

Changes in trees, groundlayer diversity, and deer-preferred plants across 18 years in oak (*Quercus*, Fagaceae) forests of northwestern Ohio^{1,2}

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Abstract. The persistence of *Quercus* forest ecosystems in eastern North America is uncertain with replacement of *Quercus* spp. by other trees, invasion by nonnative plants, and alteration of native ground layers through deer herbivory and other factors. In northwestern Ohio, we examined changes in tree strata and ground layers (herbs, shrubs, and tree seedlings) at eight *Quercus* forest sites measured in 2002, 2015, 2018, and 2019. Mortality averaged 2.0% per year for small (1–40 cm in diameter at 1.4 m) and 0.7% per year for large (≥ 40 cm in diameter) *Quercus* trees. Assuming continued lack of recruitment and linear continuation of mortality rates, live *Quercus* trees would be absent on these sites by the year 2042 in the small size class and by 2165 in the large size class. Despite their density declining by half between 2002 and 2019, *Acer rubrum*, *Sassafras albidum*, and *Prunus serotina* remained the most abundant tree species in the understory (stems 1–10 cm in diameter). Contrasting with many studies, nonnative plants remained nearly absent, never exceeding 0.2% cover (compared with 27–48% average cover of native ground layer plants among years). A major change in the ground layer was a nine-fold increase in cover of deer-preferred, native forbs between 2015 and 2019. This increase coincided with deer management after 2015 and three consecutive wet early summers from 2017–2019. Based on the long-term dataset, we discuss five scenarios of future ecosystems under different potential conservation strategies, ranging from managing for forests with canopy gaps encouraging *Quercus* regeneration, to facilitating transitions to non-*Quercus* forests. Although lack of *Quercus* recruitment highlighted uncertainty in persistence of *Quercus* trees, trends in ground layer communities suggested sustained dominance by native plants.

Key words: diversity, ground flora, nonnative species, Oak Openings region, regeneration, tree mortality rate, understory

Quercus forests in eastern North America are trending toward replacement by other tree species and are experiencing other changes in biophysical factors, such as nonnative plant invasions, herbivory, and shifting climatic patterns. If continued, *Quercus* replacement by other species and alterations to understory layers are likely to influence habitat values across vast areas (Chapman and McEwan 2016, Augspurger and Buck 2017, Palus

et al. 2018). In 2017, *Quercus* forest constituted a third (57 million ha) of eastern USA forest area and was the most widespread forest type (Oswalt *et al.* 2019). Exemplifying their special habitat values, *Quercus* trees support unique assemblages of invertebrate species via the trees' rough bark, abundant foliage, and branching structure, features not necessarily provided by trees that could replace *Quercus* (Rodewald and Abrams 1992). Moreover, at least 100 species of birds and mammals consume acorns in eastern North America (Brose *et al.* 2014).

Eastern *Quercus* forests are thought to have been maintained historically by fires (often human-ignited) interacting with dry soils and other disturbances including droughts, windstorms, and cutting (McEwan *et al.* 2011). These are all factors that perpetuate *Quercus* given its traits such as resprouting, thick bark conferring fire resistance, and drought tolerance (Abrams 1996). In closed-canopy forests without disturbances that produce multi-tree canopy openings, *Quercus* recruitment

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is poor (Lorimer 1993, Lowney *et al.* 2016, Abella *et al.* 2018). As a result, current forests with *Quercus* overstories have generally been transitioning toward increasing canopy importance of other species already dominating understories, such as *Acer rubrum* L., on nearly all but the driest sites (Reid *et al.* 2008, Palus *et al.* 2018). Although a trend for *Quercus* replacement has been widespread, variability in specific changes in tree and understory layers is not as well understood. For example, if *Quercus* recruitment continues to be poor, *Quercus* tree mortality rates determine how long *Quercus* forests will persist and frame temporal windows in which to potentially implement *Quercus* conservation actions. Anticipating *Quercus* mortality rates is difficult, however, as they have ranged 10-fold from < 1% to nearly 10% per year across the eastern USA (*e.g.*, Pedersen and McCune 2002, Lowney *et al.* 2016).

In addition to replacement of *Quercus* by other trees, *Quercus* forest ground layers (herbaceous and low woody plants) could be altered by intensive herbivory by densely populated deer (*Odocoileus virginianus*), nonnative plant invasions, and other factors in ways still being understood. Dense populations of deer have often reduced preferred food plants while increasing unpalatable ones, but plant community recovery after lowered deer populations has been variable, if present (Asnani *et al.* 2006, Jenkins *et al.* 2014, Webster *et al.* 2017). Some studies in *Quercus* forests have found that nonnative plants are increasing (*e.g.*, Rogers *et al.* 2008, Katz *et al.* 2010, Augspurger and Buck 2017), while others have not (Jenkins *et al.* 2014). Deer herbivory, nonnative plant invasions, and lack of fire corresponded with impoverished native species and community diversity in some *Quercus* forests (Rogers *et al.* 2008).

The objective of our study was to determine changes in tree strata and ground layers in *Quercus* forests across 18 years between 2002 and 2019 in the Midwestern USA. Questions we examined included: (a) Did tree diameter distributions change through time, indicative of shifts in density of small or large trees among species groups (*Quercus* and non-*Quercus* species)? (b) What were mortality rates of small and large *Quercus* trees? (c) Did ground layer cover, species richness, and species composition change through time? (d) Did nonnative plants increase and native diversity

decrease? (e) Did cover of deer-preferred plants and browse on *Quercus* regeneration vary through time? To address these questions, we established long-term permanent plots augmented with recent inventories of deer populations and browse severity.

