

## RESEARCH ARTICLE

# Variation in characteristics and conservation values of plant communities on abandoned agricultural lands with and without fires

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## Abstract

**Question:** Which plant community characteristics most consistently vary with prior land use?

**Location:** Oak Openings Preserve, Ohio, USA.

**Methods:** In 2020, we measured plant communities on 22 sites encompassing three prior land uses: (a) contemporary *Quercus* forests continuously forested since before the 1930s; (b) former agricultural lands, under cultivation in the 1930s and abandoned 70–80 years before our study and that were unburned; and (c) former agricultural lands also abandoned 70–80 years earlier and that were burned in 2013 prescribed fires. Among the three land uses, we compared 12 plant community variables, categorized into four groups characterizing different sets of community properties (structure, diversity, composition, and conservation values).

**Results:** A multivariate combination of the 12 community variables differed among all three land uses, each of the four categories of variables differed between at least two land uses, and eight of 12 individual variables differed between at least two land uses. Community structure displayed a gradient of decreasing tree canopy and understorey plant cover and increasing lichen–moss cover from continuously forested to unburned and burned formerly cultivated sites. Understorey plant species richness did not vary with land use, but species diversity was higher on cultivated sites, irrespective of fire history. While all three land uses now contain *Quercus* tree overstories, each land use exhibited unique understorey species composition. Only formerly cultivated sites contained state-listed endangered species. Cultivated sites had a lower proportion of native species cover than did continuously forested sites, but native species still comprised over 90% of the plant cover on cultivated sites. Compared with continuous forests, the soil organic layer (O horizon) was five times thinner and loss on ignition in the 0–15 cm mineral soil 49% (unburned) and 66% (burned) lower on previously cultivated sites.

**Conclusions:** Community characteristics varied in their sensitivity to land use history, with species composition among the most sensitive to prior land use. A dense sapling layer of *Acer rubrum* forming in long-unburned *Quercus* forests across much of eastern North America was absent in our study on formerly cultivated sites, possibly due to dry, infertile soil. From a restoration and conservation standpoint of the

study region's pre-settlement, frequently burned and open savannas and woodlands, previously cultivated sites may be easier to keep open via prescribed fire. Moreover, perhaps precisely because much of the flora historically developed in open savannas and woodlands which previously cultivated sites on the contemporary landscape most closely mimicked, previously cultivated sites presently contain higher species diversity and more conservation priority species than do continuously forested sites.

#### KEYWORDS

biocrust, land use history, *Quercus* forest, savanna, soil, species composition, species richness

## 1 | INTRODUCTION

The abandonment of cultivated agricultural lands has been a driver of spatio-temporal variation in land use globally and is projected to continue to be so over the next century (Perpiña Castillo et al., 2021). With a third (5 billion ha) of Earth's land area currently under cultivation as cropland or pasture, vegetation dynamics under past and present agricultural abandonment can exert enormous influence over global changes in biodiversity, climate, and future land use options (Cramer et al., 2008; FAO, 2020). Between 2000 and 2018, the amount of land under cultivation globally declined by 2%, partly via conversion to impervious surfaces (e.g., urban areas), but mostly via fallowing or abandonment resulting in land open to colonization by new plant communities (Su et al., 2018; Yu & Lu, 2018; FAO, 2020). Exemplifying potential for this trend to persist, agricultural land abandonment in Europe is projected to continue at a rate of 400,000 ha/year through the 2030s, such that abandoned lands could comprise as much as 11% of the entire area that had been under cultivation in 2000 (Perpiña Castillo et al., 2021).

Accumulating literature has established that previous land uses, including agricultural cultivation, can influence plant communities for decades to millennia (Inouye et al., 1987; Foster et al., 2003; Hermy & Verheyen, 2007). Which features of plant communities are most consistently or persistently influenced by previous land uses is less well understood, however (Brudvig et al., 2013). Focusing on examples from temperate regions, plant species richness in >30-year-old communities on formerly cultivated lands has been higher (Motzkin et al., 1996), similar (Dyer, 2010; Brudvig et al., 2013), or lower (Holmes & Matlack, 2018) than on lands not previously cultivated. Illustrating variation among community structural variables, tree canopy cover has been lower (Glitzenstein et al., 1990), understory cover has been similar (Bossuyt et al., 1999), and ground cover of biocrust organisms (lichens and mosses) has been greater (Corbin & Thiet, 2020) on formerly cultivated compared to non-cultivated lands. Species composition on formerly cultivated and non-cultivated lands has differed in several studies (Eberhardt et al., 2003; Dyer, 2010; Brudvig et al., 2013; Holmes & Matlack, 2018) but in contrasting ways among studies or plant growth forms (Csecserits & Rédei, 2001; Singleton et al., 2001; Kepfer-Rojas et al., 2015). Highlighting variation in floristic quality conservation values, non-native plants on previously cultivated sites have been abundant (Stover & Marks, 1998; Von

Holle & Motzkin, 2007; Holmes & Matlack, 2019) but so have endangered native plants (Prévosto et al., 2011). These examples reinforce both the significance of legacy effects from prior land uses and that variability in the nature of the effects among studies suggests that further research may help elucidate potential patterns in variability among ecosystems and land use histories.

One of the potential sources of variability in plant community development on formerly cultivated sites is occurrence of further disturbances, such as fires (Katz et al., 2010). In a 50-year-old abandoned field, for example, prescribed fire intended to restore open-habitat halved cover of lichens in soil biocrust in Minnesota, USA (Johansson & Reich, 2005). In Spain, burning 50-year-old abandoned fields shifted plant communities toward shrublands, contrasting with formation of coniferous forests on unburned abandoned fields (Santana et al., 2010). Similarly, in Russia, fires produced grasslands, rather than deciduous forests, on former agricultural lands (Khanina et al., 2018). These studies suggest that fires, including those implemented as part of ecological restoration to reinstate ecological processes, could shape numerous characteristics of plant communities developing on former agricultural lands.

Here, in a *Quercus*-dominated region, we compared plant communities on three types of prior land uses: forest sites continuously forested for 100+ years since before the 1930s, and previously cultivated sites abandoned 70–80 years before vegetation data collection in 2020 that were either unburned or burned in 2013 prescribed fires. We examined 12 vegetation variables, three each in four categories of plant community characteristics: (a) structure (e.g., understory plant cover); (b) diversity (e.g., evenness of cover among growth forms); (c) composition (e.g., forb cover); and (d) conservation values (e.g., cover of rare native plants). We compared plant community variables among land uses in a hierarchical analytical approach ranging from multivariate combinations of all 12 variables to each univariate variable.

## 2 | METHODS

### 2.1 | Study area

Located within the 45,000-ha Oak Openings region in northwestern Ohio, USA, the study area was the 1,737-ha Oak Openings Preserve, administered as part of a public lands conservation system

by Metroparks Toledo (Schetter et al., 2013). The preserve is a sandy landscape of low relief (generally <10 m) that formed from sand deposited along shorelines of expanding and contracting glacial lakes (Fisher et al., 2015). Based on 1820s land surveys before widespread Euro-American settlement, the region historically contained a mixture of frequently burned, open habitats, predominately *Quercus savanna*-woodland (Brewer & Vankat, 2004). By the 1930s, half the land that would become the preserve was under cultivation, mostly as small (<50 ha), homesteaded farms (Figure 1; Appendix S1). According to Moseley (1928), some of the principal crops grown in the region included corn, potatoes, wheat, rye, and pumpkins. Interspersed with the cultivated fields, forests present in the 1930s had likely resulted from increasing tree density and canopy closure in the absence of fire in the formerly open savanna-woodland habitats (Brewer & Vankat, 2004). While not cleared for cultivation,

these forests were likely inhabited by domestic livestock (Sitterley & Falconer, 1938). Many of the farms were abandoned during and after the Great Depression in the 1930s. Some were acquired by the county government in the 1940s–1950s to form the preserve and have been protected since their acquisition. The formerly cultivated sites in the contemporary preserve now contain tree overstories (<70–80 years old) of *Quercus velutina* and *Quercus alba*, are often surrounded by evidence of fence lines demarcating the previous fields, and contain homestead debris nearby (e.g., glass, cookware, and tools). Surrounding the former fields, contemporary forest in patches of 16+ ha is also dominated by *Quercus velutina* and *Quercus alba* but with older trees, 100–200+ years old (Table 1). In addition to analyzing 1930s aerial photos to determine minimum ages of the forests (Appendix S1), we confirmed the >100-year age of dominant *Quercus* trees in the forests by collecting and cross-dating cores

