

Forest Vegetation Response to White-Tailed Deer Population Reductions in a Large Urban Park

Authors: Jenkins, Michael A., and Howard, Brenda S.

Source: Natural Areas Journal, 41(2) : 114-124

Published By: Natural Areas Association

URL: <https://doi.org/10.3375/043.041.0206>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Forest Vegetation Response to White-Tailed Deer Population Reductions in a Large Urban Park

Michael A. Jenkins^{1,3} and Brenda S. Howard²

¹Department of Forestry and Natural Resources and the Hardwood Tree Improvement and Regeneration Center, Purdue University, 715 West State St., West Lafayette, IN 47907

²Office of Land Stewardship, Department of Public Works, 1200 South Madison Ave., Indianapolis, IN 46225

³Corresponding author: jenkinma@purdue.edu; 765-494-3602

Associate Editor: Nathan DeJager

ABSTRACT

Overabundance of white-tailed deer (*Odocoileus virginianus*) constitutes a threat to the biological diversity and ecosystem function of forested natural areas. Managers of Eagle Creek Park, a large forested park in Marion County, Indiana, that is surrounded by densely populated residential housing, implemented a deer population reduction program in 2014 to reduce negative impacts to park ecosystems. Starting in 2013, we instituted a monitoring program within two nature preserves imbedded within Eagle Creek Park to track the response of vegetation communities to population reductions. We found positive response in the heights of two published indicator species, *Arisaema triphyllum* (jack-in-the-pulpit) and *Actaea pachypoda* (white baneberry). We also observed increased richness and density of native woody species and an overall reduction in the proportion of twigs browsed at both preserves. The reduction efforts coincided with heavy mortality of overstory *Fraxinus* (ash) trees from emerald ash borer (*Agrilus planipennis*). Consequently, while we observed recovery of native woody species at both sites, one of the preserves also experienced a large increase in the abundance of nonnative woody plants in response to increased light availability and reduced browse pressure. Overall, our monitoring showed that deer population reductions have allowed the recovery of vegetation communities in the park. However, continued monitoring is needed to track vegetation community response to continued management of the deer population in conjunction with other human pressures on biological communities in the park.

Index terms: browse intensity; forest regeneration; herbivory; indicator species; understory vegetation

INTRODUCTION

In many parts of eastern North America, chronic herbivory by overabundant white-tailed deer (*Odocoileus virginianus* Zimmerman) populations has had lasting negative effects on forests, driving the local extirpation of browse-sensitive species (Rooney et al. 2004; Thiemann et al. 2009) and shifting species composition toward browse-tolerant and non-preferred species (Waller and Alverson 1997; Rossell et al. 2005; Tanentzap et al. 2011). Particularly problematic, invasive plant species are often not palatable to deer and may increase in abundance in heavily browsed forests (Webster et al. 2008; Knight et al. 2009; Schmit et al. 2020). In addition, chronic herbivory can change the structure of forests by reducing stem density (Jenkins et al. 2015), leaf litter depth (Bressette et al. 2012; Lessard et al. 2012), and soil permeability (Heckel et al. 2010; Harada et al. 2020). These changes in forest structure, in turn, reduce total arthropod abundance (Bressette et al. 2012) and the taxonomic diversity of litter and soil arthropods (Lessard et al. 2012). Overabundant deer populations also affect higher trophic levels. For example, overabundant deer populations on an island in British Columbia, Canada, were associated with lower songbird abundance and a shift in bird species composition toward species that were not dependent upon understory vegetation (Allombert et al. 2005).

Even when deer populations are reduced, recovery of biological communities can be a slow process. Increased cover

and abundance of plants are often evident, typically due to increased abundance of readily dispersed woody species (Jenkins et al. 2014, 2015). However, palatable species that are dispersal limited are typically slow to recolonize sites (Webster et al. 2005; Royo et al. 2010a; Harada et al. 2020), and decades- or centuries-long disruptions to forest ecosystem structure and function may persist as “ghosts of herbivory past” (Nuttle et al. 2014). As such, overabundant deer populations interact with human disturbance, intensive land use, and invasive species to erode ecological memory and increase resilience debt (loss of resilience not apparent until the next occurrence of disturbance; Webster et al. 2018), possibly leading to an undesired transition to an alternate stable state (Stromayer and Warren 1997).

In natural areas managed to reduce human impacts, hunting is often prohibited. Under such a system, deer populations fluctuate through time and typically become overabundant, a response that is augmented in fragmented landscapes with abundant edge habitat and/or mild winters (Alverson et al. 1988; Cadenasso and Pickett 2000; Rooney 2001). Within the Midwest region of the United States, overabundant deer populations in natural areas are particularly problematic where woodlots and forests are surrounded by a matrix dominated by agriculture and exurban development (Hurley et al. 2012). Many natural areas have struggled with the decision of whether or not to control deer populations. While active population reductions through the use of professional sharpshooters or public hunting may reduce negative impacts on plant populations (Royo et al.

2010b) and communities (Jenkins et al. 2014), reduction efforts have attracted considerable controversy (McShea and Rappole 1997; Mitchell et al. 1997; Knackmuhs and Farmer 2017). As more natural areas consider this and other techniques to control deer populations, the need for evaluations of the effectiveness of on-the-ground control efforts is highlighted.

Like many states in the Midwest, Indiana has historically experienced large-scale changes in its statewide deer population. White-tailed deer were extirpated from Indiana in the late 1880s following decades of unregulated harvest and habitat destruction through the conversion of native habitat to other land uses (Whitaker 2010). Deer were reintroduced to the state in the 1930s–1940s, and with an abundance of edge habitat, the absence of predators, and the cessation of unregulated hunting, deer populations rebounded and greatly expanded (Whitaker 2010). This expanded statewide population is reflected in the increasing number of deer harvested annually in Indiana, which increased from 51,778 deer in 1987 to over 103,163 by 2001, and ranged between 104,428 and 136,248 annually since 2001 (Indiana Department of Natural Resources 2018).

Located in Pike Township in Marion County, Indiana, Eagle Creek Park (ECP) is one of the largest municipally owned parks in the nation and is an archetypal example of a relatively large natural area (1580 ha of land and 570 ha of lake) embedded within a fragmented matrix of suburban development (Figure 1). The park contains a mixture of vegetation types including mature flatwood and upland forest, wooded ravines, wetlands, prairie plantings, as well as reforestation and mixed successional areas. Concerns about increasing deer abundance in ECP were first raised in 1996 and three deer exclosures were erected to observe damage, but no formal data were collected. In 2001, an assessment by the Indiana Department of Natural Resources, Nature Preserves Division, observed excessive deer browse at Eagle's Crest Nature Preserve (ECNP) within ECP (unpublished letter from Indiana DNR 2001). While herbaceous plants appeared to be abundant, concern was expressed that populations could decline if deer populations were not reduced. Inspection by an Indiana Department of Natural Resources wildlife biologist in 2014 noted "the woods within the park had a similar look to one that has been grazed extensively by goats or cattle" and included a "noticeable browse line" (S. Winks, pers. comm.; Figure 2a).

Monitoring of indicator species (Webster et al. 2001) in the park between 2003 and 2007 resulted in ratings of heavy–severe browse across years (ECP, unpub. data). Efforts to implement reductions started in 2012, when the process of obtaining necessary permits and approvals began. The deer management program was initiated in 2014 to reduce the negative impacts of overabundant white-tailed deer and restore balance to the park's ecosystems (Department of Public Works 2014).

Beginning in 2014–2015, 640 deer have been culled from the park, with 243 removed in 2014–2015, 173 in 2017, 123 in 2018, and 101 in 2019 (after data were collected for this study). The initial phase of reductions occurred 28–30 November 2014, on the east side of ECP, during daylight hours. With the park closed, recovering servicemen and women with Wounded Warrior Outdoors participated in a three-day managed hunt. For the second phase in January 2015, USDA APHIS Wildlife

Services professional sharpshooters, using thermal imaging infrared technology and baited sites, culled deer on the west side of ECP for five nights. Reduction efforts in 2017, 2018, and 2019 were accomplished entirely by nighttime sharpshooters. Except for a few deer taken home by veterans in the initial managed hunt, all deer removed were processed and the meat donated to the local food bank.

