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DEER OVERABUNDANCE IN THE PIEDMONT OF NEW JERSEY:

IMPLICATIONS FOR OLD FIELD SUCCESSION

By

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ABSTRACT OF THE THESIS

Deer Overabundance in the Piedmont of New Jersey: Implications for Old Field

Succession

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Densities of white-tailed deer, *Odocoileus virginianus*, in New Jersey have increased dramatically since the 1970s. Selective browse of hardwood tree species by overabundant deer has become problematic and can result in degraded secondary forests with diminished biodiversity. This thesis investigates the impact of overabundant deer browse on post agricultural succession communities related to three distinct plant assemblages responsible for driving succession: aboveground vegetation, the seed bank, and seed rain. The Hutcheson Memorial Forest Center (HMFC) in Somerset County of the New Jersey Piedmont served as the study location. Within HMFC are two old fields released from agriculture: the first field released in 1967 and the second field in 1984, each with permanent plots open and exclosed to deer that were installed in 1984. The goal of the first chapter of this thesis was to determine changes in aboveground vegetation of released agricultural fields over time and how the successional trajectories of the released fields change in presence of increased deer density. To do this, historic vegetation data collected in the 1990s was compared to 2017 data. Permutational multivariate analysis of

variance (PERMANOVA) and nonmetric multidimensional scaling (NMDS) were used to investigate change over time. Linear mixed-effects models and ANOVA determined differences in cover between hardwood tree species and *Juniperus virginiana* (JUVI) between fields and plot treatments over time. Accelerated Piedmont succession was only observed in exclosed plots that received fencing immediately upon release from agriculture. Delayed Piedmont succession was observed in plots open to deer. The objective of the second chapter was understanding potential impacts of deer browse cascading from aboveground vegetation to the other two assemblages, the seed bank and seed rain. The focus of this chapter was to examine changes in tree species frequency between plot treatments and fields across all three assemblages. Analysis using NMDS and PERMANOVA determined a difference in average community composition of tree species relative abundance caused by field age across all three assemblages, while differences caused by plot treatment was only found in the aboveground vegetation. Spearman correlations determined that deer browse, similar to predation and disturbance, acts as a local, plot-scale process that shape tree species frequency in aboveground vegetation. Seed rain did not respond to deer browse and instead persisted in the presence of deer. Communities within each field were largely driven by successional stage/field age, a coarser, patch-scale process. Field age played a strong role in shaping communities largely due to the difference in timing of exclosure installation after each field's release from agriculture. The focus of future research should include larger, more persistent samplings of each assemblage type that provides a better comprehension of interactions among the different assemblages.

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Chapter 1

Introduction

Overabundance of white-tailed deer (*Odocoileus virginianus*) became problematic in the eastern United States starting in the latter half of the 20th century (Côté et al., 2004). After near extirpation in the 19th century (Rooney, 2001), hunting game laws and conservation measures were put in place (Shorger, 1953; McShea et al., 1997). European settlement also resulted in many natural predators of deer being extirpated from eastern North America (Rooney, 2001). Deer populations, now with limited predators, began to increase exponentially and flourish in habitats that had been logged or converted to agricultural fields, creating young, nutrient-rich, fragmented, forest stands. (Rooney, 2001). As human populations increased, so did habitat for the deer, increasing carry capacity of the species (Rooney, 2001). Increased carrying capacity has led to historic highs in deer densities of over 15 deer per square kilometer in states like New Jersey (Kelly 2019). Deer overabundance has also been documented in Pennsylvania, Maryland and Virginia, with estimates of over 60 deer per square km in some areas (Walters et al., 2016).

Particularly, in temperate deciduous forests in the northeastern United States, white-tailed deer are ecosystem engineers (Baiser et al., 2008; Aronson and Handel, 2011). Continuous browse of forest landscapes can cause exclusion or limited regeneration of species in plant communities (Watson, 1983). Selective browse by deer and other small mammals causes a decrease in species richness and a decrease in forest

community biomass of preferred palatable species (Crawley, 1989; Gutierrez et al., 1997; Horsley et al., 2003). High browse pressure changes woody species composition to be dominated by unpreferred species that are not affected by herbivory (Crawley, 1989; Gutierrez et al., 1997; Horsley et al., 2003). Browsing has both indirect and direct effects on plant communities. Indirect effects include the alteration of nutrient, space, and light availability. Direct effects are seen through selective foraging that impacts species differentially (Huntly, 1991; Hobbs, 1996).

Selective browse also delays the establishment of woody species and allows the extended dominance of herbaceous species during succession (Inouye et al., 1994). The impacts of herbivores varies with successional stage of the community (Armesto and Pickett, 1985). White-tailed deer thrive in post-agricultural habitats where they selectively browse tree seedlings, directly influencing the abundance and dispersal of seeds and potentially altering seed bank composition (DiTommaso et al., 2014; Loomis et al., 2015). Deer have also been shown to largely influence successional trajectories during the stand initiation phase of a forest by directly impacting patterns of relative abundance and vegetation dynamics (Côté et al., 2004). Increased levels of deer browse are also likely to delay succession, slowing the rate of canopy closure (DiTommaso et al., 2014).

My objective was to understand how deer influence the successional trajectories in the Piedmont physiographic region of New Jersey, a region heavily impacted by overabundant deer. To do this, I used a series of enclosure/open plots that were established in the 1980s at Hutcheson Memorial Forest Center (HMFC) in Somerset County, New Jersey. I examined community composition changes in open and enclosed

plots of two different aged secondary successional fields at HMFC to determine how deer alter the outcome of succession. HMFC is also home to one of the longest-running succession studies, the Buell-Small Succession Study (BSS) providing a historical context to compare to open plots. If deer selectively browse upon preferred hardwood species, open plots are expected to show a compositional change compared to their exclosed plot counterparts. This change will likely result in a delayed Piedmont successional trajectory that is transitioning slower through successional stages dominated by tree species.

Hypotheses

I predict that composition of differing plot treatments (open and exclosed) to be most similar immediately after plot installation in 1984, while overall composition between fields will remain distinct. Conversely, as succession progresses, I expect differing treatment communities to diverge, while overall composition of each field converges. Exclosed plots will likely have higher composition of hardwood species as they are free from browse pressure of deer. I suspect that higher composition of hardwood species in exclosed plots will likely result in a more closed canopy within these plots.

If these fields follow traditional successional trajectories, herbaceous percent cover is expected to decrease over time, while woody tree species percent cover will increase in both fields (Bard, 1952; Meiners et al., 2007). I suspect that if each plot was installed immediately after release, the older 1967 field's exclosed plots would have the highest percent cover and numbers of hardwood species of the four treatments. Since the 1967 field did not receive fencing until 17 years after release, I believe browse pressure

has likely shaped both open and exclosed plot communities in this field by selectively browsing out more palatable hardwood seedlings prior to plot installation. Timing of browse, related to plot installation after agricultural release, will heavily influence a community. Specifically, I believe plots that have been free from deer since release will exhibit natural succession patterns or even expedited succession. Alternatively, plots that have suffered from deer browse the longest and immediately after release will likely reflect a delayed succession characterized by slower canopy closure and communities composed largely of unpreferred and/or unpalatable tree species.

Methods

Study Site

Vegetation communities were sampled at Rutgers University's Hutcheson Memorial Forest Center (HMFC) in Somerset County (40°30'N, 74°34'W), New Jersey. The use of HMFC as a model system to study successional differences among old fields is important as it provides a chronosequence of successional forest communities and an uncut old-growth forest, Mettler's Woods (Bard, 1952). Soils at HMF are of Piedmont origin and typically include shallow, clayey, red soils and contain fragments of shale (Ugolini, 1964). However, HMF soils are not entirely derived from shale like many Piedmont soils. Instead, gravel, from natural glaciation, provides greater thickness and a deeper brown color than most Piedmont soils (Ugolini, 1964). Soils of HMFC also vary throughout the forest with changes in moisture, slope, and elevation.

The old-growth forest of HMFC, the projected successional endpoint, is a mixed-oak/hickory deciduous forest dominated by several *Quercus* species. Species of *Carya*, *Fraxinus*, and *Acer* were also present. The understory was once dominated by *Cornus florida* and *Viburnum acerifolium* and lowland forest areas consisted of a *Fraxinus americana*, *Acer rubrum*, and *Nyssa sylvatica* canopy with an understory of largely *Lindera benzoin* and *Viburnum dentatum* (Frei and Fairbrothers, 1963). Evidence of these species in today's forest exist but are less common because of changes in the composition due to species loss and additions from invasions by: *Rosa multiflora*, *Berberis thunbergii*, *Lonicera* spp., *Ailanthus altissima*, and *Aralia spinosa* among others (Meiners et al., 2007).

Experimental Design.

Two successional fields were sampled in this study. The first field, hereafter referred to as the 1984 field, was last plowed and disked in 1984 and left fallow. The second field, hereafter referred to as the 1967 field, was plowed and disked 17 years earlier and left fallow. Each field is approximately 0.5 ha. Plots were established in each of the fields in 1984 with no established vegetation in the 1984 field, while the 1967 field had vegetation that established for 17 years (Figures 1.1 and 1.2). A total of eight plots, 5m x 5m in size, were established in each of the fields; of these, four were exclosed plots and four were open plots. The plots were centralized within each field and separated by no less than 10m (Cadenasso et al., 2002). Exclosed plots were built using sheet metal buried 0.5m below ground to 1m above soil surface. Additionally, wire fencing and wood frameworks were used to create the plots and exclude cottontail rabbits (*Sylvilagus floridanus*),

meadow voles (*Microtus pennsylvanica*), and wire mesh to exclude white-tailed deer (*Odocoileus virginiana*). Wooden corner posts and framing were used in construction of open plots to simulate possible perching that might occur in the exclosed plots. No fencing or sheet metal were used for the open plots to allow for unimpeded movement of herbivores within the plots. During the current study period, there were signs of small mammal browse in the exclosed plots, but deer still remain absent from these plots. Signs of both small mammal and deer browse are present in all open plots

In 1986, each plot was planted with 20 seedlings each of *Acer rubrum*, *Juniperus virginiana*, and *Cornus florida*. in randomly arrayed groups of six seedlings. These seedlings were planted to quantify the experimental test role of mammalian herbivores during old field succession (Cadenasso et al., 2002).



Figure 1.1. Study site and location of 1967 field and 1984 field within HMFC.

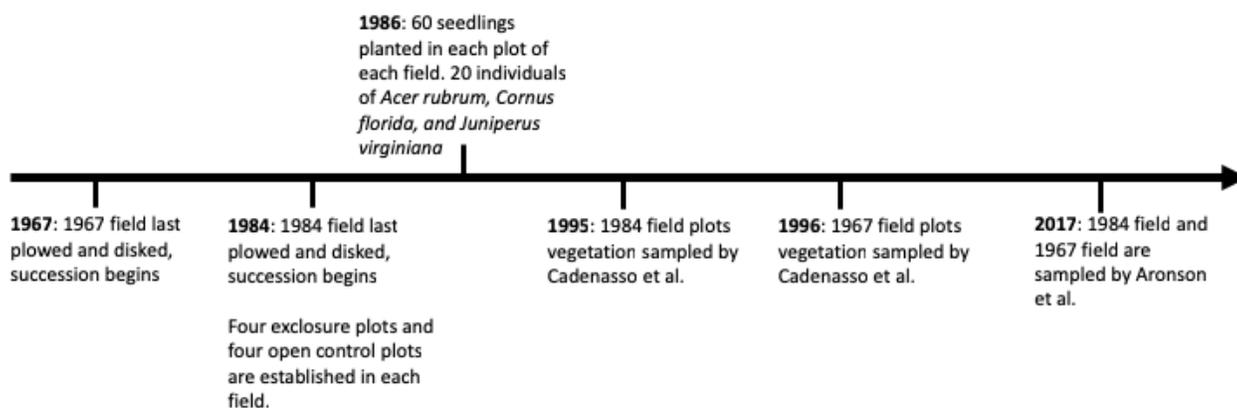


Figure 1.2. Experimental timeline and history of successional fields.

Vegetation data was collected in 1995 in the 1984 field, 1996 in the 1967 field, hereafter referred to as the 1990s sampling, and a second time in 2017 for both the 1984 field and the 1967 field, hereafter referred to as the 2017 sampling (Figure 1.2).

Vegetation data was collected using four, 0.5m x 2.0m, subplots established by Cadenasso et al. 2002 within each of the 16 plots throughout the two fields. During the first sampling by Cadenasso et al. in the 1990s, percent cover data of each species in the form of all strata together (herbaceous, shrub, canopy) was recorded in each of the subplots. During the 2017 sampling, percent cover of each species was recorded in each of the subplots with data for each strata separated. Strata was categorized as: groundcover, seedlings, saplings, and canopy trees. Seedlings consisted of all tree species

<1m in height, saplings were >1m height but <8cm DBH, and adults were >8cm DBH. Seedling, sapling, and adult frequency were also recorded during the 2017 sampling both inside the subplots and within the plots.

