

Rapid increase in sensitive indicator plants concurrent with deer management in an oak forest landscape

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Abstract

Wildlife managers are implementing programs to reduce abundant populations of large herbivores, such as white-tailed deer (*Odocoileus virginianus*) in eastern North America, with renewed research interest in understanding these programs' ecological effects. To examine plant community change following culling of white-tailed deer in oak (*Quercus* spp.) forests in Ohio, USA, we measured browse severity on tree seedlings and cover of 43 deer-sensitive, native indicator plant species across 20 years spanning pre- (2002–2015) and post- (2016–2021) deer culling periods. After culling halved deer abundance from 16.7 deer/km² to 8.6 deer/km², browse patterns on tree seedlings reversed from most seedlings exhibiting browse damage to most being undamaged. Cover of deer-sensitive indicator plants increased 7-fold in the 6 years after deer culling. Five of 6 indicator plant groups (e.g., Liliaceae) and 32 of 43 indicator species (74%) increased in cover after deer culling. Rhizomatous, clonally reproducing and early flowering (May–Jun) species were generally most responsive. The rapid increase in deer-sensitive plants after deer culling in our study is among the fastest and largest reported among eastern North American studies. The plant community resilience observed in this study could partly relate to the relatively short duration (~10 yr) that deer populations were elevated before culling began, allowing persistence of local plant

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regeneration potential. Deer culling enabled a moderate deer population to coexist with a rising sensitive plant population.

KEYWORDS

clonal reproduction, culling, forage, herbivory, hunting, population reduction

In many locations globally, increasing populations of mammalian herbivores pose challenges for contemporary wildlife management to balance herbivore abundance with conserving sensitive plants and other ecosystem values (Côté et al. 2004, Laurent et al. 2017, Nagy et al. 2022). For example, increasing grey kangaroo (*Macropus giganteus*) populations in Australia corresponded with loss of conservation-priority native plants and altered population distribution of several species of birds, reptiles, and invertebrates (Gordon et al. 2021). After forest disturbances in Japan, areas with abundant sika deer (*Cervus nippon*) developed depauperate understories containing poor-quality forage (Suzuki et al. 2021). Herbivory by abundant red deer (*Cervus elaphus*) in Europe tempered woody plant growth during otherwise favorable climatic conditions, reducing cover available to wildlife (Vuorinen et al. 2020). In eastern North America, wildlife managers are often confronted with abundant white-tailed deer (*Odocoileus virginianus*). These herbivores create management challenges on landscapes currently devoid of large predators and that have also undergone anthropogenic changes such as fragmentation, increased availability of deer food subsidies (e.g., agricultural crops surrounding forest patches), and vegetation change (Rooney and Waller 2003, Côté et al. 2004, Fisichelli and Miller 2018). Contemporary goals for managing white-tailed deer in an ecological context often include maintaining moderate deer populations to sustain deer as an important wildlife component while recovering or conserving plant populations (and their associated fauna) sensitive to severe herbivory (deCalesta and Stout 1997, McShea 2012, Nagy et al. 2022).

Research on forage nutritional content and preference by white-tailed deer, utilization of different plant species including in settings protected and unprotected from herbivory, and plant distributions and characteristics (e.g., flowering frequency) along gradients of deer abundance has identified sets of indicator plant species sensitive to high deer populations (Russell et al. 2001, Kirschbaum and Anacker 2005, Jenkins and Howard 2021). Examples of indicator plants widely applicable in eastern North American forests include certain species of tree seedlings, several species in the Liliaceae family, and certain groups of forbs not necessarily most palatable to deer but that commonly decline where deer are abundant (Williams et al. 2000, Frankland and Nelson 2003, Shelton et al. 2014). Seedlings of tree species, such as oak (*Quercus* spp.) and red maple (*Acer rubrum*), can be heavily browsed (Horsley et al. 2003). Loss of foliage, twigs, and buds under chronic herbivory can reduce density and size of seedlings, potentially limiting forest regeneration (Walters et al. 2020). Liliaceae plants are palatable to deer and may contain optimal nutritional combinations (Abell and Gilbert 1974). Some less palatable forbs, exemplified by Jack-in-the-pulpit (*Arisaema triphyllum*), can nevertheless receive herbivory, perhaps when more favored plants are sparse (Ruhren and Handel 2000). Less palatable species also correlate negatively with abundant deer potentially via indirect effects, such as changes in soil chemistry or litter inputs from herbivory on other, more favored plants (Heckel et al. 2010).

Two of the main strategies for managing abundant deer on contemporary landscapes in an ecological management context include constructing fencing to exclude deer from variously sized areas (exclosures) and regulating deer populations via culling through controlled hunting (Ward and Williams 2020, Jenkins and Howard 2021, Nagy et al. 2022). Exclosures provide deer-free refugia and express plant community change in the absence of deer herbivory (Russell et al. 2001). Not all exclosure studies show increases in indicator plants, such as when dense woody layers form or non-native plants increase instead, but several exclosure studies have revealed increases in abundance or fitness of indicator plants (e.g., Thomas-Van Gundy et al. 2014, Webster et al. 2017, Wilbur et al. 2017). Which indicator species increase and at what rate has been variable (Russell et al. 2001, Hurley and Flaspohler 2005, Pendergast et al. 2016).

Reducing deer populations via culling avoids the cost and infrastructure of fencing and involves exposing plant communities to some deer instead of no deer as in exclosures (Royo et al. 2010, Tanentzap et al. 2011, Almendinger et al. 2020). Compared with the number of exclosure studies, Jenkins et al. (2014) noted a paucity of research on changes in plant communities after deer culling. Moreover, 11 studies in eastern North America that assessed vegetation change after deer culling reported inconsistent outcomes, with 6 studies meeting a management goal of increasing sensitive indicator plants (Table 1). The other 5 studies reported mixed effects, with about equal proportions of indicator plants increasing or decreasing after deer density was lowered. There could be numerous factors associated with this variability in responses, such as length of time deer were abundant, magnitude of deer population reduction and remaining population size, weather conditions, or traits of indicator species predominating among sites (Simard et al. 2013). Plant traits that could influence vegetation recovery after deer culling include whether species can clonally reproduce, compared to only via seed, and phenological timing such as before or after tree canopy leaf out (Lapointe et al. 2010). As interest continues in managing deer populations in an ecological context, the limited and inconsistent results of vegetation change after deer culling

TABLE 1 Summary of published literature reporting change in deer-sensitive indicator plants after white-tailed deer culling in eastern North America.

Study ^a	Location	Pre-cull (deer/km ²)	Post-cull (deer/km ²)	Duration ^b (years)	Outcome ^c	Summary ^{c,d}
1	NJ	90	14	12	+/-	Woody cover +, forb cover -
2	IL	32-50	7-9	4	-/+	Floristic quality -, some deer-preferred species +
3	IN	NA ^e	NA ^e	14	+	Tree seedling, shrub, forb cover +; MV, Liliaceae +
4	NY	20-26	6-13	15	+	Tree seedling density, MV +
5	IL	25	3	8	+	Woody, forb, PT cover +
6	MN	15-29	≥1	25	+	Tree seedling density, WG +
7	PA	10-12	4-6	4	+/-	Shrub, forb, CM cover +; many indicators (e.g., SB) -
8	MD	30-75	8-12	7	+	Tree seedling density +
9	QC	4-21	11-28	4	+/-/0	Palatable plant cover +, CM -, tree seedlings unchanged
10	ON	30-55	7	16	+	Tree seedling density +
11	MD	36	NA ^e	5	+/0/-	RG cover +, ND unchanged, other species variable
PS	OH	13-22	5-14	6	+	Five of 6 groups, 32 of 43 indicator species cover +

^a1, Almendinger et al. (2020); 2, Anderson et al. (2004, 2005); 3, Jenkins et al. (2014, 2015); 4, Nagy et al. (2022); 5, Nuzzo et al. (2017); 6, Ross et al. (1970); 7, Royo et al. (2010); 8, Schmit et al. (2020); 9, Simard et al. (2013); 10, Tanentzap et al. (2011); 11, Tyndall (2020); PS, present study.

^bLength of time measurements were made after and during deer culling, as follow-up culling often continued after initial culls.

^c+, increase; 0, unchanged; -, decrease.

^dCM, Canada mayflower (*Maianthemum canadense*); MV, mapleleaf viburnum (*Viburnum acerifolium*); ND, northern dewberry; PT, prairie trillium (*Trillium recurvatum*); RG, roundleaf greenbrier; SB, sessileleaf bellwort; WG, wintergreen (*Gaultheria procumbens*).

^eNA, not available. In these studies, authors noted general reductions in deer abundance but magnitudes were uncertain.

suggests that further research could aid understanding ecological responses to changing deer abundance and potential effects of deer management strategies.

We collected 3 datasets to assess change in sensitive plants after culling reduced white-tailed deer abundance. Our data included deer browse damage on tree seedlings, long-term plots measuring change in cover of 43 indicator plant species during a 20-year period including before and after deer culling, and recent plots spanning a 4-year period during culling. We assessed the following hypotheses: 1) browse severity on deer-favored oak and red maple tree seedlings would decline after deer culling while remaining unchanged on the expected less-preferred black cherry (*Prunus serotina*; Tilghman 1989, Horsley et al. 2003), 2) species richness and cover of indicator plants and all 6 groups of indicator plants (e.g., Liliaceae) would increase from before through during deer culling on the long-term plots and through time during culling on the recent plots, and 3) indicator plant species categorized by flowering timing (early or late in the growing season) and reproduction modes (ability or inability to spread via rhizomes and clonal reproduction) would all respond similarly by increasing through time after deer culling.

STUDY AREA

We performed our study in black oak (*Quercus velutina*)-white oak (*Quercus alba*) forests in the 1,737-ha Oak Openings Preserve (41°33'12"N, 83°50'8"W), within the 45,000-ha Oak Openings region in northwestern Ohio, USA. Climate is temperate, including daily average temperature ranges of -9 – 0°C in January and 16 – 29°C in July and 85 cm/year of precipitation (34 cm from May through Aug; Figure S1, available in Supporting Information). Land use surrounding the preserve is predominately rural, consisting of agriculture, woodlots, state forestland, and low-density residential. Oak forests in the preserve are dominated by black and white oaks in the overstory, non-oaks such as red maple and black cherry in the subcanopy tree layer, and mixtures of herbaceous plants, shrubs, and tree seedlings in the understory (Figure 1). Almost all (>98%) of the understory plant cover consists of native species. In

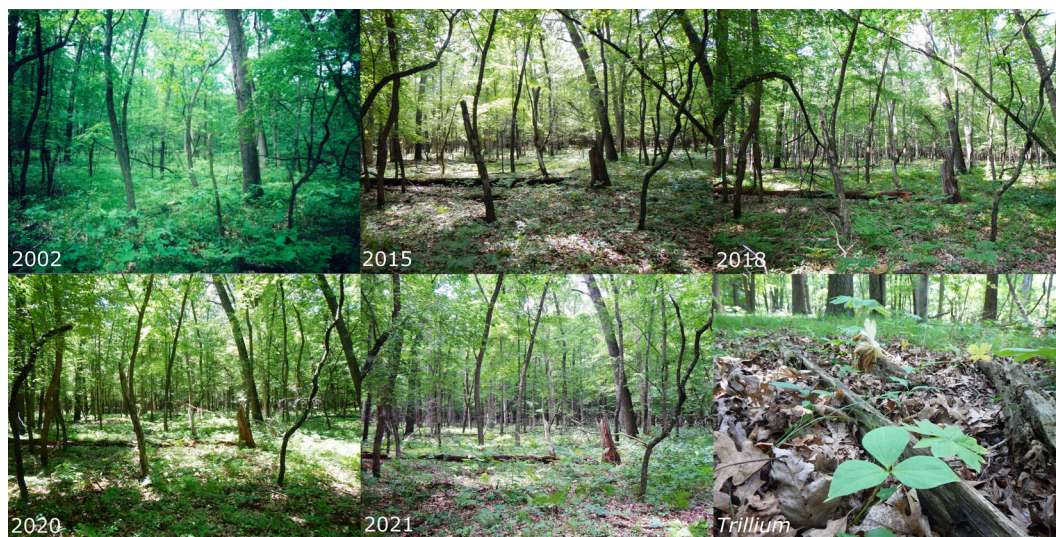


FIGURE 1 Vegetation change during a 20-year period between 2002 and 2021 on an example plot during a study of white-tailed deer culling in northwestern Ohio, USA. By 2015 when deer were abundant, a browse line appeared, and understory plant cover was low compared with 2002. This was despite 2002 having the fourth driest summer and 2015 having the third wettest summer in the last 67 years. After deer culling began in 2016, understory plant cover increased, including the appearance of new plants of white trillium, a deer-sensitive species (center foreground of the bottom right photo). Photos by S. R. Abella.

2002 when we began the study, tree canopy cover averaged 84% and forest basal area averaged 38 m²/ha (76% oak). These measures changed little by the end of the study in 2021, when tree canopy cover averaged 82% and basal area averaged 44 m²/ha (75% oak). Additional study site descriptions, such as soil properties, are in an expanded study area description (available in Supporting Information).

METHODS

White-tailed deer population characteristics and culling

Deer abundance was low (1–2 deer/km²) in northwestern Ohio in the 1960s (Nixon et al. 1970). Although deer abundance had increased by the 1990s (McWilliams et al. 2018), land managers did not observe severe browse impacts (e.g., appearance of a browse line; Figure 1) and sharply rising deer abundance until 2005–2010 (K. S. Menard, Metroparks Toledo, personal communication). In 2013–2015 before deer culling began, systematic surveys via helicopter in winter (Dec or Jan, with at least 8 cm of snow on the ground; Stoll et al. 1991) produced estimates of 13–22 deer/km² in a 25-km² area including the study area surrounded by a 500-m buffer (Figure 2).