Materials and Methods. **STUDY AREA.** We performed the study within the 340-km² Oak Openings region lying north and west of the Maumee River, west of the city of Toledo in northwestern Ohio. During 1817–1832 historical land surveys, this sandy region contained 72% *Quercus* savanna-woodland, 27% wet prairie, and 1% floodplain forest (Brewer and Vankat 2004). Like most *Quercus* savanna areas in the Midwest, the region's open ecosystems were thought to have been maintained in part by frequent fires, with closed-canopy forest forming within decades without fire (Brewer and Vankat 2004). Our specific study area was the 1,692-ha Oak Openings Preserve, managed by Metroparks Toledo, in the south-central part of the region. Climate, recorded 8 km from the preserve at the Toledo Express Airport from 1955 through 2019, averaged 85 cm/year of precipitation (34 cm of which occurred from May through August; Fig. S1) and daily minimum/maximum temperatures of –9/0 °C in January and 16/29 °C in July (Midwestern Regional Climate Center, Champaign, IL).

As long-term study sites, we randomly selected eight of about 20 polygons of upland mature *Quercus* forest displayed in a digitized 1939 aerial photo of the preserve. These sites were on sandy soil classified as Udipsamments. Overstories consisted of two *Quercus* species (*Q. velutina* Lam. and *Q. alba* L.). Stand basal area ranged from 56–92% *Quercus* in 2002 when we began the study (Table 1, Fig. 1). Based on cross-dated increment cores, dominant *Quercus* trees were 100–200 years old in 2019. The sites are thought to have been mostly unmanaged (limited tree cutting, fire, or livestock grazing) since at least the 1930s–1950s when they started to be acquired for the preserve. One site was partly burned by low-severity fire in 2014, but as species composition changed little, we retained it in the dataset. The sites were 2–5 ha in size and primarily surrounded by other forests, mainly deciduous forested wetlands.

DATA COLLECTION FOR LONG-TERM PLOTS. We established a 20 m × 25 m (0.05 ha) permanent plot in the center of each site. We measured

Table 1. Characteristics of *Quercus* forest sites studied across an 18-year period in the Oak Openings region, northwestern Ohio.

Site	Basal area, m ² /ha (% <i>Quercus</i> / <i>Acer</i> /other) ¹				Soil series	Texture ²	pH ²	C (%) ²	Top four dominant herbaceous and shrub species ³
	2002	2015	2018	2019					
1	44 (56/43/1)	32 (23/75/2)	33 (24/74/2)	34 (23/75/2)	Ottokee	LS	4.4	4.7	<i>Carex pensylvanica</i> , <i>Gaylussacia baccata</i> , <i>Vaccinium angustifolium</i> , <i>Smilax rotundifolia</i>
2	55 (76/16/8)	67 (62/25/13)	54 (79/17/4)	54 (78/19/3)	Oakville	LS	4.6	1.8	<i>Aralia nudicaulis</i> , <i>Carex pensylvanica</i> , <i>Vaccinium pallidum</i> , <i>Maianthemum racemosum</i>
3	43 (66/32/2)	53 (70/28/2)	56 (68/30/2)	57 (67/31/2)	Oakville	LS	4.3	2.2	<i>Carex pensylvanica</i> , <i>Vaccinium angustifolium</i> , <i>Vaccinium pallidum</i> , <i>Uvularia sessilifolia</i>
4	22 (70/2/28)	28 (77/4/19)	29 (77/4/19)	29 (75/5/20)	Ottokee	LS	4.6	2.0	<i>Carex pensylvanica</i> , <i>Pteridium aquilinum</i> , <i>Vaccinium pallidum</i> , <i>Eurybia macrophylla</i>
5	33 (92/5/3)	31 (87/10/3)	30 (80/16/4)	30 (79/18/3)	Ottokee	S	4.4	4.0	<i>Carex pensylvanica</i> , <i>Gaylussacia baccata</i> , <i>Vaccinium angustifolium</i> , <i>Rubus hispidus</i>
6	32 (87/13/0)	49 (85/15/0)	51 (85/15/0)	51 (84/16/0)	Ottokee	LS	4.5	4.5	<i>Gaylussacia baccata</i> , <i>Carex pensylvanica</i> , <i>Vaccinium pallidum</i> , <i>Hamamelis virginiana</i>
7	28 (78/2/20)	30 (80/4/16)	32 (80/4/16)	32 (81/5/14)	Oakville	S	4.9	1.9	<i>Hamamelis virginiana</i> , <i>Carex pensylvanica</i> , <i>Aralia nudicaulis</i> , <i>Desmodium nudiflorum</i>
8	46 (91/8/1)	54 (89/10/1)	56 (90/10/0)	57 (90/10/0)	Ottokee	LS	4.6	1.6	<i>Hamamelis virginiana</i> , <i>Carex pensylvanica</i> , <i>Smilax rotundifolia</i> , <i>Desmodium nudiflorum</i>

¹ *Quercus* includes *Q. alba* and *Q. velutina*. *Acer* is *A. rubrum*. Other includes mostly *Sassafras albidum* and *Prunus serotina*, with some *Cornus florida*, *Crataegus* spp., *Nyssa sylvatica*, and *Robinia pseudoacacia*.

² Soil properties are for 0–15 cm mineral soil, analyzed from a composite sample (four 207-cm³ cores, one from each corner of a 20 m × 25 m plot at each site) collected at each site in August 2017 (texture via the hydrometer method with LS = loamy sand and S = sandy; pH as 1:1 soil:H₂O; and C as organic C by weight using dry combustion in a C analyzer).