In June and July of 2013, we instituted a monitoring study to determine the effects of white-tailed deer herbivory in ECNP and Spring Pond Nature Preserve (SPNP), two areas within ECP where past monitoring of browse indicator species has been conducted. This assessment included measuring the height of two indicator species (*Arisaema triphyllum* [L.] Schott [jack-in-the-pulpit] and *Actaea pachypoda* Elliott [white baneberry]) identified by Webster and Parker (2000), tallying the density of seedlings and saplings by species, and assessing the occurrence of browse on woody twigs. We repeated this sampling in June and July of 2016, 2017, and 2019 in both nature preserves to quantify (1) changes in the height of indicator species, (2) changes in woody species composition, diversity, and stem density in forest understories, and (3) changes in the frequency of browse on woody species in forest understories.

METHODS

Study Sites

ECNP is a 120 ha late-successional forest reserve comprised of ridges and eroded ravines derived from glacial till. Soils are Miami and Hennepin loams and silt loams with slopes ranging from 2% to 50% (Soil Survey Staff 2020). The overstory of ECNP is dominated by *Acer saccharum* Marshall (sugar maple), *Quercus rubra* L. (northern red oak), and *Fagus grandifolia* Ehrh. (American beech). *Acer saccharum* heavily dominates the sub-canopy and sapling layers, while *Asimina triloba* (L.) Dunal (paw paw) and *Lindera benzoin* (L.) Blume (spicebush) dominate the shrub layer. The herbaceous layer contains a mixture of mesic forest species including *Asarum canadense* L. (wild ginger), *Sanicula* spp. L. (black snakeroot), *Polygonatum biflorum* (Walter) Elliott (smooth Solomon's seal), and *Laportea canadensis* (L.) Weddell (Canadian woodnettle).

SPNP is an 18 ha, poorly drained forest located east of the Eagle Creek Reservoir. Soils are derived from swales and waterlain moraines and consist of Crosby silt and Treaty silty clay loams (Soil Survey Staff 2020). The overstory at SPNP is heavily dominated by *Fraxinus pennsylvanica* Marshall (green ash) and *A. saccharum* with *Carya cordiformis* (Wangenh.) K. Koch (bitternut hickory), *Ulmus rubra* Muhl. (slippery elm), *Acer saccharinum* L. (silver maple), and *Quercus palustris* Münchh (pin oak) present as secondary components. By our last two surveys in 2017 and 2019, most of the overstory *F. pennsylvanica* was dead from emerald ash borer (*Agrilus planipennis* Fairmaire; EAB). The sub-canopy consists largely of *A. saccharum* and *F. pennsylvanica*. The shrub layer is dominated by *A. triloba* and *L. benzoin* and several nonnative shrubs including *Rosa multiflora* Thunb. (multiflora rose), *Lonicera maackii* (Rupr.) Herder (Amur honeysuckle), and *Elaeagnus umbellata* Thunb. (Autumn olive). The herbaceous layer of SPNP is dominated by seedlings of *F. pennsylvanica* and other species, thickets of *A. triloba* and *L.*

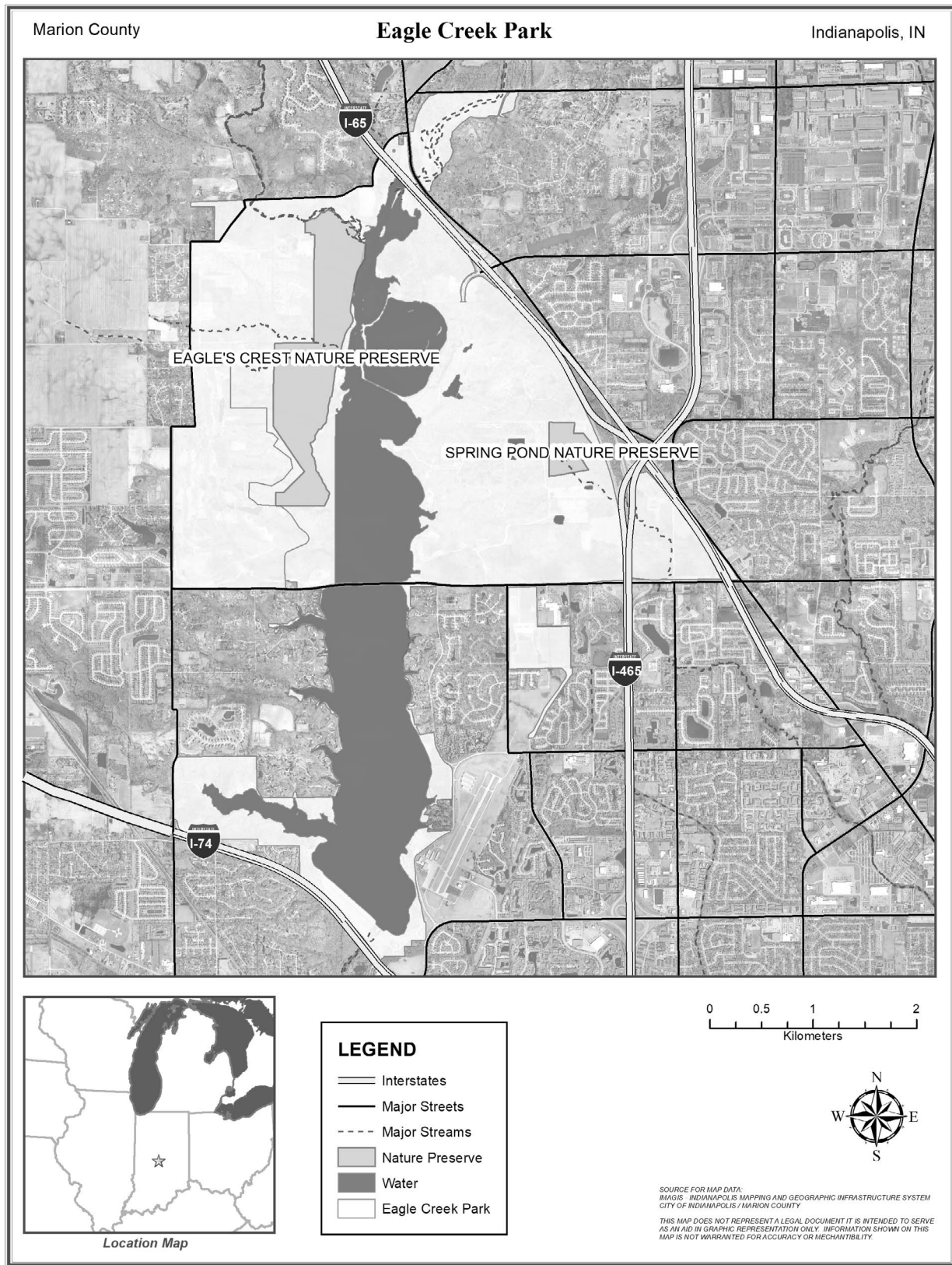


Figure 1.—Eagle’s Crest and Spring Pond Nature Preserves within Eagle Creek Park, Indianapolis, Indiana.

