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THE VERTICAL DIMENSION OF DEER BROWSE EFFECTS ON FOREST

UNDERSTORIES

by

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ABSTRACT OF THE DISSERTATION

The Vertical Dimension of Deer Browse Effects on Forest Understories

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Dr. Claus Holzapfel

Throughout their range, white-tailed deer (*Odocoileus virginianus*) have significantly altered the diversity and productivity of plants upon which they browse in forest understories as well as the average heights of many of these species, yet traditional vegetation surveys can fail to capture changes occurring at higher levels in the vertical dimension.

In Chapter 1 I examine fine-scale understory changes in the vertical dimension by measuring vegetation density and species richness at 20 cm intervals from ground level to two meters at 44 pre-existing deer exclosures of various ages in New Jersey and Maryland forests. I found that vertical vegetation density and species richness were significantly greater at every height when protected from deer. Deer affected density at all heights somewhat evenly but the impact on species richness was significantly greater in the lower heights. The impact on species richness was significantly correlated to exclosure age at virtually every height. My results indicate that multiple heights must be measured to obtain a full picture of deer impacts.

In Chapter 2 I explored the relationship of the vertical species richness profile to deer densities by measuring species richness at 20 cm intervals up to two meters across 10 forests in the Washington D.C. region with a gradient of deer densities (5 deer/km^2 to 78 deer/km^2). Vertical profiles of species richness followed a negative exponential distribution for all sites with the coefficient of the exponential describing the rate of understory species loss in the vertical dimension. This species attenuation coefficient was linearly related to the deer density explaining 31% of the variation.

In Chapter 3 I test various floristic quality indicators for their ability to capture the effects of deer on forests. Using data collected at the same exclosures and forests as above, I found that the Floristic Quality Assessment Index (FQAI) and the Plant Stewardship Index (PSI) indicated increased quality inside deer exclosures that increased slowly the longer the plots had been protected from deer browse. FQAI and PSI were also well-correlated to deer densities ($r^2 = 0.25$ and 0.31, respectively) showing decreased quality as deer density increased.

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INTRODUCTION

Browsing by white-tailed deer (*Odocoileus virginianus* Zimm.) is a major influence on the dynamics of the vegetation in the eastern deciduous forests (Russell et al. 2001, Côté et al. 2004). Deer have even been called keystone herbivores (Waller and Alverson 1997) for their power to cause dramatic alterations in forest structure and composition. Increasing deer densities have been related to regeneration failure of canopy species, declining forest understories, reduced populations of specific species, and increased abundances of other species (Côté et al. 2004).

Browsing by white-tailed deer is known to decrease the average height of particular species and to decrease the diversity of understories in forests (Rooney and Waller 2003); however, no research has been done to understand these combined effects in the vertical dimension. The effect of deer on average heights of some species is so well correlated to the size of deer populations that indices have been proposed that use surveys of these species to track deer densities and as surrogates to understand the impact of deer on the broader community (Anderson 1994, Williams et al. 2000, Webster et al. 2001, Morellet et al. 2001).

The floristic quality assessment index (FQAI) is a diversity measure that incorporates the use of a weight that is assigned to each species called a coefficient of conservatism. The index weights plant species by factors which have some correlation with their vulnerability to being lost from the community (Taft et al. 1997). Floristic quality indices are often tested against another measure known to degrade habitat. In past applications of

the FQAI, degradation has referred to anthropogenic changes to hydrology or water quality in wetland habitat (Andreas et al. 2004, Lopez and Fennessy 2002, Miller and Waldrop 2006) or disturbance caused by fire in prairie communities (Bowles et al. 1996, Bowles et al. 2006). Deer browse is generally recognized as one of the major factors impacting the integrity of eastern deciduous forest (Russell et al. 2001, Côté et al. 2004). So it is crucial to test how well the FQAI in eastern deciduous forests reflects degradation caused by deer browsing before the index can be widely applied. Anderson et al. (2004) compared floristic quality changes due to deer browse using several methods in deer exclosures in prairie ecosystems, but few studies have specifically tested floristic quality measures in relationship to levels of deer browse or to deer densities in forests.

My research addresses the hypotheses that (1) increasing deer densities affect diversity and density within different height classes in the understory and that these effects occur at different deer density thresholds than effects on traditional measures of species diversity, that (2) since the average heights of many species are affected by deer browse, a vertical measure of species richness within understories would encapsulate this effect and allow estimation of deer density across multiple communities without requiring the presence of specific plant species, and that (3) these impacts would also result in a decrease in the floristic quality of the forest understory.

I predicted that diversity and vegetation density would decrease at different rates at different heights in forest understories when exposed to deer and that the greatest impact on vegetation density and diversity would be measured within height classes occurring in

the browse zone. I expected the middle heights in the understory to lose species more rapidly under increasing deer density levels. I also predicted that floristic quality would be higher in protected plots within deer exclosures than in unprotected plots and would decrease in the unprotected forest plots as the deer density within the surrounding forest increased.

To determine whether vertical measures of plant diversity and density were impacted by deer, I collected data at pre-existing deer exclosures in New Jersey and Maryland. I studied the relationship of deer density to species richness in the vertical dimension in forests in national parks in the greater Washington D.C. area (National Capital Region Network) with a gradient of deer densities. I then examined the impacts of deer on floristic quality using data from both the pre-existing deer exclosures and the forests in national parks in the Washington D. C. area.

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CHAPTER 1: Effects of Deer on Vertical Vegetation Density and Diversity

ABSTRACT

Throughout their range, white-tailed deer (*Odocoileus virginianus*) have significantly altered the diversity and productivity of plant species upon which they browse in forest understories. Measurements of deer browse impacts on plant species diversity typically use percent cover estimates from plots laid out at ground level and viewed from above. However such measurements collapse information into two dimensions and can fail to capture changes in diversity occurring at higher levels in the vertical dimension. Vertical vegetation diversity is an important determinant of the diversity and population dynamics of a variety of taxa including birds, spiders, and butterflies. Measuring the effects of deer browse on vegetation in the vertical dimension may be critical to assessing the long-term effects of deer on forest communities and explaining their indirect effects on other fauna.

I measured biomass (vegetation density) and vegetation diversity (species richness) at 20 cm height intervals from ground level up to two meters within 44 pre-existing deer exclosures in New Jersey and Maryland forests and at corresponding control plots outside each exclosure.

Vegetation density in the forest understory was significantly greater at every height up to two meters when protected from deer browse. However, the change in vegetation density was not significantly different among the heights implying that deer reduced density of all heights somewhat evenly. The change in vegetation density was significantly correlated to the exclosure age at the 60-80 cm height ($F_{85}=4.5292$, p=0.04) indicating

that this height is critical to survey to capture effects on vegetation density over time. Species richness inside deer exclosures was significantly greater at every height class in the understory. Furthermore, the change in species richness was significantly different between many of the height classes indicating that the effect of deer varied among heights. The difference in species richness was greatest in the lowest height classes but was correlated to exclosure age at virtually every height except 60-80 cm indicating that multiple heights must be measured to obtain a full picture of deer impacts. Diversity computed from percent cover quadrats was significantly greater in the protected exclosure plots compared to the unprotected plots, however, diversity was not significantly correlated to the age of exclosure ($p=0.0667$, $r^2=-0.03$).

Measuring species richness and vegetation density at multiple heights gives a more detailed picture of impacts of deer browse on forest understories that is also more highly correlated to the length of time the vegetation has been exposed to or protected from deer than standard percent cover quadrats. These vertical measures may be useful in investigating indirect effects of deer on other taxa, tracking deer densities and monitoring forest understory regeneration.

INTRODUCTION

White-tailed deer are recognized as a major threat to the species diversity of forests in the northeastern U.S. (Rooney 2001, Russell et al. 2001, Horsley et al. 2003, Côté et al. 2004). Browsing by white-tailed deer removes understory vegetation changing species composition and successional patterns (Stromeyer and Warren 1997, Waller and

Alverson 1997, Augustine et al. 1998, Horsely et al. 2003). Populations of species preferred by deer are reduced or eliminated including many of the young tree seedlings needed for the future forest canopy (Frelich and Lorimer 1985, Tilghman 1989, Apsley and McCarthy 2004). Herbivory by deer reduces the diversity of the understory (Gill 1992, Russell et al. 1999, Gill and Beardall 2001, Côté et al. 2004) and the average heights of individual species (Balgooyen and Waller 1995, Anderson 1994, Rooney 1997, Williams et al. 2000). The effect on average heights of some species is so well correlated to the size of deer populations that indices have been proposed that use surveys of these species to track deer densities and as surrogates to understand the impact of deer on the broader community (Anderson 1994, Williams et al. 2000, Webster et al. 2001, Morellet et al. 2001).

Deer are known to browse more intensely within an area known as the "browse zone" (Côté et al. 2004). In a review paper, Gill (1992) noted that with red deer "most browsing occurs at an intermediate level between ground and full reach resulting in smaller and larger trees being relatively protected". Although there is no standardized definition of the browse zone, several studies allow a range to be estimated. Kittredge and Ashton (1995) found that seedlings shorter than 50 cm (19.7 in) were browsed significantly less by white-tailed deer than seedlings between 50 cm and 91 cm (36 in) tall. Rooney et al. (2002) found that every sapling of *Tsuga candensis* over 30 cm was eliminated. In studies involving red deer or roe deer, saplings between 30-60 cm tall were generally more vulnerable to browse (Côté et al. 2004, Welch et al. 1991, Kay 1993). The heights at which deer browse are the locations at which many understory species bear their

flowers and fruit. Analysis of deer pellets has revealed seeds of many species (Myers et al. 2004). The capability of deer to eliminate the future generations of populations by preventing individuals from attaining heights necessary to flower (Rooney and Waller 2001), eliminating flowers before seed set (Fletcher et al. 2001) and consuming fruit and seed (Lay 1965) makes it critical to understand impacts in the vertical dimension across the community.

Despite these known effects of deer on heights of species and uneven impacts on species at different heights, the consequences of deer browse on vegetation diversity in the vertical dimension have been largely overlooked. Nevertheless, several studies have provided some evidence to suggest that the mean height of species might serve as a leading indicator of impacts on species richness in the community. In a 10 year study in which deer densities were controlled, Horsley (2003) found that the mean height of the tallest stem typically increased with time but decreased with increasing deer densities. He also found that over time increasing deer density reduced understory density, species richness and diversity. However, the reductions in mean heights became apparent at the lower deer densities over a shorter time period (3-5 years) than reductions in species diversity.

This effect on mean heights was seen by Apsley and McCarthy (2004) who found that the average height of individuals decreased when exposed to a six deer/km^2 density, yet the overall species richness and abundance did not differ from protected plots. This deer density is considered to be fairly low (Alverson et al. 1988, Tilghman 1989, Horsley et al.

2003), so it might require a longer period of time before impacts would become apparent. As average heights of species are reduced, measurement of species richness at these heights would capture a decrease in diversity before the species is actually lost from the plot. These results imply that examining the vertical dimension can provide information about impacts to the community that is not captured by traditional diversity measures.

Foliage height diversity has been used to study the structural composition of forests and forest understories in the vertical dimension (MacArthur and MacArthur 1961, Berger and Puettmann 2000, Fahey and Puettmann 2008). It refers to a measure of structural complexity of the forest vegetation but is related to the density or volume of vegetation at various heights (MacArthur and MacArthur 1961). Foliage height diversity has been shown to be important in structuring avian communities (MacArthur and MacArthur 1961, Pearson 1971, Roth 1976, Wiens 1973) and web spiders (Greenstone 1984). Although most studies of the foliage height diversity index are applied over the whole height of the forest (Aber 1979) and not measured within the understory, altered forest understory resulting from herbivory by deer has been related to reduced populations of forest nesting birds (McShea and Rappole 2000), insects (Allombert et al. 2005) and spiders (Miyashita et al. 2004).

Studies that monitor plant species diversity have traditionally used plot-based or transect-based techniques (Stohlgren 2007) which collapse diversity into a 2-dimensional horizontal plane. The assumption underlying this approach is that observations made at ground-level are sufficient for expressing plant diversity in a manner that is meaningful

to the rest of the community. However, vertical differences in the plant species present may result in vertical differences in the abundances of pollinators or phytophagous insects (Haddad et al, 2001, Loyola and Martins 2008, Sobek et al. 2009) both of which have implications on prey abundances for birds and spiders. The identities of the plant species, and not simply their physical or structural characteristics, in the vertical dimension may also be relevant. For certain butterflies, vertical differences in plant species, specifically the larval host plants, resulted in the vertical stratification of adult ithomiine butterflies (Beccaloni 1997). DeVries et al. (1997) examined the species diversity of butterflies in Ecuador over horizontal, vertical and temporal dimensions and found significant diversity differences in each dimension. They argued for the importance of studying diversity in all three dimensions.

Deer impacts also result in altered vegetation density (Hough 1965, Tilghman 1989, Knops et al. 2000, Gill and Beardall 2001) leading to changed niche space, or habitat availability, for many taxa (McShea and Rappole 2000, Haddad et al. 2001). Yet, there are only a handful of studies which provide historical vegetation density data for the deciduous forest understory measured in the vertical dimension. Nudds (1977) studied habitats for wildlife cover and measured understory vegetation density at four height classes using a coverboard method in a deciduous forest. He found that vegetation density did not vary significantly between classes. Aubin et al. (2000) measured percent cover (viewed from above) of understory vegetation at three height classes in six different forest types and showed that all deciduous types had the greatest cover from 0-50 cm.

White-tailed deer are known to reduce both vegetation diversity and density of the understory but effects on these factors at various heights within the understory are not known. If vertical measures do not provide any new information, then vegetation diversity and density should decrease uniformly at all heights when subjected to deer browse, and diversity changes should be consistent with the results obtained from percent cover plots. However, if vertical measures of vegetation diversity and biomass do provide additional information, there should be significant differences among the height classes in terms of the magnitude of the effect of deer or results that provide a better correlation with deer pressure than the results obtained from percent cover plots.

I predicted that diversity and vegetation density would decrease at different rates at different heights in forest understories when exposed to deer and that the greatest impact on vegetation density and diversity would be measured within height classes occurring in the browse zone. Therefore, I expected the effects to be seen primarily in the heights from 30 cm to one meter within the understory. However, since the heights are not independent, vegetation removed from the middle range may also result in impact to the higher height classes.

The length of time the area was protected from deer browse should be related to the magnitude of the effects of deer on diversity and density at various heights as vegetation recovers and grows over time. I predicted that differences in vegetation density and diversity between protected and unprotected plots would be correlated to the length of time the plots have been protected. I expected the middle and higher height classes to

have a greater correlation to time since they are likely to be affected first and it would

take longer for species to grow to these heights during recovery.

I tested these predictions by measuring vegetation diversity and density in 20 cm height

increments within the forest understory when protected from deer browse and exposed to

deer browse at a collection of pre-existing deer exclosures of various ages.

METHODS

Sites

To determine whether vertical measures of plant diversity and density were impacted by

deer, I collected data at 44 pre-existing deer exclosures in New Jersey and Maryland

(Table 1.1). Studies using fencing to exclude deer from areas of forest to demonstrate the

effect of deer browse on vegetation dynamics have been conducted since the 1960's

(Côté et al., 2004). I chose exclosures that were situated in forests, had not undergone

manipulation in the form of herbicide application, physical removals or plantings, and

were erected at least one growing season prior to the study. All exclosures were

structurally intact and showed no evidence of recent deer browse inside the exclosure at

the time of sampling. Twenty eight of the selected exclosures were located across

northern and central New Jersey at 14 separate sites, and 16 were located in eastern

Maryland and Washington D.C. at four sites (Figure 1.1). The average age of the

exclosures was 9.7 years at the time of sampling and ages ranged from 1 to 30 years.

Table 1.1 List of deer exclosures sampled.

Location	Site Name	Exclosure size(m^2)	Year installed
1. Englewood, NJ	Flat Rock Brook Nature Center	36	2004
2. Upper Freehold, NJ	Clayton Park	81	2003
3. Highlands, NJ	Hartshorne Woods	81	2003
4. Highlands, NJ	Hartshorne Woods	81	2005
5. Middletown, NJ	Tatum Park	81	2003

6.	Lincroft, NJ	Thompson Park	81	2003
7.	Freehold, NJ	Turkey Swamp Park	81	2004
8.	Freehold, NJ	Turkey Swamp Park	81	2005
9.	Morristown, NJ	Morristown National Historic Park	36	1987-88
10.	Morristown, NJ	Morristown National Historic Park	36	1987-88
11.	Morristown, NJ	Morristown National Historic Park	36	1987-88
12.	Morristown, NJ	Morristown National Historic Park	36	1987-88
13.	Morristown, NJ	Morristown National Historic Park	100	1995
14.	Morristown, NJ	Morristown National Historic Park	100	1997
15.	Morristown, NJ	Morristown National Historic Park	100	1997
16.	Morristown, NJ	Morristown National Historic Park	100	1997
17.	Sandyston, NJ	Stokes State Forest	116	1986
18.	Ringwood, NJ	Wanaque Reservoir	21	2003
19.	Frelinghuysen, NJ	Johnsonburg Swamp Preserve – Nat. Cons.	1600	2005
20.	Frelinghuysen, NJ	Johnsonburg Swamp Preserve – Nat. Cons.	1600	2005
21.	Frelinghuysen, NJ	Johnsonburg Swamp Preserve – Nat. Cons.	1600	2005
22.	Frelinghuysen, NJ	Johnsonburg Swamp Preserve – Nat. Cons.	1600	2005
23.	Mountainside, NJ	Watchung Reservation	116	1995
24.	Mountainside, NJ	Watchung Reservation	116	1995
25.	Harding, NJ	Great Swamp Watershed Association	97	2006
26.	Basking Ridge, NJ	Lord Stirling Park – Somerset Co.	~100	2007
27.	Walpack,NJ	Delaware Water Gap Nat'l Rec. Area[+]	100	2005
28.	Walpack,NJ	Delaware Water Gap Nat'l Rec. Area[+]	100	2005
29.	Sharpsburg, MD	Antietam National Battlefield	25	2005
30.	Sharpsburg, MD	Antietam National Battlefield	25	2005
31.	Sharpsburg, MD	Antietam National Battlefield	25	2005
32.	Sharpsburg, MD	Antietam National Battlefield	25	2005
33.	Sharpsburg, MD	Antietam National Battlefield	25	2005
34.	Thurmont, MD	Catoctin Mountain Park	400	~1988
35.	Thurmont, MD	Catoctin Mountain Park	400	~1988
36.	Thurmont, MD	Catoctin Mountain Park	400	~1988
37.	Thurmont, MD	Catoctin Mountain Park	400	~1988
38.	Thurmont, MD	Catoctin Mountain Park	400	~1988
39.	Frederick, MD	Monocacy National Battlefield	25	2005
40.	Frederick, MD	Monocacy National Battlefield	25	2005
41.	Frederick, MD	Monocacy National Battlefield	25	2005
42.	Frederick, MD	Monocacy National Battlefield	25	2005
43.	Washington, DC	Rock Creek National Park[++]	100	~1978
44.	Washington, DC	Rock Creek National Park[++]	100	~1978

+ Delaware Water Gap exclosures are areas randomly selected from one large 5600 m^2 exclosure
++ Rock Creek Park exclosures are areas randomly selected from the forested area in one large 10,000 m^2 exclosure (the fenced amphitheater).

I sampled New Jersey exclosures from late May 2008 through early July 2008, and I

sampled Maryland exclosures in July and August 2008. I collected data from both inside

the exclosure (effective deer density 0 deer/km^2) and outside the exclosure (ambient deer

density), in each case. I sampled the inside and outside plots for an exclosure either on

the same day or on successive days. At the majority of these sites, no reliable deer density estimates were available.

Precipitation and temperature in New Jersey during the sampling periods were slightly below average and slightly above average, respectively while precipitation and temperature in Maryland were below normal and near normal respectively (Table 1.2).

Table 1.2 Precipitation and temperature in study regions during sampling.