With a goal of reducing browse impacts and increasing health of individual deer, managers began a deer culling program in 2016 that continued for 6 years through the end of the study in 2021. Managers set a range of desired maximum deer abundance, rather than a single target abundance, because of 1) uncertainty and likely temporal variability in the study area's deer abundance before Euro-American settlement, 2) the range within a generalized estimate of 3–8 deer/km² in pre-settlement forests of eastern North America (McCabe et al. 1997), 3) different published thresholds of deer abundance at which severe browse effects occur (Tilghman 1989, deCalesta and Stout 1997, Jenkins et al. 2014), and 4) expected temporal fluctuations in deer abundance such as with annual climatic variation (Schmit et al. 2020). As a result, managers set a target maximum range of 6–8 deer/km² to be within the general estimate of pre-settlement deer abundance in eastern forests and as an adaptive management target that

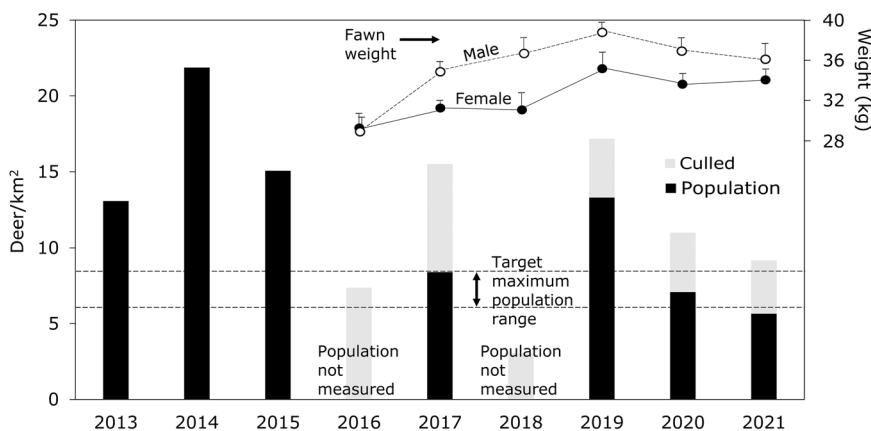


FIGURE 2 Estimated density of white-tailed deer before and after culling began in 2016 in northwestern Ohio, USA. Deer exceeded the target maximum range of 6–8 deer/km² in all 3 years before culling but in only 1 of 4 years with data available after culling. Deer abundance surveys were not performed in 2016 and 2018 because of a lack of snow cover. The elevated deer density in 2019 may relate to autumn 2018 being a mast year of abundant acorn production (Ohio Department of Natural Resources, Division of Wildlife, unpublished data). Mean (+1 SE) weight of fawns (≤ 1 yr) is shown on the secondary y-axis. Mean weight of female fawns in 2016 was lower ($P < 0.05$, Tukey tests) than in 2019 and 2021 (one-way analysis of variance $F_{5,117} = 5.41$, $P < 0.001$). Mean weight of male fawns in 2016 was lower ($P < 0.05$) than in all subsequent years ($F_{5,81} = 13.71$, $P < 0.001$).

could be adjusted depending on plant responses. Culling emphasized removing antlerless deer (~95%) and was performed annually in October–December through a controlled archery program and in January–February by professional shooters with the United States Department of Agriculture-Wildlife Services and Metroparks Toledo law enforcement. We designate the year of culling as the late winter of the calendar year in which culling was completed (e.g., culling from Oct 2015 through Feb 2016 is designated as 2016). Culling removed 185, 178, 77, 97, 98, and 88 deer annually from 2016 through 2021. Removals represented 3.1–7.4 deer/km²/year and reduced the average 2013–2015 pre-culling deer density (16.7/km²) by 49% to an average of 8.6 deer/km² (Figure 2). Culled deer other than for the public archery program were evaluated for general condition, weighed, sexed, and aged using estimates from the tooth replacement technique (Gee et al. 2002). Our evaluations suggested that most deer were generally healthy with no visible signs of emaciation and few had visible signs of physiological stress. Of the 569 culled deer that were measured, 70% were females, 37% were ≤1 year old, 50% were 1–4 years old, and 13% exceeded 4 years old with the oldest being 9 years. Average weights for fawns ≤1 year old increased after the first year of culling in 2016 and were 5 kg (females) and 7 kg (males) heavier in 2021 (Figure 2).

Data collection

We categorized deer browse damage on seedlings (4–139 cm tall) of red maple, black cherry, and oak (black and white oak combined) annually from 2015 through 2021 in March–April before leaf out. We conducted the browse surveys by systematically arranging transects every 200 m throughout the study area and inventorying a circular browse plot (7 m²) every 60 m along transects. Depending on whether plots contained a focal seedling species, we inventoried 221–314 browse plots annually. In each browse plot containing at least one of the focal species, we classified browse severity into 5 categories ranging from no to severe browse, specifically for deer browse distinguished from browse by other animals (Benner 2007). The 5 categories included not browsed (no visible damage to seedlings), lightly browsed (<50% of stems browsed), moderately browsed (≥50% of stems browsed), heavily browsed (seedlings severely hedged with twigs browsed back to the main stem but main stem >15 cm tall), and severely browsed (same as heavily browsed but main stem browsed down to ≤15 cm tall; Benner 2007).

We used a body of 46 published papers of deer indicator plants based on deer foraging selectivity (i.e., comparing deer diets with plant species availability) and differences in plant abundance within and outside deer enclosures to identify groups of indicator plants for eastern North America that occurred in the study area (Table S1, available in Supporting Information). These groups included Liliaceae (e.g., white trillium [*Trillium grandiflorum*]), Fabaceae (e.g., nakedflower ticktrefoil [*Desmodium nudiflorum*]), other primary indicators (e.g., wild sarsaparilla [*Aralia nudicaulis*]), secondary indicators (e.g., bigleaf aster [*Eurybia macrophylla*]), and species in the *Rubus* and *Smilax* genera. The primary indicators were species other than Liliaceae and Fabaceae that were either highly palatable to deer or if less palatable, that had negative relationships (e.g., for plant height, flowering, or cover) with deer abundance across multiple studies (Ruhren and Handel 2000, Heckel et al. 2010, Shelton et al. 2014). Secondary indicators included species reported as only moderately preferred forage or only moderately increasing in enclosures (based on criterion set by individual studies) or that were plant species likely preferred but assessed in fewer than 2 studies (Table S1).

We measured cover of the indicator species on 16 plots, including 8 long-term and 8 recent plots. In 2002 to establish the long-term plots, we randomly located 8, 0.05-ha (20 m × 25 m) plots using random coordinates in mature (≥80 yr) oak forests. Plots were separated by an average of 1.4 km (range = 0.3–3.1 km). We categorized aerial cover, for each indicator species rooted in each plot, using cover classes including 0.1, 0.25, and 0.5% for cover less than 1%, 1% intervals for cover to 10%, and 5% intervals to 100%. The same investigator (SRA) made cover categorizations each year, eliminating among-observer variation in cover categorization. We inventoried indicator plants on the long-term plots in 2002 and 2015, before deer culling, and in 2018–2021 annually after deer culling commenced in 2016. To augment the long-term plots, we used recent plots to measure change in indicator

plants in 2018, 2020, and 2021 during ongoing deer culling. The 8 recent plots were also randomly located (separated by an average of 1.4 km, range = 0.1–2.3 km) in mature oak forest and sampled using the same methods as for long-term plots. All 16 plots in total were separated by an average of 1.7 km (range = 0.1–4.4 km). We inventoried all plots near mid-summer (Jul–Aug), the peak growing period overall in our study area for the set of indicator plants. Our inventories occurred when early flowering species persist vegetatively or have senescent flowers and later-flowering species are near or at flowering stage.

Data analysis

We analyzed tree seedling browse data by consolidating plots into 3 browse categories (no browse, low-moderate browse, and heavy-severe browse). Separately by tree species, we conducted chi-square tests of independence to analyze if the proportion of browse plots in the 3 browse categories changed across years. Change across years was significant ($P < 0.05$) for each species, so we proceeded with comparing proportions of browse categories within years using chi-square goodness-of-fit tests under a null equal distribution.

Separately for long-term and recent plots, we analyzed the mean number of deer-sensitive indicator plant species (species richness per 0.05-ha plot), total cover of indicator plants, and cover of each indicator group across years using repeated measures analysis of variance. If these tests were significant at $P < 0.05$, we separated means using Tukey tests. To improve normality and equality of variance, we Box-Cox transformed data for analyses (Osborne 2010). Also separately for long-term and recent plots and to accommodate zero-inflated data (from many species absences initially), we used one-way, repeated measures permutational analysis of variance (9,999 permutations) to compare mean change of the cover per individual indicator species within species trait categories for reproduction (yes, no for rhizomatous and clonal reproduction) and flowering timing (early [May–Jun] or late [Jul–Sep]; Table S2, available in Supporting Information). The repeated measures comparisons were between 2015 (yr before deer culling) and 2021 (6 yr after culling began) for long-term plots and between 2018 and 2021 for recent plots. We performed statistical analyses in PAST 4.05 (Hammer 2021).

RESULTS

Browse on red maple, black cherry, and oak seedlings declined similarly following deer culling (Figure 3). Distributions of browse severity categories reversed after deer culling, switching from most seedlings exhibiting browse damage before to most being undamaged after culling. In 2015 before deer culling, for example, oak seedlings exhibiting no damage were rare, while 62–75% of them were undamaged from 2018–2021 by 3–6 years after culling began. Meanwhile, seedlings with heavy-severe browse damage declined from 38–67% among species before deer culling to only 6–14% by 2017, the year after culling began.

On long-term plots, the average number of deer-sensitive, indicator plant species present nearly doubled from a 2015 low, before deer culling, to a 2021 high after 6 years of culling (Figure 4; Table S3, available in Supporting Information). The 2021 high was 36% above 2002 when the study began. Trends were similar during culling on recent plots, with indicator species richness rising each year between 2018 and 2021 (Figure 4). The increase in indicator plants from 2018 to 2021 was consistent across the landscape, with all 16 plots including long-term and recent plots displaying some increase in species richness and cover of indicator plants.

Mean total cover of indicator plants and cover of 3 of the 6 indicator groups varied among years on long-term plots (Figure 4; Table S3). From a low in 2015, the year before deer culling began, cover of indicator plants more than doubled by 2018 and increased over 7 times by 2021. Covers of the Liliaceae, primary indicator, and *Smilax* groups all increased above 2015 levels before or in 2021. On recent plots, mean total cover of indicator plants increased each year as deer culling proceeded, with 5 times more cover in 2021 than in 2018 (Figure 4). Liliaceae,

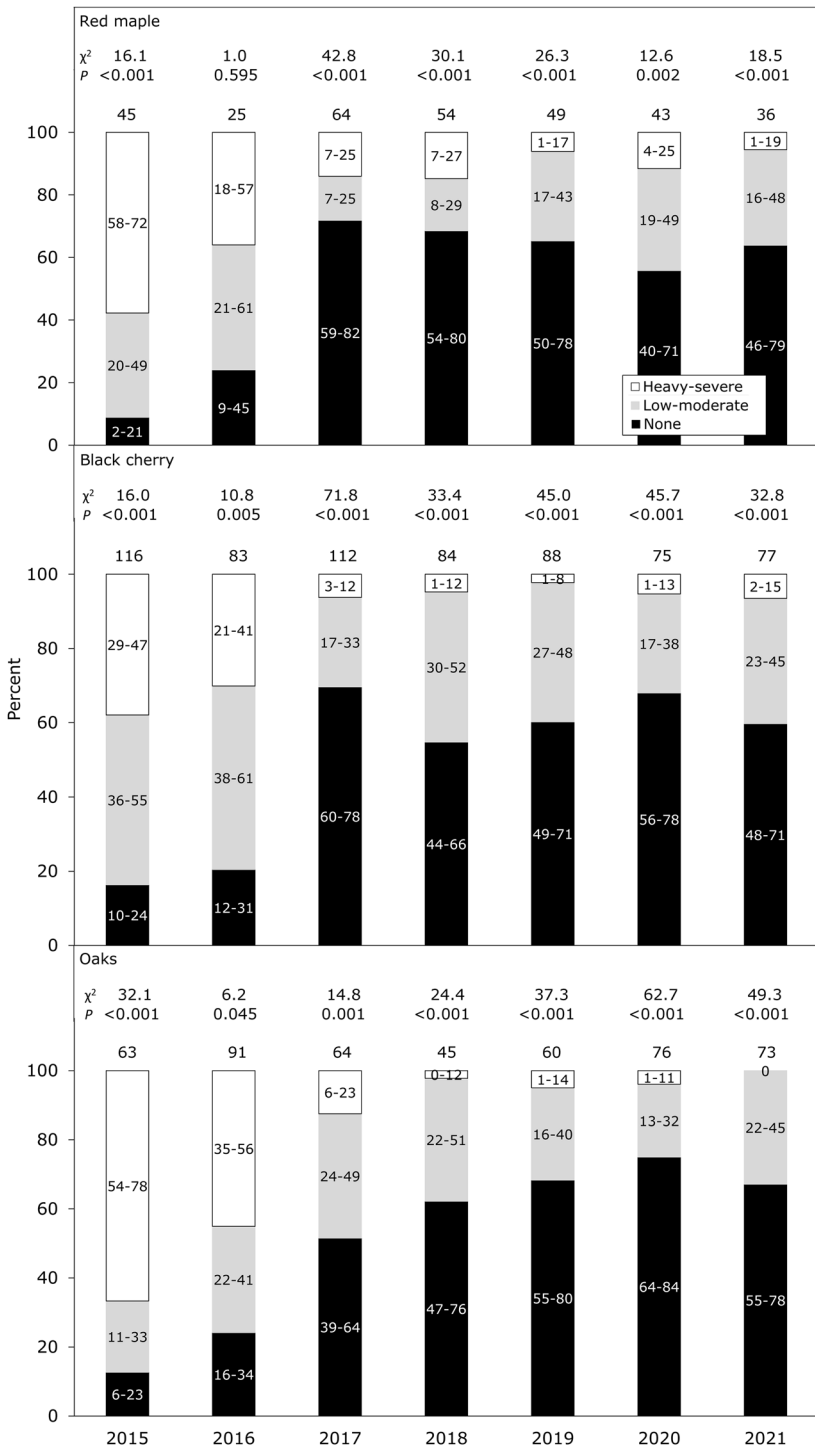


FIGURE 3 Percent of browse plots in 3 browse severity categories for seedlings of 3 tree species before (2015) and after (2016–2021) white-tailed deer culling in northwestern Ohio, USA. For each tree species, the number of plots containing the species are listed above the bars along with statistics for chi-square goodness-of-fit tests of equal distributions among browse categories within years. Within each browse category, 95% confidence intervals of browse category percentages are shown within bars. The browse category none indicates no browse.

