Deer impacts on vegetation and communities in the

Leonard Preserve, Manchester, MI

2014

Prepared for

Washtenaw County Parks and Recreation Commission

September 2015

Jacqueline Courteau, Ph.D.
Consulting Ecologist
Ann Arbor, MI
734–680–5258
jbcourteau@gmail.com

INTRODUCTION AND STUDY PURPOSE

WCPARC's Leonard Preserve in Manchester, MI, contains over 259 acres of post-agricultural land along the River Raisin. The Preserve supports a rich diversity of habitats and species, including remnant prairies, oak barrens, young oak woodlands, and floodplain forest. These habitats are home to ruffed grouse, American woodcock, and wild turkey, as well as rare species including box turtle, grasshopper sparrow, white lady's slipper, and goldenseal.

Leonard Preserve is also home to a robust deer population. No hunting is allowed on the property, and the surrounding mix of agricultural fields, forest, and suburban lawns offers ideal habitat. Aerial flights in 2009 revealed a density of 248 deer/square mile and in 2013 a deer population of 76 deer/square mile was recorded. The reasons for the apparent decrease are not clear[1], but even the lower count is significantly higher than estimates that deer densities before European settlement ranged from 4–20 deer/square mile (McShea et al. 1997).

Since the Preserve was acquired in 2005, WCPARC's Natural Area Preservation Program (NAPP) staff and volunteers have worked to reduce invasive species and to nurture native plant species and their communities. Stewardship and management activities have included mowing, burning, prairie planting, floodplain forest planting, and manual removal of invasive species. Despite considerable effort, the prairies and young oak forests at Leonard retain the sharp, clean edges of the post-agricultural landscape, the fields lack tree recolonization and shrub cover, the prairies have low diversity, and the floodplain forest planting did not survive. Park staff have observed many signs of deer impact on vegetation (damage from browsing and trampling), and wondered whether the fact that native vegetation has been slow to recover, despite considerable and sustained efforts, could be due to deer overabundance.

To assess deer impacts on vegetation, NAPP staff constructed two 32' X 32' (roughly 10 m square) fenced plots or exclosures in 2009. One exclosure is in a dry-mesic prairie and the other is at the edge of a floodplain forest. Plots were sited in consultation with local biologists with expertise in vegetation and wildlife habitat, but no systematic surveys were conducted before fences were constructed to assess baseline conditions in fenced vs. adjacent unfenced plots.

Photo monitoring since 2009 has suggested that vegetation is taller and denser inside the exclosures, where protected from deer browsing, than in the adjacent control plots. Although the visual evidence is compelling, there has been no quantitative analysis of vegetation differences.

---

[1] Aerial deer population counts are often unreliable (Morellet 2001). Counts using aerial flyovers with human observers often miss some animals under dense cover, especially in areas with conifers (Potvin and Breton 2005), and only provide snapshot of deer in the area on a given day, whereas deer may bed down and move across territories of several dozen to several hundred acres or more over the course of a season. Accuracy of counts with human observers ranged from 37–83% of known populations in a deer exclosure study (Potvin and Breton 2005).

This study was contracted by NAPP to analyze the extent to which deer are affecting the diversity, abundance, and reproduction of plant species, including wildflowers, fruiting shrubs, and trees, in forest and grassland plots. We assess the amount of herbivore damage by deer as well as small mammals and insects. This study also considers whether and how deer are affecting forest succession and making changes in habitat and food sources for other species, such as pollinators (native bees and butterflies) and birds. We also focus on tree recolonization in old-field areas. The goal is to present an overview of deer impacts on Leonard Preserve plant and animal communities.

BACKGROUND

White-tailed deer (*Odocoileus virginianus*) are abundant throughout eastern North America (Côté et al. 2004). After population declines due to overhunting during the 19th and early 20th centuries, wildlife management policies to control hunting, along with habitat management and changes in land use, have allowed populations to rebound. By some estimates, current deer populations significantly greater than before European settlement, so that deer are considered "overabundant" (N, Horsley et al. 2003, Côté et al. 2004).

Documented impacts of deer overabundance in forest and old field areas include reduced tree regeneration and recolonization, reduced abundance and flowering of native spring flora, and alterations in vegetation structure (Côté et al. 2004, Rawinski 2008, Ferker et al. 2014). Deer have been dubbed a "keystone herbivore" because they can exert wide-ranging influences on the distribution and abundance of other species at various trophic levels, altering plant community structure, with potential consequences for pollinators (bees and butterflies), birds, and small mammals (DeCalesta 1994, Waller and Alverson 1997, Côté et al. 2004, Rooney and Waller 2003).

Deer impacts have also been widely reported in suburban areas starting in the 1990s (McAninch 1997). Deer have adapted well to suburban and even urban areas that lack a top predator and provide ample food resources (Hobbs et al. 2000, Rooney & Waller 2003). Municipal and county parks, as well as some state and national parks, often restrict or prohibit hunting; deer populations may grow almost unchecked. Deer interact with landscapes and habitats already fragmented by roads and housing developments; it can be hard to tease apart the impact of deer on plant and animal species on natural areas already affected by human disturbance, including agriculture and invasive species. However, many communities have concluded that deer are affecting vegetation in public park systems and have taken steps to assess and manage deer populations and impacts (e.g., Indianopolis parks, Indy.gov 2015; Indiana Department of Natural Resources 2011; Montgomery County Parks 2004; NPS 2014; Doerr at al. 2001).

METHODS AND MEASUREMENTS

We assessed deer impacts on vegetation in the forests and grasslands in three ways:

1. ***Quadrats:*** Surveying all plants in randomly selected quadrats (subplots) within the existing fenced exclosures and adjacent controls, in order to assess vegetation diversity, density, reproduction, and herbivore damage (by deer as well as small mammals and insects).
2. ***Indicator species:*** We conducted targeted surveys of selected several species characteristic of the forest spring flora, fall woodland flowers, and grassland wildflower species in exclosures, control plots, and surrounding areas.
3. ***Oak regeneration survey:*** We surveyed oak seedlings along a field edge extending from a fenceline of large bur oaks (*Quercus macrocarpa*) to examine deer impacts on oak recolonization of old fields.

Although the initial proposal also outlined plans for assessing deer impacts on bird habitat (e.g., branch architecture and stem density relevant for ground nesting or low-canopy nesting birds), that work proved to be too time-consuming for the project budget. However, by analyzing the quadrat and indicator data to assess flowering plants that supply nectar resources and fruits to various bird species, we can suggest some potential impacts and directions for future study.

1. Quadrats in exclosures and control plots: Vegetation diversity, abundance, flowering/fruiting, and herbivore damage

Exclosure studies are used to compare how vegetation diversity, abundance (density), and reproduction differ between areas that are protected from animal browsing (the fenced areas are referred to as “exclosures” because they exclude animals) and adjacent control plots, where animal browsing is freely allowed. Ideally, sites are relatively homogeneous, so that site conditions (slope and position on slope, aspect, soil, canopy cover, etc.) and vegetation types are similar in fenced and unfenced plots, which should be established with initial baseline surveys. Fences may be constructed of a small mesh wire, to exclude all mammalian browsers, or they may use a larger wire mesh that excludes only large herbivores—in this ecosystem, deer. Depending on exclosure size, vegetation may be inventoried in full fenced plots or sampled in smaller subplots, known as quadrats.

For rigorous quantitative analysis, exclosures should be replicated several times within each community type. Use of multiple quadrats within a single exclosure (rather than across different exclosures) allows for complete sampling of species diversity per unit area, as well as stem counts and measurements of size, flower and fruit numbers, and browse damage. The resulting data can be compiled, and averages for quadrats within the exclosure can be statistically compared to those of quadrats in an adjacent control plot. However, it is important to note that multiple quadrats within a single plot are not truly independent statistical samples, and thus comprise *pseudoreplication* (Hairston 1989, Hurlbert 1984). Analyses of multiple quadrats within one pair of exclosure and control plots can establish whether the differences between the two plots are significant, but conclusions are strong and generalizable as they would be with true replication within each community. Threes ways to strengthen the inferences are to measure additional plots, to assess whether differences are consistent across multiple variables (e.g., species number, plant size, flowering/fruiting), and to assess browse damage directly.

In this study, the existing exclosures were constructed in 2009 for public demonstration rather than quantitative research, and the purpose was to show how deer are affecting different plant communities—a floodplain forest and a grassland/savanna. These two areas were characterized by different plant communities with very little overlap in plant species. Therefore, they cannot be used as replicates for statistical analysis. To partly compensate for the absence of replication, we established and sampled two control plots in each community—one adjacent to the fenced plot (the "near control) and a second "distant control" that was 50–55 m away from each exclosure. This allowed us to assess the extent to which differences in presence of abundance of plant species between exclosure and control quadrats might have been due to natural spatial heterogeneity in plant distribution or were likely to be due to deer impacts.[2] In establishing distant plots, we aimed to find locations similar to existing exclosures, with similar slope, aspect, and canopy cover and, in the forest, a similar distance to the field edge. While the forest control plot was quite similar to the exclosure in general characteristics, the grassland area was topographically diverse and featured heterogeneous vegetation, so although the distant control was the best match we could find, with similar slope, position on slope, and aspect, the tree and shrub cover in the vicinity were visibly higher, leading to more somewhat shading of the plot.

To assess deer impacts on plant species diversity, density, and flowering/fruiting, we randomly placed quadrats (subplots) within exclosures as well as near and distant control plots. The "near control" plots were placed 2 m away from the fenced areas to avoid trampling and deer paths that had formed along fencelines. The "distant control" plots were 50–55 m from the exclosure. We assessed all plants in 5 quadrats in each plot.

We sampled forest plots in 18–24 May 2014 for spring flora but did not sample grassland plots at that time as an initial survey showed little plant growth. We then sampled both forest and grassland plots 13 September–19 October 2014 and analyzed the following variables, summarized in Table 1:

Plant diversity: All plants were identified to species when possible, allowing for comparison of species richness (average number of species per quadrat, and cumulative total species). Many

---

[2] Some studies in Western grasslands have found that vegetation distribution can be so variable that spatial distribution has been associated with greater differences in species richness and abundance than grazing (Stohlgren et al. 1998).

plants were small and lacking flowers or fruit for positive identification; some were still seedlings with only cotyledon or early leaves, and others were heavily browsed so that few leaves or buds remained, or so that growth patterns may have been altered. When specific identification was unclear, we aimed to identify genus or classed unknowns by functional group (wildflowers vs. grasses or sedges vs. woody plants). The total number of unique species—species richness—was tallied for each quadrat and the averages compared across plots (exclosure, near control, far control).

Species richness—the number of species per unit area—indicates biodiversity, but doesn't distinguish between common or weedy species or invasives vs. rare or unique species. Many states have developed "floristic quality assessments" to allow consideration of species considered important for conservation due to the specificity of their site preferences, the likelihood that they are found in undisturbed sites (fidelity to presettlement conditions), or their relative rarity (Swink and Wilhelm 1994). The Michigan Floristic Quality Assessment program first developed in 1996 and now maintained in an online database (Reznicek et al. 2014), assigns to each species found in Michigan a coefficient of conservatism (known as C or CC), from which a floristic quality index (FQI) can be calculated.

Although the FQI offers valuable botanical information as an indicator of the presence of rare and "conservative" plants at a given point in time, it is based on simple presence/absence rather than abundance or population size. It was designed for use with comprehensive site inventories, partly to assess restorability of sites by ascertaining whether the site conditions could support particular species. Thus, it is not well-suited to compare quadrat or small plot data, or to monitor changes in species populations or viability. A finding of a single stem of *Trillium* in a site where the species had been browsed repeatedly until only one stem was left would receive the same score in an FQI as a site with an abundant and thriving population. Although some studies do compare FQIs or mean CC values for quadrat or transect data, we do not present an FQA analysis here. However, species lists collected in this study are posted in the UniversalFQA website, where details on floristic quality can be viewed (http://universalfqa.org).

Plant abundance and size: In forest plots, all individual stems were counted in May and October in order to calculate plant density (# stems/m^2). In grassland plots, both woody plants (trees and shrubs) and forbs (wildflowers) were counted in September–October, but because grasses are dense and numerous, we estimated % cover rather than doing individual stem counts. Estimates of cover are a common technique for assessing large or densely vegetated plots (Bonham 1989, Causton 1988). We summed total number of stems of all species to look at overall vegetation density, and also summed number of individuals per species to allow for detailed assessment of species frequency.

