

From forest to city: Plant community change in northeast Ohio from 1800 to 2014

Kathryn M. Flinn¹  | Tylor P. Mahany¹ | Constance E. Hausman²¹Biology Department, Baldwin Wallace University, Berea, OH, USA²Cleveland Metroparks, Parma, OH, USA**Correspondence**

Kathryn M. Flinn, Biology Department, Baldwin Wallace University, Berea, OH, USA.

Email: kflinn@bw.edu

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Abstract

Questions: This study compares the extent of habitat types, species composition of plant communities and abundance of individual tree species in northeast Ohio between 1800 and 2014. This comparison allows us to test hypotheses about the drivers of community change, including climate change, fire suppression and disturbance frequency, and to evaluate the impact of urbanization on biotic homogenization.

Location: Cuyahoga County, Ohio, USA.

Methods: Ranked timber observations from early land surveys were compared with vegetation plots throughout the Cleveland Metroparks system. We used ordination, cluster analysis and indicator species analysis to compare plant communities in the two time periods. We tested whether differences in species frequency and dominance from 1800 to 2014 depended on climate, fire and shade tolerance and life-history strategy.

Results: In 1800, 94% of Cuyahoga County was forested, 5% wetlands and <1% open oak woods. Most forests in 1800 were dominated by *Fagus grandifolia* (47%), *Quercus* (28%) or *Acer* (11%). At the community level, the largest changes from 1800 to 2014 were decreases in communities dominated by *F. grandifolia* and *Quercus* and an increase in communities dominated by *Acer*. *Fagus grandifolia*, *Castanea dentata*, *Tilia americana* and *Carya* decreased in frequency, and *Acer*, *Prunus serotina* and *Ulmus* increased. The best predictor of changes in frequency was life history; species with a ruderal strategy tended to increase. Climate, fire and shade tolerance did not predict changes in frequency. Plant communities in 2014 vegetation plots were more similar to each other than plant communities on the 1800 survey lines.

Conclusions: The urbanization of northeast Ohio led to regionally homogenous vegetation and plant communities in which ruderal species are frequent and dominant.

KEYWORDS

biotic homogenization, climate change, disturbance, ecological restoration, fire, land-use history, life-history strategy, northeast Ohio, pre-settlement vegetation, urbanization

1 | INTRODUCTION

Understanding how biological communities have changed over time is important for several reasons. First, because ecological restoration helps ecosystems recover the processes that propelled their “historic

trajectory” (Society for Ecological Restoration 2004), efforts to restore natural communities depend on accurate historical information to set specific and defensible targets (Higgs et al., 2014; Jackson & Hobbs, 2009). In North America, early land surveys play a key role in informing restoration goals because they provide vegetation

records from the time period just prior to the landscape transformation associated with European settlement (Liu, Mladenoff, Keuler, & Moore, 2011; Schulte & Mladenoff, 2001; Thompson, Carpenter, Cogbill, & Foster, 2013). These historical data fill a crucial gap in time scale between paleoecology and contemporary ecology (Jackson & Blois, 2015). Spatially, they cover areas lacking remnant stands representative of pre-settlement vegetation. Early land surveys provide quantitative information on the extent of habitat types, the species composition of communities and the abundance of individual species. This information is valuable for determining the potential of restored ecosystems.

The second, and larger, reason for seeking to understand community change over time is that assessing the effects of past land-use decisions enables us to make predictions about the consequences of our current actions. In particular, it is critical to assess the effects of urbanization on biological communities as urban development accelerates worldwide (DeFries, Rudel, Uriarte, & Hansen, 2010; Foley et al., 2005). Over 82% of North Americans now live in urban areas, and the proportion of the world's population in cities is expected to reach 66% by 2050 (United Nations 2014). Globally, urban land area is projected to triple by 2030, with major impacts on biological diversity (Seto, Güneralp, & Hutyra, 2012). The habitat loss and modification associated with urbanization not only endanger more species than any other human activity (Czech, Krausman, & Devers, 2000), but also radically transform the biological communities that remain. Yet very few studies have used early land surveys to evaluate vegetation changes in landscapes that became cities (but see Fahey, Bowles, & McBride, 2012).