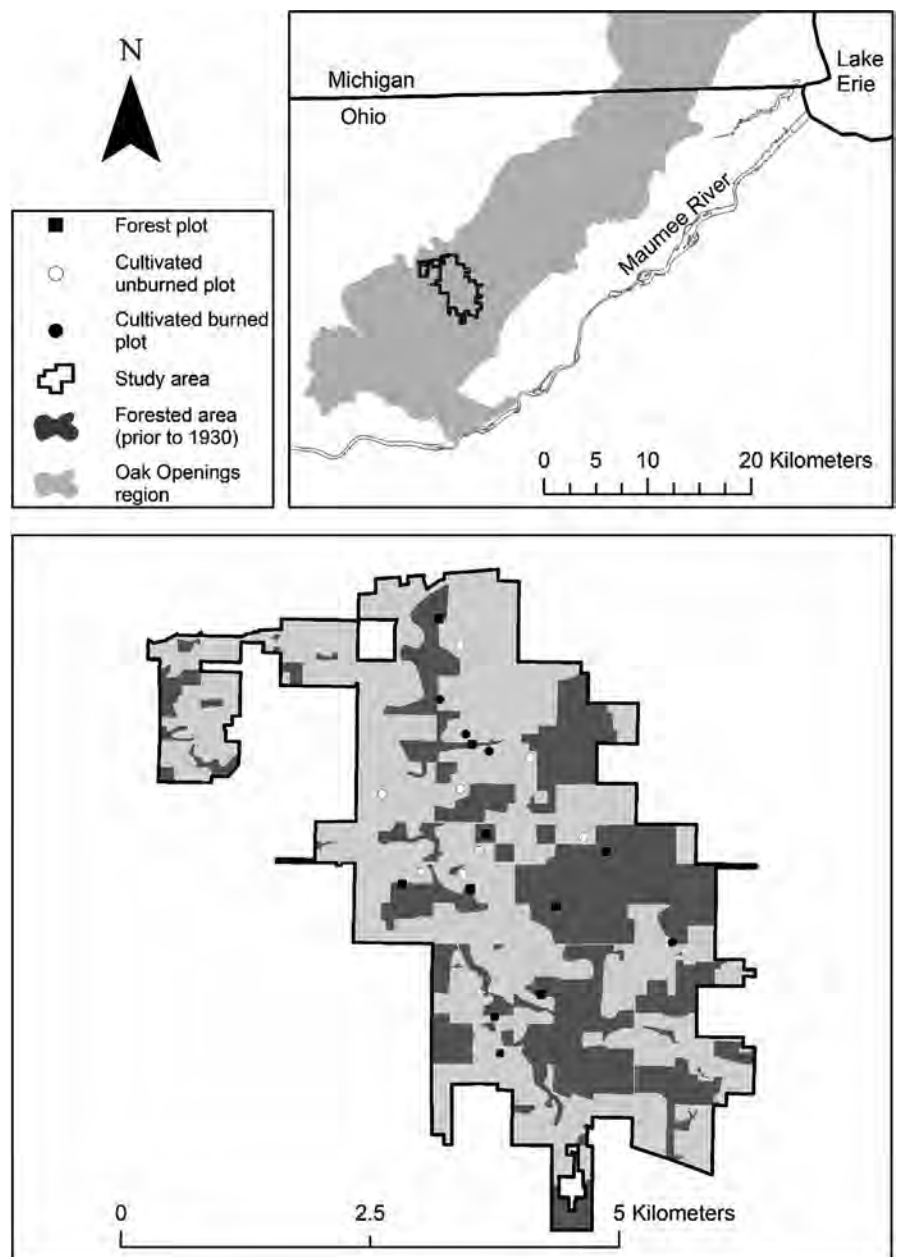


FIGURE 1 Location of the 1,737-ha Oak Openings Preserve study area within the Oak Openings region, Ohio, USA. The study area map shows 22 plots in areas forested before the 1930s and in areas under agricultural cultivation in the 1930s

(using increment borers at a height of 1.4 m up the trunk) from two or more trees near study sites. Soils across the land uses are similarly sandy textured and classified as Udipsamments (Stone et al., 1980).

## 2.2 | Data collection

We randomly located a 20 m × 25 m (0.05 ha) plot within each of eight randomly selected sites in contemporary forests that had been forest in the 1930s and in eight sites that had been under cultivation in the 1930s (based on aerial photos) and with no history of having burned since at least the 1940s (Figure 1; Appendix S1). We also randomly located a plot within each of six sites formerly cultivated in the 1930s and that received prescribed burning in April 2013 to reintroduce fire as an ecological process and manage for open habitats. The burns consisted of low-severity, dormant-season fires using backing and strip headfires with flame lengths generally <2 m. In total, we sampled 22 geographically non-contiguous sites, each containing one plot, for a total of 22 plots (Table 1). We sampled vegetation in plots in summer (July–August) 2020, a near-average climatic year with 95% of the 86-cm average annual precipitation and 91% of the 34-cm average summer (May–August) precipitation (Toledo Airport weather station, 5 km northeast of the study area; National Centers for Environmental Information, Asheville, NC, USA). Since 2015, density of the largest herbivore in the study area, *Odocoileus virginianus*, has typically averaged <10–12 individuals/km<sup>2</sup> and averaged 6/km<sup>2</sup> in 2020 during vegetation sampling.

We focused vegetation sampling on structural and community measures from which to derive a diverse array of community metrics characterizing community structure, diversity, composition, and floristic quality. On each plot, we measured tree canopy cover in percent using a densitometer in a vertical projection above a height of 2.5 m by averaging eight measurements (each to the nearest 5%) per plot every 5 m along the plot diagonal. We also measured ground coverage of biocrust (lichen and moss; Neher et al., 2003) using the same cover categories described for vascular plants below. We measured vascular plant communities by recording areal cover for each species (including seedlings and sprouts <1 cm in diameter at a height of 1.4 m for tree species) using cover categories. These categories were 0.1, 0.25, 0.5, and 1% intervals for 1–10% cover and 5% intervals for 10–100% cover. Areal cover for a species could not exceed 100%, but total cover for all species on a plot could exceed 100% if foliage of multiple species overlapped in vertical projection. Individuals were identified to species, except for some *Cratageus* or *Viola* lacking diagnostic features for reliable identification, so we retained those individuals at the genus level. In total on plots, we detected 161 taxa, of which 159 (99%) were identified to species and two to genus. We collectively refer to these as species as the *Cratageus* or *Viola* kept at genus each likely included individuals from at most 1–2 species. Nomenclature and classification of growth form (e.g., forb) and nativity to the United States follow Natural Resources Conservation Service (2021).

To examine potential environmental correlates with vegetation patterns, we sampled soils on each plot in September 2021. At the southwestern and northeastern corners of plots 1 m outside of plots, we recorded thickness of the litter layer (primarily leaves of deciduous trees) and measured thickness of the surface organic layer (O horizon; Soil Science Division Staff, 2017). After scraping away litter and the O horizon at each sample location, we collected 200 cm<sup>3</sup> of the 0–15 cm mineral soil layer to concentrate on the upper layer likely experiencing cultivation influences (Compton et al., 1998). We averaged the litter and O horizon measurements and composited the mineral soil samples from the two locations per plot. We analyzed mineral soil samples for loss on ignition as a surrogate for soil organic matter (Konen et al., 2002). We first oven-dried 8-g samples in 10-ml crucibles at 110°C for 24 h to remove moisture, then placed samples in a muffle furnace for two hours at 300°C. Loss on ignition in mid-western North American soils is positively related to organic carbon, soil fertility indicators such as nitrogen, and soil available water especially on sandy soils such as those of our study area (Konen et al., 2002; Yost & Hartemink, 2019; Pellegrini et al., 2020). We also measured soil pH (1:1 soil:H<sub>2</sub>O).

## 2.3 | Data analysis

We calculated 12 plant community variables, with three each in four categories consisting of community structure, diversity, composition, and conservation value (Table 2, Appendixes S2, S3). Structural variables included tree canopy, biocrust, and understory vascular plant cover. Diversity measures for the understory plant community included species richness (species/0.05 ha plot), the Shannon diversity index (calculated using species cover), and the evenness of cover among plant growth forms (graminoids, forbs, ferns, shrubs, and seedlings + sprouts of tree species) computed in PC-ORD 7.07 (McCune & Mefford, 1999). Understorey community compositional variables included the proportion of understory cover provided by forbs, a uniqueness frequency index, and species composition. We computed the uniqueness index as the proportion of a plot's species that occurred in two or fewer plots out of the 22 total plots, with high proportions signifying plots containing species infrequent among plots. For species composition, we used ordination axis 1 (accounting for 65% of total variance) from a non-metric multi-dimensional scaling ordination (stress = 14 on a 0–100 scale). The ordination was based on cover relativized by plot (cover of species<sub>*i*</sub>/sum of cover of all species on a plot) and computed using Sørensen distance with “thorough” default settings in PC-ORD 7.07. The three variables of understory community conservation value for each plot included a floristic quality index (sum of species coefficients of conservatism divided by the square root of native species richness; Andreas et al., 2004); cover of rare, state-listed plant species (Ohio Department of Natural Resources, 2020); and the proportion of plant cover supplied by native species. Coefficients of conservatism and the floristic quality index followed procedures customized for Ohio flora (Andreas et al., 2004). The coefficients range from 1

TABLE 1 Summary of 22 study sites in an investigation of plant communities developing on three types of historical land uses in *Quercus* ecosystems, northwestern Ohio, USA

	Forest	Cultivated unburned	Cultivated burned
Number of plots	8	8	6
Age (years)	100+	<70–80	<70–80
Protection year median (range)	1944 (1938–1946)	1945 (1944–1975)	1946 (1940–1972)
Soil	Udipsammets	Udipsammets	Udipsammets
Lichen cover (mean %)	0 ± 0	0.8 ± 0.3	0.2 ± 0.1
Moss cover (mean %)	0 ± 0	1.1 ± 0.4	0.3 ± 0.1
Understorey flora (total species detected)	87	96	84
Annuals and biennials (mean species/0.05 ha)	1 ± 0	2 ± 1	2 ± 1
Perennials (mean species/0.05 ha)	33 ± 4	33 ± 2	30 ± 3
Annuals and biennials (mean cover, %)	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1
Perennials (mean cover, %)	42 ± 9	19 ± 6	10 ± 3
Overstorey dominants	<i>Quercus velutina</i> <i>Quercus alba</i>	<i>Quercus velutina</i> <i>Quercus alba</i>	<i>Quercus velutina</i> <i>Quercus alba</i>
Understorey top four indicator species	<i>Vaccinium angustifolium</i> <i>Hamamelis virginiana</i> <i>Maianthemum racemosum</i> <i>Carex pensylvanica</i>	<i>Amelanchier arborea</i> <i>Rubus flagellaris</i> <i>Viola sagittata</i> <i>Lysimachia quadrifolia</i>	<i>Rumex acetosella</i> <i>Rhus copallinum</i> <i>Rubus occidentalis</i> <i>Apocynum cannabinum</i>



Note: Land uses represent sites that in the 1930s were in forest or under agricultural cultivation and include those unburned or burned in 2013. Protection year represents when sites were incorporated into a preserve. Means include ± SEM. The full list of indicator species is in Appendix S5.

(ruderal, widespread species tolerant of anthropogenic disturbance) to 10 (species largely restricted to high-quality natural areas).

To compare community variables among the three land uses (continuous forest and formerly cultivated unburned and burned sites), we conducted a hierarchical set of analyses. From broad to fine, these analyses included a multivariate combination of all 12 variables, multivariate combinations of the three variables within each of the four categories (structure, diversity, composition, and conservation value), and each of the 12 variables individually. We used non-parametric, permutational multivariate analysis of variance (PERMANOVA) to evaluate multivariate combinations of variables (Anderson, 2001). The 12 variables were measured on different scales. To ensure each variable was weighted equally in multivariate analyses, we relativized values of each variable on each plot as the proportion of the sum of each variable. At the finest level of the analysis, we analyzed each of the 12 variables in univariate permutational analysis of variance (Anderson, 2001). For all permutational analyses, we used Euclidean distance and 9,999 permutations. If models were significant at  $p < 0.05$ , we separated land uses

using sequential Bonferroni tests at  $p < 0.05$ . We performed analyses using PAST 4.02 (Hammer, 2020). Accompanying the hierarchical analysis, we performed PERMANOVA directly on a species compositional matrix (relative cover) followed by sequential Bonferroni comparisons of land uses. We conducted indicator species analysis (Dufrêne & Legendre, 1997) using relative cover to identify species associated with particular land uses with all three land uses included and separately comparing forest:cultivated unburned and cultivated unburned:burned sites. We analyzed soil variables (Appendix S4) using the same permutational analysis of variance procedures as for univariate vegetation variables.