While abundance is one gauge of plant success, plant size may be correlated with potential survival and reproductive success.[3] We measured plant height as a quick indicator of plant size, because it relevant to whether deer are likely to browse plants (deer most commonly browse between 0.2 and 1.5 meters in height, but we observed browse damage at anywhere from 0.05 to 1.75 m). Although plant height may be partly a response to light or competition rather than an indication of plant vigor—plants in low-light or crowded conditions will often grow tall rather than bushy—within similar conditions of light and competition (under forest canopy, or out in open grasslands), plant height can serve as a general sign of plant success. Leaf area, or leaf area index, is another common indicator of plant success, but the time and equipment needed to measure it were beyond the scope of this study. We analyzed average height of all stems per quadrat as an indicator of density, and looked at average height of individual species when applicable.

More reliable than height, but destructive to measure, is biomass, which we sampled in quadrats adjacent to the ones that we had initially measured so that we would have the option of repeating measurements in the established quadrats. We harvest biomass 28 September 2014 in the grassland and 19 October 2014 sampling period and clipped all standing (above-ground) material, dried it to constant mass at 140° C, and weighed it. Plant material was sorted by species to the extent possible, but it was difficult to sort out all grasses, so they were grouped into general native and non-native grass categories.

Because individual species were not consistently found in every quadrat, we grouped species into categories based on functional groups to allow for comparisons that indicate potential community-wide effects, such as forest regeneration and resources for trophic food webs:

- ***Wildflowers.*** Forest spring flora, as well as later-blooming forb species in both forests and grasslands, provide important nectar resources for a wide range of pollinators (including bees and butterflies as well as birds), and may also produce fruit important in the diets of various insects (including ant species), small mammals, and birds.

- ***Woody plants: trees and shrubs.*** The presence of tree seedlings and saplings indicate whether trees are regenerating within a forest or (re)colonizing a grassland, and the species composition can indicate the successional trajectory. Many forest understory and grassland shrubs provide flowers and fruits that supply a range of pollinators, birds, and small mammals with food resources.

---

[3] Although it seems intuitively obvious that larger plants have more resources to devote to reproduction, previous studies have not consistently shown increased reproductive effort with increased plant size (cf. Samson and Werk 1986). However, within individual populations (such as those in this study), the correlation is more consistent. Furthermore, some studies have found a clear correlation between plant size and flowering in spring flora species such as *Trillium* (Hanzawa and Kalisz 1993).

- ***Graminoids: grasses and sedges.*** In *forests*, where trees dominate the canopy, ground cover plants include spring flora and later-season wildflowers, woody plants (tree, shrub, and vine seedlings and saplings) and graminoids. While graminoids may play an important role as part of ground-nesting bird habitat, various studies have noted that a shift in dominance toward sedges when deer are overabundant, and then sedges in turn may outcompete both tree seedlings and spring flora (e.g., Randall and Walters 2005. Powers and Nagel 2009), which could ultimately reduce resources for some bird species. In dry to dry-mesic *grasslands* including open prairies and partly tree-covered savannas, grasses and sedges typically dominate the ground cover; however, forbs (wildflowers) are a key component of overall species diversity, and their flowers and fruits provide vital resources for insect pollinators including butterflies and bees, as well as for birds and small mammals. Forb establishment is a major goal in prairie restoration, and a major restoration handbook suggests seeding prairies with 50–60% forbs (Packard and Mutel 2005).

Plant reproduction and resources for community food webs: flowering and fruiting
All plants other than grassland grasses were assessed for whether they were flowering and fruiting, and for most species, the number of flowers and/or fruits was also recorded. It was not practical within the time constraints to record flower number for species with many small flowers, such as goldenrod (*Solidago* species) or bedstraws (*Galium* species).

Herbivore damage: deer vs. other species
Browse damage by deer can be reliably assessed on woody plants, and distinguished from other mammalian herbivores (woodchucks, rabbits, voles) by the characteristic shreddy bark and a broken appearance of the twig, because deer tend to rip and tear plant material, in contrast to rabbits and woodchucks, which cut cleanly at a 45° angle (see MDNR web site, http://www.michigan.gov/dnr/0,4570,7-153-10370_12148-61306--,00.html). Deer browse can be clearly identified on many grassland perennials with fibrous or pithy stems, such as goldenrods and asters, which show the same shreddy pattern. Deer browse on tender herbaceous plants, such as many spring flora, can be harder to assess if complete leaves or a large part of the stem is removed, as tender stems tend to wilt or wither within days of damage, so that patterns of torn or shredded leaves or stems do not persist long.

While the focus of this study was deer damage, all individually counted plants were assessed for whether they showed signs of damage from any herbivore—deer as well as small mammals (generally chipmunks or squirrels in the forest, rabbits in the grassland) and insects—to allow comparison of deer damage to other types of herbivore damage. Plants were rated for presence of herbivore damage (yes/no), type of herbivore (deer, small mammal, insect), and estimated % of plant damaged. It can be difficult to estimate how much plant material has been removed, but we used indications such as the number and amount of leaves or stems that were damaged. Most plants can tolerate occasional, moderate levels of browsing, but browse levels of 50% or more may be linked to higher mortality or reduced reproduction, so we calcuated the proportion of plants that had damage levels of 50% or more.

Quadrat data were tabulated and descriptive statistics and graphs compiled in Excel (for Mac 2011) separately for forest and grassland plots. Analyses used plots as treatments (independent variables): Exclosure, Near Control (2 m), Distant Control (50–55 m). Some data sets violated assumptions of the standard parametric statistical analysis of variance (ANOVA) that would typically be used to compare these data—for example, variability often differed significantly across treatments, and measurements of herbivore damage had missing values (that is, every plot did not have damaged plants). Non-parametric methods, such as resampling or bootstrapping, were beyond the scope of this study. Therefore, average data are displayed in figures with standard error bars; results from ANOVA tests to compare treatments are presented only when appropriate. ANOVAs were conducted in R or Excel to assess main effects followed by Tukey HSD to examine pairwise comparisons.

2. Indicator species

Quadrat data allows for comparison of overall vegetation trends, but the random samples do not always include enough individuals to allow focused analysis of particular species of concern. Studies of deer impacts sometimes focus on one or a few indicator species as representative of larger concerns. Target species have been chosen because they are known to be preferred or moderately preferred by deer (e.g., Winchcombe 2015, Boulanger et al. 2014, NPS 2014), because they represent key community functions, or to assess populations of species of special concern (threatened or endangered, or likely to become so). For example, spring flora, such as *Trillium*, offer important resources for several pollinator species, as do many other showy and beloved wildflower species, while various tree species can indicate forest regeneration and successional trajectories. Orchid species are relatively rare and many are of special concern, and have been the focus of systematic naturalist observations in the Huron-Clinton Metroparks (Courteau, unpublished report).

In this study, we focused on indicator species that offer important resources to native pollinators and seed-eaters including butterflies, bees, and birds. For forest spring flora and fall wildflowers, we established 2m transects and surveyed as many transects as needed in exclosure, near-control, and distant-control plots to locate 25–50 individuals of the following species that were blooming abundantly at sampling times:

<u>Forest: spring flora</u>

- Trillium, *Trillium grandiflorum*
- Bloodroot, *Sanguinaria canadensis*
- Creeping strawberry-bush, *Euonymus obovatus*
- Wild blue phlox, *Phlox divaricata*

In addition, although not specifically sampled outside of quadrats, several additional species of spring flora were numerous enough to allow analysis using the quadrat data:

- Spring beauty, *Claytonia virginica*
- Yellow trout lily, *Erythronium americanum*
- Cut-leaved toothwort, *Cardamine concatenata*

Forest: fall wildflowers

- Bluestem goldenrod, *Solidago caesia*
- Heart-leaved aster, *Symphyotrichum cordifolium*
- Woodland sunflower, *Helianthus divaricatus*

Population densities were calculated from the amount of area sampled to locate 25–50 stems. In the case of two fall wildflower species—heart-leaved aster and woodland sunflower—few or stems were found in the near control and/or distant control plots, so we extended our survey to sample adjacent areas in order to find enough stems for comparison.

For grassland areas, we selected wildflowers that provide resources to pollinators and assessed full plots (exclosure, near control, distant control) to count all flowering stems of the following late-summer species:

Grassland wildflowers (forbs)

- Smooth aster, *Symphyotrichum laeve*
- Stiff goldenrod, *Solidago rigida*
- Wild lettuce, *Lactuca canadensis*
- Swamp thistle, *Cirsium muticum*

While all of these species are visited by a range of native pollinators, swamp thistle is also the obligate host of the swamp metalmark butterfly, *Calephelis mutica*, listed as Special Concern in Michigan and several other Midwestern states.

For all indicator species, we assessed abundance within a given area to calculate population density, and recorded data on reproduction (flowering and fruiting) and herbivore damage as in quadrats.

3. Oak regeneration

Various studies conducted in a range of sites in the northeastern U.S. have shown that deer can slow or prevent forest tree regeneration, was well as inhibit recolonization of old fields by trees. Although much of the Leonard Preserve is post-agricultural land, the circa 1800 vegetation maps show that area included mixed savanna and oak barrens as well as oak-hickory and mixed-oak forests, so oak species have previously grown on the site and could be expected to return.

To assess whether deer browse is affecting oak recolonization, we searched for oak saplings in a belt transect (16 m wide by 200 m long) in an old field adjacent to a fenceline of large old bur oaks (*Quercus macrocarpa*). It is not clear whether these oaks were planted, volunteered in the fencerow, or remained from presettlement days. However, the trees supplied a seed source and the field lay in a site that could support oak growth and where oak saplings had been noted by park staff.

We surveyed saplings during leaf-off and snow-cover conditions, 14 March 2015, when winter browse damage would be easy to observe. We plotted oak sapling locations on ARC-GIS Collector, and assessed each individual height, condition, and herbivore damage (including deer, small mammals, and gall-forming insects). We noted whether the sapling had been topped by browsing, and also recorded a qualitative assessment of whether it appeared likely to grow into the next size class.

We exported data from ARC-GIS to Excel to tally the proportion of saplings browsed, browser identity, amount of damage, and proportion of seedlings with >50% browse damage. Spatial data, maps, and photos of saplings are available on request.

RESULTS

Forest

We measured a total of 829 plants of 48 different species in the 15 randomly placed quadrats in the forest exclosure, near control, and distant control during May 2014.

Plant diversity: species richness and composition

Springtime average species richness per quadrat where vegetation is protected from deer browsing, than both controls (Figure 1). Cumulative species number was also higher in exclosures (Figure 2, Table 2). Fall species richness of forbs (wildflowers) was significantly higher in exclosure than control plots ($p=0.02$, $F=5.67$, $df=2$; Figures 3a and 3b). Woody species followed a similar pattern but with considerable variability among plots, so that the difference was just past the $\alpha=0.05$ level ($p=0.059$, $F=3.63$, $df=2$; Figure 3c).

Plant abundance and size

Plant density was higher, on average, in exclosure quadrats than either near or distant controls (68 stems per exclosure quadrat, compared to 50 or fewer for control plots, Figure 4). The cumulative stem total for plants in all quadrats shows that the exclosure has 25% more plants than either control plot. However, the density has not yet reached a point of overcompetition, because plants in the exclosure are larger in terms of both height and biomass (Figures 6 and 7).

Forest indicators: Trillium, bloodroot, creeping strawberry-bush, trout lily, and spring beauties

Trillium, *Trillium grandiflorum* was significantly taller and had a significantly higher proportion of flowering individuals in protected exclosures than in either the near or distant control plots, based on a sample of 50 individuals from each area. The total density of *Trillium* plants was three times higher in the exclosure than either near or distant control plots ($6.25/m^2$, $0.94/m^2$, and $1.89\ /m^2$ respectively, Table 3 and Figure 8). Trillium in the exclosure had a higher total number of flowers (18 were blooming in the exclosure, 6 times as many flowers as in both control plots) and a significantly higher proportion of flowers in bloom ($p<0.0001$, $F=10.79$, $df=2$; Figure 9). Plants were also significantly taller in the exclosure ($p<0.0001$, $F=61.41$, $df=2$; Figure 10). Size distribution data for all plants suggest that more plants bloom at larger sizes (Figure 11).

Bloodroot (*Sanguinaria canadensis*) showed a similar pattern to trillium, with higher densities and a higher proportion of plants flowering or fruiting in the exclosure than in control plots. (Figure 12). Plants were larger on average (Figure 13), and the size distribution suggests that plants are more likely to bloom at the sizes found in the exclosure than in the control plots (Figure 14).

