Urban Ecosystems
https://doi.org/10.1007/s11252-023-01459-0

How a city shapes its forests: Land use change and forest distribution around Cleveland, Ohio over 220 years

Kathryn M. Flinn[1] · **Zachary R. Hughes**[1]

Accepted: 21 October 2023

Abstract
As cities consume increasing land area worldwide, we need more investigation of the effects of urbanization on forests. Here we provide a comprehensive example of how the growth of a city shapes its surrounding forests. We examine how forest area changed through time, the importance of fragmentation, and the drivers behind the spatial distribution of land uses. To assess land use change and its dependence on topography and soils, we interpreted aerial photographs of Cuyahoga County, Ohio, USA from 1938, 1979, and 2021. Over the past 220 years, Cuyahoga County experienced massive forest loss, to a minimum of 12% of the landscape, and modest recovery of forests on former farmland, to 21%. While clearing for agriculture was the primary cause of deforestation in the nineteenth century, development became the main agent of forest loss from the twentieth century to the present. One-third of current forests (6.7% of the landscape) were likely never cleared for agriculture. Most post-agricultural forests originated between 1938 and 1979. The median size of forest patches is 18 hectares, and 75% of points in forest fall within 50 m of an edge. Steeper slopes and lower elevations were more likely to remain and become forests. *Quercus* forests were three times more likely to be preserved than *Fagus* forests. To preserve forest biodiversity, conservation efforts should focus on protecting remaining forests from development—especially forests that were never cleared for agriculture and *Fagus*-dominated forests—and learning how to restore native biodiversity to developing post-agricultural forests.

Keywords Aerial photographs · Edge effects · Fragmentation · Historical ecology · Land use history · Post-agricultural forests

Introduction

Historical land use is the paramount influence on forest biodiversity in many landscapes. Forests on former agricultural land remain recognizable in species richness and composition (Flinn and Vellend 2005; Hermy and Verheyen 2007), and the effects of past agriculture can persist for millennia (Dupouey et al. 2002; Dambrine et al. 2007; Plue et al. 2008; Hejcman et al. 2013). Land use change not only transforms individual forest patches, but it also alters their landscape context through habitat loss and fragmentation. The extent of forest clearance affects plant diversity as forests regrow, because remnant forests serve as seed sources for recolonization (Vellend 2003; De Frenne et al. 2011). In addition, human land use imposes spatial patterns that continue to impact colonization and extinction dynamics via patch size, shape, and isolation (Peterken and Game 1984; Matlack 1994a; Flinn and Marks 2004; Vellend et al. 2006; Brunet et al. 2021; Uroy et al. 2023). At the landscape level, past agricultural use homogenizes community composition, reducing beta diversity (Vellend et al. 2007; Grman et al. 2015). The geography of land use may depend on environmental factors like soils and topography that also shape species composition (Matlack 1997; Flinn and Vellend 2005; Wulf et al. 2010; Abadie et al. 2018). If so, then surviving forests represent a biased sample of historical forests, in which certain species are underrepresented or overrepresented compared to their past abundances. Given these lasting impacts, it is critical to specify historical land use patterns to understand and manage current forests.

✉ Kathryn M. Flinn
kflinn@bw.edu

Zachary R. Hughes
zhughes20@bw.edu

[1] Department of Biology and Geology, Baldwin Wallace University, 275 Eastland Road, Berea, OH 44017, USA

Much of Europe and eastern North America experienced a common pattern called a forest transition (Mather 1992), in which a period of forest clearance for agriculture was followed by a period when many forests regrew on former agricultural land (Rackham 1980; Williams 1989; Whitney 1994; Peterken 1996). More recently, some tropical regions have undergone a similar transition (Thompson et al. 2002; Etter et al. 2005; Lira et al. 2012; Uribe et al. 2020). Most of these landscapes lost over 80% of their extensive forest cover, but subsequent forest expansion has created huge opportunities for the recovery of biodiversity. Many studies of this land use pattern have examined rural areas which are now largely forested again (Foster 1992; Smith et al. 1993; Verheyen et al. 1999; Monsted and Matlack 2021). However, urban landscapes may provide a counterexample in which development overwhelmed forest regrowth (Matlack 1997; Sanderson and Brown 2007; Fahey and Casali 2017). As cities consume increasing land area worldwide, we need more investigation of the effects of urbanization on forests. Here we present a case study of land use patterns and their consequences for forests in the county surrounding Cleveland, Ohio, USA. To our knowledge, this is the first such study of a near-completely forested landscape that became a major city, among the ten largest cities in the United States for most of the twentieth century.

First, we aim to quantify how forest area changed through time and what proportion of current forests have remained continuously forested throughout the historical period. It is important to know the minimum extent of forests at the peak of agriculture to gauge the landscape's potential for recovery (Vellend 2003; De Frenne et al. 2011). Identifying forests present at that time also allows us to distinguish remnants that were likely never cleared for agriculture, called primary forests, from post-agricultural forests (Smith et al. 1993; Flinn and Vellend 2005; Monsted and Matlack 2021). Further, we assess the proportions of post-agricultural forests of different ages. Primary forests typically harbor greater plant diversity than post-agricultural forests, in which plant diversity often increases with age (Bossuyt et al. 1999; Bellemare et al. 2002; Flinn and Marks 2004; Jamoneau et al. 2011). Though not old-growth, primary forests may also have species composition more representative of the region's native forests. Therefore, distinguishing forests of different history can help inform conservation priorities and set targets for restoration.

Our second aim is to assess the importance of fragmentation in this urban landscape. Forest fragmentation is an increasing concern, as 20% of the world's remaining forest is within 100 m of an edge (Haddad et al. 2015). The reduced patch area, increased isolation, and increased proportion of edge habitat associated with fragmentation can strongly reduce species richness, change composition, degrade function, and impede ecological succession (Haddad et al. 2015). In addition, forest edge habitats can be more vulnerable to invasion (Honnay et al. 2002; Yates et al. 2004). In this study, we look at the sizes and shapes of forest patches, the distance to a forest edge, and the distance from one forest patch to another. This information will aid in assessing the susceptibility of ecological communities to the negative effects of fragmentation, including future extinction debt.

Thirdly, we examine the drivers behind the spatial distribution of land uses and their implications for current forests. Creating transition matrices of land use change indicates which land uses expanded at the expense of forests, as well as which land uses were responsible for forest expansion. While larger socioeconomic forces certainly shaped land use patterns, previous work shows that local environmental factors also affected many decisions. In particular, slope and soil type are often key influences on clearance and abandonment for agriculture (Thompson et al. 2002; Flinn and Vellend 2005; Abadie et al. 2018; Cervera et al. 2019; Wulf et al. 2010; Monsted and Matlack 2021). To the extent that such environmental factors impacted the spatial distribution of land uses, remaining forests will occur on specific subsets of the landscape and contain specific subsets of the native biota. Thus, we explore how topography and soils may have influenced land use transitions. If forests adjacent to rivers and streams were more likely to be preserved, for example, then riparian forest species are likely overrepresented in the present landscape. Finally, we directly assess which forest types have been disproportionately lost. With these analyses, we hope to provide a comprehensive example of how the growth of a city shapes its surrounding forests.

Methods

Study area

Cuyahoga County, Ohio, USA covers 1184 km^2 of land on the south shore of Lake Erie (Fig. 1). Climate is humid continental, with a mean annual precipitation of 99.4 cm and a mean temperature of 10.8 °C (Midwestern Regional Climate Center 2017). Elevation ranges from 238 to 400 m. The shale and sandstone bedrock are covered with glacial deposits and largely silt loam soils with clay-rich subsoils (Musgrave and Holloran 1980). Three major rivers draining into Lake Erie cut valleys 30–45 m below the surrounding land. Prior to European settlement, the county was 98.7% forested (including 4.7% forested wetlands), with primarily *Fagus-Acer* forests on the higher-elevation Allegheny Plateau and *Quercus*, *Castanea*, and *Carya* forests on the Central Lowlands and river valleys (Flinn et al. 2018, in review). One example of old-growth *Fagus-Acer* forest survives within the county (Williams 1936; Flinn et al. 2019, 2022).