### 3 | RESULTS

Among land uses, community characteristics varied hierarchically from across the broadest multivariate combination of all 12 variables to the finest level of 12 variables individually (Table 2). All three land uses differed in the multivariate combination of all 12 variables,

while forests separated from formerly cultivated sites (irrespective of fire history) for two categories (community structure and conservation value). At least one land use differed from others for the other two categories (diversity and composition). At the finest level of the hierarchy, 8 of 12 variables in univariate analyses differed significantly between two or more land uses.

### 3.1 | Structure

Multivariate community structure differed between forest and formerly cultivated sites but did not further differ with fire on cultivated sites (Figure 2). Forests exhibited a unique multivariate combination of high tree canopy and understory plant cover and an absence of biocrust cover. In univariate analyses, tree canopy and understory cover decreased along a gradient from forest, cultivated unburned, to cultivated

**TABLE 2** Hierarchical permutational analysis of variance comparing characteristics of plant communities developing on sites spanning three types of historical land uses in *Quercus* ecosystems, Ohio, USA

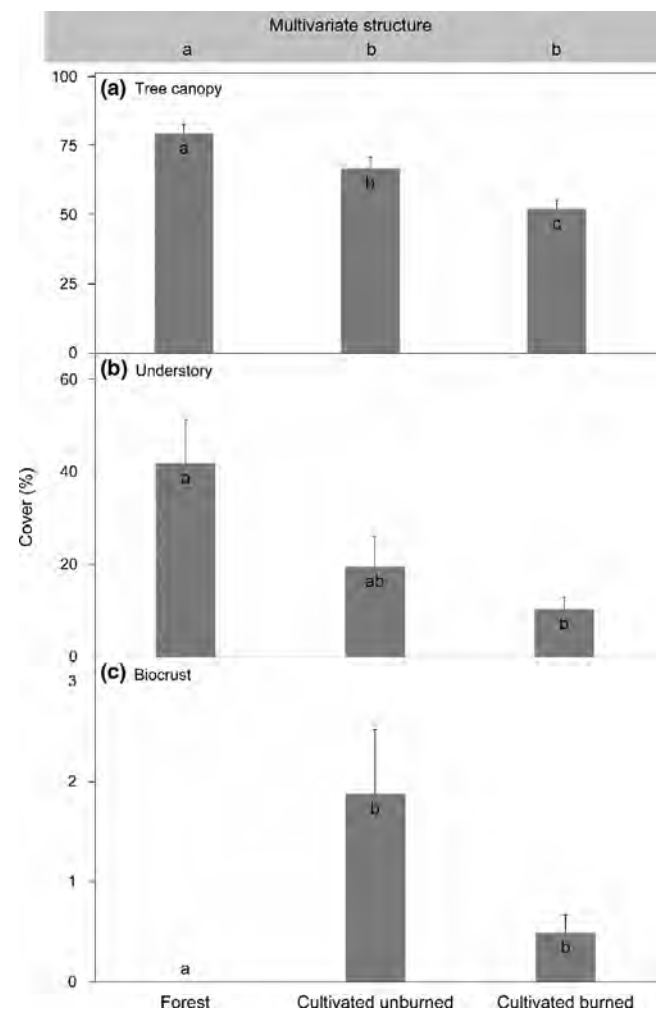
	Pseudo-F	p-Value	Sum of squares	
			Within groups	Total
<b>All 12 variables</b>	<b>4.7</b>	<b>&lt;0.001</b>	<b>0.2</b>	<b>0.3</b>
<b>Structure</b>	<b>5.7</b>	<b>&lt;0.001</b>	<b>0.1</b>	<b>0.2</b>
Canopy cover	5.9	0.006	24	39
Understory cover	4.8	0.018	7,538	11,350
Biocrust cover	13.0	<0.001	1,870	4,435
<b>Diversity</b>	<b>3.4</b>	<b>0.008</b>	<b>0.004</b>	<b>0.006</b>
Species richness	0.2	0.813	1,175	1,201
Shannon diversity	8.3	0.003	3.4	6.4
Evenness growth form	4.4	0.028	0.2	0.3
<b>Composition</b>	<b>3.3</b>	<b>0.006</b>	<b>0.04</b>	<b>0.06</b>
Ordination axis 1	34.7	<0.001	3.8	17.6
Uniqueness	0.1	0.935	0.1	0.2
Proportion forb cover	0.4	0.711	0.2	0.3
<b>Conservation</b>	<b>4.2</b>	<b>0.031</b>	<b>0.07</b>	<b>0.10</b>
Floristic quality	3.4	0.056	116	157
Rare species cover	4.2	0.033	0.2	0.3
Proportion native cover	4.1	0.021	0.1	0.2

*Note:* Land uses included sites that in the 1930s were in forest or under agricultural cultivation including those unburned or burned in 2013. Rows in bold represent multivariate analyses including all 12 plant community characteristics (broadest level of analysis) and combinations of three variables within each of four categories of community characteristics. Rows not in bold are univariate analyses. Degrees of freedom for each analysis: 2 (land use), 19 (residual), 21 (total).

burned sites. Biocrust only inhabited formerly cultivated sites, covering nearly 2% of the ground in unburned and 0.5% in burned sites.

### 3.2 | Diversity

Species richness did not differ significantly among land uses, while Shannon diversity was highest on formerly cultivated sites (Figure 3). Evenness of cover among plant growth forms was higher in cultivated unburned sites than in forests. While the dominant plant group (e.g., graminoid or shrub) could vary among forest sites, generally one or two groups dominated cover, compared with more equitable cover among plant growth forms on cultivated unburned sites.

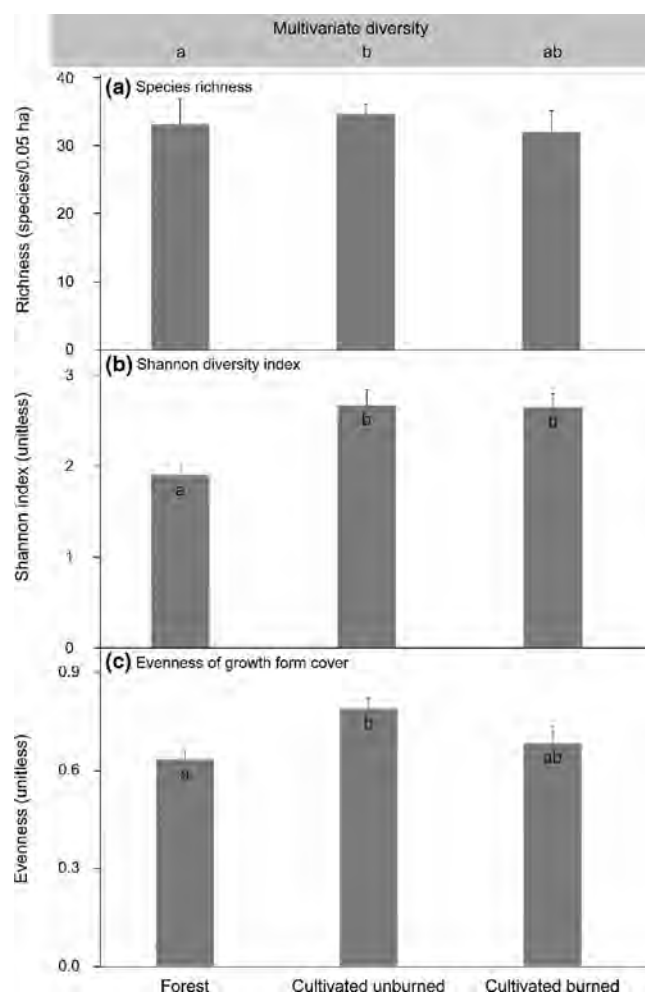


**FIGURE 2** Structural characteristics of plant communities developing on three types of historical land uses in *Quercus* ecosystems, Ohio, USA. Land uses included sites that in the 1930s were in forest or under agricultural cultivation including those unburned or burned in 2013. Bars are means and error bars are one standard error of means. Means without shared letters differ at  $p < 0.05$  (univariate permutational analysis of variance and sequential Bonferroni post-hoc tests). Letters in the top gray rectangle compare multivariate combinations of the three variables across land uses (permutational multivariate analysis of variance)

### 3.3 | Composition

The floral uniqueness index and the proportion of forb cover did not differ significantly among land uses, while species composition varied significantly among land uses (Figure 4). Illustrating these differences, an ordination displayed separation of species composition with land use (Figure 5). Additionally, PERMANOVA revealed that species composition of all three land uses differed from each other (pseudo- $F = 4.19$ ,  $p < 0.001$ ;  $p < 0.003$  for all sequential Bonferroni pairwise comparisons). Indicator species analysis further identified species uniquely distributed among land uses (Appendix S5). Of 161 species detected on plots, 17 were associated (indicator value  $\geq 50$  and  $p < 0.05$ ) with a particular land use when including all three land uses, 14 were indicators in comparing forests with cultivated

unburned sites, and five were indicators in comparing cultivated unburned and burned sites. As examples for native perennial forbs, *Hieracium scabrum* and *Solidago rugosa* were associated with cultivated unburned sites, *Apocynum cannabinum* with cultivated burned sites, and *Maianthemum racemosum* with forest sites. No annual or biennial forbs were associated with a particular land use. Among native perennial graminoids, *Danthonia spicata* and *Dichanthelium oligoanthos* were associated with cultivated unburned sites, while *Carex pensylvanica* was associated with forest sites. Among native shrubs, *Amelanchier arborea* and *Rubus flagellaris* were associated with cultivated unburned sites, *Rhus copallinum* with cultivated burned sites, and *Vaccinium angustifolium* and *Vaccinium pallidum* with forest sites.