Creeping or running strawberry-bush, *Euonymus obovatus*, a woody ground-creeping plant that provides resources for native pollinators (several species of bees and flies) and birds (which eat and disperse the fruit), was heavily browsed by deer in control plots, occurring only at the edges of fallen logs or under fallen branches (coarse woody debris). It responded strongly to protection from deer, with significantly longer stems ($p<0.001$, $F=17.75$, $df=2$), a higher proportion of plants flowering or fruiting ($p=0.002$, $F=6.38$, $df=2$), and more flowers per individual ($p=0.004$, $F=5.93$, $df=2$); Table 4. The woody stems of *Euonymus* showed clear signs of browse damage, which could be attributed to mammalian herbivores. More than half of the plants in near and distant control plots had been browsed (all by deer), whereas only a single plant in the exclosure had been (by a small mammal), and this difference was highly significant ($p<0.0001$, $F=18.96$, $df=2$). There were 14 individuals were blooming in the exclosure plot with a total of 146 flowers, whereas the near control plot had 3 stems in bloom (3 flowers total) and the distant control had 1 blooming stem (2 flowers). During the fall resampling period, 6 fruits were found in the exclosure but none in control plots (or anywhere else in the forest outside the fence).

Other spring flora and fall wildflower indicators: Trout lily, bluestem goldenrod, heart-leaved aster, and woodland sunflower all showed similar patterns to the above species: plants were more abundant and/or in greater densities, in general larger, and with a higher total and/or proportion of flowering plants (data not displayed here but available on request). Several showed clear signs of browse damage.

Indicator species not reduced by deer

Wild blue phlox, *Phlox divaricata,* was the only species that did not appear to be strongly affected by deer presence (data not displayed, but available on request). Although it was sparsely distributed in the forest overall, and found in only one of the two control plots, the plant density, average size, and proportion of flowering plants did not differ in notable ways between the exclosure and the control plot.

Spring beauty, *Claytonia virginica*, did not show a consistent response to protection from deer. Although plants were on average slightly larger (9.7 cm) in the exclosure vs. 9.3 cm and 8.8 cm in near and distant control plots), the adjacent control actually had the highest number of flowers and highest proportion of reproductive plants, while the exclosure was intermediate, and the distant control had the fewest (data not displayed here but available on request). Spring beauty may benefit from the reduced competition in heavily browsed plots—many plots where it did well had a considerable amount of bare ground—as is often blooms before it reaches the 10 cm height considered to be the lower range of the deer browse zone. (Only 2 stems of the 97 sampled in control plots showed signs of deer browsing, although we did note browse damage on 8–10 individuals outside the established plots.) Spring beauty is often abundant in woodlots heavily grazed by cattle (Tony Reznicek, personal communication), which suggests that it might be able to tolerate trampling and escape heavy browsing.

Grassland

Plant diversity, abundance, and size (biomass)
Despite the appearance of visible differences in wildflower abundance and blooming in the overall exclosure compared to the near control and other areas adjacent, the average and total (cumulative) species richness diversity did not show clear differences across plots. This could be partly because many plants in control plots were present as seedlings or in the basal rosette stage, but not blooming, making them less apparent in casual observation. In addition, some plant material was in poor condition so that identification was not always accurate to the species level. (Cumulative species lists available on request.) However, the clearest data from grassland quadrats is on plant size, indicated by standing (aboveground) biomass (Figure 16).
Average biomass per plot of all species differed significantly between the deer exclosure and the distant control but not the near control plot ($p=0.02$, $F=6.16$, $df=2$). However, biomass of wildflower (forb) species, which include wildflower species that provide resources for native pollinators and birds, was significantly lower in both control plots where deer can browse than in the fenced plot protected from deer ($p=0.02$, $F=6.13$, $df=2$), and wildflowers comprised a signicantly higher proportion of total biomass (Figure 17). Biomass of woody species (shrubs including *Cornus foemina* and *Rubus* spp.) varied considerably within and across plots so that

although the average was higher in the exclosure, the difference was not significant ($p=0.32$, $F=2.30$, $df=2$; data not displayed here but available on request).

Indicator species: late summer wildflowers

Smooth aster (*Symphyotrichum laeve*), stiff goldenrod (*Solidago rigida*), swamp thistle (*Cirsium muticum*) and wild lettuce (*Lactuca canadensis*) A survey of complete 10 X 10 m plots located blooming stems of 4 species **ONLY** in exclosure plots. Basal rosettes of all species except *Lactuca canadensis* were located in quadrats or full plots, suggesting that species may be present but unable to bloom due to deer browsing. Although not fully captured in plot surveys, both *Solidago rigida* and *Symphyotrichum laeve* were heavily browsed by deer in the grassland near established plots. *S. laeve* was also browsed by rabbits in the deer exclosure (4 of 16 plants); rabbit browsing reduced plant height from 114 cm to 22 cm (averaged for all unbrowsed vs. browsed plants), and reduced flower number from an average of 5 or more to 2. However, deer browsing was more common in the grassland as a whole. *Lactuca canadensis* appeared to be particularly desirable to deer, as plants growing within exclosures but near the fence edge had been browsed at a height of ~1m by deer reaching through the fence (which the ~10 X 15 cm mesh size was large enough to allow). *Cirsium muticum* was also relatively rare in the grassland, and browsed by both rabbits and deer—some stems in the exclosure had evidence of browse at 1m or more, suggesting that deer might have jumped the fence on one or more occasions to browse inside.

Oak recolonization

Of the 38 bur oak (*Quercus macrocarpa*) saplings sampled along a field edge, 31 were browsed by deer (81%), and a total of 56% of them had 50% or more of all buds and twigs browsed. The high proportion of seedlings browsed, and the large amount of damage when browsed, have been linked to increased mortality risk and reduced tree regeneration in other studies (e.g., Boulanger 2014). Therefore, this level of browsing is likely to be slowing oak recolonization of old fields.

Other herbivores may also be slowing regeneration. Many saplings also showed signs of small mammal damage, from voles as well as rabbits and/or woodchucks, and many also had galls from parasitic wasps. Previous studies have found that meadow voles (*Microtus pennsylvanicus*) can reduce tree colonization (Ostfield and Canham 1998), and that oak seedlings are winnowed down by mammalian herbivores from seed predation to seedlings to saplings (Courteau 2005).

The oaks sampled here likely represent a small proportion of germinated seedlings that grew to sapling size. The only saplings found in the survey were located in dense cover, either thick stands of goldenrods and grasses, or under fallen branches. This suggests that mammalian browsing may already have eliminated significant numbers of seedlings.

DISCUSSION: IMPLICATIONS FOR PLANT COMMUNITIES, WILDLIFE, AND NATIVE POLLINATORS

Presence of deer is correlated with significant reductions in plant species composition, abundance and flowering, with the potential to reduce populations of spring and fall wildflowers in both forests and grasslands, and to reduce oak recolonization in old fields. 13 out of 15 indicator species in forest and grassland plots were both more abundant and more likely to flower/fruit in areas protected from deer. Although species composition and abundance data alone do not demonstrate that deer has caused the declines, the combination of data on indicator species (including clear signs of deer browse damage) strengthens the case.

Effects ripple to communities and tropic levels beyond plant populations, however, because the affected species provide key resources for a range of insect, small mammal, and bird species.

Plant population effects

- ***Potential for Trillium decline or extirpation in forest.*** Deer presence is correlated with a six-fold reduction in total *Trillium* flowering and thus floral density.
  - Fewer flowers will result in fewer seeds.
  - *Trillium* pollination appears more successful at intermediate than low or high densities,[6] so reduced floral density could result in reduced pollination success, further decreasing reproductive success.
  - Smaller plant size and lower flowering rates could be due to deer browsing in previous years.
- ***Potential declines in many other forest spring flora and fall wildflowers.*** All indicator species other than wild blue phlox and spring beauty were more abundant, larger, and more likely to be blooming in exclosures where protected from deer. It is important to note that many sensitive species have likely already been eliminated—often by the time managers notice that deer may be a problem and install fenced plots, deer-preferred species such as orchids may have long since been eliminated (Tony Reznicek, personal communication), a problem that can be referred to as "the ghost of herbivory past" (Connell 1980, Howe & Brown 2003). Deer exclosures can demonstrate whether species that have been reduced can recover over time with protection from deer, but

- ***Decreased forb growth and flowering in grassland.*** Grassland forb species showed significantly lower biomass in control plots open to deer browse, which could lead to diminished resources to support flowering and reproduction in future years.

- ***Slowed forest regeneration or altered succession.*** Although many plants can tolerate occasional and moderate amounts of browse damage, severe browsing on woody plants has the potential to decrease forest regeneration and alter succession. Winchcombe (2015) has noted that when 50% or more twigs or buds are browsed on tree saplings less than 2 meters tall, browse damage can be fatal. Boulanger et al. (2014) suggest that browse damage on more than 15% of the seedlings of a species per year can place a generation of tree seedlings at risk. The fact that 81% of surveyed oak saplings had been browsed by deer, with 56% showing 50% or more damage, suggests that deer could indeed be inhibiting oak recolonization, so that this site may continue to be a grassland rather than succeeding to savanna or forest.

Effects on pollinators and fruit/seed eaters

Table 5 summarizes trophic interactions among some of the deer-affected wildflowers that provide important resources to species including bees, butterflies, and birds.

- ***Decreased pollen and nectar resources for native pollinator species including bees and butterflies.*** Significantly lower flowering outside deer exclosures across a range of species could affect both specialist and generalist pollinators, although further measurements are needed to assess total floral availability at multiple scales. Species such as *Cirsium,* which were heavily browsed by deer and not flowering within 200+ m of the grassland exclosure, are host to a specialist pollinator, the digger bee, *Melissodes desponsa*, and is also the preferred host plant for the caterpillars of an uncommon butterfly, *Calephelis mutica* (Swamp Metalmark, Hilty 2004).

- ***Decreased food sources for birds and small mammals.*** Although many seed eaters rely on diverse food sources, a large reduction in seed production by many forest spring flora and grassland forb species could lead to lowered abundance of both birds and small mammals. Further study would be necessary to precisely quantify links between seed production and animal populations.

FIGURES AND TABLES

Table 1. Summary of methods and measurements. Forest plots and indicators were sampled 18–24 May and 18 October 2014. Grassland plots and indicators were sampled 13–28 September 2014. Oak saplings were surveyed 14 March 2015.

Method	Index of population or community status	Community	Measurement
1. Quadrats (0.25 m square) 5 per plot (exclosure, near control, distant control)			
	Plant diversity (species composition)	Forest and grassland	species richness (# species/quadrat)
			cumulative species--total found in plot
	Plant abundance	Forest	# of stems of each species
		Grassland	# stems of wildflower and woody species
			% cover of grasses and sedges
	Plant size	Forest	height (cm) of all stems
			standing (aboveground) biomass (gm)
		Grassland	standing (aboveground) biomass (gm)
	Plant reproduction	Forest	flowering/fruiting (yes/no)
			# flowers/fruits per plant (for flowers>1cm diameter)
		Grassland	flowering/fruiting (yes/no), wildflowers only
			# flowers/fruits per plant for indicator species only
	Herbivore damage	Forest	herbivore damage (yes/no) all stems
			herbivore identity (deer, small mammal, insect)
			estimated % damage
		Grassland	herbivore damage, identity, % for wildflowers only
2. Indicator species, transects or full plots			
	Spring flora	Forest	stem height (cm)
	Trillium grandiflorum		flowering/fruiting (yes/no)
	Sanguinaria canadensis		# flowers/fruits per plant (for flowers>1cm diameter)
	Euonymus obovatus		herbivore damage (yes/no) all stems
	Phlox divaricatus		herbivore identity (deer, small mammal, insect)
	*Claytonia virginica**		estimated % damage
	*Erythronium americanum**		** Assessed from quadrat data rather than additional focused transects.*
	Fall wildflowers		
	Helianthus divaricatus		
	Solidago caesia		
	Symphyotrichum cordifolium		
	Wildflowers	Grassland	
	Cirsium muticum		total # flowering stems within full plot
	Lactuca canadensis		stem height (cm), *Symphotrichum only*
	Solidago rigida		herbivore damage and identity, *Symphyotrichum* onll
	Symphotrichum laeve		

<u>3. Oak regeneration/recolonization</u>

Oak sapling status		
	Old field	stem height (cm)
Quercus macrocarpa		herbivore damage (yes/no) all stems
		herbivore identity (deer, small mammal, insect galls)
		estimated % damage
		topped by browsing (yes/no)
		likely to succeed? (yes/no--qualitative assessment)
		map, photos: available on request

Table 2. Forest species composition, May 2014.