Urbanization is a complex, composite change whose causes and effects can be difficult to disentangle. Most North American landscapes that became cities underwent timber harvesting, agricultural use, residential and industrial development, introduction of exotic species, alteration of fire and other disturbance regimes, and climate changes during a relatively short span of several hundred years. By investigating how habitat types, community composition and species abundances changed as cities developed, we can begin to understand which drivers were most important and which effects are salient. This will provide insight into current debates over the role of fire and Native Americans in shaping North American landscapes (Vale, 2002). According to the “mesophication” hypothesis, frequent fires mostly set by Native Americans maintained open, “park-like” communities composed of fire-tolerant species across most of eastern North America prior to European settlement (Day, 1953; Lafon, Hoss, & Grissino-Mayer, 2005; Nowacki & Abrams, 2008). With fire suppression during the 20th century, these communities were replaced with closed forests composed of fire-sensitive, shade-tolerant species, a process called “mesophication” (Nowacki & Abrams, 2008). This view is often used to justify the use of fire in ecological restoration (Abrams, 2005; Brose, Schuler, Van Lear, & Berst, 2001; Hutchinson et al., 2005). However, others argue that the effects of fire and other Native American activities were more localized (Matlack, 2013; Russell, 1983). It is also possible that the effects of fire suppression were swamped by the effects of other,

concurrent changes, such as climate change, which would favour warm-adapted species, or logging, clearing and fragmentation, which would favour shade-intolerant species. Documenting which species increased or declined over the past several hundred years, and how these changes depended on species traits, will contribute much-needed evidence to this controversy.

Here we assess changes in northeast Ohio plant communities from 1800 to 2014 by comparing early land surveys of Cuyahoga County to current vegetation in the Cleveland Metroparks system. This contemporary data set allows us to evaluate how well present-day protected areas across the county represent former vegetation and to set restoration goals for these areas. Our comparison also enables us to test hypotheses about which drivers of vegetation change had the strongest impacts. The “mesophication” hypothesis predicts that open habitats would have been common prior to European settlement but declined over time, and that fire-tolerant species and vegetation types would have declined as well. If climate change were an important cause of community change, warm-adapted species should have increased at the expense of cold-adapted species. If logging, clearing and fragmentation had a dominant impact, shade-intolerant species should have increased at the expense of shade-tolerant species. If increasing disturbance frequency drove community change, then species with a ruderal life history strategy should have increased (Grime, 2001). We also test the hypothesis that urbanization homogenized the vegetation of the region, i.e. reduced β -diversity (Groffman et al., 2014; McCune & Vellend, 2013; McKinney, 2006). Thus we address the following questions:

1. How did the area in different habitat types change between 1800 and 2014?
2. How did the species composition of plant communities change?
3. Did community composition become more homogenous?
4. How did tree species change in frequency and dominance?
5. Did these changes depend on species' tolerance of climate, fire, shade or disturbance?

2 | METHODS

2.1 | Natural history of the study area

Cuyahoga County contains 1,184 km² in northeast Ohio, along the south shore of Lake Erie. The region has a humid continental climate with a mean annual temperature of 10.8°C, mean annual precipitation of 99.4 cm, including 173 cm of snow, and a median frost-free season of 189 days (Midwestern Regional Climate Center 2017). Elevation ranges from 238 to 400 m. The county includes two physiographic regions, both glaciated: the lower lake plains and till plains of the Central Lowland province to the north and west, and the higher Allegheny Plateau province to the south and east (Ohio Division of Geological Survey 1998). The Portage Escarpment divides the two regions. Three major rivers drain into Lake Erie, the



Rocky, Cuyahoga and Chagrin, with river valleys 30–45 m below the land surface. Throughout the county, shale and sandstone bedrock is overlain by glacial deposits. Large areas have silt loam soils with clay-rich subsoils, which can impede drainage (Musgrave & Holloran, 1980).

2.2 | Human history of the study area

There is archaeological evidence of inhabitants hunting, fishing, gathering and gardening in Cuyahoga County from 8000 BCE to 1500 CE (Grabowski, 2017). Permanent agricultural villages were occupied from 1500 to 1640, but the area appears to have had no permanent occupation between 1640 and 1742, when Ottawa people from Detroit established a fur trading post on the Cuyahoga River (Grabowski, 2017). The land became part of Connecticut's Western Reserve and opened to European-American settlement after 1800.

The city of Cleveland grew where the Cuyahoga River enters Lake Erie in the centre of Cuyahoga County. In 1900, 87% of the county's population was in Cleveland, and the acreage in cultivation had already peaked at one-third of the county's land area (Musgrave & Holloran, 1980). Cleveland's population peaked in 1950 at 915,000 (US Census Bureau 2017). Suburban development exploded after World War II, as the suburban share of the county's population jumped from 28% in 1940 to 62% in 1970 (Grabowski, 2017). From 1970 on, the county's urban and suburban populations declined. As of 2016, Cleveland had 386,000 people and Cuyahoga County 1.25 million (US Census Bureau 2017).

