

White-tailed deer herbivory impacts
on plant community composition and recruitment
in western New York deciduous forests

by

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Abstract

In high densities, white-tailed deer (*Odocoileus virginiana*) have a multitude of detrimental effects on plant communities, particularly in forest ecosystems. Through intensive herbivory and dispersal of native and invasive seeds, deer can be considered ecosystem engineers in the Northeastern and Midwestern United States. To measure how removal of deer herbivory changes plant community composition over time, I constructed four fenced deer exclosures and delineated four unfenced control plots in a Brockport, NY deciduous forest fragment with an estimated population of 17 deer/km². After three summers of data collection, the average height of all tree seedlings and root suckers less than 2 m tall was significantly greater in each fenced plot than unfenced plot. Ground-level percent cover, abundance, and species richness were not yet affected by treatment, but percent cover of woody vine foliage was higher in the fenced plots. As expected, removing herbivory pressure has affected plant communities in Brockport Woods. To determine whether deer are concurrently transporting invasive species in this and other disturbed forests, I collected deer fecal pellet piles across 11 months. The average number of seeds found in each whole pellet pile was 11.4 (± 11.6). Over 50% of the seeds and germinates found were from non-native species, seeds of which were particularly prevalent in pellet piles collected in the fall and winter. Of the 17 species that survived the gut and germinated in outdoor pots, only one species (*Persicaria virginiana*) successfully germinated under a forest canopy. As movers of an average of 388 seeds per day, many of which are

non-native, deer are important contributors to Northeast and Midwest seed dispersal and ecosystem dynamics.

Keywords: Deer overpopulation, herbivory, exclosures, plant communities, endozoochory, seed dispersal

General Introduction

From a cumulation of many anthropogenic factors, white-tailed deer (*Odocoileus virginiana*) are overpopulated in much of the Northeastern and Midwestern United States (Behrend *et al.* 1970, Smith 1991). As generalist herbivores, overabundant deer can impact plant productivity and fitness through direct herbivory of leaves, stems, and reproductive material (Rooney and Waller 2001, Wiegmann and Waller 2006). With browse pressure at rates beyond what native plant species have evolved to tolerate, differences in plant palatability and deer preferences can alter competitive interactions for light and other resources among native and invasive species and influence plant community composition, function, and succession across trophic levels and ecosystems (DiTommaso *et al.* 2014, Shelton *et al.* 2014, Stromayer 1997, Tanentzap *et al.* 2011). In forests with high deer densities, tree recruitment can be completely inhibited by deer as bud browsing limits a seedling's ability to grow out of the reach of deer and fill canopy gaps (Shelton *et al.* 2013). Additionally, areas that have experienced longer-term deer herbivory may have depleted seed banks, as they have lacked seed inputs from reproductive plants for a longer duration (Christopher *et al.* 2014).

Deer are also agents of seed dispersal through endozoochory: the consumption and passing of viable seed in fecal pellets. As deer occupy habitats like early and late successional forests, fragmented suburban gardens, and agricultural fields, seed can easily be spread between these landscapes (Williams *et al.* 2007). Although many species have evolved to benefit from this method of seed transport, the seeds of some

invasive plant species use this advantage too and can survive passage through the gut (Traveset 1998). The introduction of invasive species into natural areas can then be facilitated by the movement of deer and exacerbated by their overabundance.

Understanding the complex, interactive effects deer have on plant communities can provide insight into how ecosystems will react to disturbance, land use modifications, habitat restoration efforts, and different hunting regulations. For the first chapter of my master's thesis, I constructed four exclosure fences and paired control plots in a Brockport, New York deciduous woodlot to monitor plant traits and productivity with and without browse pressure from deer. For my second chapter, I collected deer fecal pellet piles in three sites across Monroe County, New York over 11 months to determine which seeds deer are consuming and their viability after gut passage. After collection, I placed the pellets outside in protected sun and shade plots and dissected a portion of each pile to directly identify consumed seeds.

Chapter 1: The impacts of long-term overpopulation of white-tailed deer
on plant community composition in a deciduous Western New York woodlot

K. Broz

Introduction

White-tailed deer (*Odocoileus virginianus*) are the most abundant large herbivore in eastern North America (Behrend *et al.* 1970, Smith 1991). High tolerance for disturbed, fragmented habitat has allowed their populations to increase rapidly as agriculture and urban sprawl divide forests, predators are extirpated, and hunting pressures are lessened (Rooney and Waller 2001). It is now estimated that deer density is 2-4 times that of pre-European settlement (Russell *et al.* 2001). In such large concentrations, these generalist herbivores have the capability to alter plant and animal community composition and function at many trophic levels, allowing deer to assume a position as ecosystem engineers (Rooney and Waller 2001, Wiegmann and Waller 2006, Dornbush and Hahn 2013, Christopher *et al.* 2014, DiTommaso *et al.* 2014, Shelton *et al.* 2014).

Although deer can consume both leafy and woody material, they initially select plant material that may be more palatable or nutritious -- typically young, nitrogen-rich leaves or buds. This selection can then modify the strength of interspecific competition among remaining plants. A species that may be a dominant competitor in the absence of deer may be a preferred consumptive species in the presence of deer, leading to a decrease in its abundance and an increase in the available light and space

for other, less competitive or less palatable plants (DiTommaso *et al.* 2014, Shelton *et al.* 2014). For example, multiple researchers have found that in the presence of high deer densities, graminoids and ferns increased as herbaceous and woody species decreased (Riemenschneider *et al.* 1995, Rooney and Waller 2001, Wiegmann and Waller 2006, Rooney 2008, Tanentzap *et al.* 2010, Dornbush and Hahn 2013, Christopher *et al.* 2014, Shelton *et al.* 2014). These preferences can exert ecosystem-wide impacts through changes in decomposition rates, nutrient availability, invasive species facilitation and suppression, and altered successional trajectories (Stromayer 1997, Tanentzap *et al.* 2011, Christopher *et al.* 2014, Shelton *et al.* 2014).

When deer abundance is extremely high, palatability and preferences matter less and forests may lose much of their ground-level vegetation (Rooney and Waller 2001, Christopher *et al.* 2014). These understories contribute significantly to nutrient cycling and energy resources for small mammals, birds, invertebrates, and pollinators (Dornbush and Hahn 2013). Although herbaceous plants are particularly vulnerable, as they do not have a large capacity for nutrient storage, sapling recruitment may be completely inhibited by browse from high enough deer densities (Shelton *et al.* 2014). Browse lines on trees, where trees cannot maintain leafy vegetation below the reach of deer, are apparent under these conditions.

Even if browse pressure is lessened, forests will likely still have a difficult time recovering from long-term deer overabundance. For example, seed-bank depletion can be a direct result of reduced plant fitness. In many species, flowering probability positively correlates with plant height, and therefore, plants must allocate resources

toward regeneration of photosynthetic material instead of reproduction when they are continually browsed (Webster *et al.* 2005, Dornbush and Hahn 2013, Christopher *et al.* 2014). However, deer are not the only force of change operating in temperate forest succession. Fire suppression, invasive species, and introduced tree and soil pests have led to age- and species-structure homogenization across forested Great Lakes landscapes (Amatangelo *et al.* 2011). Sugar maple (*Acer saccharum*), for example, has been particularly successful as a highly competitive, fire-sensitive, herbivory-resistant species. Its dense foliage creates deep shade and litter, changing light, soil, and moisture regimes within forests and altering resource availability for understory plants (Nowacki and Abrams 2008).

To help understand successional and plant community change in the context of deer, we can experimentally study plant responses to herbivory through increasing hunting pressure in an area, extirpating deer from a closed system, or building enclosure fences. Enclosures allow experimental and control plots to be placed across environmental gradients in tree groupings representative of the overall forest composition. However, researchers must ensure that their enclosures are constructed for long-term study, as natural change over time may initially be difficult to observe (Collard *et al.* 2010, Tanentzap *et al.* 2011).

Objective

As deer overpopulation has become one of the greatest threats to temperate forest diversity in eastern North America, I sought to understand the magnitude of their impacts in these ecosystems. Thus, my objective was to use a series of fenced

deer exclosures to determine how release from long-term white-tailed deer overabundance changed existing plant community composition in the Brockport woodlot. I hypothesized that the height of woody seedlings, shrubs, and collar sprouts and the abundance, percent cover, and richness of herbaceous plants would be greater inside fenced exclosures. I also hypothesized that, over time, similarity between paired fenced and unfenced plots would decrease.

Methods

Site description

To examine current deer herbivory pressures in a typical western New York deciduous forest fragment, I established paired fenced and unfenced vegetation plots in a 10 ha portion of a second-growth, sugar maple (*Acer saccharum*) dominated, deciduous woodlot approximately 60 ha in size located on campus at the College at Brockport in Monroe County, New York (43.208466, -77.959953). The woodlot has sparse, ground-level foliage, few young saplings, and maintains a distinct browse line. It is also rapidly undergoing change because of invasive plant encroachment and infestation from the invasive pests emerald ash borer (*Agrilus planipennis*), beech scale (*Cryptococcus fagisuga*), and many species of European earthworm. Using fecal pellet pile calculations, the population size of deer in the woodlot was estimated to be 1t deer/km² (Appendix I); tree seedling abundance decreases after a forest reaches a density of 10.4 deer/km² (Behrend *et al.* 1970) or even just 5.8 deer/km² (Russell *et*

al. 2001). Thus, the high level of browse intensity that the Brockport woodlot experiences would provide more readily observable results for my short-term study.

The Brockport woodlot was designated as a Natural Area by the College in 2015. The woodlot's topography is varied, but overall, the southern portion tends to remain wetter than the northern portion. Aerial photos indicate that the forest has been intact for at least 100 y and has also been a fragment, directly surrounded by agricultural fields or roads, for this same duration (Figure 1, Official Site of Monroe County, New York, 2015). Because it is located on a college campus, hunting has not been allowed since at least its acquisition in the mid-1960s (Bernstein 1974). Temperature and precipitation data for Brockport, NY were acquired through weather history from the website Weather Underground (TWC Product and Technology LLC 2014, 2018).

Exclosure placement and construction

Exclosure placement was based on tree community composition, size class, and abiotic conditions representative of four different subcommunities within the overall forest. This was determined through an inventory of 2,700 trees in the woodlot. Four distinct plot types were identified after surveys: Beech Maple, Diverse Wet, Maple Regeneration, and Sparse Maple. Between April and May 2016, I constructed four, approximately 22 x 22 m deer-exclosure-treatment plots in the Brockport woodlot using high tensile wire and 2.4-m-tall plastic deer fencing, with trees as corner posts (Appendix II). Each exclosure was paired with an unfenced

control plot of the same size 5 to 10 m from each other and delineated with PVC pipe stakes.

Measures of plant community composition change

At the start of the experiment, diameter at breast height (DBH) of all woody plants was measured within plots, and basal area was calculated with the equation $BA = 0.00007854 \times DBH^2$. The species composition and structure of the woody components of the four fenced and unfenced plots were compared across three size classes-- overstory (trees >15 cm DBH), understory (trees and shrubs 5-15 cm DBH), and regeneration and shrub layers (trees and shrubs <5 cm DBH). To assess light availability in each plot, at the end of August 2017 during peak canopy leaf-out, the canopy at the center of each plot was hemispherically photographed using methods from Chianucci and Cutini (2012) and analyzed through GLA Version 2.0 light-gap software (Cary Institute of Ecosystem Studies, Millbrook, NY).

To evaluate ground-layer vegetation, ten 1-m² quadrats were randomly placed in each plot and permanently marked with rebar stakes. Number of individuals and percent cover of each plant species rooted in the quadrats were recorded in July or August 2016, 2017, and 2018. In August 2017, the height of all woody seedlings under 2 m (including root suckers more than 10 cm away from tree bases) and the lowest leaf height of all woody plants over 2 m tall were measured within each plot. Number of collar sprouts within 10 cm of the base of the tree and growing below 1 m in height were counted. Additionally, the highest collar sprout bud was measured and the number of sprouts with browse evidence was recorded.

Native species were planted inside the fenced and unfenced plots in the spring of 2016 and 2017 to quantify deer preferences and differences in traits of individual plants. However, drought in 2016 and flooding in 2017 resulted in high mortality that constrained statistical analysis (Appendix III).

Faunal Measurements

I live-trapped small mammals in the fall of 2016 and 2017 to determine if the fenced plots influenced small mammal habitat use; my assumption was that I would capture more small mammals inside the enclosure, due to increased cover and food resources following release from browsing pressure. However, trap success in both years was too low for statistical comparison. I also extracted earthworms from the soil inside and outside of fenced plots to determine their density in each treatments (Appendix IV). Earthworms decay leaf litter abnormally quickly and transport those nutrients deep into the soil, out of the reach of new or shallow-rooted seedlings and, in doing so, homogenize soil horizons (Dvalos 2015). The soil they produce collects as compacted casts that make it more difficult for seedlings to establish (Dobson and Blossey 2015). Earthworms are also predators of small seeds (Cassin and Kotanen 2016). The Eastern U.S. is impacted by 16 species of invasive earthworm and by sampling them, I wanted to have a better understanding of their abundance in the woodlot so that my conclusions regarding deer impacts on plant community composition could be analyzed in this context.

Statistical analyses

I analyzed exclosure placement based on tree species and size class via an exploratory resemblance matrix on PRIMER Version 7 (PRIMER-e Auckland, New Zealand) and a NMDS ordination with PC-ORD Version 7 (MJM Software Design, Gleneden Beach, OR). I used PRIMER to calculate Bray-Curtis similarity coefficients to compare the overstory between fenced and unfenced plots. I also performed a linear regression and independent t-test of basal area and percent canopy openness across all paired unfenced and fenced plots (Microsoft Excel Version 1807, Redmond, WA). I used Minitab 17 to calculate Shannon-Weiner diversity indices for woody plants (Minitab 17 Statistical Software, State College, PA). To assess quadrat data between control and treatment plots, I performed Shapiro-Wilk normality tests and independent t-tests with SPSS for percent cover (after arcsine square root transformation) and richness comparisons with Holm-Bonferroni sequential corrections applied to p-values to control for Type 1 error (SPSS, IBM Corporation, Armonk, NY). I tested the average height of woody species and stump sprouts across all plots with the non-parametric hypothesis test Mann-Whitney U after normality could not be attained via transformations. Finally, to determine if lowest leaf height differed between fenced and unfenced plots, I ran a chi-square test for association in SPSS. Only having four exclosures resulted in statistical limitations and pseudoreplication (Hurlbert 1984) was necessary to compare some metrics.

Results

Weather conditions during study

During May-August 2016, the first growing season of the study, it was hot and dry, which defoliated understory trees, while the 2017 growing season was cool and very wet. The spring of 2018 was the warmest of the springs in the study, and the season overall experienced similar rainfall to that of 2016 (Figure 2).

Overstory

The Beech Maple fenced and unfenced plots were characterized by similar numbers of *Fagus grandifolia* and *Acer saccharum*. The most abundant overstory species in the Diverse Wet plots was *Tilia americana*, while the understory was composed of mainly *Carpinus carolinana* and *Lindera benzoin*. The Maple Regeneration plots were overwhelmingly dominated by almost 200 individuals of regenerating *A. saccharum* saplings across both plots. The Sparse Maple plots were comprised of an entirely *A. saccharum* overstory and understory, except for one understory *Ulmus americana* (Figure 3).

Across the three size classes of woody vegetation in fenced and unfenced plots, the basal area (BA) of the Beech Maple plots matched almost exactly, each with a BA of 1.5 per 487 m² (the average size of all plots), while the Sparse Maple plots differed most, with a 0.5 BA difference between unfenced (2.5) and fenced (1.9) plots (Figure 4). A linear regression of BA and percent canopy openness across all paired unfenced and fenced plots showed a significant, positive relationship between the percent of canopy openness and basal area ($R^2 = 0.68$, F-stat=12.66, df=6, P-value=0.01, Figure 5). The Bray-Curtis similarity resemblance matrix of overstory abundance revealed that the most similar plot pair was Maple Regeneration with a

similarity coefficient of 85.1, while the least similar was Sparse Maple, with a coefficient of 72.4 (Table 1). Overall, pairs within each plot type were more similar to one another than to plots in other plot types.