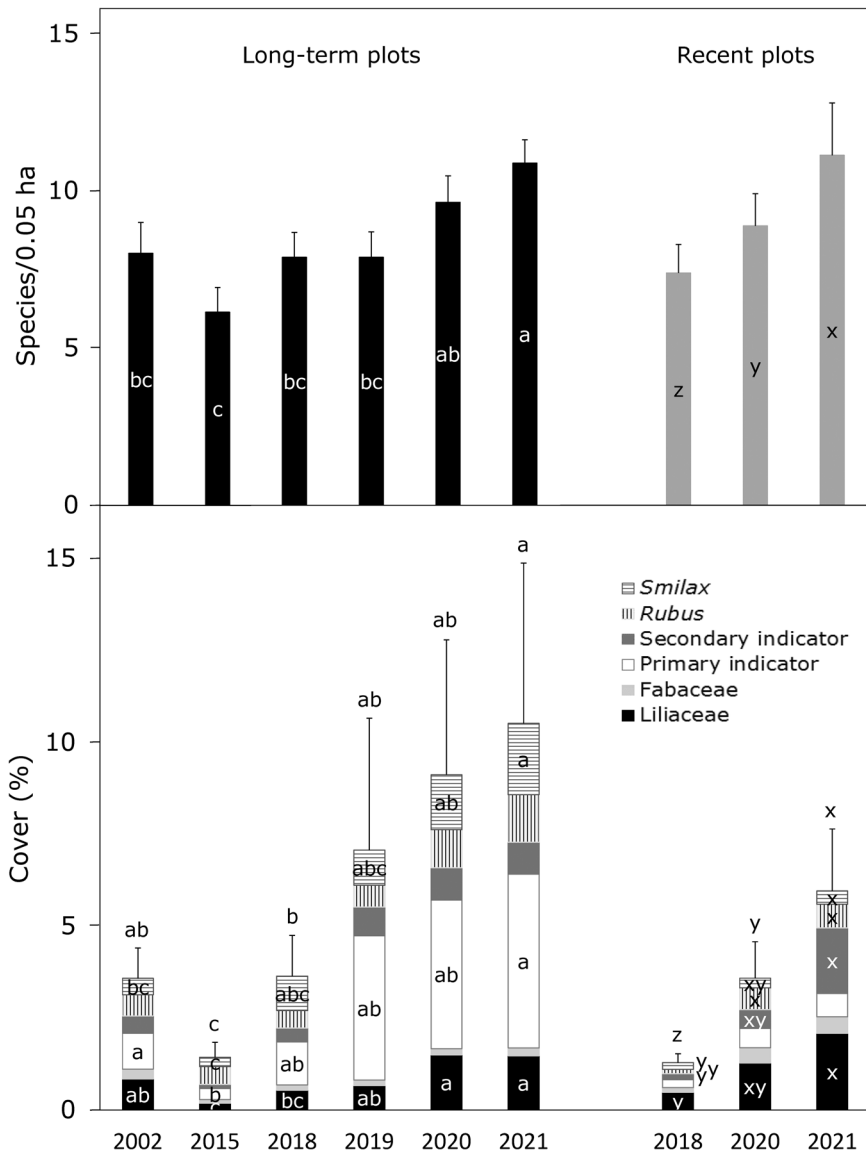


FIGURE 4 Change in mean species richness and cover of indicator plants sensitive to white-tailed deer herbivory during a study of deer culling in northwestern Ohio, USA. On long-term plots, 2002 and 2015 were before deer culling, which began in 2016 and continued through 2021. We sampled recent plots during ongoing deer culling. Error bars are one standard error of means. Means without shared letters differ at $P < 0.05$ across years within sets of comparisons. Years are compared separately within long-term and recent plot sets. For cover, total cover of indicator plants and each individual indicator group are compared across years separately (letters for total cover are shown above error bars). If letters are not shown for an indicator group, means did not differ across years at $P < 0.05$.

secondary indicator, *Rubus*, and *Smilax* groups each had greater cover in 2021 than in 2018. In total, 5 of the 6 indicator plant groups (the exception being Fabaceae) significantly increased in cover during deer culling on either long-term or recent plots.

Of 43 individual indicator species, 32 (74%) increased in cover above 2002 or 2015 levels after 2018 on long-term plots or between 2018 and 2021 on recent plots (Table S4, available in Supporting Information). Species with the

greatest cover increases after 2015 on long-term plots included wild sarsaparilla (increasing from 0.26% in 2015 to 4.53% in 2021), roundleaf greenbrier (*Smilax rotundifolia*; 0.05% to 1.17%), sessileleaf bellwort (*Uvularia sessilifolia*; 0.01% to 1.12%), bristly dewberry (*Rubus hispida*; 0.01% to 0.88%), bigleaf aster (*Eurybia macrophylla*; 0.03% to 0.67%), cat greenbrier (*Smilax glauca*; 0.20% to 0.57%), false lily of the valley (*Maianthemum racemosum*; 0.11% to 0.23%), and nakedflower ticktrefoil (0.09% to 0.18%). Only 4 species, most of which had low cover, decreased in cover between 2015 and 2021 on long-term plots (Table S4). No species declined in cover between 2015 and 2021 on recent plots.

Species with the greatest increase in frequency (number of plots species inhabited) on long-term plots included sessileleaf bellwort, which inhabited only 1 of 8 plots in 2015 but 7 plots in 2021; white avens (*Geum canadense*),

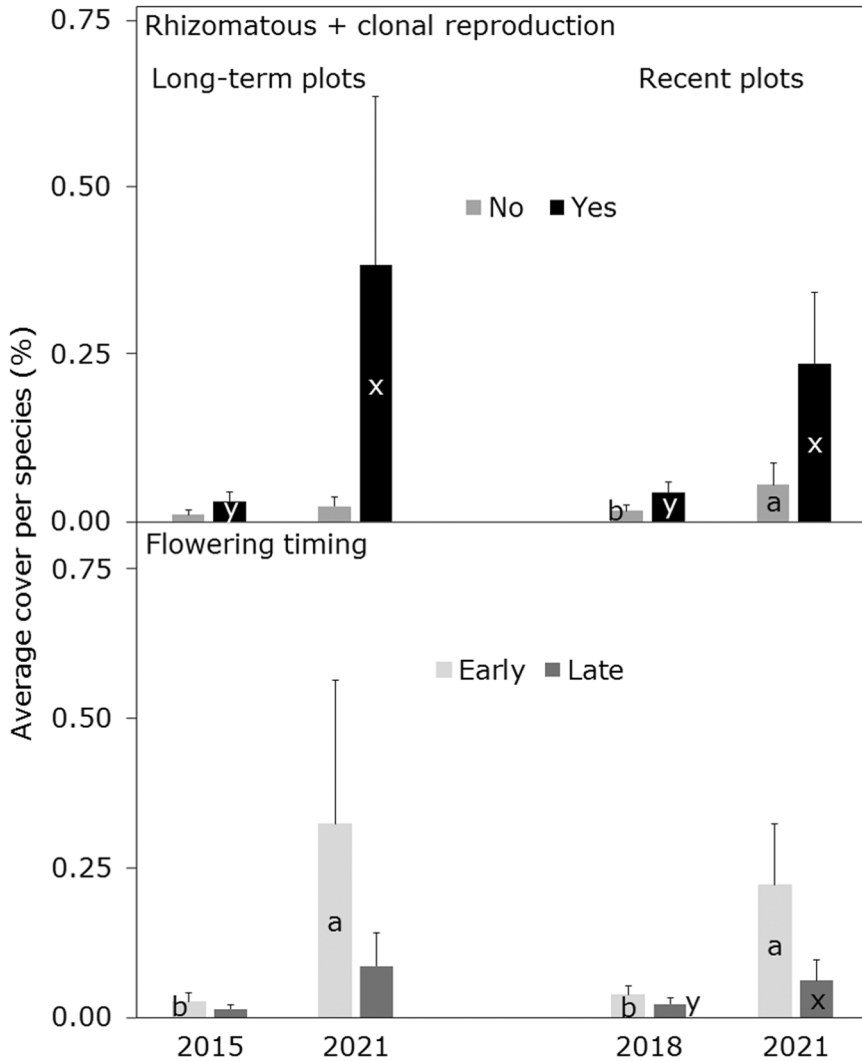


FIGURE 5 Average cover per plant species among the traits of possessing rhizomes and clonal reproduction and flowering timing (early [May–Jun], late [Jul–Sep]) during a study of white-tailed deer culling in northwestern Ohio, USA. Long-term plots compare before (2015) and after 6 years of deer culling (2021). Recent plots compare change between 2018 and 2021 during deer culling. Separately for long-term and recent plots within a trait category (e.g., early flowering species) cover per species is compared between years using repeated measures permutational analysis of variance (different letters note differences significant at $P < 0.05$). Error bars are one standard error of means.

which inhabited 1 plot in 2002, 0 in 2015, and 6 plots in 2021; bristly greenbrier (*Smilax tamnoides*), which was absent from plots in 2002 and 2015 but inhabited 5 plots in 2021; and cat greenbrier, increasing from 3 plots in 2015 to 7 plots in 2021 (Table S4). In addition to many of the same species that increased in frequency on long-term plots, major species with increases in frequency on recent plots included the Liliaceae cucumber-root (*Medeola virginiana*), the primary indicators Jack-in-the-pulpit and wild geranium (*Geranium maculatum*), the secondary indicator mayapple (*Podophyllum peltatum*), and northern dewberry (*Rubus flagellaris*). The Liliaceae white trillium was absent early in the study but colonized 2 plots after deer culling.

Rhizomatous, clonally reproducing species disproportionately increased in cover after deer culling compared to species without rhizomes and clonal reproduction (Figure 5; Table S5, available in Supporting Information). Species lacking rhizomes and clonal reproduction did not increase significantly after deer culling on long-term plots. While species lacking rhizomes and clonal reproduction did increase on recent plots during culling, their mean cover per species was 4 times less than that of rhizomatous, clonally reproducing species. Similarly, early flowering (May–Jun) species increased in cover more relative to later-flowering (Jul–Sep) species (Figure 5).

DISCUSSION

Potential factors contributing to the rapid response

Climate could be considered generally favorable for plant establishment and growth during the study, although the potential role of climate in the changing abundance of deer indicator plants is uncertain. During the 2002–2021 period encompassing inventories of the long-term plots, 12 of 20 years had above-average summer (May–Aug) precipitation (Figure S1). However, before deer culling years of 2002 and 2015 did not follow a pattern of above-average precipitation years supporting greater abundance of indicator plants. Although 2002 had the fourth driest summer in the last 67 years, it supported twice the cover of deer indicator plants than did 2015, which had the third wettest summer of the last 67 years. Thereafter during the deer-culling period (2016–2021), several years similarly had high precipitation as deer herbivory of tree seedlings declined to an apparently lower equilibrium while cover of deer indicator plants increased nearly linearly. After deer culling began, 4 of 6 full summers (May–Aug) and 5 of 6 early summers (May–Jun) had above-average precipitation. It is possible that favorable early summer precipitation facilitated increasing cover of early flowering species. For example, Jacques et al. (2015) found that early flowering species could only benefit from extended early growing seasons under warmer temperatures if early precipitation was favorable. The early growing season is key for many forest forbs to enable growth before leaf out of the tree canopy and before competitive late-summer flowering plants have initiated most growth (Jacques et al. 2015). Longer-term monitoring in our study, including evaluating if indicator plants continue increasing even in drier years during ongoing deer culling, may provide insight into the potential role of climate or its interaction with deer abundance in influencing deer-sensitive plants.

In addition to potentially favorable climate, another factor possibly contributing to rapidly responding indicator species was the relatively short duration that deer were abundant. In the mid-1940s when several areas of the United States contained abundant deer, Leopold et al. (1947) mapped deer as absent to scarce in Ohio on a national-scale map. In the 1960s, Ohio had the lowest deer population of any midwestern state, and northwestern Ohio (encompassing our study area) contained only 1–2 deer/km² (Nixon et al. 1970). Deer abundance remained generally low in northwestern Ohio through the 1980s at <6 deer/km² (Gladfelter 1984, Stoll et al. 1991, McWilliams et al. 2018). It was not until the mid-2000s that high deer populations and impacts were noted by managers in our study area. Thus, the period that deer were abundant was short (~10 yr) in our study area compared with many other locations, particularly areas with chronically abundant deer since the 1940s (McWilliams et al. 2018). Although some areas with long-term, abundant deer have recovered sensitive plants when deer were excluded or reduced, many have only minimally recovered (Hurley and Flaspohler 2005, Tanentzap et al. 2011, Nuttle et al. 2014). If chronic herbivory over a long period results in local extirpation of mature forest plant species,

necessitating long-distance dispersal of seed, recovery can be especially recalcitrant (Forrester et al. 2006). Our study was instead characterized by a short period of abundant deer, potential retention of on-site plant propagules, and a rapid increase in sensitive plants when deer populations were reduced.

Species traits

Although conducting a demographic assessment tracking the origin of individual plants was outside the scope of our study, the species composition and trait data suggested that possessing rhizomes and capability for clonal reproduction conferred advantages for responding to alleviation of herbivory pressure. Aboveground occurrence of rhizomatous, clonally reproducing species was minimal in 2015 before deer culling, but these species may have maintained belowground structures with little aboveground cover visible by summer sampling. Deer browse many Liliaceae species early in spring while the plants are still unfolding (Lapointe et al. 2010). If browsed, some Liliaceae species, such as white trillium, do not necessarily re-grow aboveground until the next year (Knight 2003), or they may persist as a briefly appearing, single juvenile leaf (Webster and Jenkins 2014). While many of the mature forest forbs, such as in the Liliaceae, may form only limited soil seed banks, they can form rhizome banks in soil where intact or fragmented rhizomes can produce new plants (Whittle et al. 1998).

