Floristic Composition and Soils of Three Grassy Forest Openings on the Unglaciated Allegheny Plateau, Strouds Run State Park, Ohio, U.S.A.

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Floristic composition and soils of three grassy forest openings on the unglaciated Allegheny Plateau, Strouds Run State Park, Ohio, U.S.A.

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ABSTRACT

Grassy openings are relatively uncommon on the unglaciated Allegheny Plateau, and the limited sites that do exist contribute disproportionately to the diversity and biological heritage of the region by providing habitat for locally uncommon plant species. Three grassy openings with areas of 0.1–0.2 ha are present on limestone-capped ridgetops at Strouds Run State Park in Athens County, Ohio. Although previous inventories of the park have documented the presence and character of these openings, the sites had not been thoroughly surveyed. Here we describe the vascular flora and soils of the openings and recommend management activities to conserve grassy openings within the park. The openings were surveyed monthly during the 2013 growing season, with frequent additional visits during the growing seasons in 2014–2019. Soils were collected from the openings and adjacent forest for analysis of pH, texture, and bulk density. We documented 135 species of vascular plants across the three sites; 27 were nonnative. The openings were dominated by forbs and grasses intermixed with woody species characteristic of limestone glades (e.g., *Celtis pumila* and *Juniperus virginiana*) and other open habitats. *Andropogon gerardi* was the dominant grass and openland forbs such as *Asclepias tuberosa*, *Lithospermum canescens*, and *Ratibida pinnata* also occurred in the three openings. Soil pH was significantly higher in openings and edge zones than in the forest matrix, suggesting that soils are a contributing factor shaping the grassy communities. However, woody plant encroachment was progressing inward from the edges of the openings, suggesting that a lack of disturbance is threatening the persistence of these unique communities. We suggest selective thinning of woody species to maintain the character and diversity of these sites; the practicality of controlled burns in small sites at close proximity to residential structures is limited.

Key words: grassland communities, prairie plants, woody encroachment

INTRODUCTION

Rare habitats that support uncommon species contribute disproportionately to biodiversity at both local and regional scales. In the heavily forested eastern United States, patches of grassland and scrub vegetation are a prime example of this phenomenon (Latham 1993; Noss 2013). Small, isolated patches of uncommon habitats make a disproportionate contribution to plant biodiversity by hosting rare and endemic species and disjunct populations of species outside their primary range (Cartwright 2019). Distinct habitats also

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contribute to regional beta-diversity; therefore, understanding them can be an essential component of managing and conserving biodiversity across landscapes and regions (Socolar et al. 2016).

On the Allegheny Plateau of Ohio, prairie-like openings with rare and unusual plant species are scattered within a matrix of deciduous forest. Distinctive sites include Buffalo Beats in Athens County, Hinckley Reservation Prairie in Medina County, a limestone bank prairie in Belmont County, and other small, scattered openings in Stark, Wayne, Meigs, and Jackson counties (Cusick and Troutman 1978; Jones 1944). Further east, Jennings Environmental Education Center in western Pennsylvania also hosts a remnant grassy opening notable for its rich forb community (Borsari et al. 2004; Waltman and Ciolkosz 1995). It is likely that many other openings once existed in Pennsylvania and Ohio but were destroyed by European settlement and agriculture, fire suppression, and other land use changes in the late 18th and 19th centuries before they could be properly documented (Cusick and Troutman 1978; Sears 1926).

The factors leading to the origin and persistence of grassland openings in otherwise forested landscapes are often attributed to edaphic conditions; it is clear that variation in soil physicochemical properties can be key drivers of vegetation structure in mixed grassland and forest regions (Lawless et al. 2006; Whitney and Stieger 1985; Wistendahl 1975). For example, grassy openings that have been called prairies in the literature often occur on calcareous substrates such as the shallow dolomite-derived soils of Lynx Prairie, a xeric limestone prairie in Adams County, Ohio (Annala et al. 1983), and the low-nutrient limestone soils that support glade and prairie communities in other regions of North America (Aldrich and Bacone 1981; Lawless et al. 2006; McClain and Ebinger 2014; Rhoades et al. 2005). The Buffalo Beats prairie in Athens County, Ohio, is another xeric limestone prairie that reflects unusual soil characteristics. It is located on two clay lenses that are higher in pH, water-holding capacity, and exchangeable cations than the surrounding shale-derived soils, conditions that favor herbaceous vegetation and partially inhibit establishment of most tree species (Hardin 1988; Wistendahl 1975). At this site, the distributions of prairie-associated plant species end abruptly in a narrow transition zone at the edges of the clay deposits (Wistendahl 1975). Similar distinct edges tracing geologic and edaphic borders are typical of many eastern xeric limestone prairie communities, which often end abruptly with their underlying parent material and do not continue onto adjacent acidic soils (Lawless et al. 2006). In contrast to these sites on unusual or extreme substrates, vast areas of the eastern United States that were formerly cleared for pasture or agriculture have rapidly reverted to forest vegetation (Drummond and Loveland 2010; Monsted and Matlack 2021).

Besides unusual edaphic or geological conditions, anthropogenic disturbance can also create and maintain grassland vegetation in the forested regions of the eastern United States (Hanberry and Noss 2022; Noss 2013). For example, prior to European settlement, Indigenous land-use practices included intentional burns to manage for useful plant and animal species and are thought to have created and maintained grasslands (Baskin et al. 1994; Lawless et al. 2006). Paleoecological evidence from pollen in sediment cores indicates that species associated with prairie openings were widespread near human settlements in southeastern Ohio before European colonization (Abrams et al. 2014; Shane et al. 2001). Both historical records and the presence of charcoal in sediment cores dating back to 400 CE indicate the use of fire as a land management tool by Indigenous peoples (Abrams et al. 2014; Sutherland 1997). European land-use practices in the post-settlement period may have also aided survival of prairie plants through grazing by introduced livestock, burning, soil disturbance, and tree clearing (Auffenorde and Wistendahl 1985; Havercamp and Whitney 1983; Laughlin 2004). Since many native grassland species are adapted to herbivory by large mammals, such as bison (Anderson 2006), herbivory by introduced livestock may similarly benefit such species and plant communities (Lawless et al. 2006).