³ Ranked by 2019 cover from the first to the fourth most cover.



FIG. 1. Repeat photos for three of the eight study sites in *Quercus* forests, northwestern Ohio. Overstories were dominated by *Q. velutina* and *Q. alba*. Understory trees were mostly *Acer rubrum*. Ground layer vegetation was primarily *Carex pensylvanica*, tree seedlings, shrubs such as *Vaccinium pallidum*, and forbs such as *Desmodium nudiflorum*. Photos correspond with Sites 1 (left column), 3 (middle column), and 8 (right column) of Table 1. Photos by S. R. Abella.

vegetation in plots in summer between June–August once each year in 2002, 2015, 2018, and 2019. On each plot each year, we recorded the diameter at 1.4 m for each tree (defined as ≥ 1 cm in diameter at 1.4 m) for all tree species and tracked *Quercus* trees individually. We categorized aerial cover of each ground layer species (vascular herbs, shrubs, and trees < 1 cm in diameter at 1.4 m) in each 0.05-ha plot using cover classes (0.1, 0.25, 0.5, and 1%; 1% intervals from 1–10%; and 5% intervals above 10% cover). The same investigator (SRA) participated in cover categorizations each year to facilitate consistency. Double sampling to compare consistency of cover categorizations by different members of the research team were within one cover class. Nomenclature and classification of potential longevity (e.g., annual, perennial), growth form (e.g., forb), and nativity of species to the United States followed Natural Resources Conservation Service (2019). Woody

species that can be vines but that usually grew as low shrubs (e.g., *Toxicodendron radicans* (L.) Kuntze) were classified as shrubs. Species lists and growth forms for the tree and ground layers are in Table S1 and S2.

DATA ANALYSIS FOR LONG-TERM PLOTS. We performed univariate analyses in PAST 3.26 (Hammer 2019) and multivariate analyses in PC-ORD 7.07 (McCune and Mefford 1999). Data for tree and ground layer parametric analyses met assumptions of equal variance (Levene's test) and normality (Shapiro-Wilk W test), except cover of deer-preferred plants, which we analyzed on a Box-Cox transformed scale.

We conducted three analyses to assess change in tree basal area, size class distribution, and *Quercus* demographic data. To assess temporal variation in mean basal area of *Quercus*, *Acer rubrum*, and other species combined (primarily *Sassafras albidum* (Nutt.) Nees and *Prunus serotina* Ehrh., with

additional minor species in Table 1), we performed repeated measures analysis of variance (ANOVA). When the ANOVA P -value was < 0.05 , means were compared with Tukey tests. Using Epps-Singleton tests, we tested for equality of diameter distributions between 2002 and 2019 separately for *Quercus*, *Acer rubrum*, and other species. For *Quercus* tracked individually, we divided diameter classes into similarly sized small (1–40 cm in diameter) and large (≥ 40 cm) classes and tested whether the proportion of trees that died between 2002 and 2019 differed between the classes using a Fisher's exact test. We further calculated mortality rates (trees/ha/yr) in the two size classes. As no *Quercus* recruitment of stems ≥ 1 cm in diameter occurred during the study, we calculated projected years to depletion of *Quercus* trees from observed mortality rates in each size class.

We performed a set of univariate (nonparametric and parametric) and multivariate (similarity and ordination) analyses for assessing change in the ground layer. To accommodate the count data, we analyzed median native and nonnative richness (species/0.05 ha) across years using Friedman tests, and for $P < 0.05$, Wilcoxon tests to separate medians. We analyzed change in ground layer mean cover, Shannon's Diversity Index (calculated using cover), floristic quality, and cover of nine deer-preferred species (identified from literature; Williams *et al.* 2000, Augustine and deCalesta 2003, Kirschbaum and Anacker 2005, Webster *et al.* 2017) using repeated measures ANOVA with Tukey tests. We did not subdivide plant cover into native and nonnative for analysis because nonnative cover was negligible ($< 0.2\%$). Floristic quality is a dimensionless index, which we computed omitting nonnative species following Andreas *et al.* (2004). Higher values indicate sites with species typifying high-quality natural habitats, while lower values indicate sites with widespread, ruderal species. To portray multivariate change in ground layer species composition and community heterogeneity, we calculated pairwise Sørensen dissimilarities among plots each year and between years for each plot using relative cover (cover of species, / \sum cover of all species on a plot). We ordinated species composition (relative cover) using nonmetric multidimensional scaling (Sørensen distance, 250 real and randomized runs with default settings in PC-ORD 7.07; McCune and Mefford 1999).

DEER POPULATION INVENTORY, MANAGEMENT, AND BROWSE SURVEY. We inventoried the deer popula-

tion within a 25 km² area encompassing the preserve surrounded by a 500 m buffer. We counted deer using a helicopter survey protocol (Stoll *et al.* 1991) by systematically flying transects in winter (December or January) with at least 8 cm of snow on the ground. Deer management commenced in 2016 by culling 184 deer ($\sim 7/\text{km}^2$), 48% of the 2015 population. Culling of 179, 77, and 97 individuals continued in 2017, 2018, and 2019. Deer culled in the winter months immediately following the helicopter surveys were subtracted from yearly population estimates. We designated the years of population estimates as the calendar year of the spring immediately following the winter population inventory and culling. Accordingly, we had deer population estimates for 2014, 2015, 2017, and 2019 (no inventories were completed for 2016 and 2018 due to inadequate snow cover or windy or poor-visibility weather).