FOREST SPECIES	Exclosure	Adjacent control	Distant control	C	N/A	PHYS	COMMON NAME
Acer saccharum	X		X	5	N	Nt Tree	SUGAR MAPLE
Actaea sp. [pachypoda or rubra)			X	7	N	Nt P-Forb	DOLL'S-EYES OR RED BANEBERRY
Agrimonia gryposepala?	X	X		2	N	Nt P-Forb	TALL AGRIMONY
Allium tricoccum	X	X	X	5	N	Nt P-Forb	WILD LEEK
Anemone quinquefolia	X			5	N	Nt P-Forb	WOOD ANEMONE
Asclepias sp.	X						MILKWEED
Aster, likely Symphyotrichum cordifolium	X			4	N	Nt P-Forb	HEART-LEAVED ASTER
Brachyelytrum erectum			X	7	N	Nt P-Grass	LONG-AWNED WOOD GRASS
Cardamine concatenata	X		X	5	N	Nt P-Forb	CUT-LEAVED TOOTHWORT
Carex blanda			X	1	N	Nt P-Sedge	SEDGE
Carex pensylnanica		X		4	N	Nt P-Sedge	SEDGE
Carex sp.	X	X	X				SEDGE
Carex woodii		X		8	N	Nt P-Sedge	SEDGE
Carya cordiformis	X			5	N	Nt Tree	BITTERNUT HICKORY
Claytonia virginica	X	X	X	4	N	Nt P-Forb	SPRING-BEAUTY
Erythronium americanum	X	X	X	5	N	Nt P-Forb	YELLOW TROUT LILY
Euonymus obovata	X			5	N	Nt Shrub	RUNNING STRAWBERRY BUSH
Forb unknown sp #1	X					Forb	
Forb unknown sp #2	X					Forb	
Fraxinus sp (pennsylvanica or americana)	X		X	2/5	N	Nt Tree	RED ASH OR WHITE ASH
Galium aparine	X			0	N	Nt A-Forb	ANNUAL BEDSTRAW
Galium concinnum		X	X	5	N	Nt P-Forb	SHINING BEDSTRAW
Geranium maculatum	X	X	X	4	N	Nt P-Forb	WILD GERANIUM
Geranium sp (robertianum?)			X	3	N	Nt A-Forb	HERB ROBERT
Glyceria striata	X	X		4	N	Nt P-Grass	FOWL MANNA GRASS
Grass sp.			X				GRASS species
Helianthus sp. (likely divaricatus)	X					Forb	(WOODLAND) SUNFLOWER
Ostrya virginiana	X	X	X	5	N	Nt Tree	IRONWOOD; HOP HORNBEAM
Parthenocissus quinquefolia	X			5	N	Nt W-Vine	VIRGINIA CREEPER
Phlox divaricata	X	X		5	N	Nt P-Forb	WOODLAND PHLOX
Polygonatum biflorum	X	X	X	4	N	Nt P-Forb	SOLOMON-SEAL
Prenanthes alba	X	X	X	5	N	Nt P-Forb	WHITE LETTUCE
Prunus serotina	X		X	2	N	Nt Tree	WILD BLACK CHERRY

FOREST SPECIES	Exclosure	Adjacent control	Distant control	C	N/A	PHYS	COMMON NAME
Quercus rubra			X	5	N	Nt Tree	RED OAK
Ranunculus abortivus	X		X	0	N	Nt A-Forb	SMALL-FLOWERED BUTTERCUP
Rosa multiflora	X			*	A	Ad Shrub	MULTIFLORA ROSE
Rosa sp			X			Shrub	ROSE species
Sanguinaria canadensis	X	X	X	5	N	Nt P-Forb	BLOODROOT
Sanicula odorata			X	2	N	Nt P-Forb	BLACK SNAKEROOT
Smilax sp (illinoensis or lasioneura)			X	4/5	N	Nt P-Forb	CARRION-FLOWER
Solidago caesia	X	X		7	N	Nt P-Forb	BLUE-STEMMED GOLDENROD
Symphyotrichum lateriflorum	X			2	N	Nt P-Forb	SIDE-FLOWERING ASTER
Taraxacum officinale			X	*	A	Ad P-Forb	COMMON DANDELION
Trillium grandiflorum	X	X	X	5	N	Nt P-Forb	COMMON TRILLIUM
Ulmus rubra	X			2	N	Nt Tree	SLIPPERY ELM
Ulmus sp. (americana or rubra)		X	X	1/2	N	Nt Tree	AMERICAN ELM OR SLIPPERY ELM
Uvularia grandiflora			X	5	N	Nt P-Forb	BELLWORT
Uvularia sp. or Polygonatum sp.	X	X	X	4/5	N	Nt P-Forb	BELLWORT OR SOLOMON-SEAL

Table 3. Indicator species: *Trilium grandiflorum*. Trillium occurred at more than 3 times the density in the exclosure than in control plots, and both a higher total number and higher proportion of plants were blooming.

Trillium	**Density (per m^2)**	**Total # blooming in full plot**	**Mean height (cm) of blooming plants**
Exclosure	6.25	18	22.56
Near Control	0.94	3	20.33
Distant Control	1.89	2	16.00

Table 4. Indicator species: *Euonymus obovatus,* creeping strawberry-bush. A small creeping woody plant providing resources for insect pollinators (native bees and flies) and fruit eaten by birds. Flowering was significantly higher inside the exclosure, resulting in at least 6 fruits that were found during fall sampling, whereas no fruits were found in control plots.

Euonymus obovatus	**Total # blooming in full plot**	**Total # flowers in full plot**
Exclosure	14	146
Near Control	3	3
Distant Control	1	2

Table 5. Trophic level (community) interactions for which plant species provides resources. Various species identified as more numerous or with more biomass or flowers

		Pollinators (nectar eaters)					Seed dispersers and predators			
Habitat	**Plant species**	**Bees**	**Beetles**	**Butterflies & Moths**	**Flies**	**Hummingbirds**	**Ants**	**Birds**	**Small mammals**	**Deer**
Forest	***Trillium grandiflorum***	**X**					**X**		**X**	**X**
	Euonymus obovatus	**X**			**X**			**X**		
Grassland*	***Cirsium muticum***	**X**		**X**		**X**		**X**		
	Desmodium paniculatum	**X**	**X**	**X**				**X**	**X**	**X**
	Hypericum perfoliatum	**X**						**X**	**X**	
	Solidago rigida	**X**		**X**				**X**	**X**	
	Symphyotrichum (aster) laevis	**X**		**likely**				**X**	**X**	
	Rubus allegheniensis	**X**		**likely**				**X**	**X**	
	Rubus flagellaris	**X**		**likely**				**X**	**X**	

*Species only found in or only blooming in exclosure quadrats.

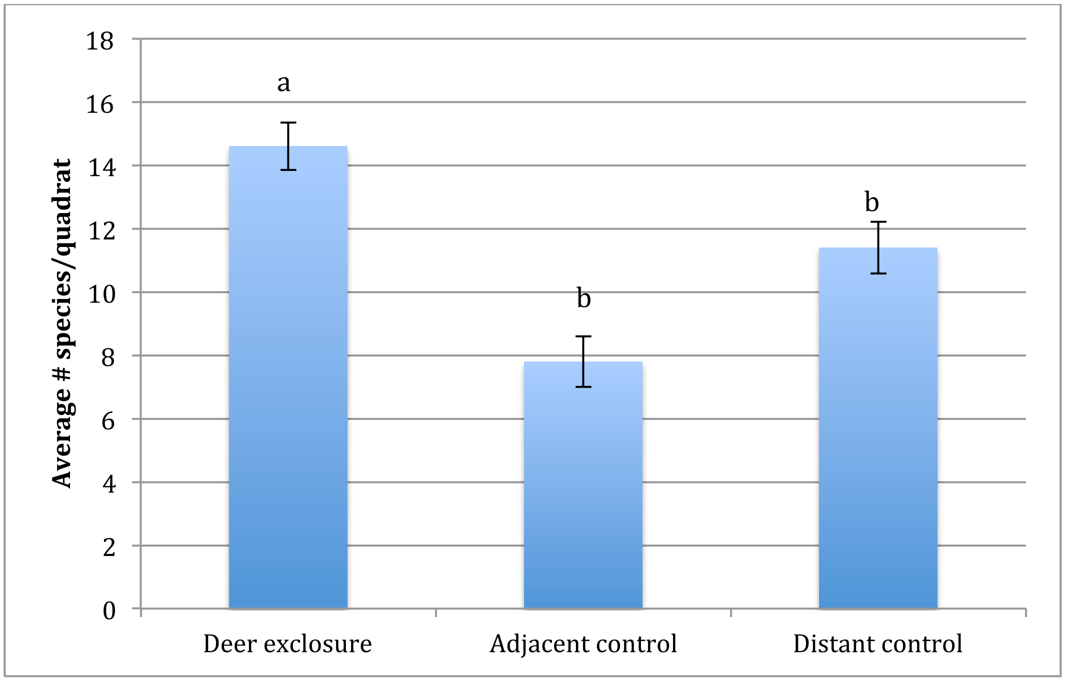

Figure 1. Forest species diversity: average species richness in spring. Average # species per 0.25 m^2 quadrat sampled in Leonard Preserve, May 2014, was significantly higher in exclosures, where plants are protected from deer browsing and trampling, than in adjacent (near) and distant control plots ($p=0.01$, $F=6.45$, $df=2$). Adjacent and distant controls differed in average richness per plot, but the difference is not significant, likely due to higher variability within control plots.

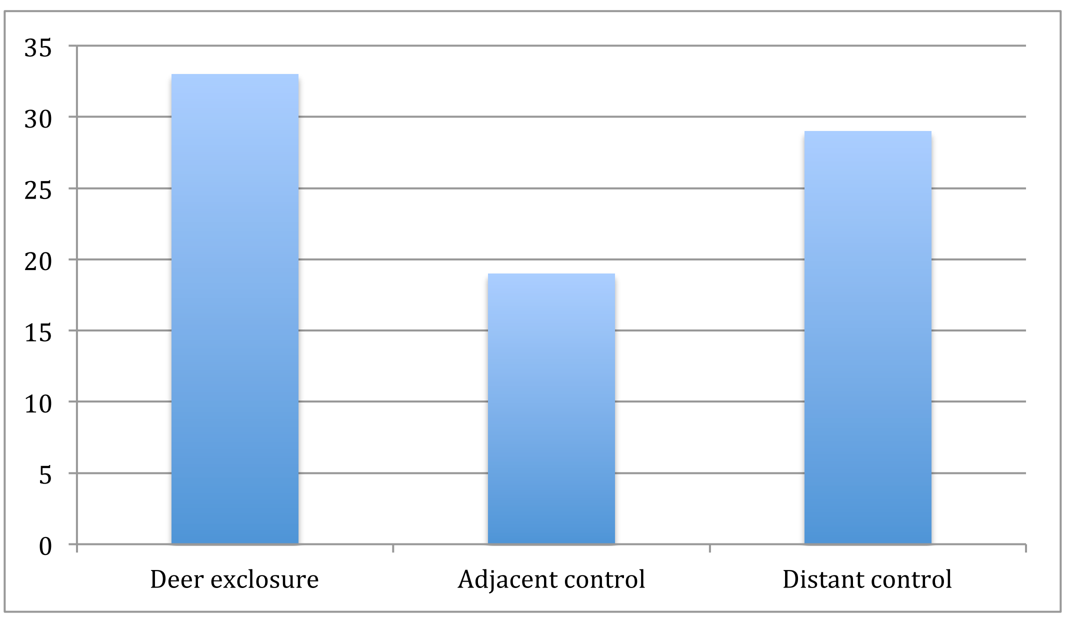

Figure 2. Cumulative total species in forest quadrats in spring. Total of all species found in 5 randomly placed 0.25 m^2 quadrats per plots, sampled in Leonard Preserve, May 2014.