**FIGURE 3** Diversity characteristics of plant communities developing on three types of historical land uses in *Quercus* ecosystems, Ohio, USA. Land uses included sites that in the 1930s were in forest or under agricultural cultivation including those unburned or burned in 2013. Bars are means and error bars are one standard error of means. Means without shared letters differ at  $p < 0.05$  (univariate permutational analysis of variance and sequential Bonferroni post-hoc tests). Letters in the top gray rectangle compare multivariate combinations of the three variables across land uses (permutational multivariate analysis of variance)

### 3.4 | Conservation

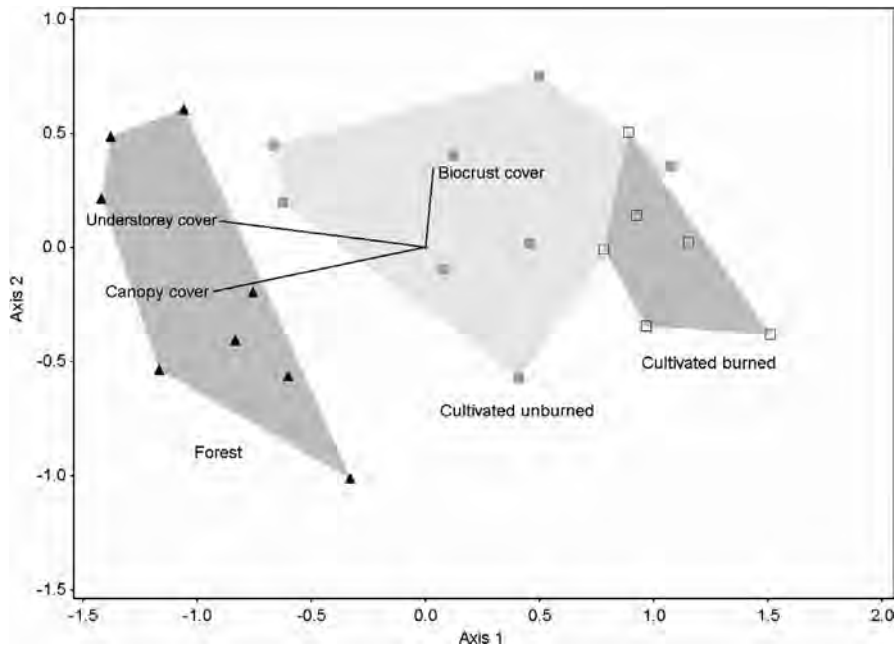
A multivariate combination of conservation variables differed between plant communities of forests and formerly cultivated sites (Figure 6). Only formerly cultivated sites contained state-listed rare plant species. There were seven state-listed rare species in total on plots in formerly cultivated sites. While forests did not contain rare species, they did contain species with at least moderate (4–7) coefficients of conservatism, such as the shrub *Gaylussacia baccata*, forb *Actaea pachypoda*, and fern *Osmunda regalis*, resulting in similar floristic quality index means among land uses. Forests contained the highest proportion of native species cover. However, even the cultivated sites had proportionately over 0.90 of cover supplied by natives and there was no significant difference with burning on cultivated sites. In total, 17 non-native species were detected, but these generally had low cover across land uses.

### 3.5 | Soils

Formerly cultivated sites contained soil organic layers (O horizons) five times thinner and only half to a third the loss on ignition percentage in the 0–15 cm mineral soil compared with continuously forested sites (Table 3). On cultivated sites, burned sites had 33% lower loss on ignition than unburned sites. Although cultivated sites contained patches of exposed mineral soil not covered by litter, lowering average thickness of the surficial litter layer, litter thickness did not differ significantly among land uses. Neither did mineral soil pH, which ranged from 5.4 to 5.8 among land uses.

## 4 | DISCUSSION

Contemporary sites previously under agricultural cultivation 70–80 years earlier were distinguished from continuously forested sites by having: (a) less tree canopy and understory plant cover; (b) higher understory plant diversity; (c) the presence of biocrust and state-listed rare plant species of open habitats; (d) distinctive



**FIGURE 4** Non-metric multidimensional scaling ordination of understorey species composition (relative cover) of plant communities developing on three types of historical land uses in *Quercus* ecosystems, Ohio, USA. Land uses included sites that in the 1930s were in forest or under agricultural cultivation including those unburned or burned in 2013. Points are individual plots ( $n = 22$ ). Axis 1 represented 65% and axis 2 12% of the variance in community composition. Showing relationships with community compositional variation, vectors are structural variables that exhibited  $r^2$  values exceeding 0.20

species composition; (e) a higher but still relatively low (proportionally  $<0.10$  of total cover) proportion of understorey cover supplied by non-native plants; and (f) less soil organic matter. These results raise questions discussed in the following sections regarding potential colonization processes, why non-native plants were not especially abundant despite the severe disturbance, how long soils may require to recover, why dense sapling layers of *Acer rubrum* were largely lacking on formerly cultivated sites and contrasting with many other studies, effects of overlaying contemporary prescribed burning on land use history, whether formerly cultivated sites in part function as surrogates for lost open habitats, and potential implications for the restoration of conservation priority oak savanna species.

#### 4.1 | Potential colonization processes and dispersal

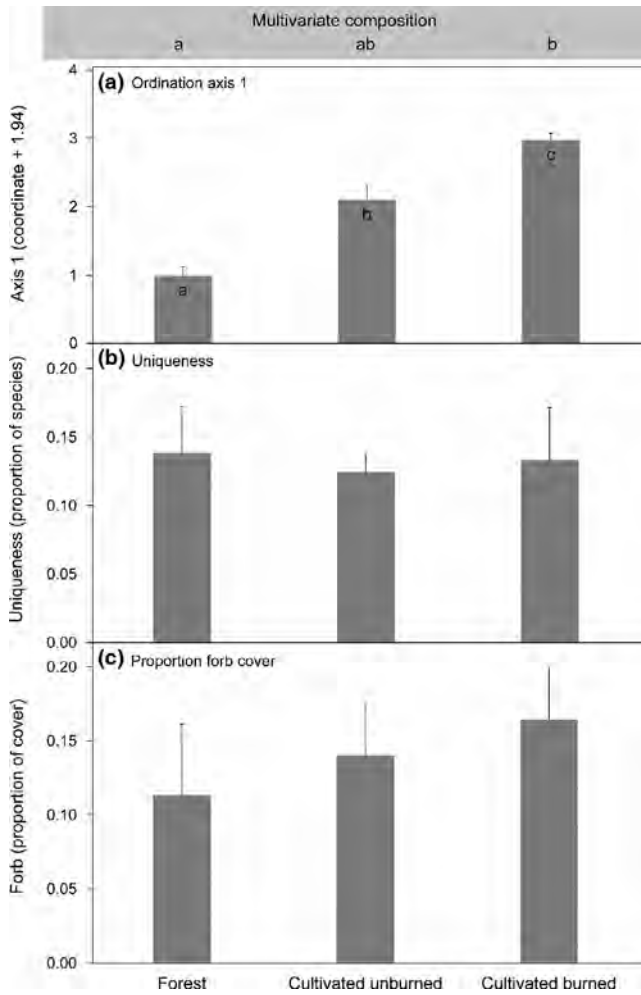
While formerly cultivated sites had a distinctive understorey species composition, they frequently lacked diagnostic species (e.g., *Asclepias tuberosa*, *Lupinus perennis*) typifying the region's pre-Euro-American-settlement savannas and open woodlands and inhabiting contemporary savanna-woodland restoration sites (Brewer & Vankat, 2004; Abella, Menard, et al., 2020). We suggest three hypothesized scenarios for the frequent absence of these species on previously cultivated sites.

A first possibility is that cultivation activities could have largely eliminated on-site plants and seed sources, combined with existing or developing forest near the fields curtailing dispersal of savanna plant species. As a result, flora on the previously cultivated sites may have developed without savanna species ever being much part of the post-cultivation colonization process, potentially because of both dispersal limitations and lack of light below the tree canopies (which were less dense than forest but more dense than typical of

savannas; Brewer & Vankat, 2004). Alternatively, a second possibility is that some residual seed banks, on-site plants (such as along field edges), or some dispersal from nearby could have maintained or fostered some colonization of at least small populations of savanna plants after farm abandonment. The savanna species could then have largely disappeared, concomitant with formation of the tree canopy. Third, perhaps propagule availability has limited colonization by these species throughout the abandonment period, and the sites even now could support populations of savanna plants, at least in more open locations, and more shade-tolerant woodland plants throughout.

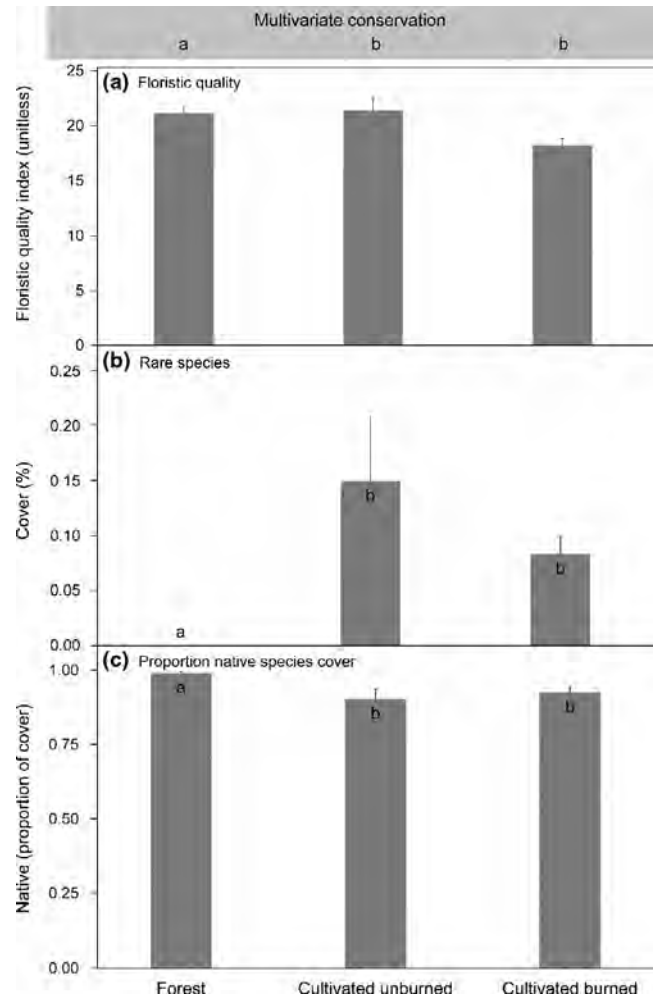
The third hypothesis would likely be easiest to test on the contemporary landscape using propagule introduction experiments to test for seed and dispersal limitations. In ecological restoration contexts on sites where tree canopy cover is low or has been reduced via cutting and fire, some studies have found that open-habitat species in midwestern North American prairie-savanna landscapes are strongly seed-limited (Foster & Tilman, 2003; Brudvig et al., 2011). Whether in our study formerly cultivated sites with moderately dense tree canopies, potentially making too much shade a primary limiting factor, would be seed-limited is unclear. Potential for impeded seed dispersal of savanna species to the cultivated sites seems high because of landscape structure where the cultivated sites are surrounded by forest (Appendix S1). Savanna species would need to be sourced primarily from remnant openings and restoration sites, then disperse through at least several hundred meters of dense forest lacking savanna species. Savannas contain many species with wind- and animal-dispersed seeds, along with some species with unassisted dispersal, which tend not to disperse far (Sperry et al., 2019). Even many wind- and bird-dispersed species rarely disperse more than 100–150 m, particularly through closed-canopy forest (Lawson et al., 1999; Hewitt & Kellman, 2002; Gardescu & Marks, 2004).