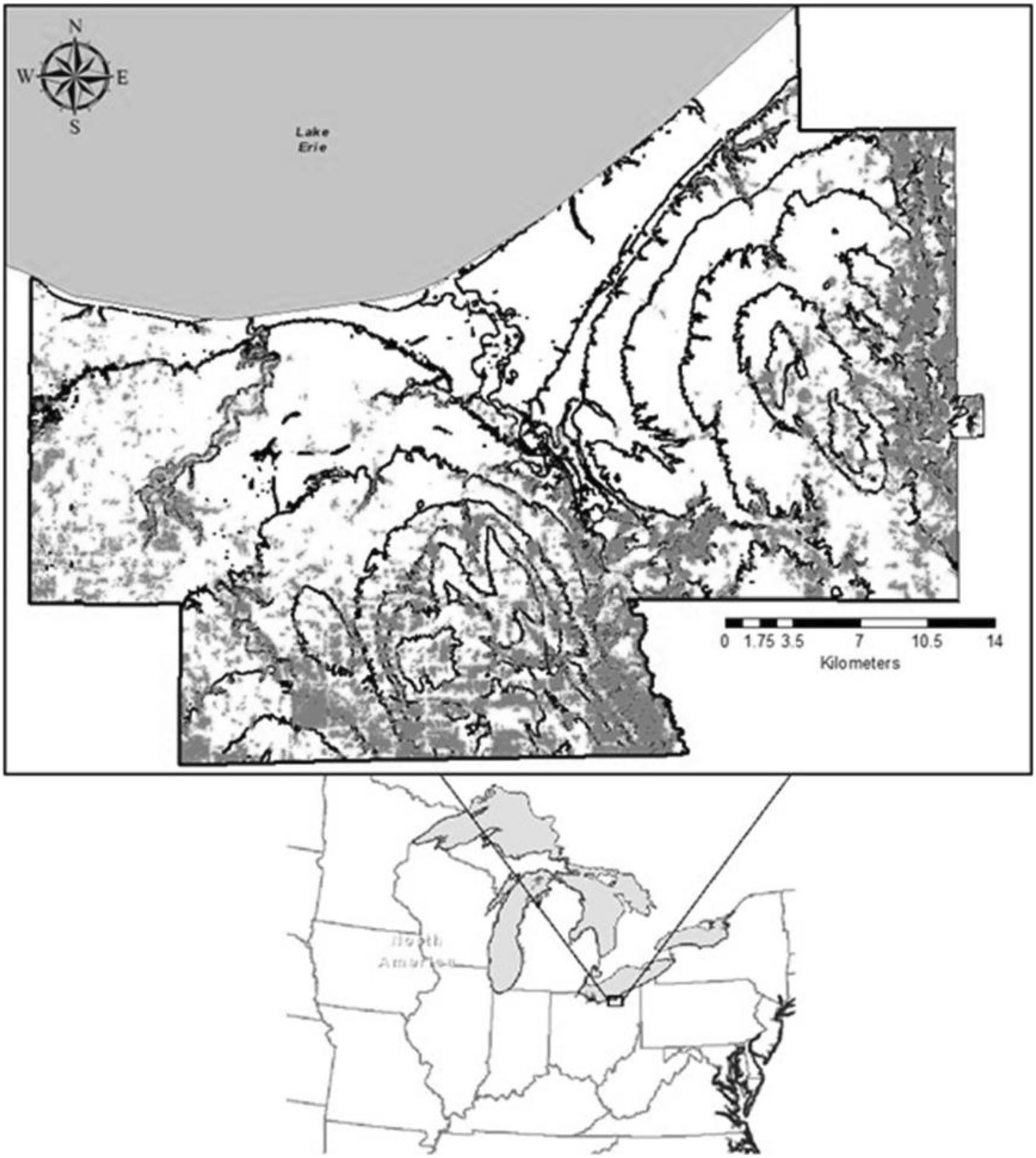

Fig. 1 Map of Cuyahoga County, Ohio, showing its location on the south shore of Lake Erie in midwest USA. Black lines show 30-m contours, and forest cover is in gray

Prehistoric inhabitants cleared small areas of floodplain forest for agricultural fields; this activity was likely greatest between 1500 and 1640 CE (Brose 1994, 2000; Grabowski 2023) and within 10–15 km of the village at the confluence of Tinkers Creek and the Cuyahoga River (Brose 1994, 2000; Tulowiecki and Larsen 2015; E. Olson, personal communication). Settlers of European heritage began clearing forests for agriculture after 1796 (Grabowski 2023). Prior to 1830, 90% of the county's population was rural, with a density of 9 humans/km^2 (United States Census Bureau 2023). Clay tile drainage became widespread by the 1850s, allowing for cultivation of many of the county's poorly drained soils (Weaver 1964). According to the agricultural census, land in farms peaked in 1880 at 91% of the county (United States Department of Agriculture, National Agricultural Statistics Service 2023). The 91% is likely an overestimate due to an issue with the 1880 census (Smith et al. 1993; Wang et al. 2010); reports of land in farms from surrounding decades (1860–1900) are closer to 80%. Nevertheless, it is likely that land in farms peaked in 1880 between 80–90%, and it remained above 80% through 1900. At that time, about half the land in farms was tilled, 13% wooded, and much of the rest in pasture and meadow (United States Department of Agriculture, National Agricultural Statistics Service 2023). Therefore, agricultural census records indicate that forest cover was reduced to a minimum of 12–20% during the period 1880–1900. At the peak of agriculture, population density was 166 humans/km^2 (United States Census Bureau 2023).

The city of Cleveland began to grow quickly after the 1825–1832 construction of the Ohio and Erie Canal. As industry expanded, its population multiplied by 800 times from 1830 to 1930 (Grabowski 2023; United States Census Bureau 2023). By 1900, 87% of the county's population lived in Cleveland (United States Census Bureau 2023). Cleveland's population reached 98% of its peak by 1930 and peaked in 1950 at 915,000 (United States Census Bureau 2023). Suburban development boomed after World War II, with the number of housing units increasing 71% between 1940 and 1980 (Manson et al. 2023). The suburban share of the county's population increased from 28% in 1940 to 62% in 1980 (United States Census Bureau 2023). The county's population peaked in 1970 at 1,721,000 (1454 humans/km^2; United States Census Bureau 2023). From 1980 to the present, the city's and the county's populations have declined, and housing units have increased by only 3%; current population density is 1068 humans/km^2 (Manson et al. 2023; United States Census Bureau 2023). Urban and suburban development have replaced agriculture as the primary land use, and forests now cover 21.5% of the county (including 1.5% forested wetland; according to Hausman 2015). Many current forests are dominated by *Acer*, now the most common tree genus in natural areas (Flinn et al. 2018).

Data collection

We obtained 1937–1938 aerial imagery at 1:20,000 scale taken by the Agricultural Adjustment Administration of the United States Department of Agriculture from the United States National Archives and Records Administration, College Park, MD (negatives scanned by Michael Constandy, Westmoreland Research, Alexandria, VA). The 1979 aerial imagery at 1:15,840 scale was taken by the Natural Resources Conservation Service of the United States Department of Agriculture from Cleveland Public Library, Cleveland, OH. We georeferenced each photograph in ArcMap 10.8.1 (ArcGIS, Environmental Systems Research Institute, Redlands, CA) with 3 to 7 reference points per photograph. High-resolution aerial imagery from 2021 was provided by Cuyahoga County Planning Commission, Cleveland, OH. All photographs had resolution sufficient to distinguish land use and individual tree crowns. We chose the 1938 photographs because they are the earliest available, and they were close enough in time to the peak of agriculture to allow us to identify forests that were likely never cleared for agriculture, or primary forests. The 1979 photographs were useful not only because they gave us two evenly spaced intervals of about 40 years each, but also because these intervals cover distinct phases of landscape development. The 1938–1979 interval captures the first wave of suburban expansion, while the 1979–2021 interval represents the period of population decline and sprawl.

We determined land use at 657 points on a regular grid covering the county, spaced 1.2 km apart. This spacing was chosen to ensure independence among points, as it exceeded the size of management units (Matlack 1997). Based on tree height, crown size, and uniformity of cover, we distinguished "young" and "mature" forests. "Young" forests had a closed canopy with a homogenous texture, indicating a high density of small trees of similar age (Monsted and Matlack 2021). Tree plantations were rare ($<0.5\%$) and included with young forests. "Mature" forests, by contrast, had a coarse, heterogeneous, or "broccoli" canopy texture. Points appearing as "mature" forests in 1938 must have established no later than 1880–1900 (Monsted and Matlack 2021). Because agricultural land use peaked in 1880–1900 in Cuyahoga County, and these points were forested at that time, it is unlikely they were ever cleared for agriculture; thus, we call them primary forests (Smith et al. 1993; Flinn and Vellend 2005; Monsted and Matlack 2021). Successional "old fields" included trees and shrubs, but crowns of individual plants were separate and canopy cover was less than 30% (Matlack 1997). Arable fields and active pastures, which could not always be distinguished, were grouped as "agricultural fields." For analysis, hedgerow trees and orchards were included with agricultural fields. We grouped together roofs, pavement, roads, and railroads as "development." Lawns, lawn trees, cemeteries, and golf courses were included in "lawns." The small area ($<2\%$) covered by rivers, streams, lakes, and open wetlands was collectively called "water." There was also a small area ($<4\%$) of "disturbed soil," such as quarries. For points in forest, we measured the area and perimeter of the forest and the distance from the point to the nearest forest edge, road, water, and other forest patch.