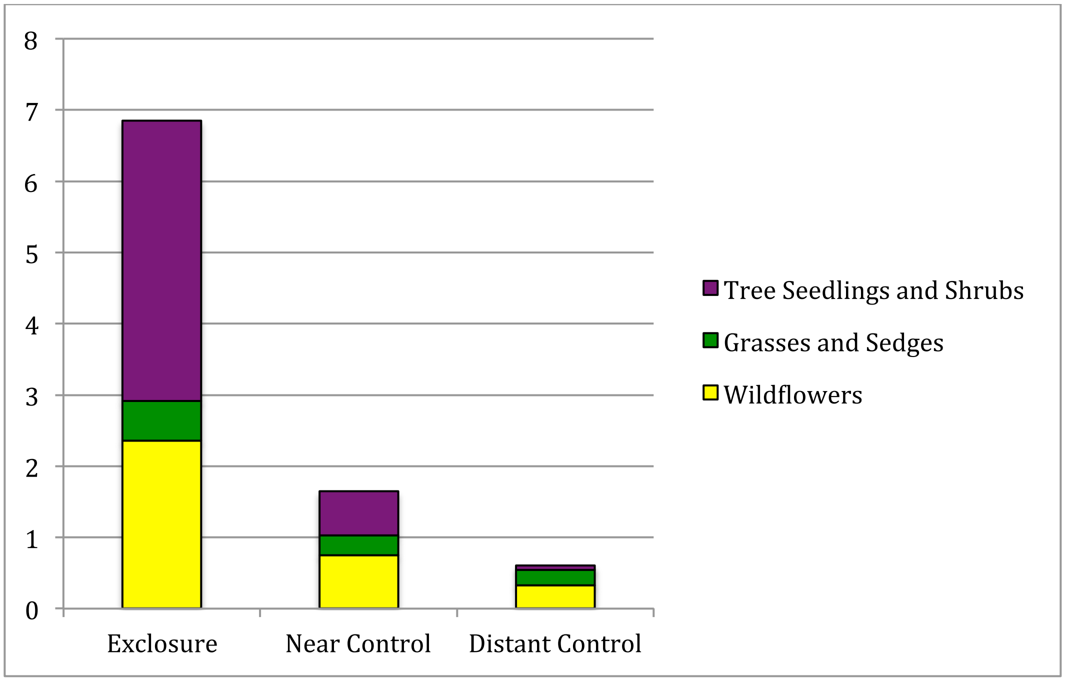

Figure 3a. Forest diversity in fall: average species richness of wildflowers, trees and shrubs, and graminoids.

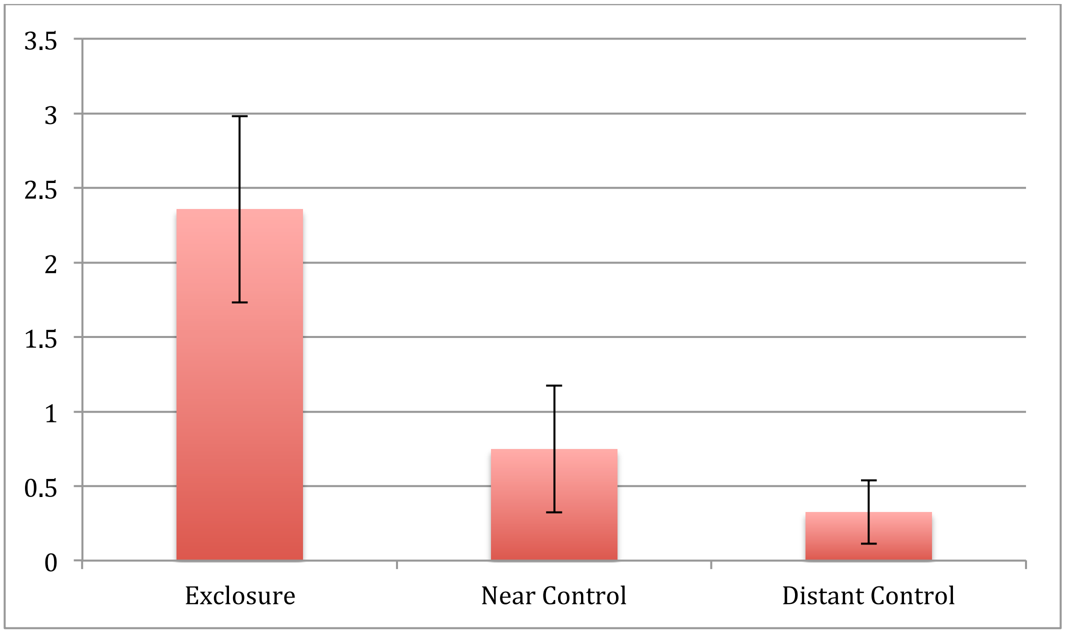

Figure 3b. Forest wildflower diversity in fall: average species richness. Average species # per quadrat of wildflower species (forbs) sampled in October. (Spring flora other than wild geranium had died back and were not included in this count). The exclosure had on average 3 times more wildflower species than control plots.

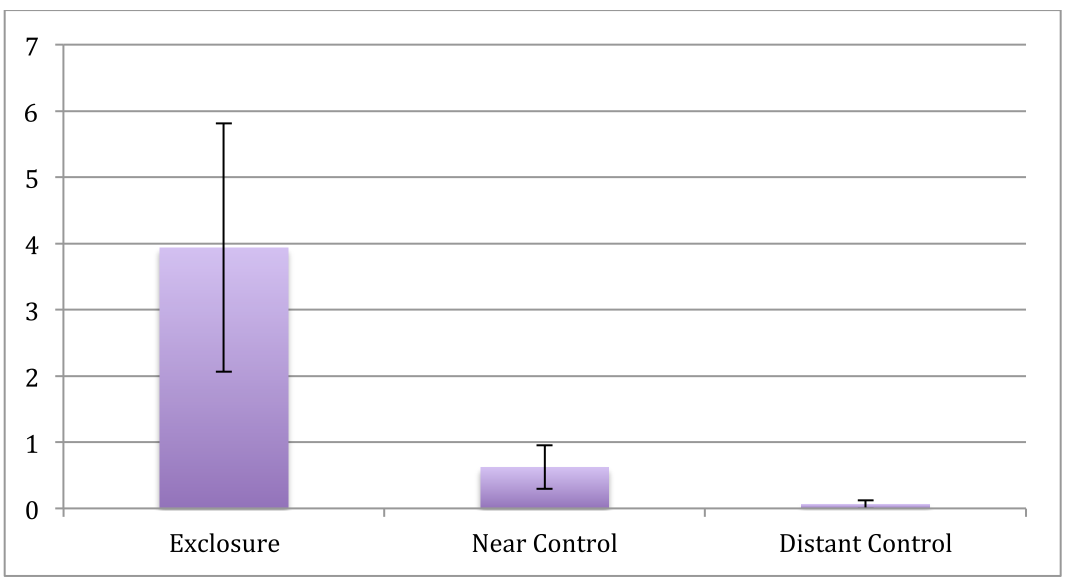

Figure 3c. Fall tree and shrub diversity: average species richness. The average number of woody plants species sampled in Leonard Preserve quadrats in October 2014. Species composition was quite variable, but on average 4 times higher in the exclosure than in control plots, which both had low numbers.

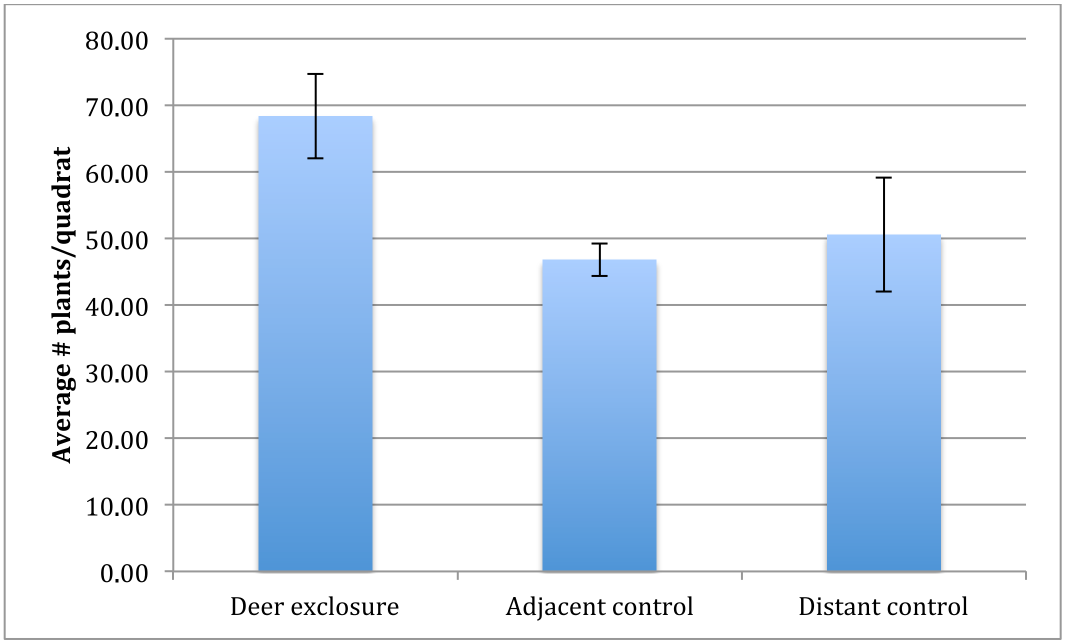

Figure 4. Forest plant abundance: stem density. Average number of individuals of all species in 0.25 m^2 quadrats per plots, sampled in Leonard Preserve, May 2014.

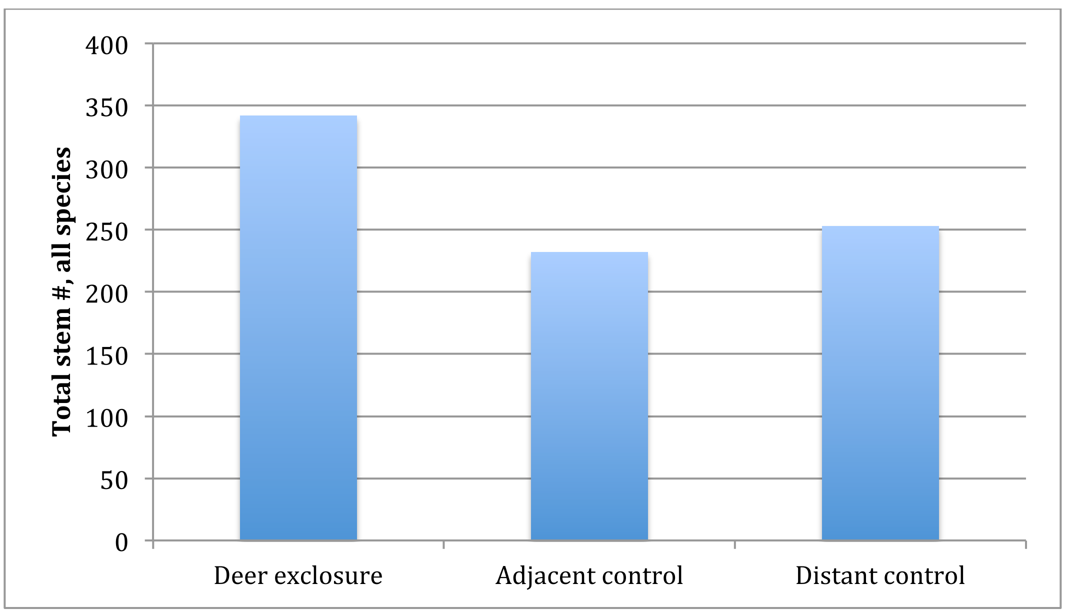

Figure 5. Forest plant abundance: Cumulative plot totals. Total number of individuals of all species found in the total 1.25 m^2 from all quadrats combined, sampled in Leonard Preserve, May 2014.