Light measurements were recorded during the month of the 2019 summer solstice in each of the 16 plots using a LICOR LI-250A light meter and 191R quantum sensor. Light measurements were recorded in 15 second averages. A measurement was recorded one meter from the plot perimeter for each cardinal direction and within the center of the plot over two different days with similar open-sky light levels. Measurements were conducted within two hours of solar noon to determine difference in canopy closure between open and exclosed plots caused by canopy tree species. The quantum sensor was held at 1.37 m off the ground to limit shading on the sensor from herbaceous and shrub layers within each plot.

Data analysis

Species percent cover collected in the subplots during both the 1990s and 2017 was used to determine relative abundance of each species for each sample year. Relative abundance was then used to understand community change over time via NMDS ordination using the vegan package in R version 3.5.1. Permutational multivariate analysis of variance (PERMANOVA) of compositional data was run to determine if differences in community composition were caused by either sample year, field, plot treatment type, or a combination of the three.

Difference in light intensity between treatments was analyzed separately between fields using a Wilcoxon rank test to determine differences between open and exclosed plots.

Percent cover of herbaceous species and woody species were determined separately for each plot during each sample year. These percent covers were then used in a Linear Mixed-Effects Model to understand change in herbaceous species percent cover and woody tree species percent cover between the two sample periods. Linear Mixed Effects Models were created using the lme4 and lmerTest packages in R where plots were random factors within the models. As this experiment only contains one replicate of each the 1967 field and the 1984 field, precautions were taken to avoid pseudoreplication errors. When possible, Linear Mixed-Effects Models were created with the data to correct for limited replicates of each field. When Linear Mixed-Effects Models could not be used, fields were analyzed separately to prevent confounding error that would arise from pseudoreplication when using field as a factor.

Percent total cover of native species in each sample year was calculated and compared with 50 years of percent total cover of native species from the reference Buell Small Succession Study (BSS) (Meiners et al., 2015). BSS study fields used were averaged data of four fields composed of 48 similar 2m x 0.5 subplots released in 1964. These fields provided data points of native species succession prior to extreme deer overabundance.

Linear Mixed-Effects Models of hardwood tree species and *J. virginiana* (JUVI) percent cover were created to determine difference in hardwood tree percent cover and *J. virginiana* percent cover between fields and plot treatments.

Two one-way analysis of variance tests (ANOVA), one for each field, were performed separately to determine differences caused by plot treatment on proportion of seedlings and saplings palatable to deer within plots during the 2017 sample year. Proportion of seedlings and saplings palatable to deer was determined from numbers of seedling and sapling individuals within each respective plot. Of the 16 tree species present across all plots in 2017, three species were determined to be more unpalatable to deer using the U.S. Forest Service's Fire Effects Information System (USDA FEIS, 2019) online database. These three species included: *Ailanthus altissima*, *Ilex opaca*, and *J. virginiana*.

Results

Community Divergence

In the 1990s, composition of the two fields differed (Figure 1.3A), but there was little difference in composition between open and exclosed plots. By 2017, the composition of the two fields had converged (Figure 1.3B), but the composition between open and exclosed plots had become more distinct (Figure 1.3A). Compositional differences occurred by sample year, plot treatment type, and field, independent from one another and also for an interaction of sample year and field (PERMANOVA all $p < 0.01$). *J. virginiana* was a uniformly dominant species for the 1967 field in both treatments (blue and yellow ellipses of Figure 1.3A). During the 2017 sample year, *A. rubrum* and *C. florida* were central species in both open and exclosed plots of the 1984 field (red and

green ellipses of Figure 1.3B) while *J. virginiana* remained central for both treatments of the 1967 field (blue and yellow ellipses of Figure 1.3B).

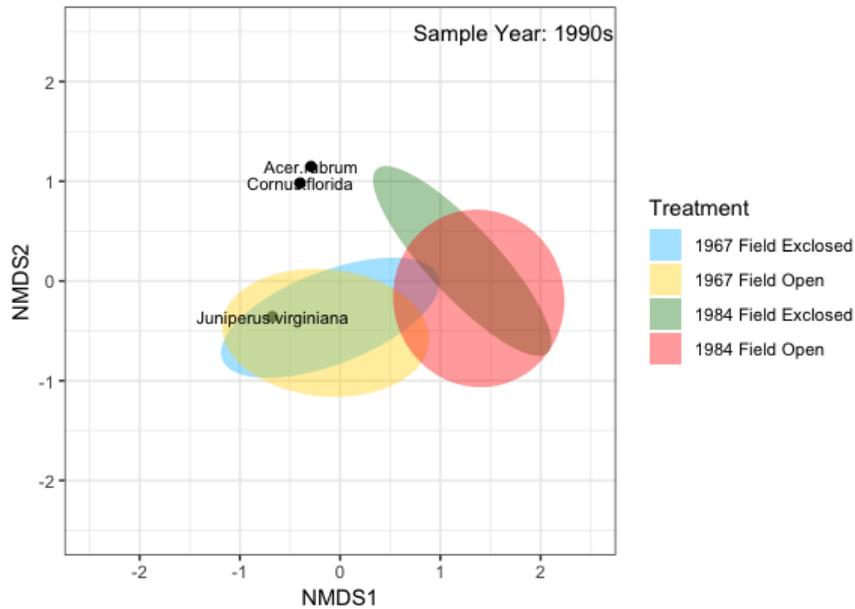


Figure 1.3A. NMDS ordination of percent cover for four treatments during the 1990s sample year. Four treatments include: 1967 field exclosed plots (n=4, blue ellipse) 1967 field open plots (n=4, yellow ellipse), 1984 field exclosed plots (n=4, green ellipse), and 1984 open plots (n=4, red ellipse) for the 1990s sample year. Tree species planted in 1986 are indicated within the ordination, stress=0.109.

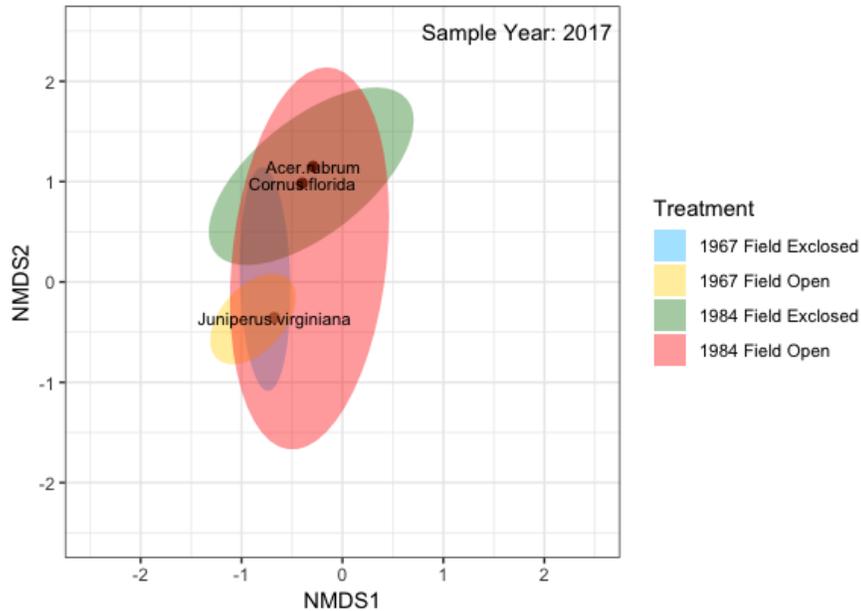


Figure 1.3B. NMDS ordination of percent cover for four treatments during the 2017 sample year. Four treatments include: 1967 field exclosed plots (n=4, blue ellipse) 1967 field open plots (n=4, yellow ellipse), 1984 field exclosed plots (n=4, green ellipse), and 1984 open plots (n=4, red ellipse) for the 2017 sample year. Tree species planted in 1986 are indicated within the ordination, stress=0.109.

Light Measurements

Light levels were significantly higher among open plots compared to exclosed plots of the 1984 field (Figure 1.4; Wilcoxon rank test, $W=16$, $p<0.05$). Light levels showed no significant difference among plots within the 1967 field likely due to several gaps created from uprooted and snowbent trees in two of the four exclosed plots of the 1967 field.

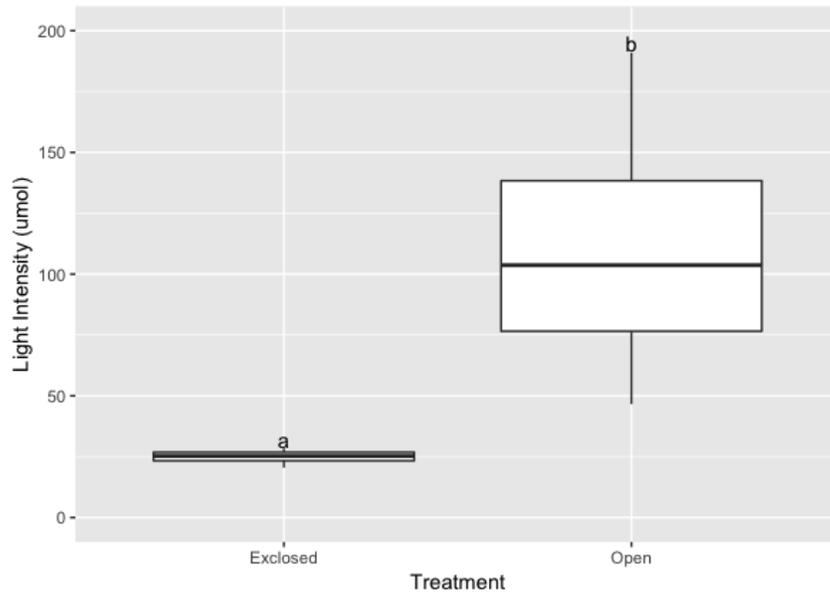


Figure 1.4. Light levels of 1984 field between grouped open and exclosed plots. Each box plot represents grouped plot treatments for the 1984 field, n=4 open plots and n=4 exclosed plots. Lowercase letters indicate difference among plot treatments.

Herbaceous to Woody Percent Cover Comparison Through Time

For both fields combined, total herbaceous cover significantly decreased from 1990s to 2017 (Figure 1.5; Linear Mixed-Effects Model; $F_{1,15}=26.404$, $p<0.001$). Total woody tree species percent cover significantly increased from 1990s to 2017 (Figure 1.5; Linear Mixed-Effects Model; $F_{1,30}=35.893$, $p<0.0001$).

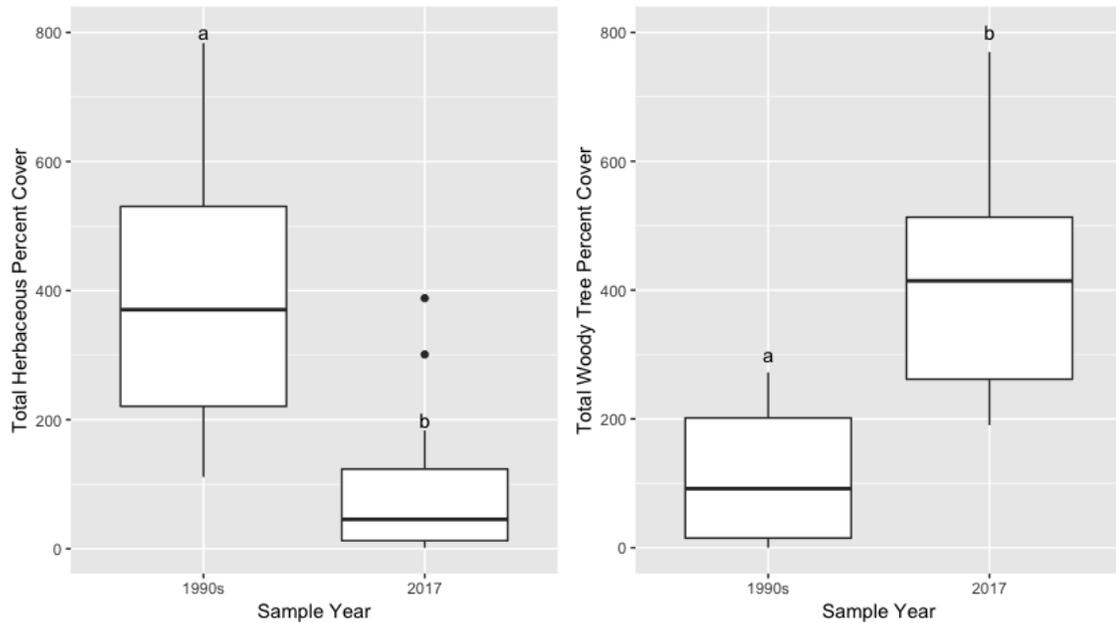


Figure 1.5. Change in both herbaceous and tree species percent cover between sample years for all plots. Each box plot represents all plots across the two fields, $n=16$. Lower case letters indicate significant difference among sample years.