For trees and shrubs taller than 2 m, the most diverse plots were the Diverse Wet fenced and unfenced plots, with Shannon-Weiner Diversity indices (H') of 1.81 and 1.78, respectively, while the lowest diversity plots were the Sparse Maple fenced and unfenced plots, where H' was 0.43 and 0.12, respectively (Table 2). The average height of the browse-line (lowest leaf heights of all trees taller than 2 m) did not show any difference between the fenced and unfenced plots after one year of deer exclusion (χ^2 stat = 0.056, p-value=0.814, df = 1, Table 3, Figure 6). Across all 504 trees within the eight plots, the average height of the browse line in the Brockport woodlot was 170 cm in 2017 (Table 4). This average included each individual with branches above 2 m (taller than the reach of deer) as 200 cm.

Understory

In 2017, after one year of deer exclusion, the average height of shrubs less than 2 m tall was taller in the fenced plots for the native shrub species *Lindera benzoin* (U-stat=473, p=0.0006) and the invasive shrub species *Ligustrum* sp. (U-stat=239, p=0.0006) and *Rosa multiflora* (U-stat=296, p=<0.0001, Figure 7). The native shrub species *Rubus* sp. averaged 0.8 cm taller in the unfenced plots but this difference was not significant (U-stat=451, p=0.810). Sample size was too small to compare *Lonicera* sp. statistically. There was no trend in the number of shrubs of this size seen across fenced and unfenced plots.

The average height of all 1,882 tree seedlings and root suckers less than 2 m tall across all plots in 2017 was significantly greater in each fenced plot than its paired, unfenced plot (Beech Maple: U-stat=19436.0, $p < 0.0001$, Diverse Wet: U-stat=7000.5, $p = 0.0008$, Maple Regeneration: U-stat=20859.5, $p < 0.00001$, Sparse Maple U-stat=10401.0, $p < 0.00001$, Figure 8). Across all plots, the average height of four tree seedling species was significantly higher in the fenced plots than the unfenced plots: *Carpinus caroliniana* (U-stat=455, $p = 0.0035$), *Carya cordiformis* (U-stat=5316.5, $p = 0.00034$), *Fagus grandifolia* (U-stat, 6304, $p < 0.00001$), and *Fraxinus* spp. (U=33621.5, $p < 0.00001$, Figure 9). The average height of *Ostrya virginiana* was not significantly higher in the fenced plots (U-stat=11389, $p = 0.089$). The average height of all fenced tree seedlings was 16.6 cm (± 14.3) and the average height of all unfenced seedlings was 10.4 (± 7.7). Only two *Fraxinus* spp. grew taller than 100 cm. The average height of *F. grandifolia* seedlings and root suckers was more than twice as great in the fenced Beech Maple plot as in the unfenced plot (36.2 cm and 15.0 cm, respectively) and number of *F. grandifolia* seedlings and root suckers was more than twice as great in the unfenced Beech Maple plot than the fenced plot (278 and 127 individuals, respectively). The overall number of tree seedlings was greater in unfenced plots than in fenced plots in three of four plot pairs. Abundance of *Prunus serotina* seedlings across all plots was 51 in the fenced plots and 2 in the unfenced plots.

The most abundant collar sprouts in 2017 were in the Diverse Wet plots and analyses were only performed in this pair. Collar sprouts were seen on *Carpinus*

carolinana, *Fraxinus pennsylvanica*, *Lindera benzoin*, *Lonicera* spp., *Ostrya virginiana*, *Prunus serotina*, and *Tilia americana*. Among plot type and species, the average number of sprouts per collar did not vary substantially (Figure 10). The average leaf or bud height of the tallest collar sprout was greater in the fenced plots, and sprout browsing was only observed in unfenced plots. For the two species with a large enough sample size to test, the collar sprout height was significantly taller in the fenced plots for *C. carolinana* (U-stat=1, p=0.00168) and *L. benzoin* (U-stat=22.5, p=<0.00001).

Ground-level

Average percent cover of ground-level vegetation in 1-m² quadrats increased in both fenced and unfenced plots across the summers of 2016, 2017, and 2018 in all but the Beech Maple unfenced plot, which decreased slightly in 2018 (Figure 11). None of these differences in percent cover were significant after Holm-Bonferroni corrections were performed on independent t-tests (Table 5).

In 2018, *Acer saccharum* masted across Western New York, and in the summer of that year, *A. saccharum* increased in percent cover across all plots except in the Diverse Wet plot, while the Sparse Maple fenced plot showed the largest increase in percent cover of these seedlings in its unfenced pair and among plots overall.

Species richness in the 1-m² quadrats varied across years and treatment types. No distinct change-over-time trends were seen. However, the richest plots were the fenced Diverse Wet plot and the unfenced Sparse Maple plot, nearing or exceeding an

average of five species per quadrat in most years (Figure 12, Appendix V for total species lists). None of these differences in richness between fenced and unfenced plots were significant after Holm-Bonferroni corrections were performed on independent t-tests (Table 5).

The woody vines *Parthenocissus quinquefolia* (Virginia creeper) and *Toxicodendron radicans* (poison ivy) increased in average percent cover by 0.72 and 0.39 percent, respectively from 2016 to 2018 among all fenced plots containing these species. Between all unfenced plots containing these species, the average percent cover of *P. quinquefolia* decreased by 0.83 percent, and average percent cover of *T. radicans* increased by 0.33 percent. Between all plots containing these species across all three years, there was an average of 0.06 percent more *P. quinquefolia* and 1.02 percent more *T. radicans* in the fenced plots than in the unfenced plots (Figure 13).

Bray-Curtis similarity coefficients of ground-level species abundance between unfenced and fenced plots from 2016 to 2018 revealed no clear trend (Figure 14). Additionally, liquid extraction confirmed that invasive earthworms were present across the woodlot in all of my fenced and unfenced plots.

Discussion

Over just three summers of deer exclusion, fenced plant communities in the Brockport woodlot showed a positive response to their release from herbivory. This was most apparent in the average height of tree seedlings after one year, as those in fenced plots were significantly taller than those in unfenced plots. Based on my results, the ability of woody seedlings to survive herbivory and mature depends

largely on the frequency at which they are browsed. In just three growing seasons of release from browse pressure, seedlings of four species of native tree were able to grow significantly taller in the fenced plots and *Prunus serotina* seedlings grew almost exclusively in the fenced plots. This indicates that the seedlings in the Brockport woodlot are heavily browsed. Most are able to survive but cannot grow past the reach of deer, which indicates that overpopulated deer are compromising the ability of trees to regenerate. Although beech-maple-basswood forests in western New York tend to create low-light understories (Shanks 1966), browse intensity seems to be a greater factor in tree regeneration than limited light in this study system.

Interestingly, the number of tree seedlings does not seem limited by deer, as all of the plots had 95 or more seedlings regardless of treatment type. This trend was also seen by Kittridge and Ashton (1995) in a 22 y exclosure study in which the number of stems did not differ between fenced and unfenced plots; however, species richness was greater and height of seedlings was taller in fenced plots (Marquis 1981). Although deer eat seedlings, many species are well-defended with high concentrations of secondary metabolites that can be toxic if consumed in large enough quantities (Swihart and Bryant 2001). Woody browse is an important food source for many mammals in winter, and because higher and generally colder latitudes have lower species diversity than warmer ones, there is stronger selection pressure for vulnerable seedlings to evolve defenses against herbivory (Swihart and Bryant 2001). These defenses likely explain the abundance of seedlings throughout

my unfenced and fenced pairs. However, each unfenced plot, except the Diverse Wet plot, had more seedlings than the fenced plots. It is possible that fenced seedlings and other herbaceous material may be able to grow larger and fill more above-and below-ground niches because they are not being browsed and can outcompete less vigorous seedlings, reducing the number that can survive inside the fencing. In contrast, unfenced seedlings, despite seedling defenses, are subject to herbivory and thus biomass suppression, filling less space and allowing a higher number of smaller seedlings to survive.

Including both herbaceous and woody seedlings in measurements, I did not see a distinct change in richness, abundance, and percent cover across quadrats though I would expect similarity in these metrics to decrease over time between fenced and unfenced plots. It is possible that overabundant deer have been impacting herbaceous seedlings long enough in the Brockport woodlot that many species are now locally extirpated or have been unable to flower and seed before being browsed. Although seeds of many species can survive for decades in seed banks, intensive browsing in the woodlot has likely been occurring for decades, so as observed in other studies, it may take years to see an increase in richness from these dormant individuals or from dispersal into the fenced plots (Collard 2010, Levine *et al.* 2012, DiTomaso *et al.* 2014).

Some of the subtle increases in ground-level percent cover were from woody species like *Parthenocissus quinquefolia* or *Toxicodendron radicans*, which were likely stems of high-light canopy vines. This trend may strengthen over time as

unbrowsed woody vines have more opportunity to spread throughout the exclosures. Deer prefer *T. radicans* as a browse species over *P. quinquefolia* although both can comprise a large proportion of deer diets in the growing season (Sotala and Kirkpatrick 1973). At least 75 species of birds eat the fruits of *Toxicodendron* spp. (Baird 1980) and small mammals use it, *P. quinquefolia*, and other ground-layer vegetation as protective cover (Shelton *et al.* 2014). Because of their growth habits, *T. radicans* and *P. quinquefolia* may climb out of reach of deer despite intense herbivory and therefore fruit; however, deer may impact their ability to function as protective ground cover and negatively influence small mammal populations (Flowerdew and Ellwood 2001).

Effects of weather

In my study, weather conditions varied considerably over the three summers and reduced my ability to make direct growth comparisons between years. The dry summer of 2016 prevented the survival of native plantings (Appendix III) and likely slowed plant growth and seed germination. By July, most understory sugar maple trees were defoliated. This may be a result of increased drought sensitivity of sugar maple elevated by earthworms affecting soil hydrology and root penetration (Larson *et al.* 2010). However, defoliation would have allowed increased light to reach the ground and possibly assisted herbaceous and woody seedling maturation during late summer rains. Conversely, 2017 was extremely wet and prevented the survival of additional native plantings due to flooding.

Beyond affecting survival of native plantings, the extreme weather difference initiated masting in *Acer saccharum* in fall of 2017, resulting in thousands of seedlings across the woodlot during 2018. This mast was triggered because the summer of 2015 was much cooler than the summer of 2016, as previous research has shown (Cleavitt and Fahey 2017). Masting increases recruitment probability, as it overwhelms seed predators and widens the potential for germination in more favorable microhabitats. However, under high deer browsing pressure, the proportion of *A. saccharum* mast survivors is lower than it would be under lower browse pressure, even while accounting for other seedling mortality factors (Macmillian and Aarssen 2017). My study showed that in the Sparse Maple plots, which contained the highest percentage of mature *A. saccharum* and had the greatest basal area of all of the plots, the percent cover of *A. saccharum* mast seedlings was significantly greater in the fenced plot than the unfenced plot (Figure 11). As evidenced by the predominately maple overstory, this upland area of the woodlot is an ideal location for *A. saccharum* to grow (Gardescu, 2003), so I may have already seen the impacts of deer herbivory operating on first-year mast seedlings in the unfenced plot. The difference between these plots also may have been caused by the closer proximity of the unfenced plot to the edge of the woodlot, with maple seedlings encountering more competition from the aggressive invasive herb *Alliaria petiolata* (garlic mustard), which was observed in the unfenced plot in all three sample years.

Diverse Wet plots

The Diverse Wet plots were in the wettest portion of the woodlot and had the greatest tree and shrub Shannon-Weiner Diversity of the plots. Average richness of ground-layer plants was also high. I attribute this to the wetter conditions in the Diverse Wet plots than in the other three plot pairs, which allowed for a greater diversity of species to persist, especially through the drought of 2016. Conversely, the flooding of 2017 may have then reduced percent cover in the Diverse Wet plots, where it would have been exacerbated. Without considering Holm-Bonferroni corrections, the difference in ground-layer percent cover between the fenced and unfenced plots approached significance in each sampling year. A substantial difference like this only a few months after deer exclusion indicates that abiotic conditions in the plot pairs may not have been as closely matched as initially assumed. Canopy openness in the fenced plot was about twice as much as the unfenced plot (9.2% openness and 5% openness respectively) and observations in spring and after heavy rainfall revealed that the unfenced plot was inundated with water much longer than the fenced plot. However, ground-layer similarity between fenced and unfenced plots (when excluding *A. saccharum* seedlings) was lower in 2018 than it had initially been in 2016, indicating that deer may be visibly impacting the understory in these plots before the other plots. The herbaceous species *Circaea lutetiana* (enchanter's nightshade) and *Persicaria virginiana* (jumpseed) are both preferred deer browse species (Augustine and Jordan 1998, Chapter 2 of this thesis), and both were found in the fenced plot. Percent cover of *P. virginiana* within the Diverse Wet fenced plot was twice as great as in the unfenced plot. No *C. lutetiana*

was found in unfenced quadrats, although it did appear in the overall species list for the unfenced plot. These sensitive species seed in late summer, so continuous browse would have prevented seeding prior to deer exclusion. It would then be more likely that the increase in ground-layer percent cover was a result of their larger leaves and new seedlings.

Trunk collar sprouts on mature trees and shrubs were most prolific in the fenced Diverse Wet plot and were an average of 73% taller than in the unfenced plot. Sprouting in certain species of mature trees and shrubs is an induced response to disturbance or changes in resource availability. The advantage sprouting yields over seedling recruitment is persistence in the community; a tree replaces itself in its own space using its stored resources, while recruitment requires seed dispersal into another resource-rich space (Del Tredici 2001). Thus, as disturbance increases, the success of sprouters compared to seedlings increases and sprout traits may then become indicators of browse impacts (Royo *et al.* 2016). Considering the differences in trunk collar sprout response between the Diverse Wet fenced and unfenced plots, deer may have a substantial impact on woody species regeneration if sprouts on *Tilia americana* and the less palatable *Lindera benzoin* cannot grow unprotected (Averill *et al.* 2016).

The Diverse Wet fenced plot also contained the greatest abundance of invasive woody taxa, including *Ligustrum* sp., *Lonicera* sp., and *Rosa multiflora*. These taxa are classified as low to moderately palatable to deer but are browsed more frequently when deer populations are high (Averill *et al.* 2016). While *R. multiflora*

has the advantage of defensive prickles, its palatability decreases as stems age and thicken, so smaller plants may still experience intensive browse. This was demonstrated in my results, as more and taller *R. multiflora* was found inside the exclosures, indicating that deer may be controlling these invasives in the forest understory. The tendency of invasives to increase following release from herbivory has also been observed in a ten-year-old western New York deer exclosure (Janis 2018) and throughout the Northeast (Christopher *et al.* 2014, Averill *et al.* 2016). Invasive shrubs in the Northeast leaf out earlier in the spring than natives, providing the first new growth for overwintering deer browse (Fridley 2012). Averill *et al.* (2016) and others have found that deer consume the most biomass in the spring, so this synchronicity between plant phenology and deer overabundance may be contributing to the limited invasive shrub takeover across the interior of the woodlot, even in canopy gaps like the Sparse Maple unfenced plot.

Maple-dominated plots

The Beech Maple plots saw the most drastic differences in release from herbivory in the response of *Fagus grandifolia* root suckers. The ability of *F. grandifolia* to root-sucker is advantageous, as it allows for the tree to recover easily from disturbance, respond to disease, or preemptively establish itself further from the parent tree and wait for canopy gaps. Royo *et al.* (2010) suggested that *F. grandifolia* is an ideal deer browse impact indicator, as its sprouts are prolific throughout beech-maple-basswood forests and, despite its moderate palatability to deer, if other more palatable species are unavailable, it can be heavily browsed. My results showed that

the average height of *F. grandifolia* seedlings and root suckers was more than twice as great in the fenced Beech Maple plot than the unfenced plot but interestingly, the number of *F. grandifolia* seedlings and root suckers was more than twice as great in the unfenced plot. I suggest that this may be a result of the tree responding to chemicals found in deer saliva, as seen in Roe deer (*Capreolus capreolus*) and *Fagus sylvatica* (Ohse *et al.* 2016). Oshe *et al.* (2016) found that deer saliva stimulated the tree to produce more protective acid in its browsed buds and leaves and increase its growth hormones to produce more new shoots from other buds. Thus, the number of *F. grandifolia* root suckers may have been greater in unfenced plots because of this induced growth response to herbivore disturbance.