State	Month	Precipitation (in.)	Temperature (°F)
		Mean	Mean
New Jersey (north)	June	Mean: 4.07	Mean: 68.2
		2008: 3.47	2008: 73.1
New Jersey (south)	June	Mean: 3.7	Mean: 69.9
		2008: 3.33	2008: 74
Maryland (BWI aiport)	July	Mean: 4.07	Mean: 77.0
		2008: 5.47	2008: 77.5
	August	Mean: 3.29	Mean: 75.1
		2008: 1.48	2008: 73.6

(Sources: New Jersey and Maryland State Climatologist Offices)

Exclosures were located over a broad geographical area across five different physiographic provinces: Coastal Plain (7 in NJ), Piedmont (4 in NJ, 4 in MD), Ridge and Valley (6 in NJ, 4 in MD), Highlands (8 in NJ), and Blue Ridge (5 in MD) (Figure 1.1).
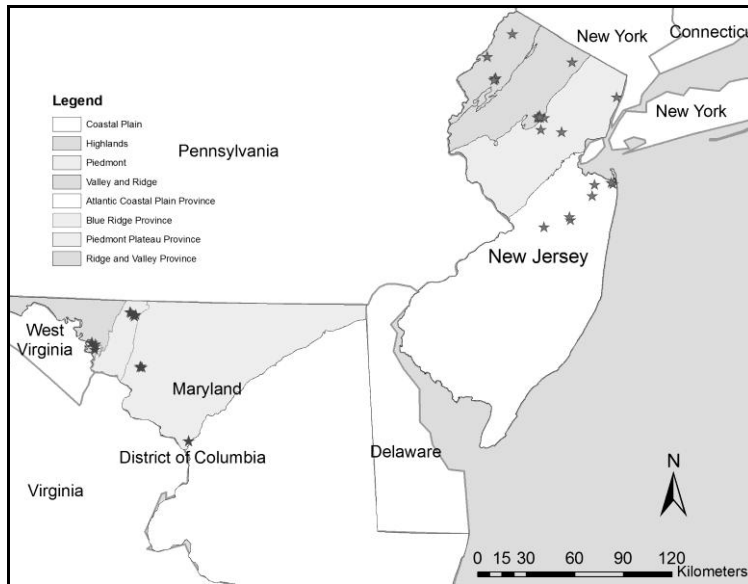
Figure 1.1 Map of deer exclosure locations with physiographic provinces.

Vertical Measures

At each location, I established a 2-m radius circular plot (12.6 m^2) in the center of the exclosure sample area as the inside plot. The outside plot was located adjacent to the exclosure on the side of the exclosure which appeared most similar in topography and vegetative cover to the inside plot and centered the same distance away from the exclosure fence as the inside plot. In the rare case that a control area had been identified when the exclosure was erected, I placed my outside plot in the center of that area. I measured diversity in the vertical dimension as vascular plant species richness within the plot at each of ten height classes in 20 cm intervals from ground level up to two meters. Above two meters, I recorded species richness at three additional height classes of 2-3 m, 3-4 m, and above 4 m.

I also measured biomass in the vertical dimension as vegetation density within each 20 cm height class up to two meters. I recorded vegetation density by estimating percent

coverage of a 20 x 20 cm card placed at the plot center and viewed horizontally at each of eight equally spaced points around the margin of the plot (Figure 1.2). This method is similar to that proposed by Collins and Becker (2001) to measure horizontal cover.
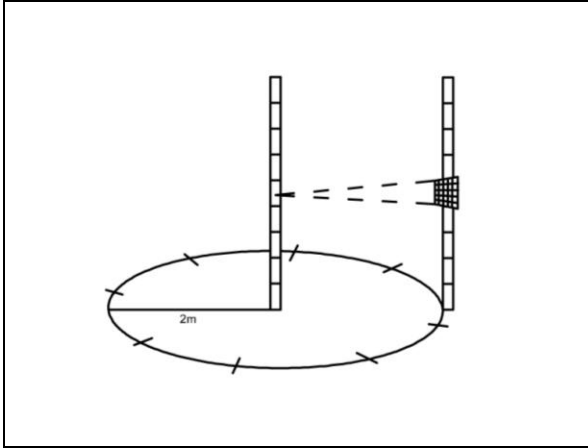
Figure 1.2 Illustration of vertical density measurement.

Covariates

At each plot, I collected soil moisture and canopy closure measurements as covariates. Because both moisture and light availability may influence diversity and production of biomass (Terborgh 1985, Tilman and Pacala 1993), ensuring that these factors in the control plots did not vary significantly between the control and exclosure plots was crucial. I measured soil moisture as volumetric water content (a percentage) using a Hydrosense^{TM} moisture meter (Campbell Scientific, Inc., Logan, Utah, USA) with 20 cm probes. I measured canopy closure using a hemispherical photograph taken at the plot center from a height of two meters with a Kodak Z740 camera and a fisheye lens. I used Gap Light Analyzer (GLA) software, version 2.0 (Frazer et al. 1999) to obtain percent canopy openness. I analyzed all photographs using the same configuration settings, with the blue color plane and a pixel threshold of 150.

Percent Cover Quadrats

I sampled traditional ground-level percent cover quadrats at each New Jersey deer exclosure. I recorded percent cover of each vascular plant species in 1% increments as the percentage of ground obscured by that species within a 1-m^2 quadrat when viewed from above at a height of approximately one meter. I estimated cover for each species as if other species were not present, and I included only those individuals rooted within the plot. I randomly selected each 1-m^2 quadrat from a grid of 1x1 m cells laid over the exclosure area. I excluded a one meter buffer along the fence line from the sample area. I selected the number of quadrats approximating 10% of the sample area, for example, 10 quadrats would be sampled for a 100 m^2 sample area. I sampled the same quadrats outside the exclosure in the paired control plot area. For large exclosures which were greater than 400 m^2 in area, to select a practical number of quadrats to sample, I divided these exclosures into 10 x 10 m sections and randomly selected one section to sample. All quadrats were permanently marked at each corner with labeled stakes.

Validating the Relationship of Vegetation Density to Biomass

To confirm the relationship between my vertical measure of vegetation density to biomass, I collected data away from the main study sites at Turkey Swamp Park in Monmouth County, New Jersey (40°12'50" N 74°19'25" W). I selected this park because it contained a variety of densities of understory vegetation, an important aspect for the comparison. I laid out three 50 m transects through sections of forest. At every five meters along each transect, I placed a 0.5 x 2 m plot perpendicular to the transect. I

measured vertical vegetation density at each of the 20 cm height classes from ground level to 180 cm as described above. Then, I carefully clipped and bagged the vegetation for each height class. I dried the samples at 60 °C for 20-24 hrs then weighed them using a Mettler-Toledo PB602-S balance (Mettler-Toledo Inc., Columbus, OH). I also recorded whether the vegetation biomass included substantial woody material since woody and herbaceous vegetation would not be distinguished when sampling percent cover, but woody vegetation would have a much greater mass than herbaceous vegetation.

Statistical Methods

All analyses were performed using R software version 2.11.1 (R Development Core Team 2010). Box and whisker plots were produced using the default R boxplot function. Heavy lines across each box represent the median. Boxes represent the first through third quartiles. The step is calculated as one and a half times the inner quartile range between the first and third quartiles. Points outside a step from the first or third quartile are shown as outlying dots. Whiskers are draw to the maximum and minimum point within the step (Murrell 2005).

 ➢ *Analysis of Comparable Controls - Covariates*

I analyzed soil moisture and canopy closure to ensure that there was no significant difference in these factors between plots inside exclosures and the corresponding plots outside the exclosures. I checked the soil moisture residuals for normality then I ran a paired t-test on the paired soil moisture samples. I checked the canopy closure residuals for normality and transformation failed to result in normality, so I ran the non-parametric

Wilcoxon signed rank test on the paired canopy closure samples. In addition, since there may have been some interaction between soil moisture and canopy closure and therefore these variables should not be treated as independent, I ran Hotelling's paired-sample t-squared test (HotellingsT2 function, ICSNP 1.0-7 library) to confirm that there were no significant differences in these variables between inside and outside plots. Hotellings' paired-sample t-squared test is a multivariate form of the student's paired-sample t-test (Anderson 2003).

➢ *Analysis of Vertical Vegetation Density*

For each height class, the eight density readings for a plot were averaged together. For each 20 cm height class, I checked the set of these average vegetation densities for the plots for normality. They were not normal and transformations failed to result in normality. I ran Hotelling's paired-sample t-squared test on the paired inside and outside plots. The change in vegetation density was computed as the difference between inside and outside plot density for each paired sample at each height. Then to determine which heights contributed to the difference between inside and outside plots, I ran a MANOVA and extracted the ANOVA tables for each height class from this model. Finally, I calculated Tukey's HSD comparison of means to determine which heights differed significantly from other heights.

➢ *Correlation between Biomass and Vertical Vegetation Density Measure*

I expressed vertical vegetation density as a proportion and then applied an arcsine-square-root transformation to meet assumptions of normally-distributed data. I used a natural log

transformation on dry weight biomass to produce normality. I ran a linear regression between the transformed dry weight biomass and vegetation density data with a Boolean factor of whether the sample was primarily woody or not.

➢ *Analysis of Vertical Vegetation Diversity*

For each height class, I calculated species richness as the number of species present in that height class. Data were not normal and transformations failed to result in normal data. I compared species richness from inside plots to outside plots at each height using the same analysis as I used for vertical vegetation density.

➢ *Analysis of Diversity from Percent Cover Quadrats*

For each exclosure, the percent cover quadrats were used to calculate diversity as the effective number species expressed as the exponential of Shannon's entropy, exp H' (Equation 1.1) where p_i is the species frequency within the plot (Jost 2006). exp H' expresses diversity as a number of species rather than an entropy.

$$D = \exp\left(-\sum_{i=1}^{s} p_i \ln p_i\right)$$

(1.1)

The data were natural log-transformed to meet the assumption of normality. The diversity inside exclosures was compared to the diversity outside exclosures using a paired-sample test.

➢ *Correlation of Age of Exclosure to Vertical Density, Vertical Diversity, Percent*
   Cover Diversity

To determine if the age of the exclosure was correlated to the difference in vegetation density between inside and outside plots, I ran an ANOVA with vertical vegetation density as the response, the plot type (inside or outside) as a fixed factor and age of the exclosure as a predictor variable. I repeated the same analysis using the vertical species richness between inside and outside plots to determine if the age of exclosure was correlated to changes in vegetation diversity at each height. Finally, I ran a linear regression between the difference in diversity as calculated from the percent cover quadrats between inside and outside plots against the age of the exclosure to determine if there was a correlation.

RESULTS

Comparable Controls - Covariates

The mean soil moisture inside exclosures was 15.28% $\pm$ 1.36 and outside the exclosures it was 16.79% $\pm$ 1.51. In the paired t-test, soil moisture did not differ significantly inside and outside exclosures (t=-1.6631, df=41, p = 0.104). Note that there are 44 deer exclosures, but one outside plot and one inside plot had no soil moisture readings (due to inability to insert the probe in rocky ground) resulting in only 42 pairs of complete data and hence 41 degrees of freedom for the t-test. The mean canopy closure inside the exclosures was 76.16% $\pm$ 1.85 and outside the exclosures it was 75.73% $\pm$ 1.88. Canopy closure did not differ significantly inside and outside the exclosures in the Wilcoxon signed-rank paired-sample test (V=383, p=0.6397). The multivariate paired-sample test, Hotelling's t-squared, confirmed that soil moisture and canopy closure were not

significantly different between paired inside and outside plots ($T^2= 0.2774$, d.f.$= 2,83$, p=0.7584).

Vertical Vegetation Density

The vertical vegetation density profile showed the greatest vegetation density at the lowest height class decreasing to a consistent level in the upper classes (Figure 1.3).
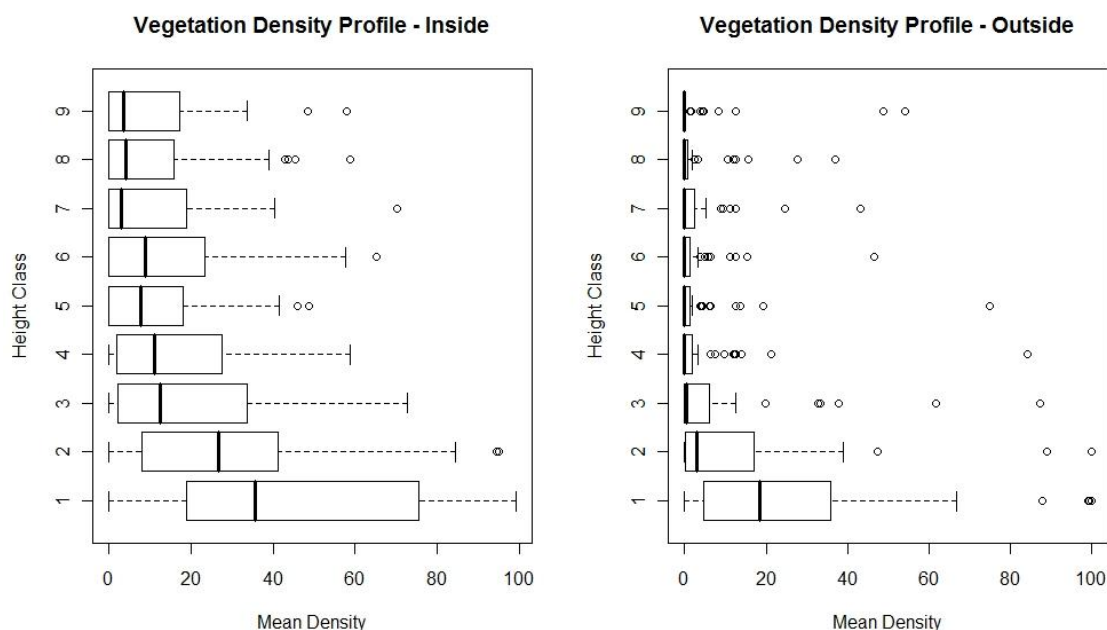
Figure 1.3 Vertical vegetation density profiles. Each class represents a 20 cm layer from 0-20 cm at height class 1 up to 160-180 cm at height class 9. n=44.

Inside exclosures the mean densities decrease from a high near 43% at the lowest height class and stabilize around 10% in the top three heights. Outside the exclosures the mean density is lower, starting at near 27% and dropping to single digits by the third height class (40-60 cm) where it remained (Table 1.3).

Table 1.3 Mean vegetation densities for each height at deer exclosures.

Class	Height (cm)	Mean Density ± SE	
		Inside (%)	Outside (%)
9	160 – 180	10.1 ± 2.1	3.3 ± 1.6
8	140 – 160	10.8 ± 2.3	2.9 ± 1.1
7	120 – 140	11.0 ± 2.3	3.4 ± 1.2
6	100 – 120	14.2 ± 2.4	2.6 ± 1.2
5	80 – 100	12.2 ± 2.1	3.4 ± 1.8
4	60 – 80	15.6 ± 2.3	4.4 ± 2.0
3	40 – 60	19.7 ± 3.0	7.7 ± 2.7
2	20 – 40	29.5 ± 4.0	12.7 ± 3.2
1	0 – 20	42.6 ± 4.8	26.6 ± 4.3

Hotelling's paired sample t-squared test shows that the vegetation density is significantly different between the paired inside and outside plots (T^2=2.9313, d.f.=9, p=0.005) The differences between vegetation densities inside exclosures and outside exclosures is graphed in Figure 1.4 implying that, at every height class, the vegetation density inside the exclosures is greater than the density outside the exclosures.
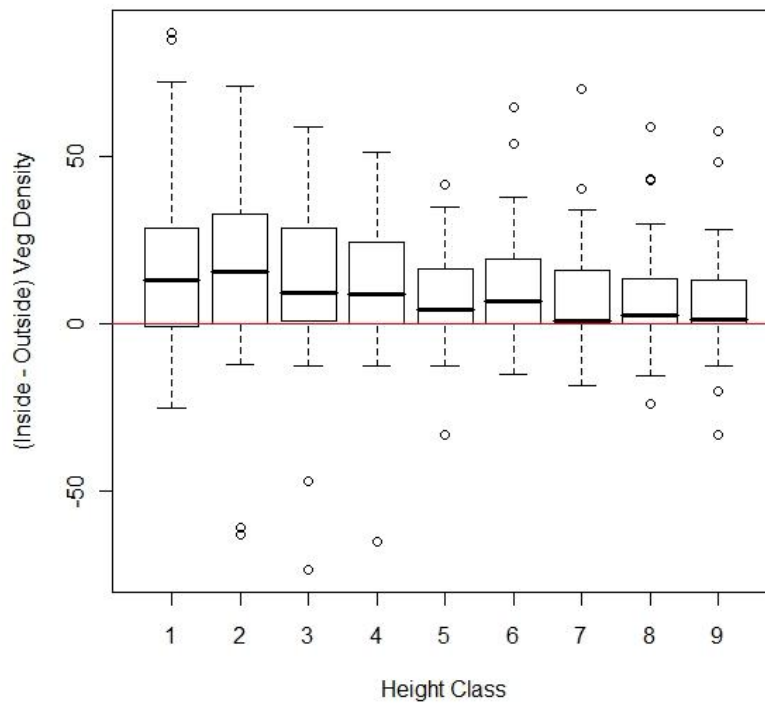
Figure 1.4 Difference in mean densities between inside and outside plots. Points above the zero line indicate densities that are greater in the inside plots.

The MANOVA confirms that the vegetation density is significantly different between the inside and outside plots (F=2.9313, d.f.=9,78, p=0.005) giving the same results as the Hotelling t-squared test, and the ANOVA tables show that each height contributes to this difference (all p-values < 0.01, d.f. =86) as is apparent in Figure 1.4.

The mean difference in vegetation density between inside and outside plots at each height class shows that vegetation density is an average of 7 to almost 17% greater inside the exclosures than outside (Table 1.4).

Table 1.4 Mean density difference (inside – outside) for each height

Class	Height (cm)	Mean Density Difference $\pm$ SE (%)
9	160 – 180	7.0 $\pm$ 2.4
8	140 – 160	8.0 $\pm$ 2.5
7	120 – 140	7.6 $\pm$ 2.5
6	100 – 120	11.6 $\pm$ 2.5
5	80 – 100	8.8 $\pm$ 2.2
4	60 – 80	11.2 $\pm$ 2.8
3	40 – 60	12.0 $\pm$ 3.4
2	20 – 40	16.8 $\pm$ 4.2
1	0 – 20	16.0 $\pm$ 3.8

An analysis of variance and Tukey's HSD comparison of means showed that there was not a significant difference in the change in vegetation density when protected from deer among the height classes (all p-values > 0.05). Vegetation density at each height had a response that was not significantly different from the other heights when protected from deer.

The ANOVA with vertical vegetation density and exclosure age showed that age was significantly correlated with the difference in vegetation density only at height class 4 (60-80 cm) (F=4.5292, d.f.=85, p=0.036) but not with any of the other heights.

Vegetation Density Relationship to Biomass

The mean vegetation density of the samples in this study was 19.3% $\pm$ 2.7 SE with samples ranging from 0% to 100% density, and the mean dry weight biomass of the vegetation in a sample was 16.0 g $\pm$ 3.2 SE with weights ranging from 0 to 229 g. Of the 135 samples, 24 were primarily woody biomass while the remaining 111 were primarily herbaceous biomass. The linear regression of the transformed data with vegetation

density as the predictor variable, biomass as the response and whether the sample was woody as a Boolean factor showed that a strong positive linear relationship existed (F=405.5, d.f.=2,132, p<<0.001, r^2= 0.86). The data are graphed with regression lines in Figure 1.5.
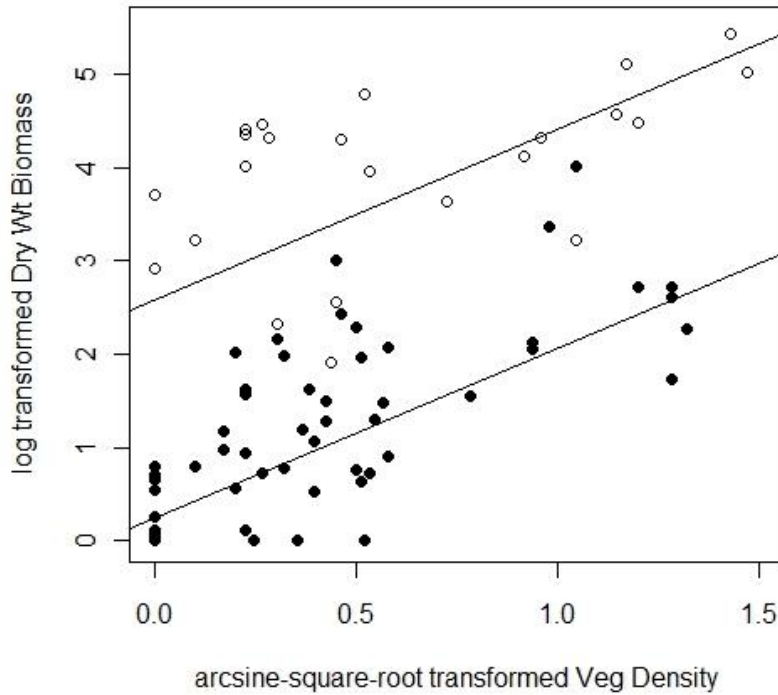
Figure 1.5 Relationship between vegetation density and biomass. Black points are primarily non-woody vegetation. White points are primarily woody vegetation. The lines are regression lines drawn using the intercept and coefficients from the regression. n=135, r^2= 0.86.