2.3 | The 1800 survey data

The private Connecticut Land Company had the Western Reserve surveyed into townships 5 miles square (65 km²), requiring surveyors to keep "a regular field book, in which they would accurately describe the situation, soil, waters, kinds of timber and natural productions of each township" (Connecticut Land Company Articles of Association, quoted in Williams, 2015). The surveyors recorded features such as wetlands, open habitats and evidence of recent fires. The land east of the Cuyahoga River was surveyed in 1796–1797 and the land west of the Cuyahoga River in 1806–1807 (Williams, 2015). Some townships were also subdivided into lots at this time. For simplicity, we refer to all of these data as the 1800 surveys. None of these surveys were part of the federal (General Land Office) system that began elsewhere in Ohio.

For this project, we obtained all available field books from surveys of Cuyahoga County between 1796 and 1807. We searched the Western Reserve Historical Society Research Library, the Washington, Jefferson, Trumbull, Geauga and Cuyahoga County Archives (the land was part of all of these counties at one time), the Ohio State Archives and the Connecticut State Library. We found surveys from throughout Cuyahoga County, including all township outlines. Because only some townships were

subdivided at this time, our data include more information from some areas of the county than others. However, the data are not methodologically biased because we included all field books we found and we are confident that we found all field books that are extant.

From the field books, we recorded ranked timber observations, in which surveyors noted up to 12 tree species on each half-mile (0.8 km) line, in descending order of abundance (Dupuis, Arseneault, & Sirois, 2011; Jackson, Pinto, Malcolm, & Wilson, 2000; Scull & Richardson, 2007; Seischab, 1990, 1992). Listing tree species in descending order of abundance was common practice, and by 1804, instructions to federal surveyors in the mid-west required listing species in this way (Bourdo, 1956; White, 1984). Their assessment of abundance was qualitative. Such line descriptions include more species per unit area than more commonly used witness tree data (Seischab, 1992). Though possibly affected by bias and variation among surveyors, line descriptions are free of known biases inherent to witness tree data (Liu et al., 2011; Williams & Baker, 2010). A comparison of line description data to early vegetation surveys showed that estimates of species prevalence and dominance derived from ranked timber observations were highly accurate (Terrail, Arseneault, Fortin, Dupuis, & Boucher, 2014). Line descriptions also produced species distribution models with better predictive performance than witness tree data (Tulowiecki, 2014). Because surveyors did not always specify tree species, we lumped observations by genus when necessary. Nomenclature follows USDA Natural Resources Conservation Service (2013). Our search yielded 1288 surveyed lines, 826 lines with ranked timber observations, and 4,234 individual tree observations.

2.4 | The 2014 vegetation data

For comparison with recent vegetation, we used a vegetation data set consisting of 400 0.1-ha plots located in Cleveland Metroparks and sampled between 2010 and 2014 (Hausman & Robison, 2010). For simplicity, we refer to these as 2014 vegetation data. Established in 1917, Cleveland Metroparks was the first metropolitan park system in the United States, and many parks outside the city were protected prior to the suburban development of the late 20th century. The 93-km² park system is spread throughout the county, covers 7% of its land area, and includes about 70% of its natural areas. The park system covers both physiographic regions, but much of it surrounds the major rivers. The plots were located randomly throughout the natural areas of the park system and spatially balanced based on a Generalized Random-Tessellation Stratified design (Stevens & Olsen, 2004). All trees in plots were recorded, but we used only stems ≥ 10 cm DBH. Using larger trees improved comparability with the 1800 surveys, which likely included only canopy-sized trees. At the same time, including stems down to 10 cm DBH allowed us to include less mature forests in the 2014 data set. Most plots (365) had at least one tree of this size.

2.5 | Analysis

2.5.1 | Changes in area of habitat types between 1800 and 2014

From the field books, we recorded any mention of habitat type or vegetation structure. We calculated the percentage of all lines described as “swamp” and “wet woods” (i.e. forested wetland), “open wet land,” “bog” and “marsh” (i.e. open wetland), and “open woods” (i.e. open oak woods; all instances of open woods were oak-dominated). For 2014, we used a detailed, ground-truthed vegetation map produced by Lake Erie Allegheny Partnership for Biodiversity covering all of Cuyahoga County (Hausman, 2015).

2.5.2 | Changes in plant community composition between 1800 and 2014

We used non-metric multidimensional scaling (NMS) ordination to describe changes in plant community composition between 1800 and 2014. To supply species abundances for the ranked timber observations, we assumed the commonly observed log-normal distribution of abundance (i.e. a sigmoid relationship between rank and log(abundance); Whittaker, 1965; Wilson, 1991). Small samples from communities with this distribution, especially samples limited to the most abundant species, such as the ranked timber observations, are best represented by geometric series (i.e. a linear relationship between rank and log(abundance); Whittaker, 1965; Bazzaz, 1975). Therefore, we used the method of Seischab (1992) to generate relative abundance values in geometric series, ranging from 0% to 100%. For the 2014 vegetation data, we calculated relative abundance as the percentage of all stems (≥ 10 cm DBH) in a plot belonging to each species, also ranging from 0% to 100%.