Although unusual or extreme soil conditions are likely a prerequisite for the initial persistence of grassland openings, ongoing disturbance regimes are also believed to be a key to their maintenance and longer-term persistence. The importance of disturbance in maintaining these communities becomes especially apparent in its absence. Abandonment from pasturing caused the Lynx Prairie in Ohio to lose more than half of its grassland area to forest between 1938 and 1971 (Annala et al. 1983). Buffalo Beats has also been colonized by woody plants in the absence of disturbance; for example, an important episode of tree recruitment and encroachment from 1910 to 1930 was likely the result of decreased fire frequency in the region (McClenahen and Houston 1998). Overall, disturbance may play an even more critical role than geology in the maintenance of grassland openings. In the absence of regular disturbance by fire or grazing, woody plants are generally able to colonize and transform even the most geologically and edaphically challenging sites in the eastern United States (Laughlin 2004).

In this study, we investigated the botanical composition and environmental context of three small grassy forest openings at Strouds Run State Park in Athens County, Ohio. These sites contribute distinctively to the flora of this otherwise heavily forested park and represent a prime example of the biodiversity value of rare and unusual habitats (Harrelson and Cantino 2006). Although some Allegheny Plateau grasslands, such as Buffalo Beats, have been well studied (Hardin 1988; Kalisz and Boettcher 1990; Wistendahl 1975), the openings at Strouds Run State Park had not yet been thoroughly inventoried. The openings exist on protected public land but, like other grasslands in the region, appear to be threatened by woody plant encroachment, loss of disturbance, and activities such as trail building. The baseline data collected in this study will be important for understanding the factors supporting this unusual vegetation type, for guiding its management and protection, and for understanding the contributions of these sites to biodiversity within the park, county, and region as a whole. The objectives of our study were to inventory the vascular flora of the three openings, compare soil properties between the openings and surrounding forest matrix, and develop management recommendations for the conservation of these unusual prairie-like plant communities.

MATERIALS AND METHODS

Strouds Run State Park (39°21′N, 82°2′W) is located in Athens County, Ohio, in the Marietta section of the unglaciated Allegheny Plateau (Brockman 1998). Local topography is highly dissected and characterized by narrow ridges separated by steep, eroded valleys. Pennsylvanian sedimentary bedrock strata, primarily sandstones and shales, are the main bedrock types, with occasional outcrops of limestone belonging to the Monongahela Series (Brockman 1998). Soils are silty loams and silty clay loams derived from the local Pennsylvanian sedimentary strata (Lucht et al. 1985). Loess deposits have not been documented at the site. Naturally occurring upland vegetation is deciduous forests dominated by *Quercus* L., *Carya* Nutt., and *Acer* L. species typical of the Low Hills Belt of the Mixed Mesophytic Forest association (Braun 1950). Plantations of *Pinus strobus* L., an uncommon species in natural regrowth forest in the study area, are present on some former agricultural land.

Three distinctive grassy openings in the upland forests were located and surveyed in the eastern half of Strouds Run State Park along Lake Hill Road (39°20′48.6″N, 82°00′44.5″W), Pete Smith Trail (39°21′27.1″N, 82°01′41.3″W), and Ent Point (39°20′57.5″N, 82°01′31.5″W); these names will be used hereafter to identify the three sites. The openings occur on and around ridgetop limestone exposures within a surrounding matrix of soils derived primarily from sandstones and shales (Figure 1). The Pete Smith site is located on the Upshur-Elba complex of silty clay loams derived from calcareous shale and limestone (United States Department of Agriculture 1985). The Lake Hill Road opening is located on the Gurnsey-Upshur complex of silty and silty clay loams derived from siltstone, and the Ent Point site is located on the Westmoreland-Upshur complex of silty and silty clay loams; both complexes include patches of carbonate-derived Elba soils on ridgetops (United States Department of Agriculture 1985). Two of the openings are surrounded by oak-dominated second-growth forest, while the Ent Point opening is partially surrounded by a *Pinus strobus* plantation.

Land-use history in Strouds Run State Park following European settlement was primarily agricultural. In early surveys and historical aerial photos from 1939, all three of the openings appear as open grasslands, most likely pastures or hayfields (United States Department of Agriculture 2013). Active agriculture had declined by the 1930s, and land abandonment initiated widespread forest regrowth in the mid-20th century (McConnel 1963; Monsted and Matlack 2021; Payne 1957). Early successional forest surrounding the openings appeared in the 1960s, and most adjacent land had converted to forest by 1980. The openings appeared as small open patches 0.1–0.2 ha in size surrounded by second-growth forest by 2000.

To inventory and document the vascular plant composition of the three openings, the sites were surveyed monthly during the growing season (May–October) in 2013. Additional site visits and collections were made in 2014 and from 2016 to 2019. Within each site, the boundaries of the openings were determined from vegetation structure, primarily the density of trees, and vegetation was surveyed within the openings and edge areas. Data on plant species present in the openings were collected via meander surveys; thorough sampling of the sites in this fashion was possible due to their small size and the frequency of visits. Vegetation surveys did not extend into the forest surrounding the openings. Our dataset on plant species composition also includes observations recorded by Jason Larson of the Richland County Parks District (unpublished data) from a previous visit and initial survey of the sites in 2010. Voucher specimens were collected and deposited in the Bartley Herbarium (BHO) at Ohio University. Species present in small populations or only as juvenile individuals were identified to species but not collected

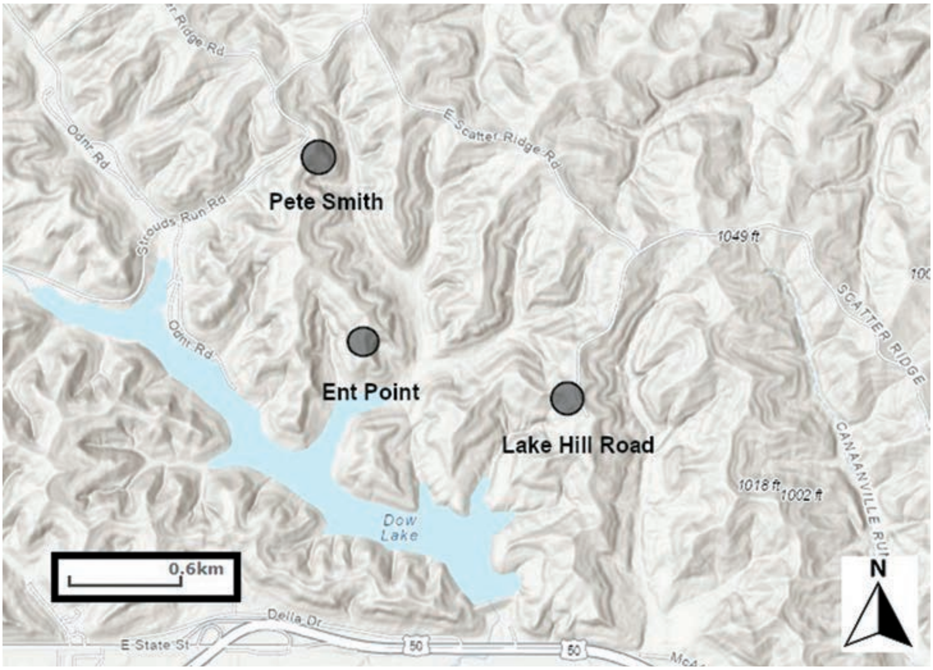

Figure 1. Topographic map of the study area (approximately 39°21′42.9″N to 39°20′06.1″N and 2°02′44.6″W to 82°01′45.0″W) at Strouds Run State Park in Athens County, Ohio, with the names and locations of the three grassy openings investigated in this study. LH = Lake Hill Road, PS = Pete Smith, and EP = Ent Point.

and vouchered. Some species were so heavily damaged by herbivory that collection of an adequate specimen was not possible. Nomenclature follows Weakley (2020).