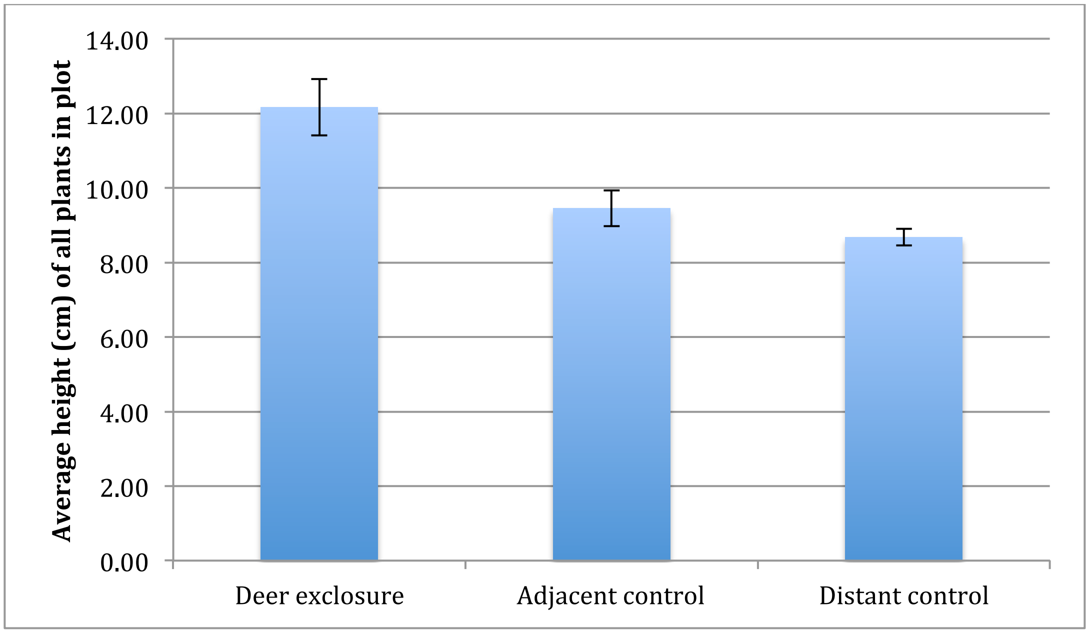

Figure 6. Forest plant size: average height of all individuals of all species. Average height of individuals of all species in 0.25 m^2 quadrats per plots, sampled in Leonard Preserve, May 2014. Although typical plant heights vary with and are constrained by species identity, the average of all plants combined is an indicator of overall plant vigor in quadrats.

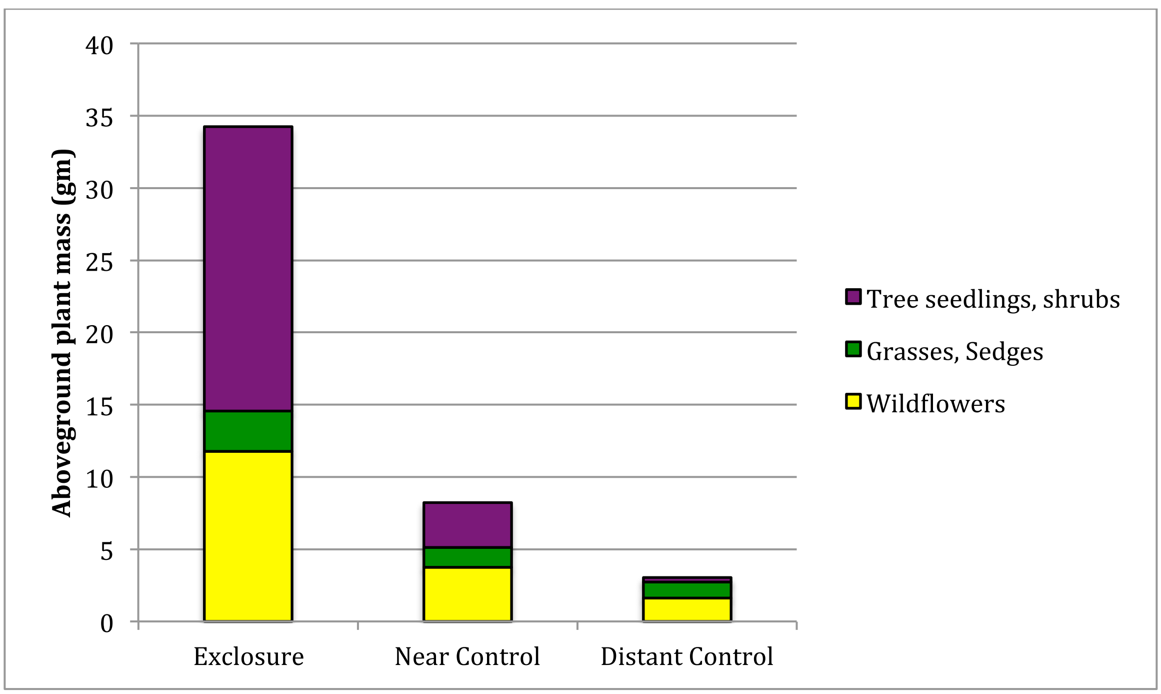

Figure 7. Forest plant size: total standing (aboveground) biomass. All standing plants in all quadrats were clipped, dried at 140° C to constant mass (all moisture removed), then weighed. Woody plants—tree seedlings and shrubs—dominated the exclosure plots, indicating tree regeneration, and wildflowers make up 1/3 of total biomass. Control plots have lower woody plant and wildflower biomass, and the distant control has a high proportion of grasses and sedges—a shift often noted where deer are overabundant.

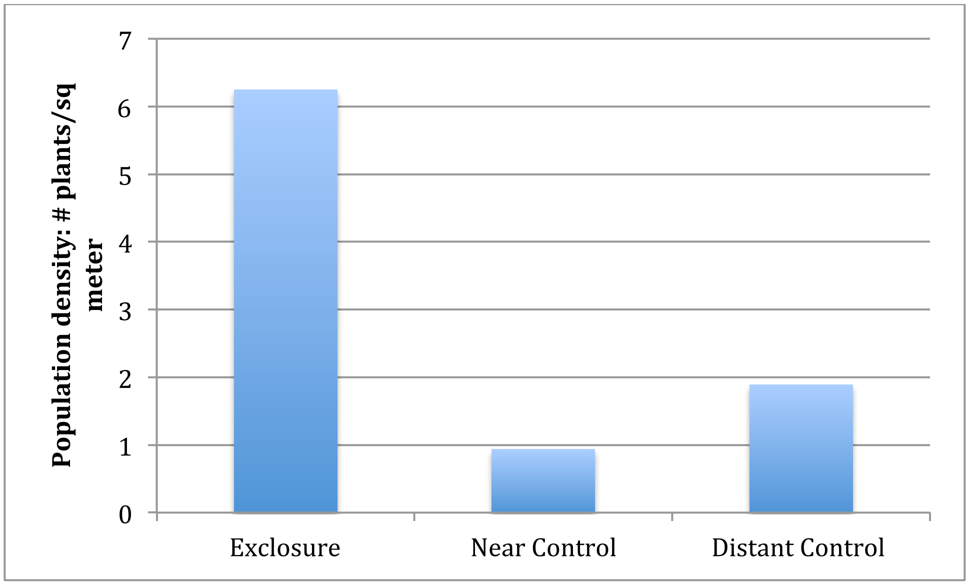

Figure 8. Forest indicator species: population density of *Trillium grandiflorum*. Densities calculated from plants encounter in 2-meter wide transects until a minimum of 50 plants were located. Trillium are more than 3 times denser in exclosure than either control plot.

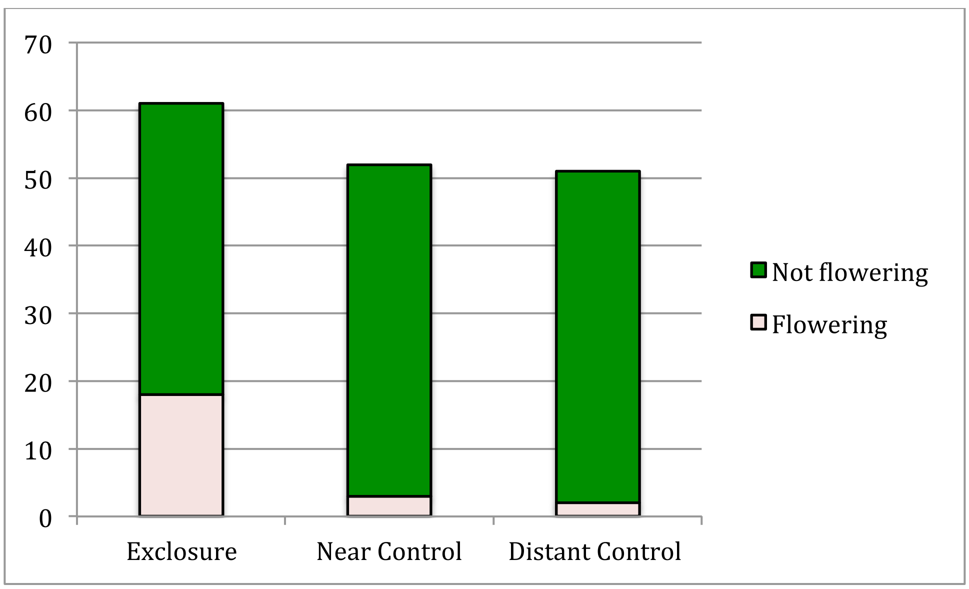

Figure 9. Forest indicator species: Proportion of sampled trillium in bloom, May 2014. Both the total number of blooms and the proportion of plants blooming was higher in the exclosure than in near or distant control plots.

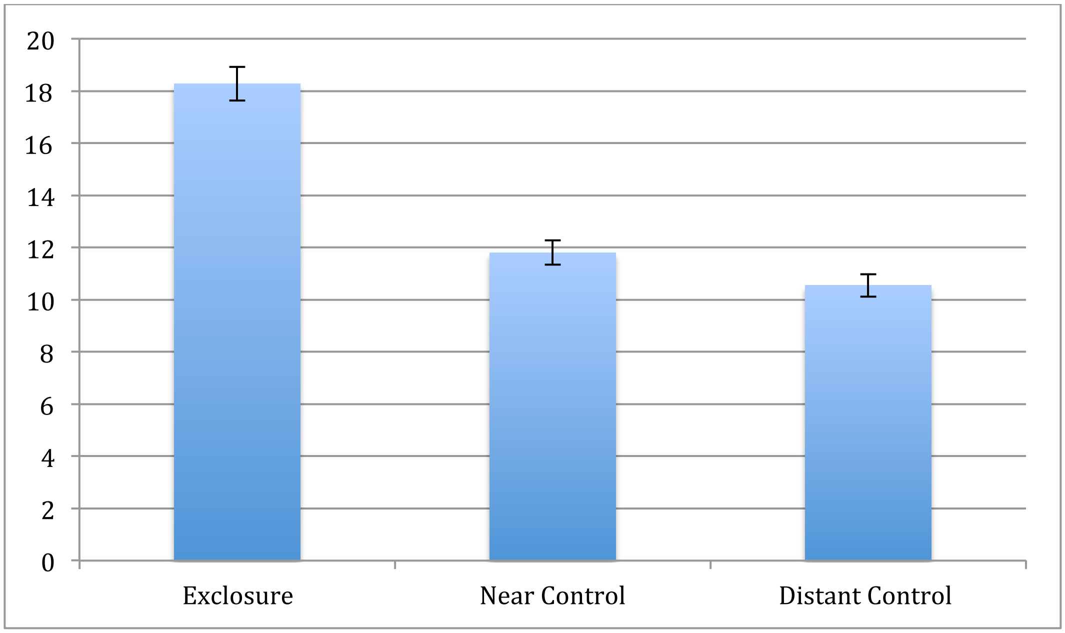

Figure 10. Forest indicator species: average height of *Trillium grandiflorum*, May 2014. Plants in the exclosure were significantly taller than plants in control plots.