In the Sparse Maple plot, ground-layer quadrat percent cover in 2018 was significantly greater in the unfenced plot than the fenced plot. I attribute this to the location of the unfenced plot compared to the fenced plot-- closer to the western edge of the woodlot and the progressing invasion of “edgy,” non-native, un-palatable species towards the interior of the woodlot. Additionally, percent canopy openness in these plots was twice as great as in all other plots. Overall, I expect these plots to be the most influenced by herbaceous invasives, as those that are present (*Alliaria petiolata*, *Vincetoxicum rossicum*, and *Leonurus cardiaca* (motherwort)) are considered unpalatable to deer (Averill *et. al* 2016, DiTommaso *et. al* 2004). However, plant life-history traits also need to be considered in analyses of change, as the total average percent cover decreased in the unfenced plot between 2017 and 2018. I attribute this to the biennial invasive *A. petiolata*. The first-year basal rosette

growth habit of this species covers more ground than its second-year growth habit, so I would expect these cover-change fluctuations to continue over time and complicate measures of plant-community change.

The Maple Regeneration plots had the lowest overall basal area of the plots and the greatest number of *Acer saccharum* with a DBH of less than 5 cm. However, these trees remain small despite having one of the highest shade tolerances among trees in late-successional deciduous forests (Beatty 1984). The abundance of smaller DBH trees in this area is likely from a large storm in September 1998 that opened up the canopy. The total deer take in Sweden, New York in 1998 was 257 as compared to 405 in 2011 (DEC, 2016). This population index suggests that the small maples in the Maple Regeneration plots were able to grow past the reach of deer and may have survived as a result of this lower deer abundance.

Future study possibilities

As the woodlot continues to experience disturbance from herbivory, tree pests/pathogens, and invasive species, the fences will continue to exclude deer, ideally for decades, and many more metrics of community change can be measured. Measuring heights and phenology of plants in quadrats would be valuable to make inferences about potential seedbank depletion of native plants and seedbank loading from invasive plants. Tracking survival of *A. saccharum* mast seedlings across years may show how successful this species is in this reproductive strategy in the presence or absence of deer. More extensive earthworm studies (abundance estimates, species ID, biomass) could be conducted to study how deer interact with them and how they

facilitate invasive plant species success or hinder seedling recruitment (Dávalos 2015). Measures of faunal differences are possible, too; however, range sizes of the study animal need to be considered, as edge effects from fencing may be severe. For example, wind-blown litter build-up at the bottom of the fence may impact invertebrate communities and soil compaction and fecal pellet nutrient loading from deer walking the perimeter of the fence may influence earthworm presence. The fence itself acting as a perch for woodland birds may produce biased results, as unfenced plots would not be affected by this same habitat modification (Allombert *et al.* 2004). Changes in growth rates of trees may also be influenced by deer, so dendrometer bands could be applied to groups of different tree species and size classes and tracked over time (Anemaet *et al.* 2013).

One limitation of my study design resulted in pseudoreplication, as four exclosures were not a large enough sample size for robust statistical comparisons. Closely matching fenced and unfenced plots as they related to tree composition and size classes limited placement in the small, multi-use, on-campus woodlot. However, non-parametric tests, p-value corrective calculations, and independent analysis of exclosure pairs allowed me to draw broad conclusions from my data.

The future of the Brockport woodlot

The Brockport woodlot was estimated as having a population of 17 deer/km², yet research has demonstrated that densities as low as 5.8 to 10.4 deer/km² decreases tree seedling survival (Behrend *et al.* 1970, Russell *et al.* 2001). Harvest reports also indicate that deer take in the Town of Sweden has been steadily increasing since the

early 1990's. This excessive herbivory pressure on plant communities is not atypical in western New York, as these woodlots are refuges for deer in an agricultural/suburban matrix. Deer using crops as a supplemental food source augments the carrying capacity of surrounding forests and further inhibits herbaceous and seedling recovery (Augustine and Jordan 1998). Deer population-control programs like bait-and-shoot and controlled hunts may need to become a first step in the conservation plans of forest managers (Doerr *et al.* 2001). However, even after deer populations have been reduced, their legacy effects may still require years of planting and seeding to restore ecosystem function (Tanentzap *et al.* 2011). This intense active management may be the only way to promote the long-term viability of the Northeast's deciduous forests.

The desperate state of a campus woodlot may be considered trivial to a college administration, and proposing a resolution that is lethal/controversial (bait-and-shoot) or expensive (woodlot perimeter fencing) will likely result in inaction. Student-led restoration efforts focused on tree seedlings in this woodlot could include fencing individual seedlings until they are large enough to withstand herbivory. When implemented over time, this would diversify the age class of trees in the woodlot. However, native, herbaceous plants would still be at risk of extirpation; thus, deer population control proposals should be introduced consistently to campus administration as a crucial component of improving the resiliency of the Brockport woodlot.

Study implications

My enclosure study can help predict the successional trajectory of the Brockport woodlot under excessive herbivory pressure from deer. The lack of tree seedlings at varied and more conspicuous heights is my primary concern. Unfenced seedlings are unable to grow much beyond 10 cm in height, and there is a distinct browse line, which indicates that the forest is not able to grow past the reach of deer. As invasive pests like the emerald ash borer kill *Fraxinus* sp., or the invasive beech scale insect increases the susceptibility of *Fagus grandifolia* to the fungal beech bark disease, high-light niches will be available for seedlings. The presence of invasive earthworms is also likely compounding the impact deer are having on plant survival in the woodlot. However, if seedlings cannot survive herbivory, the woodlot may slowly transition into a deer-resistant plant community composed of unpalatable invasive shrubs and browse tolerant grasses (Tanentzap *et al.* 2011).

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Tables

Table 1: Square-root-transformed Bray-Curtis similarity coefficients derived from a resemblance matrix of overstory abundance from initial 2016 measurements in four unfenced and fenced plots in Brockport, NY. Bolded numbers represent similarity between paired unfenced and fenced plots.

	Beech Maple Unfenced	Beech Maple Fenced	Diverse Wet Unfenced	Diverse Wet Fenced	Maple Regeneration Unfenced	Maple Regeneration Fenced	Sparse Maple Unfenced
Beech Maple Unfenced							
Beech Maple Fenced	82.6						
Diverse Wet Unfenced	37.8	50.2					
Diverse Wet Fenced	39.4	47.9	83.9				
Maple Regeneration Unfenced	55.7	59.4	49.6	44.2			
Maple Regeneration Fenced	52.2	47.8	32.4	26.5	85.1		
Sparse Maple Unfenced	50.7	42.6	19.2	21.6	41.8	50.5	
Sparse Maple Fenced	68.3	51.8	40.6	42.6	59.8	60.6	72.4

Table 2: Overstory (trees and shrubs over 2 m) characteristics from initial 2016 measurements in four unfenced and fenced plots in Brockport, NY.

	Species Richness	% <i>Acer</i> sp.	% Canopy openness	Shannon-Weiner Diversity (H')
Beech Maple Unfenced	6	56	10.6	0.94
Beech Maple Fenced	7	47	4.0	1.20
Diverse Wet Unfenced	9	11	5.0	1.78
Diverse Wet Fenced	7	13	9.2	1.81
Maple Regeneration Unfenced	7	90	7.0	0.75
Maple Regeneration Fenced	5	87	5.2	0.51
Sparse Maple Unfenced	2	97	26.0	0.12
Sparse Maple Fenced	4	90	21.4	0.43

Table 3: Number (N) and percentage of trees in all unfenced and fenced plots with lowest leaf heights below and above 2 m in Brockport, NY, after one year of deer exclusion.

	Unfenced N (%)		Fenced N (%)		p-value (χ^2 stat) df
	<2m	>2m	<2m	>2m	
Beech Maple	53 (68)	28 (35)	52 (53)	47 (47)	0.814 (0.056) df = 1
Diverse Wet	10 (23)	33 (77)	19 (31)	43 (69)	
Maple Regeneration	43 (48)	47 (52)	46 (58)	34 (43)	
Sparse Maple	11 (46)	13 (54)	10 (43)	13 (57)	
Total overall	117	121	127	137	

Table 4: Average lowest leaf height (cm) and standard deviation (\pm SD) of woody plants over 2-m tall in four paired unfenced and fenced plots in Brockport, NY, August 2017.

Tree/Treatment	All plots N	Overall \bar{x} Height cm (\pm SD)
<i>Acer</i> sp./Unfenced	132	167.6 (\pm 37.6)
<i>Acer</i> sp./Fenced	137	167.8 (\pm 41.3)
<i>Carpinus</i> sp./Unfenced	4	200.0 (\pm 0.0)
<i>Carpinus</i> sp./Fenced	6	156.0 (\pm 36.1)
<i>Carya</i> sp./Unfenced	7	194.9 (\pm 13.6)
<i>Carya</i> sp./Fenced	18	188.3 (\pm 28.2)
<i>Fagus</i> sp./Unfenced	30	145.5 (\pm 37.5)
<i>Fagus</i> sp./Fenced	42	157.5 (\pm 46.7)
<i>Fraxinus</i> sp./Unfenced	11	198.3 (\pm 5.7)
<i>Fraxinus</i> sp./Fenced	13	193.9 (\pm 19.6)
<i>Ostrya</i> sp./Unfenced	11	197.0 (\pm 10.0)
<i>Ostrya</i> sp./Fenced	6	193.1 (\pm 19.4)
<i>Prunus</i> sp./Unfenced	10	182.0 (\pm 25.4)
<i>Prunus</i> sp./Fenced	7	174.9 (\pm 44.8)
<i>Tilia</i> sp./Unfenced	15	200.0 (\pm 0)
<i>Tilia</i> sp./Fenced	21	193.0 (\pm 32.3)
All plots		
Overall/Unfenced	238	170.2 (\pm 39.4)
Overall/Fenced	264	169.5 (\pm 39.6)

Table 5: Independent t-test T-stats and P-values of percent cover and richness between ten, 1m² quadrats in unfenced and fenced plots from 2016-2018 in Brockport, NY. Bolded values indicate significant p-values <0.05 after Holm-Bonferroni corrections. Displayed graphically in Figures 11 and 12.

	T-stat, P Value						
<i>Plot</i>	<i>Acer sp. seedling percent cover 2018</i>	<i>Percent cover 2016</i>	<i>Percent cover 2017</i>	<i>Percent cover 2018</i>	<i>Richness 2016</i>	<i>Richness 2017</i>	<i>Richness 2018</i>
Beech Maple	-0.08, 0.94	-0.179, 0.86	-0.256, 0.80	1.119, 0.28	-1.31, 0.99	-1.90, 0.07	-0.47, 0.64
Diverse Wet	-1.5, 0.17	-1.857, 0.08	1.840, 0.08	1.935, 0.07	0.43, 0.08	0.68, 0.50	0.65, 0.46
Maple Regeneration	0.87, 0.41	0.932, 0.36	-0.781, 0.44	0.70, 0.385	0.46, 0.65	-0.27, 0.79	0.15, 0.88
Sparse Maple	3.8, 0.004	-0.990, 0.34	-1.95, 0.07	3.141, 0.006	-0.81, 0.43	-2.79, 0.01	-1.33, 0.20

Figures



Figure 1: The Brockport woodlot (outlined in white), Monroe County Brockport, NY, in the year 1930 (Official Site of Monroe County, New York, 2015).

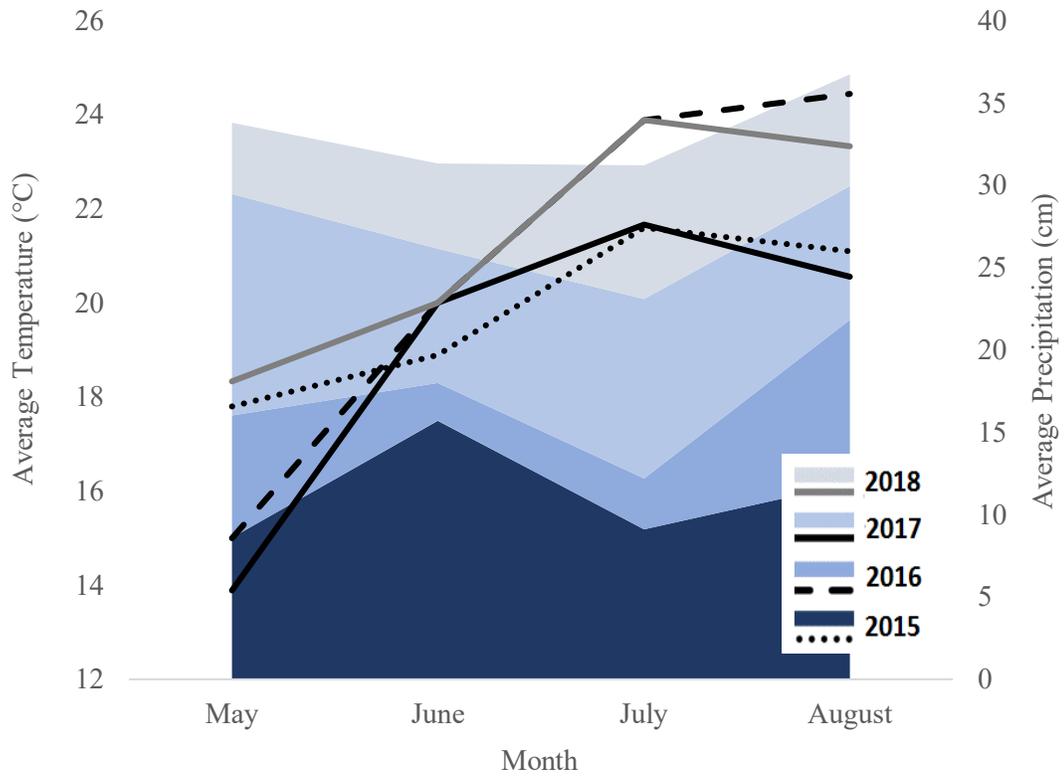


Figure 2: Average temperature (°C) represented by lines and total precipitation (cm) represented by stacked area from 2015-2018 in Brockport, NY (data from Weather Underground website).

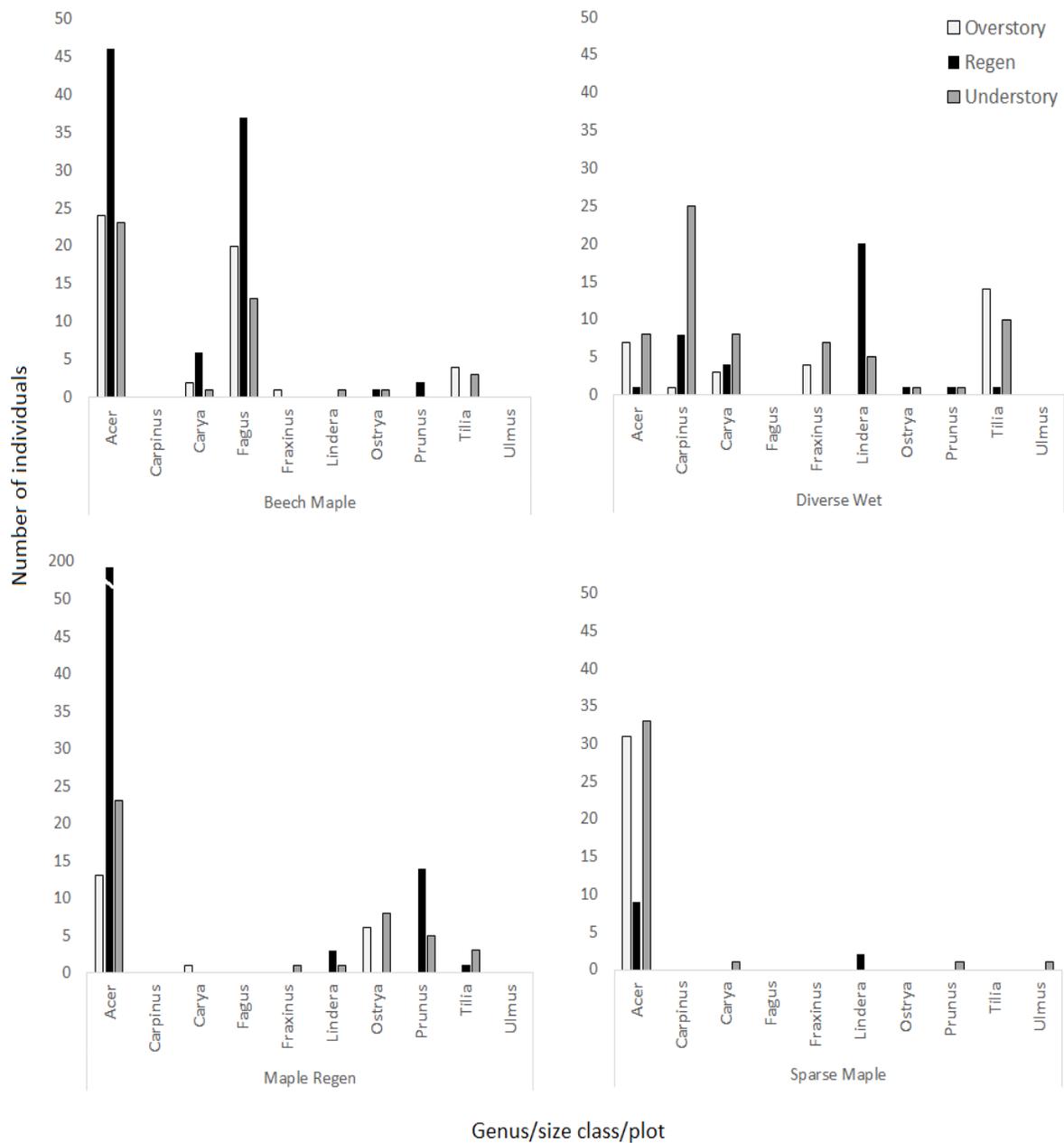


Figure 3: Number of individuals of each tree genus in three size classes overstory (trees >15 cm DBH), understory (trees and shrubs 5-15 cm DBH), and regeneration and shrub layers (trees and shrubs <5 cm DBH) combining unfenced and fenced plot pairs with each other from initial 2016 measurements in Brockport, NY.