We performed NMS using Sørensen (Bray-Curtis) distance, a random starting point, 50 runs with real data and 249 runs with randomized data. We found a two-dimensional solution and varimax-rotated it. To test whether community composition differed between 1800 and 2014, we used a multiresponse permutation procedure (MRPP) based on Sørensen distance. To specify how species composition differed, we tested whether 1800 and 2014 communities differed along each ordination axis using *t*-tests, and we conducted an indicator species analysis (ISA) to identify species associated with each time period (Dufrière & Legendre 1997). ISA combines information on species' concentration of abundance and faithfulness of occurrence in each time period. Indicator values (IV) range from 0 (no indication) to 100 (perfect indication). We used a Monte Carlo test with 4,999 randomizations to evaluate the significance of the IVs. To define groups of plant communities, we conducted a hierarchical, agglomerative cluster analysis based on Sørensen distance using the flexible beta linkage method with $\beta = -0.25$. We performed another ISA to characterize the groups. All of these analyses were conducted in PC-ORD 5.31 (MjM Software Design, Gleneden Beach, OR, USA).

2.5.3 | Homogenization in community composition

To compare β -diversity between 1800 survey lines and 2014 vegetation plots, we used the index of Raup and Crick (1979). We chose this index because it is not affected by differences in species richness (Anderson et al., 2011; Chase, Kraft, Smith, Vellend, & Inouye, 2011). It uses presence-absence data, calculates the probability that two samples share fewer species than expected for samples drawn randomly from the species pool, and ranges from 0 to 1, with higher values indicating greater β -diversity. We used the package ‘vegan’ in R to calculate Raup-Crick β -diversity between all pairs of 1800 survey lines and between all pairs of 2014 vegetation plots (R Foundation for Statistical Computing, Vienna, Austria). We then used a *t*-test to compare β -diversity between 1800 survey lines and 2014 vegetation plots. Because the measures were pair-wise, we used 1,188 *df* to reflect the true sample size.

2.5.4 | Changes in species abundance between 1800 and 2014

We calculated the frequency of each tree species in 1800 as the percentage of all tree observations belonging to that species (each record of a tree species in a line description was one tree observation; Scull & Richardson, 2007). We calculated the dominance of each tree species as the percentage of all line descriptions in which the species ranked first (Scull & Richardson, 2007). For comparability, we calculated frequency and dominance from the 2014 vegetation data in the same way. The frequency of each tree species was the percentage of all tree observations belonging to that species (considering each record of a tree species in a plot as one tree observation), and dominance was the percentage of all plots in which the species had the highest stem density.

2.5.5 | Effects of species traits on changes in abundance

We calculated differences by subtracting frequency in 1800 from frequency in 2014, and dominance in 1800 from dominance in 2014. We then tested whether these differences depended on tree species traits. To characterize species traits, we obtained fire, shade and minimum temperature tolerance information from the PLANTS database (USDA Natural Resources Conservation Service 2013). We coded fire and shade tolerance classes as ordinal variables. We obtained CSR strategies (Grime, 2001) from Wonkka, Lafon, Hutton, and Joslin (2013) and classified species as either including or not including a ruderal strategy. We tested whether differences in species frequency and dominance from 1800 to 2014 depended on species' climate, fire and shade tolerance and life-history strategy using GLM. We tested all possible pair-wise interactions and dropped those that were not significant.

3 | RESULTS

3.1 | Changes in area of habitat types between 1800 and 2014

According to surveys, 94.0% of Cuyahoga County was forested in 1800 (Table 1). Most of the remainder was covered by wetlands, 87% of which were also forested, and 0.54% was open oak woods. No terms such as “prairie,” “plains” or “grassland” were used, although these terms appeared in contemporary surveys elsewhere. No burned areas were described, although burned areas were described

TABLE 1 Proportions of habitat types in Cuyahoga County, Ohio, in 1800 and 2014. For 1800, $N = 1,288$ line descriptions in surveyors’ field books. For 2014, cover information came from a vegetation map of Cuyahoga County produced by Lake Erie Allegheny Partnership for Biodiversity (Hausman, 2015)

Habitat type	% in 1800	% in 2014
Forest	94.0	19.6
Wetland, total	5.43	2.17
Forested wetland (e.g. swamp, wet woods)	4.74	1.52
Open wetland (e.g. bog, marsh)	0.70	0.65
Open woods, i.e. open oak woods	0.54	0
Development, including lawns	0	76.9
Agriculture	0	0.93
Old-field	0	0.36

in contemporary surveys elsewhere. Several Native American paths and one “Indian sugar camp” were mentioned, but no settlements or clearings. By 2014, the area of forest in the county had decreased to 19.6% and the area of wetland had been reduced by more than half. Nearly all of the forest and wetland area lost was developed.