Vertical Vegetation Diversity

The vertical species richness profile shows that the greatest number of species occurs in the lowest height class and the number of species decreases in the higher classes (Figure 1.6).
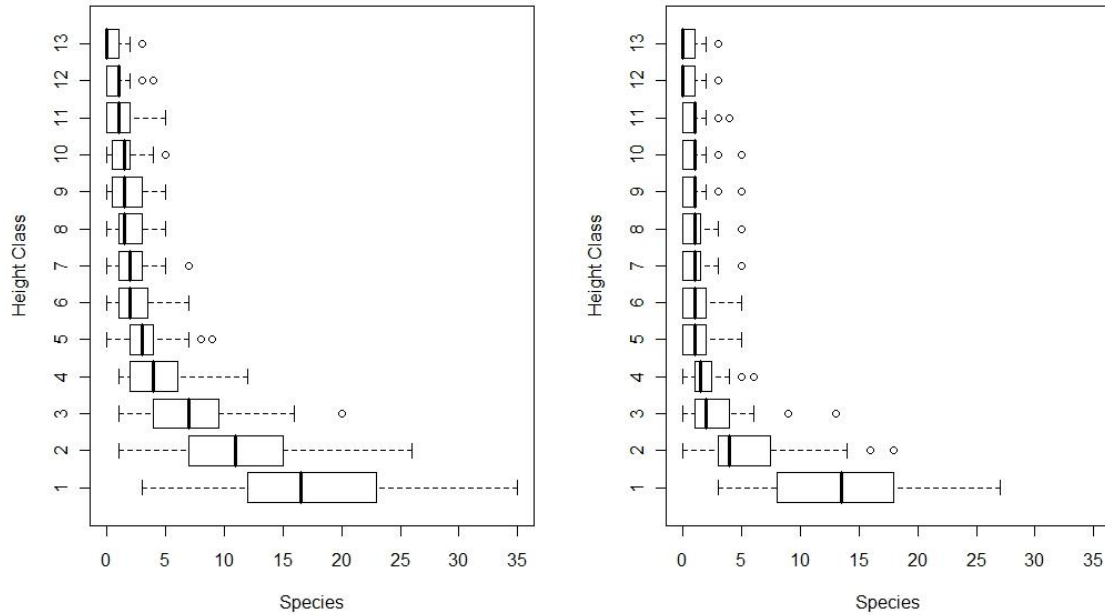
Figure 1.6 Vertical vegetation species richness profiles. Each class represents a 20 cm layer from 0-20 cm at height class 1 up to 180-200 cm at height class 10 while height class 11 is from 2-3 m, class 12 is from 3-4 m, and height class 13 is everything above 4 m. n=44.

Inside exclosures the mean species richness decreases from a maximum near 18 species in the lowest height class, and as the height increases, gradually drops to around one species at two meters (height class 11) and above. Outside the exclosures the species richness starts at a lower number of species with 14 in the lowest height, and quickly drops to around one species at a height of about 80 cm (height class 5) and remains at about one species for all the heights above that.

The paired-sample Hotelling t-squared test indicated that the species richness at the various heights differs significantly between the paired inside and outside plots (T^2=49.7052, d.f.=13, p=<<0.001).

The differences between species richness inside exclosures and outside exclosures are graphed in Figure 1.7 suggesting that, at every height class up to two meters, the species

richness inside the exclosures is greater than the species richness outside the exclosures. However, Figure 1.7 also suggests that in the upper height classes there may not be a significant difference in species richness.
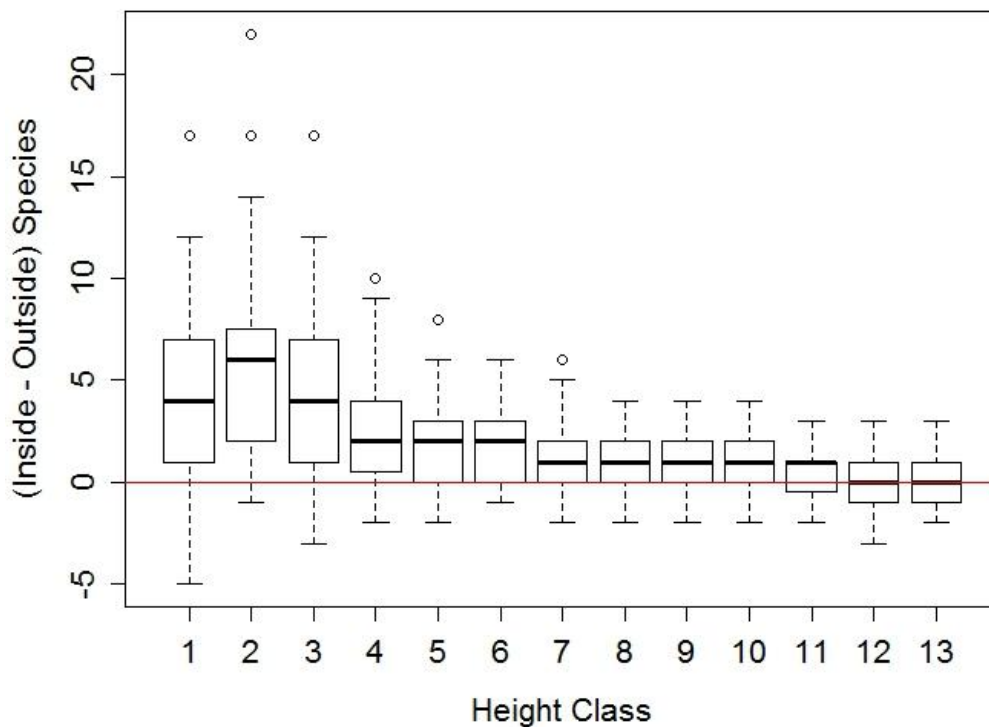
Figure 1.7 Difference in mean species richness between inside and outside plots. Points above the zero line indicate greater species richness in the inside plots.

The MANOVA results were consistent with the above test and showed that species richness between inside and outside plots differed significantly (F=3.29, d.f.=13,74, p=<0.001). Each height up to and including class 11 (2-3 m) was significantly different between the inside and outside plots (p-values < 0.05). However, species richness above three meters (classes 12 and13) was not significantly different between inside and outside plots, consistent with Figure 1.7 (p-values 0.24 and 0.42 respectively). Tukey's HSD comparison of means between the changes in species richness among the height classes

indicated that height 1 differed significantly from height 2 and 6 through 10, height 2 differed significantly from heights 4 through 10 and height 3 differed significantly from heights 5 through 10. The impact of deer on species richness was stronger in height classes 1-3 (0-60 cm) than in the upper classes.

Analysis of variance with the covariate of exclosure age showed that age was significantly correlated with the difference in species richness at most heights except for height class 4 (60-80 cm).

Percent Cover Quadrats

Using the percent cover quadrat data collected at the New Jersey exclosures, the mean diversity, D, inside the exclosures was 6.72 ± 0.83 SE and ranged from 1 to 18.1 while outside the exclosures the mean diversity, D, was 5.01 ± 0.77 SE ranging from 0 to 17.8. The diversity was an average of 1.7 greater inside the exclosures. The diversity measured by quadrats inside and outside the exclosures was significantly different in a paired t-test on the transformed data (t = 3.8351, df = 27, p-value = <0.001).

The change in diversity, D, inside the exclosure compared to outside is graphed against the age of the exclosure in Figure 1.8 using untransformed data. The graph shows that most exclosures had greater diversity inside the exclosure. However, the linear regression between the change in diversity (inside-outside) did not show a significant relationship to the age of the exclosure ($F_{1,26}$=0.1891, p=0.667, r^2 = -0.03).
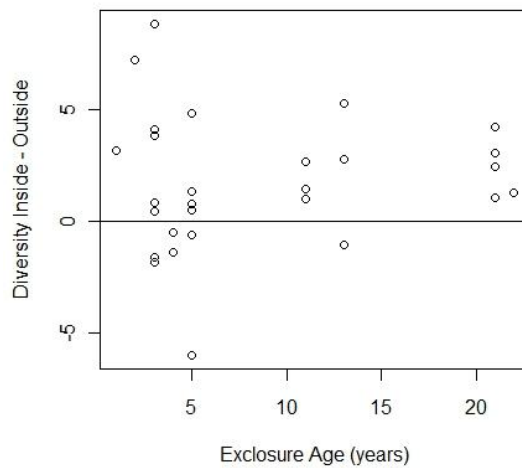
Figure 1.8 Difference in quadrat diversity, D vs. age of exclosure. (n=28). Positive values for the diversity difference (y-axis) indicate greater diversity inside the exclosure, negative values indicate greater diversity outside the exclosure. Shown with a zero line.

DISCUSSION

The vertical profile of vegetation density (Figure 1.3) showed that vegetation density was greatest at the lowest height and decreased as height increased in the understory. This pattern is consistent with the pattern of vegetation density reported by Aubin et al. (2000) for vegetation density in forest understories in three of the six forest types they tested and contrary to Nudds (1977) who found that there was not a significant variation between heights. Aubin et al. (2000) found this understory density pattern in forests with canopies of mixed deciduous-conifer, white birch, and closed conifer. In the white birch and mixed deciduous-conifer forests, the largest numbers of species in the lowest height class (0-50 cm) were made up of herbaceous plants. These two forest types are consistent in general composition with the deciduous forests in which my studies were conducted.

I predicted that vegetation density would decrease at different rates at different heights in the forest understory when exposed to deer, and I expected the greatest impact on density to occur in the browse zone between 30 – 100 cm (height classes 2 to 5). Vegetation density did decrease significantly in all heights up to 2 meters when exposed to deer browse; however, Figure 1.4 and Tukey's HSD test showed that there was no significant difference in the decline in vegetation density among heights. This result indicates that specific heights do not have a greater response to deer browse but rather that all respond similarly. This result is somewhat surprising considering the different ages of the deer exclosures. It might be expected that vegetation would recover more quickly in the lower height classes as new plants establish and more slowly in the higher height classes since it takes some time for plants to grow into these classes and some species simply are physiologically incapable of growing to those heights. Additional study is needed to examine the mechanisms behind this pattern in the change in vegetation density under deer browse.

The vertical profile of species richness in plots protected from deer (Figure 1.6) showed that species richness was greatest at the lowest height and decreased as height increased in the understory. This pattern also held true for plots outside the exclosures which were exposed to deer browse but at each height the number of species was reduced. This pattern of vertical species richness is consistent with a large number of herbaceous species in the understory and fewer woody species at taller heights as found by Aubin et al. (2000) in deciduous forests.

I predicted that vegetation diversity would decrease at different rates at different heights in forest understories when exposed to deer and that the greatest impact on vegetation diversity would be measured within height classes occurring in height classes 2 to 5 (30 cm to 100 cm) within the understory. Figure 1.7 and the results of the Tukey's HSD tests showed that species richness did change differently at different heights with more species being lost in height classes 1-3 (0-60 cm) than in the upper heights when exposed to deer browse. This result is only partially consistent with predictions. Species richness within the putative browse zone did decline and at a greater rate than species richness from 1-2 meters but not at a greater rate than ground-level species richness. In addition, species richness in the height classes representing the upper end of the browse zone (60 cm-1 meter) did not change at the highest rate as expected. The greater change in the lower heights could mean that exclosures result in greater establishment and survival of young plants or short-statured species. Royo et al. (2010) and Tanentzap et al. (2011) had found slower than expected recovery in deer exclosures and suggested that legacy effects from browse-resistant species or lack of propagules of browse-sensitive species may prevent recovery. The greater change in species richness in the lower heights in my study argues that these issues are not occurring in this case, at least not in enough cases to influence the overall result. Royo et al. (2010) did find increases in heights of several browse-sensitive species and I suggest that vertical measurement of species richness might have captured this effect as perhaps a leading indicator of recovery.

Diversity as measured from ground-level percent cover quadrats also showed a decline when exposed to deer browse giving a result consistent with the vertical measure of

species richness. These results are also consistent with previous studies that concluded deer reduce diversity in forest understories (Gill 1992, Russell et al. 1999, Gill and Beardall 2001, Côté et al. 2004).

Soil moisture and canopy closure readings taken for the exclosures at the paired unprotected plots outside the exclosures showed that no differences in these variables were present between the protected and unprotected plots indicating that the outside plots were appropriately chosen. Therefore there were no differences in soil moisture or light availability that might have influenced the differences in species richness or vegetation density seen between the protected and unprotected pair. The biomass comparison to vegetation density study also showed that my measure of vegetation density provided a good surrogate measure for biomass (Figure 1.5) with a strong correlation when woody and herbaceous material types were taken into consideration explaining 86% of the variation.

I predicted that differences in vegetation density and diversity between protected and unprotected plots would be correlated to the length of time the plots have been protected. I expected the middle and higher height classes to have a greater correlation to time. The vertical vegetation density was only related to the age of exclosure at the 60-80cm height which seems to support the prediction that deer would have a greater impact on the middle heights. This result suggests that when measuring vegetation density to track impacts from deer it is critical to measure the 60-80 cm height. However, this height class was the only class from ground-level to two meters in which the species richness was not

related to the age of exclosure. This result implies that multiple heights must be measured to track changed in species richness caused by deer browse. That species richness in the lowest height class is also related to age provides further evidence that legacy effects are not preventing re-establishment of species in these locations. The significance of age may simply be reflecting the time it took seedlings which established after protection to reach that height class.

Percent cover quadrats indicated that diversity was reduced in plots not protected from deer, but when looking at Figure 1.8 we see that the age of the exclosure was not able to be correlated with the change in diversity at deer exclosures. Vertical species richness was correlated to the age of exclosure at almost every height, including ground-level, providing more information than was available from percent cover quadrats alone. This result is surprising since percent cover quadrats should have given a more accurate measure of ground-level diversity. Since the diversity measure includes a component of evenness as well as a component of richness, it is possible that a few dominant species may be influencing the diversity result. In this study, the richness component seems to be the factor most correlated to exclosure age.

These results have some interesting implications on the structuring of other taxa within the understory. Since vegetation density changes caused by deer browse do not occur in different magnitudes in different strata with the understory, for other taxa which may be tied to vegetation density such as phytophagous insects this implies that the effect of deer browse will be the same at all heights. However, since vegetation diversity does change

differently in different understory strata, taxa which may be dependent on specific species or may be related to a diversity of species will be affected differentially at different heights. Further investigation is needed to elucidate what this change in vertical diversity among strata in the understory may mean to other taxa.

If patterns of impact to diversity in the vertical dimension are well-correlated to deer densities, species richness within height classes could be used to monitor deer populations. In general, deer densities have been found to be well-correlated with vegetative impacts (Russell et al. 2001, Tilghman 1989, Horsely et al. 2003). Several individual plant species have been proposed as indicators of deer impact (Frelich and Lorimer 1985, Balgooyen and Waller 1995, Anderson 1994, and Williams et al. 2000); however, the usefulness of these indices is often restricted to communities in which the target species is relatively common. Only a few studies have suggested using a suite of species as indicators of deer pressure (Williams et al. 2000, Fletcher et al. 2001, Webster et al. 2001, Benner 2006). In ecology, the community measures of species diversity and biomass (vegetation density) are widely used and are applicable across broad geographical ranges. Species diversity and productivity can be strongly influenced by abiotic factors (Tilman and Pacala 1993) and these measures taken on a two-dimensional level may not be sensitive enough to capture the effect of deer in forest understories especially given the strong effect of deer on the vertical heights of species. However, by including a vertical dimension, a stronger correlation to deer densities might be shown.

These studies have shown that measuring species richness and vegetation density at multiple heights gives a more detailed picture of impacts of deer browse on forest understories that is also more highly correlated to the length of time the vegetation has been exposed to or protected from deer than standard percent cover quadrats. These vertical measures may be useful in investigating indirect effects of deer on other taxa, monitoring deer densities, and monitoring forest understory regeneration. Additional study is needed to determine how these impacts at the various heights correlate to the actual deer densities present at the sample sites which will be explored in the next chapter.

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CHAPTER 2: Relationship of Understory Species Heights to Varying Deer Density

ABSTRACT

Deer overbrowse affects forests across the northeastern United States. Despite many studies suggesting various plant species could be used as phyto-indicators of deer overpopulation, a single measure which captures the subtle impacts of deer at lower densities and the regeneration of newly protected forests and is applicable across a broad geographic area has not been found. Since the average heights of many species are affected by deer browse, I hypothesized that a vertical measure of species richness within understories would encapsulate this effect and allow estimation of deer density across multiple communities without requiring the presence of specific plant species. I collected vertical data in plots across 10 forests in the greater Washington D.C. area with a gradient of deer densities ranging from 5 deer/km^2 to 78 deer/km^2 and from within pre-existing deer exclosures to represent 0 deer/km^2. Vertical profiles of species richness followed a negative exponential distribution for all sites with the coefficient of the exponential describing the rate of species loss in the vertical dimension in the understory, which I am calling the species attenuation coefficient. The species attenuation coefficient was linearly related to the deer density across the various sites explaining 31% of the variation (p=0.04, r^2=0.31). The increasing rate of species loss across the height strata was clearly tied to increasing deer density; however neither species richness nor diversity measured from percent cover quadrats were significantly related to deer densities. Species height profiles followed the reverse-J distribution within the understory across these forests. This relationship provides a baseline against which to test in other geographical regions, in other types of forest stands, and under other types of disturbance. Forest modelers who

seek to understand understory dynamics may also make use of this relationship since it provides information about the development of understory height structure and potentially a leading-edge indication of biodiversity loss under a given deer density.

INTRODUCTION

The effects of deer browse on forest communities in the northeastern United States has been well documented (Kittredge and Ashton 1995, Russell et al. 2001, Côté et al. 2004). Deer densities have often been found to be correlated with impacts to vegetation (Russell et al. 2001, Tilghman 1989, Horsley et al. 2003, Benner 2006), and some are now suggesting managers use plants as phyto-indicators of deer overpopulation (Morellet et al. 2001, Morellet et al. 2007, Benner 2006, Royo et al. 2010).

Heights of several herbaceous species have been linked to deer browse intensity. Anderson (1994) found that heights of *Trillium grandiflorum* decreased as deer browse intensity increased, and Koh et al. (2010) correlated heights of *Trillium grandiflorum* to deer density. Webster and Parker (2000) and Webster et al. (2001) correlated the heights of *Arisaema triphyllum, Acteae pachypoda* and *Osmorhyza claytonii* with deer, and suggested that the development of equations that predict deer browse damage using the heights of plants may help managers monitor deer impacts. In many plant species, height is correlated with sexual maturity and flowering capability and therefore is an important predictor of fitness (Webster et al. 2001). Several other plant species have been proposed as indicators of deer impact such as *Acer saccharum* (Frelich and Lorimer 1985), *Clintonia borealis* (Balgooyen and Waller 1995), *Chelone glabra* (Williams et al. 2000),

Maianthemum canadense (Kirschbaum and Anaker 2005), and *Medeola virginiana* (Diefenbach and Fritsky 2007) However, the usefulness of these indices is often limited to communities in which the target species is relatively common restricting their widespread application. For example, Webster et al. (2005) found that although spring flowering plants recovered significantly in diversity when protected from deer browse, *Trillium* spp. were present in too few numbers to analyze statistically.

Deer have been known to preferentially browse within certain heights. This is often referred to as the "browse zone". Kitteridge and Aston (1995) found that saplings taller than 19.7 in were browsed proportionately more often than seedlings below 19.7 in of height regardless of tree species. The height of the plant was a greater predictor of likelihood of being browsed than the species identity. Carter and Frederickson (2007) also found that larger saplings > 0.5 m tall were browsed more often than seedlings < 0.5 m although they caution that small seedlings could have been browsed so severely as to remove them completely and so would not have been counted.

Some studies at low deer densities note an impact on one or a few species or simply on the heights of some species but not the overall community species diversity. Therefore, monitoring the height of species gives additional information that may not be captured if species diversity were the only measure used. Apsley and McCarthy (2004) found that deer density estimated at 6 deer/km^2 had no effect on species richness of woody species after two years in an Ohio study in mixed oak forest communities, however they found that the mean height of *Nyssa sylvatica* seedlings were significantly lower under deer

browse. Russell et al. (2000) noted in a review paper that several studies found failure of recruitment of seedlings into taller height classes at deer densities above 8.5 deer/km^2.

Recent studies have focused on recovery of forests after reduction or exclusion of deer populations and found slower than expected recovery. (Webster et al. 2005, Collard et al. 2010, Royo et al. 2010, Tanentzap et al. 2011). Collard et al. (2010) noted taller vegetation in forest plots but no significant increase in species richness while plots in canopy gaps did exhibit increased abundance. They also noted heights of *Trillium* spp. were greater in protected plots. Webster et al. (2005) noted *Trillium* spp. and other members of the Liliaceae were especially affected by deer browse.