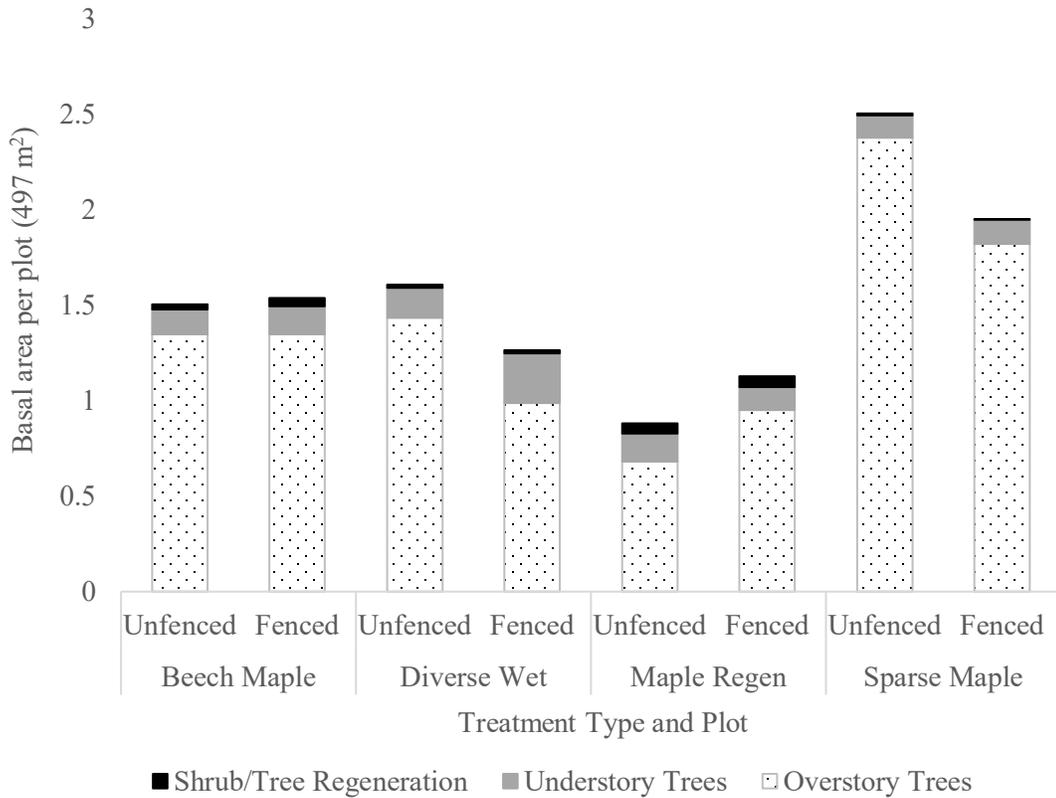


Figure 4: Total basal area per plot (497 m²) of overstory (trees >15 cm DBH), understory (trees and shrubs 5-15 cm DBH), and regeneration and shrub layers (trees and shrubs <5 cm DBH) from initial 2016 measurements in four unfenced and four fenced plots in Brockport, NY.

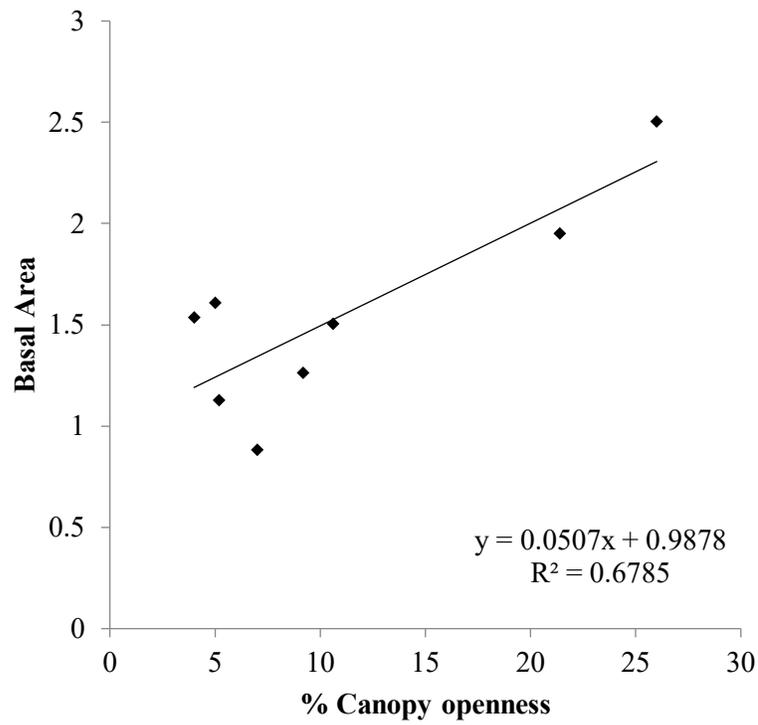


Figure 5: Linear regression of basal area and percent canopy openness across eight paired unfenced and fenced plots from initial 2016 measurements in Brockport, NY (F-stat=12.66, df=6, P-value=0.01).

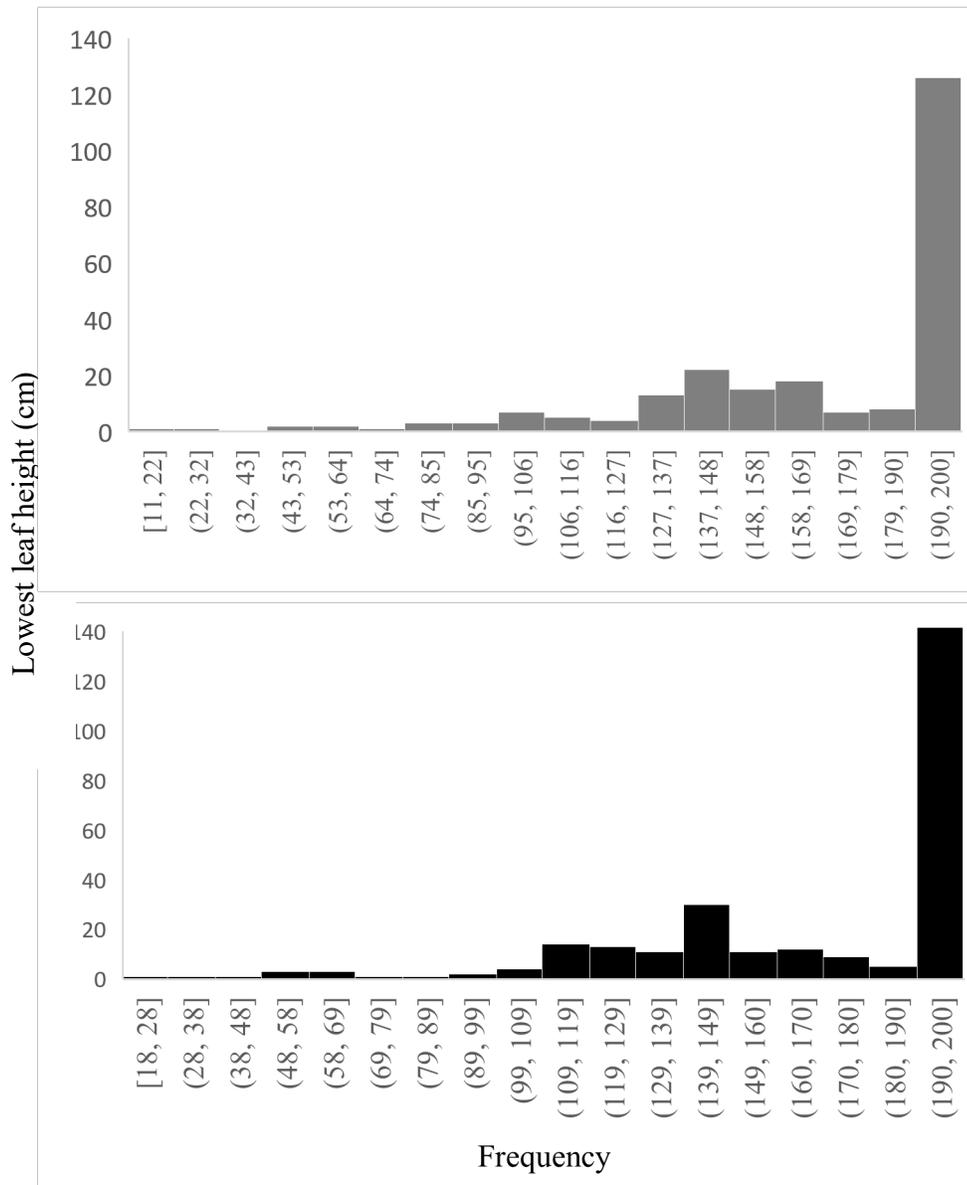


Figure 6: Frequency of lowest leaf heights (cm) of trees in all unfenced and fenced plots in Brockport, NY, after one year of deer exclusion. Trees with lowest leaf heights above 200 cm are grouped in the 190-200 cm bin.

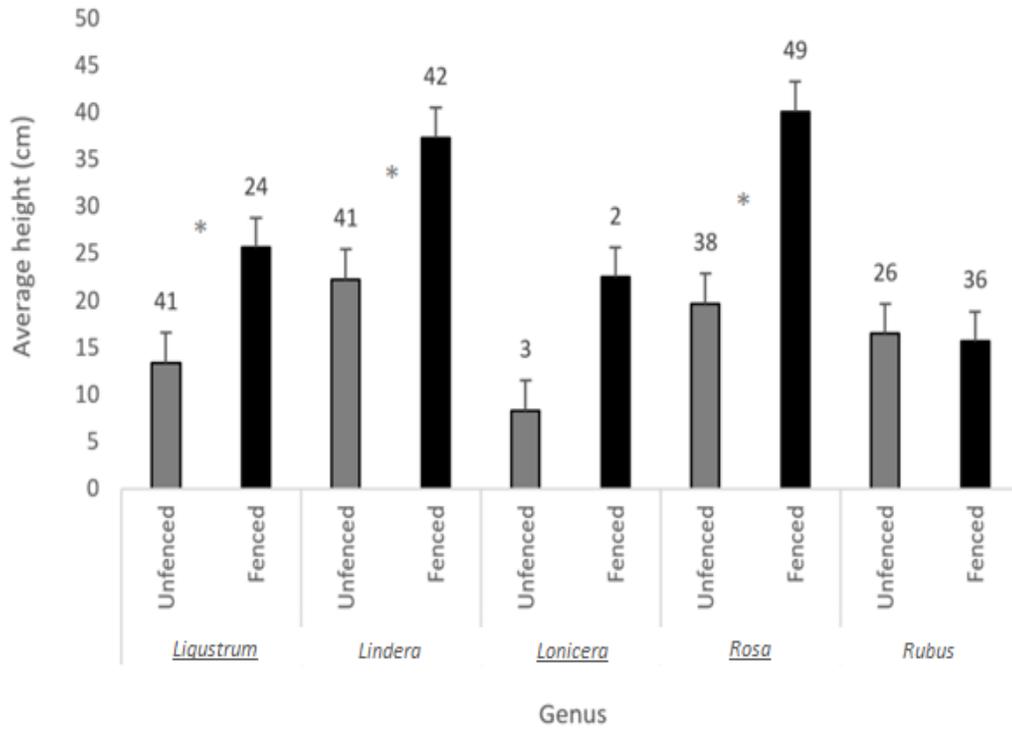


Figure 7: Average height (cm) and number (above bars) of five woody shrub species less than 2 m tall across all unfenced and fenced plots in Brockport, NY after one year of deer exclusion in 2017. Underlines represent invasive species within a genus, lines represent standard error, and stars represent significant differences in height (Mann-Whitney U test) between paired fenced and unfenced plots on species with a sample size of more than five.

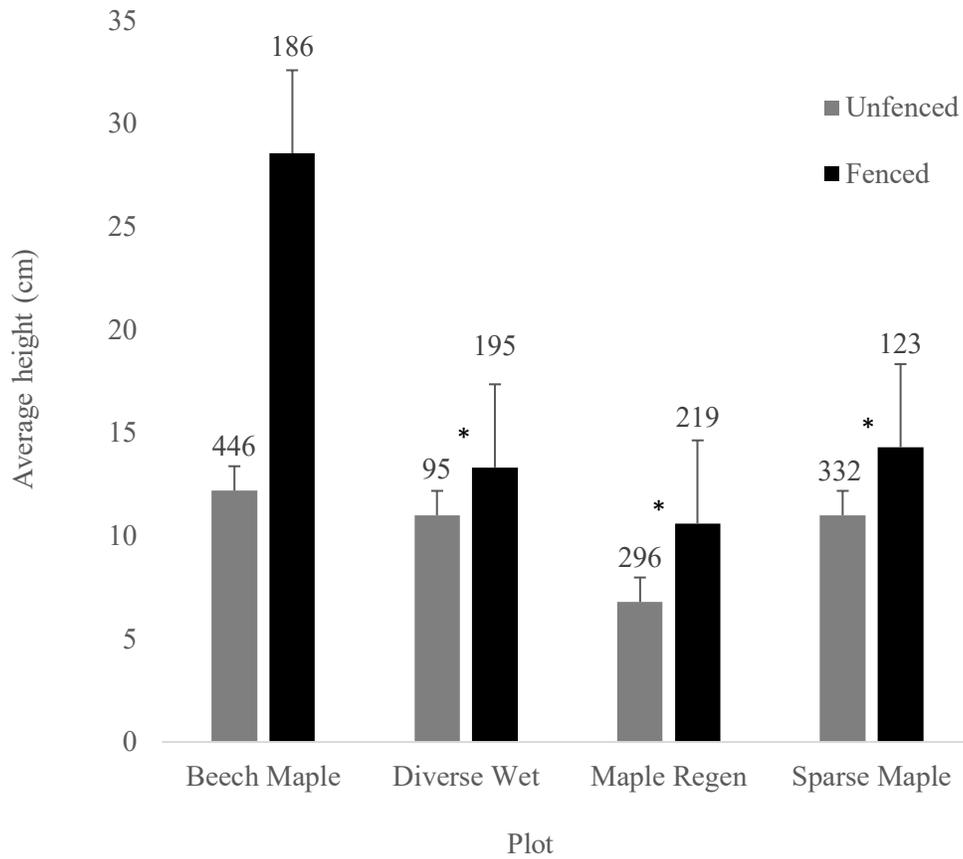


Figure 8: Average height (cm) and number (above bars) of tree seedlings (including root suckers) less than 2 m tall in four paired unfenced and fenced plots in Brockport, NY after one year of deer exclusion in 2017. Stars represent significant differences (Mann-Whitney U test) between paired fenced and unfenced plots and lines represent +1 standard error.