3.2 | Changes in plant community composition between 1800 and 2014

The NMS ordination explained 74% of the variation in plant community composition. Axis 1 described a gradient from low to high abundance of *Fagus* (Figure 1a). Plant communities in 1800 scored higher on this *Fagus* axis ($t = 17.86$, $df = 647$, $p < .0001$; Figure 1b). Axis 2 described a gradient from *Acer* to *Quercus*, *Castanea dentata* and *Carya*. Plant communities in 1800 scored higher on this axis as well, with greater abundance of *Quercus*, *C. dentata*, and *Carya* ($t = 19.58$, $df = 853$, $p < .0001$). Overall, plant communities in 1800 and 2014 differed significantly according to MRPP ($A = 0.0899$, $p < .0001$). The strongest indicator species for 1800 communities were *F. grandifolia*, *Carya*, *Quercus*, *C. dentata*, *Tilia americana* and *Fraxinus*. The strongest indicators for 2014 communities were *Acer*, *Prunus serotina* and *Ulmus* (all $IV > 30$, $p < .001$).

Cluster analysis yielded five vegetation types distinguished by different indicator species (Figure 1b). A type indicated by *Quercus*, a type indicated by *C. dentata* and *Carya*, and a type indicated by *F. grandifolia* included mostly 1800 survey lines (all $IV > 30$, $p < .001$). A total of 49% of the 1800 survey lines belonged to the *Fagus* type,

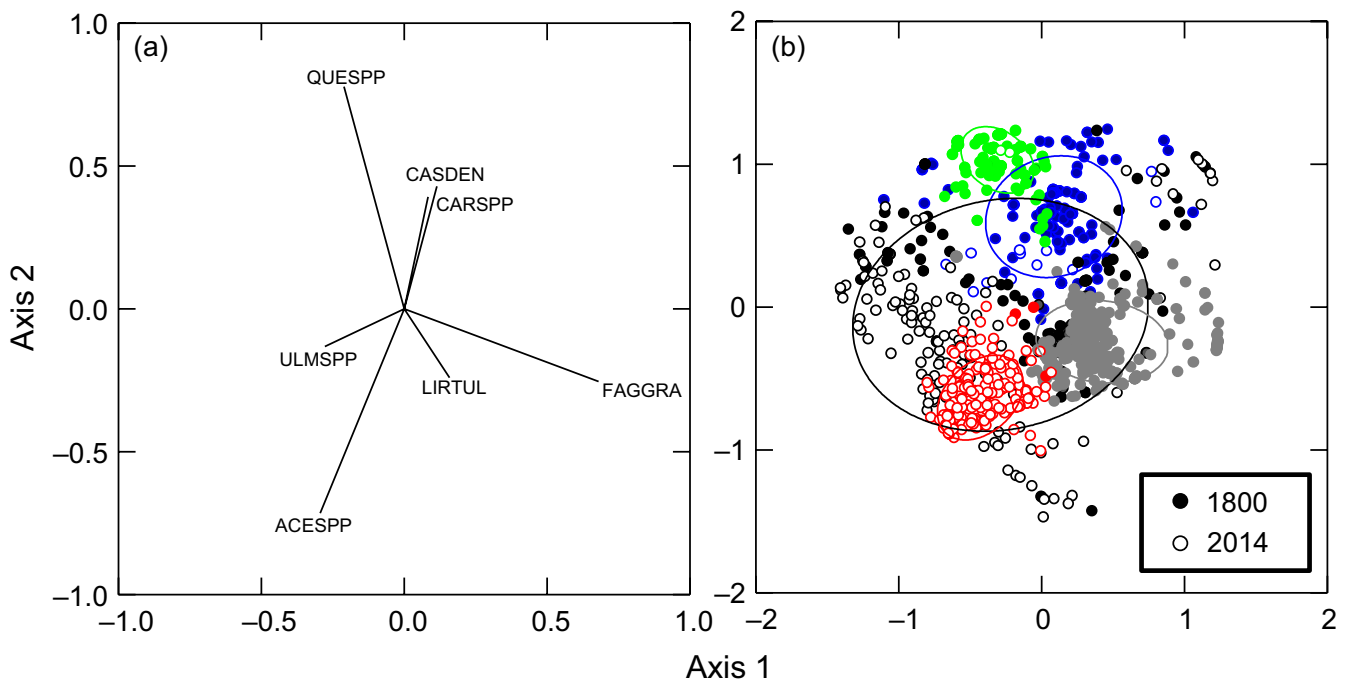


FIGURE 1 NMS ordination of plant communities of Cuyahoga County, Ohio, in 1800 and 2014. (a) Joint plot showing correlations between ordination axes and species abundances for species with $|r| > .20$. Abbreviations are the first three letters of genus and species as listed in Table 1. (b) Locations in ordination space of 1800 survey lines ($N = 825$; filled symbols) and 2014 vegetation plots ($N = 365$; open symbols). Colours indicate vegetation types identified by cluster analysis. Green symbols, *Quercus* type; blue symbols, *Castanea-Carya* type; grey symbols, *Fagus* type; black symbols, *Fraxinus-Ulmus* type; red symbols, *Acer* type (see Results)