Colonization by seed dispersal is also a possibility, though seeds of many of the forb species typically do not disperse far or may not retain viability. Hog-peanut (*Amphicarpaea bracteata*), for example, which appeared for the first time in our plots in 2021, disperses seeds ballistically for short distances up to 3 m (Trapp 1988). Several species have seeds dispersed by ants, such as ants moving white trillium seeds an average of 0.5–2.4 m from parent plants (Kalisz et al. 1999). Deer can disperse seeds farther, sometimes 3–6 km (Vellend et al. 2003, Williams et al. 2008). However, viability of seeds after ingestion by deer can be uncertain. Although seeds of some species retain viability after ingestion by deer (Myers et al. 2004, Blyth et al. 2013), Niederhauser and Matlack (2015) found that only 1% of mayapple seeds survived ingestion by deer, compared with 28% surviving ingestion by raccoons (*Procyon lotor*).

Of the 12 woody indicator species, the major increasers were 3 species of *Rubus* and 2 species of *Smilax*. *Rubus* species can reproduce vegetatively (by roots producing multiple shoots and the stems able to root) and via large, persistent, soil seed banks (Hyatt and Casper 2000, Abella et al. 2020). Of the *Smilax*, both cat greenbrier and roundleaf greenbrier reproduce via rhizomes and seed (Pogge and Bearce 1989). With the exception of cat greenbrier colonizing new plots after 2015, other increasing woody species mainly increased on the plots they already inhabited in 2015 (long-term plots) or 2018 (recent plots). This also suggested primarily local regeneration through on-site propagules.

Variation among indicator groups

The patterns in cover after deer culling varied among the 6 indicator groups and may further suggest variation in sensitivity among indicator plants. Liliaceae and *Smilax* groups were the most sensitive, increasing after deer culling on long-term and recent plots. Primary indicator plants increased on long-term plots while secondary and *Rubus* groups increased on recent plots. Although notable increases occurred in some Fabaceae species, such as quadrupling of nakedflower ticktrefoil cover on recent plots, Fabaceae as a group did not increase significantly after deer culling. Variation in response among the plant groups could be associated with 3 main factors: the relative degree that deer selectively forage on the species, tolerance and resiliency of the species to herbivory, and potential sensitivity of focal plant species to changes in habitat conditions and other species.

Relative selectivity by deer could have influenced herbivory pressure both before deer culling and after culling if remaining deer continued selecting certain plant species. In a study in Tennessee, USA, for instance, *Desmodium* species had the greatest crude protein content among species that were already highly selected by deer and were

the only plants meeting nutritional requirements for lactating females in dry years (Lashley and Harper 2012). It is possible that preferential herbivory on *Desmodium* and perhaps some other forbs in Fabaceae, coupled with lack of clonal reproduction capability, hindered a greater response in these species in our study. In tree seedlings, however, all 3 species showed similar patterns of alleviated browse damage after deer culling. This did not conform with our hypothesis that black cherry, expected to be less preferred by deer based on being unfavored browse in other studies (Tilghman 1989, Horsley et al. 2003, Lashley and Harper 2012), would display minimal change in browse damage compared with the more preferred oak and red maple (Stormer and Bauer 1980, Williams et al. 2000). Deer forage preferences can be contingent on combinations of available species (Wright et al. 2019). Apparently in our study, the tree species were nearly equally selected by deer given available winter forage. Directly comparing temporal change in availability and deer use of the indicator plants, rather than overall indicator plant community change, which was the focus of our study, would be needed to ascertain if deer culling triggered shifts in plant preferences by deer as deer abundance declined and deer-sensitive plants increased.

Tolerance to and resilience after herbivory could be promoted by clonal reproductive capability (Augustine and deCalesta 2003, Lapointe et al. 2010). The most tolerant forest forb species can sustain repeated browsing without flowering, possibly for decades, then display resiliency by sequestering sufficient resources over 1–10 years via clonal regeneration to eventually flower (Wilbur et al. 2017). In our study, wild sarsaparilla could represent one of these species with high tolerance and resiliency. Wild sarsaparilla ramets along rhizomes of clones can exceed 40 years in age and the genets could live centuries (Flanagan and Bain 1988). It is possible that the increase in cover of wild sarsaparilla shoots after deer culling arose from resilient, belowground ramets originating long before our study began.

Increases after deer culling in plants generally unpalatable to deer, such as Jack-in-the-pulpit and mayapple, could be contingent on changes in habitat and associated plant species. Although they can be browsed at low levels, especially if more palatable plants are sparse (Ruhren and Handel 2000, Frankland and Nelson 2003), Jack-in-the-pulpit contains calcium oxalate crystals and mayapple contains toxins, generally making the species unpalatable (Rust and Roth 1981, Bierzychudek 1982). When deer are abundant, Heckel et al. (2010) hypothesized that the unpalatable Jack-in-the-pulpit declined along with its palatable neighbors because of habitat changes, such as litter depth and soil chemistry, from altered plant composition and soil processes. After deer culling, mayapple could represent an example where increases in more palatable species contribute to increases in the unpalatable mayapple. Mayapple does not produce nectar but depends on nectar-seeking bees for pollination. Mayapple plants close to nectar-producing species have more frequent pollinator visits and greater seed production (Laverty 1992). Patches with increasing densities of flowers generally can promote increasing pollinator visits to multiple plant species, at least up to a point of saturated pollinator density, suggesting that alleviating herbivory pressure to enable greater flowering could benefit palatable and unpalatable species alike (Laverty 1992, Steven et al. 2003). Along with enabling fruit production in mayapple, lower deer density could result in greater seed survival of mayapple because while the foliage is unpalatable, deer do consume mayapple fruits and the seeds rarely survive ingestion by deer (Niederhauser and Matlack 2015).

Potential benefits of plant increases to wildlife and pollinators

In addition to increasing plant populations, appearance of previously absent or increasing sensitive plants after deer culling could benefit wildlife (including individual deer health) and pollinators. Deer health assessments as part of culling operations revealed that concurrent with the increase in deer-sensitive plants, deer fawn weights increased on average by 8–22% (females) and 22–35% (males) after deer culling.

Matching deer-sensitive plants with their use by fauna reported in the literature offers insight into how increases in sensitive plant populations could have further benefited fauna. For example, eastern box turtles (*Terrapene carolina*) consume fruits of mayapple (Rust and Roth 1981), a species increasing on recent plots in our study from nearly absent in 2018 to over 1% cover in 2021 as deer culling progressed. Eastern chipmunks (*Tamias striatus*) eat roots and bulbs of wild geranium (Wrazen and Svendsen 1978), which appeared on our long-term plots

for the first time in 2021 and tripled in cover on recent plots from 2018 to 2021. In forested areas, raccoons consume berries of *Smilax* species (Smith et al. 1987). *Smilax* species quadrupled in cover after deer culling on long-term plots in our study. Structural heterogeneity of understory vegetation, including a diversity of plant species varying in height and architecture, can maximize perch site availability to gray treefrogs (*Hyla versicolor*; Roble 1979). Plant diversity and cover increased during deer culling in our study, including a variable mixture of tree seedlings and herbaceous plants reported as used by treefrogs (Roble 1979). Illustrating potential benefits to pollinators, 17 invertebrate taxa including bees visited flowers during a study of wild sarsaparilla (Barrett and Helenurm 1987), which increased in cover by 22 times in our study after deer culling. These examples highlight potential for post-deer-culling increases in plant communities to stimulate diverse responses in faunal communities, highlighting utility of evaluating multi-guild responses to deer culling (Shelton et al. 2014).

Comparisons among eastern North American deer culling studies

Existing research and our results suggest that native plant metrics after deer culling in eastern North America can commonly increase, but exceptions and considerable variability in responses have occurred (Table 1). In comparing and synthesizing our study context and results with prior studies, deer density preceding culling in our study was at the low range and post-culling deer density was intermediate compared with other studies. No clear pattern seems evident with post-culling deer density and vegetation response among studies, perhaps a topic more effectively addressed by research approaches that vary deer abundance as treatments within studies (Tilghman 1989, Fletcher et al. 2001). We can conclude, however, that a post-culling target range of 6–8 deer/km² was compatible with an increase in indicator plants during our study. While several prior studies found that deer-sensitive forbs increased after deer culling, sensitive forbs failed to increase more frequently among studies than did woody plants including tree seedlings. Only one study (Simard et al. 2013) reported that woody plants failed to increase after deer culling. In our study, similar percentages of indicator woody (86%, 12 of 14 species) and forb (75%, 15 of 20 species) species increased, specifically on long-term plots between 2015 before deer culling and 2021 after 6 years of culling. Effects of time since deer culling seem difficult to identify among studies thus far; some long-term (e.g., Almendinger et al. 2020, 12 years) and short-term studies (e.g., Royo et al. 2010, 4 years) found that sensitive forbs did not increase after culling. Our study, extending 6 years after deer culling began, was within the range of 4–25 years after culling among studies. Overall, the body of literature suggests that woody plants more consistently increase following deer culling than do sensitive forbs. Further research may help identify sources of variability in plant responses to deer culling and refine likely responses in a range of ecological contexts given variability among studies thus far.

MANAGEMENT IMPLICATIONS

Our study revealed that after reducing deer abundance by 49%, browse damage to tree seedlings declined rapidly and a variety of deer-sensitive indicator plants increased rapidly. These results suggest 3 further management applications or questions. First, while results revealed that browse damage to oak seedlings declined after deer culling, the seedlings are not transitioning to larger size classes (Abella et al. 2021), consistent with widespread findings in eastern North American oak forests (e.g., Thomas-Van Gundy et al. 2014). Advancing oak seedlings to saplings often requires a combination of canopy gaps, fires, and low levels of deer herbivory (Nuttle et al. 2013, Walters et al. 2020). However, canopy gaps and fires do not necessarily benefit deer-sensitive, forest forbs, such as Liliaceae (Huebner et al. 2010). Where stimulating oak regeneration and maintaining increases in deer-sensitive forbs are both goals, further research may be necessary to identify strategies balancing these goals. Second, our results offered insight into which types of plant species are likely to be most or least resilient after deer are reduced and thus may differ in requirements for further recovery. Species regenerating *in situ* via rhizomes and clonally typically became most abundant after deer culling and appeared capable of

recovery without further assistance. Species more reliant on seed production, germination, and dispersal did not respond as vigorously after deer culling. While the rapid and positive overall plant community response to deer culling in our study may render actively restoring plants unnecessary, if active revegetation were to be conducted, it likely should focus on non-clonal species needing to colonize through seed. Third, our study revealed that deer culling corresponded with rapidly increasing deer-sensitive plants and that rising populations of these plants could coexist with a moderate, post-culling density of 6–8 deer/km². Deer culling thus was a viable management strategy for simultaneously maintaining populations of deer while increasing deer-sensitive plants across the landscape.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Plant abundance data are in Table S4, available in Supporting Information.

ETHICS STATEMENT

Culling activities occurred under deer damage control permits issued annually by the Ohio Division of Wildlife.

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REFERENCES

- Abell, D. H., and F. F. Gilbert. 1974. Nutrient content of fertilized deer browse in Maine. *Journal of Wildlife Management* 38:517–524.
- Abella, S. R., J. L. Hodel, and T. A. Schetter. 2020. Unusually high-quality soil seed banks in a Midwestern U.S. oak savanna region: variation with land use history, habitat restoration, and soil properties. *Restoration Ecology* 28:1100–1112.
- Abella, S. R., L. A. Sprow, and T. A. Schetter. 2021. Delayed tree mortality after prescribed fires in mixed oak forests in northwestern Ohio. *Forest Science* 67:412–418.
- Almendinger, T., M. Van Clef, J. F. Kelly, M. C. Allen, and C. Barreca. 2020. Restoring forests in central New Jersey through effective deer management. *Ecological Restoration* 38:246–256.
- Anderson, R. C., D. Nelson, M. R. Anderson, and M. A. Rickey. 2004. White-tailed deer (*Odocoileus virginianus* Zimmermann) browsing effects on quality of tallgrass prairie community forbs. Pages 63–69 in *Proceedings of the 19th North American prairie conference*. University of Wisconsin, Madison, USA.
- Anderson, R. C., D. Nelson, M. R. Anderson, and M. A. Rickey. 2005. White-tailed deer (*Odocoileus virginianus* Zimmerman) browsing effects on tallgrass prairie forbs: diversity and species abundances. *Natural Areas Journal* 25:19–25.
- Augustine, D. J., and D. deCalesta. 2003. Defining deer overabundance and threats to forest communities: from individual plants to landscape structure. *Ecoscience* 10:472–486.
- Barrett, S. C. H., and K. Helenurm. 1987. The reproductive biology of boreal forest herbs. I. Breeding systems and pollination. *Canadian Journal of Botany* 65:2036–2046.
- Benner, J. M. 2007. Browsing and regeneration monitoring report for Pennsylvania's state forests. Pennsylvania Department of Conservation and Natural Resources, Harrisburg, USA.
- Bierzchudek, P. 1982. Life histories and demography of shade-tolerant temperate forest herbs: a review. *New Phytologist* 90:757–776.