Comparison of Open Plots to Reference Buell Small Successional Fields

The BSS fields showed increasing native cover over time (Figure 1.6). The increase in native cover of open plots in the 1967 field ($\beta=0.14677$) was more similar to the BSS plots ($\beta=0.30074$) than of the decreased native cover of open plots of the 1984 field ($\beta=-0.95708$).

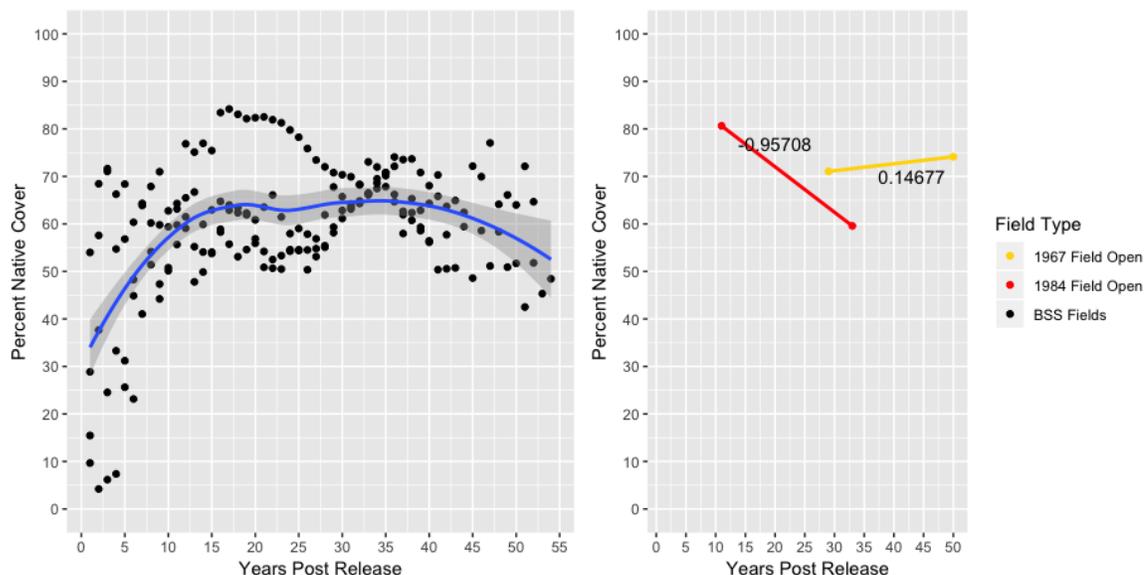


Figure 1.6. Change in percent native cover of three field types. Field types include: 1967 field open plots (four plots each with four subplots, yellow line), 1984 open plots (four plots each with four subplots, red line) and plots of four BSS fields (48 subplots per field, gray line) from the reference Buell Small Succession Study. Lines indicate each field community's percent native cover years post agricultural release with values indicating the slope of each line.

Hardwood Tree Species and Juniperus virginiana

For both fields combined, hardwood tree percent cover of all strata was significantly higher in exclosed plots than in open plots only in 2017 (Figure 1.7, Linear Mixed-Effect Model; $F_{1,12}=10.2560$, $p<0.01$). For both plot treatment types combined, *J. virginiana* (JUVI) percent cover in all strata was significantly higher in the 1967 field for both sample years (Figure 1.7, Linear Mixed-Effect Model; $F_{1,12}=0.5079$, $p=0.489673$, post-hoc Tukey test, $p<0.001$). Hardwood tree species percent cover was greatest in exclosed plots during the 2017 sample year for both the 1967 and 1984 fields (Figure 1.7).

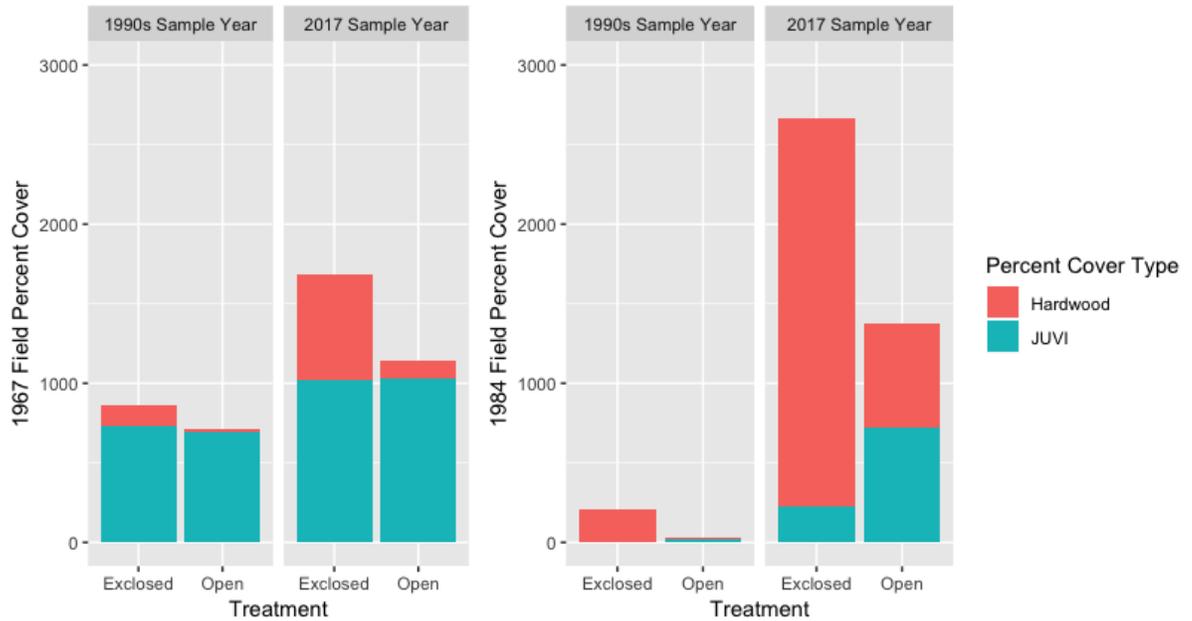


Figure 1.7. Comparison of percent cover of *Juniperus virginiana* (JUVI) and hardwood tree species across sample years, fields, and plot treatment types.

Hardwood tree species percent cover was significantly higher among 1984 field exclosed plots during the 2017 sample year compared to any other treatment during either sample year (Figure 1.8, Linear Mixed-Effect Model, $F_{1,12}=3.3888$, $p<0.001$).

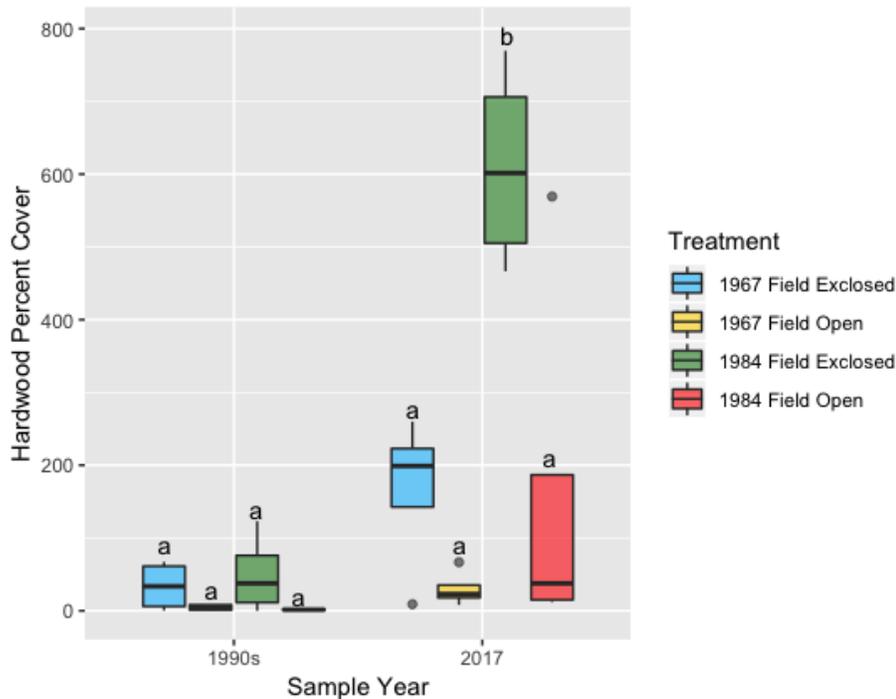


Figure 1.8. Hardwood tree species percent cover of all plots for four treatment groups. Treatment groups include: 1967 field excluded plots (n=4, blue box) 1967 field open plots (n=4, yellow box), 1984 field excluded plots (n=4, green box), 1984 open plots (n=4, red box) for both the 1990s and 2017 sample years. Lowercase letters indicate significant differences among treatments and sample years.

Species Palatability

Within the 1984 field during the 2017 sample year, mean proportion of seedlings and saplings palatable to deer was significantly greater among excluded plots compared to open plots (Figure 1.9; One-Way ANOVA, $F_{1,6} = 38.32$, $p < 0.001$). Mean proportion of palatable species in the 1967 field did not significantly differ between open and excluded plots during the 2017 sample year.

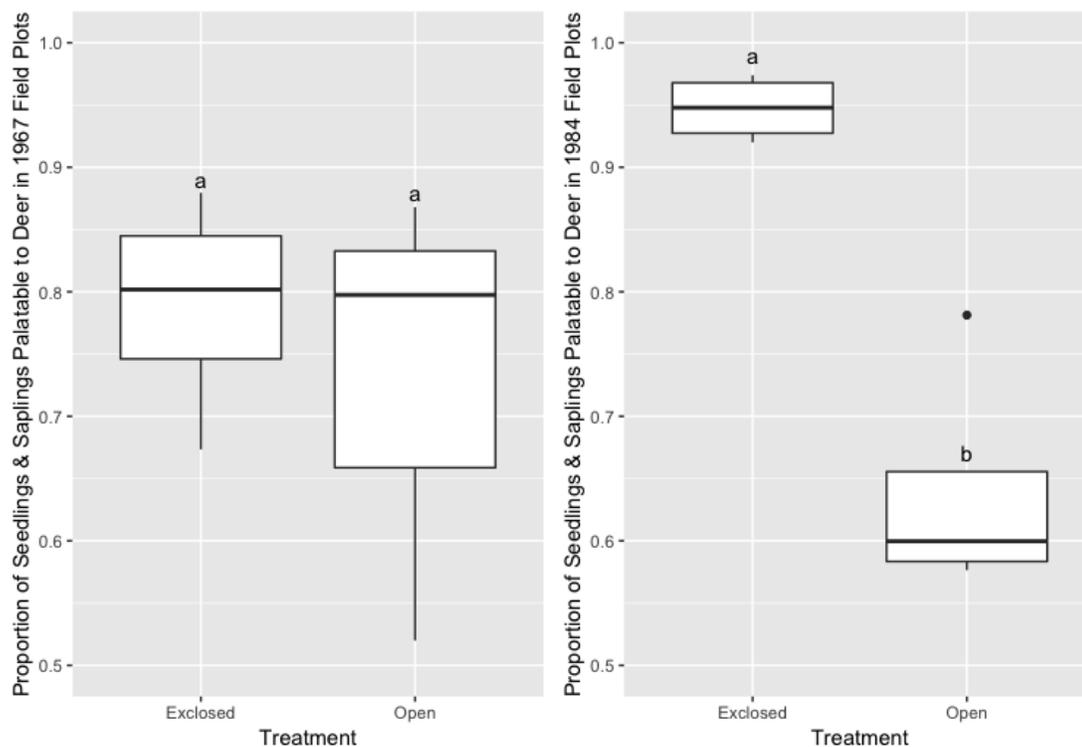


Figure 1.9. Proportion of palatable seedlings and saplings by plot treatment and field for the 2017 sample year. Each box plots represents four plots of the specified plot treatment type. Lowercase letters indicate significant differences among treatment and fields.

Discussion

Change in successional trajectories from deer overabundance was evident through several patterns. First, I found compositional differences in the plant communities of different sample years, fields, and plot treatments (open and exclosed) independent of one another. This compositional difference was also detected in communities with interactions of sample year and plot treatment variables as well as sample year and field variables. Second, an increase in percent native cover over time of the 1967 field open plots, and a decrease in percent cover over time in the 1984 field open plots is characteristic of

browse influence on succession (Knight et al., 2009). Decreasing native cover through time in the more recently released field is indicative of pressure put on these regenerating communities by high deer densities and invasive species (Knight et al., 2009; Meiners et al., 2015). Third, percent cover of hardwoods related to percent cover of *J. virginiana* serves to illustrate a successional fields position in the Piedmont successional timeline. Fields that are dominated by *J. virginiana* percent cover are at an earlier stage in the Piedmont succession timeline based on accepted theory and rate of Piedmont succession (Keever, 1950; Bard, 1952; Buell et al., 1971). Lastly, differences in the proportion of palatable seedlings and saplings to deer between open and exclosed treatments shows the impact that deer have on community composition and serves to illustrate deer as a main influence on successional dynamics. Deer densities have been strongly correlated with invasive species abundance and total tree seedling abundance (Russel et al., 2017), a trend observed throughout HMFC.

