smilax hispida Raf.

Trilliaceae
Trillium sessile L.

Uvulariaceae
Uvularia grandiflora Sm.

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*Nonnative to U.S.
**Nonnative to Ohio
†Listed in Boerner and Kooser 1991