Annually from 2015 through 2019 in March–April before leaf out, we measured deer browse on *Quercus* regeneration (seedlings and sprouts 4–139 cm tall) along transects in *Quercus* forests throughout the preserve following Benner (2007). Circular quadrats (each 7 m²) were systematically inventoried every 60 m along transects, with 223–313 quadrats inventoried annually depending on presence of *Quercus* stems and avoidance of areas where prescribed burns had occurred in the past year. In each quadrat with *Quercus* regeneration, we classified browse severity into five classes ranging from no to severe browse, specifically for deer browse distinguished from browse by other animals (Benner 2007).

Results. TREES. Between 2002 and 2019, main changes in the tree layer included decreasing (by 50% or more) density of stems across species in the 1–10 cm diameter class and increasing *Acer rubrum* basal area. *Quercus* and *A. rubrum* diameter distributions shifted toward larger trees (Epps-Singleton tests $P < 0.05$; Fig. 2). *Acer rubrum* basal area increased from 6.5 m²/ha in 2002 to 9.0–9.4 m²/ha since 2015 (repeated measures ANOVA $F_{3,21} = 5.7$, $P < 0.01$; Fig. S2). Meanwhile, mean basal area did not change significantly in total for all species ($F_{3,21} = 1.8$, $P = 0.18$), for *Quercus* ($F_{3,21} = 0.6$, $P = 0.65$), or for other species ($F_{3,21} = 1.0$, $P = 0.43$).

Tracking of individual *Quercus* trees indicated that proportionally more small (< 40 cm in

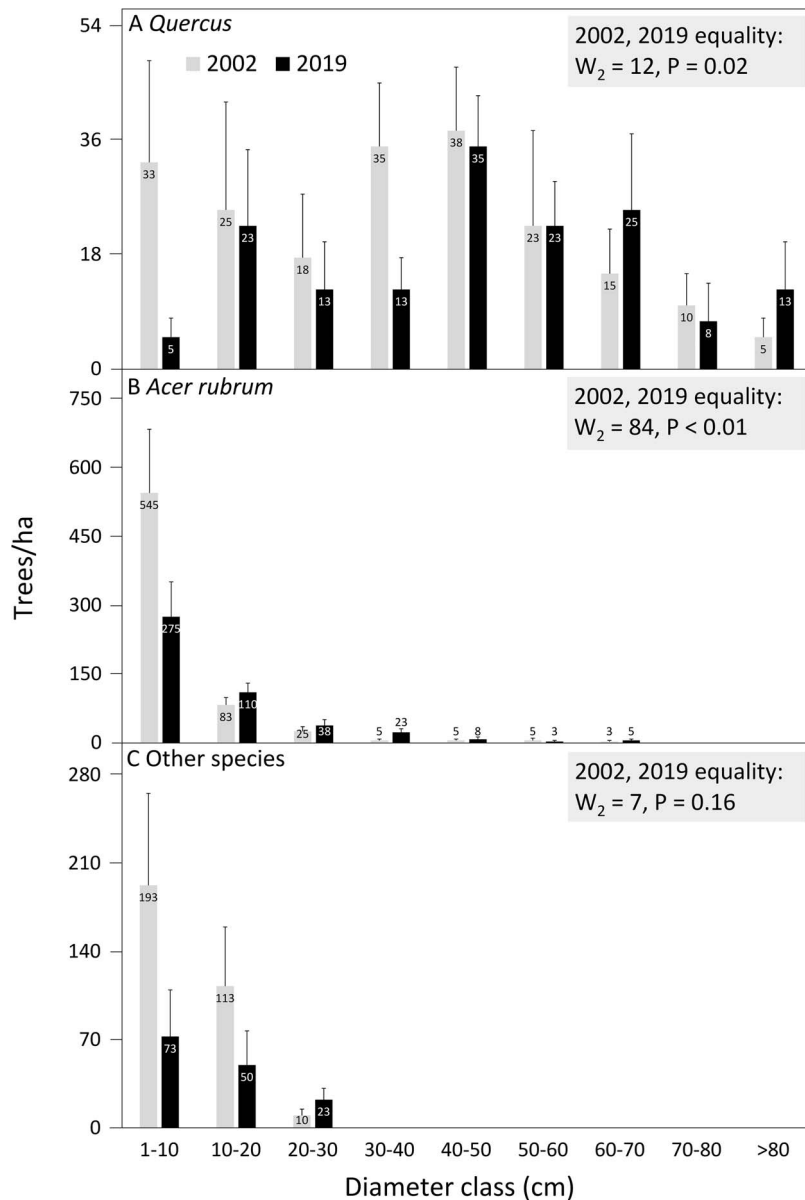


FIG. 2. Diameter distributions in *Quercus* forests, northwestern Ohio, for the first (2002) and last (2019) study years for (A) *Q. velutina* and *Q. alba*, (B) *Acer rubrum*, and (C) other tree species (primarily *Sassafras albidum* and *Prunus serotina*). Bars represent means, which are listed at the top of bars. Error bars are one standard error of means. Gray inset boxes display Epps-Singleton tests for equality of 2002 and 2019 diameter distributions (two-tailed tests).

diameter) than large (≥ 40 cm) trees died between 2002 and 2019 (Fisher's exact test $P < 0.01$; Table 2). No *Quercus* recruitment into the small size class occurred during the 18 years. From a 2019 benchmark of live tree density in each size class and assuming continuation of the average annual mortality rate and absence of

recruitment, the time to no live *Quercus* trees remaining on plots was projected to be 23 years for the small and 146 years for the large size class.