To examine environmental effects on land use decisions, we focused on five key environmental predictors: slope, elevation, aspect, soil pH, and soil drainage. Slope (°) and aspect (°) were extracted from a digital elevation model (Ohio Geographically Referenced Information Program 2023) and converted to degrees from north. The soil map came from the SSURGO database (United States Department of Agriculture, Natural Resources Conservation Service 2023). We ordered soil types by pH level, as described by the County soil survey, into eight classes ranging from "very strongly acid" to "slightly acid to neutral," and we ordered soil types into five drainage classes from "very poorly drained" to "well drained" (Musgrave and Holloran 1980).

Statistical analysis

We compared forests present in 1938, 1979, and 2021 in their area, perimeter to area ratio, distance to the forest edge, distance to the nearest road, distance to the nearest water, and distance to the nearest other forest patch. Because these variables were not normally distributed, we used nonparametric Kruskal-Wallis tests.

Logistic regressions assessed the effects of environmental predictors on land use decisions. For all points, 98.7% of which were forested in 1800 (Flinn et al. 2018), we assessed the odds of keeping forests until 1938. For forests present in 1938, we assessed the odds of keeping forests until 1979, and for forests present in 1979, we assessed the odds of keeping forests until 2021. We also looked at environmental effects on gaining forests through agricultural abandonment. For fields present in 1900 (i.e. fields, old fields, and young forests in 1938), we assessed the odds of being abandoned (becoming old fields or forests) by 1938. For fields present in 1938, we assessed the odds of being abandoned (becoming old fields or forests) by 1979. There was not enough agriculture present in 1979 (<5%) to analyze the subsequent transition. To examine the consequences of these decisions, we compared present-day primary and post-agricultural forests in slope, elevation, aspect, soil pH, and soil drainage using nonparametric Mann-Whitney U tests.

To see whether certain forest types were lost disproportionately, we used a model of forest types *circa* 1800 based on land survey records (Flinn et al. in review). This analysis tested whether the proportions of remaining primary forests belonging to each forest type differed from the proportions in the *circa*-1800 landscape with a G test. To meet the assumptions of the test, forests were grouped into two types that together covered 99% of the *circa*-1800 landscape: *Fagus* forests and *Quercus* forests.

Results

Over the past 220 years, Cuyahoga County, Ohio, USA experienced massive forest loss, including a continual decline in primary forests that were likely never cleared for agriculture, and modest recovery of forests on former agricultural land (Fig. 2). In 1938, the most common land use was agriculture, with active fields and old fields covering more than half the area (Fig. 3). Lawns and development together occupied less than one third of the county. Forests covered 16% of the landscape, including 12% of the landscape in mature forests that likely persisted through the peak of agriculture, called primary forests. By 1979, agriculture had declined dramatically, to only 4.6% of the landscape, and lawns and development had doubled to 60% of the county. At that time, agricultural abandonment had increased forest cover to 25%, but some primary forests had been cleared, so that they decreased to 8.1% of the landscape. Today, human habitat is by far the dominant land use, with lawns and development covering 72% of the county. Forest cover has decreased to 21%, and primary forests continued to be lost, so that they now cover 6.7% of the landscape. Therefore, about one third of current forests are primary, with the rest growing on former agricultural land. Most of these post-agricultural forests originated between 1938 and 1979 (Fig. 4).

From 1938 to 1979, the largest percent changes in land use were the growth of lawns by 163%, the decline of agriculture, and the expansion of forests (Fig. 5). Development increased by 57% and disturbed soil (largely future development) by 109%. The period from 1979 to 2021 saw a continued 59% gain in development. During this latter interval, the area of mature forest decreased while young forests expanded slightly.

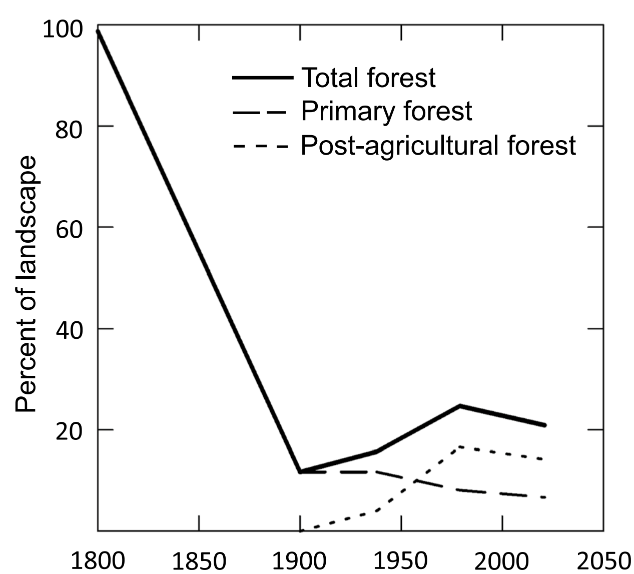

Fig. 2 Change through time in forest cover in Cuyahoga County, Ohio, USA. Primary forests were likely never cleared for agriculture, whereas post-agricultural forests developed on former agricultural fields. Forest cover *circa* 1800 is based on land survey records (Flinn et al. 2018). Forest cover from 1900 to 2021 is based on aerial photograph interpretation. N = 657 points

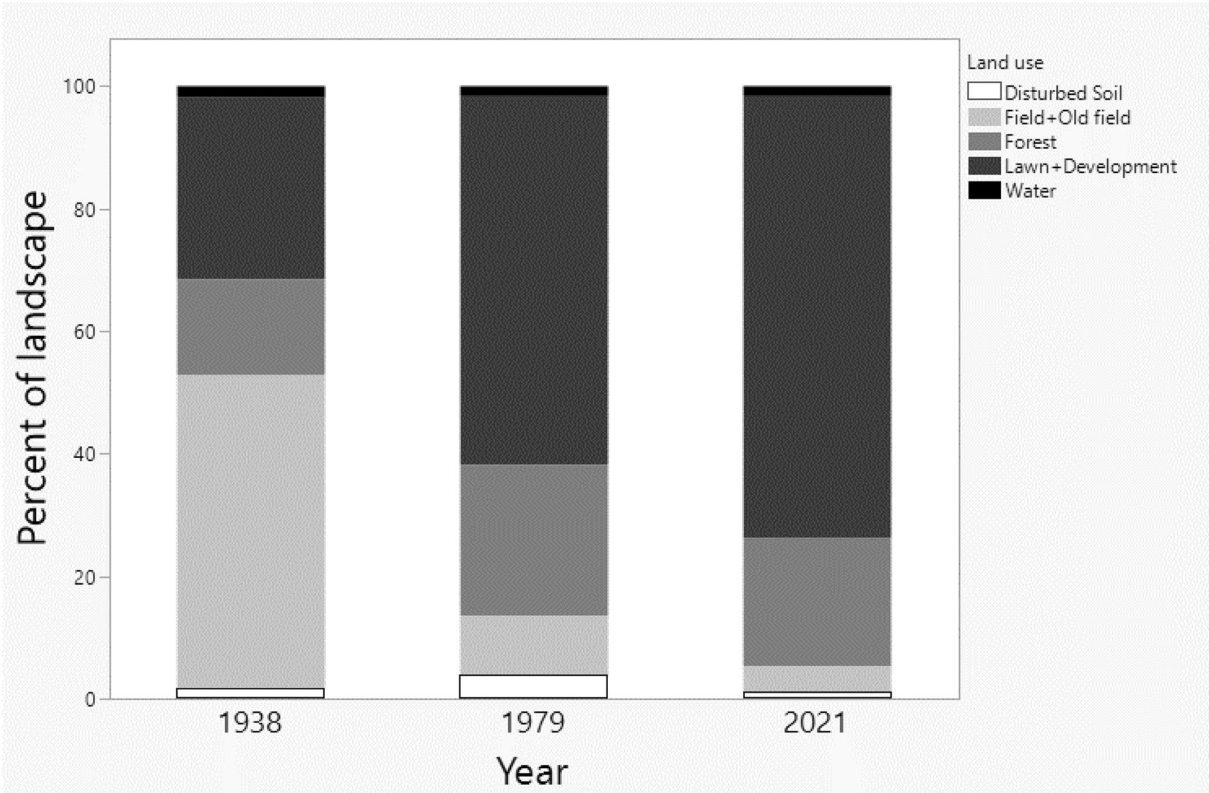

Fig. 3 Change through time in the extent of different land uses in Cuyahoga County, Ohio, USA. N = 657 points for each time