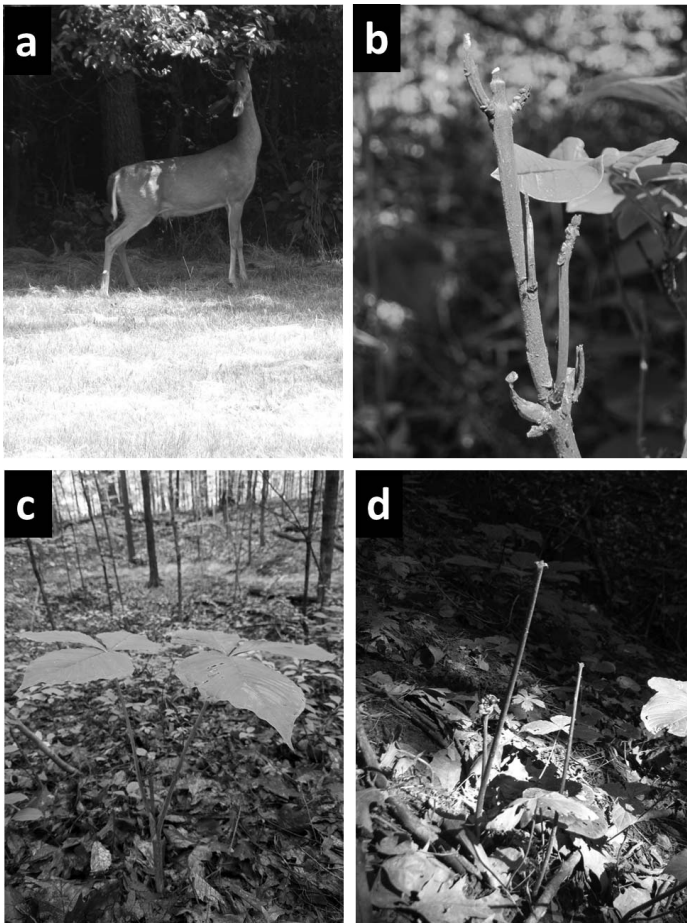


Figure 2.—(a) Browse line at Spring Pond Nature Preserve in 2013. (b) repeated browsing on *F. pennsylvanica* sapling at Spring Pond NP in 2013. (c) Flowering female *A. triphyllum* plant at Eagle's Crest NP in 2019. (d) Browsed female *A. triphyllum* plant at Eagle's Crest NP in 2013. Photo credit: M. Jenkins.

benzoin, and numerous herbaceous species including many *Carex* spp. (sedges) and Poaceae (grasses).

After plots were first sampled in 2013, we resampled vegetation three times (2016, 2017, and 2019) in both nature preserves to examine responses of indicator species and woody vegetation to deer population reductions. All sampling used the same center points as permanent plots established by Dolan and Moore (2007a, 2007b) in flora surveys of both preserves. We sampled nine plots at ECNP and eight plots at SPNP.

Indicator Species

To evaluate height changes of herbaceous indicator species, we followed the methods of Webster and Parker (2000) and Webster et al. (2001). Because the heights of *Arisaema triphyllum* and *Actaea pachypoda* have been shown to decrease in areas with overabundant deer populations (Webster and Parker 2000; Webster et al. 2001; Heckel et al. 2010), we measured the height of both species. All height measurements were taken between mid-June and early July each year.

We measured all mature *A. triphyllum* plants within variable radius plots (ranging from 10 to 20 m depending upon the abundance of focal species). *Arisaema triphyllum* was abun-

dant at ECNP and common at SPNP. However, we only observed scattered *A. pachypoda* plants at ECNP, and no plants of this species at SPNP. Therefore, we measured all individuals of this species that we encountered both on and off the plots. We performed systematic off-plot searches during each survey year at SPNP to increase the number of *A. triphyllum* plants measured. We also noted whether plants were flowering and/or had been browsed. Because *A. triphyllum* is able to change its gender and will switch to male flowering or not flower at all under environmental stress (Bierzuchudek 1984a, 1984b), the gender of flowering *A. triphyllum* plants was also identified.

To statistically examine changes in *A. triphyllum* height, we used repeated measures one-way ANOVA ($\alpha = 0.05$) to compare plot mean heights by sample year (2013, 2016, 2017) at ECNP. If the ANOVA revealed significant differences within the data, Holm-Sidak multiple comparison tests ($\alpha = 0.05$) were used to compare individual years. Because *A. triphyllum* plants were less common at SPNP, some plots contained two or fewer plants during some sample years. If a plot did not contain at least three plants during a given year, it was not used in statistical analysis for that year. Because the same plots were not analyzed for every sample year, we used a one-way ANOVA ($\alpha = 0.05$) at Spring Pond with Holm-Sidak multiple comparison tests ($\alpha = 0.05$). All data were evaluated to confirm that they met the assumptions of normality and equal variance (Neter et al. 1996). Because *A. pachypoda* occurred on so few plots (one plot in 2013, two plots in 2016, and four plots in both 2017 and 2019), and most of the plants we measured were not found on study plots, we did not calculate individual plot means or statistically compare sample year differences across plots. Instead, we calculated a mean height for all plants sampled across ECNP during each sample year.

Understory Woody Species Composition, Stem Density, and Diversity

A nested plot design was used to sample understory woody vegetation. Stems ≥ 1 m in height (saplings) were tallied by species into two diameter classes (≤ 2.5 cm dbh [1.37 m] and 2.6–10 cm dbh) within either a 300 m² (9.77 m radius) or a 200 m² (7.98 m radius) plot, depending upon stem density. Four 4 m² quadrats positioned 4 m from plot center in cardinal directions were used to tally seedlings (stems <1 m height) by species into two height classes: 0–20 cm and 21–99 cm. Mean density (stems ha⁻¹) per plot was calculated by dbh class for each sapling species and mean density per 100 m² was calculated by height class for each seedling species. We calculated native species richness, evenness (Pielou's *J'*), and Shannon's Diversity per plot for both the seedling (small and large seedlings combined) and sapling (small and large saplings combined) layers. We used relative density (density of a single species/total density across all species) as the input data for these calculations.

We used repeated measures one-way ANOVA with $\alpha = 0.05$ to compare mean total seedling and sapling densities (all species combined) and species richness, evenness, and Shannon's Diversity Index of the seedling and sapling layers calculated at the plot level by sample year (2013, 2016, 2017, 2019) at both

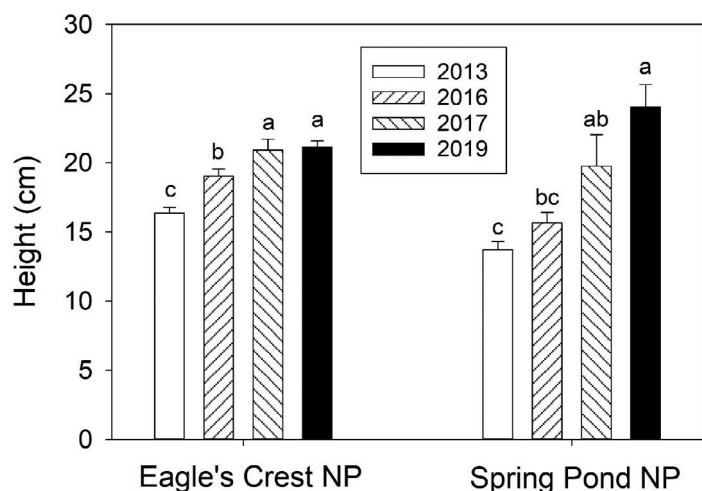


Figure 3.—Mean height (\pm standard error) of *A. triphyllum* plants calculated by plot from data collected in 2013, 2016, 2017, and 2019. For each nature preserve, bars that do not share a superscripted letter were significantly different according to one-way ANOVA with Holm-Sidak multiple comparison tests ($\alpha = 0.05$).

preserves. If the ANOVA revealed significant differences in the data, Holm-Sidak multiple comparison tests ($\alpha = 0.05$) were used to compare means for individual years. These analyses were also conducted to examine changes in the density of nonnative invasive species at SPNP. All data were evaluated to assess whether they met the assumptions of normality and equal variance (Neter et al. 1996). Because the large seedling density data from SPNP violated the assumption of normality, we used a one-way repeated measures ANOVA on ranks with Tukey multiple comparison tests ($\alpha = 0.05$) to compare mean values between years.