To evaluate the edaphic context of the openings, surface soil samples (0–10 cm depth) were collected with polyvinyl chloride pipe cores from eight points within each of three zones: opening interior (> 5 m from the edge of the opening), edge (surrounding forest < 5 m from the edge), and forest (> 10 m from opening edge). Soil sampling points were placed randomly within quadrants centered on the core opening to account for variation in soils across the opening, edge, and forest areas. In total, this protocol resulted in 72 soil samples across the three sites (i.e., 24 opening, 24 edge, 24 forest). Soil samples were sieved through 2 mm mesh and dried at ambient indoor temperatures for two weeks, after which bulk density was assessed by dry weight. Stone content in the samples was minimal, so stones were included in the dry weight. Soil pH was tested with an electronic meter (pHTestr 3+, Oakton Instruments, Vernon Hills, Illinois) using a 2:1 volume suspension of distilled water and dry soil that was agitated for two minutes and then allowed to settle for 20 minutes before testing. We assessed percentages of sand, silt, and clay by soil particle size analysis adapted from Gee and Bauder (1979).

Comparisons of soil pH, texture, and bulk density between openings, edges, and surrounding forests were assessed with generalized linear models (GLM) in the R programming language (R Core Team 2019). Plot position was used as a predictor variable. Pairwise comparisons of habitat types were performed with a post-hoc Tukey's Test in the "multcomp" package (Hothorn et al. 2008) to assess differences between each combination of positions.

RESULTS

In total, 135 vascular plant species were identified across the interiors of the three openings (excluding edge zones), of which 109 were native to Ohio and 27 were introduced (Appendix). Total species richness ranged from a high of 106 in the Lake Hill Road site (86 native, 19 introduced) to 84 at the Pete Smith site (67 native, 17 introduced) to a low of 58 at the Ent Point site (47 native, 11 introduced). The two larger openings, Lake Hill Road and Pete Smith, had the most species, while Ent Point, the smallest opening, had the fewest. Of all species identified in the sites, two (1.5%) were ferns, 22 (16.3%) were graminoids, 75 (55.6%) were forbs, and 36 (26.7%) were woody species.

Several soil properties differed significantly between the openings and the surrounding forests (Figure 2). Soil pH was significantly higher in the openings and edges ($t = -6.38$, $p = < 0.0001$), where it averaged between 7.0 and 7.5, than in the forest matrix, where it had a mean of 6.5 (Table 1). All soils were clays with clay content ranging from 34 to 61%, and averages for all three habitat zones (opening, edge, forest) were between 50 and 60% clay. Silt content was lowest in openings and highest in the forest matrix ($t = 3.84$, $p = 0.0003$). Sand content was elevated in the openings ($t = -2.0$, $p = 0.049$). Clay content and bulk density did not differ significantly between communities.

DISCUSSION

The floristic assemblages of the three grassy openings at Strouds Run State Park in Athens County, Ohio, were consistent with those reported from other prairie-like communities on the Allegheny Plateau (Jones 1944; Wistendahl 1975). Dominance of grasses such as *Andropogon gerardi* Vitman and the presence of grassland forbs such as *Lithospermum canescens* (Michx.) Lehm., *Ratibida pinnata* (Vent.) Barnhart, *Silphium trifoliatum* L., and *Physostegia virginiana* (L.) Benth. subsp. *praemorsa* (Shinners) P.D. Cantino (a prairie taxon; Cantino 1982) indicate that the openings are a prairie-like community type and not simply a successional meadow (Jones 1944). Species richness of the openings appeared to be linked to site size: the two larger openings (approximately 0.2 ha) had the largest numbers of species, both native and introduced, while the Ent Point site (approximately 0.1 ha) had the fewest species, a result to be expected considering its small size and partial occlusion by a pine plantation. The limited number of sites did not allow us to evaluate this pattern statistically.

Community composition in the openings is similar to that of nearby grassland communities, such as Buffalo Beats, with comparable species richness: 2012 floristic surveys found 79 species at Buffalo Beats (Kapolka 2014). Distinctive species of the Buffalo Beats community, such as *Andropogon gerardi* and *Ratibida pinnata*, are also common in the Strouds Run openings; however, other species that are common at Buffalo Beats, such as *Eryngium yuccifolium* Michx. and *Liatris cylindracea* Michx. (Hardin 1988; Wistendahl 1975), are absent from the Strouds Run sites. These floristic differences in