TABLE 2 Frequency and dominance of tree species in Cuyahoga County, Ohio, in 1800 and 2014. Frequency is the percentage of all tree observations belonging to each species; dominance is the percentage of all line descriptions (or plots) in which the species ranked first (had the highest stem density). Species with a ruderal life-history strategy (whose strategy includes ruderal according to Wonkka et al., 2013) are indicated with an asterisk

Tree species	Frequency		Dominance	
	1800	2014	1800	2014
<i>Acer</i> spp.*	13.9	26.3	10.6	64.4
<i>Aesculus</i> spp.	0.24	1.26	0	1.10
<i>Ailanthus altissima</i> *	0	0.05	0	0
<i>Alnus</i> spp.	0.02	0	0.12	0
<i>Betula</i> spp.*	0.14	0.75	0	0.55
<i>Carpinus caroliniana</i>	0.45	0	0	0
<i>Carya</i> spp.	12.2	6.69	0.85	2.47
<i>Castanea dentata</i>	7.68	0	6.08	0
<i>Catalpa bignonioides</i> *	0	0.15	0	0
<i>Cornus florida</i> *	0.09	0	0	0
<i>Fagus grandifolia</i>	14.6	6.24	46.5	7.95
<i>Fraxinus</i> spp.	12.6	9.76	2.79	5.21
<i>Gleditsia triacanthos</i> *	0	0.05	0	0
<i>Juglans</i> spp.	3.76	1.66	1.46	1.64
<i>Juniperus virginiana</i>	0.68	0	0	0
<i>Larix laricina</i> *	0.02	0	0.12	0
<i>Liquidambar styraciflua</i>	0	0.15	0	0
<i>Liriodendron tulipifera</i>	6.73	4.78	0.24	1.64
<i>Maclura pomifera</i>	0	0.20	0	0.27
<i>Magnolia acuminata</i> *	0.40	1.11	0	0
<i>Malus coronaria</i>	0.14	0	0	0
<i>Morus alba</i> *	0	0.05	0	0
<i>Nyssa sylvatica</i>	0.02	1.26	0	0
<i>Ostrya virginiana</i>	0	1.81	0	0.27
<i>Picea abies</i>	0	0.55	0	1.37
<i>Pinus nigra</i>	0	0.91	0	1.10
<i>Pinus resinosa</i>	0	0.45	0	0.27
<i>Pinus strobus</i>	0.09	1.11	0.12	0.55
<i>Pinus sylvestris</i>	0	0.20	0	0
<i>Platanus occidentalis</i>	0.14	0.96	0	0.27
<i>Populus</i> spp.*	0.90	0.96	0	0.82
<i>Prunus serotina</i> *	0.78	7.95	0	2.74
<i>Quercus</i> spp.	11.2	8.40	28.0	2.47
<i>Robinia pseudoacacia</i> *	0	0.86	0	0.82
<i>Salix fragilis</i> *	0	0.05	0	0.27
<i>Sassafras albidum</i> *	0.07	2.16	0	0.55
<i>Tilia americana</i> *	9.00	3.17	2.31	0.82
<i>Tsuga canadensis</i>	0.28	0.86	0.24	1.37
<i>Ulmus</i> spp.*	3.94	9.21	0.61	7.40

18% belonged to the *Castanea-Carya* type and 17% belonged to the *Quercus* type. A type indicated by *Fraxinus* and *Ulmus* had similar numbers of 1800 survey lines and 2014 vegetation plots, and a type indicated by *Acer* had mostly 2014 plots (all $IV > 30$, $p < .001$). About 52% of the 2014 plots belonged to the *Acer* type and 35% belonged to the *Fraxinus-Ulmus* type.

3.3 | Homogenization in community composition

Plant communities on 1800 survey lines had higher β -diversity than 2014 vegetation plots ($t = 48.52$, $df = 1188$, $p < .0001$).

3.4 | Changes in species abundance between 1800 and 2014

The largest changes in species frequency between 1800 and 2014 were increases in *Acer*, *Prunus serotina* and *Ulmus*, and decreases in *F. grandifolia*, *C. dentata*, *T. americana* and *Carya* (all differences $>5\%$; Table 2). The largest change in dominance was an increase in communities dominated by *Acer*, by 53% (Figure 2). Communities dominated by *Fagus* decreased by 39% and *Quercus* by 25%.