Although our data suggests notable changes in community composition due to deer overabundance, it is important to note pseudoreplication of fields in our study. As each field only had one replicate, a community's composition and change must be interpreted loosely as each field's age is confounded with location of the field. As each plot treatment, open and exclosed, had multiple replicates within a field, community composition resulting from plot treatment can be interpreted in a more robust manner.

Ecological Succession Patterns

The New Jersey Piedmont is described as having similar trends of succession to the Southern Piedmont in North Carolina (Bard, 1952). In the North Carolina Piedmont at

Duke forest, dominance of herbaceous species generally lasts until the 20th year of succession when dominance transitions to early conifer species (Keever, 1950; Office of the Duke Forest, 2019). This study showed similar trends within both successional fields at the HMFC. In the 1990s, herbaceous cover of both HMFC fields was greater than during the 2017 year. Conversely, during the 2017 sample year, tree species cover was greater in both fields than during the 1990s sample year.

My results also indicate that palatability of individual species is an important factor driving successional rates and outcomes in communities that experience extreme deer browse pressure. By 2017, seedlings and saplings palatable to deer were greater in exclosed plots in the 1984 field. Seedlings and saplings most palatable to deer are typically hardwood species that dominate in the latter half of Piedmont succession especially in the oak/hickory forest-type group (USDA FEIS, 2019; McWilliams et al., 2018). At the HMFC, hardwood trees such as *A. rubrum* and *C. florida*, while better competitors, have much higher palatability than *J. virginiana* (USDA FEIS, 2019).

As mentioned previously, all plots in both fields were planted in 1986 with seedlings of *A. rubrum* and *C. florida*, early hardwood species in Piedmont succession (Buell et al., 1971). During the 1990s sample, little to no change of hardwood species percent cover was detected between open and exclosed plots. By 2017, 30+ years after plot installation, exclosed plots had higher cover of hardwood species than open plots. These results demonstrate the accelerated capability of a Piedmont successional community to transition from a *J. virginiana* dominated stand to hardwood dominance when released from pressure of deer browse and supplemented with planted hardwood species. Although not originally intended to do so, planted hardwood seedlings have provided a

means of forest restoration and have manipulated succession by preventing an arrested phase in succession of these communities (Mansourian et al., 2005).

The effectiveness of deer exclusion provides a necessary advantage to hardwood species that is otherwise lost from browse pressure (McWilliams et al., 2018). Not only are planted hardwoods helping to prevent arrested succession, they are accelerating succession. This trend was not observed within the 1967 field. This is almost certainly due to the 17-year time lag between the field's release from agriculture in 1967 and exclosed plot installation in 1984. During this 17-year period, it is likely that browse pressure shaped this field, resulting in the exclosed treatment plots having less of an impact in protecting hardwood species planted in 1986. Hardwood species in these plots were likely scarce at the time of plot installation in 1984 due to browse between 1967 and 1984. The early succession hardwood species planted in 1986 were likely outcompeted by unpalatable species like JUVI that had established in the 17+ years since release in 1967. A similar interaction has been documented between *Juniper occidentalis*, and its early succession hardwood competitor *Populus tremuloides* in western shrub steppe communities (Miller et al., 2000).

Although deer populations were approximately four deer per km² in 1972, populations had increased by 1984 (Kelly, 2019). Deer density of over four deer per km² negatively influence hardwood seedling establishment and hardwood seedling numbers (Russel et al., 2017). This could result in limitation or exclusion of species such as *A. rubrum* and *C. florida*, species that normally appear as saplings by the tenth-year post release (Bard, 1952). By 1986, the year when 60 seedlings were planted in each plot, seedling populations of the exclosed plots of the 1967 field were likely comprised

exclusively of unpalatable species such as JUVI. This would result in a competitive disadvantage of hardwood species *Acer rubrum* and *C. florida* planted at the same time. *A. rubrum* and *C. florida* seedlings planted in the exclosed plots of the 1984 field likely endured less competition than planted species of the exclosed plots in the 1967 field due to limited establishment of competing JUVI vegetation in the 1984 field plots.

Successional Trajectories

The four fields used from the BSS study were released in 1964 (Meiners et al., 2007) and were open to deer until 2015, when two of the four fields were included in HMFC's old growth deer fencing initiative. Tree seedlings in all fields have naturally established, an important difference from the 1986 seedling planting in my study fields. The four BSS fields will therefore serve as a control for old field succession free from human interference and provide an old field successional trajectory before and after both increasing deer densities and proliferation of invasive species (Meiners et al., 2015).

Similarities between the native cover of 1967 field's open plots and the BSS plots can be attributed to similar release dates and similar browse pressure experienced during regeneration after release. A twofold increase in deer population density in New Jersey between the year 1972 and 1988 (Kelly, 2019), along with increased introduced species during this time is responsible for the sharp decline in percent native cover seen in the 1984 field's open plots between the 1990s and 2017 sampling. Whether proliferation of invasive species occurs because of their competitive advantage or because of selective avoidance by browsing of deer is likely undiscernible (Baiser et al., 2008).

Changes in successional trajectories related to turnover from one successional phase to another can be attributed to increasing deer densities, difference in enclosure time after field release from agriculture, response of planted hardwoods to competition of established vegetation, and differences between open and exclosed plot treatments. Specifically, at HMFC, planting hardwoods that experience little to no browse pressure accelerates successional trajectory to reach a hardwood dominated community earlier in succession. Alternatively, if deer are allowed to selectively browse on early establishment of hardwoods, additional plantings of hardwoods and delayed exclosure of these communities after agricultural release will have a diminished impact on successional outcome. Instead, selective hardwood browse of deer will result in delayed succession and a prolonged conifer phase dominated by *J. virginiana*. Prolonged *J. virginiana* dominance will occur with other canopy dominants that are browse resistant rather than shade tolerant as normally seen in succession (Bard, 1952; McWilliams et al., 2018). Deer densities have reached a historic high, increasing browsing pressure of communities have yielded large changes in community composition that unfavorably alter successional trajectories.

A New Model for Succession

Exposure to extreme deer densities, like those witnessed in present day New Jersey, appear to be causing an extended phase of conifer dominance and an overall delay in stage turnover during Piedmont succession at HMFC. This stage begins around year 30 of succession, where a regenerating forest stand becomes conifer dominant and likely persists as a conifer dominant stand well into year 70+ of succession when early

dominance of hardwoods would normally begin (Figure 1.10B). Conversely, with supplemented hardwood plantings early after agricultural release and immediate release from browse pressure via exclosure, we witness accelerated succession within the 1984 exclosed plots. In accelerated succession, conifer dominance is brief and transition to early hardwood species dominance occurs much earlier (Figure 1.10C).

To illustrate these concepts, I created altered successional trajectories (Figures 1.10B and 1.10C) of the traditional piedmont succession published by the Office of the Duke Forest (Figure 1.10A).

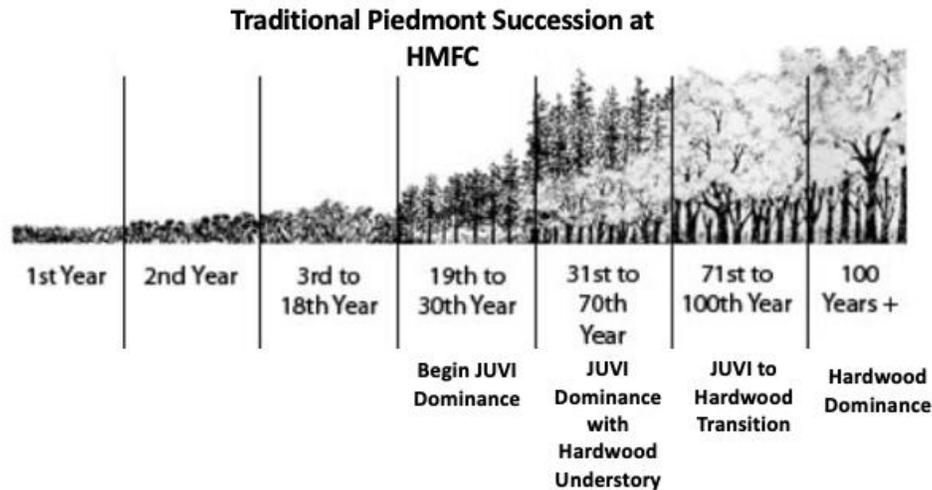


Figure 1.10A. Traditional Piedmont succession. (Office of the Duke Forest, 2019). Adapted to fit the Piedmont of New Jersey.

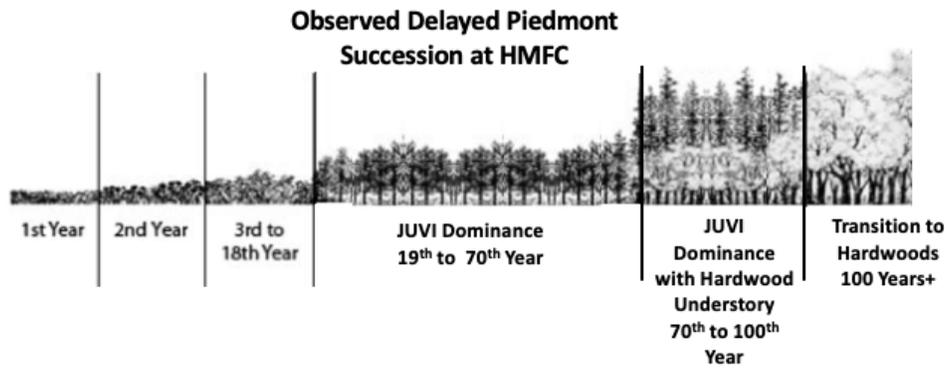


Figure 1.10B. Delayed Piedmont succession. (Office of the Duke Forest, 2019). Adapted to fit the delayed succession observed in 1967 field plots at HMFC in the Piedmont of New Jersey.

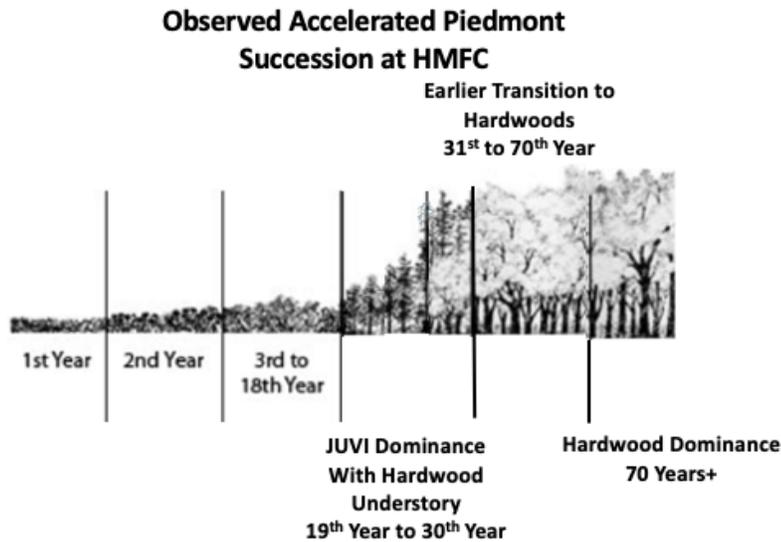


Figure 1.10C. Accelerated Piedmont succession. (Office of the Duke Forest, 2019). Adapted to fit the accelerated succession observed in 1984 field plots at HMFC in the Piedmont of New Jersey.

As agricultural land continues to be abandoned (Meiners et al., 2015), the importance of understanding change in successional trajectories becomes increasingly important. Deer overabundance accompanied by proliferation of invasive species has been shown to limit both woody species regeneration and biodiversity by modifying

community species composition (Woods, 1993; Rooney and Waller, 2003; Rooney and Rodgers, 2004; Aronson and Handel, 2011; Kelly, 2019). Understanding how the implications of these limitations impact succession is important to understand the future of released agricultural fields in a time of peak levels of deer overabundance. As lethal management of deer grows in contention, (Drummond, 1995; Messmer 1997 et al., 1997) effectiveness of nonlethal deer management such as exclosure becomes an increasingly important area of study. Understanding the implications of nonlethal deer management is important as it will likely provide the framework for future management of succeeding agricultural land. The combined use of deer exclusion and supplemental planting of early succession hardwood species can help to create an accelerated successional trajectory. This accelerated succession will yield a richer and more biodiverse stand that is more resilient to deer when deer exclusion measures must be ultimately removed later into succession.

Future Research

Pseudoreplication of each field proved to be problematic in this study. Having only one replicate of each field prevented the capability of creating a timeline of four different times in succession, year 11 (1984 field sampled in 1995), year 29 (1967 field sampled in 1996), year 33 (1984 field in 2017), and year 50 (1967 field sampled in 2017). This linear timeline would have helped to create a better understanding of transition between stages in Piedmont succession at HMFC. Lack of replication of each field also limits the ability in which to determine community composition as a result of successional age of a field rather than field location.