GROUND LAYER. Ground layer vegetation changed only subtly at the community level, with

Table 2 Demography of *Quercus* trees (combined for *Q. alba* and *Q. velutina*) between 2002 and 2019 compiled from eight study sites in the Oak Openings region, northwestern Ohio.

	<i>Quercus</i> 1–40 cm ¹	<i>Quercus</i> ≥ 40 cm ¹
Initial no. of live trees in 2002	44 (110) ²	36 (90)
No. of live trees in 2019	20 (50)	39 (98)
No. of dead trees in 2019	16 (40)	5 (12)
No. of new trees recruiting into size class between 2002 and 2019	0 (0)	8 (20)
Mortality rate (trees/ha/yr)	2.22	0.67
Mortality rate (% of initial trees/ha/yr)	2.02	0.74
Calendar year when trees depleted ³	2042	2165

¹ Diameter class based on stem diameter at a height of 1.4 m.

² Trees/ha are in parentheses.

³ From a 2019 baseline and assuming continued zero recruitment into the 1–40 cm diameter class and no further recruitment into the ≥ 40 cm diameter class. New recruitment of *Quercus* trees ≥ 1 cm in diameter was absent throughout the study between 2002 and 2019.

most of the change driven by a subset of nine deer-preferred forb species. Every plot but one retained community composition at least 50% similar among years and ordination displayed minimal separation of plots by year (Fig. 3). The optimal three-axis ordination had a final stress of 0.106 (on a 0–1 scale) and represented 87% of the variance in the distance matrix. Nonnative species richness stayed low (< 1.9 species/0.05 ha) and varied little throughout the study (across-year Friedman test $\chi^2 = 0.7$, $P = 0.86$; Fig. 4). Nonnative cover was nearly absent, averaging only 0.1–0.2% among

years (Table S2). Native species richness (across-year Friedman test $\chi^2 = 8.4$, $P = 0.03$) and floristic quality (repeated measures ANOVA $F_{3,21} = 5.6$, $P < 0.01$) were lowest in 2015 but displayed no significant net change between 2002 and 2019 (Fig. 4).

There was minimal evidence for loss of species or community diversity. Species diversity was highest in 2002, and did not change across the last three study years (Fig. 4). However, the total number of species detected (which were 92–94% native across years) for all plots increased by 20%

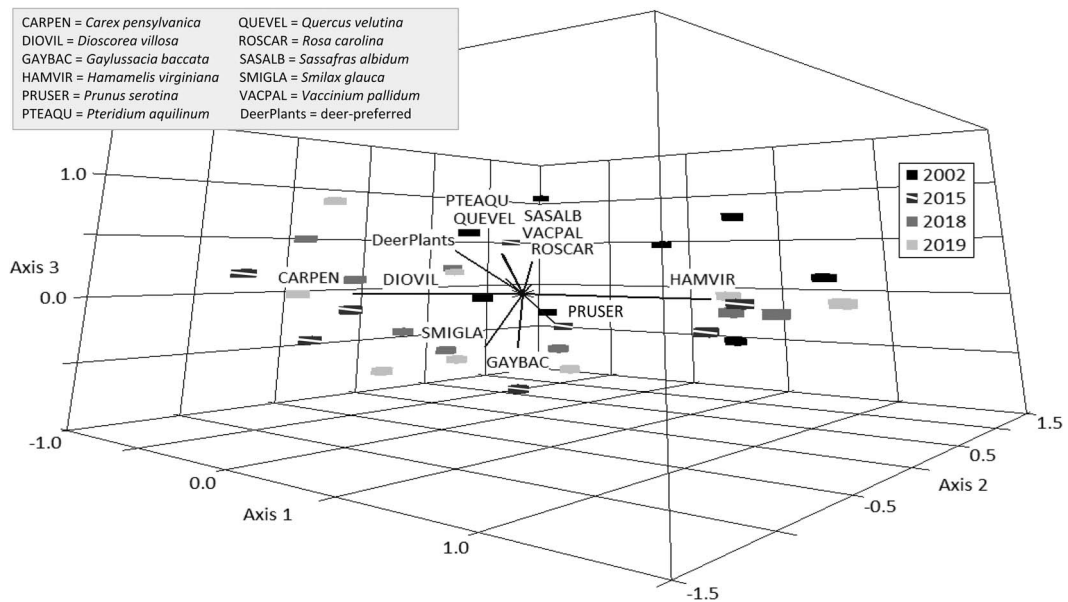


FIG. 3. Ground layer species composition (relative cover) displayed using ordination (nonmetric multidimensional scaling) in *Quercus* forests, northwestern Ohio. Ordination axes represented 41% (Axis 1), 31% (Axis 2), and 15% (Axis 3) of the variance in the distance matrix. Vectors display species correlated ($|r| \geq 0.25$) with community patterns (deer-preferred plants include nine species listed in Fig. 5).