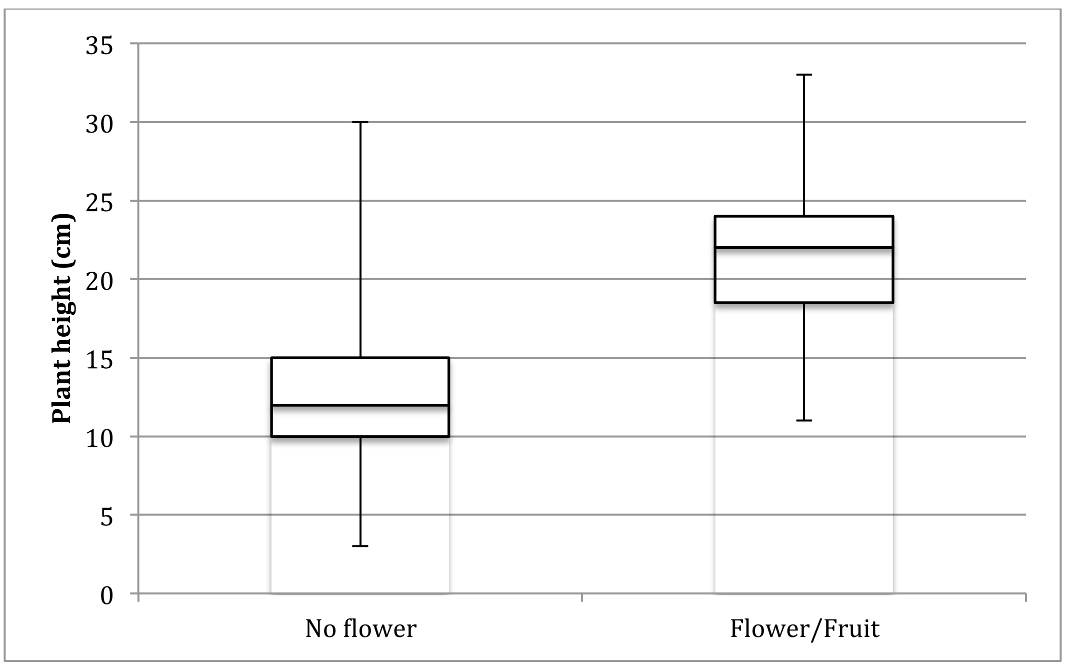

Figure 11. Forest indicator species: Size distribution of flowering/fruiting vs. non-flowering stems of *Trillium grandiflorum,* May 2014.This plot, which groups all plants together, shows the height distribution of trillium that were not in bloom compared to trillium that were in flower or fruiting at the time of the May 2014 survey. Although there was a wide range of heights of plants that were not flowering, 75% of all flowering/fruiting plants had reached a height of 18 cm or more, suggesting that flowering is more likely as plants get larger. (Box and whisker plot shows median values and quartiles.)

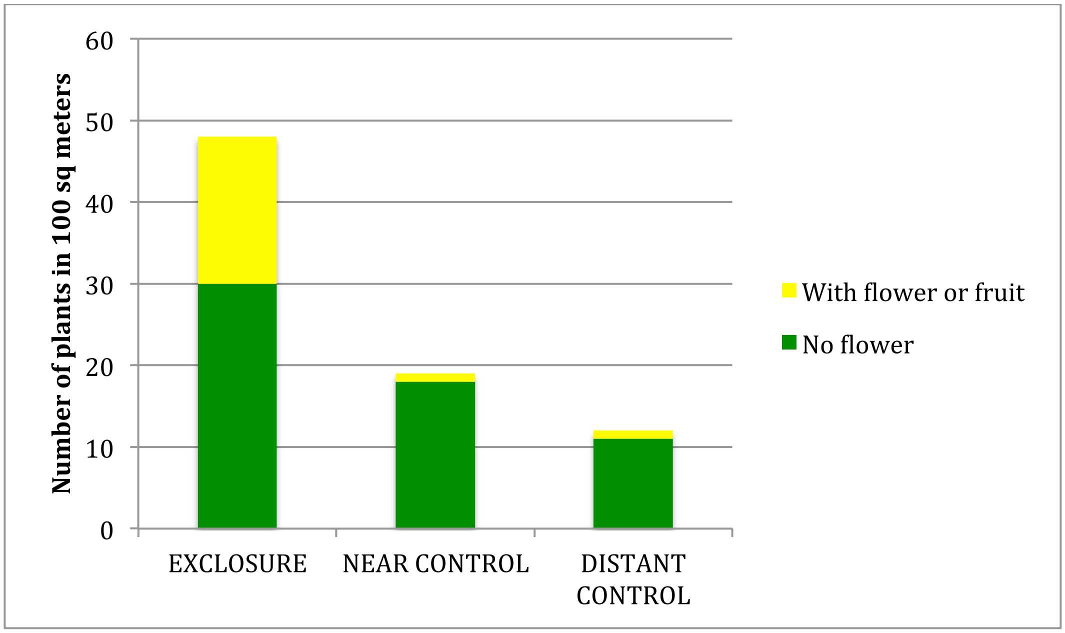

Figure 12. Forest indicator species: Density of *Sanguinaria canadensis,* bloodroot, May 2014. Plants were sampled in the full 10 X 10 meter control plots, locating a total of 48 in the exclosure, 19 in the near control and 12 in the far control. There were more plants, and a larger number and proportion in bloom, in the exclosure vs. control plots.

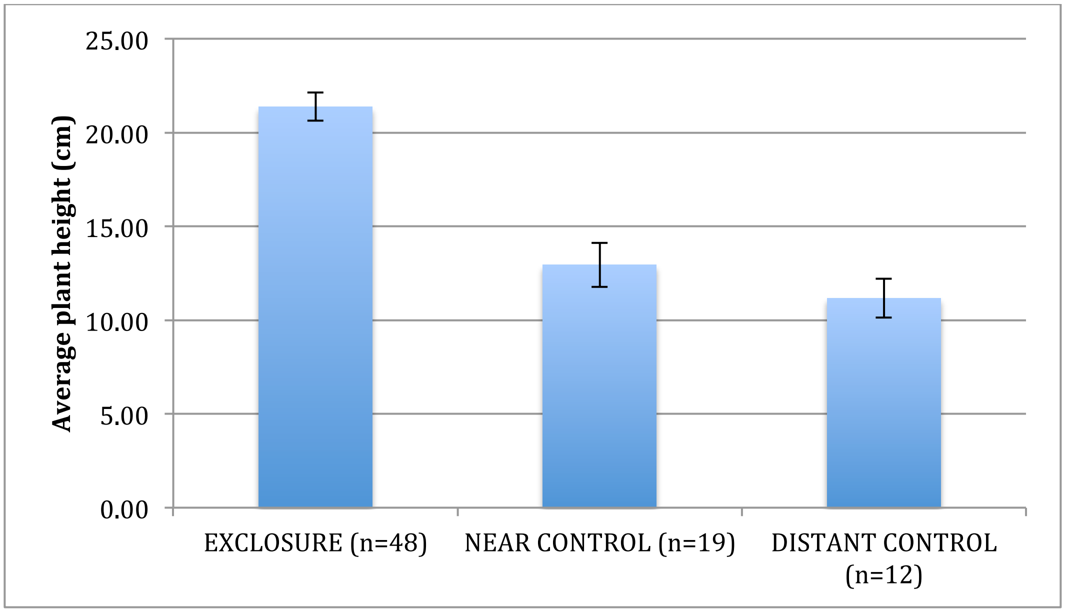

Figure 13. Forest indicator species: Average height of *Sanguinaria canadensis*, bloodroot, May 2014. Although herbivore damage is not shown here, plant height can be reduced by mammalian herbivore browsing. No plants in the exclosure showed signs of any mammalian herbivore browse damage. There were no signs of mammalian herbivore damage in the near control, but 5 of 19 plants were under a dense cover of large fallen branches (coarse woody debris) that prevented deer but not small mammal access.

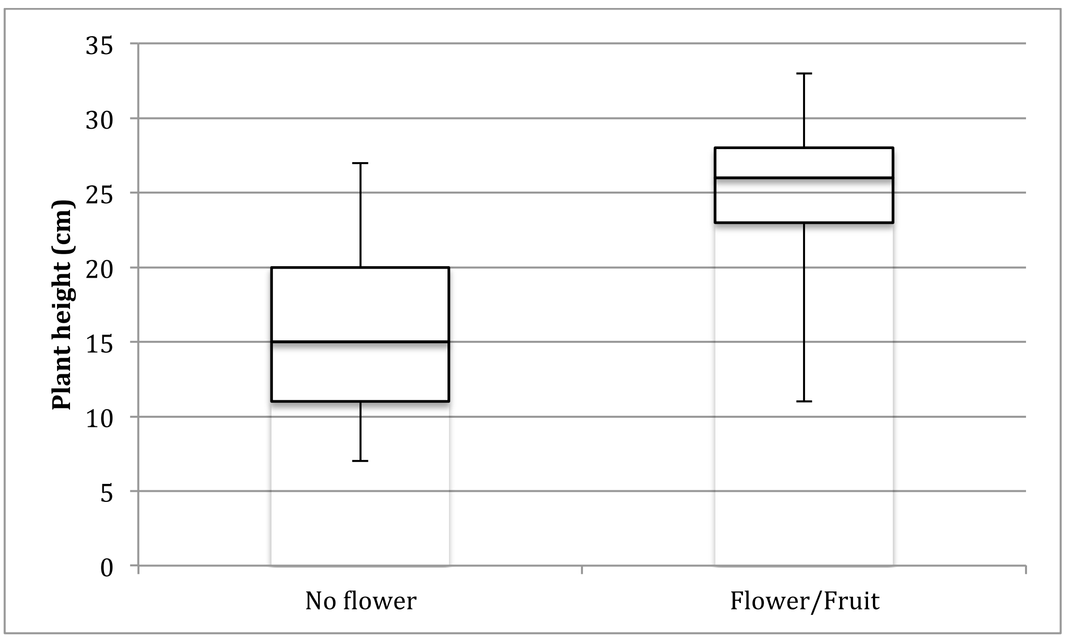

Figure 14. Forest indicator species: Size distribution of flowering/fruiting vs. non-flowering stems of *Sanguinaria canadensis,* May 2014. The height distribution flowering vs. unflowering bloodroot for all plots combined: 75% of plants that were not blooming were 20 cm tall or less, while 75% of flowering/fruiting plants were 22.5 cm or taller. (Box and whisker plot shows median values and quartiles.)

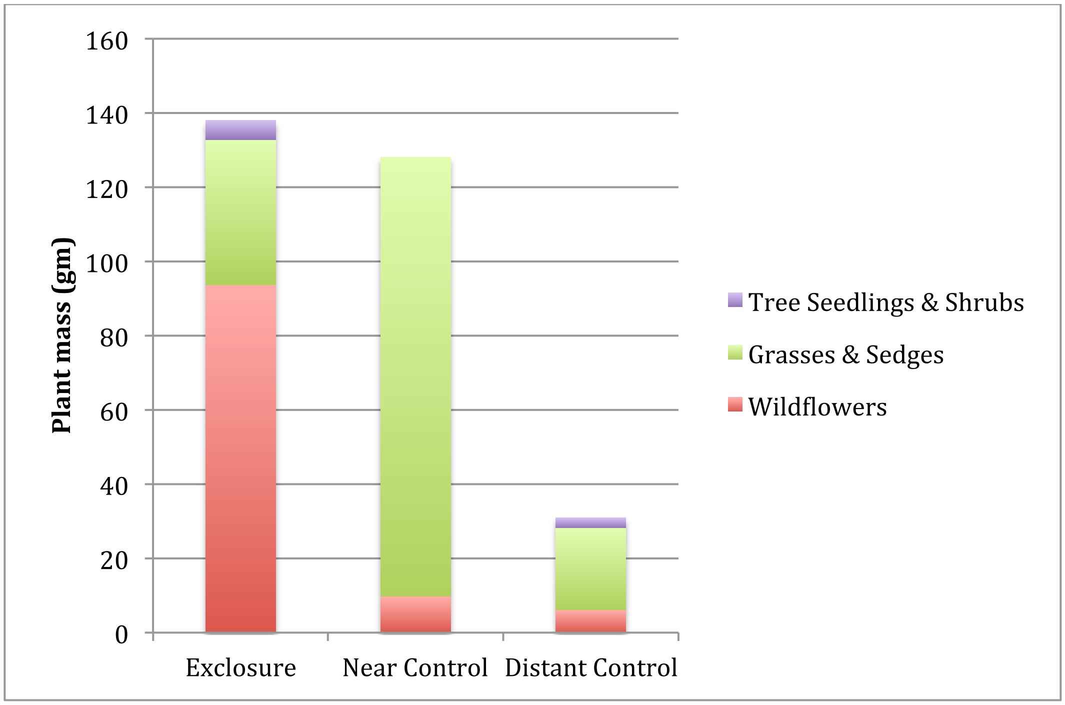

Figure 15. Grassland plant size: Total aboveground (standing) biomass at end of fall growing season, September 2014. Despite the lower total biomass of the distant control plot (likely due more shade from closer trees), the control plots were both dominated by grasses (in terms of **proportion** of total biomass), as shown in the figure below.