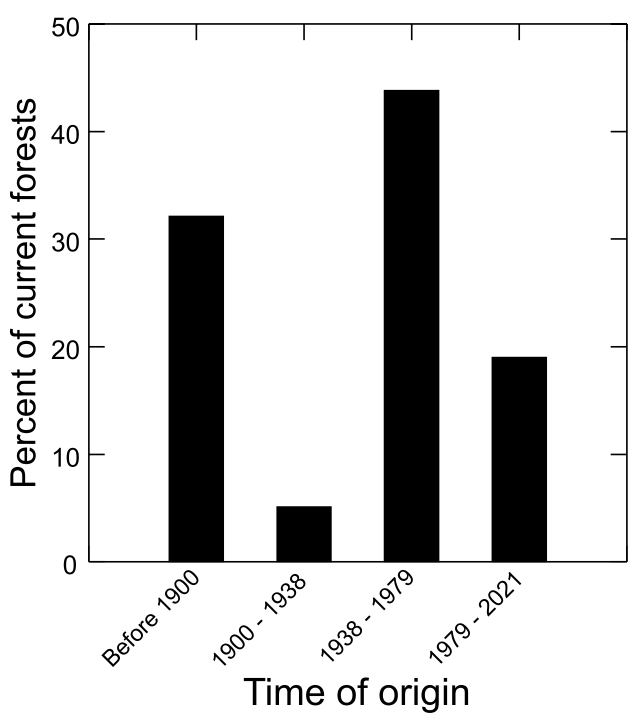

Fig. 4 Histogram showing the ages of forests in the current landscape of Cuyahoga County, Ohio, USA. In this study, forests that originated before 1900 are likely primary forests that were never cleared for agriculture. N = 137

Mature forests were relatively stable over time, with the majority of mature forests (58–68%) remaining from 1938 to 1979 and from 1979 to 2021 (Table 1). Of mature forests that were cleared, the largest share (21–24%) went to lawns and development. From 1979 to 2021, 12% of mature forests became young forests, indicating logging. While many young forests (32–39%) became mature forests over both time intervals, the largest share of young forests (39–46%) transitioned to lawns and development. In both time intervals, young forests were more likely to be developed than mature forests. From 1938 to 1979, 53% of old fields became forests, but from 1979 to 2021, only 14% of old fields became forests; instead, over half of old fields went to lawns and development during the latter interval. Across both intervals, about 60% of agricultural fields became lawns and development. Lawns and development were extremely stable land uses, with over 90% of lawns and development remaining in one of the two uses. Most disturbed soil (64–78%) later became lawns or development.

Nearly all gains in forest occurred on fields and old fields. From 1938 to 1979, new lawns and development were largely built on agricultural fields, with only 10% of new lawns and development destroying forests. From 1979 to 2021, 23% of new development and 44% of new lawns destroyed forests.

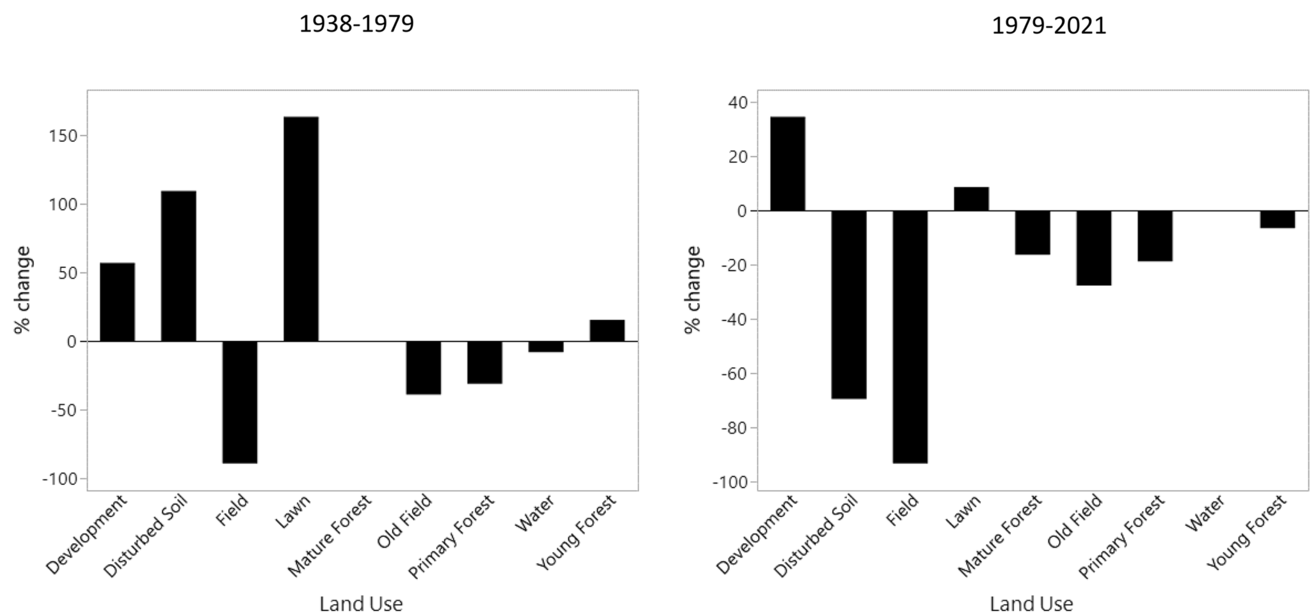

Fig. 5 Percent change in land uses in Cuyahoga County, Ohio, USA over two time intervals. Percent change over a time interval is the difference between the amount of land in a particular use in the prior year and the latter year divided by the amount of land in that use in the prior year. Note that scales differ. N = 657 points for each time interval

Table 1 Transition matrices showing changes in land use in Cuyahoga County, Ohio, USA for two time intervals. Matrices give the percent of each land use in the prior year (columns) that transitioned to each land use in the latter year (rows)

From 1938 to 1979								
Land Use %	Field	Old Field	Mature Forest	Disturbed Soil	Young Forest	Development	Water	Lawn
Field	8.7	3.4	1.3	0	3.9	0.9	0	1.2
Old Field	8.7	8.5	3.9	9.1	3.9	0.9	0	1.2
Mature Forest	11.9	44.1	67.5	9.1	38.5	2.7	33.3	2.4
Disturbed Soil	2.9	1.7	2.6	9.1	7.7	3.6	8.3	4.8
Young Forest	9.0	8.5	1.3	0	0	0	0	0
Development	24.9	8.5	7.8	9.1	19.2	55.9	0	31.0
Water	0	0	2.6	9.1	0	0	58.3	1.2
Lawn	33.9	25.4	13.0	54.6	26.9	36.0	0	58.3
N	277	59	77	11	26	111	12	84
From 1979 to 2021								
Land Use %	Field	Old Field	Mature Forest	Disturbed Soil	Young Forest	Development	Water	Lawn
Field	3.3	0	0	0	0	0	0	0.5
Old Field	13.3	22.2	4.6	0	0	1.7	0	2.3
Mature Forest	10	0	58.0	0	32.3	0.6	9.1	3.2
Disturbed Soil	0	0	0.8	17.4	0	0.6	9.1	0
Young Forest	10	13.9	12.2	4.4	29.0	0	0	0.3
Development	33.3	22.2	7.6	52.2	22.6	92.5	0	11.8
Water	3.3	0	0.8	0	0	0	81.8	0
Lawn	26.7	30.6	16.0	26.1	16.1	4.6	0	81.9
N	30	36	131	23	31	174	11	221

N = 657 points

The median size of a forest patch in the landscape today is 0.18 km^2 or 18 hectares. The size of forest patches changed over time (Kruskal-Wallis 7.14, df = 2, $P = 0.028$), first doubling from 1938 to 1979 and then decreasing from 1979 to 2021 (Fig. 6). Concomitantly, perimeter to area ratios first decreased and then increased to a median of 20 (Kruskal-Wallis 12.46, df = 2, $P = 0.002$). The distance from points in forest to the forest edge was slightly lower in 2021 than previously, with a median of only 25 m in the landscape today (Kruskal-Wallis 5.55, df = 2, $P = 0.062$). Seventy-five percent of points in forest are within 50 m of an edge. The distance from points in forest to the nearest road decreased steadily to a median of 60 m today (Kruskal-Wallis 61.57, df = 2, $P < 0.0001$). The distance from points in forest to the nearest water was much lower in 2021 than previously, a median of 156 m (Kruskal-Wallis 53.32, df = 2, $P < 0.0001$). Sixty percent of points in forest are within 200 m of water, primarily rivers. The distance from points in forest to the nearest other forest decreased steadily over time as forest patches became more clustered, to a median of 119 m (Kruskal-Wallis 27.97, df = 2, $P < 0.0001$).