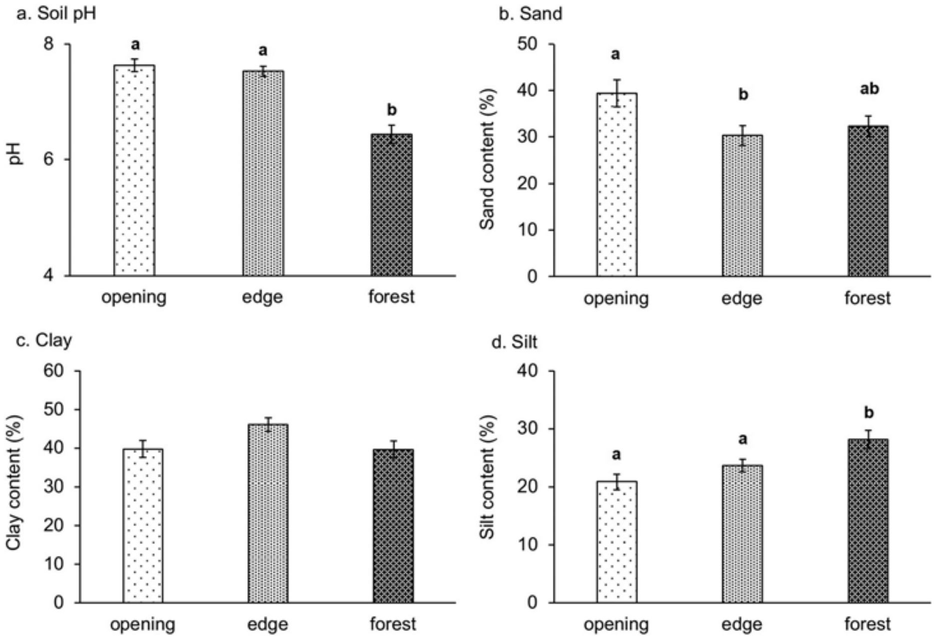

Figure 2. Soil pH and texture conditions documented in grassy opening, forest edge, and matrix forest habitats at the three study sites in Strouds Run State Park in Athens County, Ohio. Error bars indicate means ± 1 standard error. Letters denote significant differences between habitats for pH, sand, and silt; clay did not differ significantly between habitat types: a = pH; b = percent sand; c = percent clay; d = percent silt. N = 24 samples per habitat category, 72 samples total.

Table 1. Pairwise comparisons of soil variables for each habitat type: core opening, edge, and forest matrix, obtained with a post-hoc Tukey's Test, represented by the *z*-value. Bold text denotes *p*-value significance at the 0.05 level.

Soil variable	Position	Opening		Edge	
		z	*p*	*z*	*p*
pH	Opening	–	–	–	–
	Edge	–0.55	0.85	–	–
	Forest	**–6.82**	**< 0.0001**	**–6.27**	**< 0.0001**
Sand	Opening	–	–	–	–
	Edge	**–2.62**	**0.02**	–	–
	Forest	–2.03	0.10	0.58	0.83
Clay	Opening	–	–	–	–
	Edge	2.18	0.08	–	-
	Forest	–0.06	0.99	–2.23	0.07
Silt	Opening	–	–	–	–
	Edge	1.45	0.31	–	–
	Forest	**3.82**	**< 0.0001**	**2.37**	**0.047**

the Strouds Run openings might be attributable to their smaller size, the possible loss of species over time due to community drift (Vellend 2010), or herbivory by abundant white-tailed deer (Anderson et al. 2001). Some distinctive grassland species at Strouds Run, including *Gentiana alba* Muhl. ex J. McNab, *Silphium trifoliatum*, and *Onosmodium bejariense* DC. ex A. DC., are represented by fewer than five individuals in an opening and are therefore highly vulnerable to local extirpation. Of these, *Gentiana alba*, a state-threatened species known from a few scattered populations in Ohio (Andreas and Cooperrider 1981; Ohio Department of Natural Resources 2020), is of particular interest for protection.

In terms of recent land-use history, all three openings were likely kept open prior to the 1960s by haymaking and pasturing. Although it is not possible to determine the exact spatial extent of these grassy prairie-like openings before agricultural abandonment in the mid-20th century, aerial photos between 1939 and 2018 show that they have contracted in recent decades. No information is available on the pre-European history of the sites, although some circumstantial evidence might point to a deeper history as grassy openings. Specifically, work in restored post-agricultural prairies has shown that prairie-associated plant species tend to represent remnant populations that predate agriculture rather than colonization after agricultural abandonment (Kettle et al. 2000), which suggests that the occurrence of prairie species in the isolated grassy openings at Strouds Run might predate their use as hayfields or pastures by European settlers. Although the Strouds Run area does not have a documented history of extensive fire prior to European settlement, it is possible that eastern bison grazed the ridgetops prior to European colonization or that ground fires set by Indigenous peoples burned through the area on occasion. Persistence of these communities during the historical period might also be linked to patterns of land use, since surviving prairies in Ohio typically occur in areas that are undesirable for more intensive cultivation or development (Cusick and Troutman 1978). Most of the ridgetops in the region have nutrient-poor clay soils that do not support plowing and intensive row-crop agriculture but instead were favored for lower intensity pasture or hay cutting, practices that might allow the persistence of prairie-like plant communities.

In terms of their environmental setting, the three grassy openings at Strouds Run did show that soils in the openings and along their edges are chemically distinct from those of surrounding forests. Higher pH values in the openings in conjunction with lower pH in the forest matrix are consistent with limestone-based substrate surrounded by mildly acidic sandstone-derived soils. Heavy clay substrates with higher pH than surrounding forest soils are also seen at other prairie-like openings in the unglaciated Allegheny Plateau, such as Buffalo Beats (Wistendahl 1975). Higher soil pH in the openings than in surrounding forest is typical and, in fact, expected for eastern grasslands (Aldrich and Bacone 1981; Lawless et al. 2006; McClain and Ebinger 2014; Rhoades et al. 2005) whether through edaphic conditions or as a result of forbs, grasses, and trees having different effects on soil chemistry. Slightly lower bulk density in openings and edges compared to forest soils may reflect regular organic matter inputs from the fine roots of grasses and forbs (Weaver et al. 1935).

Despite differences between soils in the openings and those in the forest matrix, analysis of soil variables indicates that woody encroachment is occurring. Notably, edge soils did not differ significantly from the openings but were higher in pH than forest soils. This similarity suggests that although vegetation at the edges is more forest-like in character today, these edge zones may have once supported open, grassy, or prairie-like vegetation. Historical aerial photographs of the study area support this interpretation. Such patterns of woody plant encroachment proceeding inward from the forest edge are typical in small grass and forb-dominated openings in the absence of disturbance (Annala et al. 1983; McClenahan and Houston 1998). Environmental change occurs concurrently with change in vegetation structure, and shifts toward forest at the edges can alter micro-habitats and further facilitate transition from grassland to forest (Copenheaver et al. 2004; McClenahen and Houston 1998). Although soil conditions appear to have limited tree growth and succession in the absence of regular disturbance in recent decades, this factor is likely not sufficient to allow the openings to persist over the long term. Indeed, in an effort to slow the loss of these distinctive grassy habitats, many trees and saplings were removed from the Lake Hill Road and Pete Smith openings in 2009 and 2010 (Cantino pers. obs.). Additional experimental research is necessary to directly assess the possible limitation of tree growth by the distinctive soil conditions documented at the sites.