**FIGURE 5** Compositional characteristics of plant communities developing on three types of historical land uses in *Quercus* ecosystems, Ohio, USA. Land uses included sites that in the 1930s were in forest or under agricultural cultivation including those unburned or burned in 2013. Bars are means and error bars are one standard error of means. Means without shared letters differ at  $p < 0.05$  (univariate permutational analysis of variance and sequential Bonferonni post-hoc tests). Ordination axis 1 scores (+1.94 for ease of display) are from non-metric multidimensional scaling ordination in Figure 4. Letters in the top gray rectangle compare multivariate combinations of the three variables across land uses (permutational multivariate analysis of variance)

The first two hypotheses are more difficult to assess owing to little information on specific agricultural practices historically and limited information on the floristic composition of the agricultural landscape. A soil seed bank assay in the contemporary study area found that savanna plants were sparse to absent in seed banks of forest sites (Abella, Hodel, et al., 2020), which in the 1800s mostly supported savanna (Brewer & Vankat, 2004). These findings may indicate that regardless of whether cultivation practices enabled some residual seed banks or savanna plants to be retained (e.g., along field edges or via incomplete clearing within fields) after abandonment, these propagule sources were unlikely to persist through decades of relatively dense tree canopy cover. The 1930s air photos



**FIGURE 6** Conservation characteristics of plant communities developing on three types of historical land uses in *Quercus* ecosystems, Ohio, USA. Land uses included sites that in the 1930s were in forest or under agricultural cultivation including those unburned or burned in 2013. Bars are means and error bars are one standard error of means. Means without shared letters differ at  $p < 0.05$  (univariate permutational analysis of variance and sequential Bonferonni post-hoc tests). Letters in the top gray rectangle compare multivariate combinations of the three variables across land uses (permutational multivariate analysis of variance)

and a ground-based image in Varvel (1932) all show mature forest or dense young forest already surrounding many of the cultivated sites by the 1930s (Appendix S1). This suggests that dispersal of savanna plants from nearby could have been limited even before farm abandonment.

## 4.2 | Non-native plants

Whether non-native plants on formerly cultivated sites were introduced as part of homesteading and agricultural activities or invaded the abandoned fields after the activities ceased, or some of both, is unclear and a question also posed in previous studies (Stover & Marks, 1998; Hunter & Mattice, 2002). *Lonicera morrowii* and *Rumex*

TABLE 3 Soil properties among three types of historical land uses in *Quercus* ecosystems, Ohio, USA

	Mean $\pm$ SEM			Pseudo-F	p-Value	Sum of squares	
	Forest	Cultivated				Within groups	Total
		Unburned	Burned				
Litter thickness (cm)	3.9 $\pm$ 0.4	2.6 $\pm$ 0.3	2.3 $\pm$ 0.7	3.2	0.068	32	43
O horizon thickness (cm)	3.7 $\pm$ 0.4 a	0.7 $\pm$ 0.1 b	0.7 $\pm$ 0.2 b	44.9	<0.001	10	57
0–15 cm loss on ignition (%)	3.5 $\pm$ 0.5 a	1.8 $\pm$ 0.1 b	1.2 $\pm$ 0.1 c	12.1	<0.001	17	38
0–15 cm pH (1:1 soil:H <sub>2</sub> O)	5.4 $\pm$ 0.2	5.7 $\pm$ 0.1	5.8 $\pm$ 0.1	2.6	0.075	2	3

Note: Degrees of freedom for each analysis: 2 (land use), 19 (residual), 21 (total). Means without shared letters within a row differ at  $p < 0.05$ .

*acetosella*, the two non-native indicator species of cultivated sites in our study, both have a history of cultivation (and are associated with historical homesteads) but can also readily invade more natural landscapes (Hunter & Mattice, 2002; Stopps et al., 2011). *Rumex acetosella* has nutrient-rich leaves and was used for food and herbal medicines in Eurasia (where the species is native) and in North America (Stopps et al., 2011). As a result, *Rumex acetosella* may have been seeded or otherwise encouraged around homesteads, while the species' persistent seed bank and vigorous vegetative expansion via creeping roots enables it to persist within and invade open, disturbed sites (Stopps et al., 2011). These traits, possibly with smoke-enhanced germination (Franzese & Ghermandi, 2011), may further explain why *Rumex acetosella* was also associated with burned sites in our study. While overall our results – greater proportional cover of non-native plants in formerly cultivated compared to uncultivated sites – support those of earlier studies (Stover & Marks, 1998; Von Holle & Motzkin, 2007; Holmes & Matlack, 2019), cultivated sites in our study nevertheless were almost exclusively dominated by native plants. Thus, perhaps non-native plants were not particularly pervasive or persistent when farms were being abandoned in the 1930s–1940s, or the formerly cultivated sites and their surroundings have not been conducive to invasions of non-native plants that persistently dominate communities thus far.

### 4.3 | Soil

Thin organic layers (O horizons) and loss on ignition as a surrogate for organic matter being 49% (unburned) and 66% (burned) lower on formerly cultivated, compared with continuously forested sites, were striking differences in soil among land uses. These results suggest that cultivation can leave a legacy of depleted organic matter in upper soil lasting for at least 70–80 years on this sandy landscape. How long might it take for O horizons and organic matter to accumulate to levels found in continuously forested sites? Lichter (1998) examined soil formation along a chronosequence of sand dunes that formed during falling levels of Lake Michigan in upper Michigan north of our study area. In that study, accumulation of an O horizon to a near steady-state thickness of 4.1 cm (similar to the 3.7 cm we recorded in forests) required 285 years. Reaching a near steady-state concentration of carbon in the upper 15 cm of mineral

soil required 145 years. While likely an imperfect analog because of differences in factors such as vegetation and initial starting conditions for soil formation, Lichter's (1998) results also on a sandy landscape in the Great Lakes region suggest that the legacy of cultivation in our study is likely to persist far into the future.

Several factors associated with cultivation activities, possible soil amendments or lack thereof, and post-abandonment processes could have contributed to the persistently depleted organic contents of soils on previously cultivated sites. Cultivation activities, such as tillage, remove the O horizon and generally reduce mineral soil organic matter by disrupting processes stabilizing organic matter (McLauchlan, 2006). Soil amendments can add organic material and nutrients, but it is unclear to what extent amendments were used before and during the 1930s prior to farm abandonment and on the sandy soil (Grossmann & Mladenoff, 2008). Commercial fertilizers were not intensively and widely applied until the 1950s in the United States (Cao et al., 2018). In our study region, fertilizer application was likely limited and it is also unclear to what extent other amendments, such as manure, were applied owing to the sandy soil and sub-optimal agricultural land typically precluding expensive investments in amendments (Moseley, 1928; Varvel, 1932). These observations suggest that soil organic matter was likely low at the time of farm abandonment, then may or may not have subsequently declined further for a period of time after abandonment due to sand mobility or erosion (Grossmann & Mladenoff, 2008). Thereafter, it is possible that the persistently lower amount of tree canopy and understorey plant cover on the formerly cultivated sites, limiting organic inputs, slowed soil organic matter accumulation (Kalisz, 1986).

### 4.4 | Lack of *Acer rubrum* sapling layers

One reason for their greater canopy cover could be that continuously forested sites contained dense layers of sub-canopy *Acer rubrum* stems filling gaps between overstorey *Quercus*, whereas sub-canopy *Acer rubrum* trees were nearly absent from formerly cultivated sites. Sparseness of *Acer rubrum* on formerly cultivated sites contrasts with numerous studies where the species dominated sub-canopy or overstorey layers in forests developing on abandoned agricultural lands (Glitzenstein et al., 1990; Myster, 1993; Dyer, 2010). Given that: (a) at least in the absence of fires, *Acer rubrum* became

established as sub-canopy and canopy trees in continuously forested sites in our study during the climatic conditions since the mid-1900s; that (b) *Acer rubrum* seed sources (with seeds wind-dispersed) have been readily available near cultivated sites; and that (c) *Acer rubrum* seedlings were common on cultivated sites, it appears that failure to transition from seedlings to saplings is hindering recruitment on formerly cultivated sites.

Dry, infertile soil low in organic matter may be the major limiting factor to *Acer rubrum* sapling development on formerly cultivated sites. The species is considered a “super generalist” by having biological traits enabling the species to perform at least moderately well in a variety of ecological conditions more so than most tree species (Abrams, 1998). However, *Acer rubrum* may not perform well on the driest, most infertile part of the environmental gradient the species inhabits (Johnson et al., 1987). For example, seedling survival, sapling height growth, and overstorey biomass all have been sharply lower within landscapes on the coarsest-textured, most infertile glacial outwash soils in Great Lakes region forests (Host et al., 1988; Haag et al., 1989; Sakai, 1990). *Quercus velutina* and *Quercus alba*, in comparison, perform well on these soils (Host et al., 1988). Root development could be one of the causal mechanisms for these differences, with Maguire and Kobe (2015), for example, finding that experimental drought treatments triggered increased fine root production in *Quercus* but not in *Acer rubrum*. One of the most striking patterns of forest change in mature *Quercus* forests across much of eastern North America is a trend for replacement of *Quercus* by *Acer rubrum* in the absence of fire and large canopy gaps on all but perhaps the driest sites (Iverson et al., 2017). In our study, it appears that past agricultural cultivation has arrested this replacement process, possibly by making soil too dry and infertile for growth of *Acer rubrum* saplings.