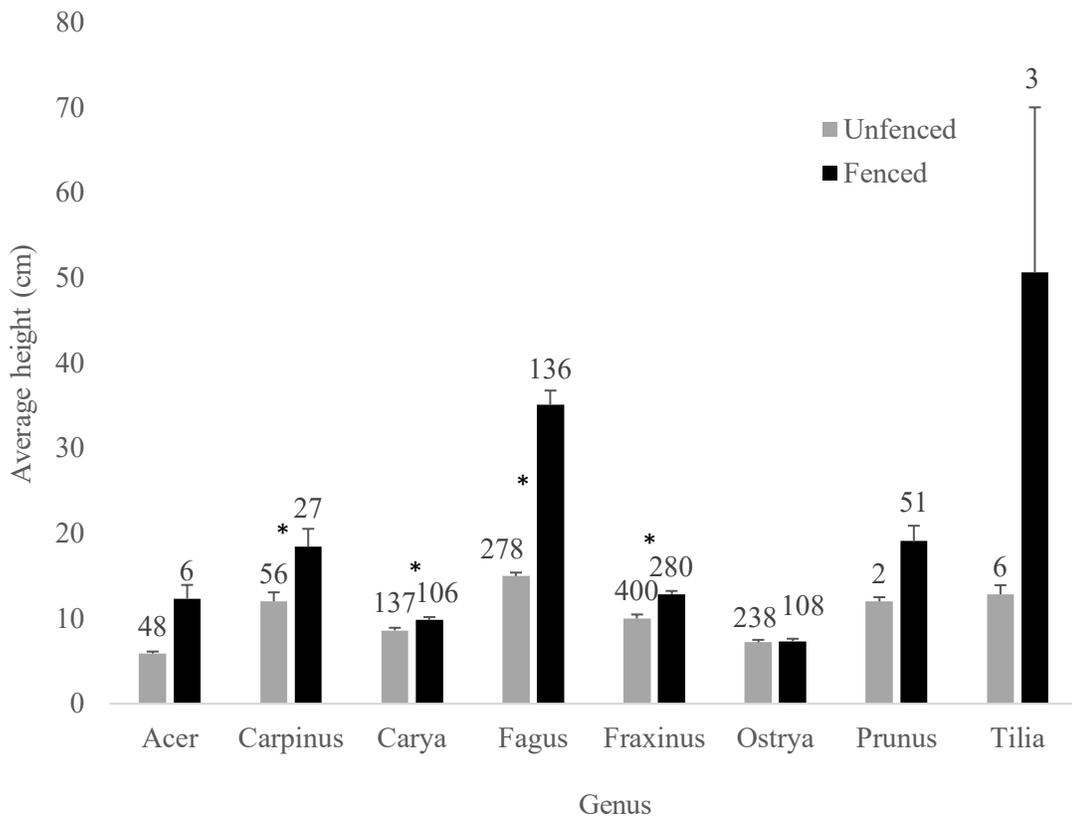


Figure 9: Average height (cm) and number (above bars) by genus of tree seedlings (including root suckers) less than 2 m tall in four paired unfenced and fenced plots in Brockport, NY after one year of deer exclusion in 2017. Stars represent significant differences (Mann-Whitney U test) between paired fenced and unfenced plots with large enough sample sizes and lines represent +1 standard error.

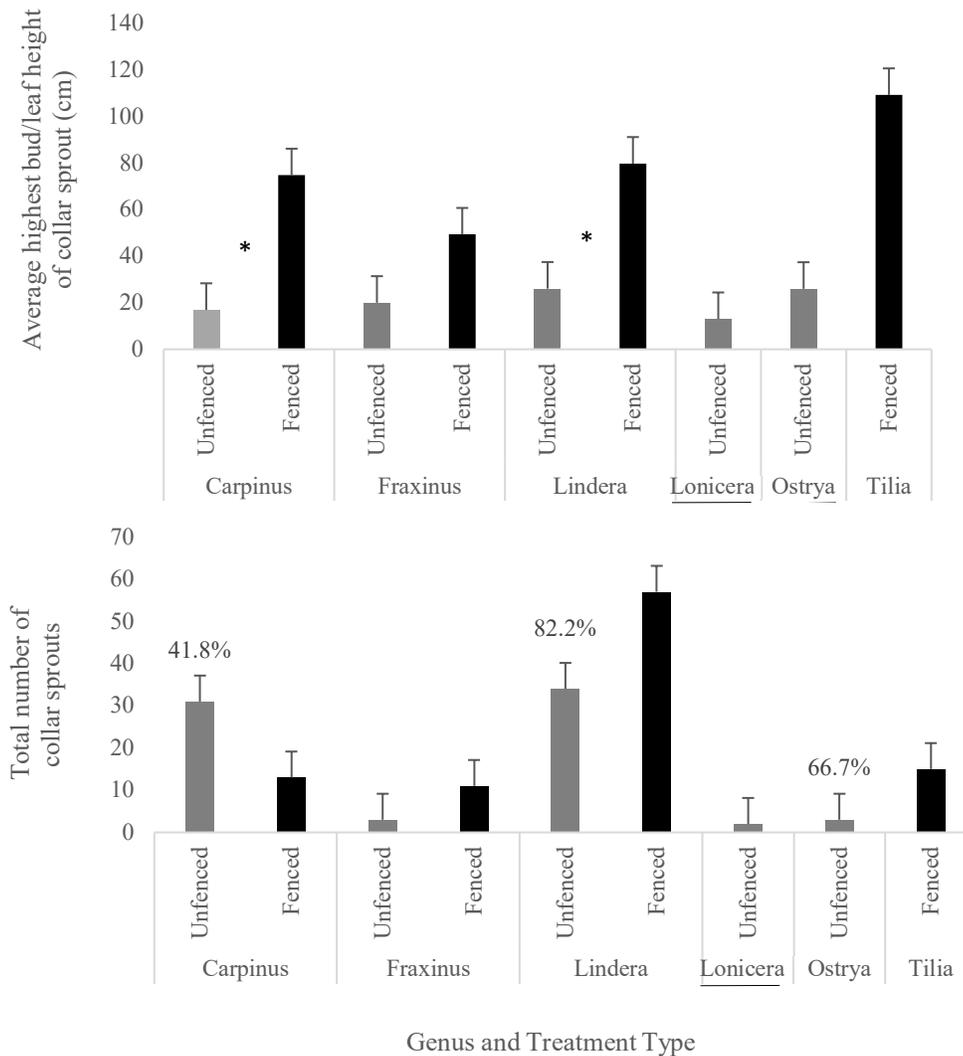


Figure 10: Average highest leaf height of collar sprouts, total number of collar sprouts, and proportion of collar sprouts browsed (above bars) of each sprouting genus in the Diverse Wet fenced and unfenced treatment plots in Brockport, NY after one year of deer exclusion. Underlines represent invasive species within a genus, lines represent standard error, stars represent significant differences between paired fenced and unfenced plots (Mann-Whitney U test) on *Carpinus caroliniana* and *Lindera benzoin* with a sample size of more than five.

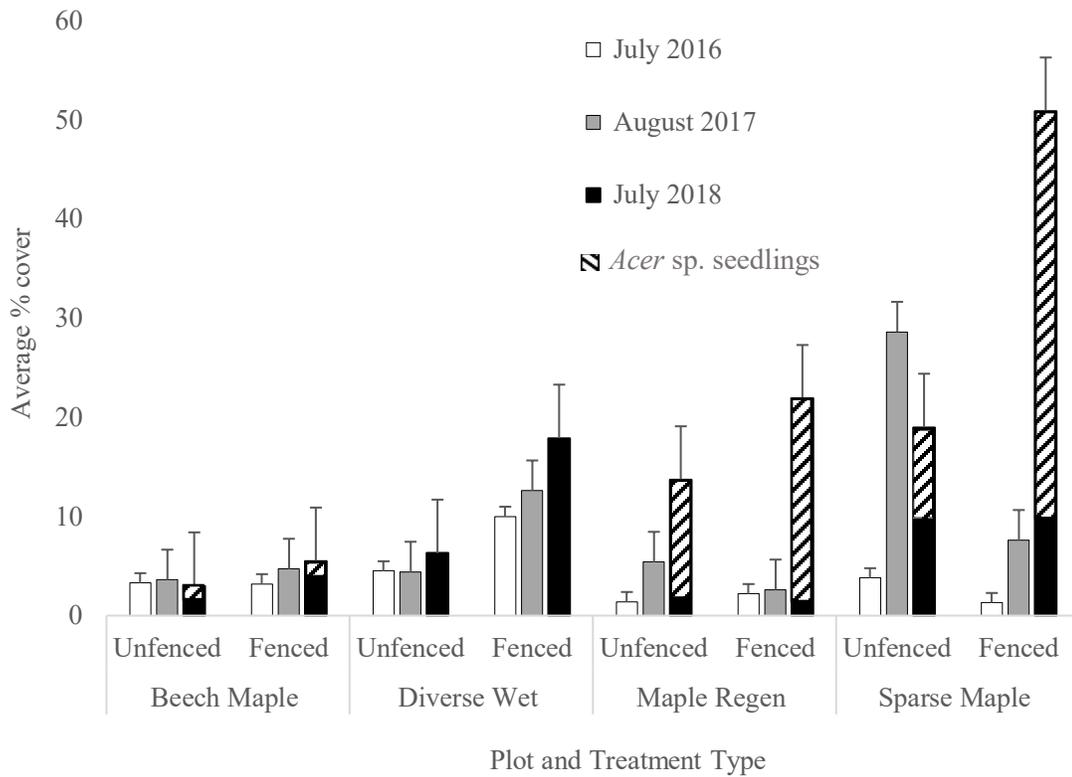


Figure 11: Average percent cover (per 1m² quadrat) of ground-level vegetation in each of four paired unfenced and fenced plots by year in Brockport, NY. Hashed bars represent percent cover of *Acer* sp. seedlings, lines represent +1 standard error.

Detailed data shown in Table 5.

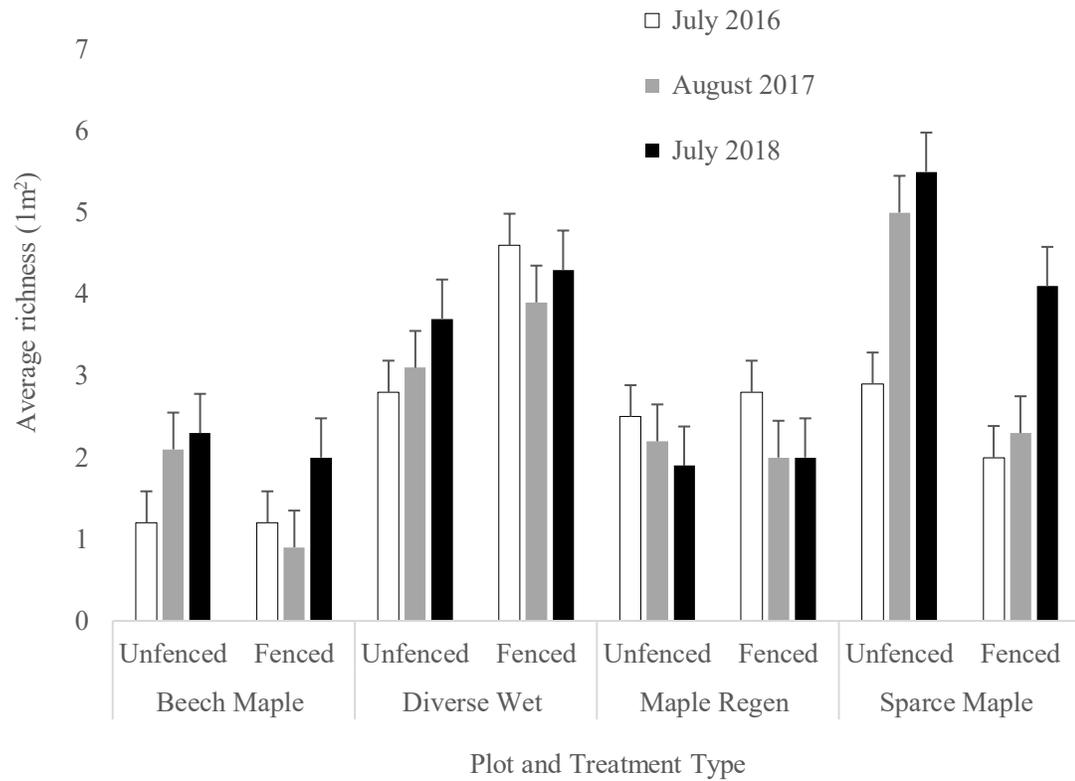


Figure 12: Average species richness (per 1m² quadrat) of ground-level vegetation in each of four paired unfenced and fenced plots by year in Brockport, NY. Lines represent +1 standard error. Independent t-test results shown in Table 5.

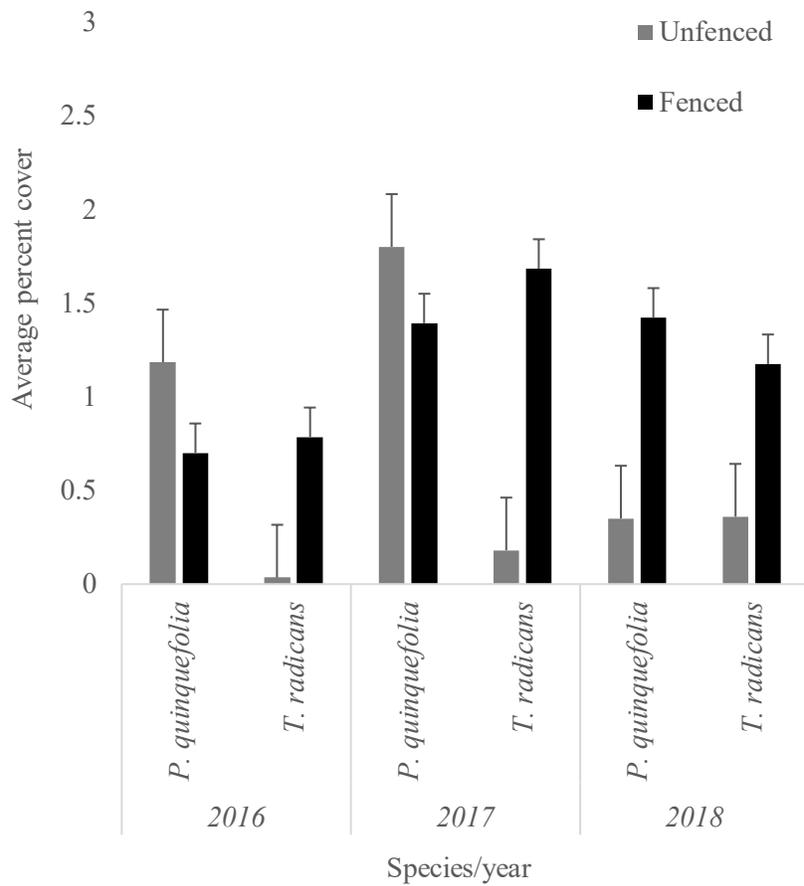


Figure 13: Average percent cover by year of ground layer vegetation of *Parthenocissus quinquefolia* and *Toxicodendron radicans* across ten 1m² quadrats in paired unfenced and fenced plots that contained these species in Brockport, NY.