Future research to further support conclusions drawn by this study include creating a more thorough sample design that includes multiple replicates of fields. By including replicates of each field, we would be able to clearly discern between changes in community composition as a result of field age rather than location.

Chapter 2

Introduction

Seed banks are important drivers of ecological succession and provide the foundation for establishment of early successional plant communities (Marks and Mohler, 1985; Dölle and Schmidt, 2009). Seed banks offer plants the opportunity to disperse through time, notably serving as means of spontaneous restoration during succession of former agricultural fields (Vandvik et al., 2015). During disturbance, seed banks help to maintain species pools by acting as a spatial and temporal reservoir for biodiversity (Vandvik et al., 2015). Seed rain, dispersal, predation, longevity, germination, and recruitment are all factors that influence how a seed enters, leaves, or persists in the seed bank. Studying these factors provides an understanding of how the seed bank allows a community to maintain itself and respond to disturbance (Leck et al., 1989).

A form of disturbance that has become problematic in Northeastern forests in recent decades is browse from highly elevated densities of white-tailed deer, *Odocoileus virginianus* (McWilliams et al., 2018). Deer have been shown to be selective browsers that preferentially consume woody species, changing competitive dynamics and species composition during succession (Chapter 1; Inouye et al., 1994; Augustine and McNaughton, 1998). Deer densities in New Jersey have increased from 4 deer per km² in the 1970s to nearly 16 deer per km² by 1998 (Rooney, 2001; Kelly, 2019). Deer thrive in post-agricultural habitats and influence both the abundance and structure of woody species in regenerating forest systems, impacting the abundance and dispersal of seeds, and potentially altering seed bank composition (DiTomamso et al., 2014). Deer browse

can often lead to site-specific extirpation of more susceptible tree species (Gill and Beardall, 2001). Deer also provide a means for dispersal of exotic and native plant species, specifically small seeded, herbaceous species (Myers et al., 2004; Williams and Ward, 2006; Knight et al., 2009).

As aboveground plant communities are altered by overabundant deer, this impact should cascade into the soil seed bank, largely driven from vegetation changes that impact seed rain inputs. It is important to understand how aboveground vegetation, seed rain, and seed banks affect successional trajectories and patterns that may occur in the aboveground vegetation of these systems, especially during disturbance events (Thompson and Grime, 1979; Bakker et al., 1996; Amiaud and Touzard, 2004). While the effects of deer herbivory on vegetation composition and community structure during succession have been well established (Chapter 1; McWilliams et al., 2018; Kelly, 2019), much less is known of how deer browse might alter the seed bank and how inputs from aboveground seed rain may be modified.

This study investigates the potential for overabundant deer browse to alter the community composition of aboveground vegetation and how these impacts may cascade into the seed rain and the seed bank of successional communities. Overabundant deer have been shown to delay succession by limiting frequency and cover of early hardwood successional species in plots open to deer, resulting in an extended dominance of the early successional conifer *Juniperus virginiana* (Chapter 1). In plots exclosed to deer, succession was shown to be more rapid through higher total cover of hardwood species at an earlier stage than is typical of Piedmont succession. Here, I wish to understand if the change in aboveground vegetation of these communities is also represented in the seed

bank and seed rain through comparison of community compositions of all three assemblages.

Collected soil cores, seed rain, and vegetation data allowed for insight of compositional differences among aboveground vegetation, seed rain, and the seed bank caused from selective deer browse. To determine if plot treatment had differing impacts among these three assemblages (aboveground vegetation, seed bank and seed rain), it is important to determine the scale of deer browse and how it might impact the assemblages differently. I expect successional field age and plot treatment to be drivers in determining community composition of all three assemblages. Community composition of aboveground vegetation is suspected to be most influenced by deer with impacts cascading through the seed rain and into the seed bank. I predict the seed bank to have the least similarities with the other assemblages as the seed bank can be highly influenced by the legacy of a site (Bekker et al., 1997). I suspect deer browse to occur at a scale large enough to impact all three regeneration assemblages, ultimately slowing the rate at which succession occurs by reducing and possibly removing important successional tree species from the species pool.

Methods

Study Site

Plots established in 1984 at Rutgers University's Hutcheson Memorial Forest Center (HMFC) in Somerset County (40°30'N, 74°34'W – New Jersey Piedmont) served as the study site. HMFC consists of old growth forest and fallowed agricultural land of various

release dates that creates a chronosequence of different successional communities. These different successional communities provide a strong understanding of how communities change overtime and how changing browse pressure can shape communities (Meiners et al., 2015).

Experimental Design

This experiment was initiated in 1984 in two separate old fields at HMFC (Cadenasso et al., 2002). The first field, hereafter referred to as the 1967 field, was last plowed and disked in 1967, then left fallow. The second field, hereafter referred to as the 1984 field, was last plowed and disked in 1984, then left fallow. Eight, 5m x 5m, plots were established within each field. Four of the plots were open (control) and four plots were exclosed, for a total of 16 plots among the two fields. The plots within each field are plot pairs containing a single open plot that is adjacent to an exclosed plot for comparison analysis. Plots were centralized within each field and separated by no less than 10m. Exclosed plots were built using buried sheet metal, wire fencing and wood structuring to exclude cottontail rabbits (*Sylvilagus floridanus*), meadow voles (*Microtus pennsylvanica*), and white-tailed deer (*Odocoileus virginianus*). In the open plots, no fencing or sheet metal was used to allow for movement of herbivores freely within the plot. Wooden corner posts and framing were used in construction of open plots to simulate possible perching that might occur in exclosed plots. Twenty seedlings each of *Acer rubrum*, *Juniperus virginiana*, and *Cornus florida* were planted in 1986 within each plot in randomly arrayed groups of six seedlings. Exclosed plots remain free from deer but show evidence of browse from small mammals.

Data Collection

Vegetation data was collected in June 2017. Percent cover vegetation data (the herbaceous, shrub, and canopy layers that are collectively the aboveground vegetation) was collected using four, 0.5m x 2.0m, subplots established by Cadenasso et al. (2002) within each of the 16 plots throughout the two fields. Individual tree species frequency was also collected within the subplots and within the entire 5x5m plot. Tree species data included three cohorts: seedlings (under 1m height), saplings (greater than 1m height but less than 8cm DBH), and canopy trees (greater than 8 cm DBH). Frequency of the cohorts was summed to provide one total dataset of tree species frequency.

Within each plot, seven soil cores (5cm diameter x 10cm depth) were collected during three different seasons: Fall 2017, Spring 2018, and Summer 2018. This approach provided a comprehensive assessment of the seed bank (Leck et al., 1985; Krinke et al., 2005). Soil cores collected during the fall and summer were cold stratified at 4.4°C for 120 days to increase likelihood of germination (Kostel-Hughes et al., 1998). Spring soil cores received no artificial cold stratification as they were naturally cold stratified the previous winter season and were collected prior to new dispersal. Soil cores within each plot were homogenized and mixed with sterile potting soil. These mixtures were then spread in separate 0.5m x 0.25m sterile greenhouse trays. Trays were placed in the New Jersey Agricultural Experiment Station Greenhouse at Rutgers University (New Brunswick, NJ) and watered when needed. Over the course of six months, emerging seedlings were counted and identified to the species level when possible (Gleason and Cronquist, 1991; Rhoads and Block, 2007). In the fall collection, the leaf litter layer

above the soil was collected separately, mixed with sterile potting soil and grown in greenhouse trays separately from their soil core counterpart.

Seed rain of woody species in each plot was collected from May 2018 through January 2019. To collect seed rain, three seed traps were placed in each plot for both fields. Seed traps were made from stacked and fastened greenhouse trays, with the top ‘catch’ tray having a webbed construction with dimensions of 0.5m x 0.25m to allow for collection of seed. This design maximized the capture of falling seed rain, while minimizing potential seed removal from traps by granivores (Piana, 2019). Seed traps were emptied every four weeks, and all collected intact and viable seeds from woody species were counted and identified to the species level when possible (Young and Young, 2009). Only woody species were identified as these were the species that deer often selectively browse and were the dominant vegetation type of our successional fields. Monthly seed rain data were summed into a running dataset of seed rain collected across the 2018 growing season into 2019.

Data Analysis

Selective browse of woody species by deer and dominance of conifers or hardwood species both play important roles in shaping successional trajectory in the Piedmont (Chapter 1; Bard, 1952; Horsley et al., 2003). Because of this, I created a dataset that restricted our data to only include the frequencies of tree species in the aboveground vegetation, soil seed bank, and seed rain. I transformed this dataset to relative frequency of each tree species found within the three assemblages. The transformed data set was examined using nonmetric multidimensional scaling, NMDS, ordination containing all

three assemblage types together. In the ordination, data were grouped by assemblage type (vegetation, seed bank, or seed rain), by plot treatment (exclosed or open) and by field age (1967 or 1984), resulting in 12 distinct groups. Permutational multivariate analysis of variance, PERMANOVA, was used to determine the importance of assemblage types, treatments, and/or fields on composition. Beta-dispersion tests were used to analyze multivariable homogeneity of group dispersion to determine if significant results were the result of change in average community composition between groups or change in dispersion within a group. I also performed NMDS on each of the assemblages separately as described above to isolate the effects within each assemblage. NMDS, PERMANOVA, and beta-dispersion tests were conducted using the *vegan* package in R version 3.5.1.

To validate the results of our NMDS ordinations for each assemblage type and determine the effect of plot treatment, two spearman correlation tests were conducted using the *ggpubr* package in R version 3.5.1. As *Acer rubrum* (ACRU), *Cornus florida* (COFL), and *J. virginiana* (JUVI) had been planted in all plots in 1986 (Cadenasso et al., 2002), these three species were the focal species in our first correlation. In this focal species correlation, a unique correlation was conducted for each focal species, across two assemblage types (vegetation and seed rain), and across the two fields, resulting in twelve correlations. Each unique correlation compared the frequency of a respective focal species between the four open and four exclosed plot pairs within a respective field.

The second correlation included all tree species detected within the plots of a respective field. A correlation was conducted across two assemblage types (vegetation and seed rain) and across the two fields, resulting in four unique correlations. Each

unique correlation compared the frequency of all tree species of grouped open plots in a respective field to the frequency of those same tree species within grouped exclosed plots of the same field.

Within the seed bank, *A. rubrum* and *J. virginiana* are considered to be poor seed banking species with short lived seed banks after dispersal (Fashingbauer and Moyle, 1963; Abbot, 1974; Hothuijzen and Sharik, 1984; Lees, 1987). At HMFC, seed banking of *A. rubrum* can persist with limited density after one season (Myster and Pickett, 1993). *C. florida* is characterized by delayed germination within the seed bank due to embryo dormancy that requires overwintering (Priester, 1979; McLemore, 1990). *C. florida* also has poor germinative capacity after the first year of forest floor burial (Meadows et al., 2006). The restrictive and fleeting nature of these species' seed banks is indicated by their poor representation within our seed bank data. Due to the limited nature of these species in our data set, correlations of the seed bank were not conducted as they would falsely represent any further relationships between the effect of plot treatment on the soil seed bank.

Results

During the 2017 above-ground vegetation sampling, a total of 68 species, woody and herbaceous, were detected across all plots. Individuals of tree species were counted across three cohorts: seedlings, saplings, and canopy trees. A total of 1,491 individuals of 16 tree species were counted across all cohorts. Seedlings were represented by 1,223 individuals across all 16 species present, the sapling cohort was represented by 156

individuals across ten of the species present, and the canopy tree cohort was represented by 112 individuals across seven of the species present (Table 2.2).

The seed rain was composed of 3,163 seeds suspected to be viable collected from 16 different woody species. Of these, 2,605 were from eight different species of trees. The seed bank sampling resulted in 3,586 total emerging seedlings across 88 different species with 109 of these seedlings from 12 different tree species (Table 2.1).

Table 2.1. Frequency of 21 tree species detected across all 16 plots within the three assemblages: vegetation, seed rain, and seed bank.

	Vegetation	Seed Rain	Seed Bank
<i>Acer platanoides</i>	9	6	0
<i>Acer rubrum</i>	417	574	1
<i>Acer saccharum</i>	1	0	0
<i>Ailanthus altissima</i>	96	5	17
<i>Carya</i> sp.	3	0	1
<i>Celtis occidentalis</i>	34	0	0
<i>Cornus florida</i>	88	268	8
<i>Fraxinus americana</i>	100	1	1
<i>Ilex opaca</i>	3	0	0
<i>Juniperus virginiana</i>	268	1559	56
<i>Morus</i> sp.	0	0	5
<i>Platanus occidentalis</i>	0	0	16
<i>Populus deltoides</i>	0	0	1
<i>Prunus avium</i>	150	0	1
<i>Prunus serotina</i>	290	181	1
<i>Quercus alba</i>	4	0	0
<i>Quercus rubra</i>	15	0	0
<i>Quercus velutina</i>	10	0	0
<i>Salix</i> sp.	0	0	1
<i>Ulmus americana</i>	3	0	0
<i>Ulmus rubra</i>	0	11	0
Assemblage total	1491	2605	109

Table 2.2. Frequency of 16 tree species detected across all 16 plots within the vegetation assemblage. Vegetation was sampled across tree cohorts: seedlings, saplings, and canopy trees. Trees characterized as canopy trees (8cm DBH and greater) are separated among three size classes: 8-12cm DBH, 12-16cm DBH, and 16+ cm DBH.