Only a few studies have suggested using a suite of species as indicators (Williams et al. 2000, Fletcher et al. 2001, Webster et al. 2001, Benner 2006). Benner (2006) proposed that a suite of woody species that are preferentially browsed by deer be used in a "browse index" to indicate level of browse pressure on the community as a whole. Benner noted that under severe browse woody seedlings may never exceed 0.5 ft (~15 cm). Sweetapple and Nugent (2004) combined the concepts of browse preference and impact on heights of species to develop an index for assessing browse impacts on forests in Hawaii and New Zealand. Their seedling ratio compares the ratio of species richness of tall seedlings to the species richness of short seedlings for groups of high-, moderate- and low-preference species. By combining a height measure with a species richness measure Sweetapple and Nugent (2004) were able to create an index that was highly correlated with browser abundance.

If patterns of impact to diversity in the vertical dimension are well-correlated to deer densities, species richness within height classes could be used to monitor deer populations. In a previous study, I found that when protected from deer browse, species richness at every height within the understory increases and that these heights are not affected in the same ways (Rohleder, unpublished data, Chapter 1). The vertical profile of species richness is a measure of community diversity that includes effects on heights of various species while being applicable over forests of differing species compositions. I hypothesized that a vertical measure of species richness within understories would encapsulate this effect and allow estimation of deer density across multiple communities without requiring the presence of specific plant species.

In this study, I sought to determine the relationship of the vertical measurement of plant species richness to deer density. I predicted that at lower deer densities, diversity at the middle heights (those within the "browse zone") will be affected whereas at the greater deer densities, all heights that are reachable by deer will experience a decrease in diversity. I further predicted that decreasing plant species richness in the vertical dimension would be related to increasing deer density. I tested my predictions using data from 10 forests with a gradient of deer densities in the Washington D.C. metropolitan area.

METHODS

Sites

In order to determine the relationship between vertical measures and various deer densities, I collected data in forests across 10 national park areas belonging to the National Capitol Region Network located in the greater Washington D.C. area (Figure 2.1). During the sampling year, deer densities in these forests formed a gradient ranging from 5 deer/km^2 to 78 deer/km^2 (Table 2.1).
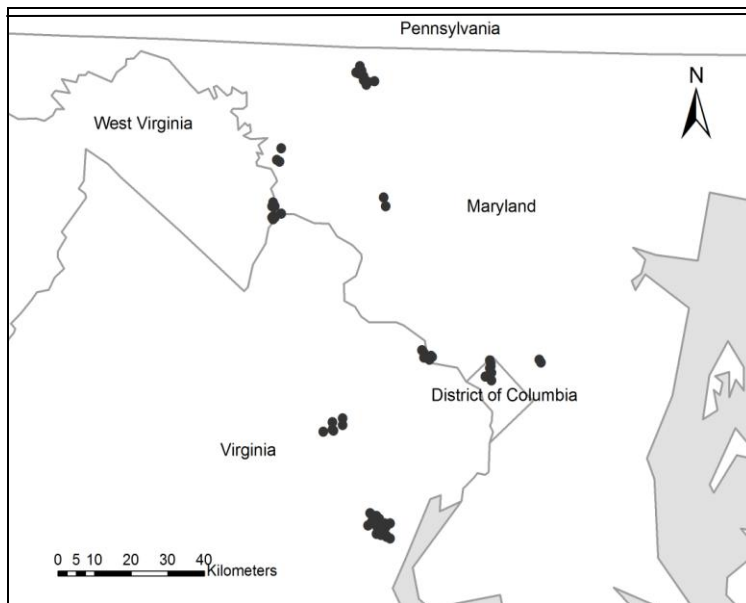
Figure 2.1 Plot locations.

I selected plot locations from the set of permanent plots established by the National Park Service Inventory and Monitoring program (J. P. Schmit, pers. comm.). The National Park Service had generated these locations by using GIS and generalized random tessellation stratified sampling (GRTS) (Stevens and Olsen 2004). A 250 x 250 m grid was intersected with the park areas. Each vertex was then defined as a candidate plot in S-Draw software (West Inc., Cheyenne, WY, USA), GRTS was used to select plots to be visited on a four year rotation such that 100 plots would be sampled each year. Plots which fell in grasslands, mowed areas, maintained areas, on roads, and areas with greater

than 30% slope were removed and replaced with the next GRTS selected plot (J. P. Schmit, pers. comm.). This method employs random plot selection to allow statistical inference while also providing balanced spatial coverage and flexibility for post-stratification of plots (Stevens and Olsen 2004).

In addition to the national forest plots, I used data collected in a previous study at deer exclosures across New Jersey and Maryland (Rohleder, unpublished data, Chapter 1). I used plot data collected from within these deer exclosures using the same methods as below to represent sites with no deer. I used data only from exclosures that were at least 10 years old at the time of sampling. Horsley et al. (2003) noted that some effects on species richness and diversity were not seen until year 10 in his study. Niewinski et al. (2006) also found that vegetation recovery took at least 5-10 years after reduction in deer herd levels.

Deer Density

Deer densities were estimated by the National Park Service using spot-light counts following a standardized protocol in all the parks except for Harper's Ferry where pellet counts were used, and the program Distance was used to analyze the data (Bates 2009). Monitoring of deer densities in these parks has been conducted annually since 2001 except for Harper's Ferry – Loudon Heights area which was surveyed for the first time in 2007 (Bates 2009). Deer populations have remained at approximately the same levels for most of these parks over the entire survey period except for Prince William which

exhibited a significant downward trend (Bates 2009). Prince William has one of the

lowest deer densities of the study sites.

Table 2.1 Deer densities for 2007 in National Capital Region Parks (Bates 2009)

Park Name	Deer Density (km^2)	95% C.I.
Antietam National Battlefield	37.14	17.99-76.68
Catoctin Mountain Park	40.39	28.43-57.37
Greenbelt Park	32.09	19.81-51.98
George Washington Memorial Parkway[1]	46.81	25.79-84.95
Harper's Ferry NHP – Loudon Heights	11.74	7.11-16.36
Harper's Ferry NHP – Maryland Heights	27.29	20.22-33.50
Manassas National Battlefield	50.09	39.04-64.25
Monocacy National Battlefield	77.66*	30.31-161.00
Prince William Forest Park	5.15	3.78-7.02
Rock Creek Park	31.83	24.86-40.75

[1]Great Falls Park; * Differs from published number- correction supplied by S. Bates (pers. com.)

In order to control for inter-annual variation in deer population estimates, I calculated the

mean deer density for the last eight years from each park where these estimates were

performed as the deer density estimates in the following statistical analyses. However, I

used the 2007 survey number for the Louden Heights area of Harper's Ferry since no

other estimates were available for that site.

Vertical Measures

At each location, I established a two meter radius circular plot (12.6 m^2). I measured

diversity in the vertical dimension as vascular plant species richness within the plot at

each of ten height classes in 20 cm intervals from ground level up to two meters by

counting plant species present in each height class.

Covariates

In addition, at each plot, I took measurements of soil moisture and canopy closure as

covariates. I measured soil moisture as volumetric water content (a percentage) using a

Hydrosense™ moisture meter (Campbell Scientific, Inc., Logan, Utah, USA) with 20 cm

probes. I measured canopy closure using a hemispherical photograph taken at the plot center from a height of two meters using a Kodak Z740 camera and a fisheye lens. I analyzed the photographs with Gap Light Analyzer (GLA) software, version 2.0 (Frazer et al. 1999) to obtain percent canopy openness and then subtracted this number from 100 to get canopy closure. All photographs were analyzed using the same configuration settings, with the blue color plane and a pixel threshold of 150.

Percent Cover Quadrats

At 45 of the vertical plot locations in the national park forests, twelve 2 x 0.5 m (1 m^2) quadrats were positioned according to the vegetation monitoring protocols of the NPS's NCRN Inventory and Monitoring team (Schmit and Campbell 2008). A tape was run at a bearing of zero degrees from center, and the quadrat frame was laid parallel to the tape and offset 10 cm to the right beginning at 3 m, then at 8 m, and finally at 13 m. This pattern was repeated at bearings of 120 and 240 degrees. At bearings of 60, 180, and 300 degrees, the quadrat was centered at 9 m from the plot center along the bearing (Figure 2.2). At each quadrat I recorded percent cover of each vascular plant species in 1% increments as the percentage of ground obscured by that species within the quadrat when viewed from above at a height of approximately one meter. I estimated cover for each species as if other species were not present, and I included only those individuals rooted within the plot.
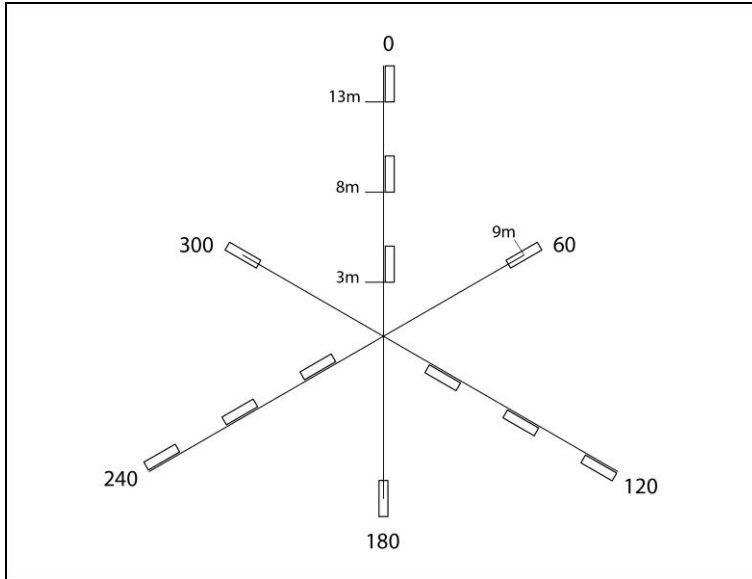
Figure 2.2 Percent cover quadrat plot layout. Lines represent compass bearings. Plot locations are shown as rectangles.

Statistical Methods

All analyses were performed using R software version 2.11.1 (R Development Core Team 2010). I viewed the vertical species richness profile for a site as a curve that began at its maximum value at the lowest height class and deceased rapidly as the heights increased. Therefore, I analyzed this curve as a negative exponential (Equation 2.1) where x is the height class, S_1 represents the number of species at height class 1 and S_x represents the number of species at height class x. The left-hand side of the equation then represents the proportion of species remaining at height x. The coefficient of x is the rate at which species are lost as the heights increase. I refer to this coefficient, –k, as the species attenuation coefficient.

$$\frac{S_x}{S_1} = e^{-kx}$$

(2.1)

To calculate the species attenuation coefficient for each site, I computed S_x/S_1 for height classes 2 through 10, took the natural log of these values and then ran a linear regression

with x, the height classes. I ran the regression with the option for no intercept. The slope of this regression line is the species attenuation coefficient, -k. Once I obtained the species attenuation coefficients for each site, I ran a linear regression of these with the deer density for each site to determine if the rate of species attenuation was correlated to the deer density.

I also analyzed the covariates to determine if they were comparable across sites. I ran an ANOVA on soil moisture for each site and on canopy closure for each site. When the ANOVA showed significant differences among sites, I ran Tukey's HSD comparison of means to identify which sites differed significantly from the others. After analyzing the covariates I determined that certain sites were significantly different from the others. I added this variable to the linear regression of species attenuation coefficients against deer density and evaluated the difference in the models.

RESULTS

The average deer densities over the eight-year period prior to the study range from lows of 11.7 deer/km^2 at Loudon Heights in Harper's Ferry Park and 11.9 at Prince William Forest Park up to a high of 77.3 deer/km^2 at Monocacy National Battlefield (Table 2.2).

Table 2.2 Deer densities by site, eight-year average (2001-2008). Based on Bates (unpublished data).

Site	Park Name	Deer Density (deer/km)
ANTI	Antietam National Battlefield	43.0
CATO	Catoctin Mountain Park	49.3
GREE	Greenbelt Park	36.2
GWMP	George Washington Memorial Parkway[1]	32.1
LOUHGT	Harper's Ferry NHP – Loudon Heights*	11.7
MDHGT	Harper's Ferry NHP – Maryland Heights	36.4
MANA	Manassas National Battlefield	61.1

MONO	Monocacy National Battlefield	65.7
PRWI	Prince William Forest Park	11.9
ROCR	Rock Creek Park	26.7

[1]*Great Falls Park; * 2007 estimate only*

The vertical species profiles showing species richness at each height class for each site are shown in Figure 2.3. The vertical profiles for all sites seem to follow the negative exponential pattern beginning with many species at the lowest height class and rapidly decreasing as the heights increase. The sites with the three lowest deer densities appear to retain more species at the upper heights than the other sites.
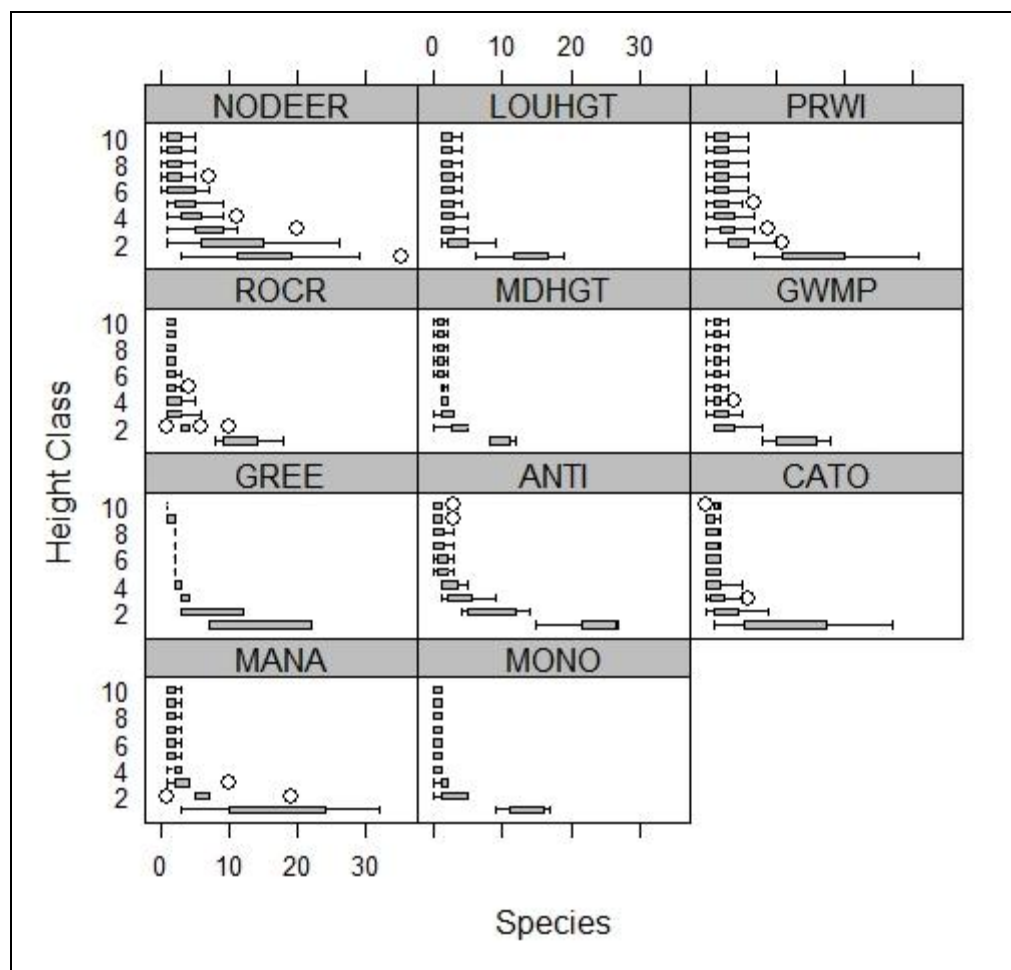
Figure 2.3 Vertical species profiles for each site. NODEER is the collection of plots from within deer exclosures. The sites are shown from lowest deer density to highest reading left to right, top to bottom. Height classes are 20 cm intervals from ground level to 2 m. n=110.

The species attenuation coefficients for each site are given in Table 2.3. The attenuation

coefficients range from -0.269 for Greenbelt Park to -0.632 for Monacacy Battlefield

Park. All the regressions were significant with $p < 0.001$ and r^2 values above 0.50. The

mean species richness of the lowest height class for each site is also given in Table 2.3.

Mean species richness at height class 1 ranged from 9.5 at Maryland Heights in Harper's

Ferry to 23.4 at Antietam National Battlefield.

Table 2.3 Species attenuation coefficients (-k) by site with linear regression results. n
is the number of vertical plots upon which the analysis is based. S is the mean species
richness of the lowest height class.

Site	n	S	-k	r^2	p-value
NODEER	18	16.28±1.94	-0.310	0.67	<0.001
ANTI	8	23.38±1.43	-0.540	0.80	<0.001
CATO	15	12.93±2.07	0.520	0.61	<0.001
GREE	2	14.50±7.50	-0.269	0.86	<0.001
GWMP	10	12.60±1.20	-0.359	0.66	<0.001
LOUHGT	7	13.57±1.67	-0.278	0.84	<0.001
MDHGT	4	9.50±9.50	-0.407	0.58	<0.001
MANA	6	18.17±4.32	-0.300	0.83	<0.001
MONO	6	13.67±1.31	-0.632	0.74	<0.001
PRWI	25	15.72±1.36	-0.325	0.61	<0.001
ROCR	9	12.11±1.26	-0.285	0.86	<0.001

The mean species richness for each site as calculated from the lowest height class was not

significantly correlated with deer density ($F_{1,9}=0.1175$, $p=0.74$, $r^2= -0.097$). The mean

species richness by site is given in Table 2.3. Species richness for each plot is graphed

against deer density in Figure 2.4. Species richness for each plot is also not significantly

correlated to deer density ($F_{1,108}=0.05225$, $p=0.82$, $r^2=-0.01$).
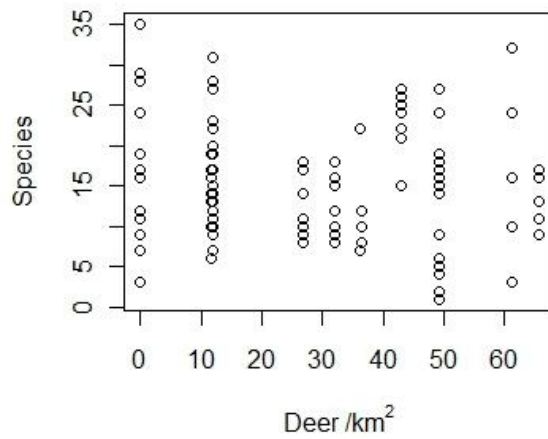
Figure 2.4 Species richness graphed against deer density. n=110**.**

 The results of the linear regression of species attenuation coefficients against deer

densities are graphed in Figure 2.5. The species attenuation coefficients are correlated to

deer density with $F_{1,9}=5.474$, $r^2 = 0.31$, p= 0.04. The solid line on the graph is the

regression line. Analysis of the regression indicates that the points for Antietam National

Battlefield (ANTI), Greenbelt Park (GREE) and Manassas National Battlefield (MANA)

are outliers. The points for these sites are labeled on the graph.
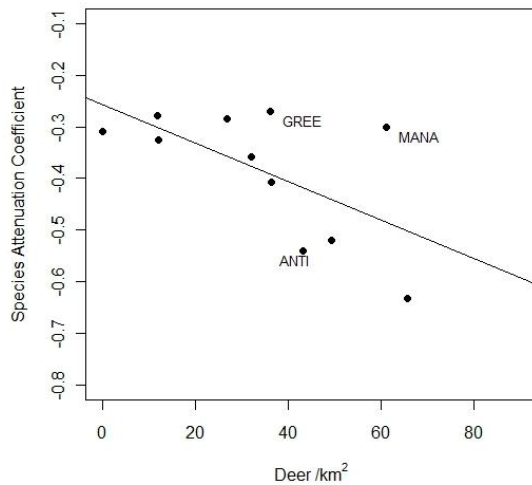
Figure 2.5 Relationship of species attenuation coefficients to deer density.

I analyzed the covariates of canopy closure and soil moisture by site to determine if any of the sites were significantly different from the other sites. Sites had a mean canopy closure between 79.2% at Monocacy National Battlefield and at George Washington Memorial Parkway and 85% at Maryland Heights in Harper's Ferry. None of the sites were significantly different from each other in canopy closure ($F_{9,98}= 0.7509$, p=0.66). Soil moisture was more variable ranging from a low of 5.78% $\pm$ 1.79 SD at Monocacy National Battlefield to a high of 30% $\pm$ 21.34 SD at Manassas National Battlefield. The overall mean of soil moisture was 15.86% $\pm$11.84 SD and all sites were within one standard deviation of this overall mean except for Manassas National Battlefield. In Tukey's HSD comparison of means, Manassas was significantly different (p<0.05) from Catoctin, Monocacy and Loudon Heights, the sites with the lowest soil moistures. Antietam National Battlefield, the site with the second highest soil moisture was also significantly different (p<0.05) from Catoctin and Monocacy. However, when soil

moisture is added in to the linear regression between the species attenuation coefficient

and deer density, the regression is not significant (p=0.06). However, if the Manassas site

is removed, the relationship between deer density and species attenuation coefficients

becomes stronger ($F_{1,8}$=15.43, r^2=0.62, p=0.004).

