November 2015

Complex Effects of Ungulate Browsers on Tree Recruitment and Herbaceous Layers in New England Temperate Forests

Edward K. Faison

COMPLEX EFFECTS OF UNGULATE BROWSERS ON TREE RECRUITMENT AND HERBACEOUS LAYERS IN NEW ENGLAND TEMPERATE FORESTS

A Dissertation Presented

by

EDWARD K. FAISON

Submitted to the Graduate School of the

University of Massachusetts Amherst in partial fulfillment

of the requirements for the degree of

DOCTOR OF PHILOSOPHY

SEPTEMBER 2015

Wildlife, Fish and Conservation Biology

COMPLEX EFFECTS OF UNGULATE BROWSERS ON TREE RECRUITMENT AND HERBACEOUS LAYERS IN NEW ENGLAND TEMPERATE FORESTS

A Dissertation Presented

by

EDWARD K. FAISON

Approved as to style and content by:

_____

Stephen DeStefano, Chair

_____

David R. Foster, Chair

_____

Thomas L. Millette, Member

_____

Curtice R. Griffin, Department Head
Department of Environmental Conservation

ACKNOWLEDGMENTS

I thank my advisor, Steve DeStefano for the invitation to pursue this doctorate and for his support, advice, and friendship throughout the process. I also thank my co-advisor David Foster for his critical feedback and support along the way that greatly improved this dissertation. I am also grateful to committee member, Thomas Millette for his enthusiasm and support of this research.

Numerous other people read and provided feedback on chapters from which I benefitted greatly and for which I am grateful. Alex Royo, Oswald Schmitz, Glenn Motzkin, Josh Rapp, and Aaron Ellison were particularly helpful. Two people provided invaluable statistical and modeling assistance – Josh Rapp and Jack Finn. Special thanks to Josh and Jack. Elizabeth Crone, Aaron Ellison, and Dave Wattles also provided important statistical advice and assistance.

Several people were instrumental in data collection for this project. Greta Van Scoy managed the remote cameras and collected woody plant data along with Bernie Kuszewski. Glenn Motzkin provided plant identification expertise and collected the herbaceous layer data for chapter 2. Bill Moorhead also provided high level plant identification and assisted with data collection for chapter 4. Andrew Moe collected much of the woody plant data for chapter 1. I am sincerely grateful to Highstead for their enthusiasm and support of this endeavor, particularly board members Peter Del Tredici, Elisabeth Dudley, Peter Ashton, and David Foster.

I would also like to thank Audrey Barker-Plotkin for logistical support at Harvard Forest, John Wisnewski and the Harvard Forest woods crew for maintaining the fenced exclosures, Dan Clark and Herm Eck for logistical and financial support of the DCR exclosures, Darel Peck for maintaining the Highstead exclosure, and Justin Compton for his significant contribution in designing and initiating the experiment used in chs. 2 and 3. Finally, thank you to Brooke, Lane, and Kip for their patience and understanding on those nights and weekends that I was working.

ABSTRACT

COMPLEX EFFECTS OF UNGULATE BROWSERS ON TREE RECRUITMENT AND HERBACEOUS LAYERS IN NEW ENGLAND TEMPERATE FORESTS

SEPTEMBER 2015

EDWARD K. FAISON, B.A., CONNECTICUT COLLEGE

M.S., UNIVERSITY OF VERMONT; M.F.S., HARVARD UNIVERSITY

Ph.D., UNIVERSITY OF MASSACHUSETTS, AMHERST

Directed by: Dr. Stephen DeStefano and Dr. David Foster

Browsing by ungulates is a leading biotic disturbance in northern forest ecosystems and an important determinant of habitat, biodiversity, and ecosystem services. A large body of work has revealed that white-tailed deer (*Odocoileus virginianus*) at high densities alter forest understories in strong and predictable ways; however, less is known about how lower densities of deer and the combined effects of multiple herbivores influence forest understory vegetation, particularly in stands following canopy disturbance. Using fenced exclosures, remote cameras and other field observations, I explored the foraging response and browsing effects of low densities of deer and moose (*Alces alces*) on tree recruitment and herbaceous layers (low shrubs, herbs, and small trees) in stands disturbed by logging and simulated Hemlock Woolly Adelgid (HWA) attack over 4-7 years in Massachusetts, USA. I also examined the effects of 15 years of deer exclusion on an intact hardwood forest in southwestern Connecticut exposed to decades of high densities of deer.