- Blyth, L. H., L. J. Ouborg, D. M. Johnson, and L. J. Anderson. 2013. The short-term germination and establishment success of deer-dispersed seeds in mesic temperate forests. *Journal of the Torrey Botanical Society* 140:334–348.
- Côté, S. D., T. P. Rooney, J. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology and Systematics* 35:113–147.
- deCalesta, D. S., and S. L. Stout. 1997. Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. *Wildlife Society Bulletin* 25:252–258.
- Fischelli, N. A., and K. M. Miller. 2018. Weeds, worms, and deer: positive relationships among common forest understory stressors. *Biological Invasions* 20:1337–1348.
- Flanagan, L. B., and J. F. Bain. 1988. The biological flora of Canada: 8. *Aralia nudicaulis* L., wild sarsaparilla. *Canadian Field-Naturalist* 102:45–59.
- Fletcher, J. D., W. J. McShea, L. A. Shipley, and D. Shumway. 2001. Use of common forest forbs to measure browsing pressure by white-tailed deer (*Odocoileus virginianus* Zimmerman) in Virginia, USA. *Natural Areas Journal* 21:172–176.
- Forrester, J. A., D. J. Leopold, and H. B. Underwood. 2006. Isolating the effects of white-tailed deer on the vegetation dynamics of a rare maritime American holly forest. *American Midland Naturalist* 156:135–150.
- Frankland, F., and T. Nelson. 2003. Impacts of white-tailed deer on spring wildflowers in Illinois, USA. *Natural Areas Journal* 23:341–348.
- Gee, K. L., J. H. Holman, M. K. Causey, A. N. Rossi, and J. B. Armstrong. 2002. Aging white-tailed deer by tooth replacement and wear: a critical evaluation of a time-honored technique. *Wildlife Society Bulletin* 30:387–393.
- Gladfelter, H. L. 1984. Midwest agricultural region. Pages 427–440 in L. K. Halls, editor. *White-tailed deer: ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Gordon, I., M. Snape, D. Fletcher, B. Howland, G. Coulson, M. Festa-Bianchet, P. Caley, S. McIntyre, T. Pople, C. Wimpenny, et al. 2021. Herbivore management for biodiversity conservation: a case study of kangaroos in the Australian Capital Territory (ACT). *Ecological Management and Restoration* 22:124–137.
- Hammer, Ø. 2021. PAST 4.05, paleontological statistics reference manual. University of Oslo, Oslo, Norway.
- Heckel, C. D., N. A. Bourg, W. J. McShea, and S. Kalisz. 2010. Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. *Ecology* 91:319–326.
- Horsley, S. B., S. L. Stout, and D. S. deCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications* 13:98–118.
- Huebner, C. D., K. W. Gottschalk, G. W. Miller, and P. H. Brose. 2010. Restoration of 3 forest herbs in the Liliaceae family by manipulating deer herbivory and overstorey and understorey vegetation. *Plant Ecology and Diversity* 3:259–272.
- Hurley, P. M., and D. Flaspohler. 2005. An assessment of long-term biodiversity recovery from intense and sustained deer browse on North Manitowish Island, Sleeping Bear Dunes National Lakeshore. Pages 85–108 in *Proceedings: forest and wildlife—striving for balance*. Society of American Foresters, St. Ignace, Michigan, USA.
- Hyatt, L. A., and B. B. Casper. 2000. Seed bank formation during early secondary succession in a temperate deciduous forest. *Journal of Ecology* 88:516–527.
- Jacques, M., L. Lapointe, K. Rice, R. A. Montgomery, A. Stefanski, and P. B. Reich. 2015. Responses of 2 understory herbs, *Maianthemum canadense* and *Eurybia macrophylla*, to experimental forest warming: early emergence is the key to enhanced reproductive output. *American Journal of Botany* 102:1610–1624.
- Jenkins, M. A., and B. S. Howard. 2021. Forest vegetation response to white-tailed deer population reductions in a large urban park. *Natural Areas Journal* 41:114–124.
- Jenkins, L. H., M. A. Jenkins, C. R. Webster, P. A. Zollner, and J. M. Shields. 2014. Herbaceous layer response to 17 years of controlled deer hunting in forested natural areas. *Biological Conservation* 175:119–128.
- Jenkins, L. H., B. D. Murray, M. A. Jenkins, and C. R. Webster. 2015. Woody regeneration response to over a decade of deer population reductions in Indiana state parks. *Journal of the Torrey Botanical Society* 142:205–219.
- Kalisz, S., F. M. Hanzawa, S. J. Tonsor, D. A. Thiede, and S. Voigt. 1999. Ant-mediated seed dispersal alters pattern of relatedness in a population of *Trillium grandiflorum*. *Ecology* 80:2620–2634.
- Kirschbaum, C. D., and B. L. Anacker. 2005. The utility of *Trillium* and *Maianthemum* as phyto-indicators of deer impact in northwestern Pennsylvania, USA. *Forest Ecology and Management* 217:54–66.
- Knight, T. M. 2003. Effects of herbivory and its timing across populations of *Trillium grandiflorum* (Liliaceae). *American Journal of Botany* 90:1207–1214.
- Lapointe, L., J. Bussi eres, M. Cr ete, and J. Ouellet. 2010. Impact of growth form and carbohydrate reserves on tolerance to simulated deer herbivory and subsequent recovery in Liliaceae. *American Journal of Botany* 97:913–924.
- Lashley, M. A., and C. A. Harper. 2012. The effects of extreme drought on native forage nutritional quality and white-tailed deer diet selection. *Southeastern Naturalist* 11:699–710.
- Laurent, L., A. M arell, P. Balandier, H. Holveck, and S. Sa id. 2017. Understorey vegetation dynamics and tree regeneration as affected by deer herbivory in temperate hardwood forests. *iForest* 10:837–844.
- Laverty, T. M. 1992. Plant interactions for pollinator visits: a test of the magnet species effect. *Oecologia* 89:502–508.

- Leopold, A., L. K. Sows, and D. L. Spender. 1947. A survey of over-populated deer ranges in the United States. *Journal of Wildlife Management* 11:162–177.
- McCabe, T. R., and R. E. McCabe. 1997. Recounting whitetails past. Pages 11–26 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. 1997. *The science of overabundance: deer ecology and population management*. Smithsonian Books, Washington, D.C., USA.
- McShea, W. J. 2012. Ecology and management of white-tailed deer in a changing world. *Annals of the New York Academy of Sciences* 1249:45–56.
- McWilliams, W. H., J. A. Westfall, P. H. Brose, D. C. Dey, A. W. D'Amato, Y. L. Dickinson, M. A. Fajvan, L. S. Kenefic, C. C. Kern, K. M. Laustsen, et al. 2018. Subcontinental-scale patterns of large-ungulate herbivory and synoptic review of restoration management implications for Midwestern and northeastern forests. General Technical Report NRS-182. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, Pennsylvania, USA.
- Myers, J. A., M. Vellend, S. Gardescu, and P. L. Marks. 2004. Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* 139:35–44.
- Nagy, C., C. Ng, N. Veverka, and M. Weckel. 2022. Assessment of a 15-year white-tailed deer management program and woody recovery in a suburban forest preserve. *Forest Ecology and Management* 503:119748.
- Niederhauser, E. C., and G. R. Matlack. 2015. All frugivores are not equal: exploitation competition determines seed survival and germination in a fleshy fruited forest herb. *Plant Ecology* 216:1203–1211.
- Nixon, C. M., M. W. McClain, and K. R. Russell. 1970. Deer food habits and range characteristics in Ohio. *Journal of Wildlife Management* 34:870–886.
- Nuttle, T., T. E. Ristau, and A. A. Royo. 2014. Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understoreys reflect past deer density treatments for at least 20 years. *Journal of Ecology* 102:221–228.
- Nuttle, T., A. A. Royo, M. B. Adams, and W. P. Carson. 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. *Ecological Monographs* 83:3–17.
- Nuzzo, V., A. Dávalos, and B. Blossey. 2017. Assessing plant community composition fails to capture impacts of white-tailed deer on native and invasive plant species. *AoB PLANTS* 9:plx026.
- Osborne, J. W. 2010. Improving your data transformations: applying the Box-Cox transformation. *Practical Assessment, Research and Evaluation* 15:1–9.
- Pendergast, T. H., S. M. Hanlon, Z. M. Long, A. A. Royo, and W. P. Carson. 2016. The legacy of deer overabundance: long-term delays in herbaceous understory recovery. *Canadian Journal of Forest Research* 46:362–369.
- Pogge, F. L., and B. C. Bearce. 1989. Germinating common and cat greenbrier. *Tree Planters' Notes* 40:34–37.
- Roble, S. M. 1979. Dispersal movements and plant associations of juvenile gray treefrogs, *Hyla versicolor* Le Conte. *Transactions of the Kansas Academy of Sciences* 82:235–245.
- Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181:165–176.
- Ross, B. A., J. R. Bray, and W. H. Marshall. 1970. Effects of long-term deer exclusion on a *Pinus resinosa* forest in north-central Minnesota. *Ecology* 51:1088–1093.
- Royo, A. A., S. L. Stout, D. S. deCalesta, and T. G. Pierson. 2010. Restoring forest herb communities through landscape-level deer herd reductions: is recovery limited by legacy effects? *Biological Conservation* 143:2425–2434.
- Ruhren, S., and S. N. Handel. 2000. Considering herbivory, reproduction, and gender when monitoring plants: a case study of Jack-in-the-pulpit (*Arisaema triphyllum* [L.] Schott). *Natural Areas Journal* 20:261–266.
- Russell, F. L., D. B. Zippin, and N. L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. *American Midland Naturalist* 146:1–26.
- Rust, R. W., and R. R. Roth. 1981. Seed production and seedling establishment in the mayapple, *Podophyllum peltatum* L. *American Midland Naturalist* 105:51–60.
- Schmit, J. P., E. R. Matthews, and A. Brolis. 2020. Effects of culling white-tailed deer on tree regeneration and *Microstegium vimineum*, an invasive grass. *Forest Ecology and Management* 463:118015.
- Shelton, A. L., J. A. Henning, P. Schultz, and K. Clay. 2014. Effects of abundant white-tailed deer on vegetation, animals, mycorrhizal fungi, and soils. *Forest Ecology and Management* 320:39–49.
- Simard, M. A., C. Dussault, J. Huot, and S. D. Côté. 2013. Is hunting an effective tool to control overabundant deer? A test using an experimental approach. *Journal of Wildlife Management* 77:254–269.
- Smith, R. A., M. L. Kennedy, and G. D. Baumgardner. 1987. Food habits of the raccoon (*Procyon lotor*) at Land Between the Lakes. *Journal of the Tennessee Academy of Science* 62:79–82.
- Steven, J. C., T. P. Rooney, O. D. Boyle, and D. M. Waller. 2003. Density-dependent pollinator visitation and self-incompatibility in upper Great Lakes populations of *Trillium grandiflorum*. *Journal of the Torrey Botanical Society* 130:23–29.
- Stoll, R. J., M. W. McClain, J. C. Clem, and T. Plageman. 1991. Accuracy of helicopter counts of white-tailed deer in western Ohio farmland. *Wildlife Society Bulletin* 19:309–314.
- Stormer, F. A., and W. A. Bauer. 1980. Summer forage use by tame deer in northern Michigan. *Journal of Wildlife Management* 44:98–106.

- Suzuki, M., T. Karukome, K. Fujihira, M. Mitsugi, and Y. Hisamoto. 2021. Clear-cutting triggers regeneration of abandoned secondary forests but risks alternative successional trajectories with high deer density. *Applied Vegetation Science* 24:e12596.
- Tanentzap, A. J., D. R. Bazely, S. Koh, M. Timciska, E. G. Haggith, T. J. Carleton, and D. A. Coomes. 2011. Seeing the forest for the deer: do reductions in deer-disturbance lead to forest recovery? *Biological Conservation* 144:376–382.
- Thomas-Van Gundy, M., J. Rentch, M. B. Adams, and W. Carson. 2014. Reversing legacy effects in the understory of an oak-dominated forest. *Canadian Journal of Forest Research* 44:350–364.
- Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *Journal of Wildlife Management* 53:524–532.
- Trapp, E. J. 1988. Dispersal of heteromorphic seeds in *Amphicarpaea bracteata* (Fabaceae). *American Journal of Botany* 75: 1535–1539.
- Tyndall, R. W. 2020. Changes in herbaceous species variables after enhanced hunting effort for white-tailed deer in Soldiers Delight serpentine ecosystem in Maryland. *Castanea* 85:327–342.
- Vellend, M., J. A. Myers, S. Gardescu, and P. L. Marks. 2003. Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. *Ecology* 84:1067–1072.
- Vuorinen, K. E. M., S. J. Rao, A. J. Hester, and J. D. M. Speed. 2020. Herbivory and climate as drivers of woody plant growth: do deer decrease the impacts of warming? *Ecological Applications* 30:e02119.
- Walters, M. B., E. J. Farinosi, and J. L. Willis. 2020. Deer browsing and shrub competition set sapling recruitment height and interact with light to shape recruitment niches for temperate forest tree species. *Forest Ecology and Management* 467:118134.
- Ward, J. S., and S. C. Williams. 2020. Influence of deer hunting and residual stand structure on tree regeneration in deciduous forests. *Wildlife Society Bulletin* 44:519–530.
- Webster, C. R., and M. A. Jenkins. 2014. Evidence of long and discontinuous juvenile periods in *Trillium catesbaei* under contrasting levels of herbivory. *Botany* 92:77–81.
- Webster, C. R., J. H. Rock, and M. A. Jenkins. 2017. Response of spring flora to nearly 2 decades of deer exclusion and resurgent woody understories within exclosures. *Journal of the Torrey Botanical Society* 144:1–14.
- Whittle, C. A., L. C. Duchesne, and T. Needham. 1998. Soil seed bank of a jack pine (*Pinus banksiana*) ecosystem. *International Journal of Wildland Fire* 8:67–71.
- Wilbur, H. M., K. L. Burke, R. B. Wilbur, and A. Rosenbauer. 2017. Recovery of the herb layer in a southern Appalachian forest following chronic herbivory by deer (*Odocoileus virginianus*). *Castanea* 82:98–113.
- Williams, C. E., E. V. Mosbacher, and W. J. Moriarity. 2000. Use of turtlehead (*Chelone glabra* L.) and other herbaceous plants to assess intensity of white-tailed deer browsing on Allegheny Plateau riparian forests, USA. *Biological Conservation* 92:207–215.
- Williams, S. C., J. S. Ward, and U. Ramakrishnan. 2008. Endozoochory by white-tailed deer (*Odocoileus virginianus*) across a suburban/woodland interface. *Forest Ecology and Management* 255:940–947.
- Wrazen, J. A., and G. E. Svendsen. 1978. Feeding ecology of a population of eastern chipmunks (*Tamias striatus*) in southeast Ohio. *American Midland Naturalist* 100:190–201.
- Wright, G. A., I. Juska, and D. L. Gorchov. 2019. White-tailed deer browse preference for an invasive shrub, Amur honeysuckle (*Lonicera maackii*), depends on woody species composition. *Invasive Plant Science and Management* 12:11–21.

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SUPPORTING INFORMATION

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

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Supporting Information
2022

Abella, S.R, T.A. Schetter, and T.D. Gallaher. 2022. Rapid increase in sensitive indicator plants concurrent with deer management in an oak forest landscape. *Wildlife Society Bulletin*.