Woody Species Browse

Browsing of woody understory stems (Figure 2b) was assessed in four 4 m² quadrats placed in cardinal directions 4 m from plot center. The techniques of Williamson and Hirth (1985) were used to quantify browse of individual twigs. Available (non-browsed) and browsed twigs (0.15–1.8 m above ground) were counted by species from up to eight randomly selected individuals per species. All woody species were quantitatively assessed except *L. benzoin*, a non-preferred species, and *A. triloba*, a highly non-preferred species. Based upon field observations, we noted light to intermittent browsing of *L. benzoin* and no browsing of *A. triloba*. Percent of twigs browsed for each species was calculated as a per plot average. All data were evaluated to confirm that they met the assumptions of normality and equal variance (Neter et al. 1996). We used repeated measures one-way ANOVA with $\alpha = 0.05$ to compare mean percent browse (twigs from all species combined on each plot) by sample year (2013, 2016, 2017, 2019) at both preserves. If the ANOVA revealed significant differences in the data, Holm-Sidak multiple comparison tests ($\alpha = 0.05$) were used to compare means for individual years.

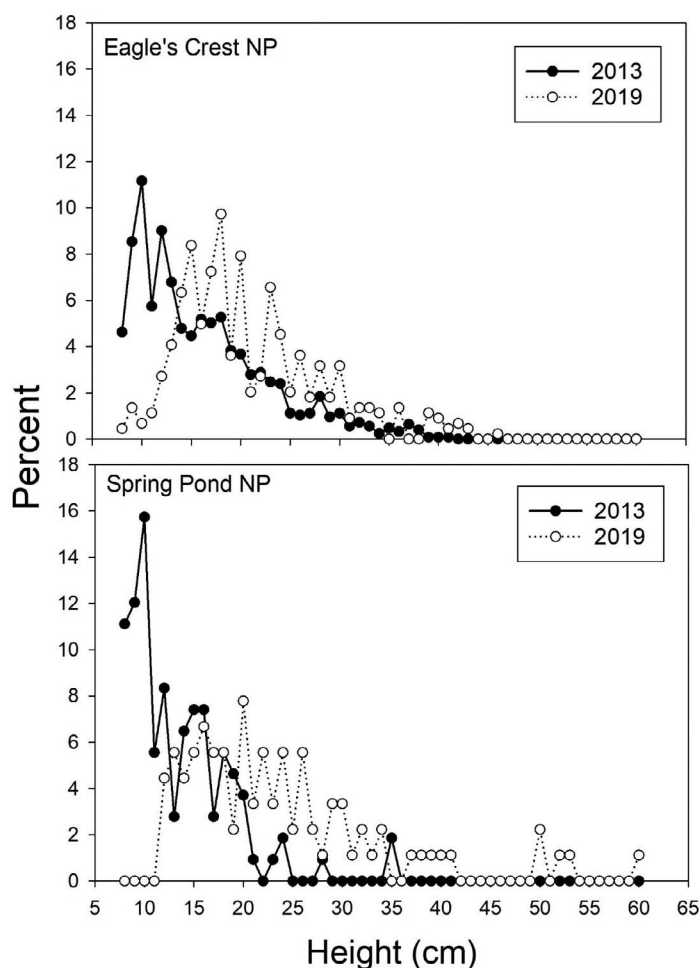


Figure 4.—Percent distribution of *A. triphyllum* plant heights at Eagle's Crest and Spring Pond Nature Preserves in 2013 and 2019.

RESULTS

Indicator Species

The per plot mean height of *A. triphyllum* plants at ECNP in 2019 did not differ significantly from the 2017 mean height ($P = 0.741$; Figure 3). However, mean height of *A. triphyllum* in both 2019 and 2017 was significantly greater than the mean height observed in 2016 and 2013 (Figure 3). The per plot mean height of *A. triphyllum* plants at SPNP in 2019 did not differ significantly from that observed in 2017 ($P = 0.13$). Mean height in 2019 was significantly greater than mean height observed in both 2016 and 2013 (Figure 3). For both sites, there has been a dramatic shift in the height distribution of plants since 2013 (Figure 4). This shift was driven by a reduction in the portion of individuals ≤ 15 cm in height, coupled with an increase in the proportion of plants > 20 cm in height.

At ECNP, only 2% of *A. triphyllum* plants were flowering in 2013, but in 2016 3% were flowering. In 2017 and 2019, 9% of plants were flowering. The ratio of male to female plants remained similar between 2013 and 2016; 17% of flowering plants were female in 2013 vs. 16% in 2016. However, in 2017 20% of flowering plants were female. In 2019, the proportion of female plants declined to 8%. In the first three sample years, few

Table 1.—Total density (all species combined; mean \pm standard error) of small seedlings (0–20 cm height), large seedlings (21–100 cm height), small saplings (0–2.5 cm dbh), and large saplings (2.6–10.0 cm dbh) at Eagle’s Crest and Spring Pond Nature Preserves. Seedling densities are stems/100 m²; sapling densities are stems/ha. Seedling and sapling densities of nonnative species are also provided for Spring Pond NP. Density values that do not share a superscripted letter were significantly different between years according to one-way ANOVA and Holm-Sidak multiple comparison tests ($\alpha = 0.05$). Woody vine species are included.

	2013	2016	2017	2019
Eagle’s Crest NP				
Small seedlings	70 \pm 29 ^b	316 \pm 85 ^a	280 \pm 81 ^a	198 \pm 65 ^{ab}
Large seedlings	66 \pm 25 ^c	76 \pm 27 ^{bc}	107 \pm 35 ^{ab}	140 \pm 41 ^a
Small saplings	585 \pm 160 ^a	540 \pm 177 ^a	707 \pm 308 ^a	869 \pm 257 ^a
Large saplings	282 \pm 67 ^a	328 \pm 111 ^a	311 \pm 103 ^a	278 \pm 84 ^a
Spring Pond NP				
Small seedlings	131 \pm 26 ^a	135 \pm 36 ^a	148 \pm 28 ^a	132 \pm 23 ^a
Small seedlings – nonnative species	4 \pm 2 ^a	7 \pm 4 ^a	5 \pm 3 ^a	12 \pm 4 ^a
Large seedlings	485 \pm 67 ^b	482 \pm 54 ^b	681 \pm 67 ^a	511 \pm 62 ^{ab}
Large seedlings – nonnative species	5 \pm 3 ^b	32 \pm 7 ^{ab}	65 \pm 15 ^a	34 \pm 15 ^{ab}
Small saplings	1208 \pm 225 ^d	2374 \pm 312 ^{cd}	3738 \pm 695 ^{bc}	5981 \pm 597 ^a
Small saplings – nonnative species	13 \pm 6 ^c	66 \pm 41 ^c	462 \pm 140 ^b	844 \pm 175 ^a
Large saplings	408 \pm 58 ^a	517 \pm 70 ^a	463 \pm 90 ^a	481 \pm 72 ^a
Large saplings – nonnative species	0 \pm 0 ^a	0 \pm 0 ^a	6 \pm 6 ^a	6 \pm 6 ^a

plants were flowering at SPNP (three plants in 2013 vs. one plant in 2016 vs. seven plants in 2017). In 2019, the number of flowering plants at Spring Pond increased to 10, and 50% of these flowering plants were female.

The mean height of *A. pachypoda* plants at ECNP in 2019 was 27 \pm 10 cm, which was greater than mean heights in 2017 (23 \pm 7 cm), 2016 (19 \pm 5 cm), and 2013 (9 \pm 3 cm). Also notable was the steady increase in the abundance of the species across the study plots and walked routes between plots. In 2013 we observed a total of four plants, while in 2019 we observed 24 plants. These results suggest that *A. pachypoda* height responds to changes in deer abundance more rapidly than *A. triphyllum* height. However, a much greater number of *A. triphyllum* plants were measured across a greater proportion of the preserve compared to *A. pachypoda*. Therefore, changes in the height of *A. triphyllum* may be more representative of browse pressure across the preserve.