3.5 | Effects of species traits on changes in abundance

Species traits explained 36% of the variation in differences in frequency between 1800 and 2014 (model: $F = 2.3589$, $df = 7, 29$, $p = .0490$). The best predictor of changes in frequency was life-history strategy; species including a ruderal strategy tended to increase, whereas species not including a ruderal strategy tended to decrease (Type III SS: $F = 4.8162$, $df = 1$, $p = .0364$; Figure 3). Climate, fire and shade tolerance did not significantly predict changes in frequency, and no interactions were significant. None of the traits explained changes in dominance.

4 | DISCUSSION

Plant communities in northeast Ohio have changed tremendously over the past 200 years. The most obvious change is the large proportion of natural habitat lost to development, but the biological communities that remain have been profoundly altered as well. This study provides new insight into the drivers of these changes. Our data give no evidence for the hypothesis that the vegetation of northeast Ohio was shaped predominantly by frequent fire and subsequent fire suppression. This could be because fire was not a dominant force shaping plant communities in northeast Ohio, or because this study was not able to detect the signature of fire history. The deep and often poorly drained loam soils, ravines and floodplains covering much of the study area are not typically associated with frequent fires (Schwartz, 1994). Plant communities dominated by *F. grandifolia*, which do not support frequent fire, covered 46.5% of the 1800 landscape. In addition, the 1800

FIGURE 2 Changes in tree species dominance in Cuyahoga County, Ohio, between 1800 and 2014. Dominance is the percentage of all line descriptions (or plots) in which the species ranked first (had the highest stem density)

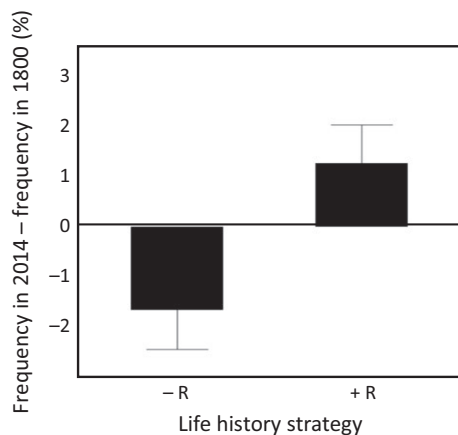
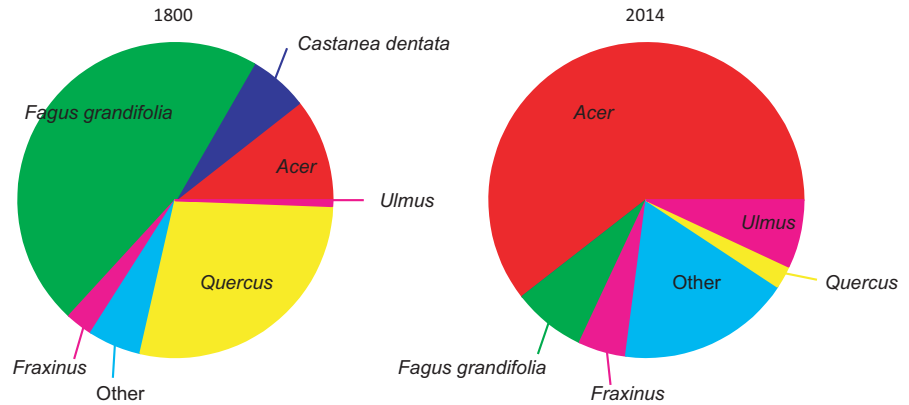


FIGURE 3 Changes in frequency of tree species in Cuyahoga County, Ohio, between 1800 and 2014 (mean \pm SE), comparing species with CSR strategies including ruderal and species with strategies not including ruderal (Grime, 2001; Wonkka et al., 2013)

landscape had no recently burned areas and only 0.54% open oak woods. By contrast, nearby parts of northeast Ohio had 3.2% of the pre-settlement landscape covered by barrens and burns (Whitney, 1982). The relative lack of recent fires and prairie or savanna habitats in this region may be explained in part by the lack of permanent Native American settlement from 1640 to 1742 (Grabowski, 2017). Fire tolerance did not emerge as a significant predictor of changes in species frequency from 1800 to 2014. Communities dominated by *Quercus*, which may have been tolerant of fire, covered 28% of the 1800 landscape and declined in extent to the present day, and fire-intolerant *Acer* increased. Fire suppression, forest clearing, deer herbivory and other factors may have contributed to this decrease in *Quercus*-dominated communities and the increase in *Acer* (McEwan, Dyer, & Pederson, 2011; Schulte, Mladenoff, Crow, Merrick, & Cleland, 2007; Thompson et al., 2013).