Although the grassy openings at Strouds Run and their characteristic plant communities have so far survived the broader regional transition from agricultural land use to forest in recent decades, continued colonization by woody plant species poses a threat to their persistence. Other openings in the Allegheny Plateau and Bluegrass regions, such as Buffalo Beats and Lynx Prairie, have suffered species loss and rapid structural change from canopy closure following fire suppression or abandonment from grazing (Annala et al. 1983; Hardin 1988; Kapolka 2014). In the past, livestock pasturing at Strouds Run likely prevented establishment of trees and shrubs, which would have benefitted grassland species by reducing shade and competition (Anderson 2006; Auffenorde and Wistendahl 1985). The end of agricultural grazing around the time of land acquisition for the park in the 1950s would have removed this disturbance factor, ending suppression of woody species and allowing gradual colonization of the openings by trees.

Woody encroachment at the Strouds Run sites takes multiple forms. For example, *Cercis canadensis* L. occurs in dense patches in the Lake Hill Road and Pete Smith openings, and small *Fraxinus americanus* L. saplings have established in all three sites. The effects of woody encroachment seem especially conspicuous at the Ent Point site, where planted *Pinus strobus* and its seedlings appear to be actively competing with and suppressing the characteristic openland species. Many openland species in this site showed stunted growth and reduced flowering compared to more open sites (Holmes pers. obs.), which are responses consistent with shading (Petranka and McPherson 1979). Although the stunted species persist at present, it is possible that reduced reproduction, stochastic mortality in small populations, and community drift (Vellend 2010) may ultimately result in population failure and species loss, with a negative effect on site diversity.

Because of their distinctive contributions to the local and regional flora, and signs that they are threatened by successional processes, the grassy openings at Strouds Run State Park merit further attention and targeted management. In particular, management of the distinctive plant communities represented in the three sites should focus on preventing further woody plant encroachment and succession to forest, if not expanding the openings into edge areas with calcareous soils that have transitioned to forest edge. Because the openings are small and populations of many grassland-associated species are small and patchy, use of heavy equipment and herbicides should be avoided. Accidental destruction of a few individuals of species, such as *Gentiana alba* or *Silphium trifoliatum*, could result in extirpation from the site and perhaps the park as a whole; as such, protection of characteristic species should be of utmost importance to any management plans. Periodic hand-thinning of native woody species, like *Cercis* and *Fraxinus,* is recommended to prevent them from shading and outcompeting the unique ground-layer plants. The high density and abundance of *Pinus strobus* seedlings at the Ent Point site makes successful management unlikely, but hand-pulling may be attempted. Of the nonnative species present in the openings, the majority are herbaceous species, such as *Leucanthemum vulgare* Lam., that do not spread aggressively within the sites and appear to coexist with native species in small numbers. Because of the potential for damage from management efforts, these species should not be prioritized for removal but rather might be considered relics from the sites' agricultural past. In contrast, more aggressive woody exotic species, such as *Rosa multiflora* Thunb., *Rubus phoenicolasius* Maxim., and *Lonicera maackii* (Rupr.) Maxim., should be targeted for removal. These invasive shrubs should be removed with hand-cutting, and any seedlings should be pulled or dug out where possible. Although controlled burns have potential as a management tool, they may not be a practical option owing to the small size of the sites and their proximity to residential structures.

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LITERATURE CITED

Abrams, E.M., A. Freter, and V. Stefanova. 2014. Environmental change since the Woodland Period in the Mid-Ohio Valley: results from Patton Bog sediment core palynological analyses. MidContinental Journal of Archaeology 39:163–178. DOI:10.1179/2327427113Y.0000000009

Aldrich, J.R. and J.A. Bacone. 1981. Limestone glades of Harrison County, Indiana. Proceedings of the Indiana Academy of Sciences 91:480–485.

Anderson, R.C. 2006. Evolution and origin of the Central Grassland of North America: climate, fire, and mammalian grazers. Journal of the Torrey Botanical Society 133:626–647. DOI:10.3159/1095-5674(2006)133[626:EAOOTC]2.0.CO;2

———, E.A. Corbett, M.R. Anderson, G.A. Corbett, and T.M. Kelley. 2001. High white-tailed deer density has negative impact on tallgrass prairie forbs. Journal of the Torrey Botanical Society 128:381–392. DOI:10.2307/3088670

Andreas, B.K. and T.S. Cooperrider. 1981. The Gentianaceae and Menyanthaceae of Ohio. Castanea 46:102–108. DOI:10.2307/4033038

Annala, A., J.D. Dubois, and L.A. Kapustka. 1983. Prairies lost to forests: a 33-year history of two sites in Adams County, Ohio. Ohio Journal of Science 83:22–27.

Auffenorde, T.M. and W.A. Wistendahl. 1985. The composition, structure, and phenology of the vegetation at the O.E. Anderson Compass-Plant Prairie in unglaciated southeastern Ohio. Ohio Journal of Science 85:50–59.

Baskin, J.M., C.C. Baskin, and E.W. Chester. 1994. The Big Barrens Region of Kentucky and Tennessee: further observations and considerations. Castanea 59:226–254. DOI:10.2307/4033696

Borsari, B., D. Johnson, W. Taylor, and V. Kefeli. 2004. Conservation efforts and natural history of a prairie habitat at Jennings Environmental Education Center, Pennsylvania, pp.149–157. *In:* D. Egan and J.A. Harrington, eds., Proceedings of the 19th North American Prairie Conference: The Conservation Legacy Lives On. University of Wisconsin Press, Madison, WI.

Braun, E.L. 1950. Deciduous Forests of Eastern North America. Blackburn Press, Caldwell, NJ.

Brockman, C.S. 1998. Physiographic regions of Ohio. State of Ohio, Department of Natural Resources, Division of Geological Survey, Columbus, OH.

Cantino, P.D. 1982. A monograph of the genus *Physostegia* (Labiatae). Contributions from the Gray Herbarium of Harvard University 211:1–105.

Cartwright, J. 2019. Ecological islands: conserving biodiversity hotspots in a changing climate. Frontiers in Ecology and the Environment 17:331–340.

Copenheaver, C.A., N.E. Fuhrman, L.S. Gellerstedt, and P.A. Gellerstedt. 2004. Tree encroachment in forest openings: a case study from Buffalo Mountain, Virginia. Castanea 69:297–308.

Cusick, A.W. and K.R. Troutman. 1978. The prairie survey project, a summary of data to date. Ohio Biological Survey Informative Circular No. 10. Ohio State University, Columbus, OH.

Drummond, M.A. and T.R. Loveland. 2010. Land-use pressure and a transition to forest-cover loss in the eastern United States. BioScience 60:286–298. DOI:10.1525/bio.2010.60.4.7

Gee, G.W. and J.W. Bauder. 1979. Particle size analysis by hydrometer: a simplified method for routine textural analysis and a sensitivity test of measurement parameters. Soil Science Society of America Journal 43:1004–1007.