#### 4.5 | Fire effects

Formerly cultivated sites that were unburned or burned seven years earlier did not exhibit a multivariate difference in all 12 variables but some univariate variation occurred. Tree canopy cover was lower on burned sites, consistent with susceptibility to fire of small non-*Quercus* trees and of suppressed sub-canopy *Quercus* stems (Abella et al., 2019). Though not statistically significant, biocrust cover was four times lower in burned sites. In previous studies in temperate sandy habitats, fire quickly reduced soil lichen cover by 50% within a year in 50-year-old abandoned fields (Johansson & Reich, 2005) and by 90% within two years in prairies (Schulden, 1985). These reductions are at least as large as the 50% average reduction in post-fire biocrust cover reported in a global meta-analysis (Briante et al., 2020). Lichen diversity recovered within 10 years after fire in heathland in Scotland (Davies & Legg, 2008), indicating that biocrust in our study could potentially still be recovering seven years after fire.

Understorey species composition differed between unburned and burned cultivated sites, a difference mostly appearing from

multivariate combinations of species as only five indicator species were significantly associated with fire presence or absence. Three species associated with burned sites included the perennial forb *Apocynum cannabinum* and the shrubs *Rhus copallinum* and *Rubus occidentalis*. Previous research with *Rhus copallinum* found that burning promoted photosynthetic activity, especially when soil disturbance occurred, and that heat stimulated seed germination (Freeman et al., 2004; Bolin, 2009). It is also noteworthy that total plant cover in the understorey was not higher on burned sites, contrasting with sharp increases occurring within 3–6 years post-fire in oak savannas–woodlands without a recent history of cultivation where fire stimulates profuse shrub and tree sprouting (Abella, Menard, et al., 2020). Our finding of some differences between unburned and burned cultivated sites, but general multivariate similarity, represents less variation than Khanina et al. (2018) reported on abandoned agricultural lands in Russia, where burning produced drastically different communities (grassland with and forest without fire).

#### 4.6 | Are formerly cultivated sites surrogates for lost open habitats?

Formerly cultivated sites supported state-listed, rare plant species and at least some other conservation priority species that inhabit open savannas–woodlands representing the region's primary pre-settlement communities (Brewer & Vankat, 2004). Some of the state-listed species included the shrub *Comptonia peregrina* and the perennial forbs *Lupinus perennis* and *Helianthemum canadense*, which are thought to have been abundant in pre-settlement savannas (Brewer & Vankat, 2004). On the contemporary landscape, these species are frequent in savannas restored in the last 2–3 decades using tree thinning and prescribed fires (Abella, Menard, et al., 2020). Other species that were significant indicators and contributed to unique community composition in formerly cultivated sites that have also inhabited (though at low covers) restored savannas–woodlands include *Apocynum cannabinum*, *Hieracium* spp., *Amelanchier arborea*, *Danthonia spicata*, and *Dichantheium oligosanthes* (Abella, Menard, et al., 2020). While overall community composition may differ between the cultivated sites and pre-settlement or restored open habitats, overlap existed in at least some subsets of light-demanding species. It is possible that the formerly cultivated sites, with their moderate levels of tree canopy cover, are partly serving as surrogates for lost open habitats and provide refugia for open-habitat species absent from forests.

#### 4.7 | Conservation and restoration implications

Results suggest at least three applications for conservation and restoration. First, findings indicate that long-abandoned agricultural lands exhibited unique conservation values and that including

them in habitat acquisition programs may help expand conservation opportunities. Further research could assist determining to what degree the accrual of conservation value of more recently abandoned lands, perhaps exposed to different influences in the contemporary landscape, is similar to the older sites we studied. It is possible that abandoned agricultural lands may hold special conservation potential where conserving open-structured habitats is a goal, such as in our study landscape historically dominated by open habitats. Second, abandoned agricultural lands could represent some of the best opportunities for maintaining open *Quercus* savannas-woodlands precisely because the abandoned sites lacked dense understories of *Acer rubrum* saplings and other non-*Quercus* trees. Third, burning the previously cultivated sites may not increase floristic quality but may be associated with unique community composition, adding to diversity at landscape scales. Overall, contemporary sites with a history of agricultural cultivation 70–80 years earlier contained appreciable conservation value, as indicated by open tree canopies resembling the study region's pre-settlement open habitats (Brewer & Vankat, 2004), presence of non-vascular communities as biocrust, enhanced plant species diversity relative to continuously forested sites, and abundance of conservation priority endangered plants.

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#### AUTHOR CONTRIBUTIONS

SRA collected field data; TAS conducted GIS analyses and SRA conducted statistical analyses; both authors prepared and edited the manuscript.

#### DATA AVAILABILITY STATEMENT

The community variables data set is in Appendix S2 and the soils data set is in Appendix S4.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**Appendix S1** Air photo showing 1939 land use

**Appendix S2** Data set of community variables

**Appendix S3** Correlation matrix of community variables

**Appendix S4** Data set of soil variables

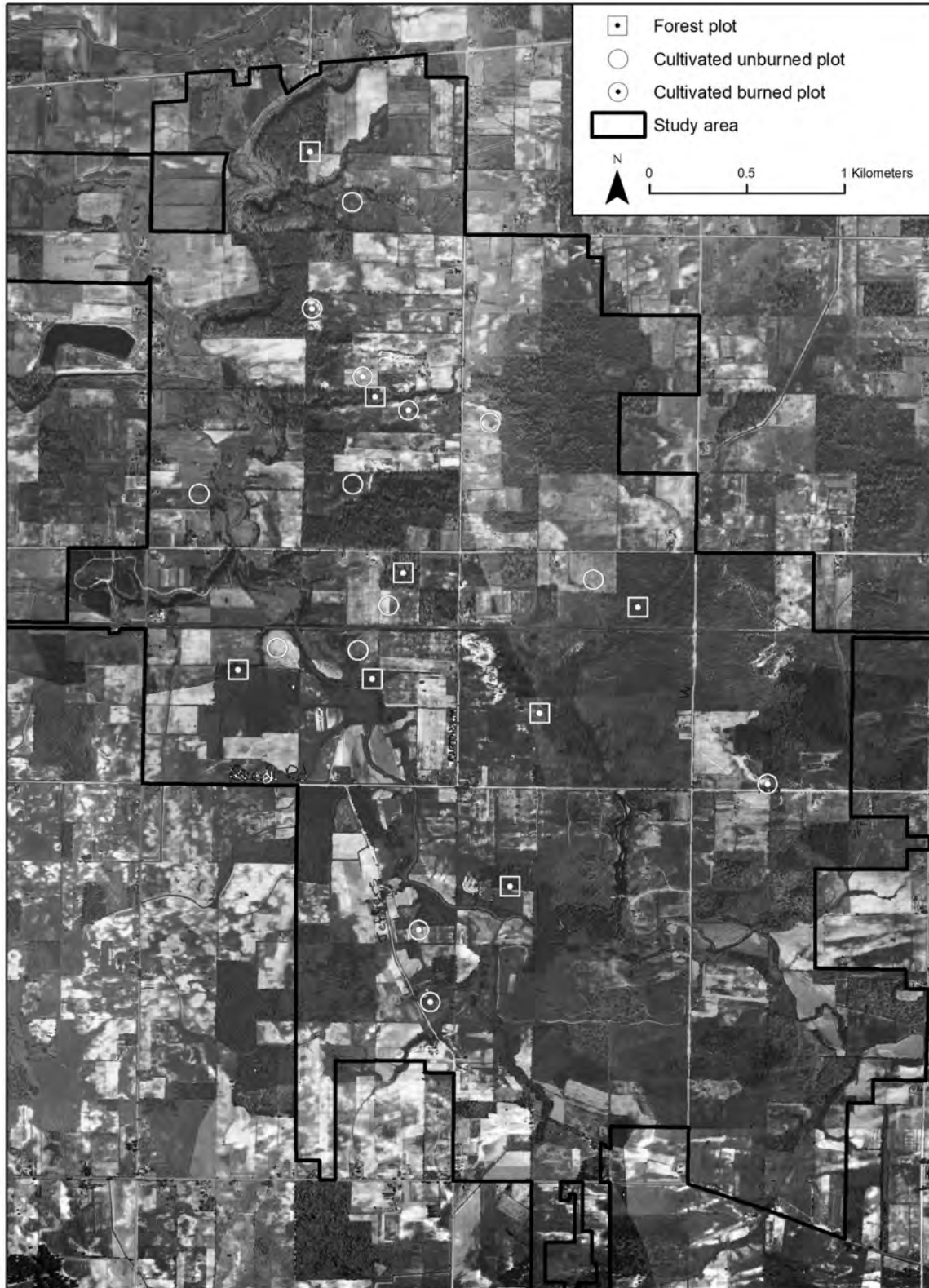
**Appendix S5** Indicator species analysis among land uses

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**APPENDIX S1** Air photo showing land use in 1939 in what would become the 1,737-ha Oak Openings Preserve, Ohio, USA



**APPENDIX S2** Data set including 12 variables in four categories for 22 study sites analyzed in an investigation of plant communities developing on three types of historical land uses in *Quercus* ecosystems, Ohio, USA. Land uses represent sites that in the 1930s were in forest or under agricultural cultivation and include those unburned (CultivatedU) or burned (CultivatedB) in 2013