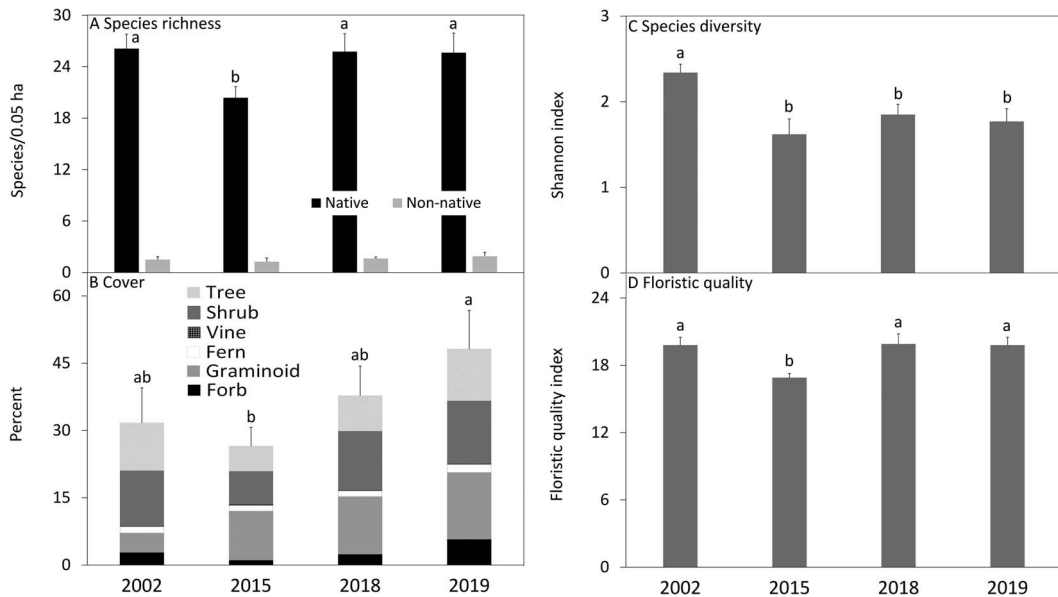


FIG. 4. Change in ground layer metrics in *Quercus* forests, northwestern Ohio. Bars represent means and error bars are one standard error of means. Letters note differences ($P < 0.05$) for median (A) native species richness (Friedman tests and Wilcoxon tests for median separation; no letters for nonnative richness because it did not differ among years), and mean (B) total cover, (C) Shannon diversity, and (D) floristic quality using repeated measures analysis of variance with Tukey mean separation. Medians in (A) for native/nonnative species richness were 26/1.5 (2002), 21/1.0 (2015), 26/2.0 (2018), and 27/1.5 (2019).

from 66 in 2002 to 80 (2018) and 79 (2019). Species composition among plots also diversified (58% average among-plot Sørensen dissimilarity in 2002 increasing to 63% in 2019).

The main change in the ground layer was increasing cover after 2015 driven primarily by forbs, specifically deer-preferred forbs. Between 2015 and 2019, total forb cover increased by 5.2 ×,

compared with the next highest increases of 1.9–2.0 × for tree seedlings and shrubs (Fig. 4). For deer-preferred forbs, mean cover ranged from 0.6% (2015) to 5.2% (2019) to vary significantly among years (repeated measures ANOVA $F_{3,21} = 5.3$, $P < 0.01$; Fig. 5). Deer-preferred forbs increased 9.4 × relative to all forbs between 2015 and 2019.

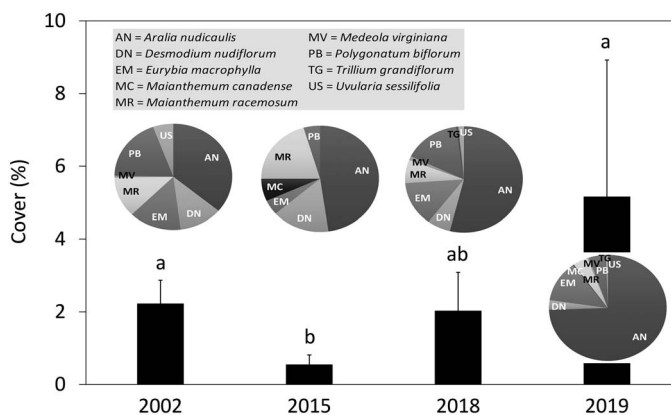


FIG. 5. Change in mean total cover of nine deer-preferred forb species in *Quercus* forests, northwestern Ohio. Error bars are one standard error of means. Means without shared letters differ at $P < 0.05$ (Tukey mean separation). Pie charts show the relative cover contributions of species for each year.

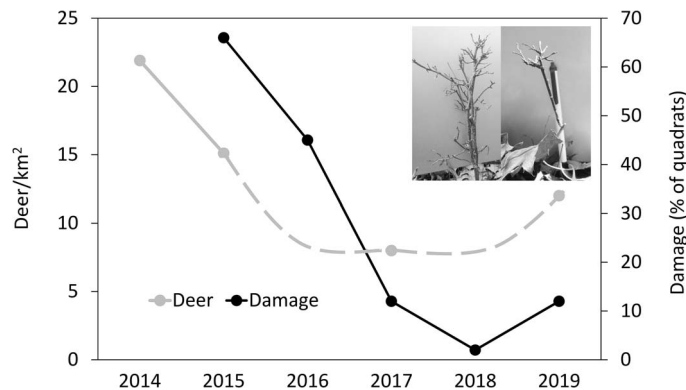


FIG. 6. Deer population size and browse damage on *Quercus* regeneration (seedlings and sprouts 4–139 cm tall) in *Quercus* forests, northwestern Ohio. Deer populations were inventoried in each year marked with a gray circle and were extrapolated (shown as dashed line segments) for 2016 and 2018 (years without helicopter surveys) using estimates from a general infrared survey. The browse measure is the percentage of quadrats with heavy to severe browse on *Quercus* regeneration. Left inset photo: Heavily browsed *Quercus* with browsed tips of twigs. Right inset photo: Severely browsed *Quercus* with small twigs nearly fully removed and tips of large twigs mostly removed.