Expanded study area description. Supplementary study site descriptions for an investigation of plant community change following culling white-tailed deer populations in northwestern Ohio, USA. The study site descriptions are for 8 long-term plots (measured during the period 2002-2021) and 8 recent plots (measured during the period 2018-2021) corresponding with deer culling beginning in 2016 and continuing through 2021. One plot was randomly located within each of the 16 sites.

The 16 study sites were acquired between 1938 and 1947 by Metroparks Toledo as part of initial acquisitions forming Oak Openings Preserve, presently including 1,737-ha of conservation lands. Based on late 1930s air photos, study sites had forest cover then. Increment boring in 2018 of dominant or co-dominant black oak (*Quercus velutina*) and white oak (*Quercus alba*) trees in and surrounding study sites revealed cross-dated ages of approximately 80-200 years. These were mature oak forest sites with 64-92% tree canopy cover in 2021. Understory tree sapling layers (trees < 15 cm in stem diameter at a height of 1.4 m) were predominately red maple (*Acer rubrum*). The litter layer (Oi horizon), primarily consisting of tree leaves, averaged 3.5 cm thick. The decomposing organic layer (Oea horizon) averaged 3.2 cm thick. Textures of the upper 15 cm of mineral soil were similar among sites as either sand or loamy sand. The pH (1:1 soil:H₂O) of this mineral soil layer ranged from 4.3-4.9. Soils were classified as Udipsamments of the Oakville and Ottokee series (Stone et al. 1980). Land use did not change for the duration of the study (2002-2021). All sites were managed as habitat conservation lands, with minimal to no evidence of human disturbance at the sites during the study. Except for one site partly burned at low severity in a 2014 prescribed fire, sites were unburned since 2002 and likely for much longer. Other than the 2014 prescribed fire at the one site, the most recent fires may have been in the early 1900s or most likely 1800s (Brewer and Vankat 2004).

Study sites provided extensive geographic coverage in mature oak forests within the study area and exhibited minimal spatial autocorrelation in plant community change following deer culling. Pairwise geographic distances between long-term plots ranged from 0.3-3.1 km and averaged 1.4 km. Among recent plots, pairwise geographic distances ranged from 0.1-2.3 km and also averaged 1.4 km. All 16 plots in total were separated by an average of 1.7 km (0.1-4.4 km range). To test for possible spatial associations among the 16 plots, we compared a matrix of geographic distances between plots based on plot locations (*x, y* coordinates in meters in Universal Transverse Mercator, North American Datum 1983) with 4 matrices of deer indicator plant variables (2021 indicator plant species/0.05 ha plot and cover and the change in these variables between 2018 and 2021) using Mantel tests (Urban et al. 2002). Mantel tests assess the degree of correlation between 2 matrices and provide a standardized Mantel statistic (*r*) and *P* value, similar in interpretation to the bivariate correlation coefficient. We implemented the Mantel test using Euclidean distance in PC-ORD 7.07 (McCune and Mefford 1999). No significant relationship occurred between geographic distance and any of the 4 deer indicator plant variables (2021 species richness: $r = -0.11$, $P = 0.321$; 2021 cover: $r = -0.04$, $P = 0.784$; change in species richness: $r = -0.07$, $P = 0.563$; change in cover: $r = -0.02$, $P = 0.0889$). In addition to rejecting a hypothesis of spatial autocorrelation among plots, the Mantel test results supported an interpretation of consistent increases in indicator plants across the landscape during deer culling. While the magnitude of the increases did vary among plots, all 16 plots consistently showed some increase in indicator plant species richness and cover from 2018 to 2021, suggesting a spatially consistent qualitative increase in indicator plants.

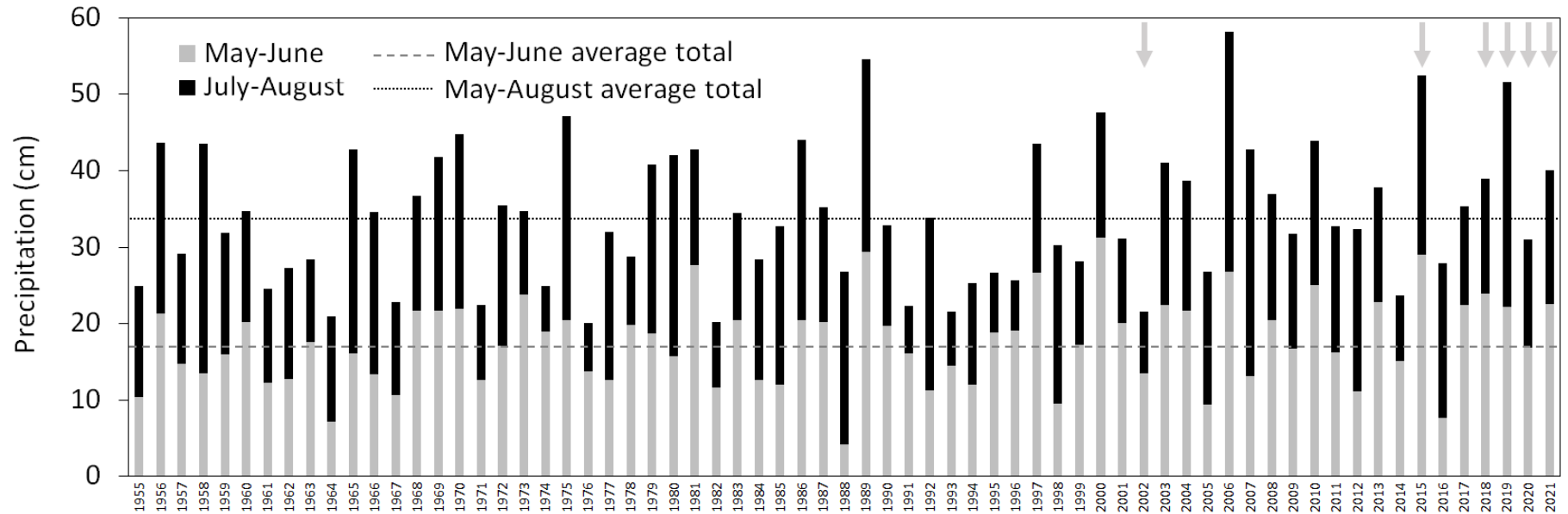


Figure S1. Summer precipitation in the long-term climate record and in 6 study years (indicated by arrows) during a study of change in plants sensitive to white-tailed deer herbivory following deer culling beginning in 2016, northwestern Ohio, USA. Precipitation is partitioned into early (May-June) and late (July-August) summer. Precipitation was recorded 5 km northeast of the study area at the Toledo Airport (National Oceanic and Atmospheric Administration, National Centers for Environmental Information, Asheville, North Carolina, USA).

Table S1. List of 43 indicator species sensitive to white-tailed deer herbivory that were monitored during a 20-year period in oak forests, northwestern Ohio, USA. The species list and species classification into 6 groups was based on 46 published studies of plant sensitivity to deer herbivory in eastern North America. Sensitivity was quantified in forage-preference (comparing selection relative to availability) and herbivory-resilience studies (e.g., resilience of plants inside deer exclosures).

Indicator group	References
Liliaceae	
<i>Maianthemum canadense</i>	Abrams and Johnson 2012, Casabon and Pothier 2008, Collard et al. 2010, Crête et al. 2001, Daigle et al. 2004, Goetsch et al. 2011, Hidding et al. 2013, Holmes and Webster 2011, Koh et al. 1996, Pekins and Mautz 1987, Rooney 2009, Stormer and Bauer 1980
<i>Maianthemum racemosum</i>	Abrams and Johnson 2012, Asnani et al. 2006, Balgooyen and Waller 1995, Fletcher et al. 2001, Frankland and Nelson 2003, Frerker et al. 2014, Goetsch et al. 2011, Murray et al. 2016, Pendergast et al. 2016
<i>Medeola virginiana</i>	Abrams and Johnson 2012, Goetsch et al. 2011, Wilbur et al. 2017
<i>Polygonatum biflorum</i>	Abrams and Johnson 2012, Dobson and Blossey 2015, Fletcher et al. 2001, Knight et al. 2009, Webster et al. 2017
<i>Trillium grandiflorum</i>	Asnani et al. 2006, Balgooyen and Waller 1995, Crête et al. 2001, Frerker et al. 2014, Holmes and Webster 2011, Knight et al. 2009, Koh et al. 1996, Koh et al. 2010
<i>Uvularia sessilifolia</i>	Balgooyen and Waller 1995, Fletcher et al. 2001
Fabaceae	
<i>Amphicarpaea bracteata</i>	Murray et al. 2016
<i>Desmodium glutinosum</i>	Lashley and Harper 2012, Snider and Asplund 1974
<i>Desmodium nudiflorum</i>	Abrams and Johnson 2012, Lashley and Harper 2012
<i>Robinia pseudoacacia</i>	Halls et al. 1960, Moore and Johnson 1967
Primary indicators	
<i>Actaea pachypoda</i>	Crête et al. 2001, Dobson and Blossey 2015, Goetsch et al. 2011, Shelton et al. 2014
<i>Aralia nudicaulis</i>	Abrams and Johnson 2012, Balgooyen and Waller 1995, Crête et al. 2001, Daigle et al. 2004, Forrester et al 2006, Frerker et al. 2014
<i>Arisaema triphyllum</i>	Abrams and Johnson 2012, Collard et al. 2010, Crête et al. 2001, Fletcher et al. 2001, Frankland and Nelson 2003, Goetsch et al. 2011, Heckel et al. 2010, Koh et al. 1996, Murray et al. 2016, Pendergast et al. 2016, Rooney 2009, Ruhren and Handel 2000
<i>Gaultheria procumbens</i>	Dahlberg 1956, Pekins and Mautz 1987, Ross et al. 1970
<i>Geranium maculatum</i>	Anderson 1994, Dobson and Blossey 2015, Williams et al. 2000
<i>Geum canadense</i>	Abrams and Johnson 2012, Dobson and Blossey 2015, Williams et al. 2000
<i>Lactuca canadensis</i>	Augustine and deCalesta 2003, Shelton and Inouye 1995, Snider and Asplund 1974

<i>Osmorhiza claytonii</i>	Abrams and Johnson 2012, Augustine and deCalesta 2003, Crête et al. 2001, Pendergast et al. 2016, Shelton et al. 2014
<i>Osmorhiza longistylis</i>	Abrams and Johnson 2012, Augustine and deCalesta 2003
Secondary indicators	
<i>Agrimonia gryposepala</i>	Dobson and Blossey 2015
<i>Anemone quinquefolia</i>	Crête et al. 2001, Koh et al. 1996
<i>Arisaema dracontium</i>	Abrams and Johnson 2012
<i>Circaea lutetiana</i>	Williams et al. 2000
<i>Comandra umbellata</i>	Anderson et al. 2004
<i>Dioscorea villosa</i>	Lashley and Harper 2012
<i>Eurybia macrophylla</i>	Balگوoyen and Waller 1995
<i>Hieracium scabrum</i>	Stormer and Bauer 1980
<i>Podophyllum peltatum</i>	Abrams and Johnson 2012, Asnani et al. 2006, Frankland and Nelson 2003
<i>Symphotrichum lateriflorum</i>	Murray et al. 2016
<i>Thalictrum dioicum</i>	Dobson and Blossey 2015
<i>Viburnum acerifolium</i>	Abrams and Johnson 2012, Frerker et al. 2014
<i>Viburnum dentatum</i>	Abrams and Johnson 2012
<i>Viola pubescens</i>	Anderson 1994, Frerker et al. 2014, Shelton et al. 2014
<i>Viola sororia</i>	Augustine and deCalesta 2003, Webster et al. 2017
<i>Rubus</i>	
<i>Rubus allegheniensis</i>	Goetsch et al. 2011, genus ^a
<i>Rubus flagellaris</i>	Dahlberg 1956, genus ^a
<i>Rubus hispidus</i>	Genus ^a
<i>Rubus idaeus</i>	Casabon and Pothier 2008, Dostaler et al. 2011, Goetsch et al. 2011, Hidding et al. 2013, Rooney 2009, genus ^a
<i>Rubus occidentalis</i>	Genus ^a
<i>Smilax</i>	
<i>Smilax glauca</i>	Abrams and Johnson 2012, genus ^a
<i>Smilax herbacea</i>	Genus ^a
<i>Smilax rotundifolia</i>	Bramble and Goddard 1953, Forrester et al 2006, Knierim et al. 1971, genus ^a
<i>Smilax tamnoides</i>	Snider and Asplund 1974, genus ^a

^aMany studies combined species within *Rubus* and *Smilax* at the genus level. Studies reporting the *Rubus* genus as indicator plants of deer herbivory include: Case and McCullough 1987, Daigle et al. 2004, Halls and Crawford 1960, Johnson et al. 1995, Lashley and Harper 2012, and Parker et al. 2020.

Studies reporting the *Smilax* genus as indicator plants of deer herbivory include: Apsley and McCarthy 2004, Bramble and Goddard 1953, Halls and Crawford 1960, Harlow et al. 1975, Johnson et al. 1995, and Lashley and Harper 2012.

Table S2. Traits of 31 forb species comprising indicator species sensitive to white-tailed deer herbivory that were assessed during a 20-year period in oak forests, northwestern Ohio, USA. Traits were obtained from published literature with an example reference provided. References were chosen to be review articles or among the most comprehensive autecology papers of a species where possible. Flowering timing is classified as early (May-June) or late (July-September). The species traits were used to construct Fig. 5 of the paper.