	Seedlings	Saplings	Canopy (8-12cm)	Canopy (12-16cm)	Canopy (16cm+)
Acer plantanoides	6	3	0	0	0
Acer rubrum	365	34	14	4	0
Acer saccharum	1	0	0	0	0
Ailanthus altissima	96	0	0	0	0
Carya sp.	3	0	0	0	0
Celtis occidentalis	33	1	0	0	0
Cornus florida	26	43	16	3	0
Fraxinus americana	92	7	0	0	1
Ilex opaca	3	0	0	0	0
Juniperus virginiana	156	48	38	15	11
Prunus avium	135	12	2	1	0
Prunus serotina	278	6	3	2	1
Quercus alba	4	0	0	0	0
Quercus rubra	14	1	0	0	0
Quercus velutina	9	0	1	0	0
Ulmus americana	2	1	0	0	0
Total	1223	156	74	25	13

Community Composition of Tree Species

When compared to both aboveground vegetation and seed rain, open and exclosed seed bank assemblages had distinct tree community composition. Composition of seed rain communities had the most similarities to vegetation communities. Significant compositional differences among communities occurred by plot treatment, assemblage type, and field, all independent from one another, and also for the interaction of plot treatment and assemblage type (Figure 2.1, PERMANOVA, $p < 0.05$). Beta-dispersion analysis was non-significant ($p > 0.05$), confirming that differences detected were within average composition of a community rather than in the variance of the community.

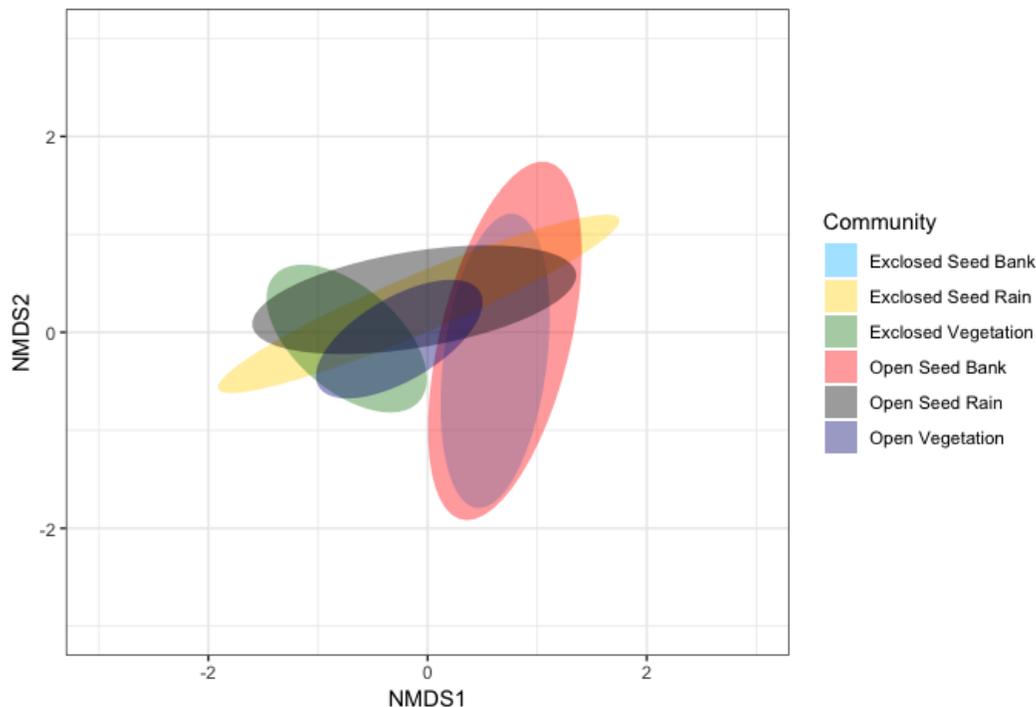


Figure 2.1 NMDS ordination of relative tree species frequency for all three assemblage types together. (4 dimensions, stress=0.057). Ellipses denote different communities determined by plot treatment (open or exclosed) and assemblage type (vegetation, seed bank, or seed rain). Distinction of 1984 and 1967 fields were not included in this figure for easier visualization but remained a factor in the PERMANOVA and betadispersion.

When analyzed separately, beta-dispersion analysis was insignificant ($p > 0.05$), confirming that there was a difference in average vegetation, seed bank, and seed rain community composition between fields rather than within fields (PERMANOVA, $p < 0.05$, Figure 2.2A-2C). For only the vegetation, composition differed between exclosed and open plots (PERMANOVA $p < 0.05$, Betadispersion $p < 0.05$, Figure 2.2A). Although there were significant differences in vegetation community composition for both field and plot treatment independent of one another, there was no interaction between field and plot treatment.

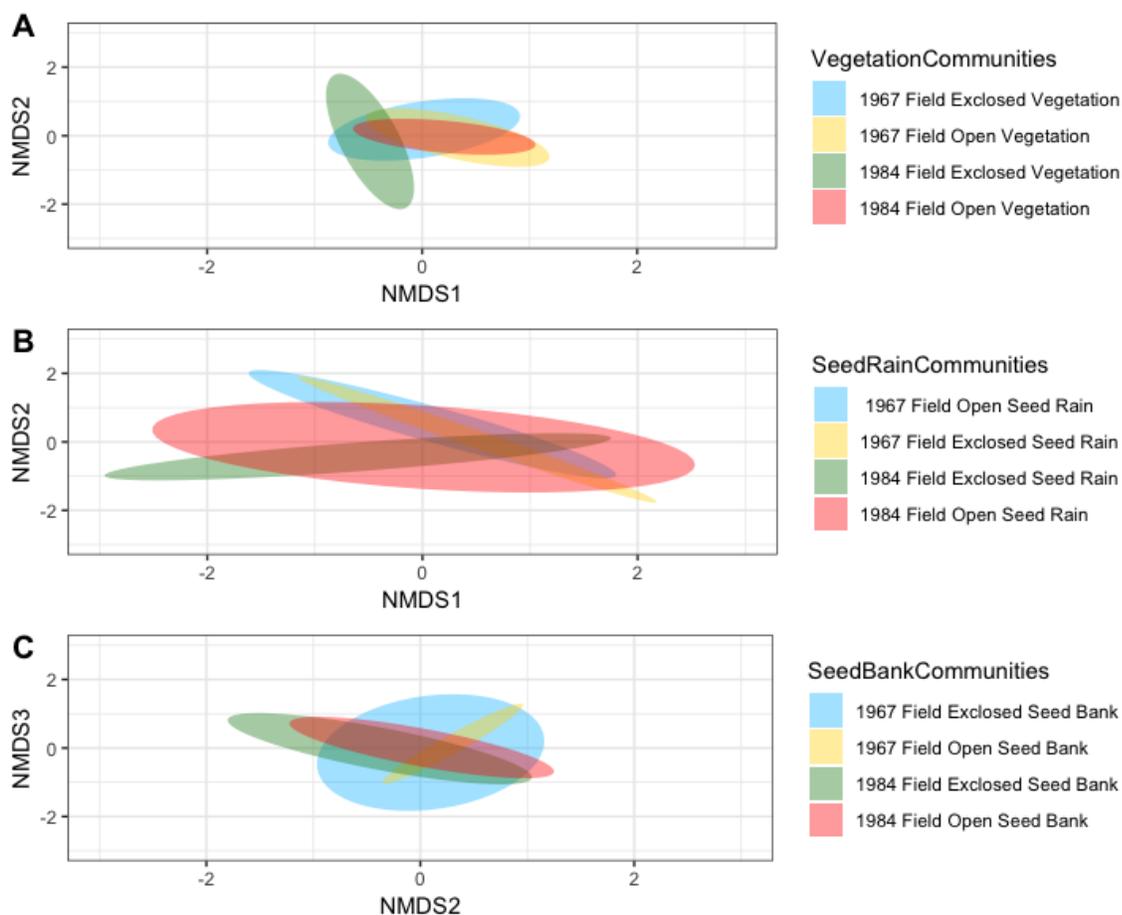


Figure 2.2(A-C). NMDS ordination of relative tree species frequency for each assemblage type separated. Ellipses denote different communities determined by plot treatment (open or exclosed), field (1984 or 1967), and community type (vegetation, seed rain, or seed bank). (Figure 2A: 2 dimensions, stress=0.058; Figure 2B: 2 dimensions, stress=0.060; Figure 2C: 3 dimensions, stress=0.024).

Within the focal species correlation analysis, some of the correlations indicated either strong negative or positive relationships, but none of these correlations were significant (Table 2.3).

Table 2.3 Spearman correlation results for all 16 correlations. Respective variables used in correlations also listed including: field, assemblage type, and comparison type.

Correlation Type	Field	Assemblage Type	Comparison Type	R Value	P-Value
ACRU Individuals	1984 Field	Vegetation	Individual Plot Pairs	-1	0.083
ACRU Individuals	1984 Field	Seed Rain	Individual Plot Pairs	-0.8	0.33
COFL Individuals	1984 Field	Vegetation	Individual Plot Pairs	0	1
COFL Individuals	1984 Field	Seed Rain	Individual Plot Pairs	0.8	0.33
JUVI Individuals	1984 Field	Vegetation	Individual Plot Pairs	0	1
JUVI Individuals	1984 Field	Seed Rain	Individual Plot Pairs	-0.8	0.33
ACRU Individuals	1967 Field	Vegetation	Individual Plot Pairs	-0.2	0.92
ACRU Individuals	1967 Field	Seed Rain	Individual Plot Pairs	0.4	0.75
COFL Individuals	1967 Field	Vegetation	Individual Plot Pairs	NA	NA
COFL Individuals	1967 Field	Seed Rain	Individual Plot Pairs	-0.33	0.67
JUVI Individuals	1967 Field	Vegetation	Individual Plot Pairs	-0.8	0.33
JUVI Individuals	1967 Field	Seed Rain	Individual Plot Pairs	-0.2	0.92
All Tree Species Individuals	1984 Field	Vegetation	All Open To Exclosed Plots	0.6	0.056
All Tree Species Individuals	1984 Field	Seed Rain	All Open To Exclosed Plots	0.78	0.039
All Tree Species Individuals	1967 Field	Vegetation	All Open To Exclosed Plots	0.69	0.026
All Tree Species Individuals	1967 Field	Seed Rain	All Open To Exclosed Plots	0.87	0.026

The correlation of tree species vegetation between open and exclosed plots within the 1984 field indicated a non-significant ($p > 0.05$) limited relationship, $R = 0.60$ (Figure 2.3A). The correlation of tree species seed rain between open and exclosed plots within the 1984 field indicated a significant ($p < 0.05$) positive relationship, $R = 0.78$ (Figure 2.3B). Within the 1967 field, correlation of tree species vegetation between open and exclosed plots indicated a significant ($p < 0.05$) positive relationship, $R = 0.69$ (Figure 2.3C). Correlation of seed rain between open and exclosed plots within the 1967 field was significant, $p < 0.05$, with a strong positive relationship, $R = 0.87$ (Figure 2.3D).