RECENT DEER POPULATION SIZE AND BROWSE SEVERITY. Between 2014 and 2019, deer populations and browse on *Quercus* regeneration varied sharply (Fig. 6). Density of deer ranged from 15–22 individuals/km² before deer management and from 8–12 individuals/km² after management began. Heavy to severe browse on *Quercus* regeneration occurred on 66% of quadrats in 2015 before deer management but on only 2–12% of quadrats in 2017–2019 during management.

Discussion. OAK PERSISTENCE. The mortality rate of 0.7% per year for large *Quercus* trees (≥ 40 cm in diameter) was at the low end for eastern *Quercus* forests. Annual mortality rates for mature *Quercus* trees were 0.6% at seven sites in the Midwest (Pedersen and McCune 2002), 0.9–1.2% in Mammoth Cave National Park in Kentucky (McCune and Henckel 1993), 1% in the southern Appalachians in North Carolina (Greenberg *et al.* 2011), and 2–9% in old-growth forests in Indiana (Lowney *et al.* 2016). Some mortality was attributable to windthrow in each study (*e.g.*, 3–28% of mortality in McCune and Henckel 1993), but most mortality was from causes hard to pinpoint. Greenberg *et al.* (2011), for example, surmised that much mortality resulted from interacting decline factors including drought, fungal infection, and competition from less fire-tolerant species in fire-free forests. While pinpointing cause of tree death was beyond our

study's scope, we suspect that wind and European gypsy moths (*Lymantria dispar dispar*) contributed to some mortality.

Our projections beyond 2019 of time to no live *Quercus* trees remaining assumed no new recruitment, no further movement of trees from the small to the large size class, and continued average mortality rates. No *Quercus* recruitment was observed during the 18-year study and future recruitment likely requires large canopy gaps (Chapman and McEwan 2016). The assumption of no further movement of trees into the large size class seems likely to be largely supported given the mortality rate observed for small trees ($3 \times$ greater than for large trees) and that many were suppressed subcanopy individuals. Both *Quercus* species can respond to growth release events at old ages of 200+ years after some suppression periods (Abrams and Downs 1990). However, release events may need to occur soon at our sites before small *Quercus* trees are already dead. Without recruitment, persistence of *Quercus* hinges on longevity of extant trees. Maximum life spans are typically 300+ years for *Q. alba* and 200+ years for *Q. velutina* (Abrams and Downs 1990). If age-related decline or pests (*e.g.*, oak wilt [*Ceratocystis fagacearum*]) accelerate mortality, large *Quercus* could be lost faster than we projected.

UNDERSTORY TREE DYNAMICS. The decline in tree density in the 1–10 cm diameter class in total across species was mostly from mortality (and lack

of recruitment), rather than from advancement of the trees into larger size classes, and could represent attrition of suppressed stems associated with forest maturation. The three most abundant understory species (*Prunus serotina*, *Sassafras albidum*, and *Acer rubrum*) have moderate shade tolerance accompanied by gap-colonizing ability. *Prunus serotina* and *A. rubrum* can survive when suppressed below overstories for at least 60 years, at which point they can still respond to release if canopy gaps form (Auclair and Cottam 1971, Hart *et al.* 2012). *Sassafras albidum* can also persist in shaded understories for indeterminate periods (Reid *et al.* 2008). However, mortality of suppressed individuals is often heavy in the three species. For example, after *P. serotina* seedlings and sprouts were suppressed for 10–15 years, growth decelerated rapidly and mortality rate rose (Auclair and Cottam 1971).

GROUND LAYER CHANGES AND DIVERSITY. Some changes in eastern *Quercus* forests observed in other multi-decade studies were not apparent in our study. Nonnative plants, sharply increasing in recent decades in some *Quercus* forests (*e.g.*, Rogers *et al.* 2008, Katz *et al.* 2010, Mattingly *et al.* 2016, Augspurger and Buck 2017), remained nearly absent throughout our study. It is difficult to pinpoint why nonnative plants remained so sparse, particularly given that roads and deer can serve as vectors for nonnative plant dispersal (McNeish and McEwan 2016). Our study sites in the fragmented landscape were within 0.5 km of roads and deer became abundant. With stand basal area in our study remaining nearly constant and few canopy gaps forming, shaded conditions could have limited nonnative cover, at least for light-demanding species. The nonnative species that were present, such as *Alliaria petiolata* (Bieb.) Cavara & Grande, are shade tolerant but did not increase either (Augspurger and Buck 2017). Climate during the study, relative to the long-term climate, would seem favorable for plant establishment (Fig. S1). The year our study began in 2002 was dry (63% of average May through August precipitation), but the study period as a whole was moist (110% of average May through August precipitation from 2002 through 2019).

Along with low abundance of nonnative plants, there was minimal evidence overall for loss of native diversity. Species diversity did decline between 2002 and 2019, which could be partly attributable to an increase in *Carex pensylvanica*

Lam., lowering community evenness. The sedge is often positively correlated with dense deer populations, because it is not preferred forage and quickly expands via rhizomes when more palatable plants decline (Rooney 2009). Lowered species diversity, however, was counterbalanced by other measures suggesting diversification, such as increasing total species richness and community heterogeneity.