Relationship of Diversity from Quadrat Data to Deer Density

Diversity for each of the sites as calculated by data from the percent cover quadrats

ranged from 5.0 to 13.83 (Table 2.4). Species richness from the quadrat data is also given

in Table 2.4 and showed that most sites had species richness of around 20-21 species

except for Antietam which had a much higher species richness (36 species) and Manassas

and Monocacy which were 29 and 28.5 species respectively.

Table 2.4 Species richness and diversity by site based on quadrat data. n is the
number of plot locations. S is the mean species richness and D is mean diversity across
plots at the given Site.

Site	n	S	D
ANTI	3	36.3	13.83
CATO	8	21.1	5.3
GREE	2	21.0	4.98
GWMP	3	20.0	5.0
LOUHGT	4	20.0	9.49
MDHGT	3	20.5	6.28
MANA	3	29.0	4.27
MONO	2	28.5	11.03
PRWI	11	21.0	6.58
ROCR	6	21.5	8.89

Diversity and species richness as calculated from the percent cover quadrats are graphed

against deer density in Figure 2.6. Diversity was not significantly correlated with deer

density ($F_{1,8}$=0.001687, p=0.968, r^2=-0.12). Species richness also was not significantly

correlated with deer density ($F_{1,8}$=3.846, p=0.085, r^2=0.24), however this non-significant

result was influenced by one outlying point, the Antietam site. If that site were removed,

species richness from the percent cover quadrats would be significantly correlated to deer density ($F_{1,7}$ = 12.13, p=0.01, r^2=0.58), but the slope (0.15) indicates increasing species richness as deer density increases.

A   B
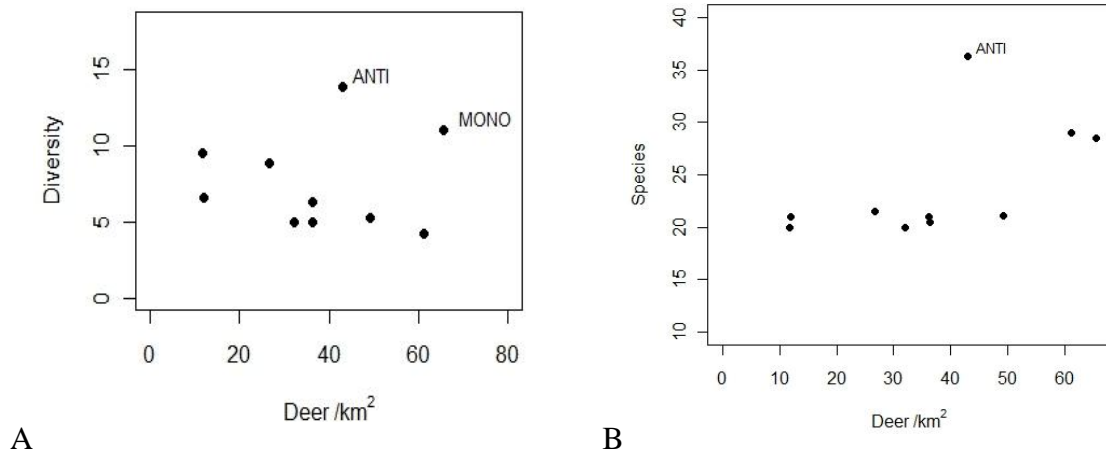
Figure 2.6 Diversity and species richness by site based on quadrat data with deer density. A) Diversity B) Species richness. n=10.

DISCUSSION

I predicted that at lower deer densities, diversity at the middle heights (those within the "browse zone") would be affected whereas at the greater deer densities, all heights that were reachable by deer would experience a decrease in diversity. My results did not support this prediction although all heights did experience species loss. The lower rate of species loss at lower deer densities (e.g. k= -0.3 for PRWI at 11.9 deer/km^2) compared to greater deer densities (e.g. k = -0.6 for MONO at 65.7 deer/km^2) corresponds to a more vertical slope of the curve in the species richness profile at low deer density arguing for a slightly more even effect of deer on all height classes. The larger rate of loss at the greater deer density is consistent with a greater impact of deer on middle heights above height class 1 (> 20 cm). Carter and Frederickson (2007) found that saplings greater than

0.5 m tall were browsed more than smaller seedlings under deer densities between 5.9 deer/km^2 and 15.4 deer/km^2, and Kitteridge and Aston (1995) found seedlings taller than 19.7 cm were browsed more than smaller seedlings. These results are consistent with my findings at higher deer densities.

One goal of this study was to determine the relationship of the vertical measurement of species richness to deer densities. My study shows that the number of species, the species richness, at various heights in the forest understory can be described by the reverse J-curve with the coefficient of the negative exponential function providing an index of the species attenuation along the height gradient. Furthermore, this species attenuation coefficient can be related to the deer density at the site. The species attenuation coefficient, a negative exponential coefficient, decreases or becomes more negative indicating an increased rate of species loss as deer density increases. In the deciduous forests of the northeastern U.S. where I conducted my studies, the species attenuation coefficient decreases linearly with increasing deer density at sites with fairly comparable canopy closures and soil moisture. It remains to be seen if this relationship will hold across other forest types and in other geographical regions.

Two of the sites I used had significantly different soil moisture than the majority of the sites, and these sites did show as outliers compared to the other sites. The site with the highest soil moisture, MANA 30%, was the most displaced from the regression line (Figure 2.5) showing that site factors can influence the species attenuation coefficient – deer density relationship. This site had a much slower rate of species loss than is

predicted from the given deer density under this linear relationship, but this result could
be explained by the increased soil moisture allowing the plant species to have increased
tolerance or resistance to deer browse. Although my analysis of the linear regression
identified the GREE and ANTI sites as outliers, if MANA is removed from the analysis
the regression line becomes much more fitted to these points, and the relationship
between the species attenuation coefficient and deer density becomes much stronger
(r^2=0.62). Based on the wide variety of sites studied, these findings are applicable across
a broad range of deciduous forests indicating a strong pattern.

Species richness and diversity calculated from percent cover quadrats (Figure 2.6) at
these same forests were not able to be correlated to deer densities in a logical way.
Although an outlying point was seen (ANTI) in the graph of species richness and when
removed a linear correlation resulted, this correlation indicated gradually increasing
species richness as deer density increased, contradictory to most published studies.
Perhaps there were not enough quadrat plots (45) taken to obtain representative samples
compared to the number of vertical species richness plots (110). But regardless of the
explanation, the vertical species richness plots in this study provided better correlation
with deer density than percent cover quadrat data.

Because the vertical species richness profile and specifically the species attenuation
coefficient are well correlated with deer density, this measurement may be used to predict
deer densities. Although indices based on single species such as *Trillium* spp.
(Kirschbaum and Anacker 2005), *Clintonia borealis* (Balgooyen and Waller 1995),

Chelone glabra (Williams et al. 2000), may work well for specific regions in which that species is abundant, in this study none of these species were encountered in any of the plots, and other species were only encountered at a few of the sites. *Acer saccharum* used in Frelich and Lorimer's (1985) sugar maple browse index and *Maianthemum canadense* (Kirschbaum and Anaker 2005) were only encountered at one of the ten sites, and *Medeola virginiana* (Diefenbach and Fritsky 2007) was only found at two sites. Consistent with Sweetapple and Nugent's (2006) seedling ratio index, use of the heights of the suite of species in the forest understory as a browser abundance index seems to work well.

Sweetapple and Nugent (2006) found a stronger correlation to browser abundance using additional information about which species were preferred by browsers; however, that information is not always known. Furthermore, deer browsing preferences change seasonally (Healy 1971, Crawford 1982, Horsley et al. 2003) and vary regionally. For example, Castleberry et al. (1999) found that preferred browse species in a southern bottomland forest in South Carolina included red maple (*Acer rubrum*), winged elm (*Ulmus alata*), greenbrier (*Smilax* spp.) and black willow (*Salix nigra*), while in Virginia Carter and Frederickson (2006) found high rates of browse on American beech (*Fagus grandifolia*), black cherry (*Prunus serotina*), and black gum (Nyssa sylvatica) among others but red maple (*Acer rubrum*) which was quite abundant was only lightly browsed. In Pennsylvania, Horsely et al. (2003) found black cherry to be a less preferred species. This variation in preferences of white-tailed deer depending on region makes it hard to

select a suite of highly preferred species which is generally applicable. The vertical species richness profile avoids this issue.

The reverse J-curve distribution is commonly used by foresters to describe the numbers of trees in diameter size classes, or age classes, in uneven-aged stands (Meyer 1943, 1952, Leak 1965, O'Hara 1998). This study extends the applicability of this concept to the lower strata of the forest. Managers of forests have used this pattern as a template against which to evaluate forest management practices such as logging to ensure quality forest structure is preserved (O'Hara 1998). In his paper on the J-curve distribution, Leak (1965) predicts that the J-curve distribution might describe other continuous variables in forests and proposed that fast growing species under pressure from competition or disturbance might likely follow this distribution. Leak (1965) even postulated that one of these variables might be height. In the forests in my study, deer provide levels of disturbance which seems to relate well to the form of the curve produced, and the vertical growth of plants combined with the strong effect of deer on their heights provides a consistent explanation for the pattern. Lindenmayer et al. (2000) identify the need for indicators of biodiversity to ensure sustainability in forest management and call for measures that include structure-based indicators as well as plant species composition indicators. Therefore, this reverse J-curve distribution of vertical species richness in the understory might be useful as a both a structural and compositional quality indicator to forest managers who wish to maintain the integrity of forest understories under various management regimes.

The finding that the species richness in forest understories follows the reverse J-curve in the vertical dimension also has implications for forest modelers seeking to understand the potential effects of various disturbances or management regimes on biodiversity. Increasing levels of disturbance or browse by deer can be modeled using greater species attenuation coefficients. Forest modelers who seek to understand understory dynamics may also make use of this relationship since it provides information about the development of understory height structure and potentially a leading edge indication of biodiversity loss under a given deer density.

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CHAPTER 3: Test of the Effects of Deer on Floristic Quality in Eastern Deciduous

Forests

ABSTRACT

White-tailed deer (*Odeocoilus virginianus*) have significant effects on the diversity and

productivity of forest understories. I looked at how these effects may be reflected in

floristic quality indices which are becoming more commonly used by land managers and

lay people to evaluate the integrity of forests under their management. Using newly

assigned coefficients of conservatism for plant species in the mid-Atlantic region of the

United States, I tested the results of several floristic quality indices at 44 pre-existing deer

exclosures in New Jersey and Maryland ranging in age from 1 year to 30 years old and at

10 forests in the metropolitan Washington D.C. area with a gradient of deer densities

from 5 deer/km^2 to 78 deer/km^2. I expected to find increased floristic quality in protected

plots within deer exclosures, to find increased quality over time, and to find decreased

quality as deer density increased. The original Floristic Quality Assessment Index (FQAI)

and the Plant Stewardship Index (PSI) both yielded results that confirmed expectations

indicating increased quality inside deer exclosures (p $<<0.001$). Furthermore, quality

increased gradually the longer the plots had been protected from deer browse (r^2=0.14

and 0.10, respectively). Species richness was also significantly higher within deer

exclosures but was only weakly related to deer densities. FQAI and PSI, however, were

well-correlated to deer densities (r^2 = 0.25 and 0.31, respectively) showing decreased

quality as deer density increased. FQAI and PSI combine species richness and quality in

a meaningful way that provides more information than species richness alone. However,

versions of floristic quality measures that are weighted more heavily toward conservatism

values may not reflect changes in deer density due to legacy effects and slowed recovery of conservative species. Land managers who wish to monitor the effects of deer on forest understories should use FQAI or PSI indices in the mid-Atlantic states and New Jersey.

INTRODUCTION

White-tailed deer have significant effects on the biodiversity of forest understories in the northeastern U.S. (Rooney 2001, Russell et al. 2001, Horsley et al. 2003, Côté et al. 2004). The species composition of the vegetation community is changed and successional patterns altered by browsing by white-tailed (Stromeyer and Warren 1997, Waller and Alverson 1997, Augustine et al. 1998, Horsely et al. 2003). Many of the woody seedlings which would become the future forest canopy are eliminated and populations of forest herbs are reduced (Frelich and Lorimer 1985, Tilghman 1989, Apsley and McCarthy 2004). These impacts make it important for forest managers to monitor biodiversity in conjunction with deer densities.

Biodiversity is generally thought to increase the stability of ecosystem processes (Loreau and de Manzancourt 2013), and preserving biodiversity has become a goal of forest managers (Lindenmayer et al. 2000). Ecological indicators have become a popular way to assess the condition of the environment (Niemi and McDonald 2004). Plants have long been recognized as indicative of environmental conditions, and Ellenberg, working in Europe, published lists of indicator values for specific plants that have been widely used in central Europe (Diekmann 2003). The floristic quality index (FQI), or floristic quality assessment index (FQAI), is one method that attempts to synthesize the

importance of individual species and their traits with the overall diversity of a community as an indicator of disturbance. These measures may be useful to forest managers seeking to relate vegetation impacts to deer densities.

The floristic quality assessment index (FQAI) uses the concept of conservatism that originates from Grime's C-S-R model of plant strategies (Grime et al. 1988). The model describes different sets of plant traits, called strategies, which evolve under different environmental conditions. C represents the Competitors, R the Ruderals, and S the Stress-tolerators. Disturbance is defined as physical damage to vegetation, and stress is defined as constraints on productivity such as shortages of light, water, or nutrients. Plants which are adapted to a higher level of disturbance are called ruderals (R), and those that have adapted to high stress environments are called stress-tolerators (S). Competitors are adapted to a productive, undisturbed environment (Grime et al. 1988).

There are intermediate strategies such as C-S. These competitive stress-tolerators would be especially good at conserving resources, including space, in mature environments, so they are known as conservative species. In reality, the levels of stress and disturbance vary throughout a community temporally, spatially, and seasonally so that communities often contain plants with a variety of strategies. As disturbance levels increase, the community would be expected to shift to a greater dominance by ruderal species (Grime et al. 1988). Therefore, by scoring the species in a community according to their strategies, a measure of the disturbance the community is experiencing could be attained. Mabry and Fraterrigo (2009) evaluated a large data set of forest species to determine if

certain species traits could be used as generalized predictors of habitat disturbance and found that the trait most consistently related to degree of disturbance was habitat specialization.

The floristic quality assessment index (FQAI) is a diversity measure that incorporates the use of a weight that is assigned to each species called a coefficient of conservatism. The index weights plant species by factors which have some correlation with their vulnerability to being lost from the community. These factors are (1) the sensitivity to disturbance and (2) fidelity to specific habitat conditions (Taft et al. 1997). A weight is assigned to each species that incorporates an evaluation of its position along these gradients. This weight is an evaluation based on subjective expert opinion since actually testing each plant species to arrive at an empirical number would be impractical for obtaining initial scores. However, validation testing over time of the assigned scores is not precluded and is a necessary part of ensuring that the tool is useful. A high weight indicates high sensitivity to disturbance and degradation of habitat conditions, while a low weight indicates high tolerance to disturbance and persistence in a variety of habitat conditions (Table 3.1). Ruderal species are expected to have low coefficients of conservatism. Coefficients for a set of species are typically assigned on a local or regional basis.

Table 3.1: Coefficient of conservatism scale. (adapted from Andreas et al. 2004)

0	Plants with a wide range of ecological tolerances. Often these are opportunistic invaders of natural areas or native taxa that are typically part of a ruderal community
1-2	Widespread taxa that are not typical of (or only marginally typical of) a particular community
3-5	Plants with an intermediate range of ecological tolerances that typify a stable phase of some native community, but persist under some disturbance
6-8	Plants with a narrow range of ecological tolerances that typify a stable or near "climax" community

9-10   Plants with a narrow range of ecological tolerances that exhibit relatively high
degrees of fidelity to a narrow range of habitat requirements

The FQAI is essentially a weighted species richness measure and is typically calculated

as the mean coefficient of conservatism multiplied by the square root of species richness

(Andreas et al. 2004). Non-native species are typically excluded from the calculation

However, certain modified indices have been proposed which do not exclude alien

species (BHWP 2006). The Plant Stewardship Index (PSI) used in BHWP (2006)

modifies the original FQAI slightly using the same formula but retaining the alien

species.

The FQAI has been used across the United States and in Canada. Swink and Wilhelm

originated the concept in Illinois (Taft et al. 1997) and, until recently, its use has been

primarily in the Midwest and Great Plains. Coefficients of conservatism have been

assigned for Ontario (Oldham et al. 1995), the Dakotas (NGPFQAP 2001), Wisconsin

(Nichols 1999), Michigan (Herman et al. 1997), Minnesota (Bourdaghs 2006), Missouri

(Ladd 1993), Indiana (Rothrock 2004), Ohio (Andreas et al. 2004), and Kansas (Jog et al.

2006). Recent applications have expanded the use of floristic quality assessment into the

southern states of Florida (Cohen et al. 2004) and Mississippi (Herman et al. 2006) and

east into Pennsylvania (Miller and Waldrop 2006), New Jersey (BHWP 2006) and the

middle Atlantic states (Chamberlain and Ingram, in press) and in New England (Bried et

al. 2012).

Floristic quality assessment has primarily been applied to wetlands as a wetlands quality

assessment technique for mitigation monitoring purposes and has been found to be well-

correlated to wetland quality (Lopez and Fennessy 2002). There have been only a few applications in forested communities. Nichols et al. (2006) applied the technique in forested wetland in southern Virginia, and floristic quality has been used in deciduous forest in Ontario (Burke and Nol 1998; Francis et al. 2000).

Nichols et al. (2006) found that calculating the floristic quality for the separate strata layers of the forest yielded a useful correlation between quality of the canopy layer and the historical land use disturbance level, and between the herbaceous layer and the current disturbance level. They suggest that due to key life history differences between the canopy species and the herbaceous layer, the herbaceous layer is more reflective of the current disturbance level and therefore makes the herbaceous layer a good candidate for evaluating the current biological integrity. They also found that the sapling layer was more reflective of gap dynamics and suggest that sapling layer assessment may prove a useful indicator of integrity following a disturbance regime. These findings imply that it would be useful to evaluate the floristic quality at different vertical heights within the forest.

Floristic quality indices are often tested against another measure known to degrade habitat. In past applications of the FQAI, degradation has referred to anthropogenic changes to hydrology or water quality in wetland habitat (Andreas et al. 2004, Lopez and Fennessy 2002, Miller and Waldrop 2006) or disturbance caused by fire in prairie communities (Bowles et al. 1996, Bowles et al. 2006). If the FQAI is to be successfully applied in forested communities, it will need to accurately reflect the major disturbances

occurring in forests. Deer browse is generally recognized as one of the major factors impacting the integrity of eastern deciduous forest (Russell et al. 2001, Côté et al. 2004). So it is crucial to test how well the FQAI in eastern deciduous forests reflects degradation caused by deer browsing before the index can be widely applied. Anderson et al. (2004) compared floristic quality changes due to deer browse using several methods in deer exclosures in prairie ecosystems, but few studies have specifically tested floristic quality measures in relationship to levels of deer browse or to deer densities in forests. In a small study, Asnani et al. (2006) evaluated floristic quality at three deer exclosures in a forested park in Ohio and found increased vegetative abundance inside exclosures but non-significant differences in diversity, species richness and floristic quality.

Because regional plant populations differ in their characteristics, coefficients are assigned on a regional basis (usually at the state level). Coefficients of conservatism were assigned by a group of expert botanists for the state of New Jersey in 2006 (BHWP 2006) and Maryland and Virginia in 2011 (Chamberlain and Ingram, in press). However, only a few scientific studies have used the coefficients for New Jersey. Ravit et al. (2008) applied New Jersey coefficients to a wetland system, and Spyreas et al. (2012) applied them in successional old fields, so the New Jersey coefficients have yet to be studied in forests. No published scientific studies to-date have used the Maryland and Virginia coefficients.

To test whether the floristic quality assessment index showed increased quality within areas of forest that were protected from browsing by deer, I sampled data from inside and outside pre-existing deer exclosures in forests in New Jersey and Maryland. In addition, I

tested the correlation of floristic quality to deer densities by sampling vegetation at 10 forests in the Washington DC metropolitan area over a gradient of deer densities.

Since deer are known to have negative effects on forest understories (Rooney and Waller 2003), I expected that floristic quality would be higher in protected plots within deer exclosures than in unprotected plots and would decrease in the unprotected forest plots as the deer density within the surrounding forest increased. I tested several different methods of calculating floristic quality against these predictions.