Understory Woody Species Composition, Stem Density, and Diversity

Eagle’s Crest NP: Across both strata at ECNP between 2013 and 2019, seven native woody species were gained on the nine plots, while two were lost, resulting in a net gain of five species. During this time span, no nonnative woody species were gained or lost from the plots. This equates to a 22% increase in the number of species found on the plots between 2013 and 2019.

Between 2013 and 2016, the density of small seedlings (0–20 cm height) increased significantly at ECNP from 71 stems/100 m² to 316 stems/100 m², but did not change significantly between 2016 and 2017 (Table 1). In 2019, the density of small seedlings displayed a nonsignificant decline. This decrease was mostly the result of reduced densities of *Fraxinus americana* L. (white ash) and *A. saccharum* seedlings, two species that initially increased in density following the initiation of deer population reductions (Online Supplemental Appendix 1). While the density of large seedlings (21–100 cm height) exhibited little change between 2013 and 2016, we observed a significantly greater density of large seedlings in 2017, and a further increase

in 2019 (Table 1). This continuing increase in density was driven by increased abundance of *F. americana* and *A. triloba* across sample years (Online Supplemental Appendix 1). We observed no significant changes in the sapling layer of ECNP across sample years. Although not statistically significant due to high inter-plot variability, small sapling (≥ 1 m height; 0–2.5 cm dbh) density increased each sample year (Table 1).

Between 2013 and 2016, we observed an increase in seedling species richness at ECNP, with significantly greater richness in 2016, 2017, and 2019 compared to 2013 (Figure 5). We observed no significant differences among years for evenness ($P = 0.435$) or Shannon’s Diversity Index ($P = 0.074$). While not statistically significant, Shannon’s Diversity Index did increase steadily between 2013 and 2019. Sapling species richness at ECNP exhibited a slight increase through time with significantly greater richness in 2019 compared to 2016 (Figure 6). Sapling species evenness and Shannon’s Diversity Index did not differ between years ($P = 0.880$ and 0.157, respectively).

Spring Pond NP: Across all strata between 2013 and 2019, we observed an increase in the number of native woody species occurring on the plots at Spring Pond. Seven species were gained across the plots, while two were lost, resulting in a net gain of five native species. Also during this time span, two nonnative woody species were gained, but none were lost.

Between 2013 and 2019, the density of small seedlings at SPNP did not change significantly (Table 1). However, the number of species tallied in this stratum increased from 10 to 17 in 2019. Similar to small seedlings, the large seedling stratum at SPNP exhibited little change in density between 2013 and 2016 (Table 1). However, density in this stratum increased significantly in 2017, but displayed a nonsignificant decline in 2019. The increased density in 2017 was largely a result of the increased abundance of nonnative species, which increased significantly from 5 stems/100 m² in 2013 to 65 stems/100 m² in 2017. However, density of nonnative species in this stratum declined to 34 stems/100 m² in 2019.

Although not statically significant, small sapling (≥ 1 m height, 0–2.5 cm dbh) density nearly doubled from 1208 stems/

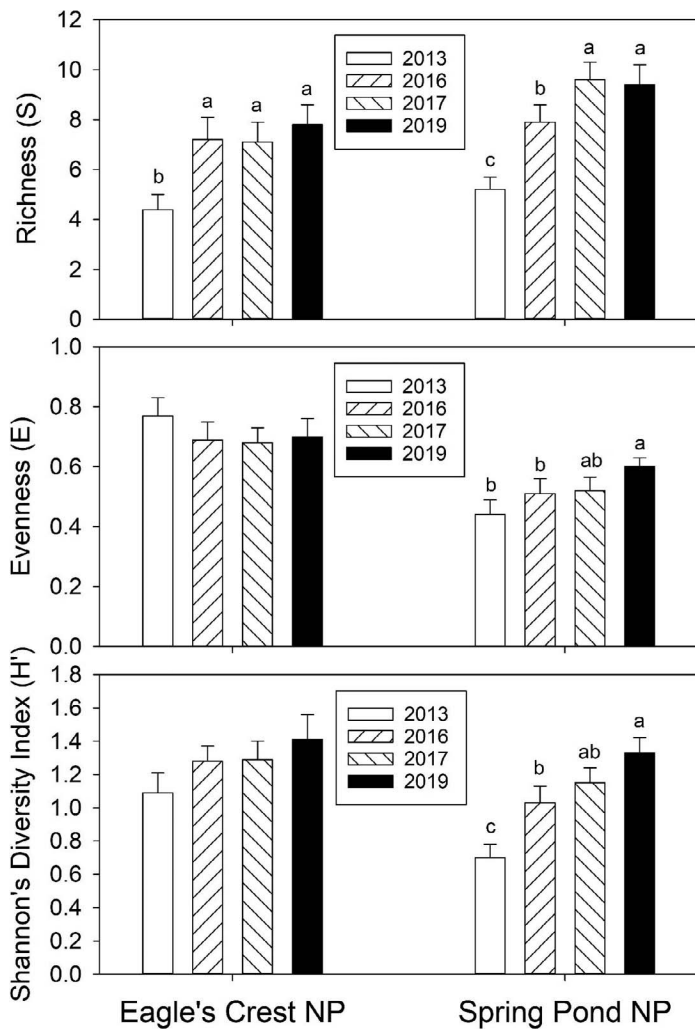


Figure 5.—Mean (\pm standard error) richness, evenness, and Shannon's Diversity Index of native seedling species at Eagle's Crest and Spring Pond Nature Preserves. For each nature preserve, bars that do not share a superscripted letter were significantly different according to one-way ANOVA with Holm-Sidak multiple comparison tests ($\alpha = 0.05$).

ha in 2013 to 2374 stems/ha in 2016. Between 2016 and 2019, density more than doubled again to 5981 stems/ha, a statistically significant increase (Table 1). The increase in density between 2013 and 2019 was largely a result of a nearly eight-fold increase in the density of spicebush and a four-fold increase in the density of *F. pennsylvanica* (Appendix 2). We observed little stump sprouting by mature *F. pennsylvanica* trees killed by EAB and nearly all of the increased density of small saplings resulted from the recruitment of seedlings. The overall increase in stem density between 2013 and 2019 also resulted from increased density of five nonnative species: *E. umbellata*, *L. maackii*, *R. multiflora*, *Euonymus alatus* (Thunb.) Siebold (burning bush), and *Celastrus orbiculatus* Thunb. (oriental bittersweet; Online Supplemental Appendix 2). This increase in density was particularly dramatic for *R. multiflora*, which was not found in this stratum in 2013, but had a density of 563 stems/ha in 2019.