DEER-PREFERRED PLANTS. Several lines of evidence suggest that reduced density of deer, potentially interacting with wet summers, triggered the observed increase in deer-preferred forbs. First, deer-preferred forbs disproportionately increased relative to all forbs and other plant groups. Second, the disproportionate increase was analogous to some increases reported in deer-exclosure experiments (*e.g.*, Rooney 2009). These experiments indicate that when recovery of sensitive plants from deer herbivory does occur, it is most evident for species able to persist with at least low cover (often as nonflowering individuals) through periods of intensive herbivory, rather than having to recolonize (Wilbur *et al.* 2017). Except for *Trillium grandiflorum* (Michx.) Salisb., which was absent at our sites before 2018, the other eight species were at least present in 2002 and 2015. Additionally, *T. grandiflorum* and *Desmodium nudiflorum* (L.) DC. were the only deer-preferred species lacking clonal reproduction. The other seven species can reproduce via rhizomes, potentially accelerating recovery (Whigham 2004, Jacques *et al.* 2015). Third, browse severity on *Quercus* regeneration dropped synchronously with the increase in deer-preferred forbs.

It is possible that wet summers enhanced the response to reduced herbivory of deer-preferred forbs. May–June precipitation from 2017–2019 was 126–136% of average (Fig. S1). Seven of the nine deer-preferred species in our study complete most of their vegetative growth and flower by May–June (Whigham 2004, Pavlovic *et al.* 2011). The exceptions are *D. nudiflorum* and *Eurybia macrophylla* (L.) Cass., which flower July–September (Huang and Boerner 2008, Jacques *et al.* 2015). These species might have benefitted from wetter late summers. July–August precipitation was below average in 2017 and 2018 but was 177% of average in 2019, third wettest of the last 65 years. Based on studying plant chemistry and deer forage selection in summer during a dry and average year, Lashley and Harper (2012) hypoth-

esized that a nuanced relationship existed between moisture any given year and deer foraging selectivity, contingent on deer population characteristics, nutrient content of plants, and availability of forage species. Examining trends in our study across future years combined with experimental approaches may offer further insight into the relative roles of herbivory, climate, and interacting factors in long-term community changes.

CONSERVATION OPTIONS AND FUTURE SCENARIOS. Our results supported widespread findings that in the absence of canopy disturbance, other tree species will likely replace the current *Quercus* overstory (Abrams and Downs 1990, Hart *et al.* 2012, Chapman and McEwan 2016), although the replacement's timeframe is often uncertain. Our data suggest that under *status quo* conditions, the depletion of large *Quercus* trees is not imminent but *Quercus* habitat functions could soon diminish. For example, acorn production may dwindle through both continued attrition of acorn-producing individuals and declining output as trees mature past optimum ages for acorn production (Greenberg 2000).

We suggest five scenarios for potential future ecosystems that could develop on these sites under different management strategies likely producing a continuum of *Quercus* abundance. First, given that the sites were formerly *Quercus* savanna-woodland (Brewer and Vankat 2004), they could be restored to those open ecosystems (Abella *et al.* 2018). Second, if *Quercus* forest is to be maintained, cutting multi-tree openings could initiate *Quercus* recruitment and diversify age structure. While minimum gap sizes required for *Quercus* recruitment might vary with many factors and require site-specific experimentation, openings exceeding 0.1 ha have supported profuse *Quercus* regeneration in some locations within the study area (Abella *et al.* 2018). Third, development of fire-resistant tree layers of non-*Quercus* species could be deterred using periodic (*e.g.*, decadal) low-severity fires or other treatments. Dormant-season burns have top-killed over 97% of *Acer rubrum* stems < 14 cm in diameter (Abella *et al.* 2019). While low-severity fires do not necessarily facilitate *Quercus* regeneration below closed canopies in the near term, the fires could maintain conditions suitable for *Quercus* regeneration as canopy *Quercus* die, by preventing understories from filling with non-*Quercus* species. Fourth, without management and with minimal canopy

disturbance, a forest dominated by *Acer rubrum* seems likely. Such a forest would seemingly provide habitat inferior to *Quercus* forest, but some species tolerant or benefitting from closed-canopy forest could be favored (Rodewald and Abrams 1992). Fifth, a transition to non-*Quercus* forest could be accompanied by enrichment plantings or other activities to encourage diversity. Herbivory-protected plantings of deer-sensitive taxa such as *Trillium* could be undertaken, as well as strategically deploying deer exclosures to stimulate patches of plant recruitment (Ruhren and Handel 2003).

Future dynamics of deer populations could affect outcomes for each of the five scenarios via interactive effects of herbivory with fire and canopy openness (Nuttle *et al.* 2013). Four years of deer culling in our study reduced density of deer by about half, to 12 individuals/km² in 2019. This still exceeded, but is closer to, the estimated 3–8 deer/km² in eastern forests before Euro-American settlement and a general threshold of 8 deer/km² above which herbivory effects become severe (Horsley *et al.* 2003). A consideration and perhaps incentive to keep deer populations near the threshold is that irrupting deer populations are apparently more recent in our study area than in many other eastern forests. As of the 1960s, Nixon *et al.* (1970) noted that Ohio had the lowest deer population in the Midwest and that northwestern Ohio at that time contained only 0.5 deer/km². In comparison, areas such as western Pennsylvania had deer densities as high as 12–23/km² from the 1930s to the 1970s (Horsley *et al.* 2003). Length of time that deer have been ecologically overabundant in a region is significant because effects can be cumulative and recovery of sensitive species, if locally extirpated, slows indefinitely (Kirschbaum and Anacker 2005). It is possible that the comparatively short history of recent deer abundance in our study area contributed to the rapid increase in deer-preferred plants coinciding with deer management.

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