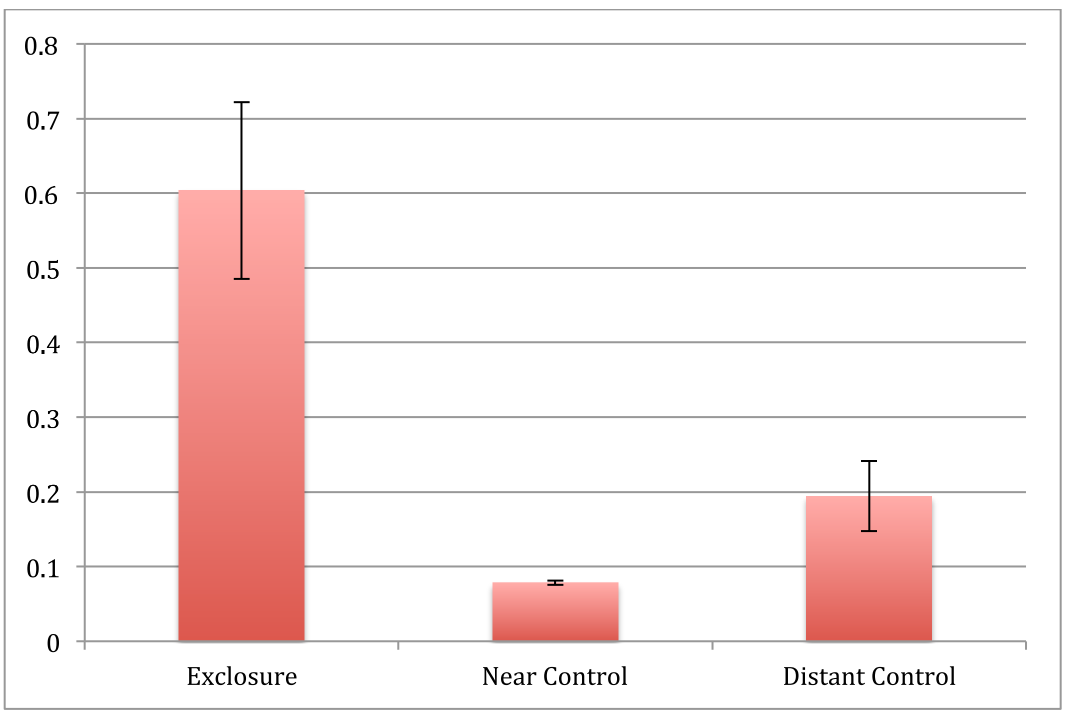

Figure 16. Grassland species composition and plant size: wildflowers as a proportion of total biomass. Grass dominance is often increased with deer. Prairie and savanna restoration projects often aim for 60-80% wildflower cover.

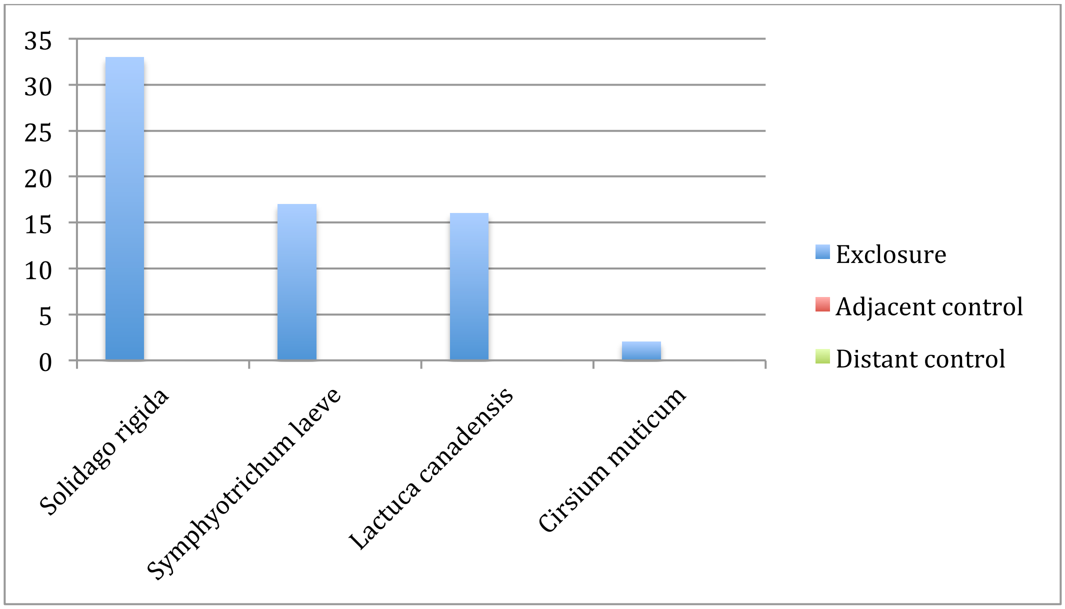

Figure 17. Grassland indicator species: Total # of blooming stems. All four indicator species were found in bloom only in the exclosure, but not in either near or distant control plots despite the presence of rosettes of three of the species (all except *Lactuca*) in quadrat samples. A few stems of *S. laeve* were observed in bloom outside the sampled plots; all were heavily browsed and severely reduced in flower number.

REFERENCES AND LITERATURE CITED

Bonham, C.D. 1989. *Measurements for Terrestrial Vegetation.* New York: John Wiley & Sons. 338 p.

Boulanger, J.R., P.D. Curtis, and B. Blossey. 2014. *An Integrated Approach for Managing White-Tailed Deer in Suburban Environments: The Cornell University Study.* Cornell University Cooperative Extension and the Northeast Wildlife Damage Research and Outreach Cooperative. 34 pp. Accessed online: http://wildlifecontrol.info/deer/Documents/IDRM_12-5-2014.pdf

Causton, D.R. 1988. *Introduction to Vegetation Analysis.* London: Unwin Hyman. 342 p.

Cincotta, C.L., J. M. Adams, and C. Holzapfel. 2009. Testing the enemy release hypothesis: a comparison of foliar insect herbivory of the exotic Norway maple (*Acer platanoides* L.) and the native sugar maple (*A. saccharum* L.). *Biological Invasions* 11(2): 379–388.

Comer, P.J., and D.A. Albert. 1997. Vegetation *circa* 1800 of Washtenaw County, Michigan: An interpretation of the land office surveys. Michigan Natural Features Inventory. Accessed online: http://mnfi.anr.msu.edu/data/veg1800/washtenaw.pdf.

Connell, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35: 131–138.

Côté, S. D, T.P. Rooney, J-P. Tremblay, C. Dussault, D.M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics* 35(1): 113-147.

DeCalesta, D. 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. *Journal of Wildlife Management* 58(4):711–718.

Doerr, M.L., J.B. McAninch, and E.P. Wiggers. 2001. Comparison of 4 methods to reduce white-tailed deer abundance in an urban community. *Wildlife Society Bulletin* 29(4): 1105–1113.

Ferker, K., A. Sabo, D. Waller. 2014. Long-term regional shifts in plant community composition are largely explained by local deer impact experiments. PLOS ONE online journal, http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0115843#abstract0. DOI: 10.1371/journal.pone.0115843.

Hairston, N.G., Sr. 1989. *Ecological Experiments: Purpose, Design, and Execution.* Cambridge: Cambridge University Press. Pp. 32–34.

Hanzawa, F.M. and S. Kalisz. 1993. The relationship between age, size, and reproduction in *Trillium grandiflorum* (Liliaceae). *American Journal of Botany* 80(4): 405–410.

Hobbs, N., Bowden, D., & Baker, D. 2000. Effects of fertility control on populations of ungulates: general, stage-structured models. *The Journal of Wildlife Management* 64: 473–473.

Hilty, J. 2004. *Illinois Wildflowers*. [Online resource: http://www.illinoiswildflowers.info]

Horsley, S., Stout, S., & DeCalesta, D. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications* 13(1): 98–118.

Howe, H.F., and J.S. Brown. 2003. The ghost of granivory past. *Ecology Letters* 4(4): 371–378.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 197–211.

Indy.gov. 2015. Deer management program: Eagle Creek Park. http://www.indy.gov/eGov/City/DPR/Pages/Deer-Management-Program.aspx.

Indiana Department of Natural Resources, Division of Fish and Wildlife. 2011?. *Urban Deer Technical Guide.* Accessed online: http://www.state.in.us/dnr/fishwild/files/fw-UrbanDeerTechnicalGuide.pdf.

Keane, R.M., and M.J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* 17(4): 164–170.

McAninch, J.B., ed. 1995. *Urban Deer: A Manageable Resource?* Proc. of the 1993 Symposium of the North Central Section, The Wildlife Society.

McShea, W.J., H.B. Underwood, and J.H. Rappole, eds. 1997. *The Science of Overabundance: Deer Ecology and Population Management.* Washington, DC: Smithsonian Press. 432 pp.

MI DNR. "Forest foods deer eat." Michigan Department of Natural Resources. Accessed online: http://www.michigan.gov/dnr/0,4570,7-153-10370_12148-61306--,00.html).

Montgomery County Parks. 2004. *Comprehensive Management Plan for White-tailed Deer in Montgomery County, Maryland, August 1995 (Updated August 2004).* Accessed online: http://www.montgomeryparks.org/PPSD/Natural_Resources_Stewardship/Living_with_wildlife/deer/documents/deerplan_update_aug2004.pdf.

Morellet, Nicolas, et al. 2001. The browsing index: new tool uses browsing pressure to monitor deer populations. *Wildlife Society Bulletin* 29(4): 1243–1252.

NPS. 2014. Cuyahoga Valley National Park Final White-tailed Deer Management Plan / Environmental Impact Statement. National Park Service. December 2014. Accessed online: http://parkplanning.nps.gov/document.cfm?parkID=121&projectID=10817&documentID=62775

Packard, S., and C.F. Mutel. 2005. *The Tallgrass Restoration Handbook for Prairies, Savannas, and Woodlands.* Society for Ecological Restoration ed. Washington: Island Press. p. 136.

Potvin, F. and L. Breton. 2005. Testing 2 aerial survey techniques on deer in fenced enclosures: visual double-counts and thermal infrared sensing. *Wildlife Society Bulletin* 33(1): 317–325.

Powers, M.D. and L.M Nagel. 2009. Pennsylvania sedge cover, forest management and deer density influence tree regeneration dynamics in a northern hardwood forest. *Forestry* 82 (3): 241–254. doi: 10.1093/forestry/cpp003.

Randall, J.A., and M.B. Walters. 2005. Deer and sedge impact tree regeneration in working forests: possible restoration treatments. Michigan State University Extension. Unpublished study available online: http://michigansaf.org/Tours/05Deer/21-RandallEtal.pdf. Accessed 8 September 2015.

Rawinski, T.J. 2008. Impacts of white-tailed deer overabundance in forest ecosystems: an overview. U.S. Forest Service, Northeastern Area State and Private Forestry Service, U.S. Department of Agriculture. http://www.na.fs.fed.us/fhp/special_interests/white_tailed_deer.pdf.

Reznicek, A.A., M.R. Penskar, B.S. Walters, and B.S. Slaughter. 2014. Michigan Floristic Quality Assessment Database. Herbarium, University of Michigan, Ann Arbor, MI and Michigan Natural Features Inventory, Michigan State University, Lansing, MI. (http://michiganflora.net/home.aspx)

Rooney, T., & Waller, D. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181(1):165–176.

Samson, D.A., and K.S. Werk. 1986. Size-dependent effects in the analysis of reproductive effort in plants. *American Naturalist* 127(5): 667–680.

Stohlgren, T.J., L.D. Schell, B. Vanden. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. *Ecological Applications* 9(1): 45-64.

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(1): 23-29. Available at: http://works.bepress.com/thomas_rooney/51

Swink, F., and G. Wilhelm 1994. *Plants of the Chicago Region.* 4th ed. Indianapolis: Indiana Academy of Science. 921 pp.

Waller, D.M., and W.S. Alverson. 1997. The white-tailed deer: a keystone herbivore. *Wildlife Society Bulletin* 25: 217–226.

Winchcombe, R.J. 2015. Monitoring deer browsing. Cary Institute project description. Accessed online: http://www.caryinstitute.org/science-program/research-projects/monitoring-deer-browsing.

ACKNOWLEDGMENTS

Thanks to Washtenaw County Parks and Recreation Commission for contracting this work, and to Shawn Severance for providing background information and guidance. Samuel Hahn provided excellent field assistance, and William Lucier for was willing to slog through cold slush to map oak saplings; we are grateful for the support of the University of Michigan Undergraduate Research Opportunity Program and the Program in the Environment for making it possible for students to engage in research for employment or academic credit. We appreciate the expert advice of Sylvia Taylor and John Russell in initial site selection of exclosures. Many thanks Tony Reznicek for assistance with plant identification and Mary Anne Evans for advice and assistance on statistical analysis; any errors that remain are my own.