Hanberry, B.B. and R.F. Noss. 2022. Locating potential historical fire-maintained grasslands of the eastern United States based on topography and wind speed. Ecosphere 13:e4098. DOI: 10.1002/ecs2.4098

Hardin, E.D. 1988. Succession in Buffalo Beats prairie and surrounding forest. Bulletin of the Torrey Botanical Club 115:13–24.

Harrelson, S.M. and P.D. Cantino. 2006. The terrestrial vascular flora of Strouds Run State Park, Athens County, Ohio. Rhodora 108:142–183. DOI:10.3119/05-10.1

Havercamp, J. and G.G. Whitney. 1983. The life history characteristics of three ecologically distinct groups of forbs associated with the tallgrass prairie. American Midland Naturalist 109:105–119.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. Biometrical Journal: Journal of Mathematical Methods in Biosciences 50:346–363. DOI:10.1002/bimj.200810425

Jones, C.H. 1944. Studies in Ohio floristics-III. Vegetation of Ohio prairies. Bulletin of the Torrey Botanical Club 71:536–548.

Kalisz, P.J. and S.E. Boettcher. 1990. Phytolith analysis of soils at Buffalo Beats, a small forest opening in southeastern Ohio. Bulletin of the Torrey Botanical Club 117:445–449. DOI:10.2307/2996842

Kapolka, C.K. 2014. Assessment of prairie restoration and vegetation change at the Buffalo Beats Research Natural Area, Athens County, OH. M.S. thesis, Ohio University, Athens, OH.

Kettle, W.D., P.M. Rich, K. Kindscher, G.L. Pittman, and P. Fu. 2000. Land-use history in ecosystem restoration: a 40-year study in the prairie-forest ecotone. Restoration Ecology 8:307–317. DOI:10.1046/j.1526-100x.2000.80043.x

Latham, R.E. 1993. The serpentine barrens of temperate eastern North America: critical issues in the management of rare species and communities. Bartonia 57:61–74.

Laughlin, D.C. 2004. Woody plant invasion and the importance of anthropogenic disturbance within xeric limestone prairies. Journal of the Pennsylvania Academy of Science 78:12–24.

Lawless, P.J., J.M. Baskin, and C.C. Baskin. 2006. Scale-dependent classification of xeric limestone prairies: annual or perennial grasslands? Annals of the Missouri Botanical Garden 93:455–464. DOI:10.3417/0026-6493(2007)93[455:SCOXLP]2.0.CO;2

Lucht, T.E., D.L. Brown, and N.H. Martin. 1985. Soil survey of Athens County, Ohio. Soil Conservation Service, United States Department of Agriculture, Washington, D.C.

McClain, W.E. and J.E. Ebinger. 2014. Vascular flora of Buettner xeric limestone prairies, Monroe County, Illinois. Castanea 79:246–254. DOI:10.2179/14-015R

McClenahen, J.R. and D.B. Houston. 1998. Comparative age structure of a relict prairie transition forest and indigenous forest in southeastern Ohio, USA. Forest Ecology & Management 112:31–40.

McConnel, C.T. 1963. The vegetation of old fields in Strouds Run State Park with special reference to the ages of trees. M.S. thesis, Ohio University, Athens, OH.

Monsted, J.W. and G.R. Matlack. 2021. Shaping the second-growth forest: fine-scale land use change in the Ohio Valley over 120 years. Landscape Ecology 36:3507–3521. DOI:10.1007/s10980-021-01323-6

Noss, R.F. 2013. Forgotten Grasslands of the South: Natural History and Conservation. Island Press, Washington, D.C.

Ohio Department of Natural Resources. 2020. Rare native Ohio plants 2020–21 status list. Website (https://ohiodnr.gov/static/documents/natural-areas/2020-21+Ohio+Rare+Native+Plants+Status+List+FINAL.pdf).

Payne, W. 1957. A floristic study of the Athens State Forest, Athens County, Ohio. M.S. thesis, Ohio University, Athens, OH.

Petranka, J.W. and J.K. McPherson. 1979. The role of *Rhus copallina* in the dynamics of the forest-prairie ecotone in north-central Oklahoma. Ecology 60:956–965.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Website (http://www.R-project.org).

Rhoades, C.C., S.P. Miller, and D.L. Skinner. 2005. Forest vegetation and soil patterns across glade-forest ecotones in the Knobs region of northeastern Kentucky, USA. American Midland Naturalist 154:1–10. DOI:10.1674/0003-0031(2005)154[0001:FVASPA]2.0.CO;2

Sears, P.B. 1926. Natural vegetation of Ohio II: the prairies. Ohio Journal of Science 26:128–146.

Shane, L.C., G.G. Snyder, and K.H. Anderson. 2001. Holocene vegetation and climate changes in the Ohio region, pp. 11–55. *In*: O.H. Prufer, S.E. Pedde, and R.S. Meindl, eds., Archaic Transitions in Ohio and Kentucky Prehistory. Kent State University Press, Kent, OH.

Socolar, J.B., J.J. Gilroy, W.E. Kunin, and D.P. Edwards. 2016. How should beta-diversity inform biodiversity conservation? Trends in Ecology & Evolution 31:67–80. DOI:10.1016/j.tree.2015.11.005

Sutherland, E.K. 1997. History of fire in a southern Ohio second-growth mixed-oak forest. North Central Forest Experiment Station, Forest Service, U.S. Department of Agriculture.

United States Department of Agriculture. 2013. Aerial photographs of Athens County, Ohio (ca. 1938–1966). USDA Soil and Water Conservation Office, The Plains, Ohio, USA.

United States Department of Agriculture Soil Conservation Service. 1985. Soil survey of Athens County. Website (https://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/ohio/OH009/0/athens.pdf).

Vellend, M. 2010. Conceptual synthesis in community ecology. Quarterly Review of Biology 85:183–206.

Waltman, S.W. and E.J. Ciolkosz. 1995. Prairie soil development in northwestern Pennsylvania. Soil Science 160:199–208.

Weakley, A.S. 2020. Flora of the Southeastern United States: Southern Ohio. University of North Carolina Herbarium, Chapel Hill, NC. Website (https://ncbg.unc.edu/research/unc-herbarium/floras).

Weaver, J.E., V.H. Hougen, and M.D. Weldon. 1935. Relation of root distribution to organic matter in prairie soil. Botanical Gazette 96:389–420.

Whitney, G.G. and J.R. Steiger. 1985. Site-factor determinants of the presettlement prairie-forest border areas of north-central Ohio. Botanical Gazette 146:421–430.