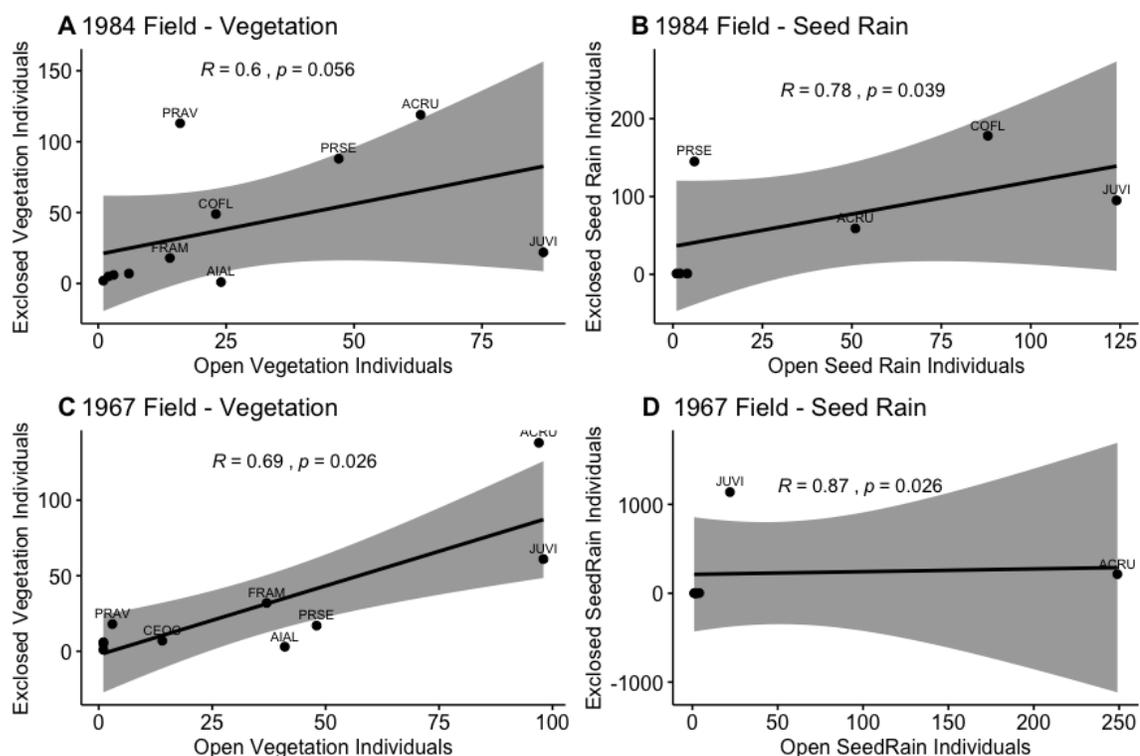


Figure 2.3(A-D). Spearman correlations conducted on grouped open and grouped excluded plots, separated by field and assemblage type. Correlation coefficients and significance values reported within each graph.

Discussion

The first chapter of this thesis explored impacts of overabundant deer browse and field age on successional vegetation communities, determining that both factors played an important role in both shaping a community and determining the community's successional trajectory. In this chapter, I have found that, although both these factors influence the three assemblage types discussed here, field, despite plot treatment, is one of the major drivers of the vegetation and the seed rain of our successional communities. The two fields were released at different periods and likely experienced different browse

pressures, however, the critical difference between the two fields is the timing of enclosure installation. The installation of plot enclosures in 1984 yielded a more effective management of browsing pressure in the 1984 field than seen in enclosures of the 1967 field.

Results of the community composition analysis support the hypothesis that the communities of the seed bank, seed rain, and aboveground vegetation are similarly influenced by field age. Enclosure of communities from deer only impacted composition of vegetation, not the seed rain nor the seed banks. These results may reflect that seed rain and the seed banks are responding to processes occurring at different scales than the enclosure treatments, which affect plant communities at hyper-local plot-scale. The soil seed bank was least similar in composition to the other two assemblage types, likely due to the limited rigor of the seed bank collection technique. The results suggest that enclosing a community from deer largely influences only vegetation, while the seed rain and seed bank persist and remain intact in the presence of deer. This indicates that vegetation is largely driven by processes at the plot scale, while seed rain and seed bank are driven by larger, patch level processes that remain unperturbed from deer browse.

Ecologists have long debated on the impacts of regional and local processes in shaping plant communities (Ricklefs, 1987; Cornell and Lawton, 1992; Lawton, 1999). Local processes have generally been identified as predation, parasitism, competition, and disturbance, while regional processes are seen as dispersal, speciation, and fluctuation in species distribution and numbers (Cornell and Lawton, 1992). Predation is a consumptive interaction that occurs at a local scale, often limiting species diversity and leading to localized extirpation of a species (Ricklefs, 1987). Deer browse, an herbivorous

consumptive interaction, can also cause localized extirpation of preferred browse species and limit diversity and frequency within a local system (McWilliams et al., 2018; Kelly, 2019). Within the 1984 field, differences in the frequency of tree species in vegetation of grouped open and exclosed plots were indicative of the vegetation responding to the impact of deer browse, a plot-scale process. This trend is supported within the first chapter of this thesis as discernible differences in more palatable hardwood species and less palatable (*J. virginiana*) tree species cover were seen between the different plot treatments in the 1984 field (Chapter 1).

No discernible differences in average community composition and frequency of tree species between the seed rain of open and exclosed plots for both the 1984 and 1967 fields. These results suggest that seed rain in these fields do not respond to the localized, plot scale process of deer browse. Instead, it is likely that seed rain of these fields would be more responsive to larger patch scale changes such as distance to neighboring seed sources and densities of fruiting species in the surrounding landscape, processes that supersede any effects caused by plot treatment. (Ricklefs, 1987; Cornell and Lawton, 1992; Lawton, 1999; Germain et al., 2017).

Age of a site is important in determining community composition of our three assemblages and if relationships exist between these assemblage types. The seed bank of a site represents dispersal through time and is largely determined by the history of the site (Bekker et al., 1997; Kalamees and Zobel, 1998). Established vegetation are more reflective of seed rain in a community that has been successfully established and will therefore be represented largely by age and availability of surrounding seed sources (Howe and Smallwood, 1982; Kalamees and Zobel, 1998). Vegetation communities of

each of the fields is driven largely by successional age of the field, a more coarse, patch-scale process. This is attributed to diversity and frequency of tree species being determined by the successional stage of a forest including interspecific competition and the light availability (Bard, 1952; Murrell et al., 2014).

Within the 1967 field, contrary to the 1984 field, there was no discernible difference in tree species frequency of the vegetation assemblage type between the open and exclosed plots. This result is likely caused by differences in fields related to plot treatment. When the exclosure plots were established in 1984, the 1967 field had been fallow for 17 years while the 1984 field had just been released. During this 17-year period between 1967 and 1984, deer selectively browsed and altered community composition and frequency of tree species, resulting in delayed succession and limited regeneration of many hardwood species in this field while simultaneously altering competitive dynamics of regenerating species (Chapter 1; Russel et al., 2017; Kelly, 2019). As field fallow time increased, the regeneration potential of plant communities within the field decreased, likely generated by the poor seed bank potential of late successional woodland species (Dölle and Schmidt, 2009).

Although I could not draw conclusions of the impact of deer browse on tree species frequency of the seedbank, it is likely that the scale of processes in which the seed bank responds to is similar to the seed rain. Both assemblage types have been attributed to being impacted by larger regional level processes such as dispersal, and species invasion that results in the formation persistent seed banks (Cornell and Lawton, 1992; Gioria et al., 2019). Land use history including past agriculture of a released field is also a driver of succession and community formation. (Cornell and Lawton, 1992;

Meiners et al., 2015). It is plausible that seed sources from surrounding communities, such as neighboring successional fields, or the old growth forest of HMFC are providing important inputs for both the seed rain and soil seed bank of our study sites (McClanahan, 1986). This process is comparable to silviculture prescriptions that clear-cut forested land and leave behind few mature trees, providing a seed source for regeneration (Burns, 1989).

Implications of Deer Overabundance

It is evident that deer are influential in altering and degrading the composition and frequency of site-specific assemblages, notably vegetation (Freker et al. 2017). Although deer have been shown to alter community composition toward less palatable, often undesirable, exotic species, (Chapter 1; Anderson, 1997; Augustine and McNaughton, 1998) dispersal serves as a patch scale process that can restore biodiversity and composition of regenerating forests (Corlett and Hau, 2000; Verheyen and Herm, 2001). New Jersey contains a large amount of abandoned farmland that now composes a significant portion of the state's successional forestland (Crocker et al., 2017). As New Jersey is plagued by deer overabundance, the incorporation of deer removal efforts, either through lethal management or nonlethal deer exclusion, forest restoration efforts, and proper management of standing forest to provide a healthy seed rain source, appears more necessary than ever.

To best manage newly released successional agricultural land, a combination of deer exclosure and/or lethal deer management to lower deer to acceptable densities along with plantings of mid to late successional tree species is recommended (Chapter 1;

Chazdon, 2008; Beguin et al., 2016). The planted trees that survive will eventually shade out competing invasive species and provide additional seed rain for seedling recruitment when they reach maturity. Our study has shown that even in the presence of overabundant deer, seed rain of tree species remains persistent among degraded successional agricultural sites largely due to patch-scale dispersal. Seed rain can serve as an important seed source for tree species that helps to progress forest succession in degraded systems. Supplemental removal of invasive species throughout succession can also help in providing a healthier, native forest system (Aronson and Handel, 2011).

Future Research and Improvements

This study has made it clear that in order to draw cross-comparisons of assemblages, it is important to have a clear understanding of each unique assemblage type. To gain clear understanding of the assemblage types, rigorous sampling methods are necessary. This studies' sampling methods proved to be a limiting factor. To improve upon sampling methods, added rigor is necessary during the sampling of each assemblage. First, using larger 10 x 10 m plots, rather than 5 x 5 m plots, would limit competition of establishing vegetation within the plots. This increased plot size would also allow for the installation of more seed rain traps to collect a larger volume of seed rain without compromising the vegetation. Increased plot area provides for a larger amount of soil volume to be sampled, providing a more comprehensive understanding of the soil seed bank. Collected soil cores were 5cm in width and 10cm in depth; this technique, while providing a comprehensive understanding of herbaceous species present in the seed bank, greatly limited the collection of larger seeded tree species. To correct this, switching the dimensions to a

5cm depth and *10cm width* soil core would provide a better sampling technique for the collection of larger seeded, short-lived tree species in the transient seed bank. More frequent seed bank collections throughout the year would also provide better resolution by allowing for collection of recently dispersed, short-lived seed banking species.

Synonymous with recommendations for improvements in Chapter 1, increasing the number of plot replicates within each field and the number of replicates of each field would prevent limitations of conclusions created from any potential pseudoreplication. Through added rigor in data collection, a more comprehensive understanding of our three assemblage types would be provided. Better comprehension of each assemblage provides the necessary foundation for additional analyses, specifically analysis of species diversity among the three assemblage types.

References

- Abbot, H. G. 1974. Some characteristics of fruitfulness and seed germination in red maple. *Tree Planters' Notes*, 25(2): 25-27.
- Armesto, J. J. and S. T. A Pickett. 1985. Experiments on disturbance in old-field plant communities: impacts on species richness and abundance. *Ecology*, 66: 230-240.
- Amiaud, B., and B. Touzard. 2004. The relationships between soil seed bank, aboveground vegetation and disturbances in old embanked marshland of Western France. *Flora – Morphology, Distribution, Functional Ecology of Plants*, 199(1): 25-35.
- Anderson, R. C. 1997. Native pests: The impact of deer in highly fragmented habitats. In: Schwartz M.W. (eds) *Conservation in Highly Fragmented Landscapes*. Springer, Boston, MA.
- Aronson, M. F. J. and S. N. Handel. 2011. Deer and invasive plant species suppress forest herbaceous communities and canopy tree regeneration. *Natural Areas Journal*, 31: 400–407.
- Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management*, 62(2): 1165-1183.
- Averill K. M., D. A. Mortensen, E. A. H. Smithwick, S. Kalisz, W. J. McShea, N. A. Bourg, J. D. Parker, A. A. Royo, M. D. Abrams, D. K. Apsley, B. Blossey, D. H. Boucher, K. L. Caraher, A. DiTommaso, S. E. Johnson, R. Masson, and V. A. Nuzzo. 2018. A regional assessment of white-tailed deer effects on plant invasion. *AoB PLANTS*, 10: plx047.
- Bakker, J. P., P. Poschlod, R. J. Strykstra, R. M. Bekker, and K. Thompson. 1996. Seed banks and seed dispersal: important topics in restoration ecology. *Acta botanica neerlandica*, 45(4): 461-490.
- Bard, G. E. 1952. Secondary succession on the Piedmont of New Jersey. *Ecological Monographs*, 22(3): 195-215.
- Baiser B., J. L. Lockwood, D. La Puma, and M. F. J Aronson. 2008. A perfect storm: two ecosystem engineers interact to degrade deciduous forests of New Jersey. *Biological Invasions*, 10: 785–795.
- Beguín, J., J.-P. Tremblay, N. Thiffault, D. Pothier, S. D. and Côté. 2016. Management of forest regeneration in boreal and temperate deer–forest systems: challenges, guidelines, and research gaps. *Ecosphere*, 7(10): e01488.