Indicator group	Rhizomatous	Clonal	Flowering	Example reference
Liliaceae				
<i>Maianthemum canadense</i>	Yes	Yes	Early	Lapointe et al. 2010
<i>Maianthemum racemosum</i>	Yes	Yes	Early	Brundrett and Kendrick 1990
<i>Medeola virginiana</i>	Yes	Yes	Early	Cook 1988
<i>Polygonatum biflorum</i>	Yes	Yes	Early	Ownbey 1944
<i>Trillium grandiflorum</i>	Yes	No	Early	Knight 2003
<i>Uvularia sessilifolia</i>	Yes	Yes	Early	Wijesinghe and Whigham 2001
Fabaceae				
<i>Amphicarpaea bracteata</i>	No	No	Late	Trapp 1988
<i>Desmodium glutinosum</i>	No	No	Late	Buss et al. 1969
<i>Desmodium nudiflorum</i>	No	No	Late	Huang and Boerner 2008
Primary indicators				
<i>Actaea pachypoda</i>	No	No	Early	Sobey and Barkhouse 1977
<i>Aralia nudicaulis</i>	Yes	Yes	Early	Flanagan and Bain 1988
<i>Arisaema triphyllum</i>	No	Yes	Early	Levine and Feller 2004
<i>Geranium maculatum</i>	Yes	Yes	Early	Martin 1965
<i>Geum canadense</i>	Yes	Yes	Late	Baskin and Baskin 1985
<i>Lactuca canadensis</i>	No	No	Late	Shelton and Inouye 1995
<i>Osmorhiza claytonii</i>	No	No	Early	Baskin and Baskin 1991
<i>Osmorhiza longistylis</i>	No	No	Early	Baskin and Baskin 1984
Secondary indicators				
<i>Agrimonia gryposepala</i>	Yes	Yes	Late	Greller 1977
<i>Anemone quinquefolia</i>	Yes	Yes	Early	Keener 1975
<i>Arisaema dracontium</i>	No	Yes	Early	Yang et al. 1999
<i>Circaea lutetiana</i>	Yes	Yes	Late	Verburg et al. 2000
<i>Comandra umbellata</i>	Yes	Yes	Late	Piehl 1965
<i>Dioscorea villosa</i>	Yes	Yes	Late	Albrecht and McCarthy 2006
<i>Eurybia macrophylla</i>	Yes	Yes	Late	Jacques et al. 2015
<i>Hieracium scabrum</i>	Yes	Yes	Late	French 2021
<i>Podophyllum peltatum</i>	Yes	Yes	Early	Krochmal et al. 1974
<i>Symphyotrichum lateriflorum</i>	Yes	Yes	Late	Chmielewski and Semple 2001
<i>Thalictrum dioicum</i>	No	No	Early	Steven and Waller 2004
<i>Viola pubescens</i>	Yes	No	Early	Culley 2002
<i>Viola sororia</i>	Yes	Yes	Early	Antlfinger et al. 1985
Smilax				
<i>Smilax herbacea</i>	Yes	No	Early	Sawyer and Anderson 1998

Table S3. Statistical results for change in species richness and cover of indicator plants among years in a white-tailed deer culling study in oak forests, northwestern Ohio, USA. Results are from repeated-measures analysis of variance comparing vegetation response variables across years and correspond with Fig. 4 of the paper.

	Long-term plots		Recent plots	
	$F_{5,42}$	P	$F_{2,21}$	P
Species richness	6.28	<0.001	16.02	<0.001
Total cover	10.90	<0.001	50.82	<0.001
Liliaceae	11.45	<0.001	6.58	0.010
Fabaceae	0.48	0.787	1.28	0.310
Primary indicator	3.83	0.007	2.97	0.084
Secondary indicator	2.02	0.101	9.41	0.003
<i>Rubus</i>	0.81	0.547	17.30	<0.001
<i>Smilax</i>	5.43	<0.001	6.41	0.011

Table S4. Mean cover and frequency of 43 indicator plant species of white-tailed deer herbivory among study years in oak forests, northwestern Ohio, USA.

Indicator group	Long-term plots					Recent plots			
	2002	2015	2018	2019	2020	2021	2018	2020	2021
Liliaceae	Mean percent cover (frequency) ^a								
<i>Maianthemum canadense</i>	– ^b	0.04 (3)	–	0.01 (1)	0.01 (1)	0.01 (1)	–	–	–
<i>Maianthemum racemosum</i>	0.28 (7)	0.11 (5)	0.14 (6)	0.21 (6)	0.34 (7)	0.23 (8)	0.09 (7)	0.11 (7)	0.14 (8)
<i>Medeola virginiana</i>	0.01 (1)	–	0.03 (2)	0.03 (2)	0.03 (1)	0.04 (2)	0.13 (1)	0.38 (1)	0.51 (2)
<i>Polygonatum biflorum</i>	0.01 (1)	0.01 (1)	0.01 (1)	0.03 (2)	0.04 (2)	0.04 (3)	–	–	–
<i>Trillium grandiflorum</i>	–	–	0.01 (1)	0.01 (1)	0.01 (1)	0.03 (1)	–	–	0.01 (1)
<i>Uvularia sessilifolia</i>	0.54 (7)	0.01 (1)	0.34 (5)	0.37 (5)	1.06 (7)	1.12 (7)	0.26 (4)	0.79 (5)	1.42 (5)
Fabaceae									
<i>Amphicarpaea bracteata</i>	–	–	–	–	–	–	–	–	0.03 (2)
<i>Desmodium glutinosum</i>	–	–	–	–	–	–	0.01 (1)	0.01 (1)	0.01 (1)
<i>Desmodium nudiflorum</i>	0.27 (6)	0.09 (7)	0.13 (6)	0.15 (6)	0.14 (5)	0.18 (6)	0.11 (5)	0.40 (3)	0.41 (4)
<i>Robinia pseudoacacia</i>	–	0.01 (1)	0.01 (1)	–	0.03 (1)	0.03 (1)	–	–	–
Primary indicators									
<i>Actaea pachypoda</i>	–	–	–	–	–	–	0.01 (1)	0.03 (1)	0.03 (1)
<i>Aralia nudicaulis</i>	0.80 (5)	0.26 (2)	1.09 (4)	3.84 (4)	3.91 (4)	4.53 (4)	–	–	0.01 (1)
<i>Arisaema triphyllum</i>	0.03 (1)	–	–	–	0.01 (1)	0.03 (1)	0.04 (2)	0.06 (3)	0.16 (2)
<i>Gaultheria procumbens</i>	0.08 (2)	0.01 (1)	0.01 (1)	0.01 (1)	0.01 (1)	0.03 (1)	0.01 (1)	0.01 (1)	0.01 (1)
<i>Geranium maculatum</i>	–	–	–	–	–	0.01 (1)	0.13 (1)	0.39 (2)	0.39 (2)
<i>Geum canadense</i>	0.01 (1)	–	0.04 (3)	0.04 (3)	0.05 (4)	0.09 (6)	0.03 (2)	0.04 (3)	0.04 (3)
<i>Lactuca canadensis</i>	–	0.01 (1)	–	–	0.01 (1)	–	–	–	–
<i>Osmorhiza claytonii</i>	0.03 (3)	0.01 (1)	0.03 (2)	0.03 (2)	0.04 (2)	0.03 (2)	–	–	–
<i>Osmorhiza longistylis</i>	0.03 (2)	–	–	–	–	–	–	–	–
Secondary indicators									
<i>Agrimonia gryposepala</i>	–	–	–	–	–	–	–	0.01 (1)	0.01 (1)
<i>Anemone quinquefolia</i>	–	–	–	–	–	–	–	–	0.04 (2)
<i>Arisaema dracontium</i>	–	–	–	–	–	–	–	–	0.01 (1)
<i>Circaea lutetiana</i>	0.05 (3)	0.01 (1)	0.03 (2)	0.03 (2)	0.04 (2)	0.04 (2)	0.06 (5)	0.11 (4)	0.14 (4)
<i>Comandra umbellata</i>	0.01 (1)	–	–	–	–	0.01 (1)	–	–	–

<i>Dioscorea villosa</i>	0.04 (3)	0.03 (2)	0.04 (2)	0.04 (2)	0.03 (2)	0.03 (2)	0.04 (3)	0.04 (3)	0.04 (3)
<i>Eurybia macrophylla</i>	0.32 (3)	0.03 (2)	0.28 (3)	0.65 (3)	0.67 (3)	0.67 (3)	0.01 (1)	0.03 (2)	0.04 (3)
<i>Hieracium scabrum</i>	–	–	–	–	–	–	–	0.01 (1)	0.01 (1)
<i>Podophyllum peltatum</i>	0.01 (1)	–	0.01 (1)	0.01 (1)	0.04 (2)	0.04 (2)	0.03 (2)	0.29 (4)	1.42 (5)
<i>Symphyotrichum lateriflorum</i>	–	–	–	–	–	–	–	–	0.01 (1)
<i>Thalictrum dioicum</i>	0.01 (1)	–	–	–	–	–	0.01 (1)	0.01 (1)	0.01 (1)
<i>Viburnum acerifolium</i>	–	0.01 (1)	0.01 (1)	0.03 (1)	0.06 (1)	0.03 (2)	–	–	–
<i>Viburnum dentatum</i>	–	–	–	–	–	0.01 (1)	–	–	–
<i>Viola pubescens</i>	0.02 (1)	0.01 (1)	–	0.01 (1)	0.01 (1)	0.01 (1)	0.01 (1)	0.01 (1)	0.01 (1)
<i>Viola sororia</i>	0.01 (1)	0.03 (2)	0.01 (1)	0.01 (1)	0.03 (2)	0.03 (2)	–	–	0.03 (2)
<i>Rubus</i>									
<i>Rubus allegheniensis</i>	–	0.04 (3)	0.04 (3)	0.03 (2)	0.09 (6)	0.10 (4)	0.01 (1)	0.07 (4)	0.06 (3)
<i>Rubus flagellaris</i>	0.58 (7)	0.41 (4)	0.41 (4)	0.17 (3)	0.18 (4)	0.31 (4)	0.09 (6)	0.49 (7)	0.52 (7)
<i>Rubus hispidus</i>	–	0.01 (1)	0.01 (1)	0.38 (1)	0.76 (2)	0.88 (1)	0.01 (1)	0.03 (1)	0.04 (2)
<i>Rubus idaeus</i>	–	0.01 (1)	–	–	–	–	–	–	–
<i>Rubus occidentalis</i>	–	0.01 (1)	0.01 (1)	0.03 (2)	–	0.01 (1)	–	–	0.03 (2)
<i>Smilax</i>									
<i>Smilax glauca</i>	0.03 (2)	0.20 (3)	0.24 (7)	0.23 (6)	0.31 (8)	0.57 (7)	0.06 (5)	0.08 (5)	0.12 (5)
<i>Smilax herbacea</i>	–	–	–	–	0.01 (1)	0.01 (1)	–	0.01 (1)	0.03 (2)
<i>Smilax rotundifolia</i>	0.41 (5)	0.05 (4)	0.68 (4)	0.72 (4)	1.17 (5)	1.28 (4)	0.11 (7)	0.14 (7)	0.14 (5)
<i>Smilax tamnoides</i>	–	–	0.01 (1)	0.01 (1)	–	0.08 (5)	0.01 (1)	0.03 (2)	0.08 (5)

^aCover is the mean by year on 8 long-term plots and 8 recent plots. Frequency is the number of plots a species inhabited (out of 8 plots).

^b– signifies species not present.

Table S5. Statistical results of repeated measures permutational analysis of variance evaluating whether cover changed between 2015 and 2021 (long-term plots) or 2018 and 2021 (recent plots) for deer-sensitive forbs classified according to species traits. Flowering timing is classified as early (May-June) or late (July-September). The statistical results correspond with Fig. 5 of the paper.

Test comparison	DF ^a	<i>F</i>	<i>P</i>
Long-term plots			
Rhizomatous + clonal reproduction			
No	1, 24	2.91	0.130
Yes	1, 34	2.17	0.003
Flowering timing			
Early	1, 36	1.72	0.005
Late	1, 22	1.84	0.094
Recent plots			
Rhizomatous + clonal reproduction			
No	1, 24	2.79	0.014
Yes	1, 34	4.03	< 0.001
Flowering timing			
Early	1, 36	4.08	< 0.001
Late	1, 22	2.63	0.008

^aDegrees of freedom.

References

- Albrecht, M.A., and B.C. McCarthy. 2006. Seed germination and dormancy in the medicinal woodland herbs *Collinsonia canadensis* L. (Lamiaceae) and *Dioscorea villosa* L. (Dioscoreaceae). *Flora* 201:24-31.
- Anderson, R.C. 1994. Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. *Ecological Applications* 4:104-109.
- Anderson, R.C., D. Nelson, M.R. Anderson, and M.A. Rickey. 2004. White-tailed deer (*Odocoileus virginianus* Zimmermann) browsing effects on quality of tallgrass prairie community forbs. Pp. 63-69 in Egan, D., and J.A. Harrington (eds.). Proceedings of the 19th North American prairie conference. University of Wisconsin, Madison, Wisconsin. 292 pp.
- Antlfinger, A.E., W.F. Curtis, and O.T. Solbrig. 1985. Environmental and genetic determinants of plant size in *Viola sororia*. *Evolution* 39:1053-1064.
- Apsley, D.K., and B.C. McCarthy. 2004. White-tailed deer herbivory on forest regeneration following fire and thinning treatments in southern Ohio mixed oak forests. Pp. 461-471 in Yaussy, D.A., D.M. Hix, P.C. Goebel, and R.P. Long (eds.). Proceedings: 14th central hardwood forest conference. General Technical Report GTR-NE-316. U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA. 539 pp.
- Asnani, K.M., R.A. Klips, and P.S. Curtis. 2006. Regeneration of woodland vegetation after deer browsing in Sharon Woods Metro Park, Franklin County, Ohio. *Ohio Journal of Science* 106:86-92.
- Augustine, D.J., and D. deCalesta. 2003. Defining deer overabundance and threats to forest communities: from individual plants to landscape structure. *Ecoscience* 10:472-486.
- Baskin, J.M., and C.C. Baskin. 1984. Germination ecophysiology of the woodland herb *Osmorhiza longistylis* (Umbelliferae). *American Journal of Botany* 71:687-692.
- Baskin, J.M., and C.C. Baskin. 1985. Role of dispersal date and changes in physiological responses in controlling timing of germination in achenes of *Geum canadense*. *Canadian Journal of Botany* 63:1654-1658.
- Baskin, J.M., and C.C. Baskin. 1991. Nondeep complex morphophysiological dormancy in seeds of *Osmorhiza claytonii* (Apiaceae). *American Journal of Botany* 78:588-593.
- Bramble, W.C., and M.K. Goddard. 1953. Seasonal browsing of woody plants by white-tailed deer in the Ridge and Valley section of central Pennsylvania. *Journal of Forestry* 51:815-819.
- Brewer, L.G., and J.L. Vankat. 2004. Description of the vegetation of the Oak Openings of northwestern Ohio at the time of Euro-American settlement. *Ohio Journal of Science* 104:76-85.
- Brundrett, M., and B. Kendrick. 1990. The roots and mycorrhizas of herbaceous woodland plants. I. Quantitative aspects of morphology. *New Phytologist* 114:457-468.
- Buss, P.A., D.F. Galen, and N.R. Lersten. 1969. Pollen and tapetum development in *Desmodium glutinosum* and *D. illinoense* (Papilionoideae; Leguminosae). *American Journal of Botany* 56:1203-1208.
- Casabon, C., and D. Pothier. 2008. Impact of deer browsing on plant communities in cutover sites on Anticosti Island. *Ecoscience* 15:389-397.
- Case, D.J., and D.R. McCullough. 1987. The white-tailed deer of North Manitou Island. *Hilgardia* 55:1-57.
- Chmielewski, J.G., and J.C. Semple. 2001. The biology of Canadian weeds. 113. *Symphyotrichum lanceolatum* (Willd.) Nesom [*Aster lanceolatus* Willd.] and *S. lateriflorum* (L.) Löve & Löve [*Aster lateriflorus* (L.) Britt.]. *Canadian Journal of Plant Science* 81:829-849.
- Collard, A., L. Lapointe, J. Ouellet, M. Crête, A. Lussier, C. Daigle, and S.D. Côté. 2010. Slow