METHODS

Exclosure Sites

To determine whether floristic quality measures reflect impacts by deer browsing, I collected data at 44 pre-existing deer exclosures in New Jersey and Maryland. I chose exclosures which were situated in forests, had not undergone manipulation in the form of herbicide application, physical removals or plantings, and were erected at least one growing season prior to the study. When sampled all exclosures were structurally intact and showed no evidence of recent deer browse inside the exclosure (Table 3.2). Of the selected exclosures, 28 were located across northern and central New Jersey at 14 separate sites, and 16 were located in eastern Maryland and Washington D.C. at 4 sites (Figure 3.1). The average age of the exclosures was 9.7 years at the time of sampling.

Table 3.2 Deer Exclosures.

Location	Site Name	Exclosure size(m^2)	Year installed
1. Englewood, NJ	Flat Rock Brook Nature Center	36	2004
2. Upper Freehold, NJ	Clayton Park	81	2003
3. Highlands, NJ	Hartshorne Woods	81	2003
4. Highlands, NJ	Hartshorne Woods	81	2005
5. Middletown, NJ	Tatum Park	81	2003

6.	Lincroft, NJ	Thompson Park	81	2003
7.	Freehold, NJ	Turkey Swamp Park	81	2004
8.	Freehold, NJ	Turkey Swamp Park	81	2005
9.	Morristown, NJ	Morristown National Historic Park	36	1987-88
10.	Morristown, NJ	Morristown National Historic Park	36	1987-88
11.	Morristown, NJ	Morristown National Historic Park	36	1987-88
12.	Morristown, NJ	Morristown National Historic Park	36	1987-88
13.	Morristown, NJ	Morristown National Historic Park	100	1995
14.	Morristown, NJ	Morristown National Historic Park	100	1997
15.	Morristown, NJ	Morristown National Historic Park	100	1997
16.	Morristown, NJ	Morristown National Historic Park	100	1997
17.	Sandyston, NJ	Stokes State Forest	116	1986
18.	Ringwood, NJ	Wanaque Reservoir	21	2003
19.	Frelinghuysen, NJ	Johnsonburg Swamp Preserve – Nat. Cons.	1600	2005
20.	Frelinghuysen, NJ	Johnsonburg Swamp Preserve – Nat. Cons.	1600	2005
21.	Frelinghuysen, NJ	Johnsonburg Swamp Preserve – Nat. Cons.	1600	2005
22.	Frelinghuysen, NJ	Johnsonburg Swamp Preserve – Nat. Cons.	1600	2005
23.	Mountainside, NJ	Watchung Reservation	116	1995
24.	Mountainside, NJ	Watchung Reservation	116	1995
25.	Harding, NJ	Great Swamp Watershed Association	97	2006
26.	Basking Ridge, NJ	Lord Stirling Park – Somerset Co.	~100	2007
27.	Walpack,NJ	Delaware Water Gap Nat'l Rec. Area[+]	100	2005
28.	Walpack,NJ	Delaware Water Gap Nat'l Rec. Area[+]	100	2005
29.	Sharpsburg, MD	Antietam National Battlefield	25	2005
30.	Sharpsburg, MD	Antietam National Battlefield	25	2005
31.	Sharpsburg, MD	Antietam National Battlefield	25	2005
32.	Sharpsburg, MD	Antietam National Battlefield	25	2005
33.	Sharpsburg, MD	Antietam National Battlefield	25	2005
34.	Thurmont, MD	Catoctin Mountain Park	400	~1988
35.	Thurmont, MD	Catoctin Mountain Park	400	~1988
36.	Thurmont, MD	Catoctin Mountain Park	400	~1988
37.	Thurmont, MD	Catoctin Mountain Park	400	~1988
38.	Thurmont, MD	Catoctin Mountain Park	400	~1988
39.	Frederick, MD	Monocacy National Battlefield	25	2005
40.	Frederick, MD	Monocacy National Battlefield	25	2005
41.	Frederick, MD	Monocacy National Battlefield	25	2005
42.	Frederick, MD	Monocacy National Battlefield	25	2005
43.	Washington, DC	Rock Creek National Park[++]	100	~1978
44.	Washington, DC	Rock Creek National Park[++]	100	~1978

+ Delaware Water Gap exclosures are areas randomly selected from one large 5600 m^2 exclosure
++ Rock Creek Park exclosures are areas randomly selected from the forested area in one large 10,000 m^2 exclosure (the fenced amphitheater).

Figure 3.1 Deer exclosure sites marked by stars.

Forest Sites

I also collected data in forests across 10 national park areas belonging to the National

Capitol Region Network located in the greater Washington D.C. area for which deer

density estimates were available (Figure 3.2). I selected plot locations from the set of

permanent plots established by the National Park Service Inventory and Monitoring

program (J. P. Schmit, pers. comm.). These plot locations were generated using GIS and

generalized random tessellation stratified sampling (GRTS) (Stevens and Olsen 2004). A

250 x 250 m grid was intersected with the remaining areas. Each vertex was then defined

as a candidate plot in S-Draw software (West Inc., Cheyenne, WY, USA), GRTS was

used to select plots to be visited on a four year rotation such that 100 plots would be

sampled each year. Plots which fell in grasslands, mowed areas, maintained areas, on

roads, and areas with greater than 30% slope were removed and replaced with the next

GRTS selected plot (J. P. Schmit, pers. comm.). This method employs random plot

selection to allow statistical inference while also providing balanced spatial coverage and

flexibility for post-stratification of plots (Stevens and Olsen 2004). I supplemented the data from these forest plots with data I collected at deer exclosures at the same sites. I considered plots outside the deer exclosure to be at the same deer density as the rest of the site. I also used plots from within deer exclosures at the same sites to represent vegetation at 0 deer/km^2.
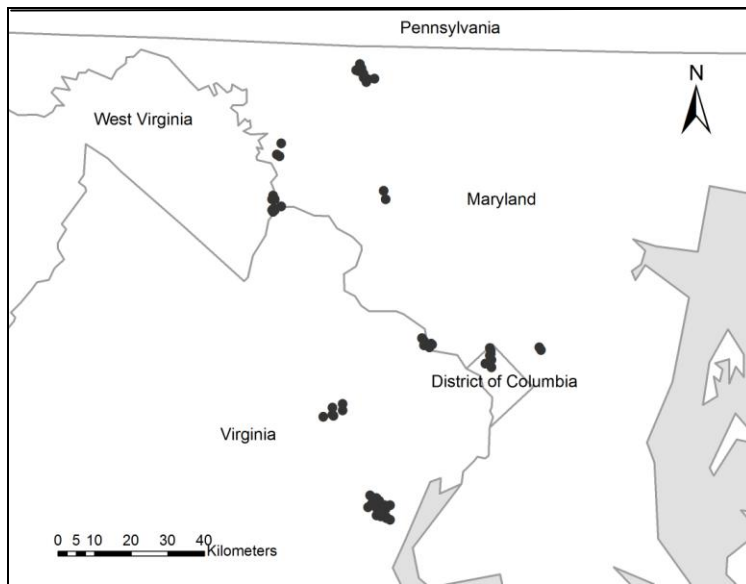
Figure 3.2 Forest Plots

Deer Density

Deer densities were estimated by the National Park Service using distance sampling in all the parks except for Harper's Ferry where pellet counts were used (Bates 2009). Monitoring of deer densities in these parks has been conducted annually since 2001 except for Harper's Ferry – Loudon Heights area which was surveyed for the first time in 2007 (Bates 2009). During the sampling year, deer densities in these forests formed a gradient ranging from 5 deer/km^2 to 78 deer/km^2 (Table 3.3).

Table 3.3 Deer densities for 2007 in National Capital Region Parks. (Bates 2009)

Park Name	Deer Density (deer/km^2)	95% C.I.
Antietam National Battlefield	37.14	17.99-76.68
Catoctin Mountain Park	40.39	28.43-57.37
Greenbelt Park	32.09	19.81-51.98
George Washington Memorial Parkway[1]	46.81	25.79-84.95
Harper's Ferry NHP – Loudon Heights	11.74	7.11-16.36
Harper's Ferry NHP – Maryland Heights	27.29	20.22-33.50
Manassas National Battlefield	50.09	39.04-64.25
Monocacy National Battlefield	77.66*	30.31-161.00
Prince William Forest Park	5.15	3.78-7.02
Rock Creek Park	31.83	24.86-40.75

* Differs from published number- correction supplied by S. Bates (pers com)
[1]Great Falls Park

In order to control for inter-annual variation in deer population estimates, I averaged the

deer densities for the last eight years from each park where these estimates were

performed to obtain the deer density estimates used in the following statistical analyses.

Data Collection

I established circular plots with a 2-m radius (12.6 m^2 each) and identified all vascular

plant species within the plot. At each exclosure, I established one circular plot inside the

exclosure and one plot outside the exclosure.

Covariates

In addition, at each plot, I took measurements of soil moisture and canopy closure as

covariates. Soil moisture was taken as volumetric water content (a percentage) using a

Hydrosense^{TM} moisture meter (Campbell Scientific, Inc., Logan, Utah, USA) with 20 cm

probes. Canopy closure was measured using a hemispherical photograph taken at the plot

center from a height of 2 m using a Kodak Z740 camera with a fisheye lens. I analyzed

the photographs with Gap Light Analyzer (GLA) software, version 2.0 (Frazer et al.

1999) to obtain percent canopy openness. I analyzed all photographs using the same configuration settings, with the blue color plane and a pixel threshold of 150.

STATISTICAL ANALYSIS

All analyses were performed using R statistical software version 2.7.2 (R Development Core Team 2008).

Analysis of Comparable Controls - Covariates

I analyzed soil moisture and canopy closure to ensure that there was no significant difference in these factors between plots inside exclosures and the corresponding plots outside the exclosures. I checked the soil moisture residuals for normality then I ran a paired t-test on the paired soil moisture samples. I checked the canopy closure residuals for normality and transformation failed to result in normality, so I ran the non-parametric Wilcoxon signed rank test on the paired canopy closure samples. In addition, since there may have been some interaction between soil moisture and canopy closure and therefore these variables should not be treated as independent, I ran Hotelling's paired-sample t-squared test (HotellingsT2 function, ICSNP 1.0-7 library) to confirm that there were no significant differences in these variables between inside and outside plots. Hotellings' paired-sample t-squared test is a multivariate form of the student's paired-sample t-test (Anderson 2003).

Calculation of floristic quality

I calculated floristic quality using the traditional formula of mean coefficient of conservatism of native species, C_N, multiplied by the square root of native species richness, N (Equation 3.1).

$$FQAI = \overline{C_N} \times \sqrt{N}$$ (3.1)

However, there are several problems with this formula. Since the FQAI incorporates species richness in its calculations, the result varies as a function of the area sampled (Francis et al. 2000, Matthews 2003). Additionally, only native species are included in the classic formula even though exotic species are often facilitated by disturbance (Crawley 1987, Kotanen 1997). Another criticism of the FQAI formula is that it confounds information by multiplying two possibly independent factors, mean C and species richness, together (Rooney and Rogers 2002).

The Plant Stewardship Index (PSI) modifies the formula to include exotic species in the calculation. The PSI is calculated as the mean coefficient of conservatism of all species, C_s, multiplied by the square root of species richness, S (Equation 3.2).

$$PSI = \overline{C_S} \times \sqrt{N}$$ (3.2)

To address the issue of dependence on species richness, Rooney and Rogers (2002) proposed a modified floristic quality index that is not sensitive to sample size or sample effort. They suggested that the measure should simply be the mean coefficient of conservatism for all species. Exotics are assigned a coefficient of conservatism of zero.

Miller and Wardrup (2006) also proposed a modified index, FQAI' (Equation 3.3). Their index attempts to dampen the influence of species richness, especially non-native richness and increase the influence of the coefficient of conservatism on the overall floristic quality score (Miller and Wardrup 2006). N is the number of native species, S is overall species richness, and C_s is the mean coefficient of conservatism of all species.

$$\text{FQAI}' = \frac{\overline{C_S}}{10} \times \sqrt{\frac{N}{S}} \times 100$$

(3.3)

Floristic quality at deer exclosures

I compared floristic quality as measured by each of these formulas for inside and outside plots at deer exclosures using paired sample t-tests. I computed the difference between each floristic quality measure inside and outside for each exclosure as the change in quality, and I ran a linear regression of the change in quality against the exclosure age to determine the relationship of each floristic quality measure to the length of time the vegetation had been protected from deer browse. I also conducted these same analyses with the simple measure of species richness, S.

Floristic quality relationship to deer density

I calculated the floristic quality using each of the measures described above for each plot within the 10 national park forests. For each floristic quality measure, I ran a linear regression against the deer density at the corresponding site.

RESULTS

Comparable Controls - Covariates

The mean soil moisture inside exclosures was 15.28% $\pm$ 1.36 and outside the exclosures

it was 16.79% $\pm$ 1.51. In the paired t-test, soil moisture did not differ significantly inside

and outside exclosures (t=-1.6631, df=41, p = 0.104). Note that there are 44 deer

exclosures, but one outside plot and one inside plot had no soil moisture readings (due to

inability to insert the probe in rocky ground) resulting in only 42 pairs of complete data

and hence 41 degrees of freedom for the t-test. The mean canopy closure inside the

exclosures was 76.16% $\pm$ 1.85 and outside the exclosures it was 75.73% $\pm$ 1.88. Canopy

closure did not differ significantly inside and outside the exclosures in the Wilcoxon

signed-rank paired-sample test (V=383, p=0.6397). The multivariate paired-sample test,

Hotelling's t-squared, confirmed that soil moisture and canopy closure were not

significantly different between paired inside and outside plots (T^2= 0.2774, d.f.= 2,83,

p=0.7584).

Floristic quality at deer exclosures

The mean floristic quality measurement for each index is given in Table 3.4 for plots

inside and outside deer exclosures.

Table 3.4 Mean species richness and floristic quality ($\pm$ SE) inside and outside deer exclosures as measured by various indices. (n=44)

Floristic Quality measure	Inside	Outside
Species richness	16.5 $\pm$ 1.1	13.0 $\pm$ 1.0
FQAI	16.8 $\pm$ 0.8	13.9 $\pm$ 0.9
PSI	14.9 $\pm$ 0.9	11.0 $\pm$ 1.0
Mean C_s	4.0 $\pm$ 0.2	3.8 $\pm$ 0.2
FQAI'	37.9 $\pm$ 1.9	35.0 $\pm$ 2.5

Species richness was significantly different between the inside and outside plots (t =

5.5981, d.f. = 43, p <<0.001). The results of paired sample t-tests of floristic quality

inside and outside the exclosures are shown in Table 3.5. The FQAI and PSI also showed

a significant difference in floristic quality (n=44, p<<0.001). However, the mean Cs and

FQAI' measures were not significantly different inside and outside the exclosures.

Table 3.5 Results of paired sample t-tests of species richness and floristic quality inside and outside deer exclosures. (n=44, df=43)

	t	p-value
Species richness	5.5981	**<<0.001**
FQAI	5.2006	**<<0.001**
PSI	4.4814	**<<0.001**
FQAI'	1.7982	0.0792
Mean C_s	1.7827	0.0817

The change in species richness was linearly related to the age of the deer exclosure

(Table 3.6) with the difference between the protected and unprotected plots increasing the

longer the deer exclosure had been in place (Figure 3.3 A). The change in FQAI in the

deer exclosures was also linearly related to the age of the exclosure (Table 3.6, Figure 3.3

B), and the change in PSI also displayed a similar increase with deer exclosure age.

(Table 3.6, Figure 3.3 C). Virtually all exclosures over 10 years of age (16 of 18, 89%)

had greater floristic quality in the protected plots as measured by species richness, FQAI

or PSI. However, the change in mean C_s and change in FQAI' between inside and

outside plots were not related to the ages of the deer exclosures (Table 3.6, Figure 3.3 D

& E).

Table 3.6 Results of linear regression of change in species richness and floristic quality measures against deer exclosure age. (n=44, df=1,42)

	F	p-value	r^2	Slope	Intercept
Species richness	7.636	**0.008**	0.13	0.194	1.664
FQAI	8.112	**0.007**	0.14	0.177	1.212
PSI	5.936	**0.019**	0.10	0.184	1.214
FQAI'	1.123	0.079	0.00	na	na
Mean C_s	1.22	0.082	0.00	na	na

na = not applicable
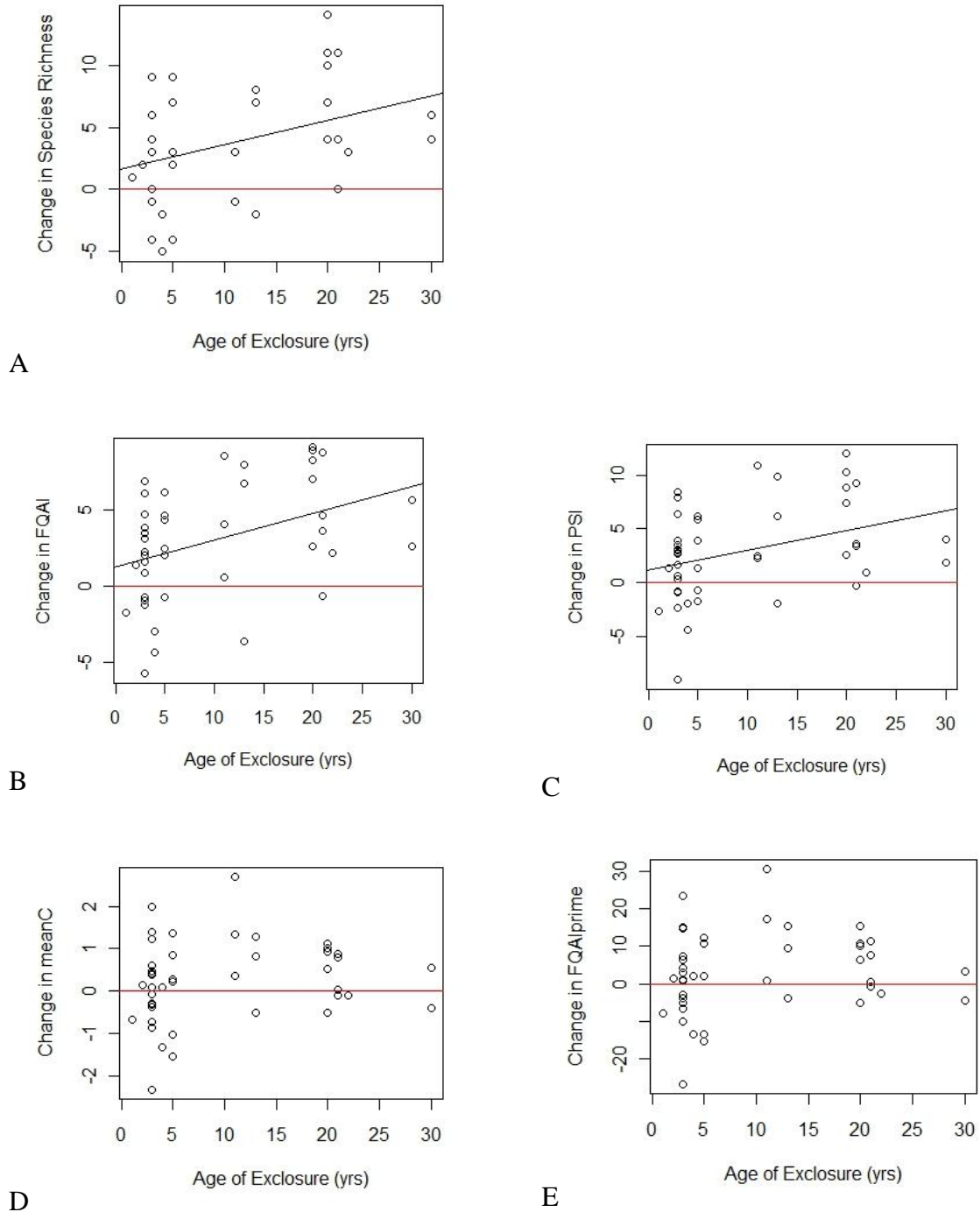
Figure 3.3 Relationship of the change in species richness and floristic quality measures to age of exclosures. A) Species richness, B) FQAI, C) PSI, D) mean C_s, E) FQAI'. Results are shown with a zero line and the regression line, if applicable. The regression line is shown with intercept and slope as in Table 3.6. Points above the zero line indicate greater quality inside the exclosure. n=44.

Floristic quality across varying deer densities

The average deer densities over the eight-year period prior to the study ranged from lows

of 11.7 deer/km^2 at Loudon Heights in Harper's Ferry Park and 11.9 at Prince William

Forest Park up to a high of 65.7 deer/km^2 at Monocacy National Battlefield (Table 3.7).

Table 3.7 Deer densities by site, eight-year average (2001-2008). Based on Bates
(unpublished data).