- Bekker, R. G. Verweij, R. Smith, R. Reine, J. Bakker, and S. Schneider. 1997. Soil seed banks in European grasslands: Does land use affect regeneration perspectives? *Journal of Applied Ecology*, 34(5): 1293-1310.
- Buell, M. F., H. F. Buell, and J. A. Small. 1954. Fire in the history of Mettler's Woods. *Bulletin of the Torrey Botanical Club*, 81: 253-255.
- Buell, M. F., H. F. Buell, and J. A. Small. 1971. Invasion of trees in secondary succession on the New Jersey Piedmont. *Bulletin of the Torrey Botanical Club*, 98(2): 67-74.
- Burns, R.M. 1989. The scientific basis for silvicultural and management decisions in the national forest system. General Technical Reports. WO-55. Washington, DC: USDA Forest Service.
- Cadenasso, M. L., S. T. A. Pickett, and P. J. Morin. 2002. Experimental test role of mammalian herbivores on old field succession: Community structure and seedling survival. *Journal of the Torrey Botanical Society*, 129(3): 228-237.
- Chazdon, R. L. 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science*, 320(5882): 1458-1460.
- Corlett, R. and B.C.H. Hau. 2000. Seed dispersal and forest restoration. In: *Forest Restoration for Wildlife Conservation* (eds. Elliott, S., J., Kerby, D. Blakesley, K. Hardwick, K. Woods and V. Anusarnsunthorn). International Tropical Timber Organization and The Forest Restoration Research, Chiang Mai University, Thailand. 317-325.
- Cornell, H. V. and J. H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology*, 61: 1-12.
- Côté, S.D., T. P. Rooney, J. P. Tremblay, C. Dussault, and D. M. Wallter. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics*, 35: 113-147.
- Crawley, M. J. 1989. Chance and timing in biological invasions. *In: J. A. Drake, H. A. Mooney, F. diCasti, R. H. Groves, F. J. Kruger, M. Rejmanek and M. Williamson (eds.), Biological Invasions: A Global Perspective*. John Wiley & Sons, New York, 407-423.
- Crocker, S J., C. J. Barnett, B. J. Butler, M. A. Hatfield, C. M. Kurtz, T. W. Lister, D. M. Meneguzzo, P. D. Miles, R. S. Morin, M. D. Nelson, R. J. Piva, R. Riemann, J. E. Smith, C. W. Woodall, W. Zipse. 2017. *New Jersey Forests 2013*. Resour. Bull. NRS-109. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 90 p.

- DiTommaso A., S. H. Morris, J. D. Parker, C. L. Cone, and A. A. Agrawal. 2014. Deer browsing delays succession by altering aboveground vegetation and belowground seed banks. *PLoS ONE*, 9(3): e91155.
- DiTommaso A., S. H. Morris, J. D. Parker, C. L. Cone, and A. A. Agrawal. 2014. Deer browsing delays succession by altering aboveground vegetation and belowground seed banks. *PLoS ONE*, 9(3): e91155.
- Dölle, M., and W. Schmidt. 2009. The relationship between soil seed bank, above-ground vegetation and disturbance intensity on old-field successional permanent plots. *Applied Vegetation Science*, 12(4): 415-428.
- Drummond, F. 1995. Lethal and non-lethal deer management at Ryerson Conservation Area, Northeastern Illinois. *Urban deer: a manageable resource*. Wildlife.org.
- Fashingbauer, B. A. and J. B. Moyle. 1963. Nutritive value of red-osier dogwood and mountain maple as deer browse. *Minnesota Academy of Science Proceedings*, 31(1): 73-77.
- Fire Effects Information System (FEIS). 2019. Forest Service. United States Department of Agriculture.
- Frei, K. R., and D. E. Fairbrothers. 1963. Floristic study of the William L. Hutcheson Memorial Forest (New Jersey). *Bulletin of the Torrey Botanical Club* 90:338–355.
- Freker K., A. Sabo, and D. Waller. 2017. Long-term regional shifts in plant community composition are largely explained by local deer impact experiments. *PLOS ONE*, 12(9): e0185037.
- Germain, R. M., S. Y. Strauss, and B. Gilbert. 2017. Experimental dispersal reveals characteristic scales of biodiversity in a natural landscape. *Proceedings of the National Academy of Sciences*, 114(17): 4447-4452.
- Gill, R. M. A., and V. Beardall. 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry: An International Journal of Forest Research*, 74(3): 209-218.
- Gioria, M., J.J. Le Roux, H. Hirsch, and L. Moravcová. 2019. Characteristics of the soil seed bank of invasive and non-invasive plants in their native and alien range distribution. *Biological Invasion*, 21: 2313-2332.
- Gleason, H.A. and A. Cronquist. 1991. *Manual of vascular plants of Northeastern United States and adjacent Canada*. 2nd Edition, The New York Botanical Garden, Bronx, NY.

- Gutierrez, J. R., P. L. Meserve, S. Herrera, L. C. Contreras, and F. M. Jaksic. 1997. Effects of small mammals and vertebrate predators on vegetation in the Chilean semiarid zone. *Oecologia*, 109: 398-406.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management*, 60: 695-713.
- Holthuijzen, A. M. A. and T. Sharik. 1984. Seed longevity and mechanisms of regeneration of eastern red cedar (*Juniperus virginiana* L.). *Bulletin of the Torrey Botanical Club*, 111(2): 152-158.
- Horsley, S. B., S. L. Stout, and D. S. DeCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications*, 13: 98-118.
- Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, 13(1): 201-228.
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 22: 477-503.
- Inouye, R. S., T. D. Allison, and N. C. Johnson. 1994. Old field succession on a Minnesota sand plain-effects of deer and other factors on invasion by trees. *Bulletin of the Torrey Botanical Club*, 121: 266-276.
- Kalamees, R., and M. Zobel. 1998. Soil seed bank composition in different successional stages of a species rich wooded meadow in Laelatu, Western Estonia. *Acta Oecologica*. 19(2): 175-180.
- Keever, Catherine. 1950. Causes of succession on old fields of the Piedmont, North Carolina. *Ecological Monographs*, 20(3): 229-250.
- Kelly, J. 2019. Regional changes to forest understories since the mid-Twentieth Century: Effects of overabundant deer and other factors in northern New Jersey. *Forest Ecology and Management*, 444: 151-162.
- Knight, T.M., J. L. Dunn, L. A. Smith, J. Davis, and S. Kalisz. 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. *Natural Areas Journal*, 29: 110-116.
- Kostel-Hughes, F., T. P. Young, and M. J. McDonnel. 1998. The soil seed bank and its relationship to the aboveground vegetation in deciduous forests in New York City. *Urban Ecosystems*, 2: 43-59.

- Krinke, L., L. Moravcova, P. Pysek, V. Jarosik, J. Pergl, and I. Perlova. 2005. Seed bank of an invasive alien, *Heracleum mantegazzianum*, and its seasonal dynamics. *Seed Science Research*, 15: 239-248.
- Lawton, J. H. 1999. Are there general laws in ecology? *Oikos*, 84: 177-192.
- Leck, M. A., V. T. Parker, and R. L. Simpson. 1989. *Ecology of Soil Seed Banks*. Academic Press, Inc. San Diego, California.
- Lees, J. C. 1987. Clearcutting as an even-aged reproduction method. In: Nyland, Ralph D., editor. *Managing northern hardwoods: Proceedings of a silvicultural symposium; 1986 June 23-25; Syracuse NY. Faculty of Forestry Miscellaneous Publication No. 13 (ESF 87-002); Society of American Foresters Publication No. 87-03. Syracuse NY: State University of New York, College of Environmental Science and Forestry: 115-127.*
- Loomis, J. D., S. F. Matter, and G. N. Cameroon. 2015. Effects of invasive amur honeysuckle (*Lonicera Maackii*) and white-tailed deer (*Odocoileus virginianus*) on survival of sugar maple seedlings in Southwestern Ohio forest. *The American Midland Naturalist*, 174(1): 65-73.
- Mansourian, S., D. Vallauri, and N. Dudley. 2005. *Forest restoration and landscape: beyond tree plantings*. eds. (in cooperation with WWF International) Springer, New York.
- Marks, P. L. and C. L. Mohler. 1985. Succession after elimination of buried seeds from a recently plowed field. *Bulletin of the Torrey Botanical Club*, 112: 376-382.
- McClanahan, T.R. 1986. The effect of a seed source on primary succession in a forest ecosystem. *Vegetatio*. 65: 175–178.
- McLemore, B. F. 1990. *Cornus florida* L. flowering dogwood. In: Burns, R. M.; Honkala, B. H., technical coordinators. *Silvics of North America. 2. Hardwoods. Agric. Handb. 654*. Washington, DC: USDA, Forest Service: 278-283.
- McShea, W. J., H. B. Underwood, and J. H. Rappole. 1997. *The science of overabundance: deer ecology and population management*. Washington, DC: Smithsonian Institution Press.
- McWilliams W. H., J. A. Westfall, P. H. Brose, D. C. Dey, A. W. D'Amato, Y. L. Dickinson, M. A. Fajvan, L. S. Kenefic, C. C. Kern, K. M. Laustsen, S. L. Lehman, R. S. Morin, T. E. Ristau, A. A. Royo, A. M. Stoltman, and S. L. Stout. 2018. Subcontinental-scale patterns of large-ungulate herbivory and synoptic review of restoration management implications for midwestern and northeastern forests. Gen. Tech. Rep. NRS-182. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station, 24 p.

- Meadows, J. S., F. T. Bonner, J. D. Haywood. 2006. Soil-seed bank survival in forest of the southern United States. *New Forests*, 32: 335.
- Meiners, S. J., M. L. Cadenasso, and S. T. A. Pickett. 2007. Succession on the piedmont of New Jersey and its implications for ecological restoration. Pages 145-161, in V. A. Cramer and R. J. Hobbs (eds.) *Old Fields: Dynamics and Restoration of Abandoned Farmland*. Island Press, Washington DC.
- Meiners, S. J., S. T. A. Pickett, and M. L. Cadenasso. 2015. *An integrative approach to successional dynamics: Tempo and mode of community change*. Cambridge University Press.
- Messmer, T. A., S. M. George, and L. Cornicelli. 1997. Legal considerations regarding lethal and nonlethal approaches to managing urban deer. *Wildlife Society Bulletin*, 25(2): 424-429.
- Miller, R. F., T. J. Svejcar, and J. A. Rose. 2000. Impacts of western juniper on plant community composition and structure. *Journal of Range Management*, 53: 574-585.
- Murrell, E. G., A. R. Ives, and S. A. Juliano. 2014. Intrinsic and extrinsic drivers of succession: Effects of habitat age and season on an aquatic insect community. *Ecological entomology*, 39(3): 316–324.
- Myers, J. A., M. Vellend, S. Gardescu, and P. L. Marks. 2004. Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia*, 139: 35-44.
- Myster, W., and S. T. A. Pickett. 1993. Effects of litter, distance, density, and vegetation patch type on postdispersal tree seed predation in old fields. *Oikos*, 66: 381-388.
- Office of the Duke Forest. 2019. Piedmont Forest Succession Model.
<https://dukeforest.duke.edu/forest-environment/forest-succession>
- Piana, M. R. 2019. *Plant recruitment dynamics in urban forests: consequences for seed and seed establishment*. Rutgers University. New Brunswick, New Jersey.
- Priester, D. S. 1979. Stump sprouts of swamp and water tupelo produce viable seeds. *Southern Journal of Applied Forests*, 3(4): 149-151.
- Rhoads, A. F. and T. A. Block. 2007. *The plants of Pennsylvania: An illustrated manual*. Philadelphia: University of Pennsylvania Press.

- Ricklefs, R. W. 1987. Community diversity: relative roles of local and regional processes. *Science*, 235: 167-171.
- Rooney, T.P. and D. A. Rogers. 2004. Monitoring nonnative plant invasions over fifty years in Wisconsin. *Weed Technology*, 18: 1266-1268
- Rooney, T.P. and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management*, 181: 165–176.
- Russel, M. B., C. W. Woodall, K. M. Potter, B. F. Walters, G. M. Domke, and C. M. Osalt. 2017. Interaction between white-tailed deer density and the composition of forest understories in the Northern United States. *Forest Ecology and Management*, 384: 26-33.
- Schorger, A. W. 1953. The white-tailed deer in Wisconsin. *Transactions of the Wisconsin Academy of Sciences, Arts, and Letters*, 42: 197-247.
- Thompson, K., J. P. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology*, 67: 893–921.
- Ugolini, F. C. 1964. Soil development on the red beds of New Jersey. *William Hutcheson Memorial Forest Bulletin*, 2(1):1-34.
- Vandvik, V., K. Klsanderud, E. Meineri, I. E. Måren, and J. Topper. 2016. Seed banks are biodiversity resevoirs: species-area relationships above versus below ground. *Oikos*, 125: 218-228.
- Verheyen, K. and M. Herm. 2001. The relative importance of dispersal limitation of vascular plants in secondary forest succession in Muizen Forest, Belgium. *Journal of Ecology*, 89: 829-840.
- Walters, B.F., C. W. Woodall, and M. B. Russell. 2016. White-tailed deer density estimates across the eastern United States, 2008. Minneapolis, MN: University of Minnesota Digital Conservancy.
- Watson A. 1983. Eighteenth century deer numbers and pine regeneration near Braemar, Scotland. *Biological Conservation*, 25: 289–305.
- Williams, S. C., and J. S. Ward. 2006. Exotic seed dispersal of white-tailed deer in southern Connecticut. *Natural Areas Journal*, 26(4): 383-390.
- Woods, K. D. 1993. Effects of invasion by *Lonicera tartarica* L. on herbs and tree seedlings in four New England forests. *American Midland Naturalist Journal*, 130: 62–74.

Young, J. A., and C. G. Young. 2009. *Seeds of woody plants in North America*. Timber Press.