Wistendahl, W.A. 1975. Buffalo Beats, a relict prairie within a southeastern Ohio forest. Bulletin of the Torrey Botanical Club 102:178–186.

APPENDIX

Terrestrial vascular plant species found in three grassy forest openings at Strouds Run State Park, Athens County, Ohio

Species names are listed alphabetically by family within larger groups. Taxonomy follows Flora of the Southeastern United States: Southern Ohio (Weakley 2020). Openings where each species occurs are abbreviated as follows: Lake Hill Road (LH), Pete Smith (PS), Ent Point (EP). Species marked with "*" are nonnative in Ohio; the species preceded by "T" is listed as "threatened" in Ohio (Ohio Department of Natural Resources 2020). All specimens have been deposited in the Floyd Bartley Herbarium (BHO) at Ohio University.

PTERIDOPHYTA

ASPLENIACEAE

Asplenium platyneuron (L.) Britton, Sterns, & Poggenb.—EP, LH, PS; *Holmes 2018-008*

OPHIOGLOSSACEAE

Botrychium virginianum (L.) Sw.—EP, LH, PS; *Holmes 2013-004*

CONIFEROPHYTA

CUPRESSACEAE

Juniperus virginiana L.—EP, LH, PS; *Holmes 019-005*, *Holmes 2018-001*

PINACEAE

Pinus strobus L.—EP; Not collected

MAGNOLIOPHYTA

ACERACEAE

Acer saccharum Marshall—PS; Not collected

ALLIACEAE

**Allium vineale* L.—LH; *Holmes 2018-010*

ANACARDIACEAE

Toxicodendron radicans (L.) Kuntze—LH; Not collected

APIACEAE

**Daucus carota* L.—EP, LH, PS; *Holmes 2013-115*

APOCYNACEAE

Apocynum cannabinum L.—EP, LH, PS; Not collected
Asclepias syriaca L.—LH; Not collected
Asclepias tuberosa L.—EP, LH, PS; *Holmes 2019-021*

ASTERACEAE

**Achillea millefolium* L.—EP, LH, PS; *Holmes 2019-020*
Ageratina altissima (L.) R.M. King & H. Rob.—EP, LH, PS; *Holmes 2013-112*
Ambrosia artemisiifolia L.—PS; Not collected
Antennaria plantaginifolia (L.) Hook.—EP; *Holmes 2013-011*
Arnoglossum atriplicifolium (L.) H. Rob.—EP, LH, PS; *Holmes 2013-129*
Cirsium discolor (Muhl. ex Willd.) Spreng.—LH, PS; *Holmes 2013-127*
Conoclinium coelestinum (L.) DC.—PS; Not collected
Erigeron strigosus Muhl. ex Willd.—LH, PS; *Holmes 2013-094*
Helianthus hirsutus Raf.—LH; *Holmes 2013-124*
**Leucanthemum vulgare* Lam.—EP, LH, PS; *Holmes 2013-049*

Packera aurea (L.) Á. Löve & D. Löve—EP; Not collected
Pseudognaphalium obtusifolium (L.) Hilliard & B.L. Burtt—PS; *Holmes 2017-016*
Ratibida pinnata (Vent.) Barnhart—LH, PS; *Holmes 2013-097*
Silphium trifoliatum L.—LH; Not collected
Solidago nemoralis Aiton—LH, PS; *Holmes 2017-006*
Symphyotrichum cordifolium (L.) G.L. Nesom—LH, PS; *Holmes 2013-140*
Symphyotrichum lateriflorum (L.) Á. Löve & D. Löve—LH, PS; *Holmes 2018-006*
Symphyotrichum undulatum (L.) G.L. Nesom—LH; *Holmes 2018-003*
**Taraxacum officinale* F.H. Wigg.—LH, PS; Not collected
**Tragopogon pratensis* L.—EP, PS; *Holmes 2013-086*

BERBERIDACEAE
**Berberis thunbergii* DC.—PS; *Holmes 2017-011*

BORAGINACEAE
Cynoglossum virginianum L.—EP, LH, PS; Not collected
Lithospermum canescens (Michx.) Lehm.—EP, LH, PS; *Holmes 2013-010*
Lithospermum latifolium Michx.—EP, LH, PS; Not collected
Onosmodium bejariense DC. ex A. DC.—LH; *Holmes 2013-047*

BRASSICACEAE
Cardamine douglassii Britton—EP, LH, PS; *Holmes 2013-017*
**Lepidium campestre* (L.) W.T. Aiton—PS; *Holmes 2019-013*
**Thlaspi alliaceum* L.—LH, PS; *Holmes 2013-053*

CAMPANULACEAE
Campanulastrum americanum (L.) Small—EP, LH, PS; *Holmes 2014-021*

CAPRIFOLIACEAE
**Lonicera japonica* Thunb.—EP, LH, PS; *Holmes 2013-133*
**Lonicera maackii* (Rupr.) Maxim.—LH; *Holmes 2018-011*
Symphoricarpos orbiculatus Moench—LH, PS; *Holmes 2017-007*
Triosteum aurantiacum E.P. Bicknell—LH; Not collected
Viburnum prunifolium L.—LH; *Holmes 2017-002*

CARYOPHYLLACEAE
**Dianthus armeria* L.—EP, LH, PS; *Holmes 2013-074*

CELASTRACEAE
**Celastrus orbiculatus* Thunb.—PS; *Holmes 2017-008*

CONVOLVULACEAE
Calystegia spithamaea (L.) Pursh—LH; Reported by J. Larson

CORNACEAE
Cornus florida L.—EP, LH, PS; *Holmes 2019-002*

CYPERACEAE
Carex communis L.H. Bailey—LH, PS; *Holmes 2013-045*, *Holmes 2019-011*
Carex hirsutella Mack.—EP, LH; *Holmes 2013-071*, *Holmes 2019-018*
Carex hitchcockiana Dewey—EP, PS; *Holmes 2013-076, Holmes 2019-010*
Carex juniperorum Catling, Reznicek, & Crins—LH, PS; *Holmes 2019-001*, *Holmes 2019-006*
Carex meadii Dewey—LH; *Holmes 2019-014*
Carex oligocarpa Schkuhr ex Willd.—LH, PS; *Holmes 2019-003*, *Holmes 2019-007*

Carex pensylvanica Lam.—LH, PS; *Holmes 2013-059*
Carex striatula Michx.—EP, PS; *Holmes 2013-012*
Carex umbellata Schkuhr ex Willd.—LH; Reported by J. Larson