In Massachusetts, large variations in tree densities developed over time in different stand disturbance types (simulated HWA attack, logging), altering the foraging response of herbivores and mitigating browsing effects. Still, moose + deer browsing delayed tree recruitment by about three years in logged stands, whereas deer alone had relatively minor effects. Delayed tree recruitment by browsers corresponded with reduced abundance of forest indicator herbs and

shrubs and greater abundance of open/disturbance indicator plant species in plots browsed by deer + moose. Richness of native herbs and low woody plants also increased with the addition of browsers. Among major tree taxa, pin cherry (*Prunus pensylvanica*) and oak (*Quercus* spp.) recruitment declined with browsing. In the Connecticut forest, sedge and exotic species abundance and richness generally declined with deer exclusion, whereas forb abundance increased. The direction in which native species richness was altered by deer exclusion depended on the plant functional group (i.e., shrub richness increased, but herb richness declined). My results revealed complex effects of herbivory over time on forest understories, highlighting the importance of examining ungulate-forest interactions across a range of ungulate densities and forest conditions and utilizing ≥3 browser treatments whenever feasible.

TABLE OF CONTENTS

Page

ACKNOWLEDGMENTS iv

ABSTRACT v

LIST OF TABLES ix

LIST OF FIGURES x

INTRODUCTION……1

CHAPTER

1. FUNCTIONAL RESPONSE OF UNGULATES IN DISTURBED HEMLOCK FORESTS.. ..4

1.1 Abstract……4

1.2 Introduction…….....5

1.3 Materials and Methods……..7

1.4 Results……11

1.5 Discussion……...13

2. TWO UNGULATE BROWSERS DELAY SUCCESSION AND PROMOTE HERBACEOUS LAYER DIVERSITY IN LOGGED TEMPERATE FORESTS……...25

2.1 Abstract……...25

2.2 Introduction…….26

2.3 Materials and Methods……28

2.4 Results…….33

2.5 Discussion……...34

3. EFFECTS OF UNGULATE BROWSERS ON TREE RECRUITMENT IN LOGGED TEMPERATE FORESTS……47

3.1 Abstract……...47

3.2 Introduction…….48

3.3 Materials and Methods……50

3.4 Results…….55

3.5 Discussion……...57

4. LONG-TERM DEER EXCLUSION HAS COMPLEX EFFECTS ON DIVERSITY AND COMPOSITION IN A SUBURBAN HARDWOOD FOREST……. 69

4.1 Abstract……...69

4.2 Introduction…….70

4.3 Materials and Methods……72

4.4 Results…….75

4.5 Discussion……...77

CONCLUSION……...86

BIBLIOGRAPHY……...88

LIST OF TABLES

Table Page

1.1 Comparison of functional response models of combined moose and white-tailed deer foraging (number of stems browsed) in relation to woody stem food supply……...17

2.1 Characteristics of study site blocks in central Massachusetts, USA……...….....39

2.2 Herb and shrub species associated with forest and open/disturbed habitats used in species composition analysis……...40

2.3 Mean abundance of common plant species and growth form groups in the herbaceous layer (<2m in height) by ungulate browser treatment in 2013……41

3.1 Characteristics of study site blocks in central Massachusetts, USA……...62

3.2 Browsing selectivity by deer alone and moose + deer combined on the 10 most common tree species.....63

4.1 Mean abundance of common plant species and growth form groups in the herbaceous layer (<2m in height) by treatment in 2013……...81

LIST OF FIGURES

Figure Page

1.1. Three major functional responses plotted as the proportion of prey eaten relative to forage density……..18

1.2 Comparison of woody stem densities (0.3-3 m in height) by treatment in 2008 and 2012……19

1.3 Comparative photos of three canopy treatments and understory vegetation response……...20

1.4 Ungulate pellet group densities in relation to woody stem densities in 2008 (a) and 2012 (b)…..21

1.5 Total moose visitation time (a) and weighted ungulate visitation time (b) recorded by remote cameras in the eight treatment plots from Dec 2011-April 2013.……...22