Stem density in the large sapling stratum (2.6–10 cm dbh) did not change significantly across sample years (Table 1). While the

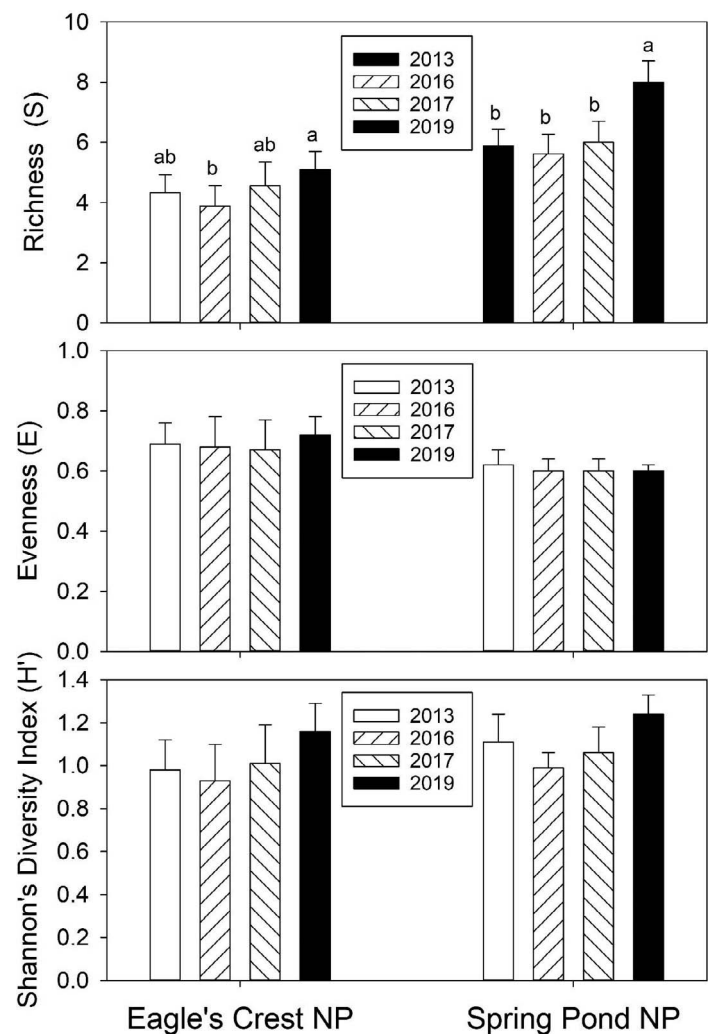


Figure 6.—Mean (\pm standard error) richness, evenness, and Shannon's Diversity Index of native sapling species at Eagle's Crest and Spring Pond Nature Preserves. For each nature preserve, bars that do not share a superscripted letter were significantly different according to one-way ANOVA with Holm-Sidak multiple comparison tests ($\alpha = 0.05$).

density of most species in this layer were similar between 2013 and 2019, the density of paw paw increased nearly 50% (Online Supplemental Appendix 2). The density of nonnative species did not change significantly across sample years.

Seedling species richness at Spring Pond increased significantly at each remeasurement between 2013 and 2017, but did not change between 2017 and 2019 (Figure 5). Evenness was significantly greater in 2019 compared to both 2013 and 2016. Shannon's Diversity Index increased steadily between 2013 and 2019 with significantly greater diversity in 2016, 2017, and 2019 compared to 2013. Sapling species richness was significantly greater in 2019 compared to 2013–2017 (Figure 6). Sapling species evenness and Shannon's Diversity Index did not differ significantly across years ($P = 0.951$ and 0.136 , respectively).

Woody Species Browse

Across both sites, the rate of browsing on woody stems generally decreased between 2013 and 2019 (Table 2). Overall,

Table 2.—Total percent browse of woody stems (all species combined; means \pm standard error) at Eagle’s Crest and Spring Pond Nature Preserves. Mean percent values without a standard error resulted when browse for a given species was measured on a single plot. Total percent browse values that do not share a superscripted letter were significantly different between years according to one-way ANOVA and multiple comparison tests ($\alpha = 0.05$).

	2013	2016	2017	2019
Eagle’s Crest NP	28.9 \pm 7.1 ^a	26.3 \pm 8.9 ^{ac}	6.5 \pm 2.1 ^b	8.3 \pm 3.3 ^{bc}
Spring Pond NP	77.4 \pm 3.3 ^a	68.4 \pm 3.6 ^a	33.4 \pm 1.1 ^b	24.4 \pm 2.6 ^c

the percent of twigs browsed at ECNP did not change between 2013 and 2016, but decreased significantly in 2017 before rebounding slightly in 2019. Browse rates were very similar in 2013 and 2016 for most species, but browse rates of most individual species decreased in 2017 (Online Supplemental Appendix 3). Although browsing rates of individual species were highly variable across plots and were not compared statistically, browsing of *Vitis* spp. (grape species), *Q. rubra*, and *F. americana* appeared to increase between 2017 and 2019, coupled with a decrease in the browse of *Fraxinus quadrangulata* Michx. (blue ash). Percent browse decreased significantly across sample years at SPNP, declining from 77% in 2013 to 24% in 2019.

DISCUSSION

In our study, we observed recovery of the vegetation community following deer reductions. Across both nature preserves, we observed increased height of indicator species, increased stem density and richness of native woody species in the understory, and decreased rates of browse on woody stems. By examining multiple descriptors of the vegetation community, our monitoring allowed more concrete conclusions about the effects of reductions than examinations of a single metric.

Studies have shown that some species exhibit changes in height, abundance, and reproduction with changes in deer abundance, allowing them to be used as indicators of browse intensity (Anderson 1994; Webster and Parker 2000; Williams et al. 2000; Koh et al. 2010). Between 2013 and 2019, we observed sustained increases in the heights of *A. triphyllum* and *A. pachypoda*, two indicator species of deer overabundance in Indiana (Webster and Parker 2000). Between 2013 and 2017, we also observed increased rate of flowering and increased proportion of female plants in *A. triphyllum* at both sites (Figure 2c). This increase in the proportion of fertile female plants suggests that reduced browse pressure has allowed plants to shift more resources toward reproduction (Bierzuchudek 1984a, 1984b). Unlike most other herbaceous indicators of browse intensity, deer rarely browse *A. triphyllum*, likely due to the presence of sharp crystals of calcium oxalate in the sap (Pickett 1915). In our study, we observed only six browsed *A. triphyllum* plants over our four surveys. Of the six browsed plants, five were flowering, and of these four were female (Figure 2d). While deer do not typically browse *A. triphyllum*, their movement around plants results in soil compaction and reduces litter depth, which creates stress on plants and reduces their growth (Heckel et al. 2010). Reduced deer densities at ECP have likely resulted in reduced environmental stress on *A. triphyllum* plants, although

other abiotic and demographic factors may influence flowering in a given year. Although the limited abundance and distribution of plants precluded statistical testing, we observed a 3 \times increase in the mean height of *A. pachypoda* between 2013 and 2019, suggesting that this species may be a more sensitive indicator of browse intensity than *A. triphyllum*.

Prior to attack of EAB, *F. pennsylvanica* comprised 14% of the overstory basal area in plots distributed across SPNP (Dolan and Moore 2007b). Increased light levels resulting from overstory mortality of *F. pennsylvanica* from EAB (Engelken et al. 2020) and damage to surrounding tree canopies by falling dead *Fraxinus* trees may have contributed to the increased height of *A. triphyllum* plants at SPNP. However, *A. triphyllum* plants at SPNP, along with other herbaceous species associated with closed-canopy forests, were overtopped by dense woody reproduction and early seral vegetation, reestablishing heavy shading of the herbaceous layer. Consequently, it has become time consuming to find *A. triphyllum* plants on many of our plots at SPNP and overall abundance of the species may have declined due to heavy competition from woody understory and early seral species. Abella et al. (2019) observed increased cover of *A. triphyllum* 2 y after the arrival of EAB in an Ohio swamp forest; however, cover of the species subsequently declined to pre-EAB levels 12 y after initial infestation.

As a likely result of increased light availability from EAB-caused mortality at SPNP (Abella et al. 2019), we also observed increased density of two species of low palatability to deer (Liang and Seagle 2002; Slater and Anderson 2014), *L. benzoin* (small saplings: 675% increase) and *A. triloba* (large saplings: 46% increase). We also observed a 3 \times increase in the density of *F. pennsylvanica* in the small sapling layer between 2016 and 2019. While heavily browsed, this species has persisted at SPNP as a result of its browse tolerance, a characteristic of members of the genus *Fraxinus* (Rossell et al. 2005), and its increased density was likely a result of both increased light and reduced browse pressure.