Site	Park Name	Deer Density (deer/km)
ANTI	Antietam National Battlefield	43.0
CATO	Catoctin Mountain Park	49.3
GREE	Greenbelt Park	36.2
GWMP	George Washington Memorial Parkway[1]	32.1
LOUHGT	Harper's Ferry NHP – Loudon Heights*	11.7
MDHGT	Harper's Ferry NHP – Maryland Heights	36.4
MANA	Manassas National Battlefield	61.1
MONO	Monocacy National Battlefield	65.7
PRWI	Prince William Forest Park	11.9
ROCR	Rock Creek Park	26.7

[1]Great Falls Park; * 2007 estimate only

Species richness and floristic quality values for each site are shown in Table 3.8. Species

richness ranged from a mean of 20.62 at Antietam to 9.0 at Greenbelt. FQAI ranged

from a mean of 17.78 at Prince William to 9.53 at Maryland Heights – Harper's Ferry.

PSI ranged from a mean of 17.41 at Greenbelt to 6.0 at Maryland Heights. The mean

coefficients of conservatism (mean C_s) ranged from 2.17 at Antietam to 4.80 at Prince

William. Miller and Wardrup's modified FQAI (FQAI') ranged from 44.77 at Greenbelt

to 17.63 at Antietam.

Table 3.8 Mean ($\pm$SE) species richness and floristic quality measures by site. n is the
number of 2-m radius plots. S is species richness. Sites are listed in order of increasing
deer density. The NODEER site represents a collection of plots within deer exclosures.

Site	n	S	FQAI	PSI	mean C_s	FQAI'
NODEER	16	18.19$\pm$1.61	16.76$\pm$0.95	14.58$\pm$1.15	3.77$\pm$0.24	35.40$\pm$2.73
LOUHGT	7	12.29$\pm$1.82	14.04$\pm$1.47	12.17$\pm$1.67	3.75$\pm$0.2	34.73$\pm$2.47
PRWI	25	14.08$\pm$0.92	17.78$\pm$0.54	17.41$\pm$0.54	4.80$\pm$0.12	47.60$\pm$1.29
ROCR	9	11.67$\pm$1.41	14.00$\pm$0.83	11.88$\pm$1.06	3.84$\pm$0.27	35.56$\pm$3.19
GWMP	10	11.30$\pm$1.21	13.89$\pm$0.59	12.59$\pm$0.56	4.04$\pm$0.17	35.88$\pm$1.98
GREE	2	14.00$\pm$7	15.97$\pm$2.36	15.53$\pm$1.93	4.52$\pm$0.62	44.77$\pm$6.66
MDHGT	4	9.00$\pm$0.91	9.53$\pm$1.05	6.00$\pm$1.08	2.50$\pm$0.26	19.85$\pm$2.86
ANTI	8	20.62$\pm$1.34	12.13$\pm$0.74	8.07$\pm$0.73	2.17$\pm$0.11	17.63$\pm$1.17
CATO	15	10.80$\pm$1.86	12.48$\pm$1.46	10.40$\pm$1.26	3.81$\pm$0.28	35.53$\pm$3.06

MANA	6	14.67±3.74	12.40±1.62	10.37±1.43	3.35±0.41	31.41±4.7
MONO	6	11.83±1.19	10.81±1.09	7.52±0.89	2.62±0.24	21.90±2.35

The linear regression of each floristic quality measure against deer density is shown in

Table 3.9. The result of the regression of species richness against deer density is shown

for comparison. Species richness was marginally significantly related to deer density

($p=0.048$, $r^2=0.03$). All floristic quality measures decreased with increasing deer density

as shown by the negative slopes and were significantly related to deer densities

($p<<0.001$). The FQAI and PSI had the strongest relationships with 25% and 31% of the

variation explained by deer density.

**Table 3.9 Results of linear regressions of species richness and floristic quality with
deer density.** (n=108, df=1,106)

	F	p-value	r^2	Slope	Intercept
Species richness	4.0	**0.048**	0.03	-0.056	15.43
FQAI	36.14	**<<0.001**	0.25	-0.102	17.38
PSI	45.82	**<<0.001**	0.31	-0.127	16.24
Mean Cs	21.26	**<<0.001**	0.16	-0.021	4.39
FQAI'	21.54	**<<0.001**	0.16	-0.243	42.58

The relationship between the various floristic quality measures and deer density is

illustrated in the graphs in Figure 3.4.
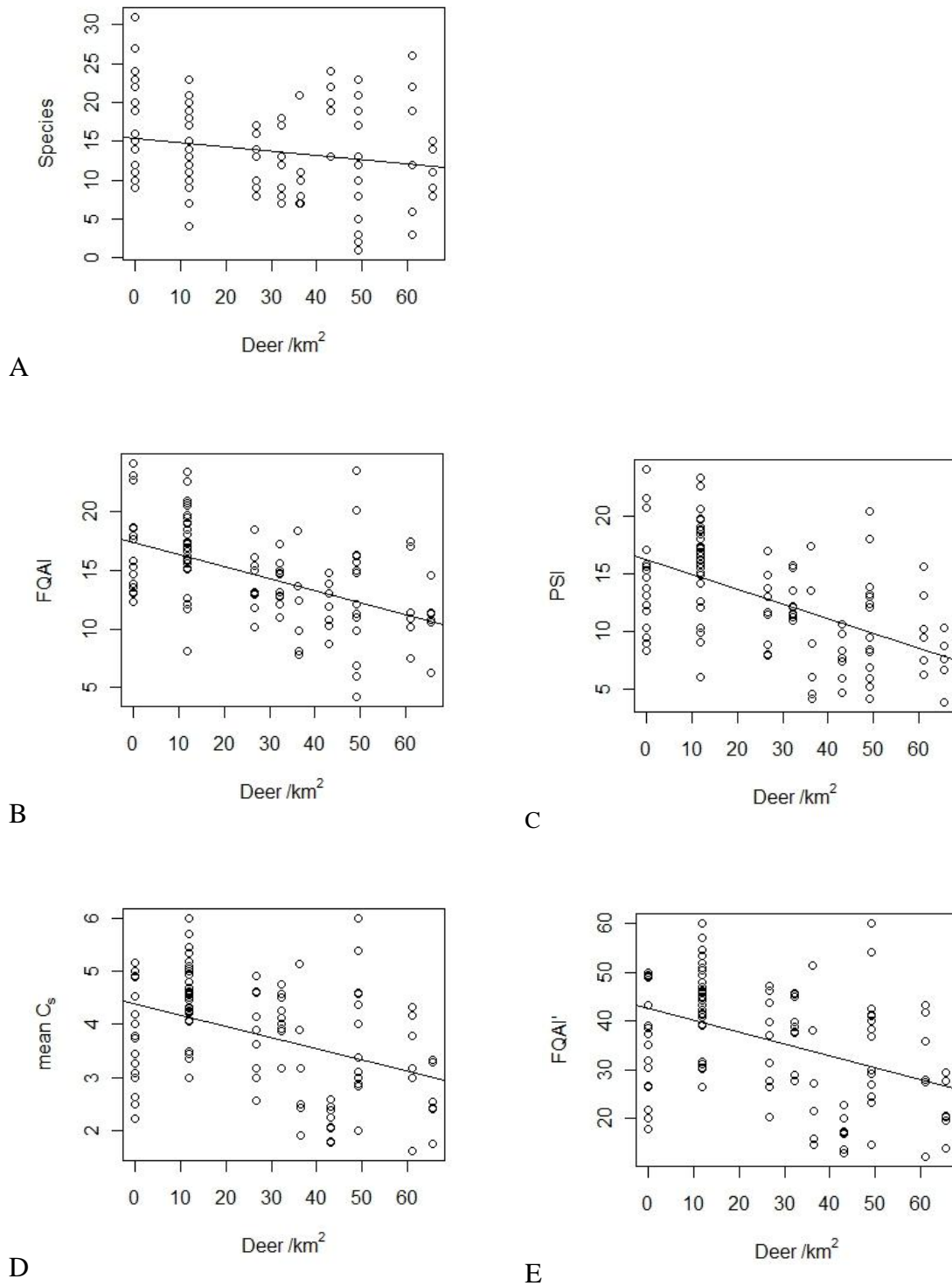
Figure 3.4 Species richness and floristic quality relationship to deer density. A) Species richness B) FQAI C) PSI, D) mean C_s, E) FQAI'. Each point represents a 2-m radius plot (n=108). The regression line is shown with intercept and slope as in Table 3.9.

DISCUSSION

I predicted that floristic quality should be greater in plots protected from deer browse inside deer exclosures. Table 3.4 shows that the mean values for all measures appear greater inside the exclosures, however, only species richness, FQAI and PSI were significantly different in the statistical test (Table 3.5). Since both FQAI and PSI give more weight to species richness, it is likely that the significant difference between the paired plots is due primarily to a difference in the number of species rather than differences in their average conservatism. FQAI' and mean Cs both attempt to minimize the influence of species richness and emphasize the coefficients of conservatism, and neither shows a significant difference between the paired plots. These results imply that deer are reducing the overall number of species but not having a measureable influence on the overall conservative level of the community.

Anderson et al. (2004) also found that the mean coefficient of conservatism showed no difference between protected and unprotected plots after a decade in a prairie community but suggested that deer do have an effect on conservative species by reducing their abundance and correspondingly increasing the abundance of browse-tolerant species which tend to have a lower coefficient of conservatism value. My results are consistent with this non-significant change in conservative value but differ from Anderson et al. (2004) in that FQAI did differ significantly between protected and unprotected plots.

One explanation for the lack of an effect on conservatism may be that many of the exclosures were erected after conservative species had already been eliminated from the site and we are seeing a legacy effect within the exclosures (Russell et al. 2001). Royo et al. (2010) found that in a landscape level study after reduction in deer densities that species richness and evenness did not recover despite increases in the abundances of certain browse-sensitive species. They suggest that legacy effects of long-term intensive browsing by deer may have created depauperate forests that may need more active restoration measures to recover.

Another possible reason that conservative species are not recovering within exclosures is that other constraints on their regeneration are present such as invasive earthworms, slugs, or lack of propagules. Invasive earthworms have been shown to decrease species richness and decrease the establishment of forest herbs and these effects have been linked to indirect effects of deer (Fisichelli et al. 2013, Holdsworth et al. 2007). Invasive slugs can also limit species richness and establishment of forest herbs and woody seedlings and prevent regeneration even in areas protected from deer browse (Joe and Daehler 2008, Côté et al. 2005, Holdsworth 2006).

Finally, another explanation may be that the coefficients of conservatism that were assigned to these species do not accurately reflect their tolerance to the chronic disturbance of deer browse. Further study is needed to determine if any of these explanations is correct.

When the change in FQAI and change PSI between protected and unprotected plots at the exclosures were regressed against the age of the exclosure, it showed that there is a weak linear increase in both the FQAI and PSI the longer the plots were protected (Table 3.6, Figure 3.3). The r^2 values are low (r^2=0.14 and 0.10 respectively); however, virtually all exclosures more than 10 years old experienced an increase in floristic quality inside the exclosures. Species richness also showed a similar relationship to the age of exclosure (r^2=0.13). One caveat should be mentioned here; however, which is that land managers may not be motivated to maintain an exclosure over a long period of time if it is not showing a difference in vegetation. This bias may create an older cohort of exclosures which will always show statistical differences from the surrounding forest.

When I examined the correlation of floristic quality measures with the deer densities across several forests, the results (Table 3.9) showed that the weakest correlate with deer density was species richness. I had predicted that floristic quality should decrease as deer density increased. Floristic quality did show a negative linear relationship with deer density (Table 3.9, Figure 3.4). All floristic quality measures were more strongly correlated with deer density than species richness was. However, the measures based primarily on coefficient of conservatism, the adjusted FQAI and mean C_s, were only weakly correlated with deer densities as indicated by the low r^2 values. The FQAI and PSI were more closely correlated with deer densities. The PSI has a stronger relationship explaining 31% of the variation while the FQAI only explains 25%. PSI may provide a better fit because it includes invasive species in its calculation. The PSI r^2 value of 0.31 is good for ecological data indicating that there is a real relationship and is consistent with

the presence of a multitude of factors in addition to deer influencing floristic quality. These results suggest that the PSI floristic quality measure should be the preferred measure for use in forests where deer browse pressure is expected since it most strongly shows decreasing quality under increasing deer pressure.

These studies have shown that the floristic quality indices FQAI and PSI combine species richness and quality in a meaningful way that provides more information than species richness alone. Floristic quality measures which are weighted more heavily toward conservatism values, such as mean C_s and Miller and Wardrup's modified FQAI, may not adequately reflect changes in the floristic community due to deer. In the mid-Atlantic states and New Jersey, land managers who wish to monitor the effects of deer on forest understories should prefer FQAI or PSI indices to provide an indication of deer browsing impact.

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APPENDIX

Appendix 3.1. Table of plant species found and their coefficients of conservatism.
Nativity of N means Native, I means Invasive. Nomenclature follows USDA NRCS
Plants Database (http://plants.usda.gov, accessed October 2009).

Species Code	Scientific Name	Common Name	Family	Nativity	C NJ	C Mid-Atl
ACNE2	*Acer negundo*	box elder	Aceraceae	N	2	2
ACPA2	*Acer palmatum*	Japanese maple	Aceraceae	I	0	0
ACPL	*Acer platanoides*	Norway maple	Aceraceae	I	0	0
ACRU	*Acer rubrum*	red maple	Aceraceae	N	3	1
ACSA2	*Acer saccharinum*	silver maple	Aceraceae	N	5	5
ACSA3	*Acer saccharum*	sugar maple	Aceraceae	N	5	6
ACMI2	*Achillea millefolium*	common yarrow	Asteraceae	I	0	0
ACRAR	*Actaea racemosa*	black cohosh	Ranunculaceae	N	9	6
ADPE	*Adiantum pedatum*	maidenhair fern	Pteridaceae	N	7	7
AGAL5	*Ageratina altissima*	rough snakeroot	Asteraceae	N	3	3
AGCA	*Agrostis capillaris*	colonial bentgrass	Poaceae	I	0	0
AGPE	*Agrostis perennans*	upland bentgrass	Poaceae	N		4
AIAL	*Ailanthus altissima*	tree-of-heaven	Simaroubaceae	I	0	0
ALJU	*Albizia julibrissin*	mimosa	Fabaceae	I	0	0
ALPE4	*Alliaria petiolata*	garlic mustard	Brassicaceae	I	0	0
ALVI	*Allium vineale*	wild garlic	Liliaceae	I	0	0
AMAR2	*Ambrosia artemisiifolia*	ragweed	Asteraceae	N	0	1
AMAR3	*Amelanchier arborea*	common serviceberry	Rosaceae	N	7	6
AMCA4	*Amelanchier canadensis*	coastal serviceberry	Rosaceae	N	8	7
AMBR7	*Ampelopsis brevipedunculata*	porcelainberry	Vitaceae	I	0	0
AMBR2	*Amphicarpaea bracteata*	hog peanut	Fabaceae	N	4	4
ANQU	*Anemone quinquefolia*	wood anemone	Ranunculaceae	N	7	7
ANTH5	*Anemonella thalictroides*	rue anemone	Ranunculaceae	N	7	
ANOD	*Anthoxanthum odoratum*	sweet vernal grass	Poaceae	I	0	0
ARNU2	*Aralia nudicaulis*	wild sarsaparilla	Araliaceae	N	5	7
ARSP2	*Aralia spinosa*	devil's walking stick	Araliaceae	N		3
ARTR	*Arisaema triphyllum*	jack-in-the-pulpit	Araceae	N	5	5
ASCA	*Asarum canadense*	wild ginger	Aristolochiaceae	N	8	7
ASTR	*Asimina triloba*	pawpaw	Annonaceae	N	10	5
ASPL	*Asplenium platyneuron*	ebony spleenwort	Aspleniaceae	N	3	3
ASRH2	*Asplenium rhizophyllum*	walking fern	Aspleniaceae	N	10	9
ATFI	*Athyrium filix-femina*	lady fern	Dryopteridaceae	N	7	5
BAVI3	*Bartonia virginica*	yellow screwstem	Gentianaceae	N	5	7
BETH	*Berberis thunbergii*	Japanese barberry	Berberidaceae	I	0	0
BEAL2	*Betula alleghaniensis*	yellow birch	Betulaceae	N	10	7
BELE	*Betula lenta*	black birch	Betulaceae	N	6	5
BEPO	*Betula populifolia*	gray birch	Betulaceae	N	2	5
BIBI7	*Bidens bipinnata*	Spanish needles	Asteraceae	N	1	1
BIDEN	*Bidens sp.*	beggarticks	Asteraceae			
BOCY	*Boehmeria cylindrica*	false nettle	Urticaceae	N	5	5
BOVI	*Botyrichium virginianum*	rattlesnake fern	Ophioglossaceae	N	6	5
BRAR9	*Brachyelytrum aristosum*	northern shorthusk	Poaceae	N	10	7

Species Code	Scientific Name	Common Name	Family	Nativity	C NJ	C Mid-Atl
BRER2	*Brachyelytrum erectum*	bearded shorthusk	Poaceae	N	7	6
CARA2	*Campsis radicans*	trumpet creeper	Bignoniaceae	N	3	2
CAIM	*Cardamine impatiens*	narrowleaf bittercress	Brassicaceae	I	0	0
CAAL25	*Carex albicans*	stellate sedge	Cyperaceae	N	7	6
CAAM8	*Carex amphibola*	eastern narrowleaf sedge	Cyperaceae	N	10	7
CABL	*Carex blanda*	eastern woodland sedge	Cyperaceae	N	6	3
CACO7	*Carex communis*	fibrous root sedge	Cyperaceae	N		7
CADE5	*Carex debilis*	white edge sedge	Cyperaceae	N	6	4
CADER	*Carex debilis var. rudgei*	white-edge sedge	Cyperaceae	N	5	6
CADI5	*Carex digitalis*	slender woodland sedge	Cyperaceae	N	7	6
CAFE3	*Carex festucacea*	fescue sedge	Cyperaceae	N	7	5
CAFR3	*Carex frankii*	Frank's sedge	Cyperaceae	N		2
CAGR24	*Carex grisea*	inflated narrow-leaf sedge	Cyperaceae	N	6	5
CAHI6	*Carex hirsutella*	fuzzy sedge	Cyperaceae	N	4	4
CAHI5	*Carex hirtifolia*	pubescent sedge	Cyperaceae	N	10	6
CAIN12	*Carex intumescens*	bladder sedge	Cyperaceae	N	5	5
CAJA2	*Carex jamesii*	James' sedge	Cyperaceae	N	10	8
CALA18	*Carex laxiculmis*	spreading sedge	Cyperaceae	N	8	7
CALA19	*Carex laxiflora*	broad looseflowered sedge	Cyperaceae	N	6	5
CAPE6	*Carex pensylvanica*	Pennsylvania sedge	Cyperaceae	N	5	5
CARA	*Carex radiata*	eastern star sedge	Cyperaceae	N	7	7
CARE9	*Carex retroflexa*	reflexed sedge	Cyperaceae	N	7	7
CASC11	*Carex scoparia*	pointed broom sedge	Cyperaceae	N	3	4
CAST5	*Carex stipata*	awl-fruited sedge	Cyperaceae	N	3	3
CAST6	*Carex straminea*	eastern straw sedge	Cyperaceae	N		8
CASW	*Carex swanii*	Swan's sedge	Cyperaceae	N	6	4
CATO10	*Carex tonsa*	shaved sedge	Cyperaceae	N	6	6
CAUM4	*Carex umbellata*	parasol sedge	Cyperaceae	N	6	5
CACA18	*Carpinus caroliniana*	American hornbeam	Betulaceae	N	7	6
CAAL27	*Carya alba*	mockernut hickory	Juglandaceae	N	5	6
CACO15	*Carya cordiformis*	bitternut hickory	Juglandaceae	N	8	5
CAGL8	*Carya glabra*	pignut hickory	Juglandaceae	N	7	6
CAOV2	*Carya ovata*	shagbark hickory	Juglandaceae	N	7	6
CADE12	*Castanea dentata*	American chestnut	Fagaceae	N	5	5
CAPU9	*Castanea pumila*	chinkapin	Fagaceae	N	4	8
CATH2	*Caulophyllum thalictroides*	blue cohosh	Berberidaceae	N	9	7
CEOR7	*Celastrus orbiculatus*	oriental bittersweet	Celastraceae	I	0	0
CEOC	*Celtis occidentalis*	common hackberry	Ulmaceae	N	4	4
CECA4	*Cercis canadensis*	eastern redbud	Fabaceae	N	8	5
CHLA6	*Chasmanthium laxum*	slender woodoats	Poaceae	N	4	4
CHAL7	*Chenopodium album*	lambs quarters	Chenopodiaceae	I	0	0
CHMA3	*Chimaphila maculata*	striped wintergreen	Pyrolaceae	N	7	6
CIAR2	*Cinna arundinacea*	wood reed	Poaceae	N	4	5
CILU	*Circaea lutetiana*	enchanter's nightshade	Onagraceae	N	6	2
CLVI5	*Clematis virginiana*	virgin's bower	Ranunculaceae	N	5	3