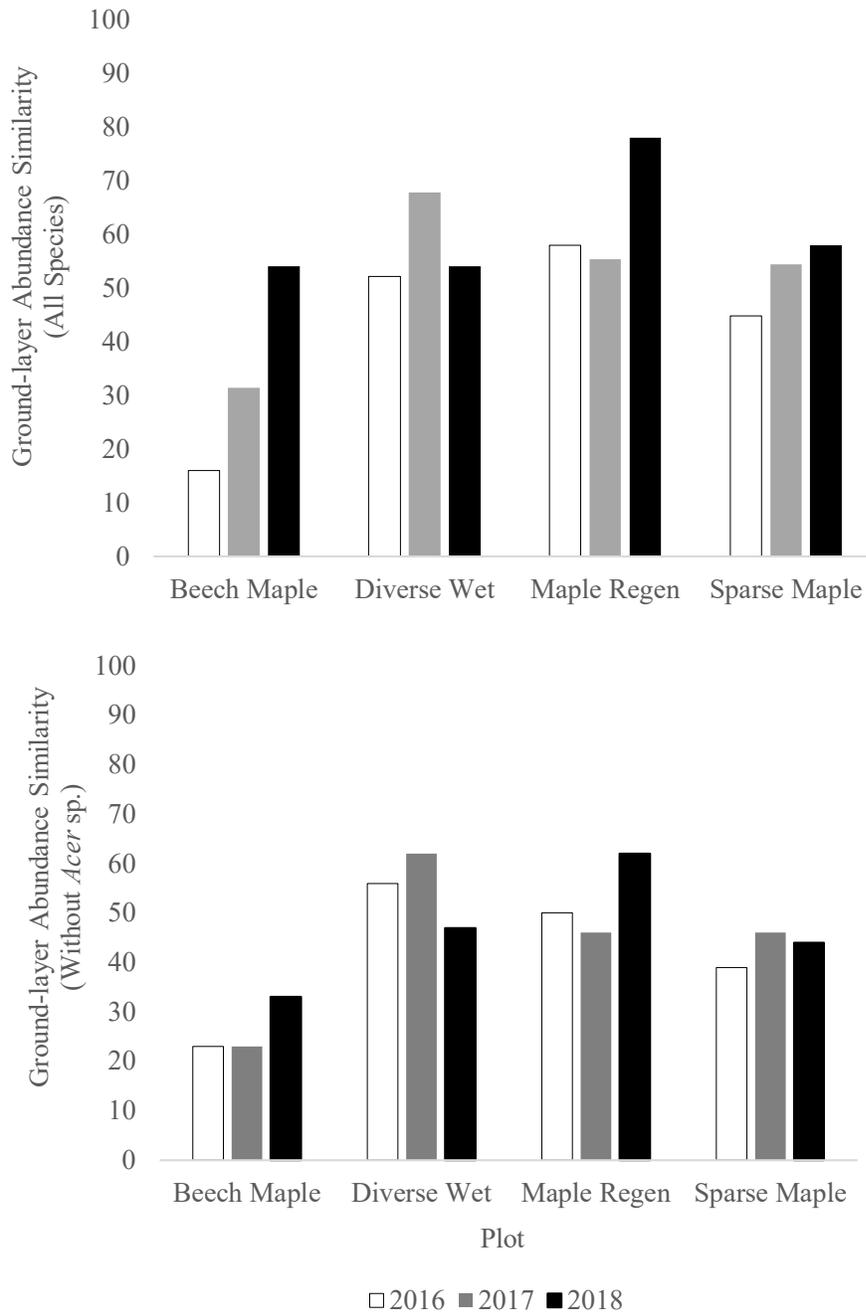


Figure 14: Square-root-transformed Bray-Curtis similarity coefficients of ground-level plant species abundance with and without *Acer* sp. seedlings between four unfenced and fenced plots in Brockport, NY.

Appendix

I. Deer density estimate

To evaluate density of deer in the Brockport woodlot, undergraduate student Chris Plummer and I employed a commonly used methodology to estimate deer density per square kilometer by systematically counting fecal pellet groups. Three parallel line transects were run approximately 150 m apart throughout the length of the woodlot. Every 20 m along each transect, 1.2-m-radius plots were established, and the numbers of pellet groups were counted within the circles (DeCalesta 2013, Shelton *et al.* 2014). The number of pellet groups produced by deer per day was needed for our calculation, and Rogers (1992) was referenced for this value. To calculate deer density, I used the DeCalesta (2013) equation:

$$\text{Density} = (\text{Total \# pellet group}) \div (\text{pellet groups per deer per day} * \text{time since fall leaf off} * \text{total sample area in square miles})$$

II. Exclosure construction details

I conducted the tree community composition inventory 30 m from treeline edges in a 270 x 70 m area gridded into eighty, 15 m² flagged plots where all trees within each plot were identified and placed into size classes based on DBH. Approximately 2,700 trees were inventoried and analyzed to identify similar tree communities characterized by species and size using a resemblance matrix, spreadsheet comparisons, and a NMDS ordination. Similarity between the plots was

confirmed once delineated through additional tree inventories, species comparisons, and matching total basal area and biomass calculations between the plots.

The size of experimental and control plots was approximately 22 x 22 m; however, dimensions were ultimately determined by presence of trees deemed ideal for fence corners. I used 12.5-gauge, rust-proof, aluminized high-tensile wire, 2.4-m-tall plastic deer fencing (maximum deer jumping height), and trees greater than 20-cm DBH as corner posts. The wire was installed as close to the ground and as close to the top of the fence as possible. Topography created intermittent ground-level gaps no greater than 15 cm and allowed for small mammal access, while the fence's 12.7 x 12.7 cm mesh permitted entry of smaller animals. Heavy duty tent stakes were added to the bottom of the fences every 2-3 m, and bamboo support sticks were added to sagging fence tops to ensure deer exclusion. One corner of each enclosure was secured with removable zip-ties to provide researcher access. Each enclosure was paired with an unexclosed control plot of approximately the same size and clearly marked with PVC pipe stakes with the tops spray-painted orange (a color deer have difficulty seeing) to prevent their attraction to the control area. Laminated "Do Not Disturb" signage was attached to each side of the enclosures to discourage human interference. Bright blue flagging tape was strung along the outside of the enclosures at deer eye-level to prevent deer from running into and damaging the fences. Blue was used, as it is a color that deer can see during the day and night (VerCauteren and Pipas 2003). Throughout the experiment, fences were visited as often as possible and

repaired as necessary, especially during rut and after heavy winds when damage to fencing was severe and provided open access to enclosed plots intermittently.

Construction of the deer exclosures was led by Michael Ashdown, a research assistant employed by Cornell University who has experience building numerous exclosures across New York State. His on-site expertise was used to construct the first two exclosures on 16 March 2016 and allowed us to lead the construction of the other two fences on 10 April 2016 with volunteers.

Fence construction materials:

# Needed	Item	Brand/Company	Size/Count
4	Extra strength deer fence with reinforced edge	Deer Busters	2.3 m tall x 100.6 m roll
1	High Tensile Wire Double Pack	Zareba Systems	609.6 m 12.5 Gauge
1	High Tensile Wire	Zareba Systems	304.8 m 12.5 Gauge
8	In-Line Wire Strainer	Zareba Systems	
4	Large Fence Tension Spring	Zareba Systems	
1	Gritted Crimping Sleeve 2-3	Zareba Systems	25 ct.
1	4 Slot High Tensile Wire Crimping Tool	Zareba Systems	
1	In-Line Strainer Handle	Zareba Systems	
3	Nail-On Claw Insulator	Kencove	25 ct.
1	Hog Ring Pillars Kit	Dewalt/Tractor Supply	1 pillar with 1000 1.7 cm rings
1	Hog Rings	Dewalt/Tractor Supply	1000 1.7 cm rings
3	Top Choice #2 Prime Pressure Treated Lumber	Lowe's	0.6 x 1.8 x 3.7 m
2	Grip-Rite Hot-Dipped Galvanized Smooth Box Nails	Lowe's	2.27 kg, 16D, 1 m
2	Grip-Rite Hot-Dipped Galvanized Smooth Joist Hanger Nails	Lowe's	0.45 kg, 9-Gauge, 0.38 m
5	Blue Hawk Zinc-Plated Standard (SAE) Fender Washers	Lowe's	25 Count, 0.79 cm x 3.81 cm
1	Black zip ties	Lowe's	500 ct.

III: Native plantings

In April 2016, I received 45 individuals of six species of native plants shipped in a dormant state from Izel Native Plants (Izel Plants, Washington, D.C.). I ordered five extra plants of each species in case of mortality prior to planting. Plant selection focused on different habits of woodland species that are adapted for the understory, vary in known deer palatability, and have at one time been recorded as being present in Monroe County. I planted two dicot herbaceous species, *Trillium grandiflorum*- a NYS exploitably vulnerable native plant, *Cardamine diphylla*, the fern *Polystichum acrostichoides*, the woody shrub *Viburnum acerifolium*, the sedge *Carex plantaginea*, and the tree *Acer saccharum*.

I stored the plants in a refrigerator for approximately 5 d and then planted them individually in pots with a potting soil and peat mix. Pots were color-coded by species to reduce mistakes by planting volunteers. I watered the plants every other day and allowed them to break dormancy in a greenhouse at temperatures above 21°C. Three days prior to planting, I placed the plants in their pots inside an enclosure to acclimatize them to the outdoors. The day prior to planting, I measured each plant for highest leaf height, greatest flower height, number of leaves, length and width of largest leaf or frond, and whole plant percent herbivory (including insect damage).

In May 2016, I divided treatment and control plots in half with white flagging to include a north-south moisture gradient. One half was randomly selected and allowed to regenerate naturally, and the other half was planted with six species of native plants (five individuals of each species), totaling 30 plantings in each plot.

Three plantings were placed along 10 line transects spaced 2 m apart. Using random number generators, I assigned planting locations for each species at least 1 m apart from each other and marked with 12 cm, color-coded bamboo stakes. Depression areas that fell on the transect lines that were known for flooding were avoided. The plant size measurements I initially took were repeated once per month on all plants throughout the growing season. Similar planting techniques have been used successfully to determine herbivory impacts in several temperate forest and riparian studies (Cornett *et al.* 2000, Opperman and Merenlender 2000, and Ruhern and Handel 2003).

During the first week after planting, I checked plants every day. Those that were dug up by eastern chipmunks (*Tamias striatus*) and other small mammals were replanted *in situ* as often as encountered. I estimated survival and herbivory by comparing current plant condition to previously recorded plant condition two times per week during the first two weeks after planting and then once per week after that.

In April 2017, I received 75 individuals of three species of native plants from Izel Native Plants shipped in a dormant state. I stored the plants in a refrigerator and bareroot planted them within a week of arrival. I ordered five extra plants of each species in case of mortality. Plants included the herbaceous species *Actaea pachypoda*, *Cardamine diphylla*, and *Carex plantaginea*. I planted plants 1 m from the edge of one side of the treatment and control plots, with the goal of all being visible from the edges of the plots to reduce in-plot trampling. Order of plantings was randomly determined, and I avoided planting locations with known flooded

depressions. I tracked survival twice per month throughout the growing season, while digging disturbance from small mammals was ignored.

IV: Faunal measurements

I trapped white-footed mice (*Peromyscus leucopus*) on 17-19 October 2016 and 23-25 October 2017 utilizing 48 Sherman livetraps baited with oats and stuffed with polyester fiber filling for warmth over three consecutive trapping nights. In the fenced plots, 25 mice were trapped, and 20 were trapped in the unfenced plots in 2016. In 2017, only one chipmunk was trapped, so this dataset was not robust enough to draw conclusions about mice preferring fenced or unfenced plots.

I also liquid-extracted earthworms from three 35cm x 35cm sample trays randomly placed in each fenced and unfenced plot on 8 October 2017 after a few days of rain using the methods described by Dávalos (2015). I made a 4-L solution of food-grade mustard powder and water at a concentration of 10g/L and poured it into the sample tray over the course of ten minutes. This solution irritated the earthworms' skin, and they emerged at the surface, where I collected and preserved them in 70% isopropyl alcohol and then transferred them to formalin. However, the earthworms broke down in the formalin before counting or identification could occur, so the only data I could gather were that earthworms were present in all of the 18 sample trays on which I used liquid extractant and, thus, were present in all of my experimental plots. (Tip: place worms back into 70% isopropyl alcohol after 24 hours in formalin, and they will likely be better preserved).

V. Total species list of plants in each experimental plot across all years. Planted: (P)

Beech Maple Fenced

Acer saccharum
Acer saccharum (P)
Acer saccharum seedling
Actaea pachypoda (P)
Arisaema triphyllum
Cardamine concateratar
Cardamine dyphylla (P)
Carex plantaginea (P)
Carya cordiformis
Carya cordiformis seedling
Caulophyllum thalictroides
Cyperaceae
Dentaria lacinata
Dryopteris sp.
Epipactis helleborine
Erythronium americanum
Fagus grandifolia
Fagus grandifolia root sucker
Fraxinus americana
Fraxinus americana seedling
Galium aparine
Geranium maculatum
Geum sp.
Ostrya virginiana
Ostrya virginiana seedling
Parthenocissus quinquefolia
Poaceae
Podophyllum peltatum
Polygonatum biflorum
Polystichum acrostichoides (P)
Prenanthes alba
Prunus serotina
Rosa multiflora
Thalictrum pubescens
Tilia americana
Toxicodenden radicans

Beech Maple Unfenced

Acer saccharum
Acer saccharum (P)
Acer saccharum seedling
Actaea pachypoda (P)
Aster diveracatus
Asteraceae
Cardamine concateratar
Cardamine dyphylla (P)
Carex plantaginea (P)
Carex sp.
Carya cordiformis
Carya cordiformis seedling
Caulophyllum thalictroides
Claytonia virginica
Cyperaceae
Dentaria lacinata
Erythronium americanum
Fagus grandifolia
Fagus grandifolia root sucker
Fraxinus americana
Fraxinus americana seedling
Galium aparine
Geranium robertianum
Geum aleppicum
Geum sp.
Impatiens capensis
Ligustrum sp.
Lindera benzoin
Monotropa uniflora
Persicaria virginiana
Poaceae
Polygonatum biflorum
Polystichum acrostichoides (P)
Populus deltoides seedling
Prenanthes alba
Prenanthes serpentaria

Trillium grandiflorum (P)
Viburnum acerifolium (P)
Vitis riparia

Prunus serotina
Rosa multiflora
Rubus sp.
Taraxacum officinale
Tilia americana
Toxicodendron radicans
Trillium grandiflorum (P)
Viburnum acerifolium (P)
Vitis riparia

Diverse Wet Fenced

Acer saccharum
Acer saccharum (P)
Acer saccharum seedling
Actaea pachypoda (P)
Alliaria petiolata
Arisaema triphyllum
Cardamine dyphyllia (P)
Carex plantaginea (P)
Carpinus caroliniana
Carpinus caroliniana seedling
Carpinus seedling
Carya cordiformis
Carya cordiformis seedling
Circaea lutetiana
Cornus sp. seedling
Cyperaceae
Epipactis helleborine
Erythronium americanum
Eurybia divaricata
Fraxinus americana
Fraxinus americana seedling
Geranium maculatum
Geum aleppicum
Geum laciniatum
Geum sp.
Hieracium pratense
Impatiens capensis

Diverse Wet Unfenced

Acer saccharum
Acer saccharum (P)
Acer saccharum seedling
Actaea pachypoda (P)
Alliaria petiolata
Allium schoenoprasum
Arisaema triphyllum
Cardamine dyphyllia (P)
Carex penslyvanica
Carex plantaginea (P)
Carpinus caroliniana
Carpinus caroliniana seedling
Carpinus caroliniana root sucker
Carya cordiformis
Carya cordiformis seedling
Cyperaceae
Epipactis helleborine
Erythronium americanum
Eurybia divaricata
Fraxinus americana
Fraxinus americana seedling
Geum laciniatum
Geum sp.
Impatiens capensis
Ligustrum sp.
Lindera benzoin seedling
Lindera benzoin

Ligustrum sp.
Lindera benzoin root suckers
Lindera benzoin
Lindera benzoin seedling
Lonicera sp.
Lysimachia nummularia
Oxalis stricta
Parthenocissus quinquefolia
Persicaria virginiana
Poaceae
Polystichum acrostichoides (P)
Prunella vulgaris
Prunus serotina
Ranunculus abortivus
Ranunculus sp.
Rosa multiflora
Rubus sp.
Taraxacum officinale
Tilia americana
Tilia americana seedling
Trillium grandiflorum (P)
Toxicodendron radicans
Viburnum acerifolium (P)
Viola subsinuata
Vitis riparia

Lonicera sp.
Lonicera sp. seedling
Lycopus americanus
Lysimachia nummularia
Ostrya virginiana
Parthenocissus quinquefolia
Persicaria virginiana
Poa compressa
Poaceae
Polystichum acrostichoides (P)
Prunus serotina
Rosa multiflora
Rubus sp.
Taraxacum officinale
Tilia americana
Tilia americana seedling
Trillium grandiflorum(P)
Toxicodendron radicans
Veronica officinalis
Viburnum acerifolium (P)
Vitis riparia