Topography, but not soil type, consistently impacted land use decisions. Forests on steeper slopes and at lower elevations were more likely to be preserved at all time intervals (Table 2). In addition, fields on steeper slopes and at lower elevations were more likely to become forests. Present-day primary forests are located on steeper slopes than post-agricultural forests (Mann-Whitney U 2957, df = 1, $P < 0.0001$). Primary forests also tend to occur at lower elevations (Mann-Whitney U 1683, df = 1, $P = 0.094$). Forests of different history did not differ in aspect or soil type.

Forest types were not cleared randomly, but rather, *Fagus* forests were lost disproportionately, with only 3% of the *Fagus* forests that existed in 1800 remaining as primary forests today (G = 11.9, df = 1, P 0.0006). By contrast, 10% of *Quercus* forests remain. Thus, *Quercus* forests were three times more likely to be preserved than *Fagus* forests. Seventy-seven percent of today's primary forests were *Quercus* forests *circa* 1800.

Discussion

In only 220 years, the county surrounding Cleveland, Ohio, USA underwent two major transformations: first, from a near-completely forested landscape to an agricultural landscape, and second, from an agricultural landscape to a major city and suburban hinterland. In the first transformation,

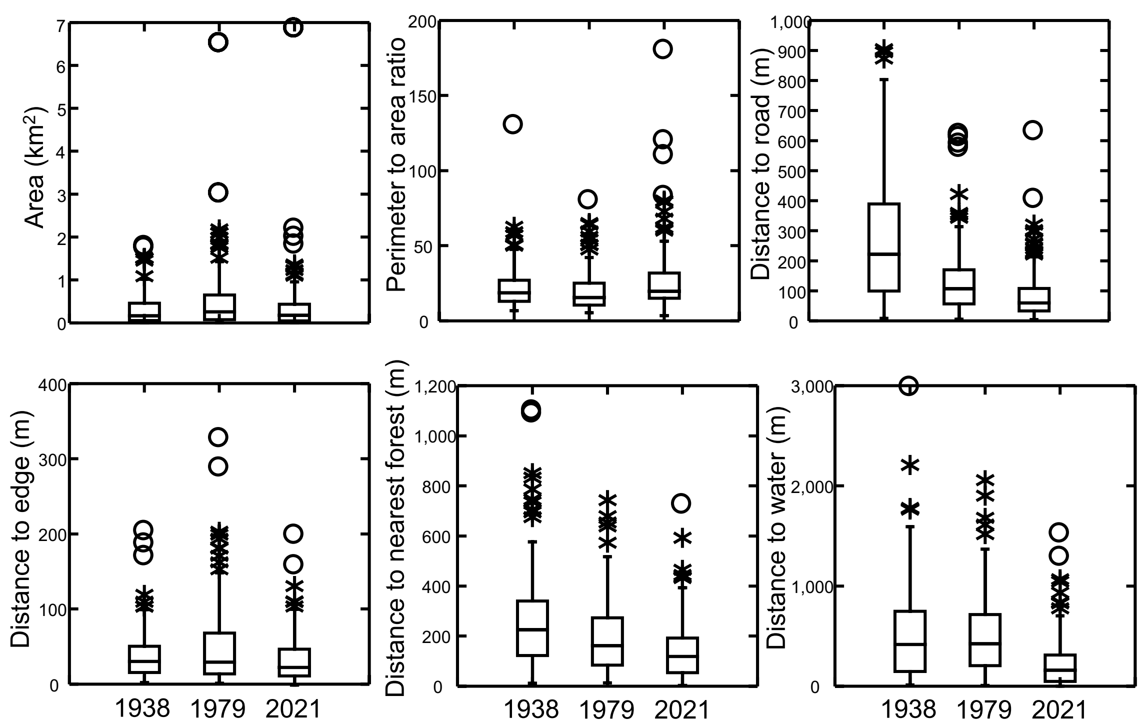

Fig. 6 Box plots showing spatial characteristics of forests present in 1938, 1979, and 2021 in Cuyahoga County, Ohio, USA. The center line shows the median, the box edges show the first and third quartiles, and the whiskers show the range of observed values that fall within 1.5*(interquartile range) of the box edges. Values between 1.5*(interquartile range) and 3*(interquartile range) of the box edges are plotted with asterisks. Values beyond 3*(interquartile range) of the box edges are plotted with empty circles. N = 103 for 1938, N = 162 for 1979, N = 137 for 2021

Table 2 Logistic regressions of the effects of environmental predictors on land use decisions in Cuyahoga County, Ohio, USA

For forests in 1800, odds of keeping forests until 1938. N = 653		
	Z	*P*
Slope	**6.795**	**< 0.0001**
Elevation	**-5.786**	**< 0.0001**
Aspect	-1.773	0.076
pH	-0.064	0.949
Drainage	0.188	0.851
For forests in 1938, odds of keeping forests until 1979. N = 103		
	Z	*P*
Slope	**3.264**	**0.001**
Elevation	**-2.408**	**0.016**
Aspect	1.263	0.206
pH	0.471	0.638
Drainage	1.141	0.254
For forests in 1979, odds of keeping forests until 2021. N = 162		
	Z	*P*
Slope	**2.796**	**0.005**
Elevation	-1.868	0.062
Aspect	1.725	0.085
pH	0.287	0.774
Drainage	1.394	0.163
For fields in 1900, odds of letting fields become forests by 1938. N = 362		
	Z	*P*
Slope	**2.384**	**0.017**
Elevation	**-2.111**	**0.035**
Aspect	-1.178	0.239
pH	-0.03	0.976
Drainage	-1.086	0.278
For fields in 1938, odds of letting fields become forests by 1979. N = 277		
	Z	*P*
Slope	**3.413**	**0.001**
Elevation	**-4.158**	**< 0.0001**
Aspect	0.263	0.792
pH	1.291	0.197
Drainage	0.27	0.7

The Z value is the ratio of the estimated coefficient to its standard error. Significant effects are in bold

during the nineteenth century, 88% of the county's forests were lost, leaving 12% of the landscape in forests that were likely never cleared for agriculture, or primary forests. This change coincided with the spectacular population growth of Cleveland and environs during the nineteenth and early twentieth century. During the second transformation, forest expansion on former agricultural land doubled forest cover to 25% by 1979; this process seems similar to the transition to forest regrowth observed throughout Europe and eastern North America (Rackham 1980; Williams 1989; Whitney 1994; Peterken 1996). Here, much of the forest regrowth resulted from the demise of Cuyahoga County's robust dairy industry during the mid-twentieth century (Grabowski 2023). However, this county contrasts with many other landscapes in that the trend toward forest increase was derailed by development; since 1979, forest cover has declined. The intense suburbanization begun after World War II has continued to destroy forests even though, with Cleveland's industrial decline, the county's population has decreased since 1970. It is unclear how development came to cover an additional 12% of the county's land area since 1979 while the number of housing units increased by only 3% (Manson et al. 2023).

Cuyahoga County, Ohio provides a counterexample to the typical forest transition (Mather 1992). Other landscapes like nearby Wayne County, Ohio never experienced a trend toward forest regrowth, but remained largely agricultural (Whitney and Somerlot 1985). This suggests, rather than a single model of forest transition, at least three possible trajectories for forested landscapes that became agricultural landscapes: they could transition to forest regrowth, as in many parts of Europe and eastern North America with weaker development pressure; transition to suburbia, as here; or remain agricultural. For the eastern USA overall, forest regrowth may have reached a maximum *circa* 1970 (Drummond and Loveland 2010). The decline in forest area in Cuyahoga County since 1979 mirrors a larger picture of forest loss and urban expansion throughout the conterminous USA since 1973 (Drummond and Loveland 2010; Sleeter et al. 2013; Sohl et al. 2014). However, in the eastern USA overall, the dominant mechanism of forest loss was logging (Drummond and Loveland 2010), whereas surrounding Cleveland, timber harvesting was not prevalent, and development was the primary agent of forest destruction.