- responses of understory plants of maple-dominated forests to white-tailed deer experimental exclusion. *Forest Ecology and Management* 260:649-662.
- Cook, R.E. 1988. Growth in *Medeola virginiana* clones. I. Field observations. *American Journal of Botany* 75:725-731
- Côté, S.D., T.P. Rooney, J. Tremblay, C. Dussault, and D.M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology and Systematics* 35:113-147.
- Crête, M., J. Ouellet, and L. Lesage. 2001. Comparative effects on plants of caribou/reindeer, moose and white-tailed deer herbivory. *Arctic* 54:407-417.
- Culley, T.M. 2002. Reproductive biology and delayed selfing in *Viola pubescens* (Violaceae), an understory herb with chasmogamous and cleistogamous flowers. *International Journal of Plant Sciences* 163:113-122.
- Dahlberg, B.L., and R.C. Guettinger. 1956. The white-tailed deer in Wisconsin. Technical Wildlife Bulletin 14. Wisconsin Conservation Department, Madison, WI. 282 pp.
- Daigle, C., M. Crête, L. Lesage, J. Ouellet, and J. Huot. 2004. Summer diet of two white-tailed deer, *Odocoileus virginianus*, populations living at low and high density in southern Québec. *Canadian Field-Naturalist* 118:360-367.
- Dobson, A., and B. Blossey. 2015. Earthworm invasion, white-tailed deer and seedling establishment in deciduous forests of north-eastern North America. *Journal of Ecology* 103:153-164.
- Dostaler, S., J. Ouellet, J. Therrien, and S.D. Côté. 2011. Are feeding preferences of white-tailed deer related to plant constituents? *Journal of Wildlife Management* 75:913-918.
- Flanagan, L.B., and J.F. Bain. 1988. The biological flora of Canada: 8. *Aralia nudicaulis* L., wild sarsaparilla. *Canadian Field-Naturalist* 102:45-59.
- Fletcher, J.D., W.J. McShea, L.A. Shipley, and D. Shumway. 2001. Use of common forest forbs to measure browsing pressure by white-tailed deer (*Odocoileus virginianus* Zimmerman) in Virginia, USA. *Natural Areas Journal* 21:172-176.
- Forrester, J.A., D.J. Leopold, and H.B. Underwood. 2006. Isolating the effects of white-tailed deer on the vegetation dynamics of a rare maritime American holly forest. *American Midland Naturalist* 156:135-150.
- Frankland, F., and T. Nelson. 2003. Impacts of white-tailed deer on spring wildflowers in Illinois, USA. *Natural Areas Journal* 23:341-348.
- French, K. 2021. Invasion by hawkweeds. *Biological Invasions* 23:3641-3652.
- Frerker, K., A. Sabo, and D. Waller. 2014. Long-term regional shifts in plant community composition are largely explained by local deer impact experiments. *PLoS ONE* 9:e115843.
- Goetsch, C., J. Wigg, A.A. Royo, T. Ristau, and W.P. Carson. 2011. Chronic over browsing and biodiversity collapse in a forest understory in Pennsylvania: results from a 60 year-old deer exclusion plot. *Journal of the Torrey Botanical Society* 138:220-224.
- Greller, A.M. 1977. A vascular flora of the forested portion of Cunningham Park, Queens County, New York, with notes on the vegetation. *Bulletin of the Torrey Botanical Club* 104:170-176.
- Halls, L.K., and H.S. Crawford. 1960. Deer-forest habitat relationships in north Arkansas. *Journal of Wildlife Management* 24:387-395.
- Harlow, R.F., P.A. Shrauder, and M.E. Seehorn. 1975. Deer browse resources of the Oconee national Forest. Research Paper SE-137. U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, NC. 16 pp.
- Heckel, C.D., N.A. Bourg, W.J. McShea, and S. Kalisz. 2010. Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. *Ecology* 91:319-326.
- Hidding, B., J. Tremblay, and S.D. Côté. 2013. A large herbivore triggers alternative successional trajectories in the boreal forest. *Ecology* 94:2852-2860.

- Huang, J., and R.E.J. Boerner. 2008. Shifts in morphological traits, seed production, and early establishment of *Desmodium nudiflorum* following prescribed fire, alone or in combination with forest canopy thinning. *Botany* 86:376-384.
- Jacques, M., L. Lapointe, K. Rice, R.A. Montgomery, A. Stefanski, and P.B. Reich. 2015. Responses of two understory herbs, *Maianthemum canadense* and *Eurybia macrophylla*, to experimental forest warming: early emergence is the key to enhanced reproductive output. *American Journal of Botany* 102:1610-1624.
- Jenkins, L.H., M.A. Jenkins, C.R. Webster, P.A. Zollner, and J.M. Shields. 2014. Herbaceous layer response to 17 years of controlled deer hunting in forested natural areas. *Biological Conservation* 175:119-128.
- Jenkins, L.H., B.D. Murray, M.A. Jenkins, and C.R. Webster. 2015. Woody regeneration response to over a decade of deer population reductions in Indiana state parks. *Journal of the Torrey Botanical Society* 142:205-219.
- Johnson, A.S., P.E. Hale, W.M. Ford, J.M. Wentworth, J.R. French, O.F. Anderson, and G.B. Pullen. 1995. White-tailed deer foraging in relation to successional stage, overstory type and management of southern Appalachian forests. *American Midland Naturalist* 133:18-35.
- Keener, C.S. 1975. Studies in the Ranunculaceae of the southeastern United States. I. *Anemone L. Castanea* 40:36-44.
- Kirschbaum, C.D., and B.L. Anacker. 2005. The utility of *Trillium* and *Maianthemum* as phyto-indicators of deer impact in northwestern Pennsylvania, USA. *Forest Ecology and Management* 217:54-66.
- Knierim, P.G., K.L. Carvell, and J.D. Gill. 1971. Browse in thinned oak and cove hardwood stands. *Journal of Wildlife Management* 35:163-168.
- Knight, T.M. 2003. Floral density, pollen limitation, and reproductive success in *Trillium grandiflorum*. *Oecologia* 442:557-563.
- Knight, T.M., J.L. Dunn, L.A. Smith, J. Davis, and S. Kalisz. 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. *Natural Areas Journal* 29:110-116.
- Koh, S., T.A. Watt, D.R. Bazely, D.L. Pearl, M. Tang, and T.J. Carleton. 1996. Impact of herbivory of white-tailed deer (*Odocoileus virginianus*) on plant community composition. *Aspects of Applied Biology* 44:445-450.
- Koh, S., D.R. Bazely, A.J. Tanentzap, D.R. Voigt, and E. Da Silva. 2010. *Trillium grandiflorum* height is an indicator of white-tailed deer density at local and regional scales. *Forest Ecology and Management* 259:1472-1479.
- Krochmal, A., L. Wilkins, D. Van Lear, and M. Chien. 1974. Mayapple (*Podophyllum peltatum* L.). Research Paper NE-296. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA. 9 pp.
- Lapointe, L., J. Bussi eres, M. Cr ete, and J. Ouellet. 2010. Impact of growth form and carbohydrate reserves on tolerance to simulated deer herbivory and subsequent recovery in Liliaceae. *American Journal of Botany* 97:913-924.
- Lashley, M.A., and C.A. Harper. 2012. The effects of extreme drought on native forage nutritional quality and white-tailed deer diet selection. *Southeastern Naturalist* 11:699-710.
- Levine, M.T., and I.C. Feller. 2004. Effects of forest age and disturbance on population persistence in the understory herb, *Arisaema triphyllum* (Araceae). *Plant Ecology* 172:73-82.
- Martin, S.M.C. 1965. An ecological life history of *Geranium maculatum*. *American Midland Naturalist* 73:111-149.
- McCune, B., and M.J. Mefford. 1999. PC-ORD: multivariate analysis of ecological data. User's guide. MjM Software Design, Glenden Beach, Oregon. 237 pp.

- Moore, W.H., and F.M. Johnson. 1967. Nature of deer browsing on hardwood seedlings and sprouts. *Journal of Wildlife Management* 31:351-353.
- Murray, B.D., C.R. Webster, M.A. Jenkins, M.R. Saunders, and G.S. Haulton. 2016. Ungulate impacts on herbaceous-layer plant communities in even-aged and uneven-aged managed forests. *Ecosphere* 7:e01378.
- Ownbey, R.P. 1944. The Liliaceous genus *Polygonatum* in North America. *Annals of the Missouri Botanical Garden* 31:373-413.
- Parker, H.A., J.T. Larkin, D. Heggenstaller, J. Duchamp, M.C. Tyree, C.S. Rushing, E.J. Domoto, and J.L. Larkin. 2020. Evaluating the impacts of white-tailed deer (*Odocoileus virginianus*) browsing on vegetation in fenced and unfenced timber harvests. *Forest Ecology and Management* 473:118326.
- Pekins, P.J., and W.M. Mautz. 1987. Acorn usage by deer: significance of oak management. *Northern Journal of Applied Forestry* 4:124-128.
- Pendergast, T.H., S.M. Hanlon, Z.M. Long, A.A. Royo, and W.P. Carson. 2016. The legacy of deer overabundance: long-term delays in herbaceous understory recovery. *Canadian Journal of Forest Research* 46:362-369.
- Piehl, M.A. 1965. The natural history and taxonomy of *Comandra* (Santalaceae). *Memoirs of the Torrey Botanical Club* 22:1-97.
- Rooney, T.P. 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. *Plant Ecology* 202:103-111.
- Ross, B.A., J.R. Bray, and W.H. Marshall. 1970. Effects of long-term deer exclusion on a *Pinus resinosa* forest in north-central Minnesota. *Ecology* 51:1088-1093.
- Sawyer, N.W., and G.J. Anderson. 1998. Reproductive biology of the carrion-flower, *Smilax herbacea* (Smilacaceae). *Rhodora* 100:1-24.
- Shelton, A.L., and R.S. Inouye. 1995. Effect of browsing by deer on the growth and reproductive success of *Lactuca canadensis* (Asteraceae). *American Midland Naturalist* 134:332-339.
- Shelton, A.L., J.A. Henning, P. Schultz, and K. Clay. 2014. Effects of abundant white-tailed deer on vegetation, animals, mycorrhizal fungi, and soils. *Forest Ecology and Management* 320:39-49.
- Snider, C.C., and J.M. Asplund. 1974. In vitro digestibility of deer foods from the Missouri Ozarks. *Journal of Wildlife Management* 38:20-31.
- Sobey, D.G., and P. Barkhouse. 1977. The structure and rate of growth of the rhizomes of some forest herbs and dwarf shrubs of the New Brunswick – Nova Scotia border region. *Canadian Field-Naturalist* 91:377-383.
- Steven, J.C., and D.M. Waller. 2004. Reproductive alternatives to insect pollination in four species of *Thalictrum* (Ranunculaceae). *Plant Species Biology* 19:73-80.
- Stone, K.L., E.H. McConoughey, G.D. Bottrell, and D.J. Crouner. 1980. Soil Survey of Lucas County, Ohio. U.S. Department of Agriculture, Soil Conservation Service. U.S. Government Printing Office, Washington, D.C. 139 pp.
- Stormer, F.A., and W.A. Bauer. 1980. Summer forage use by tame deer in northern Michigan. *Journal of Wildlife Management* 44:98-106.
- Trapp, E.J. 1988. Dispersal of heteromorphic seeds in *Amphicarpaea bracteata* (Fabaceae). *American Journal of Botany* 75:1535-1539.
- Urban, D., S. Goslee, K. Pierce, and T. Lookingbill. 2002. Extending community ecology to landscapes. *Ecoscience* 9:200-212.
- Verburg, R., J. Maas, and H.J. During. 2000. Clonal diversity in differently-aged populations of the pseudo-annual clonal plant *Circaea lutetiana* L. *Plant Biology* 2:646-652.

- Wijesinghe, D.K., and D.F. Whigham. 2001. Nutrient foraging in woodland herbs: a comparison of three species of *Uvularia* (Liliaceae) with contrasting belowground morphologies. *American Journal of Botany* 88:1071-1079.
- Wilbur, H.M., K.L. Burke, R.B. Wilbur, and A. Rosenbauer. 2017. Recovery of the herb layer in a southern Appalachian forest following chronic herbivory by deer (*Odocoileus virginianus*). *Castanea* 82:98-113.
- Williams, C.E., E.V. Mosbacher, and W.J. Moriarity. 2000. Use of turtlehead (*Chelone glabra* L.) and other herbaceous plants to assess intensity of white-tailed deer browsing on Allegheny Plateau riparian forests, USA. *Biological Conservation* 92:207-215.
- Yang, J., J. Lovett-Doust, and L. Lovett-Doust. 1999. Seed germination patterns in green dragon (*Arisaema dracontium*, Araceae). *American Journal of Botany* 86:1160-1167.