Species Code	Scientific Name	Common Name	Family	Nativity	C NJ	C Mid-Atl
COCA4	*Collinsonia canadensis*	horsebalm	Lamiaceae	N	9	5
COCO3	*Commelina communis*	Asian dayflower	Commelinaceae	I	0	0
COAM	*Conopholis americana*	squawroot	Orobanchaceae	N	9	8
COAR4	*Convolvus arvensis*	field bindweed	Convolvulaceae	I		0
COFL2	*Cornus florida*	flowering dogwood	Cornaceae	N	5	4
COAM3	*Corylus americana*	American hazelnut	Betulaceae	N	5	5
CYVI	*Cynoglossum virginianum*	wild comfrey	Boraginaceae	N	10	5
CYAC3	*Cypripedium acaule*	pink lady's slipper	Orchidaceae	N	8	7
CYBU3	*Cystopteris bulbifera*	bulblet bladder fern	Dryopteridaceae	N	10	8
DAGL	*Dactylis glomerata*	orchardgrass	Poaceae	I		0
DASP2	*Danthonia spicata*	poverty oatgrass	Poaceae	N	5	3
DEPU2	*Dennstaedtia punctilobula*	hayscented fern	Dennstaedtiaceae	N		2
DEGL5	*Desmodium glutinosum*	pointedleaf ticktrefoil	Fabaceae	N	7	6
DENU4	*Desmodium nudiflorum*	nakedflower ticktrefoil	Fabaceae	N	7	6
DIAR	*Dianthus armeria*	Deptford pink	Caryophyllaceae	I		0
DIAC2	*Dichanthelium acuminatum*	tapered rosette grass	Poaceae	N		5
DIBO2	*Dichanthelium boscii*	Bosc's panicgrass	Poaceae	N	8	6
DIDI6	*Dichanthelium dichotomum*	cypress panicgrass	Poaceae	N	8	4
DIQU	*Dioscorea quaternata*	fourleaf wild yam	Dioscoreaceae	N	7	5
DIVI4	*Dioscorea villosa*	wild yam	Dioscoreaceae	N	7	5
DRCA11	*Dryopteris carthusiana*	spinulose woodfern	Dryopteridaceae	N	5	5
DRIN5	*Dryopteris intermedia*	intermediate woodfern	Dryopteridaceae	N	8	5
DRMA4	*Dryopteris marginalis*	marginal woodfern	Dryopteridaceae	N	9	6
DRYOP	*Dryopteris sp.*	woodfern	Dryopteridaceae	N		
DUIN	*Duchesnea indica*	Indian strawberry	Rosaceae	I	0	0
ELUM	*Elaeagnus umbellata*	autumn olive	Elaeagnaceae	I	0	0
ELTE	*Eleocharis tenuis*	slender spikerush	Cyperaceae	N	3	3
ELHY	*Elymus hystrix*	bottlebrush grass	Poaceae	N		5
ELVI3	*Elymus virginicus*	Virginia wild rye	Poaceae	N		4
EPCO	*Epilobium coloratum*	purple-leaved willowherb	Onagraceae	N	2	2
EPHE	*Epipactis helleborine*	broadleaf helleborine	Orchidaceae	I	0	0
ERHI2	*Erechtites hieraciifolia*	pilewort	Asteraceae	N		1
EURA	*Eubotrys racemosa*	swamp fetterbush	Ericaceae	N	6	6
EUAL13	*Euonymus alatus*	burning bush	Celastraceae	I	0	0
EUAM	*Euonymus americana*	American strawberry bush	Celastraceae	N	7	6
EUFO	*Euonymus fortunei*	wintercreeper	Celastraceae	I	0	0
EUPE3	*Eupatorium perfoliatum*	common boneset	Asteraceae	N	3	3
EUDI16	*Eurybia divaricata*	white wood aster	Asteraceae	N	4	5
FAGR	*Fagus grandifolia*	American beech	Fagaceae	N	8	6
FESU3	*Festuca subverticillata*	nodding festcue	Poaceae	N	8	6
FRVE	*Fragaria vesca*	woodland strawberry	Rosaceae	N	7	
FRAM2	*Fraxinus americana*	white ash	Oleaceae	N	7	5
FRPE	*Fraxinus pennsylvanica*	green ash	Oleaceae	N	4	5
GASP5	*Galearis spectabilis*	showy orchid	Orchidaceae	N	10	7
GAAP2	*Galium aparine*	cleavers	Rubiaceae	N	1	2
GACI2	*Galium circaezans*	wild licorice	Rubiaceae	N	8	6

Species Code	Scientific Name	Common Name	Family	Nativity	C NJ	C Mid-Atl
GALA3	*Galium lanceolatum*	lanceleaf wild licorice	Rubiaceae	N	8	8
GATI	*Galium tinctorium*	stiff marsh bedstraw	Rubiaceae	N	3	4
GATR3	*Galium triflorum*	fragrant bedstraw	Rubiaceae	N	5	5
GAPR2	*Gaultheria procumbens*	teaberry	Ericaceae	N	5	8
GABA	*Gaylussacia baccata*	black huckleberry	Ericaceae	N	8	8
GAFR2	*Gaylussacia frondosa*	blue huckleberry	Ericaceae	N	7	8
GECA7	*Geum canadense*	white avens	Rosaceae	N	5	3
GELA	*Geum laciniatum*	rough avens	Rosaceae	N	5	5
GLHE2	*Glechoma hederacea*	ground ivy	Lamiaceae	I	0	0
GLST	*Glyceria striata*	fowl manna grass	Poaceae	N	3	5
HAVI2	*Hackelia virginiana*	beggars lice	Boraginaceae	N	2	3
HAVI4	*Hamamelis virginiana*	witch hazel	Hamamelidaceae	N	7	5
HEHE	*Hedera helix*	English ivy	Araliaceae	I	0	0
HENOO	*Hepatica nobilis var. obtusa*	roundlobe hepatica	Ranunculaceae	N	9	8
HOLA	*Holcus lanatus*	velvetgrass	Poaceae	I	0	0
HOPU2	*Houstonia purpurea*	purple bluets	Rubiaceae	N		7
ILOP	*Ilex opaca*	American holly	Aquifoliaceae	N	4	4
IMCA	*Impatiens capensis*	jewelweed	Balsaminaceae	N	2	3
JUNI	*Juglans nigra*	black walnut	Juglandaceae	N	2	4
JUEF	*Juncus effusus*	soft rush	Juncaceae	N	1	2
JUTE	*Juncus tenuis*	path rush	Juncaceae	N		1
JUVI	*Juniperus virginiana*	eastern red cedar	Cupressaceae	N	2	3
KAAN	*Kalmia angustifolia*	sheep laurel	Ericaceae	N	5	8
KALA	*Kalmia latifolia*	mountain laurel	Ericaceae	N	7	5
LEVI2	*Leersia virginica*	white cutgrass	Poaceae	N	3	3
LEMI3	*Lemna minor*	common duckweed	Lemnaceae	N		4
LIGUS2	*Ligustrum sp.*	privet	Oleaceae	I	0	0
LIBE3	*Lindera benzoin*	spicebush	Lauraceae	N	5	5
LIST2	*Liquidambar styraciflua*	sweetgum	Hamamelidaceae	N	1	1
LITU	*Liriodendron tulipifera*	tulip poplar	Magnoliaceae	N	5	5
LOIN	*Lobelia inflata*	Indian tabacco	Campanulaceae	N	2	1
LOJA	*Lonicera japonica*	Japanese honeysuckle	Caprifoliaceae	I	0	0
LOMA6	*Lonicera morrowii/maackii*	Amur honeysuckle	Caprifoliaceae	I	0	0
LOTA	*Lonicera tartarica*	Tartarian honeysuckle	Caprifoliaceae	I	0	0
LYDI3	*Lycopodium digitatum*	fan clubmoss	Lycopodiaceae	N		4
LYOB	*Lycopodium obscurum*	ground pine	Lycopodiaceae	N	4	6
LYVI4	*Lycopus virginicus*	Virginia water horehound	Lamiaceae	N		4
LYAM	*Lycopus americanus*	American water horehound	Lamiaceae	N	4	4
LYUN	*Lycopus uniflorus*	water horehound	Lamiaceae	N	4	6
LYNU	*Lysimachia nummularia*	moneywort	Primulaceae	I	0	0
LYQU2	*Lysimachia quadrifolia*	whorled yellow loosestrife	Primulaceae	N	3	5
MATR	*Magnolia tripetala*	umbrella tree	Magnoliaceae	N		9
MACA4	*Maianthemum canadense*	Canada mayflower	Liliaceae	N	4	8
MARA7	*Maianthemum racemosum*	false solomon's seal	Liliaceae	N	5	5
MEVI	*Medeola virginiana*	indian cucumber	Liliaceae	N	8	7

Species Code	Scientific Name	Common Name	Family	Nativity	C NJ	C Mid-Atl
MELI2	*Melampyrum lineare*	narrowleaf cowwheat	Scrophulariaceae	N	5	7
MECA3	*Menispermum canadense*	moonseed	Menispermaceae	N	6	5
MIVI	*Microstegium vimineum*	Japanese stilt-grass	Poaceae	I	0	0
MIRE	*Mitchella repens*	partridgeberry	Rubiaceae	N	5	6
MIDI3	*Mitella diphylla*	mitrewort	Saxifragaceae	N	9	8
MORU	*Morus rubra*	red mulberry	Moraceae	N	10	6
NAPS	*Narcissus pseudonarcissus*	daffodil	Liliaceae	I	0	0
NYSY	*Nyssa sylvatica*	black gum	Cornaceae	N	4	6
ONSE	*Onoclea sensibilis*	sensitive fern	Dryopteridaceae	N	2	3
OSCL	*Osmorhiza claytonii*	sweet cicely	Apiaceae	N	4	5
OSVI	*Ostrya virginiana*	hophornbeam	Betulaceae	N	7	7
OXST	*Oxalis stricta*	yellow wood sorrel	Oxalidaceae	N	0	0
PAQU	*Panax quinquefolius*	American ginseng	Araliaceae	N	10	8
PATR2	*Panax trifolius*	dwarf ginseng	Araliaceae	N	8	8
PAVI2	*Panicum virgatum*	switchgrass	Poaceae	N	3	4
PAPE5	*Parietaria pensylvanica*	Pennsylvania pellitory	Urticaceae	N	9	2
PACA11	*Paronychia canadensis*	forked chickweed	Caryophyllaceae	N	5	6
PAQU2	*Parthenocissus quinquefolia*	Virginia creeper	Vitaceae	N	1	3
PEFR4	*Perilla frutescens*	beefsteakplant	Lamiaceae	I	0	0
PHHE11	*Phegopteris hexagonoptera*	broad beech fern	Thelypteridaceae	N	8	7
PHME13	*Photinia melanocarpa*	black chokeberry	Rosaceae	N	6	8
PHLE5	*Phryma leptostachya*	lopseed	Verbenaceae	N	8	5
PHAM4	*Phytolacca americana*	pokeweed	Phytolaccaceae	N	0	1
PIGL	*Picea glauca*	white spruce	Pinaceae	I	0	0
PIPU2	*Pilea pumila*	clearweed	Urticaceae	N	3	4
PIEC	*Pinus echinata*	short-leaf pine	Pinaceae	N		8
PIRI	*Pinus rigida*	pitch pine	Pinaceae	N	6	6
PIVI2	*Pinus virginiana*	Virginia pine	Pinaceae	N	3	3
PLMA2	*Plantago major*	common plantain	Plantaginaceae	I	0	0
POCO	*Poa compressa*	Canada bluegrass	Poaceae	I	0	0
POPE	*Podophyllum peltatum*	mayapple	Berberidaceae	N		5
POBI2	*Polygonatum biflorum*	solomon's seal	Liliaceae	N	8	7
POAR	*Polygonum arifolium*	halberd-leaf tearthumb	Polygonaceae	N	6	6
POCAL	*Polygonum caespitosum var. longisetum*	oriental ladysthumb	Polygonaceae	I	0	0
POHY2	*Polygonum hydropiperoides*	marsh waterpepper	Polygonaceae	N	6	4
POPE10	*Polygonum perfoliatum*	mile-a-minute vine	Polygonaceae	I	0	0
POPE3	*Polygonum persicaria*	spotted ladysthumb	Polygonaceae	I	0	0
POPU5	*Polygonum punctatum*	dotted smartweed	Polygonaceae	N	5	4
POSA5	*Polygonum sagittatum*	arrow-leaf tearthumb	Polygonaceae	N		3
POVI2	*Polygonum virginianum*	Virginia jumpseed	Polygonaceae	N	4	4
POAC4	*Polystichum acrostichoides*	christmas fern	Dryopteridaceae	N	7	5
POGR4	*Populus grandidentata*	big tooth aspen	Salicaceae	N	4	4
POSI2	*Potentilla simplex*	common cinquefoil	Rosaceae	N	2	3
POTEN	*Potentilla sp.*	cinquefoil	Rosaceae	N	2	
PRAL2	*Prenanthes alba*	white rattlesnakeroot	Asteraceae	N	6	7
PRTR	*Prenanthes trifoliolata*	gall of the earth	Asteraceae	N	6	7

Species Code	Scientific Name	Common Name	Family	Nativity	C NJ	C Mid-Atl
PRVU	*Prunella vulgaris*	self-heal	Lamiaceae	I	0	0
PRSE2	*Prunus serotina*	black cherry	Rosaceae	N	1	3
PTAQ	*Pteridium aquilinum*	bracken fern	Dennstaedtiaceae	N	2	4
PYAM	*Pyrola americana*	wintergreen	Pyrolaceae	N	8	8
QUAL	*Quercus alba*	white oak	Fagaceae	N	4	6
QUBI	*Quercus bicolor*	swamp white oak	Fagaceae	N	7	8
QUCO2	*Quercus coccinea*	scarlet oak	Fagaceae	N	6	7
QUFA	*Quercus falcata*	southern red oak	Fagaceae	N		5
QUIL	*Quercus ilicifolia*	bear oak	Fagaceae	N	7	8
QUMA3	*Quercus marilandica*	blackjack oak	Fagaceae	N	6	7
QUPA2	*Quercus palustrus*	pin oak	Fagaceae	N	3	5
QUPH	*Quercus phellos*	willow oak	Fagaceae	N		6
QUPR2	*Quercus prinus*	chestnut oak	Fagaceae	N	4	7
QURU	*Quercus rubra*	northern red oak	Fagaceae	N	7	6
QUVE	*Quercus velutina*	black oak	Fagaceae	N	6	6
RAAB	*Ranunculus abortivus*	littleleaf buttercup	Ranunculaceae	N	1	3
RARE2	*Ranunculus recurvatus*	hooked crowfoot	Ranunculaceae	N	3	4
RHPE4	*Rhododendron periclymenoides*	pinxterbloom azalea	Ericaceae	N	5	6
ROPS	*Robinia pseudoacacia*	black locust	Fabaceae	N	0	1
ROMU	*Rosa multiflora*	multiflora rose	Rosaceae	I	0	0
RUAL	*Rubus allegheniensis*	blackberry	Rosaceae	N	3	1
RUFL	*Rubus flagellaris*	northern dewberry	Rosaceae	N	2	1
RUHI	*Rubus hispidus*	bristly dewberry	Roseacea	N		6
RUOC	*Rubus occidentalis*	black raspberry	Rosaceae	N	1	2
RUPH	*Rubus phoenicolasius*	wineberry	Rosaceae	I	0	0
RUCA4	*Ruellia caroliniensis*	wild petunia	Acanthaceae	N	10	3
RUOB	*Rumex obtusifolius*	bitter dock	Polygonaceae	I	0	0
SACA13	*Sanguinaria canadensis*	bloodroot	Papaveraceae	N	8	5
SACA15	*Sanicula canadensis*	black snakeroot	Apiaceae	N	3	3
SAAL5	*Sassafras albidum*	sassafras	Lauraceae	N	2	3
SACE	*Saururus cernuus*	lizard's tail	Saururaceae	N	8	8
SCAT2	*Scirpus atrovirens*	black bulrush	Cyperaceae	N	3	3
SCEL	*Scutellaria elliptica*	hairy skullcap	Lamiaceae	N	5	7
SCIN2	*Scutellaria integrifolia*	hyssop skullcap	Lamiaceae	N		5
SMUV	*Smallanthus uvedalius*	hairy leafcup	Asteraceae	N		4
SMGL	*Smilax glauca*	cat greenbrier	Smilacaceae	N	3	4
SMHE	*Smilax herbacea*	smooth carrionflower	Smilacaceae	N	5	6
SMRO	*Smilax rotundifolia*	roundleaf greenbrier	Smilacaceae	N	2	2
SMTA2	*Smilax tamnoides*	bristly greenbrier	Smilacaceae	N	5	5
SOCA3	*Solanum carolinense*	Carolina horsenettle	Cyperaceae	I		0
SOCA4	*Solidago caesia*	blue-stem goldenrod	Asteraceae	N	6	6
SOFL2	*Solidago flexicaulis*	zigzag goldenrod	Asteraceae	N	7	7
SOPA2	*Solidago patula*	round-leaf goldenrod	Asteraceae	N	9	6
SORU2	*Solidago rugosa*	rough goldenrod	Asteraceae	N	2	2
SPAM	*Sparganium americanum*	bur-reed	Sparganiaceae	N		6
SYCO4	*Symphyotrichum cordifolium*	common blue wood aster	Asteraceae	N	7	5

Species Code	Scientific Name	Common Name	Family	Nativity	C NJ	C Mid-Atl
SYLAL4	*Symphyotrichum lanceolatum*	white-panicled aster	Asteraceae	N		2
SYFO	*Symplocarpus foetidus*	skunk cabbage	Araceae	N	5	5
TAOF	*Taraxacum officinale*	dandelion	Asteraceae	I	0	0
TACU	*Taxus cuspidata*	Japanese yew	Taxaceae	I		0
THPU2	*Thalictrum pubescens*	tall meadowrue	Ranunculaceae	N	5	4
THNO	*Thelypteris noveboracensis*	New York fern	Thelypteridaceae	N	3	5
THPA	*Thelypteris palustris*	eastern marsh fern	Thelypteridaceae	N		6
TIDI	*Tipularia discolor*	cranefly orchid	Orchidaceae	N		5
TORA2	*Toxicodendron radicans*	poison ivy	Anacardiaceae	N	1	1
TRBO2	*Trientalis borealis*	starflower	Primulaceae	N	1	7
ULAM	*Ulmus americana*	American elm	Ulmaceae	N	6	5
ULRU	*Ulmus rubra*	slippery elm	Ulmaceae	N		4
URDI	*Urtica dioica*	stinging nettle	Urticaceae	I	0	0
UVPE	*Uvularia perfoliata*	perfoliate-leaf bellwort	Liliaceae	N	8	6
UVSE	*Uvularia sessilifolia*	sessile-leaf bellwort	Liliaceae	N	6	6
VAAN	*Vaccinium angustifolium*	lowbush blueberry	Ericaceae	N	8	5
VACO	*Vaccinium corymbosum*	highbush blueberry	Ericaceae	N	5	6
VAPA4	*Vaccinium pallidum*	early lowbush blueberry	Ericaceae	N	7	6
VAST	*Vaccinium stamineum*	deerberry	Ericaceae	N	7	6
VEHA2	*Verbena hastata*	blue vervain	Verbenaceae	N	3	3
VEUR	*Verbena urticifolia*	white vervain	Verbenaceae	N		2
VEAL	*Verbesina alternifolia*	wingstem	Asteraceae	N	2	2
VIAC	*Viburnum acerifolium*	maple-leaf viburnum	Caprifoliaceae	N	8	6
VIDE	*Viburnum dentatum*	arrowwood	Caprifoliaceae	N	5	5
VIDI80	*Viburnum dilatatum*	linden viburnum	Caprifoliaceae	I	0	0
VIPR	*Viburnum prunifolium*	blackhaw viburnum	Caprifoliaceae	N	5	5
VIMI2	*Vinca minor*	periwinkle	Apocynaceae	I	0	0
VIPU3	*Viola pubescens*	yellow violet	Violaceae	N	7	7
VISO	*Viola sororia*	common blue violet	Violaceae	N	2	3
VITR3	*Viola triloba*	three-lobe violet	Violaceae	N		5
VIAE	*Vitis aestivalis*	summer grape	Vitaceae	N	7	4
VILA	*Vitis labrusca*	fox grape	Vitaceae	N	7	4
VITISG	*Vitis sp. (green beneath)*	grape	Vitaceae	N	4	
VITISW	*Vitis sp. (white beneath)*	grape	Vitaceae	N	7	
VIVU	*Vitis vulpina*	frost grape	Vitaceae	N	4	3
WISTE	*Wisteria sp.*	wisteria	Fabaceae	I	0	0