Maple Regeneration Fenced

Acer saccharum
Acer saccharum (P)
Acer saccharum seedling
Actaea pachypoda (P)
Alliaria petiolata
Allium schoenoprasum
Allium tricoccum
Arisaema triphyllum
Aster diveracatus
Asteraceae
Berberis tumburgenii
Cardamine concateratar

Maple Regeneration Unfenced

Acer saccharum
Acer saccharum (P)
Acer saccharum seedling
Actaea pachypoda (P)
Allium tricoccum
Arisaema triphyllum
Aster diveracatus
Asteraceae
Cardamine concateratar
Cardamine dyphylla (P)
Carex plantaginea (P)
Carya cordiformis

<i>Cardamine dyphylla</i> (P)	<i>Carya cordiformis</i> seedling
<i>Carex plantaginea</i> (P)	Cyperaceae
<i>Carya cordiformis</i>	<i>Dentaria lacinata</i>
<i>Carya cordiformis</i> seedling	<i>Dryopteris</i> sp.
<i>Caulophyllum thalictroides</i>	<i>Epipactis helleborine</i>
Cyperaceae	<i>Erythronium americanum</i>
<i>Dentaria lacinata</i>	<i>Eurybia divaricata</i>
<i>Epipactis helleborine</i>	<i>Fraxinus americana</i>
<i>Erythronium americanum</i>	<i>Fraxinus americana</i> seedling
<i>Eurybia divaricata</i>	<i>Galium aparine</i>
<i>Fraxinus americana</i>	<i>Geranium maculatum</i>
<i>Fraxinus americana</i> seedling	<i>Geranium robertianum</i>
<i>Geum</i> sp.	<i>Geum aleppicum</i>
<i>Impatiens capensis</i>	<i>Geum</i> sp.
<i>Ligustrum</i> sp.	<i>Impatiens capensis</i>
<i>Lindera benzoin</i>	<i>Intermedia marginalis</i>
<i>Lindera benzoin</i> seedling	<i>Lindera benzoin</i>
<i>Maianthemum racemosum</i>	<i>Maianthemum racemosum</i>
<i>Ostrya virginiana</i>	<i>Ostrya virginiana</i>
<i>Ostrya virginiana</i> seedling	<i>Ostrya virginiana</i> seedling
<i>Parthenocissus quinquefolia</i>	<i>Parthenocissus quinquefolia</i>
<i>Persicaria virginiana</i>	Poaceae
Poaceae	<i>Polystichum acrostichoides</i> (P)
<i>Polystichum acrostichoides</i> (P)	<i>Prunus serotina</i>
<i>Prunus serotina</i>	<i>Prunus</i> sp. Seedling
<i>Prunus</i> sp. Seedling	<i>Ranunculus</i> sp.
<i>Rosa multiflora</i>	<i>Robinia</i> seedling
<i>Solidago flexicalis</i>	<i>Rosa multiflora</i>
<i>Taraxacum officinale</i>	<i>Rubus</i> sp.
<i>Tilia americana</i>	<i>Solanum nigrum</i>
<i>Trillium grandiflorum</i> (P)	<i>Tilia americana</i>
<i>Toxicodendron radicans</i>	<i>Trillium grandiflorum</i> (P)
<i>Urtica</i> sp.	<i>Toxicodendron radicans</i>
<i>Uvularia</i> sp.	<i>Viburnum acerifolium</i> (P)
<i>Viburnum acerifolium</i> (P)	<i>Viola subsinuata</i>

Sparse Maple Fenced

Acer saccharum
Acer saccharum (P)
Acer saccharum seedling
Actaea pachypoda (P)
Allieria petiolata
Allium tricoccum
Arisaema triphyllum
Asteraceae
Cardamine concateratar
Cardamine dyphylla (P)
Carex plantaginea
Carex plantaginea (P)
Carya cordiformis
Carya cordiformis seedling
Circaea lutetiana
Cirsium vulgare
Claytonia virginica
Cyperaceae
Dentaria lacinata
Dicentra cucullaria
Erythronium americanum
Fraxinus americana
Fraxinus americana seedling
Galium aparine
Geranium maculatum
Geranium robertianum
Geum sp.
Hesperis matronalis
Hydrophyllum canadense
Lindera benozin
Ostrya virginiana
Ostrya virginiana seedling
Oxalis stricta
Parthenocissus quinquefolia
Persicaria virginiana
Phytolacca americana
Pilea pumila
Poaceae

Sparse Maple Unfenced

Acer saccharum (P)
Acer saccharum seedling
Actaea pachypoda (P)
Alliaria petiolata
Allium tricoccum
Arisaema triphyllum
Asteraceae
Cardamine dyphylla (P)
Carex plantaginea
Carex plantaginea (P)
Carya cordiformis
Carya cordiformis seedling
Circaea lutetiana
Cyperaceae
Dentaria lacinata
Dicentra cucullaria
Erythronium americanum
Fraxinus americana
Fraxinus americana seedling
Galium aparine
Geranium maculatum
Geranium robertianum
Geum sp.
Hesperis matronalis
Hieracium sp.
Impatiens capensis
Ligustrum sp.
Leonurus cardiaca
Ostrya virginiana
Ostrya virginiana seedling
Parthenocissus quinquefolia
Persicaria virginiana
Phytolacca americana
Plantago major
Poaceae
Polystichum acrostichoides (P)
Ranunculus sp.
Robinia pseudoacacia seedling

Podophyllum peltatum
Polystichum acrostichoides (P)
Prunella vulgaris
Prunus serotina
Prunus sp. seedling
Ranunculus sp.
Rosa multiflora
Rubus allegheniensis
Rubus occidentalis
Rubus sp.
Solanum nigrum
Symphotrichum lanceolatum
Taraxacum officinale
Trillium grandiflorum (P)
Toxicodendron radicans
Uvularia sp.
Vibrunum acerifolium (P)
Vincetoxicum rossicum
Vitis riparia

Rubus occidentalis
Rubus sp.
Rumex sp.
Solarum nigrum
Taraxacum officinale
Trillium grandiflorum (P)
Toxicodendron radicans
Ulmus americana
Urtica sp.
Verbascum thapsus
Vibrunum acerifolium (P)
Vincetoxicum rossicum
Viola sp.
Vitis riparia

Chapter 2: White-tailed deer endozoochory in Western New York: A year of pellet germination and analysis

K. Broz

Introduction

As ruminants with selenodont dentition, white-tailed deer (*Odocoileus virginianus*) are capable of consuming a wide variety of woody and herbaceous plant material. Within deciduous forests, their feeding habits vary seasonally based on food availability and nutritional needs (Christopher *et al.* 2014). During the winter, deer will eat dried leaves and browse-level woody stems. In the spring, deer preferentially feed on nitrogen-rich herbaceous plants and new-growth woody stems, and will continue to forage on them as plants mature during the growing season. Throughout the year, supplemental nourishment is gained from seeds, fruits, landscaping plants, and agricultural crops (Smith 1991).

This generalist diet exposes deer to many different plant species and habitats. Deer can then become a vector for seed dispersal through adhesion to fur (ectozoochory) or passage through the digestive tract (endozoochory). Endozoochory has evolved as a necessary step in germination for many species as stomach acid stratification can soften hard exocarps and break seed dormancy (Levine *et al.* 2012). In a review of 200 plant species and their vertebrate seed dispersers, the germination rate of 50% of consumed plants were impacted by ingestion, with ingestion increasing germination success approximately twice as often as hindering it (Traveset 1998). A seed in a fecal pellet is also already in a nutrient rich, moist environment,

further enhancing germination potential (Jaroszewicz and Piroznikow 2011). However, seed germination and long-term survival may be inhibited by the environment in which the pellet was deposited. Species that have specific abiotic requirements for light or moisture may not succeed if dropped in habitats that lack them (Mouissie *et al.* 2005).

Deer may disperse seeds because they are attracted to the fruit or seeds themselves or through inadvertent consumption from feeding on the palatable leaves of fruiting plants. Janzen (1984) noted that successful germination via endozoochory in livestock and wild ungulates is very common, yet most of the plants they consume (e.g. gramminoids) are not specifically adapted for this method of dispersal. If a seed is small enough to evade damage from mastication by a large herbivore and its seed-coat is hard enough to resist acid damage (an adaptation also suited for long-term dormancy in the environment or protection from insects), the seed may be able to survive passage through the ruminant gut (Myers 2004, Pellerin 2016).

Although the home ranges of deer vary seasonally and by sex, they cover territories of up to 4 km² (Webb *et al.* 2010). In fragmented, suburban habitats, deer encounter a wide variety of plants; shrubby edges of farm fields, landscaped neighborhoods, wetlands, grasslands, and forest interiors. Thus, deer have the potential to transport seeds into and out of these habitat types as they forage (Williams *et. al* 2007). Of particular concern are abundant non-native and invasive seeds originating from residential landscaping (Ward and Amatangelo 2018).

Myers (2004), Williams and Ward (2006), and others studied white-tailed deer endozoochory in the Northeast by collecting fecal pellet piles and germinating the pellets in greenhouses to determine seed viability after passage through the gut. They generated lists containing more than 50 species, which allowed researchers to better understand deer diet, native and invasive seed consumption, and how habitat and deer home range influences dispersal potential.

Objective

In Monroe County, 366, vouchered, non-native plant species are known to exist (Weldy *et al.* 2019). Of these plants, a suite of particularly invasive species threatens native plant communities, include the shrubs *Rosa multiflora* (multiflora rose), *Rhamnus cathartica* (buckthorn), and *Lonicera* spp. (honeysuckle); vines like *Celastrus orbiculatus* (oriental bittersweet); and herbaceous plants like *Alliaria petiolata* (garlic mustard). Concurrently, deer in the New York State Department of Environmental Conservation's Wildlife Management Units 8H and 8G, which encompass much of Monroe county in western New York, are overpopulated-- with deer habitat in the region considered some of "the most productive in the state" (Wasilco, 2018). Thus, my objective was to determine how white-tailed deer overabundance in western New York facilitates seed dispersal of native and invasive plants in the region. I hypothesized that deer consume the fruits of both invasive and native seeds and that of the seeds that survive the digestive tract, significantly more of them will germinate in high light conditions.

Methods

Study sites

I collected deer fecal pellet piles from three sites across Monroe County, New York: a mixed deciduous, coniferous forest at Mendon Ponds County Park in Honeoye Falls, NY (43.021875, -77.575868), a mixed deciduous, coniferous in Northampton Park in Brockport, NY (43.184192, -77.887207), and a deciduous forest in a designated Natural Area on The College at Brockport campus in Brockport, NY (43.208466, -77.959953). Each collection site was within 100 m of a road, adjacent to recreational lawns, and included a diverse overstory, high light edge habitats, and the presence of several invasive plant species common in western New York.

Pellet germination

I collected a total of 155 samples from three sites across 11 months in 2016 and 2017. I divided each pellet group into thirds and either stored them in a freezer or placed outside to germinate in potting soil filled pots. Two plots contained the pots—a sun plot on open grass and a shade plot under a beech-maple-basswood forest canopy. I protected pots from animal interference by building large, shallow planter boxes with a removable 1.27 cm mesh hardware cloth top. I also placed a monthly control pot containing just potting soil with the pellet groups. I recorded species and abundance of each plant as germination occurred.

Seed extraction

I thawed the stored third of each pellet pile and processed them in water for two to three minutes in a soil dispersion mixer equipped with a smooth-edge stirring

paddle. I then rinsed the slurry through a 1mm mesh sieve, until only undigested material remained, and dried it at room temperature. I then picked the seeds out of each sample and identified them to genus or species with visual reference guides and a dissecting scope (Martin and Barkley 1961, Montgomery 1977, Musil 1979).

Statistical Analysis

I performed a non-parametric Kruskal-Wallis test in Minitab 17 (Minitab 17 Statistical Software, State College, PA) to determine the difference in the number of seeds found among the collection months after normality of the dataset could not be attained through transformations. Percent germination of each species in each whole pellet pile was estimated by dividing the number of germinated seeds by the number of seeds found in one-third pellet pile multiplied by three.

Results

In the one-thirds portion of all pellet piles from which I extracted seeds, 652 seeds were found; of these, 606 were identifiable to species or genus (Table 1). The highest average number of native seeds found in pellet piles was in fall (September, October, and November), while the highest average number of non-native seeds found in pellet piles was in winter (December, January, February, and March) (Figure 1). Multiplying the average of what I found in the one-thirds portion of each pellet pile by three, the average number of seeds in each whole pellet pile was 11.4 (± 11.6). My Kruskal-Wallis test revealed no difference in the number of seeds found among the seasons grouped into growing season, fall, and winter (H-stat= 0.704, p=0.702).

In the pots, 105 plants from 17 different species with dispersal mechanisms suited for intentional or incidental ingestion germinated; 82.9% of these were in the sun plot while 17% were in the shade plot (Table 1). The only species that germinated in both the sun (N = 17) and shade plots (N = 18) was the native herb *Persicaria virginiana* (jumpseed), which was calculated to have a germination rate of 14.6% across both plots (Table 1). Fifty percent of all identified species that germinated or were found as seed were not native to North America. Two of the control pots sprouted *Artemisia vulgaris* (mugwort) and *Solidago canadensis* (Canada goldenrod), indicating that contamination from wind dispersal or potting soil must be considered in my analysis. In total, 98 individual plants comprised of 11 species with dispersal mechanisms suited for wind germinated. Excluding these species in the total number of plants that germinated in all pots, 107 plants were observed. The sun pots contained germinates of ten species not found as seeds in dissected pellets, and ten species found as seeds in dissected pellets did not germinate in pots (Table 1).

My study sites were two county parks, North Hampton Park and Mendon Ponds Park, and the Brockport Woods, a campus natural area, all of which contained plant communities impacted by invasive species. Based on germinates from pellet piles and the seeds extracted from pellet piles, North Hampton had a species richness of ten (five were non-native species), Mendon Ponds had a species richness of 11 (three were non-native species), and Brockport woods had a species richness of four (three were non-native species). Two species were found at all three sites; *Vitis riparia* (river grape) which had an 11.6% germination rate and *Trifolium pratense*

(red clover) which had a 17.5% germination rate. Across all three sites, the park with the most non-native seeds per pellet pile was Mendon Ponds Park, while North Hampton Park had the most native species per pellet pile (Figure 2). The Brockport Woods had the fewest seeds overall, and relative to the number of native seeds, the most within-park, non-native seeds per pellet pile. A non-parametric Kruskal-Wallis test revealed no difference in the number of seeds between the three sites (H-stat= 5.2037, p=0.074).

Discussion

Deer are capable of spreading native and non-native, viable seed across landscapes throughout the year. Even seeds without obvious adaptations for endozoochory were able to germinate after consumption by deer, mainly in the sun plots. As expected, deer are moving seeds of non-native species from backyards to natural areas. For example, *Panicum miliaceum* (proso millet), a common bird feeder seed, was found within five pellet piles from two sites and successfully germinated once in the sun plot. This non-native is not yet naturalized in New York (Werier 2017); however, because deer regularly access bird feeders, this increases the chances of it escaping into natural areas. Deer also ate the most non-native seeds during the winter months. The leaves of invasive species in the Northeast and Midwest persist later into the winter than native species (Fridley *et al.* 2012). Invasives also tend to fruit almost a month later and have a longer fruiting season than native species (Galliant *et al.* 2017). With less options in the winter, it is likely that deer feeding

preferences are less selective so an increased consumption what is available—more non-native fruits and seeds—may result.

Contrary to previous research, invasive *Lonicera* spp. did not germinate in my study although it was the most common seed found in pellet piles (Averill *et al.* 2016). Deer feed preferentially on *Lonicera* spp. and disperse its seeds; however, their viability decreases after gut passage (Myers 2004, Castellano and Gorchov 2013). In a study by Riley (2013), viability of *Lonicera maackii* (Amur honeysuckle) was lowest in the summer and highest in late October/November when fruits were brightest. In my study, *Lonicera* spp. were consumed only in July and August so it is possible that the deer had fed on unripe fruit and passed unviable seed in the summer. However, ripening times between *Lonicera* spp. do vary and I was unable to classify the seeds in my samples to species due to their similarities in appearance.