At SPNP, we also observed large increases in the density of woody invasive shrubs and vines. While Dolan and Moore (2007b) documented the increasing presence of invasive plants at SPNP, invasives were absent from the preserve during an earlier survey in 1997 (Dolan et al. 2015). Deer browse invasive shrubs and vines (Rossell et al. 2007; Martinod and Gorchov 2017), and overabundant deer populations have been shown to suppress their growth and spread (Griggs et al. 2006; Ward et al. 2017). At SPNP, reduced browse pressure and increased light levels from EAB have likely allowed the density of woody invasive species to increase dramatically (Hoven et al. 2017), and active management may be needed to prevent their continued spread. Deer and invasive shrubs have both individual and synergistic negative effects on forest understories, and active control of both is often warranted (Owings et al. 2017; Haffey and Gorchov 2019). However, while overabundant deer populations may suppress the growth of woody invasive plants, research has shown that they can have the opposite effect on unpalatable herbaceous invasive species. Exclusion studies have shown that herbivory of more-palatable native species by deer reinforces the dominance of both *Microstegium vimineum* (Trin.) A. Camus (Japanese stiltgrass; Webster et al. 2008) and

Alliaria petiolata (M. Bieb.) Cavara & Grande (garlic mustard; Knight et al. 2009; Kalisz et al. 2014).

At ECNP, we observed increased mean species richness and abundance of woody regeneration, manifested by a greater than 2× increase in the density of both small and large seedlings. Following deer reductions, woody species often rebound quickly because of the wide dispersal of their seeds and their persistence as seed-producing trees (Jenkins et al. 2015). We also observed a 22% increase in the number of native woody species across all the plots we sampled. According to Dolan and Moore (1997), a strong straight-line wind event occurred in ECNP in 1994, uprooting and damaging many trees across the preserve. While large gaps in forests are typically associated with an increase in plant diversity (Busing and White 1997), Dolan and Moore (1997) found no difference in species diversity between gaps and the surrounding forest matrix. Our observed increases in both plot- and site-level native species richness suggests that herbivory by overabundant deer may have contributed to reduced diversity following the creation of gaps. In a large-scale experiment in Pennsylvania, Nuttle et al. (2013) found that herbivory by deer nullified the positive effects of surface fire and canopy gaps, two components of the historical disturbance regime that promoted tree species diversity. However, in forested landscapes with lower deer abundance, herbivory can promote plant species diversity in forest gaps (Murray et al. 2016).

When assessing browse, we did not attempt to determine whether browsing on a twig occurred before or after the prior sample year. Therefore, our results present an assessment of all browse on a site, not just new browse that occurred since the last sampling. Therefore, true post-2013 browse rates may be lower than what we calculated. Determining when browse occurred is problematic in long-term studies of deer herbivory that seek to track changes in browse intensity. Twig aging has recently been offered as a quick, efficient, and repeatable technique to monitor browse intensity of white-tailed deer (Waller et al. 2017) and could improve the sensitivity and utility of monitoring efforts in ECP.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Overall, the results of our 6 y of monitoring have shown that the reductions in deer abundance have had a sustained positive effect on vegetation communities in ECP. Anecdotally, park staff observed a marked increase in the diversity and distribution of spring ephemerals and other herbaceous species, including new observations of five orchid species and observations of *Panax quinquefolia* (American ginseng) on the east side of the park when it had previously only been noted on the west side. While park staff also observed increased abundance and size of native shrubs, browse still significantly impacts unfenced reforestation plots adjoining SPNP. Consequently, plans at SPNP to replant trees in canopy openings include adding cages to deter deer browse.

The reductions in deer abundance have occurred in conjunction with other ecological changes, most notable of which has been the loss of *Fraxinus* trees. While this loss has affected both preserves, it has likely contributed greatly to the increased abundance of invasive plant species in SPNP.

Managers of natural areas where reductions in deer populations occur in conjunction with overstory disturbance, such as mortality from EAB, should be prepared to dedicate additional resources to control expanding populations of invasive shrubs. Continued monitoring is needed to track vegetation response to reduced browse pressure, the loss of *Fraxinus* trees, and other agents of ecological change. While deer herbivory can serve as a driver of change in forest ecosystems (Webster et al. 2008), it is a single component of a complex disturbance regime that must be considered for successful management of forested natural areas.

ACKNOWLEDGMENTS

We thank Don Miller for advice and assistance in all parts of this study, Brittany Davis Swinford for assistance with logistics, and Dawn VanDeman for assistance with data collection. Funding was provided by the Office of Land Stewardship, Department of Public Works, Indianapolis.

Michael A. Jenkins is a Professor of Forest Ecology at Purdue University. His research interests include plant community responses to disturbance, impacts of invasive plants, insects, and disease, and the use of fire in community restoration.

Brenda S. Howard is Senior Ecologist with the Land Stewardship office at the Indianapolis Department of Public Works-Engineering. She leads natural resource management activities, writes conservation management plans, maintains GIS records, and oversees the city's Native Planting Area program.

LITERATURE CITED

- Abella, S.R., C.E. Hausman, J.F. Jaeger, K.S. Menard, T.A. Schetter, and O.J. Rocha. 2019. Fourteen years of swamp forest change from the onset, during, and after invasion of emerald ash borer. *Biological Invasions* 21:3685-3696.
- Allombert, S., A.J. Gaston, and J.-L. Martin. 2005. A natural experiment on the impact of overabundant deer on songbird populations. *Biological Conservation* 126:1-13.
- Alverson, W.S., D.M. Waller, and S.L. Solheim. 1988. Forests too deer: Edge effects in northern Wisconsin. *Conservation Biology* 2:348-358.
- Anderson, R.C. 1994. Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. *Ecological Applications* 4:104-109.
- Bierzychudek, P. 1984a. Assessing "optimal" life histories in a fluctuating environment: The evolution of sex-changing by jack-in-the-pulpit. *American Naturalist* 123:829-840.
- Bierzychudek, P. 1984b. Determinants of gender in jack-in-the-pulpit: The influence of plant size and reproductive history. *Oecologia* 65:14-18.
- Bressette, J.W., H. Beck, and V.B. Beauchamp. 2012. Beyond the browse line: Complex cascade effects mediated by white-tailed deer. *Oikos* 121:1749-1760.
- Busing R.T., and P.S. White. 1997. Species diversity and small-scale disturbance in an old-growth temperate forest: A consideration of gap partitioning concepts. *Oikos* 78:562-568.
- Cadenasso, M.L., and S.T.A. Pickett. 2000. Linking forest edge structure to edge function: Mediation of herbivore damage. *Journal of Ecology* 88:31-44.
- Department of Public Works. 2014. Deer Management Plan Fact Sheet. Department of Public Works, Indianapolis, IN. <<http://www.indy.gov>>