1.6 Functional response of ungulates in 2008 (top) and 2012 (bottom)……...23

1.7 Per capita browse consumption by ungulates in 2008 and 2012……24

2.1 Photos of experimental treatments……..43

2.2 Effect of browsers on the abundance of woody plants above the herbaceous layer (≥ 2 m in height; LRT χ^2 = 23.2; df= 2; P <0.0001) and within the herbaceous layer (<2 m in height; LRT χ^2 = 13.78; df = 2; P = 0.001)……44

2.3 Effect of browsers on the combined abundance of 13 herb and shrub species affiliated with undisturbed/forest habitat (P = 0.007) and 18 herb and shrub species associated with disturbed/open habitats (P = 0.010)……45

2.4 Effect of browsers on (A) native woody plant richness at the subplot scale (mean no. of species of trees, shrubs, and lianas in 13, 1m^2 in each plot; (LRT χ2 = 10.21; df = 2; P = 0.006); and (B) native herbaceous species richness at the plot scale (no. species of forbs, graminoids, and ferns 169 m^{-2}; LRT = χ^2 = 8.6; DF = 2; 0.013)……..46

3.1 Photos of tree recruitment.…….....64

3.2 Effects of browsers on (A) woody stem density and (B) basal area for stems ≥ 2 m in height from 2008 to 2014……...65

3.3 Effect of browsers on the recruitment density of common tree taxa above 2 m in height in 2011 (top) and 2014 (bottom).……...66

3.4 Effect of browsers on (A) species richness and (B) diversity of tall woody stems (≥2 m) in 2011 and in 2014……67

3.5 Individual based rarefaction curves (rarefied richness) by browser treatment in 2011 (left) and 2014 (right).……68

4.1 Photos of the four treatment plots in 2013……..83

4.2 Contrasting effects of deer exclusion on species richness <2 m in height at the plot scale (no. species/400m^2)……84

4.3 Effects of deer exclusion on native and exotic species richness <2 m in height at the subplot scale (mean no. of species in 13, 1m^2 subplots in each plot). …….....85

INTRODUCTION

Large herbivores are leading biotic drivers of forest dynamics worldwide and therefore important determinants of habitat, biodiversity, and a host of ecosystem services (Oliver and Larson 1996, Diaz et al. 2007, Hegland et al. 2013). Numerous recolonizations of previously extirpated or depleted forest ungulates occurred in the 20th century as a result of conservation efforts and changes in land use (Foster et al. 2002, Soule 2003, Kuijper et al. 2010). A large body of work subsequently revealed that ungulates (primarily cervids) dramatically reduce the density, height, and species richness of regenerating trees and alter species composition toward browse tolerant and unpalatable species (Russell et al. 2001, Cote et al. 2004, Gill 2006, Nuttle et al. 2013). Although most ungulate-vegetation research has focused on tree regeneration (Russell et al. 2001, Royo et al. 2010), deer herbivory has also been reported to reduce forb abundance, height, and reproductive capacity and increase graminoid, fern, and exotic species abundance (Cote et al. 2004, Eschtruth and Battles 2009, Rooney 2009, Frerker et al. 2014, Nuttle et al. 2014). As a result of this work, it is generalized by many that unregulated (by top predators or hunters) cervid browsing has caused widespread tree recruitment failure and forest degradation across Eastern North America (e.g., Soule 2003, Estes et al. 2011).

Most of what is known about ungulate-tree regeneration dynamics comes from landscapes with elevated cervid densities (>8.5 deer km^{-2} or ≥1.5 moose km^{-2}). The extent to which lower cervid densities (i.e., ≤6-7 deer km^{-2} and <1 moose km^{-2}) – which characterize large parts of North America's Eastern Deciduous Forests (Adams et al. 2009, Bergeron et al. 2011, Wattles and DeStefano 2011) – alter tree regeneration and herbaceous layer (herb, shrub, and small trees) communities is less understood and may differ from areas with high densities of cervids (Royo et al. 2010, Bergeron et al. 2011). In addition to the paucity of studies capturing the lower end of cervid density gradients, limited attention has been paid to the functional

response (the rate of consumption in relation to food availability) of cervids (Schmitz and Sinclair 1997). Understanding the functional response of ungulates is important because disturbance (e.g., logging, insect outbreaks, and blowdowns) – and the different stand structures, understory conditions, and forage densities that result – can, in some instances, override "top down" control by herbivores (Hunter and Price 1992, McLaren and Peterson 1994).