Land use	Structure			Diversity			Composition			Conservation		
	Canopy Cover (%)	Understory Cover (%)	Biocrust Cover (%)	Richness 0.05 ha	Diversity Shannon	Growth form Evenness	Spp. Comp. Axis 1	Uniqueness Index	Forbs Proportion	Floristic Quality	Rare spp. Cover (%)	Native Proportion
Forest	82	29	0.0	49	2.04	0.71	0.00	0.18	0.10	24.6	0.0	0.97
Forest	78	13	0.0	20	2.33	0.60	1.09	0.05	0.02	18.3	0.0	1.00
Forest	64	76	0.0	45	1.13	0.41	0.04	0.18	0.10	23.4	0.0	1.00
Forest	81	63	0.0	35	2.21	0.71	0.59	0.26	0.02	22.3	0.0	1.00
Forest	68	77	0.0	30	1.54	0.65	0.36	0.10	0.43	20.0	0.0	1.00
Forest	93	38	0.0	23	1.88	0.66	0.66	0.00	0.01	19.4	0.0	1.00
Forest	81	29	0.0	38	1.94	0.60	0.25	0.26	0.12	21.4	0.0	0.98
Forest	89	11	0.0	26	2.11	0.71	0.82	0.08	0.10	19.6	0.0	0.99
CultivatedU	61	7	2.0	35	3.08	0.87	1.54	0.09	0.19	21.7	0.3	0.91
CultivatedU	71	56	4.0	43	1.77	0.63	0.75	0.14	0.04	27.8	0.5	1.00
CultivatedU	68	9	5.0	31	2.94	0.89	1.92	0.10	0.17	21.6	0.0	0.97
CultivatedU	48	11	0.2	33	2.71	0.68	2.49	0.18	0.06	19.7	0.1	0.71
CultivatedU	68	8	0.4	34	3.17	0.80	1.87	0.09	0.13	18.3	0.0	0.91
CultivatedU	58	15	2.3	30	2.53	0.85	1.50	0.10	0.14	21.0	0.1	0.92
CultivatedU	86	10	0.2	36	3.02	0.86	1.83	0.14	0.34	17.8	0.0	0.83
CultivatedU	75	41	1.0	36	2.14	0.71	0.79	0.17	0.06	23.5	0.3	0.99
CultivatedB	63	5	0.4	26	2.91	0.79	2.34	0.04	0.13	19.4	0.1	0.93
CultivatedB	50	7	0.8	25	2.37	0.71	2.57	0.08	0.17	18.1	0.1	0.98
CultivatedB	50	8	0.2	26	2.24	0.59	2.20	0.04	0.05	16.4	0.0	0.95
CultivatedB	55	14	0.2	35	2.66	0.50	2.31	0.17	0.14	19.5	0.1	0.91
CultivatedB	55	7	0.2	35	3.18	0.66	2.39	0.23	0.31	19.6	0.1	0.93
CultivatedB	40	22	1.3	45	2.54	0.84	2.93	0.24	0.19	16.2	0.1	0.84



**APPENDIX S3** Pearson correlation matrix for 12 variables analyzed in an investigation of plant communities developing on three types of historical land uses in *Quercus* ecosystems, Ohio, USA. Correlations between variables that exceeded |0.50| and that were significant at  $P < 0.05$  are shown in gray highlight

	Canopy	Understory	Biocrust	Richness	Diversity	Growth form	Spp. Comp.	Uniqueness	Forbs	Floristic	Rare spp.	Native
Canopy	1.00											
Understory	0.28	1.00										
Biocrust	-0.16	-0.07	1.00									
Richness	-0.09	0.37	0.13	1.00								
Diversity	-0.30	-0.81	0.18	-0.18	1.00							
Growth form	-0.02	-0.46	0.44	-0.07	0.64	1.00						
Spp. Comp.	-0.73	-0.72	0.14	-0.24	0.74	0.36	1.00					
Uniqueness	-0.14	0.29	-0.10	0.73	-0.06	-0.15	-0.09	1.00				
Forbs	-0.17	-0.01	-0.02	0.09	0.24	0.27	0.19	0.11	1.00			
Floristic	0.33	0.55	0.41	0.52	-0.43	-0.18	-0.65	0.27	-0.26	1.00		
Rare spp.	-0.22	0.07	0.51	0.26	0.03	0.09	0.09	0.07	-0.13	0.53	1.00	
Native	0.48	0.45	0.05	-0.15	-0.56	-0.33	-0.63	-0.21	-0.18	0.39	-0.02	1.00

**APPENDIX S4** Data set of soil variables for 22 study sites analyzed in an investigation of plant communities developing on three types of historical land uses in *Quercus* ecosystems, Ohio, USA. Land uses represent sites that in the 1930s were in forest or under agricultural cultivation and include those unburned (CultivatedU) or burned (CultivatedB) in 2013. Sites are in the same order as in Appendix S2

Land use	LOI	pH	Litter (cm)	O horizon (cm)
Forest	2.8	5.8	2.5	3.0
Forest	2.1	5.7	2.5	3.5
Forest	3.2	5.7	2.5	2.8
Forest	6.6	4.4	4.0	3.8
Forest	3.0	5.8	4.0	4.5
Forest	4.9	5.4	5.0	5.0
Forest	2.7	4.9	5.6	4.8
Forest	2.9	5.7	5.0	2.3
CultivatedU	1.7	5.5	2.0	1.3
CultivatedU	2.5	5.7	2.0	1.3
CultivatedU	1.7	5.8	3.5	0.5
CultivatedU	1.5	5.7	3.5	0.5
CultivatedU	1.7	5.8	1.5	0.5
CultivatedU	1.6	5.6	3.0	0.8
CultivatedU	2.0	5.9	3.5	0.3
CultivatedU	1.8	5.9	1.5	0.3
CultivatedB	1.4	5.8	2.3	0.8
CultivatedB	1.7	6.0	0.5	0.0
CultivatedB	1.4	5.9	3.5	0.3
CultivatedB	1.2	5.7	5.0	0.8
CultivatedB	0.7	5.6	2.0	1.8
CultivatedB	0.9	5.7	0.5	0.5

*Note:* LOI, loss on ignition (300°C, 2 hours); pH, 1:1 soil:H<sub>2</sub>O; litter and O horizon thickness.

**APPENDIX S5** Indicator species analysis identifying plant species associated with three types of historical land uses in *Quercus* ecosystems, Ohio, USA. Three sets of analyses are shown, including all three land uses, continuously forested sites as compared to formerly cultivated/unburned (CU) sites, and CU compared with formerly cultivated/burned (CB) sites. Values shown are indicator values and P-values for the highest indicator value. Indicator values range from 0-100, with 0 indicating no association and 100 indicating maximal association with a land use. Gray highlight signifies indicator values  $\geq 50$  and with  $P < 0.05$ . Blanks represent absences and hence no indicator value. Asterisks note species not native to the USA. Letters in parentheses after species names signify rare species listed in the State of Ohio: E, endangered; P, potentially threatened; and T, threatened

Species	All three land uses				Forest and CU			Cultivated only		
	Forest	CU	CB	P-value	Forest	CU	P-value	CU	CB	P-value
<b>Annual or biennial forbs</b>										
<i>Alliaria petiolata</i> *	29	0	4	0.221	38	0	0.201	0	17	0.432
<i>Ambrosia artemisiifolia</i>	0	5	10	0.710	0	13	1.000	5	10	1.000
<i>Arabis laevigata</i>	0	0	17	0.273				0	17	0.427
<i>Conyza canadensis</i>	0	20	16	0.571	0	38	0.207	20	16	1.000
<i>Erechtites hieraciifolius</i>	0	0	33	0.070				0	33	0.167
<i>Galium aparine</i>	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Lactuca canadensis</i>	25	0	0	0.306	25	0	0.454			
<i>Pilea pumila</i>	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Polygala polygama</i> (T)	0	25	25	0.616	0	50	0.076	25	25	1.000
<i>Polygonum caespitosum</i> *	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Pseudognaphalium obtusifolium</i>	0	0	33	0.067				0	33	0.169
<i>Verbascum thapsus</i> *	0	5	10	0.716	0	13	1.000	5	10	1.000
<b>Perennial forbs</b>										
<i>Achillea millefolium</i>	0	3	24	0.250	0	13	1.000	3	24	0.549
<i>Actaea pachypoda</i>	13	0	0	1.000	13	0	1.000			
<i>Agrimonia gryposepala</i>	13	0	0	1.000	13	0	1.000			
<i>Antennaria plantaginifolia</i>	0	38	0	0.081	0	38	0.207	38	0	0.219
<i>Apocynum androsaemifolium</i>	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Apocynum cannabinum</i>	0	0	67	0.002				0	67	0.017
<i>Aralia nudicaulis</i>	25	0	0	0.305	25	0	0.464			
<i>Arisaema triphyllum</i>	19	3	0	0.387	19	3	0.739	13	0	1.000
<i>Asclepias amplexicaulis</i> (P)	0	0	33	0.067				0	33	0.161
<i>Asclepias tuberosa</i>	0	0	17	0.282				0	17	0.432
<i>Circaea lutetiana</i>	42	0	3	0.058	50	0	0.077	0	17	0.432
<i>Comandra umbellata</i>	0	15	7	0.753	0	25	0.459	15	7	1.000
<i>Desmodium nudiflorum</i>	55	5	1	0.161	56	5	0.298	38	4	0.295
<i>Dioscorea villosa</i>	50	0	0	0.022	50	0	0.083			
<i>Equisetum arvense</i>	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Euphorbia corollata</i>	0	25	0	0.314	0	25	0.467	25	0	0.482
<i>Eurybia macrophylla</i>	25	0	0	0.301	25	0	0.478			
<i>Fragaria virginiana</i>	0	15	7	0.758	0	25	0.468	15	7	1.000
<i>Galium asprellum</i>	13	0	0	1.000	13	0	1.000			
<i>Galium circaeans</i>	28	11	17	0.624	42	17	0.481	20	30	0.775