Further, the increase in forest cover in Cuyahoga County from 12% *circa* 1900 to 21% today masks an ongoing loss of primary forests that were likely never cleared for agriculture. In fact, during the past century, the county lost 44% of the primary forests that remained at the peak of agriculture. Only 6.7% of the landscape remains in primary forests, which harbor approximations of native vegetation, refugia for native biota, and seed sources for recolonization. The remaining two-thirds of the county's forest cover is largely less than 85 years old, has a species composition shaped by its history of agricultural use, and likely remains impoverished in native biodiversity (Flinn and Vellend 2005; Hermy and Verheyen 2007). Primary and post-agricultural forests contain very different ecosystems, as past agricultural use impacts nearly every ecological interaction that has been studied, including tree sensitivity to climate extremes (von Oheimb et al. 2014; Mausolf et al. 2018), deer herbivory (Bartel and Orrock 2023), insect herbivory (Hahn and Orrock 2015), seed-dispersal mutualisms (Buono et al. 2023), seed predation (Bartel and Orrock 2020), salamander abundance (Cosentino and Brubaker 2018), earthworm communities (Szlávecz and Csuzdi 2007), soil microbial communities (Fichtner et al. 2014; Turley et al. 2020; Yavitt et al. 2021), and mycorrhizal colonization (Boeraeve et al. 2018). To preserve the unique and valuable qualities of primary forests, it is urgent that we identify and protect the remaining remnants. As part of this study, we have assembled and made available the historical information necessary to do so. Given that most post-agricultural forests are less than 85 years old, we expect them to remain radically different from primary forests, and we need to understand in detail how they differ to see how best to restore biodiversity in developing post-agricultural forests.

Our estimate of 12% forest cover at the peak of agriculture is consistent with the lower end of the range deduced from agricultural census records (United States Department of Agriculture, National Agricultural Statistics Service 2023). Cuyahoga County's past and present forest cover levels place it on par with parts of Germany (Wulf et al. 2010), Czech Republic (Skaloš et al. 2012), and Hungary (Biró et al. 2022). Despite the dominance of development, this landscape has more primary forest than many places including Flanders (De Keersmaeker et al. 2015), much of Britain (Spencer and Kirby 1992), and the vicinity of Wilmington, DE, part of the eastern megalopolis of the USA (Matlack 1997). Of course, many other parts of eastern North America retained and recovered much more forest (Smith et al. 1993; Hall et al. 2003). Our methods were not able to detect lands cleared by Native Americans or early settlers that developed into mature forests by 1938. This could cause a slight overestimate of the amount of primary forest. On the other hand, we assumed no forests were cleared between 1900 and 1938, a fair assumption given that this was a time of agricultural decline, but this could cause a slight underestimate of the amount of primary forest present at the peak of agriculture. Regardless, the reduction in forest cover was severe. However, the ratio of primary forest to total forest is actually quite high (32%) relative to other landscapes, suggesting strong potential for recovery of restored habitats (Vellend 2003; De Frenne et al. 2011). In fact, few other locations have such a high proportion of primary forest, notwithstanding much higher total forest cover.

The spatial characteristics of current forests suggest a strong influence of fragmentation on ecological processes. Today's forest patches are generally larger and less isolated than the farm woodlots of the agricultural past. This is likely due in part to the aggregation of forests within two major park systems, Cleveland Metroparks and Cuyahoga Valley National Park. However, even the median distance of 119 m to the next forest patch can represent a substantial barrier to dispersal, such as ant dispersal of forest plants (Culver and Beattie 1978). Proximity to a forest edge can also hinder seed dispersal by wind or gravity (Warneke et al. 2022). Roads, which lie a median of 60 m from points in forest, pose additional barriers to the movement of many organisms. Therefore, the development of post-agricultural forests in this landscape is likely to be hampered in part by dispersal limitation (Matlack 1994a). In addition, 75% of points in forest are within 50 m of an edge, a zone where edge effects can alter vegetation (Palik and Murphy 1990; Fraver 1994; Matlack 1994b). The predominance of edge habitat likely promotes regeneration of early-successional and shade-intolerant trees rather than the late-successional, shade-tolerant species characteristic of local native forests (Flinn et al. 2019, 2022, in review). Forest edges are also known to harbor different insect and bird communities than the forest interiors that dominated the pre-clearance landscape, altering processes like predation and herbivory (Barbaro et al. 2012; Guimaraes et al. 2014; Dekeukeleire et al. 2019; Valente and Betts 2019). It would be worth investigating how forest interior habitats differ from edge-affected areas in this landscape to see how fragmentation has impacted species composition and ecological interactions. These spatial characteristics are common to other urban landscapes (Matlack 1997; Fahey and Casali 2017), and they may be responsible for many of the unique challenges facing urban forests.

Gains in forest area took place on former farmland. While clearing for agriculture was the primary cause of deforestation in the nineteenth century, development became the main agent of forest loss from the twentieth century to the present. None of these land use changes occurred in a spatially random fashion. Slope strongly influenced which lands remained and became forest, a common finding in other landscapes (LaGro and DeGloria 1992; Matlack 1997; Thompson et al. 2002; Flinn and Vellend 2005; Abadie et al. 2018; Cervera et al. 2019; Uribe et al. 2020; Monsted and Matlack 2021). This meant that primary forests tend to be located on steeper slopes than post-agricultural forests, and all forests tend to be located on steeper slopes than other land uses. The tendency to leave slopes forested likely contributed to the bias toward *Quercus* forests, as steeper slopes were more likely to be occupied by *Quercus* species in the *circa*-1800 landscape (Flinn et al. in review). The fact that lower elevations were more likely to remain and become forests in our study area likely reflects the tendency to keep forests along the three major river valleys, which lie 30–45 m below the surrounding land. Forested river valleys are another common feature of many landscapes (Matlack 1997; Fahey and Casali 2017; Schweizer and Matlack 2014). This pattern is clearly visible on a map of the county (Fig. 1), and the interpretation is also supported by the fact that points in forest became increasingly close to waterways. Retention of forests in river valleys is likely also responsible for the overrepresentation of *Quercus* forests in today's landscape, as *circa* 1800, river valleys were largely covered by *Quercus* forests (Flinn et al. in review). This pattern suggests that not only *Quercus* forests, but slope-associated and riparian species in general, are likely overrepresented at present, whereas *Fagus* forests and species of the flatter, higher-elevation Allegheny Plateau are scarce. It is perhaps surprising that soil properties had no effect on land use decisions, given their importance in other landscapes (Etter et al. 2005; Flinn and Vellend 2005; Wulf et al. 2010; Abadie et al. 2018). On the other hand, soil fertility is not likely a major factor in locating lawns and development, which drove much of the land use change here.

Conclusions

Most land use turnover occurred on abandoned agricultural land. During the early twentieth century, forests expanded on former farmland; currently, there is essentially no agriculture in the county, and therefore, little possibility of forest expansion in the future. There is also essentially no agricultural land left to develop. Since 1979, a substantial portion of ongoing development has been destroying forests, and this portion is likely to increase. This pattern is consistent throughout the eastern USA, where forested land was the source of 40% or more of new development since 1973 (Drummond and Loveland 2010; Auch et al. 2016). In this landscape as elsewhere, when land transitioned to development, the change was largely irreversible. To preserve forest biodiversity, therefore, conservation efforts should focus on protecting remaining forests from development—especially primary forests, and especially *Fagus*-dominated primary forests. Preserving forest biodiversity is critical because most of the native biota are forest species, as 98.7% of the landscape was forested *circa* 1800 (Flinn et al. 2018). Knowledge of the landscape history and context we present here emphasizes how precious and worthy of study are natural areas like A.B. Williams woods, the county's only old-growth *Fagus-Acer* forest (Williams 1936; Flinn et al. 2019, 2022). A second aim should be learning how to restore native biodiversity to the developing post-agricultural forests that comprise the majority of forest cover.

Acknowledgements This project would not have been possible without help from Mike Henderson of Case Western Reserve University, Chad Harris of Northeast Ohio Areawide Coordinating Agency, Kevin Leeson, Dan Meaney, and Robin Watkins of Cuyahoga County Planning Commission, Chatham Ewing of Cleveland Public Library, Steve Mather of Oberlin College, and James Watling of John Carroll University.