Although much of the eastern temperate forest of North America contains a single ungulate species – white-tailed deer (*Odocoileus virginianus*) – in northern regions moose (*Alces alces*) and white-tailed deer overlap, particularly in recent decades when moose recolonized much of their former southern range (Boer 1997, Faison et al. 2010). Few studies have examined the combined effects of multiple ungulate species on forest communities (Ritchie and Olff 1999, Wisdom et al. 2006). Two or more herbivore species may either compound (additive) or oppose (compensatory) the effects of a single herbivore species on species composition, succession, or diversity (Ritchie and Olff 1999, Hester et al. 2006). The extent to which a recolonizing herbivore will join an existing herbivore to have additive or compensatory effects is often difficult to predict because the addition of the former can initiate diet shifts in the latter (Hester et al. 2006).

In the late 20th century moose recolonized much of their former southern range in Massachusetts and northern Connecticut, creating a two-ungulate system with deer for the first time in almost two centuries in this region (Faison et al. 2010). Almost nothing is known about how low densities of moose (<0.5 km^{-2}) interact with other browsers to shape the structure and composition of temperate forests. Deer populations also increased sharply during the 20th century after deer were extirpated from large parts of the region in the 19th century (Foster et al. 2002). Today, deer densities are low to moderate in Central Massachusetts (~4.2 km $^{-}$2; McDonald et al. 2007), but reach much higher densities in southwestern CT (≥21-24 km^{-2}).

The recent arrival of moose in southern New England forests coincided with the arrival of Hemlock Woolly Adelgid (HWA) into Massachusetts in 1989, which has caused significant

mortality to eastern hemlock (*Tsuga canadensis*; Orwig et al. 2012). However, the leading forest disturbance (not converting forest to a non-forest cover) in the region is timber harvesting, predominantly low intensity selective harvesting; while moderately intensive shelterwood and intensive patch clear cuts are part of state and private forest management plans (Kittredge et al. 2003). Forest ungulates are drawn to disturbed openings, which typically undergo rapid change in the herbaceous layer in the first several years after disturbance; thus herbivores frequently have strong interactions with vegetation in these environments (Oliver and Larson 1996, Eschtruth and Battles 2008, Kuijper et al. 2009, Royo et al. 2010).

The potential interplay of these novel dynamics combined with the aforementioned knowledge gaps in ungulate-forest studies prompted me to explore the following research questions for this dissertation: (1) how does variation in forest disturbance (HWA and logging), stand structure, and accompanying food supply influence the functional response of two browsers over time (Ch. 1)? (2) how do two generalist browsers occurring at low densities influence the composition, succession, and diversity of the herbaceous layer in recent patch cut timber harvests (Ch. 2)? (3) how do two generalist browsers occurring at low densities influence tree recruitment density, richness, and composition during the first several years following canopy removal in patch cut harvests (Ch. 3); and (4) how has long-term exclusion of deer in a landscape of high deer densities influenced the composition, diversity, and abundance of native and exotic species in a suburban hardwood forest (Ch. 4)?

CHAPTER 1

FUNCTIONAL RESPONSE OF UNGULATES IN DISTURBED HEMLOCK FORESTS

1.1 Abstract

Trophic cascades in predator depleted North American landscapes are believed to be causing widespread tree recruitment failures. However, disturbance and variations in ungulate densities are a source of heterogeneity that can buffer ecosystems against herbivory. Little is known about the functional response (the rate of consumption in relation to food availability) of ungulates in northern temperate forests, and therefore how "top down" control of vegetation may vary within landscapes composed of different disturbance types, intensities, and timing. I used an existing experiment begun in 2005, which simulated severe hemlock woolly adelgid (*Adelges tsugae*) infestation and intensive logging of intact eastern hemlock (*Tsuga canadensis*) forest, to examine the functional response of combined moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) foraging across contrasting stand structures resulting from different disturbances. I sampled and compared woody regeneration among two disturbance treatments (logged and simulated insect attack) and two intact controls (hemlock and hardwood forest) in 2008 and again in 2012. I then used Akaike's Information Criterion (AIC) model selection to compare the three major functional response models (Type I, II, and III) of ungulate browsing in relation to forage density. I also examined relative intensity of use of the different stand types by comparing pellet group density and remote camera images. In 2008, total and proportional browse consumption (and use) increased with stem density, and peaked in logged plots, revealing a Type I (linear) functional response and density-dependent browsing by ungulates. In 2012, stem densities were greatest in girdled plots, but proportional browse consumption (and use) was highest at intermediate stem densities in logged plots, exhibiting a Type III (sigmoidal) functional response. Browsing was therefore density dependent at low to moderate stem densities and