EBENACEAE
Diospyros virginiana L.—LH, PS; *Holmes 2018-002*

ELEAGNACEAE
Elaeagnus umbellata Thunb.—LH; *Holmes 2013-006*

FABACEAE
Amphicarpaea bracteata (L.) Fernald—EP, LH, PS; *Holmes 2013-044*
Cercis canadensis L.—EP, LH, PS; *Holmes 2017-001*
Desmodium paniculatum (L.) DC.—EP, LH; *Holmes 2013-091*
Desmodium rotundifolium DC.—EP, LH; *Holmes 2013-122*
Gleditsia triacanthos L.—PS; Not collected
Lespedeza procumbens Michx.—EP, LH, PS; *Holmes 2018-012*
Medicago lupulina L.—EP, LH; *Holmes 2013-058*
Melilotus officinalis (L.) Lam.—EP, LH, PS; *Holmes 2013-072*
Securigera varia (L.) Lassen—EP; Not collected
Senna marilandica (L.) Link—LH; *Holmes 2013-126*
Trifolium pratense L.—LH; *Holmes 2013-098*
Trifolium repens L.—EP, LH, PS; *Holmes 2017-003*

FAGACEAE
Quercus alba L.—LH; Not collected
Quercus macrocarpa Michx.—PS; *Holmes 2017-015*
Quercus montana Willd.—EP, PS; *Holmes 2017-013*
Quercus muehlenbergii Engelm.—EP, LH, PS; *Holmes 2017-009*

GENTIANACEAE
Frasera caroliniensis Walter—EP; *Holmes 2019-019*
(T) *Gentiana alba* Muhl. ex J. McNab—PS; *Holmes 2014-020*

IRIDACEAE
Sisyrinchium albidum Raf.—LH; Reported by J. Larson
Sisyrinchium angustifolium Mill.—LH; Not collected

LAMIACEAE
Blephilia ciliata (L.) Raf. ex Benth.—LH, PS; *Holmes 2019-017*
Monarda fistulosa L.—LH, PS; *Holmes 2013-100*
Physostegia virginiana (L.) Benth. subsp. *praemorsa* (Shinners) P.D. Cantino—LH, PS; *Holmes 2013-125*
Prunella vulgaris L.—EP, LH, PS; *Holmes 2013-142*
Scutellaria serrata Andrews—PS; *Holmes 2013-081*

OLEACEAE
Fraxinus americana L.—EP, LH, PS ; *Holmes 2018-004*
Fraxinus quadrangulata Michx.—LH; Reported by D. Gibbs and P. Cantino 2019
Ligustrum vulgare L.—PS; *Holmes 2013-109*

ORCHIDACEAE
Aplectrum hyemale (Muhl. ex Willd.) Torr.—EP; Not collected
Liparis liliifolia (L.) A. Rich. ex Lindl.—EP; Not collected

OXALIDACEAE
Oxalis stricta L.—LH; Not collected

PHRYMACEAE
Phryma leptostachya L.—LH; *Holmes 2013-078*

PLANTAGINACEAE
Penstemon digitalis Nutt. ex Sims—LH, PS ; *Holmes 2019-016*

POACEAE
Andropogon gerardi Vitman– EP, LH, PS; *Holmes 2013-130*
Brachyelytrum erectum (Schreb.) P. Beauv.—EP; *Holmes 2013-090*
**Bromus arvensis* L.—LH; *Holmes 2013-057*
Bromus ciliatus L.—EP, LH, PS; *Holmes 2013-046*
Dichanthelium boscii (Poir.) Gould & C.A. Clark—EP, LH, PS; *Holmes 2013-050*
Dichanthelium villosissimum (Nash) Freckmann—LH; *Holmes 2013-054*
Elymus hystrix L.—EP, LH, PS; *Holmes 2013-082*
Elymus virginicus L.—EP; *Holmes 2013-067*
**Microstegium vimineum* (Trin.) A. Camus—LH, PS; *Holmes 2013-111*
**Phleum pratense* L.—EP, LH; *Holmes 2013-101*
**Schedonorus arundinaceus* (Schreb.) Dumort.—LH; *Holmes 2013-056*
Schizachyrium scoparium (Michx.) Nash—LH; *Holmes 2013-131*
Tridens flavus (L.) Hitchc.—LH; *Holmes 2013-132*

RANUNCULACEAE
Anemone virginiana L.—EP, LH, PS; *Holmes 2013-092*

ROSACEAE
Crataegus chrysocarpa Ashe—PS; *Holmes 2013-005*
Crataegus mollis (Torr. & A. Gray) Scheele—LH; *Holmes 2013-007*
Fragaria virginiana Mill.—LH; Not collected
Agrimonia pubescens Wallr.—PS; *Holmes 2017-012*
Gillenia stipulata (Muhl. ex Willd.) Nutt.—LH, PS; Not collected
Potentilla canadensis L.—EP; Not collected
Potentilla norvegica L.—LH; Not collected
Rosa carolina L.—LH; *Holmes 2013-043*
**Rosa multiflora* Thunb.—LH, PS; *Holmes 2013-034*
Rubus flagellaris Willd.—LH; *Holmes 2013-008*
Rubus occidentalis L.—EP, LH, PS; *Holmes 2013-096*
Rubus pensilvanicus Poir.—PS; *Holmes 2013-083*
**Rubus phoenicolasius* Maxim.—LH; *Holmes 2018-009*

RUBIACEAE
Galium circaezans Michx.—EP; *Holmes 2013-055*
Galium concinnum Torr. & A. Gray—LH; *Holmes 2013-048*
Galium pilosum Aiton—LH; Reported by J. Larson

SMILACACEAE
Smilax tamnoides L.—EP, LH, PS; *Holmes 2017-005*

SOLANACEAE
Physalis pubescens L.—EP, LH, PS; *Holmes 2018-005*
Solanum carolinense L.—LH, PS; Not collected

ULMACEAE
Celtis pumila Pursh—EP, LH, PS; *Holmes 2013-128*
Ulmus americana L.—EP, LH, PS; Not collected

VALERIANACEAE
Valerianella chenopodiifolia (Pursh) DC.—PS; *Holmes 2019-012*

VERBENACEAE
Verbena urticifolia L.—PS; Not collected

VIOLACEAE
Viola blanda Willd.—PS; *Holmes 2013-002*
Viola sororia Willd.—LH, PS; *Holmes 2013-009*
Viola triloba Schwein.—EP, LH, PS; *Holmes 2013-003*

VITACEAE
**Ampelopsis brevipedunculata* (Maxim.) Trautv.—PS; Not collected
Parthenocissus quinquefolia (L.) Planch.—EP, LH, PS; Not collected