Author contributions Both authors contributed to the study design and analysis. Zachary R. Hughes collected the data and created data visualizations. Kathryn M. Flinn led the writing.

Funding Baldwin Wallace University supported this work.

Data availability The datasets generated and analyzed during this study are available from the corresponding author on reasonable request. We are in the process of making the 1938 and 1979 aerial imagery available in a digital archive.

Declarations

Competing interests The authors declare no competing interests.

References

Abadie J, Dupouey JL, Avon C, Rochel X, Tatoni T, Bergès L (2018) Forest recovery since 1860 in a Mediterranean region: drivers and implications for land use and land cover spatial distribution. Landsc Ecol 33:289–305

Auch RF, Drummond MA, Xian G, Sayler KL, Acevedo W, Taylor JL (2016) Regional differences in upland forest to developed (urban) land cover conversions in the conterminous US, 1973–2011. Forests 7:132

Barbaro L, Brockerhoff EG, Giffard B, van Halder I (2012) Edge and area effects on avian assemblages and insectivory in fragmented native forests. Landsc Ecol 27:1451–1463

Bartel SL, Orrock JL (2020) Past and present disturbances generate spatial variation in seed predation. Ecosphere 11:e03116

Bartel SL, Orrock JL (2023) Land-use history, fire regime, and large-mammal herbivory affect deer-preferred plant diversity in longleaf pine woodlands. For Ecol Manag 541:121023

Bellemare J, Motzkin G, Foster DR (2002) Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. J Biogeogr 29:1401–1420

Biró M, Molnár Z, Öllerer K, Demeter L, Bölöni J (2022) Behind the general pattern of forest loss and gain: A long-term assessment of semi-natural and secondary forest cover change at country level. Landsc Urban Plan 220:104334

Boeraeve M, Honnay O, Mullens N, Vandekerkhove K, De Keersmaeker L, Thomaes A, Jacquemyn H (2018) The impact of spatial isolation and local habitat conditions on colonization of recent forest stands by ectomycorrhizal fungi. For Ecol Manag 429:84–92

Bossuyt B, Hermy M, Deckers J (1999) Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. J Ecol 87:517–527

Brose DS (1994) The South Park site and the late prehistoric Whittlesey Tradition of northeast Ohio. Prehistory Press, Madison, WI

Brose DS (2000) Late prehistoric societies of northeastern Ohio and adjacent portions of the south shore of Lake Erie: a review. In: Genheimer RA (ed) Cultures before contact: The late prehistory of Ohio and surrounding regions. Ohio Archaeological Council, Columbus, OH, pp 96–123

Brunet J, Hedwall PO, Lindgren J, Cousins SAO (2021) Immigration credit of temperate forest herbs in fragmented landscapes—Implications for restoration of habitat connectivity. J Appl Ecol 58:2195–2206

Buono CM, Lofaso J, Smisko W, Gerth C, Santare J, Prior KM (2023) Historical forest disturbance results in variation in functional resilience of seed dispersal mutualisms. Ecology 104:e3978

Cervera T, Pino J, Marull J, Padró R, Tello E (2019) Understanding the long-term dynamics of forest transition: from deforestation to afforestation in a Mediterranean landscape (Catalonia, 1868–2005). Land Use Policy 80:318–331

Cosentino BJ, Brubaker KM (2018) Effects of land use legacies and habitat fragmentation on salamander abundance. Landsc Ecol 33:1573–1584

Culver DC, Beattie AJ (1978) Myrmecochory in *Viola*: dynamics of seed ant interactions in some West Virginia species. J Ecol 66:53–72

Dambrine E, Dupouey JL, Laut L, Humbert L, Thinon M, Beaufils T, Richard H (2007) Present forest biodiversity patterns in France related to former Roman agriculture. Ecology 88:1430–1439

De Frenne P, Baeten L, Graae BJ, Verheyen K (2011) Interregional variation in the floristic recovery of post-agricultural forests. J Ecol 99:600–609

De Keersmaeker L, Onkelinx T, De Vos B, Rogiers N, Vandekerkhove K, Thomaes A, De Schrijver A, Hermy M, Verheyen K (2015) The analysis of spatio-temporal forest changes (1775–2000) in Flanders (northern Belgium) indicates habitat-specific levels of fragmentation and area loss. Landsc Ecol 30:247–259

Dekeukeleire D, Lantman IMV, Hertzog LL (2019) Avian top-down control affects invertebrate herbivory and sapling growth more strongly than overstorey species composition in temperate forest fragments. For Ecol Manag 442:1–9

Drummond MA, Loveland TR (2010) Land-use pressure and a transition to forest-cover loss in the eastern United States. Bioscience 60:286–298

Dupouey JL, Dambrine E, Laffite JD, Moares C (2002) Irreversible impact of past land use on forest soils and biodiversity. Ecology 83:2978–2984

Etter A, McAlpine C, Pullar D, Possingham H (2005) Modeling the age of tropical moist forest fragments in heavily-cleared lowland landscapes of Colombia. For Ecol Manag 208:249–260

Fahey RT, Casali M (2017) Distribution of forest ecosystems over two centuries in a highly urbanized landscape. Landsc Urban Plan 164:13–24

Fichtner A, von Oheimb G, Hardtle W, Wilken C, Gutknecht JLM (2014) Effects of anthropogenic disturbances on soil microbial communities in oak forests persist for more than 100 years. Soil Biol Biochem 70:79–87

Flinn KM, Marks PL (2004) Land-use history and forest herb diversity in Tompkins County, New York, USA. In: Honnay O, Verheyen K, Bossuyt B, Hermy M (eds) Forest biodiversity: Lessons from history for conservation. CABI, Wallingford, UK, pp 81–95

Flinn KM, Vellend M (2005) Recovery of forest plant communities in post-agricultural landscapes. Front Ecol Environ 3:243–250

Flinn KM, Mahany TP, Hausman CE (2018) From forest to city: Plant community change in northeast Ohio from 1800 to 2014. J Veg Sci 29:297–306

Flinn KM, Bly ER, Dickinson CS (2019) Major changes in tree community composition and structure over 86 years in an old-growth forest. J Torrey Bot Soc 146:87–95

Flinn KM, Dolnicek MN, Cox AL (2022) Gap dynamics and disease-causing invasive species drive the development of an old-growth forest over 250 years. For Ecol Manag 508:120045

Flinn KM, Litwinowicz Z, Mahany TP, Watling JI (in review) Presettlement tree distributions and forest types of northeast Ohio, USA mapped with species distribution models

Foster DR (1992) Land-use history (1730–1990) and vegetation dynamics in central New England, USA. J Ecol 80:753–771

Fraver S (1994) Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River basin, North Carolina. Conserv Biol 8:822–832

Grabowski J (ed) (2023) Encyclopedia of Cleveland history. Case Western Reserve University, Cleveland, OH. https://case.edu/ech/. Accessed 30 May 2023

Grman E, Orrock JL, Habeck CW, Ledvina JA, Brudvig LA (2015) Altered beta diversity in post-agricultural woodlands: two hypotheses and the role of scale. Ecography 38:614–621

Guimaraes CDD, Viana JPR, Cornelissen T (2014) A meta-analysis of the effects of fragmentation on herbivorous insects. Environ Entomol 43:537–545

Haddad NM, Brudvig LA, Clobert J, Townshend JR (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1:e1500052

Hahn PG, Orrock JL (2015) Land-use history alters contemporary insect herbivore community composition and decouples plant-herbivore relationships. J Anim Ecol 84:745–754

Hall B, Motzkin G, Foster DR, Syfert M, Burk J (2003) Three hundred years of forest and land-use change in Massachusetts, USA. J Biogeogr 29:1319–1335

Hausman CE (2015) A regional ecosystem monitoring and assessment program for the Lake Erie-Allegheny Plateau region. Cleveland Metroparks Technical Report 2015/NR-5, Parma, OH