Although invasive species may be abundant in a landscape, deer may not contribute to the spread of some species. The invasive species *Berberis thunbergii* (barberry) was common in two of my study sites but did not germinate in pots nor was it found in pellet piles. Williams and Ward (2006) found that *B. thunbergii* did not germinate in fecal pellet piles despite visual confirmation of consumption by deer. Because *B. thunbergii* is a large, ovate seed, up to 1 cm in length and 5mm in width, it is possible that mastication destroy it; however, other species in my study with similar-sized seeds passed through the gut undamaged so it may have a weak seed coat. Conversely, seeds of the invasive shrubs *Rosa multiflora* (2 mm, semi-round) and *Lonicera* spp. (4 mm, flat) are small and contained in a cluster within a thin

exocarp. In my study, these were seen as intact seeds in fecal pellet piles and although they both successfully germinated in other studies (Myers 2004, Williams 2006, Castellano 2013), only one *R. multiflora* germinated in mine. Bird dispersal enhances germination of *R. multiflora* (White and Stiles 1992), however stomach and gut retention time is much lower in birds compared to ruminants so it is possible that deer dispersal inhibits the growth of this species.

The native grape vine, *Vitis riparia*, germinated 24 times in my study and was found in October to May pellets from all three sampling sites, indicating that its fruits may be an important winter and spring food for deer. This may also be the first experimentally derived evidence that viable seed of this nuisance native is dispersed by deer. Plant propagation protocols for *V. riparia* do not indicate a need for acid scarification for successful germination, indicating that ingestion is not a necessary part of this plant's biology to break dormancy (Hartmann *et al.* 1990); however, its metabolically expensive flesh entices dispersal through these means. Although a non-strangling vine, *V. riparia* can break tree limbs with its weight and smother light out of canopies. Thus, a forest with high deer density may experience an increase in vine related damage from dispersal in pellet piles, although *V. riparia* success after germination could also be limited by its palatable leaves and high light requirements.

Legumes are particularly suited for ruminant endozoochory, as they have hard seed coats that benefit from acid scarification (Kimura 2012). Three non-native clover (*Trifolium* spp.) successfully germinated from pellet piles in my study. One of them, *Trifolium pratense* (red clover), germinated from all three of my sampling sites and

had the highest germination rate of passed seeds in my study (17.5%). This same species of *Trifolium* germinated in Myers *et. al* (2004) and although not present in my study, *T. repens* (white clover) germinated in Williams and Ward (2006), and *Gleditsia triacanthos* (honeylocust) germinated in Guiden (2013). Because legumes fix atmospheric nitrogen via bacteria on root nodules, deer could be considered contributors to nitrogen fixation at various scales. An agricultural hectare of *T. pratense* and *T. repens* can fix more than 500 kg of nitrogen in a year (Carlsson and Huss-Danell 2003). Thus, a natural area with legume deposits from deer would experience changes in nutrient availability and therefore changes in competitive interactions between plants, favoring species less adapted to nutrient poor soil and possibly reducing diversity at the site. Of the three *Trifolium* spp. I found in my study, one is an annual and two are perennials so, after germination from pellet piles, there is a potential for persistence at the site and consequently, long-term soil modifications.

Germination overall was very low in the shaded, forested plot. This may indicate that deer endozoochory has a greater role in shaping the species composition of early successional habitats, shrublands, and grasslands than they do in forests, as the species they consume require higher light environments. In low-light forests, seeds in pellet piles may contribute more to dormant seedbanks. In new canopy gaps created by pest-facilitated tree die-offs of vulnerable tree species [i.e. *Fraxinus* spp. (ash) and *Tsuga canadensis* (Eastern hemlock)], endozoochorous seed deposited by deer may impose an inhibitory priority effect on the understory community during

gap succession, limiting forest recovery and causing a shift towards high-light community assemblages (Williams *et. al* 2008).

The native plant *Persicaria virginiana* was capable of germination in the sun and shade plots which is consistent with observations of wild populations. This plant frequently competes with the invasive *Vincetoxisum rossicum* (pale swallowwort) in forest understories and edges. However, *V. rossicum* is unpalatable (Rawinski 2008) so deer dispersal of *P. virginiana* through endozoochory may allow it to be more competitive with the invasive despite being browsed.

Some seeds identified in pellet piles did not germinate in the pots. *Rubus occidentalis* (black raspberry), *Prunus* spp. (cherry), and *Phytolacca americana* (pokeweed) were three of these. Seeds with hard endocarps and chemical germination inhibitors are common to *Rubus* spp., especially *R. occidentalis*, which has an extremely hard seed coat requiring acid, cold, and warm scarification that can still result in low germination rates (Wada and Reed 2001). Though the *R. occidentalis* seeds in my study were acid stratified after ingestion, it is likely they needed another freeze/thaw cycle to break dormancy. Similarly, *Prunus serotina* (black cherry), germinates after acid and cold scarification; however, this species can delay germination up to three years (Marquis 1975). In addition to acid and temperature, a high-light environment is an important factor for germination of *Phytolacca americana* (Farmer and Hall 1970). These may not have germinated in my study because the pellets did not have enough time or moisture to break down and expose the small, 3-4mm *P. americana* seeds to enough sunlight to trigger germination.

Summary

Deer can transport seeds of both native and invasive plants across a landscape throughout the year via endozoochory. The relative cover of invasive shrubs in the northeast have increased significantly over the last few decades. Records from 1938 indicate that *Lonciera morrowii*, *Rosa multiflora*, *Ligustrum vulgare*, and *Berberis thubvergii* were not present in surveys across Monroe County (Hunter and Mattice 1998). Deer populations have correspondingly increased since this time, and dispersal of invasive shrub species by deer endozoochory have likely contributed to this despite few shrub seedlings germinating in my study. Williams (2006) estimated that between 500-1000 exotic seeds could be dispersed by one deer in a single day. My data estimated that each pellet pile contained an average of 12.6 seeds. When multiplied by deer defecation rate averaged across a year [34 pellet piles per day (Rogers 1992)], individual deer in my study have the potential to move an average of 428 seeds per day. Although in my study viability after gut passage varied, the large quantity of seeds deer can consume and their long gut retention times increases their potential impact on plant community composition and the scale of their facilitated dispersal distance. Coupled with their ability to change soil and light regimes through legume accumulation and grape vine smothering of canopies, overabundant deer should be considered important contributors to Northeast and Midwest seed dispersal and ecosystem dynamics.

Future study

Although my outdoor seeding of deer pellet piles provided natural stratification of seeds in my study, wind-dispersed seed contaminants limited my ability to conclude that all seedlings emerging from pots were from seeds consumed by deer. These 11 species were not included in my results because of their potential as an artifact, despite the possibility that they survived gut passage. I also may have lost seeds to seed predators undeterred by my protective hardware cloth. Other problems included disturbance from branches falling onto the shaded plot, and deer stepping through the mesh cover in the winter, which warranted repairs. To avoid these issues, additional study should include freezer-induced cold stratification of pellets and subsequent greenhouse germination on a non-soil substrate. Much longer greenhouse studies would be beneficial as well to break dormancies of seeds with multi-year freeze/thaw requirements.

When extracting seeds from the pellets, the holes in the sieve I used to rinse the pellets was 1 mm in diameter, so it is likely that I could not detect smaller seeds with this method. This may account for some of the species that germinated and were likely ingested by deer, but were not seen as seeds in pellets (Table 1). A finer sieve could be considered; however, this may be difficult as undigested cellulose in the pellets clog small holes and prevents drainage. Additionally, larger monthly sample sizes are needed to provide insight on temporal changes in feeding changes, especially while spring ephemerals are seeding. Feeding trials of seed with captive

deer (similar to Mouissie *et. al* 2005) or domestic ruminants (i.e. goats) could provide viability estimates for select native and invasive species after gut passage.

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Tables

Table 1: Number of identifiable seeds (N) found in the one-thirds portion of each sample, the number of plants germinated (N) from the two-thirds portion of each sample, and the estimated percent seed germination of plant species in 155 white-tailed deer pellet piles collected from three sites (North Hampton (NH), Mendon Ponds (MP), Brockport Woods (BP), or control (CTRL) pots in Monroe County, NY. Asterisks indicate non-native species, estimated percent seed germination= N germinated/(N seeds*3).

Species	Common name	N seeds	N germ	Est. % seed germ	Germination plot	Origin site
<i>Persicaria virginiana</i>	Jumpseed	80	35	14.6	Shade/Sun	NH, MP
<i>Vitis riparia</i>	River grape	69	24	11.6	Sun	NH, MP, BP
<i>Persicaria pensylvanica</i>	Pennsylvania smartweed	61	12	6.6	Sun	NH
<i>Trifolium pratense</i> *	Red clover	19	10	17.5	Sun	NH, MP, BP
<i>Myosotis verna</i>	Spring forget-me-not	-	5	-	Sun	BP
<i>Trifolium aureum</i> *	Palmate hop clover	-	5	-	Sun	MP
<i>Plantago major</i> *	Common plantain	-	3	-	Sun	BP
<i>Oxalis corniculata</i> *	Creeping yellow wood sorrel	-	2	-	Sun	BP
<i>Plantago lanceolata</i> *	English plantain	-	1	-	Sun	BP
<i>Panicum miliaceum</i> *	Proso millet	100	1	0.3	Sun	BP
<i>Rosa multiflora</i> *	Multiflora rose	11	1	-	Sun	BP
<i>Trifolium hybridum</i> *	Aslike clover	1	1	-	Sun	NH
<i>Juncus tenuis</i>	Path rush	-	1	-	Sun	MP, BP
<i>Polygonum aviculare</i> *	Dooryard knotweed	-	1	-	Sun	BP
<i>Oxybasis glauca</i> *	Oak-leaf goosefoot	-	1	-	Sun	BP
<i>Geum canadense</i>	White avens	-	1	-	Sun	NH
<i>Panicum dichotomiflorum</i>	Smooth panic grass	-	1	-	Sun	MP
<i>Lonicera spp.</i> *	Honeysuckle	218	0	0	-	NH, MP
<i>Rubus occidentalis</i>	Black raspberry	18	0	0	-	NH, MP
<i>Silene antirrhina</i>	Sleepy silene	12	0	-	-	MP
<i>Phytolacca americana</i>	American pokeweed	5	0	-	-	NH, MP
<i>Prunus sp.</i>	Cherry	5	0	-	-	MP
<i>Parthenocissus quinquefolia</i>	Virginia creeper	3	0	-	-	MP
<i>Solanum dulcamara</i>	Bittersweet nightshade	1	0	-	-	MP
<i>Triticum aestivum</i> *	Common wheat	1	0	-	-	MP
<i>Malus pumila</i> *	Cultivated apple	1	0	-	-	NH
<i>Cerastium arvense</i> *	Field chickweed	1	0	-	-	NH
Germinated species likely artifacts of wind contamination						
<i>Solidago canadensis</i>	Canada goldenrod	-	27	-	Sun	MP, BP, CTRL
<i>Unidentified grass</i>	Unknown	-	25	-	Sun	NH, MP

<i>Artemisia vulgaris</i> *	Mugwort	-	12	-	Sun	NH, MP, BP, CTRL
<i>Unidentified herb</i>	Unknown	-	9	-	Sun	NH
<i>Populus deltoides</i>	Eastern cottonwood	-	8	-	Sun	BP
<i>Daucus carota</i> *	Queen Anne's Lace	-	5	-	Sun	NH
<i>Juncus tenuis</i>	Path rush	-	5	-	Sun	NH, BP
<i>Festuca filiformis</i> *	Hair fescue	-	3	-	Sun	NH
<i>Unidentified aster</i>	Unknown	-	2	-	Sun	MP
<i>Epilobium ciliatum</i>	Fringed willowherb	-	1	-	Sun	NH
<i>Symphotrichum pilosum</i>	Frostweed aster	-	1	-	Sun	MP

Figures

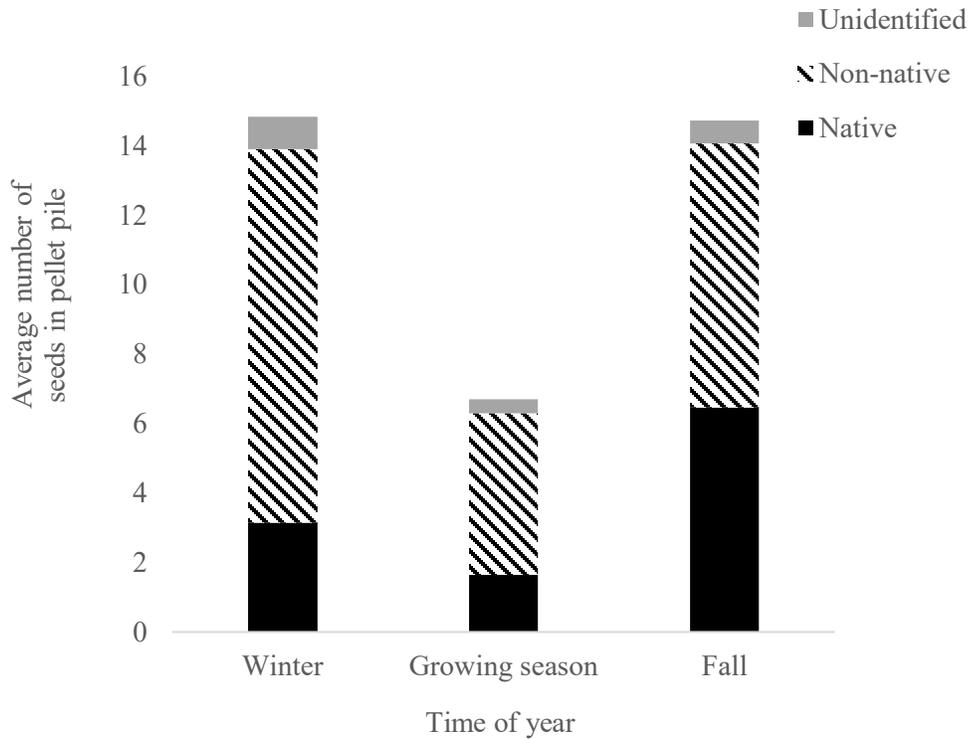


Figure 1: The average number of native, non-native, and unidentified seeds found in the one-thirds portion of pellet piles multiplied by three collected across three seasons—winter (December, January, February, March), growing season (April, May, July, August), and Fall (September, October, November) from three sites in Monroe County, New York.

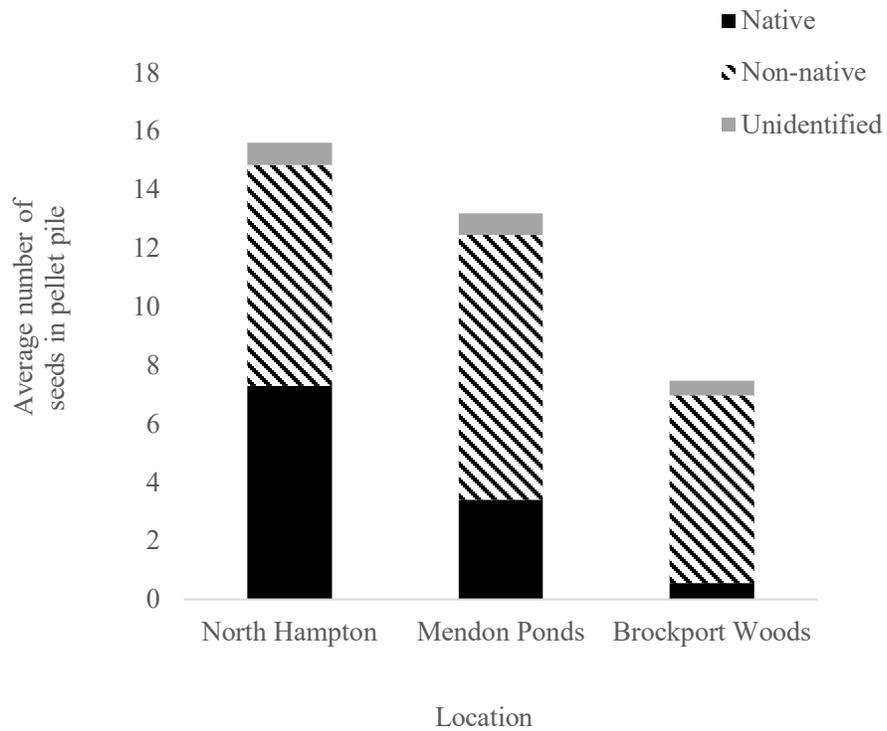


Figure 2: The average number of native, non-native, and unidentified seeds found in the one-thirds portion of pellet piles multiplied by three collected across three sites in Monroe County, New York.