Climate and shade tolerance likewise did not predict changes in species frequency. Climate change likely played some role in vegetation change from 1800 to 2014, but other factors evidently had stronger influence (Nowacki & Abrams, 2015; Pederson et al., 2015). Incorporating precipitation as well as temperature tolerance would

improve the ability to detect an effect of climate change. The lack of a pronounced decline of shade-tolerant species and the lack of increase of shade-intolerant species is somewhat surprising given the extent of forest clearing and creation of open habitats. This result was affected in part by the great decline in shade-intolerant *C. dentata* due to the fungal blight introduced in the early 1900s. Again, other factors, in this case including an introduced pathogen, obscured a clear effect.

The single best predictor of species' increases and decreases from 1800 to 2014 was their life-history strategy. Species that increased had a ruderal strategy, a combination of adaptations to frequent disturbance including fast growth, short time to reproductive maturity, large allocation to reproduction and effective seed dispersal (Grime, 2001). While ruderal species likely increased in many North American landscapes over the past several hundred years, it makes sense that urbanization would intensify this effect. Natural areas within an urban landscape are subject to frequent human disturbances, from land management to recreational use. In our comparison, the natural areas of Cleveland Metroparks are managed and heavily used, and include large areas of edge and successional habitat favouring ruderal species, including post-agricultural forests. The dominance of ruderal species may decline in the future as these forests mature, unless continuous disturbances in urban forests perpetually promote ruderal species.

Species' responses to disturbance help explain the most dramatic shifts we observed: the decline of *Fagus*-dominated communities and the rise of *Acer*. These same shifts have been documented throughout the northeast and upper mid-west United States (Schulte et al., 2007; Thompson et al., 2013). *Fagus grandifolia*, a late successional species, often takes over 100 years to recolonize cleared land (Flinn & Marks, 2007). The increase in the dominance of the genus *Acer* likely reflects a shift in species composition as well, toward the early successional and ecologically versatile *Acer rubrum*, which often dominates post-agricultural and other disturbed forests (Flinn & Marks, 2007). The majority of trees called "maple" on 1800 survey lines were likely *Acer saccharum*, whereas the composition of *Acer* in 2014 vegetation plots was 46% *A. saccharum*, 40% *A. rubrum*, 8% *A. negundo*, 5% *A. saccharinum* and 2% *A. platanoides*.

Another signature of urbanization revealed here is biotic homogenization sensu Olden and Rooney (2006). Plant communities in the 2014 vegetation plots were more similar to each other than plant communities on 1800 survey lines. The greater homogeneity of 2014 plant communities may be explained in part if particular community types, such as riparian areas, were more likely to be preserved. Many landscapes have become more homogenous over the past several hundred years (Schulte et al., 2007; Thompson et al., 2013), but this effect is likely exacerbated by urban development (McCune & Vellend, 2013; McKinney, 2006). In fact, there is evidence that humans in disparate regions impose common selective pressures, so that urban ecosystems become more similar to other, geographically distant cities than to adjacent native ecosystems (Groffman et al., 2014; Kühn & Klotz, 2006; Wittig & Becker, 2010). However, the biotic homogenization of tree communities in northeast Ohio did not result from the spread of introduced species, often considered a primary driver of such patterns globally (Qian & Ricklefs, 2006). Our study identified 11 tree species added to the flora since 1800, but all made extremely minor contributions to contemporary plant communities. The most abundant introduced species was *A. plat-anoides*, with a frequency of 1% in 2014 vegetation plots. Rather, the increased commonness of the native ruderal species *A. rubrum*, *Ulmus* and *Prunus serotina* led to homogenization across the region.

4.1 | Implications for restoration

If one goal of protected areas is to preserve historical vegetation, then our data provide a few clear priorities. Increasing the extent of *Fagus*- and *Quercus*-dominated forests, in part by identifying future land acquisitions with these forests, would make current protected areas more representative of pre-settlement plant communities. We find little historical justification for maintaining open habitats, given that 0.54% of the landscape was in open oak woods and zero in prairie. Compared to 1800, wetlands are now actually overrepresented in the county's landscape relative to forests (Table 1). This is likely due to efforts to prioritize and preserve remaining wetland habitats in protected areas. Wetlands and riparian areas are also overrepresented in 2014 vegetation plots because much of the Cleveland Metroparks system follows rivers and creeks. This riparian bias in the 2014 data set is responsible for results such as a small apparent increase in late successional *Tsuga canadensis*, which grows only in river valleys and ravines in northeast Ohio (Braun, 1961). To better represent regional vegetation in protected areas, we need to raise the priority of upland *Fagus* and *Quercus* forests relative to wetlands and open habitats and increase efforts to restore *Castanea dentata* if possible.

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ORCID

Kathryn M. Flinn  <http://orcid.org/0000-0001-5922-3610>

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