<i>Galium pilosum</i>	25	0	0	0.306	25	0	0.473			
<i>Galium triflorum</i>	11	2	7	0.937	19	3	0.731	3	13	0.736
<i>Geranium maculatum</i>	13	0	0	1.000	13	0	1.000			
<i>Geum canadense</i>	17	2	13	0.849	28	3	0.560	3	24	0.543
<i>Hackelia virginiana</i>	12	11	8	1.000	16	14	1.000	20	16	1.000
<i>Helianthemum canadense</i> (T)	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Hieracium gronovii</i>	0	25	0	0.303	0	25	0.465	25	0	0.486
<i>Hieracium scabrum</i>	0	42	17	0.118	0	63	0.026	42	17	0.554
<i>Lepidium virginicum</i>	0	0	17	0.269				0	17	0.432
<i>Lespedeza capitata</i>	0	24	12	0.420	0	38	0.201	24	12	0.837
<i>Lespedeza procumbens</i>	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Liatris aspera</i>	0	0	17	0.282				0	17	0.432
<i>Lupinus perennis</i> (P)	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Lysimachia quadrifolia</i>	0	50	0	0.024	0	50	0.077	50	0	0.086
<i>Maianthemum canadense</i>	13	0	0	1.000	13	0	1.000			
<i>Maianthemum racemosum</i>	72	3	1	0.004	77	3	0.015	15	7	1.000
<i>Medeola virginiana</i>	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Monotropa uniflora</i>	25	0	0	0.315	25	0	0.458			
<i>Osmorhiza claytonii</i>	13	0	0	1.000	13	0	1.000			
<i>Oxalis dillenii</i>	0	0	17	0.269				0	17	0.432
<i>Oxalis stricta</i>	25	0	0	0.305	25	0	0.466			
<i>Phryma leptostachya</i>	3	0	24	0.242	13	0	1.000	0	33	0.161
<i>Podophyllum peltatum</i>	25	0	0	0.317	25	0	0.466			
<i>Polygonatum biflorum</i>	34	1	0	0.193	34	1	0.451	13	0	1.000
<i>Polygonum persicaria</i> *	0	0	17	0.277				0	17	0.423
<i>Polygonum virginianum</i>	8	16	9	0.960	10	20	0.982	19	11	0.946
<i>Potentilla simplex</i>	8	8	13	0.947	13	13	1.000	11	19	0.935
<i>Prenanthes alba</i>	38	0	0	0.090	38	0	0.198			
<i>Rudbeckia hirta</i>	0	0	17	0.269				0	17	0.432
<i>Rumex acetosella</i> *	0	20	69	0.017	0	63	0.023	20	69	0.169
<i>Sanicula trifoliata</i>	13	0	0	1.000	13	0	1.000			
<i>Silene latifolia</i> *	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Smilax herbacea</i>	13	0	0	1.000	13	0	1.000			
<i>Solanum carolinense</i>	0	0	17	0.277				0	17	0.423
<i>Solidago canadensis</i>	13	0	0	1.000	13	0	1.000			
<i>Solidago nemoralis</i>	0	2	43	0.059	0	13	1.000	2	43	0.196
<i>Solidago rugosa</i>	0	41	27	0.216	0	88	0.001	41	27	0.813
<i>Taraxacum officinale</i> *	0	0	17	0.269				0	17	0.432
<i>Trillium grandiflorum</i>	13	0	0	1.000	13	0	1.000			
<i>Uvularia sessilifolia</i>	57	2	0	0.026	57	2	0.132	25	0	0.466
<i>Verbena urticifolia</i>	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Viola pubescens</i>	25	0	0	0.300	25	0	0.464			
<i>Viola sagittata</i>	0	50	0	0.019	0	50	0.076	50	0	0.085
<i>Viola</i> spp.	13	0	0	1.000	13	0	1.000			
<b>Perennial graminoids</b>										
<i>Agrostis perennans</i>	0	13	0	1.000	0	13	1.000	13	0	1.000

<i>Carex pensylvanica</i>	70	29	1	0.050	71	29	0.262	98	2	0.004
<i>Carex swanii</i>	13	0	0	1.000	13	0	1.000			
<i>Cinna arundinacea</i>	38	0	0	0.083	38	0	0.201			
<i>Danthonia spicata</i>	0	43	22	0.067	0	75	0.006	43	22	0.551
<i>Dichanthelium clandestinum</i>	38	0	0	0.090	38	0	0.198			
<i>Dichanthelium latifolium</i>	0	0	33	0.067				0	33	0.161
<i>Dichanthelium oligosanthes</i>	0	43	48	0.060	0	100	0.000	43	48	1.000
<i>Elymus canadensis</i>	13	0	0	1.000	13	0	1.000			
<i>Elymus hystrix</i>	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Leersia virginica</i>	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Schizachyrium scoparium</i>	0	0	17	0.269				0	17	0.432
<b>Ferns</b>										
<i>Botrychium dissectum</i>	0	0	33	0.067				0	33	0.173
<i>Botrychium multifidum</i> (E)	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Osmunda cinnamomea</i>	13	0	0	1.000	13	0	1.000			
<i>Osmunda regalis</i>	13	0	0	1.000	13	0	1.000			
<i>Pteridium aquilinum</i>	9	20	2	0.889	10	21	0.926	23	2	0.728
<b>Shrubs</b>										
<i>Amelanchier arborea</i>	17	77	1	0.013	17	80	0.008	96	1	0.002
<i>Aronia melanocarpa</i>	15	5	0	0.604	15	5	1.000	13	0	1.000
<i>Berberis thunbergii</i> *	4	37	2	0.121	4	41	0.310	44	2	0.205
<i>Celastrus orbiculatus</i> *	2	15	8	0.658	3	28	0.574	18	9	0.785
<i>Chimaphila maculata</i>	0	25	0	0.311	0	25	0.478	25	0	0.475
<i>Comptonia peregrina</i> (E)	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Cornus drummondii</i>	0	0	17	0.269				0	17	0.432
<i>Cornus racemosa</i>	25	0	0	0.305	25	0	0.466			
<i>Cornus rugosa</i> (P)	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Corylus americana</i>	13	0	0	1.000	13	0	1.000			
<i>Crataegus</i> spp.	27	17	8	0.679	35	22	1.000	30	13	0.630
<i>Elaeagnus umbellata</i> *	2	22	6	0.533	3	33	0.600	24	6	0.599
<i>Euonymus alatus</i> *	9	16	0	0.555	9	16	1.000	25	0	0.461
<i>Frangula alnus</i> *	0	0	17	0.282				0	17	0.432
<i>Gaylussacia baccata</i>	48	1	0	0.057	48	1	0.194	25	0	0.466
<i>Hypericum prolificum</i>	0	29	8	0.249	0	38	0.194	29	8	0.550
<i>Lindera benzoin</i>	9	4	0	0.803	9	4	1.000	13	0	1.000
<i>Lonicera dioica</i>	13	0	0	1.000	13	0	1.000			
<i>Lonicera maackii</i> *	17	0	22	0.625	50	0	0.076	0	33	0.161
<i>Lonicera morrowii</i> *	0	47	8	0.044	0	63	0.029	47	8	0.274
<i>Parthenocissus quinquefolia</i>	36	29	10	0.513	44	36	0.943	56	18	0.248
<i>Prunus virginiana</i>	9	4	0	0.793	9	4	1.000	13	0	1.000
<i>Rhamnus cathartica</i> *	0	5	10	0.718	0	13	1.000	5	10	1.000
<i>Rhus copallinum</i>	0	0	67	0.003				0	67	0.015
<i>Rhus typhina</i>	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Rosa carolina</i>	19	15	0	0.670	19	15	0.942	25	0	0.470
<i>Rosa multiflora</i> *	4	24	23	0.638	7	45	0.317	28	27	1.000
<i>Rubus allegheniensis</i>	61	0	3	0.008	75	0	0.006	0	17	0.432

<i>Rubus flagellaris</i>	4	64	23	0.004	6	89	0.000	70	25	0.076
<i>Rubus hispidus</i>	1	11	0	0.789	1	11	1.000	13	0	1.000
<i>Rubus occidentalis</i>	0	0	67	0.003				0	67	0.017
<i>Smilax glauca</i>	42	25	1	0.176	44	26	0.587	57	1	0.112
<i>Smilax rotundifolia</i>	77	7	2	0.126	80	7	0.274	60	16	0.173
<i>Smilax tamnoides</i>	9	2	16	0.829	17	4	1.000	3	24	0.534
<i>Spiraea tomentosa</i>	0	15	7	0.760	0	25	0.459	15	7	1.000
<i>Toxicodendron radicans</i>	25	27	12	0.790	33	36	1.000	45	20	0.578
<i>Vaccinium angustifolium</i>	74	2	0	0.002	74	2	0.008	13	0	1.000
<i>Vaccinium pallidum</i>	59	11	3	0.051	62	11	0.136	48	15	0.371
<i>Viburnum acerifolium</i>	13	0	0	1.000	13	0	1.000			
<i>Vitis aestivalis</i>	2	2	33	0.176	6	6	1.000	3	40	0.247
<b>Tree seedlings and sprouts</b>										
<i>Acer rubrum</i>	15	49	36	0.306	23	77	0.017	57	43	0.624
<i>Carya cordiformis</i>	15	0	7	0.752	25	0	0.466	0	17	0.423
<i>Catalpa speciosa</i>	0	0	17	0.282				0	17	0.432
<i>Cornus florida</i>	34	13	7	0.218	43	16	0.316	24	12	0.833
<i>Crataegus crus-galli</i>	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Fraxinus americana</i>	10	23	0	0.310	10	23	1.000	38	0	0.208
<i>Fraxinus pennsylvanica</i>	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Gleditsia triacanthos</i>	0	0	17	0.277				0	17	0.423
<i>Hamamelis virginiana</i>	74	0	0	0.004	74	0	0.012	25	0	0.471
<i>Juniperus virginiana</i>	0	1	30	0.196	0	13	1.000	1	30	0.425
<i>Liquidambar styraciflua</i>	0	0	17	0.282				0	17	0.432
<i>Liriodendron tulipifera</i>	0	1	30	0.193	0	13	1.000	1	30	0.426
<i>Nyssa sylvatica</i>	8	39	14	0.227	11	54	0.226	49	17	0.388
<i>Picea abies*</i>	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Picea glauca</i>	0	0	17	0.269				0	17	0.432
<i>Pinus strobus</i>	4	53	32	0.353	6	77	0.045	57	34	0.938
<i>Prunus serotina</i>	66	25	8	0.463	73	27	0.492	73	23	0.691
<i>Quercus alba</i>	34	50	11	0.536	38	56	0.708	82	18	0.247
<i>Quercus muehlenbergii</i>	0	13	0	1.000	0	13	1.000	13	0	1.000
<i>Quercus palustris</i>	2	17	13	0.844	3	28	0.556	20	16	1.000
<i>Quercus rubra</i>	13	0	0	1.000	13	0	1.000			
<i>Quercus velutina</i>	13	31	56	0.050	29	71	0.091	36	64	0.240
<i>Robinia pseudoacacia</i>	9	4	0	0.798	9	4	1.000	13	0	1.000
<i>Sassafras albidum</i>	53	20	24	0.519	70	26	0.408	42	52	0.796
<i>Ulmus americana</i>	6	6	25	0.611	13	13	1.000	8	33	0.572

# Variation in characteristics and conservation values of plant communities on abandoned agricultural lands with and without fires

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We compared plant communities and soils on sites continuously forested since before the 1930s with sites that were under agricultural cultivation in the 1930s and either burned or unburned in 2013 prescribed fires. Plant communities and soils sampled in 2020–2021 reflected legacies of the prior land uses 70–80 years earlier. The photo, taken along a historical fence line, shows a continuously forested area on the left side and a previously cultivated area on the right side.

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