- gov/eGov/City/DPR/Billboard%20Library/2016%20Fact%20Sheet.pdf>
- Dolan, R., and M. Moore. 1997. Qualitative vegetation analysis of Eagle's Crest State Nature Preserve, Eagle Creek Park, Indianapolis, IN. Friesner Herbarium, Butler University, Indianapolis, IN.
- Dolan, R., and M. Moore. 2007a. Ten year resurvey of permanent plots at Eagle's Crest Nature Preserve, Eagle Creek Park, Indianapolis, IN. Friesner Herbarium, Butler University, Indianapolis, IN.
- Dolan, R., and M. Moore. 2007b. Eleven year resurvey of permanent plots at Spring Pond Nature Preserve, Eagle Creek Park, Indianapolis, IN. Friesner Herbarium, Butler University, Indianapolis, IN.
- Dolan, R.W., J.D. Stephens, and M.E. Moore. 2015. Changes in plant species composition and structure in two peri-urban nature preserves over 10 years. *American Midland Naturalist* 174:33-48.
- Engelken, P.J., M.E. Benbow, and D.G. McCullough. 2020. Legacy effects of emerald ash borer on riparian forest vegetation and structure. *Forest Ecology and Management* 457:117684.
- Griggs, J.A., J.H. Rock, C.R. Webster, and M.A. Jenkins. 2006. Vegetative legacy of a protected deer herd in Cades Cove, Great Smoky Mountains National Park. *Natural Areas Journal* 26:126-136.
- Haffey, C.M., and D.L. Gorchov. 2019. The effects of deer and an invasive shrub, *Lonicera maackii*, on forest understory plant composition. *Ecoscience* 26:237-247.
- Harada, K., J. Ang, M. Ann, and M. Suzuki. 2020. Legacy effects of sika deer overpopulation on ground vegetation and soil physical properties. *Forest Ecology and Management* 474:118346.
- 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.
- Hoven, B.M., D.L. Gorchov, K.S. Knight, and V.E. Peters. 2017. The effect of emerald ash borer-caused tree mortality on the invasive shrub Amur honeysuckle and their combined effects on tree and shrub seedlings. *Biological Invasions* 19:2813-2836.
- Hurley, P.M., C.R. Webster, D.J. Flaspohler, and G.R. Parker. 2012. Untangling the landscape of deer overabundance: Reserve size versus landscape context in the agricultural Midwest. *Biological Conservation* 146:62-71.
- Indiana Department of Natural Resources. 2018. Indiana White-Tailed Deer Report. Indiana Department of Natural Resources, Indianapolis. <https://www.in.gov/dnr/fishwild/files/fw-DeerSummaryReport_2018.pdf>
- 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., R.B. Spigler, and C.C. Horvitz. 2014. In a long-term experimental demography study, excluding ungulates reversed invader's explosive population growth rate and restored natives. *Proceedings of the National Academy of Sciences USA* 111:4501-4506.
- Knackmuhs, E., and J.R. Farmer. 2017. Factors influencing trust in a wildlife management agency: A case study of deer management in Bloomington, Indiana. *Journal of Park and Recreation Administration* 35:48-64.
- 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., 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.
- Lessard, J.P., W.N. Reynolds, W.A. Bunn, M.A. Genung, M.A. Cregger, E. Felker-Quinn, M.N. Barrios-Garcia, M.L. Stevenson, M. Lawton, C.B. Brown, et al. 2012. Equivalence in the strength of deer herbivory on above and below ground communities. *Basic and Applied Ecology* 13:59-66.
- Liang, S.Y., and S.W. Seagle. 2002. Browsing and microhabitat effects on riparian forest woody seedling demography. *Ecology* 83:212-227.
- Martinod, K., and D.L. Gorchov. 2017. White-tailed deer browse on an invasive shrub with extended leaf phenology meets assumptions of an apparent competition hypothesis. *AoB Plants* 9:plx006.
- McShea, W.J., and J.H. Rappole. 1997. The science and politics of managing deer within a protected area. *Wildlife Society Bulletin* 25:443-446.
- Mitchell, J.M., G.J. Pagac, and G.R. Parker. 1997. Informed consent: Gaining support for removal of overabundant white-tailed deer on an Indiana state park. *Wildlife Society Bulletin* 25:447-450.
- Murray, B.D., C.R. Webster, M.A. Jenkins, M.R. Saunders, and S. Haulton. 2016. Ungulate impacts on herbaceous-layer plant communities in even-aged and uneven-aged managed forests. *Ecosphere* 7:e01378.
- Neter, J., M.H. Kutner, C.J. Nachtsheim, and W. Wasserman. 1996. *Applied Linear Statistical Models*, 4th ed. IRWIN, Chicago, IL.
- 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.
- Owings, C.F., D.F. Jacobs, J.M. Shields, M.R. Saunders, and M.A. Jenkins. 2017. Individual and interactive effects of white-tailed deer and an exotic shrub on artificial and natural regeneration in mixed hardwood forests. *AoB Plants* 9:plx024.
- Pickett, F.L. 1915. A contribution to our knowledge of *Arisaema triphyllum*. *Memoirs of the Torrey Botanical Club* 16:1-55.
- Rooney, T.P. 2001. Deer impacts on forest ecosystems: A North American perspective. *Forestry* 74:201-208.
- Rooney T.P., S.M. Wiegmann, D.A. Rogers, and D.M. Waller. 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conservation Biology* 18:787-798.
- Rossell, C.R., B. Gorsira, and S. Patch. 2005. Effects of white-tailed deer on vegetation structure and woody seedling composition in three forest types on the Piedmont Plateau. *Forest Ecology and Management* 210:415-424.
- Rossell, C.R., Jr., S. Patch, and S. Salmons. 2007. Effects of deer browsing on native and non-native vegetation in a mixed oak-beech forest on the Atlantic coastal plain. *Northeastern Naturalist* 14:61-72.
- Royo, A.A., R. Collins, M.B. Adams, C. Kirschbaum, and W.P. Carson. 2010a. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. *Ecology* 91:93-105.
- Royo, A.A., S.L. Stout, D.S. deCalesta, and T.G. Pierson. 2010b. Restoring forest herb communities through landscape-level deer herd reductions: Is recovery limited by legacy effects? *Biological Conservation* 143:2425-2434.
- 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.
- Slater, M.A., and R.C. Anderson. 2014. Intensive selective deer browsing favors success of *Asimina triloba* (pawpaw) a native tree species. *Natural Areas Journal* 34:178-187.

- Soil Survey Staff. 2020. USDA Natural Resources Conservation Service, Web Soil Survey. Accessed 16 July 2020 from <<http://websoilsurvey.nrcs.usda.gov/>>.
- Stromayer, K.A.K., and R.J. Warren. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? *Wildlife Society Bulletin* 25:227-234.
- 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.
- Thiemann, J.A., C.R. Webster, M.A. Jenkins, P.M. Hurley, J.H. Rock, and P.S. White. 2009. Herbaceous-layer impoverishment in a post-agricultural southern Appalachian landscape. *American Midland Naturalist* 162:148-168.
- Waller, D.M., and W.S. Alverson. 1997. The white-tailed deer: A keystone herbivore. *Wildlife Society Bulletin* 25:217-226.
- Waller, D.M., S.E. Johnson, and J.C. Witt. 2017. A new rapid and efficient method to estimate browse impacts from twig age. *Forest Ecology and Management* 404:361-369.
- Ward, J.S., S.C. Williams, and M.A. Linske. 2017. Independent effects of invasive shrubs and deer herbivory on plant community dynamics. *Forests* 8:1-18.
- Webster, C.R., Y.L. Dickinson, J.I. Burton, L.E. Frelich, M.A. Jenkins, C.C. Kern, P. Raymond, M.R. Saunders, M.B. Walters, and J.L. Willis. 2018. Promoting and maintaining diversity in contemporary hardwood forests: Confronting contemporary drivers of change and the loss of ecological memory. *Forest Ecology and Management* 421:98-108.
- Webster, C.R., M.A. Jenkins, and G.R. Parker. 2001. A field test of herbaceous plant indicators of deer browsing intensity in mesic hardwood forests of Indiana, USA. *Natural Areas Journal* 21:149-158.
- Webster, C.R., M.A. Jenkins, and J.H. Rock. 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. *Biological Conservation* 125:297-307.
- Webster, C.R., and G.R. Parker. 2000. Evaluation of *Osmorhiza claytonii* (Michx.) C.B. Clarke, *Arisaema triphyllum* (L.) Schott, and *Actaea pachypoda* Ell. as potential indicators of white-tailed deer overabundance. *Natural Areas Journal* 20:176-188.
- Webster, C.R., J.H. Rock, R.E. Froese, and M.A. Jenkins. 2008. Drought-herbivory interaction disrupts competitive displacement of native plants by *Microstegium vimineum*, 10-year results. *Oecologia* 157:497-508.
- Whitaker, J.O. 2010. *Mammals of Indiana*. Indiana University Press, Bloomington.
- 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.
- Williamson, S., and D.H. Hirth. 1985. An evaluation of edge use by white-tailed deer. *Wildlife Society Bulletin* 13:252-257.