Hejcman M, Karlik P, Ondracek J, Klir T (2013) Short-term medieval settlement activities irreversibly changed forest soils and vegetation in central Europe. Ecosystems 16:652–663
Hermy M, Verheyen K (2007) Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. Ecol Res 22:361–371
Honnay O, Verheyen K, Hermy M (2002) Permeability of ancient forest edges for weedy plant species invasion. For Ecol Manag 161:109–122
Jamoneau A, Sonnier G, Chabrerie O, Closset-Kopp D, Saguez R, Gallet-Moron E, Decocq G (2011) Drivers of plant species assemblages in forest patches among contrasted dynamic agricultural landscapes. J Ecol 99:1152–1161
LaGro JA, DeGloria SD (1992) Land use dynamics within an urbanizing non-metropolitan county in New York State (USA). Landsc Ecol 7:275–289
Lira PK, Tambosi LR, Ewers RM, Metzger JP (2012) Land-use and land-cover change in Atlantic Forest landscapes. For Ecol Manag 278:80–89
Manson S, Schroeder J, Van Riper D, Kugler T, Ruggles S (2023) IPUMS National Historical Geographic Information System: Version 17.0. IPUMS, Minneapolis, MN. https://doi.org/10.18128/D050.V17.0
Mather S (1992) The forest transition. Area 24:367–379
Matlack GR (1994a) Plant species migration in a mixed-history forest landscape in eastern North America. Ecology 75:1491–1502
Matlack GR (1994b) Vegetation dynamics of the forest edge—trends in space and successional time. J Ecol 82:113–123
Matlack GR (1997) Land use and forest habitat distribution in the hinterland of a large city. J Biogeogr 24:297–307
Mausolf K, Hardtle W, Jansen K, Delory BM, Hertel D, Leuschner C, Temperton VM, von Oheimb G, Fichtner A (2018) Legacy effects of land-use modulate tree growth responses to climate extremes. Oecologia 187:825–837
Midwestern Regional Climate Center (2017) Midwest Climate Summaries. Midwestern Regional Climate Center, Champaign, IL. http://mrcc.isws.illinois.edu/mw_climate/climateSummaries/climSumm.jsp. Accessed 30 May 2023
Monsted J, Matlack GR (2021) Shaping the second-growth forest: fine scale land use change in the Ohio Valley over 120 years. Landsc Ecol 36:3507–3521
Musgrave DK, Holloran DM (1980) Soil survey of Cuyahoga County, Ohio. United States Department of Agriculture, Soil Conservation Service, Government Printing Office, Washington, DC
Ohio Geographically Referenced Information Program (2023) OSIP Data for Ohio by county. Columbus, OH. http://gis3.oit.ohio.gov/geodatadownload/osip.aspx. Accessed 30 May 2023
Palik BJ, Murphy PG (1990) Disturbance versus edge effects in sugar-maple/beech forest fragments. For Ecol Manag 32:187–202
Peterken GF (1996) Natural woodland: ecology and conservation in northern temperate regions. Cambridge University Press, Cambridge
Peterken GF, Game M (1984) Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. J Ecol 72:155–182
Plue J, Hermy M, Verheyen K, Thuillier P, Saguez R, Decocq G (2008) Persistent changes in forest vegetation and seed bank 1,600 years after human occupation. Landsc Ecol 23:673–688
Rackham O (1980) Ancient woodland: its history, vegetation and uses in England. Edward Arnold, London
Sanderson EW, Brown M (2007) Manhattan: an ecological first look at the Manhattan landscape prior to Henry Hudson. Northeast Nat 14:545–570
Schweizer PE, Matlack GR (2014) Factors driving land use change and forest distribution on the coastal plain of Mississippi, USA. Landsc Urban Plan 121:55–64
Skaloš J, Engstová B, Trpáková I, Šantrůčková M, Podrázský V (2012) Long-term changes in forest cover 1780–2007 in central Bohemia, Czech Republic. Eur J Forest Res 131:871–884
Sleeter BM, Sohl TL, Loveland TR, Auch RF, Acevedo W, Drummond MA, Sayler KL, Stehman SV (2013) Land-cover change in the conterminous United States from 1973 to 2000. Glob Environ Chang 23:733–748
Smith BE, Marks PL, Gardescu S (1993) Two hundred years of forest cover changes in Tompkins County, New York. Bull Torrey Bot Club 120:229–247
Sohl TL, Sayler KL, Bouchard MA, Van Hofwegen T (2014) Spatially explicit modeling of 1992–2100 land cover and forest stand age for the conterminous United States. Ecol Appl 24:1015–1036
Spencer JW, Kirby KJ (1992) An inventory of ancient woodland for England and Wales. Biol Cons 62:77–93
Szlávecz K, Csuzdi C (2007) Land use change affects earthworm communities in Eastern Maryland, USA. Eur J Soil Biol 43:S79–S85
Thompson J, Brokaw N, Zimmerman JK, Waide RB, Everham EM III, Lodge DJ, Taylor CM, García-Montiel D, Fluet M (2002) Land use history, environment, and tree composition in a tropical forest. Ecol Appl 12:1344–1363
Tulowiecki ST, Larsen CPS (2015) Native American impact on past forest composition inferred from species distribution models, Chautauqua County, New York. Ecol Monogr 85:557–581
Turley NE, Bell-Dereske L, Evans SE, Brudvig LA (2020) Agricultural land-use history and restoration impact soil microbial biodiversity. J Appl Ecol 57:852–863
United States Census Bureau (2023). Quick facts. Washington, DC. https://census.gov. Accessed 30 May 2023
United States Department of Agriculture, National Agricultural Statistics Service (2023) Census of Agriculture. https://www.nass.usda.gov/AgCensus/. Accessed 30 May 2023
United States Department of Agriculture, Natural Resources Conservation Service (2023). Web Soil Survey. https://websoilsurvey.nrcs.usda.gov/. Accessed 30 May 2023
Uribe SV, Estades CF, Radeloff VC (2020) Pine plantations and five decades of land use change in central Chile. PLoS ONE 15:e0230193
Uroy L, Ernoult A, Alignier A, Mony C (2023) Unveiling the ghosts of landscapes past: Changes in landscape connectivity over the last decades are still shaping current woodland plant assemblages. J Ecol 111:1063–1078
Valente JJ, Betts MG (2019) Response to fragmentation by avian communities is mediated by species traits. Divers Distrib 25:48–60
Vellend M (2003) Habitat loss inhibits recovery of plant diversity as forests regrow. Ecology 84:1158–1164
Vellend M, Verheyen K, Jacquemyn H, Kolb A, van Calster H, Peterken G, Hermy M (2006) Extinction debt of forest plants persists for more than a century following habitat fragmentation. Ecology 87:542–548
Vellend M, Verheyen K, Flinn KM, Jacquemyn H, Kolb A, Van Calster H, Peterken G, Graae BJ, Bellemare J, Honnay O, Brunet J, Wulf M, Gerhardt F, Hermy M (2007) Homogenization of forest plant communities and weakening of species–environment relationships via agricultural land use. J Ecol 95:565–573
Verheyen K, Bossuyt B, Hermy M, Tack G (1999) The land use history (1278–1990) of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. J Biogeogr 26:1115–1128
von Oheimb G, Hardtle W, Eckstein D, Engelke HH, Hehnke T, Wagner B, Fichtner A (2014) Does forest continuity enhance the resilience of trees to environmental change? PLoS ONE 9:e113507
Wang YC, Larsen CPS, Kronenfeld BJ (2010) Effects of clearance and fragmentation on forest compositional change and recovery after 200 years in western New York. Plant Ecol 208:245–258
Warneke CR, Caughlin TT, Damschen EI, Haddad NM, Levey DJ, Brudvig LA (2022) Habitat fragmentation alters the distance of

abiotic seed dispersal through edge effects and direction of dispersal. Ecology 103:1–8
Weaver MM (1964) History of tile drainage in America prior to 1900. MM Weaver, Waterloo, NY. https://historicgeneva.org/products/history-of-tile-drainage-in-america-by-marion-m-weaver/
Whitney GG (1994) From coastal wilderness to fruited plain. Cambridge University Press, Cambridge
Whitney GG, Somerlot WJ (1985) A case study of woodland continuity and change in the American Midwest. Biol Cons 31:265–287
Williams AB (1936) The composition and dynamics of a beech-maple climax community. Ecol Monogr 6:317–408
Williams M (1989) Americans and their forests: a historical geography. Cambridge University Press, Cambridge
Wulf M, Sommer M, Schmidt R (2010) Forest cover changes in the Prignitz region (NE Germany) between 1790 and 1960 in relation to soils and other driving forces. Landsc Ecol 25:299–313
Yates ED, Levia DF, Williams CL (2004) Recruitment of three non-native invasive plants into a fragmented forest in southern Illinois. For Ecol Manag 190:119–130
Yavitt JB, Pipes GT, Olmos EC, Zhang JB, Shapleigh JP (2021) Soil organic matter, soil structure, and bacterial community structure in a post-agricultural landscape. Front Earth Sci 9:590103