inverse density dependent at moderate to high stem densities. My results suggest that the functional response of ungulates across the different stand types changed over time, revealing shifting top down control by herbivores at different stages of stand recovery from disturbance. It is important for forest managers to understand that cervids have complex, dynamic, and context dependent impacts on woody plant regeneration in eastern forests.

1.2 Introduction

Trophic cascades (i.e., severe herbivore consumption) in predator depleted North American forests are hypothesized to be a dominant ecological force leading to recruitment failures by unregulated ungulates (Schmitz and Sinclair 1997, Estes et al. 2011). On the other hand, system variability and heterogeneity is believed to buffer terrestrial ecosystems against severe trophic cascades (Strong 1992). Canopy disturbance (e.g., logging, insect outbreaks, windstorms, and fire) represent a key source of spatial and temporal heterogeneity in temperate forest ecosystems (Oliver and Larson 1996); variations in ungulate densities represent another source of variation (Adams et al. 2009, Royo et al. 2010). Disturbances, in turn, play a critical role in determining density and distribution of ungulates and their impacts on vegetation at various spatial scales (Struhsaker et al. 1996, Peek 1997, Geist 1998, Persson et al. 2005, Kuijper et al. 2009). Hence, the extent to which regenerating vegetation is controlled from the top down (by consumers such as ungulates) or from the bottom up (i.e., by abiotic resources) should vary and depend on the timing, type, and intensity of disturbance (Pastor et al. 1988, Hunter and Price 1992, McLaren and Peterson 1994, Sinclair and Krebs 2002).

Despite the inherent complexities of large herbivore control of vegetation in heterogeneous landscapes, limited attention has been paid to the functional response (the rate of consumption in relation to food availability) of cervids under different forest stand and disturbance conditions (Schmitz and Sinclair 1997). Predation theory identifies three major

functional response models: Type I, II, and III. A Type I response involves a linear increase in consumption rate with increasing prey density and therefore neither density dependent nor inverse density dependent predation (Fig. 1). A Type II response involves an initial increase in consumption with prey density followed by a decelerating plateau at higher prey densities, which occurs because of satiation and limitations caused by handling time (i.e., searching, pursuing, and consuming; Sinclair and Krebs 2002; Begon et al. 2006). A Type II response therefore shows inverse density dependence of prey to predators and therefore bottom up control over prey (Fig. 1). A Type III response occurs when predators avoid prey at low densities, consume prey at a greater than linear rate at intermediate food densities, and finally reach a plateau of consumption akin to the Type II response at high prey densities (Sinclair and Krebs 2002; Begon et al. 2006). This model shows initial density dependence or top down control by predators followed by bottom up control at higher prey densities (Fig. 1; Sinclair and Krebs 2002).

In northeastern temperate forests, an exotic forest insect, the hemlock woolly adelgid (*Adelges tsugae*; HWA), is causing significant mortality to eastern hemlock (*Tsuga canadensis*), resulting in stands of young deciduous (predominantly *Betula lenta,* but also *Acer rubrum, Prunus* spp., *Pinus strobus*) trees regenerating beneath the dying hemlocks (Orwig et al. 1998, 2012). Many landowners in southern New England have responded to this spreading infestation by cutting their forests, either pre-emptively or as the trees die (Orwig et al. 2012). The arrival of HWA into Massachusetts in 1989 coincided with increasing white-tailed deer (*Odocoileus virginianus*) densities in many parts of the state, and the recolonization of moose (*Alces alces*) after an almost 200-year absence (Foster et al. 2002, Faison et al. 2010, Wattles and DeStefano 2011). The potential interplay of these changing conditions prompted us to assess what effect, if any, there would be on the functional response of two forest ungulates to their food supply. In other words, to what extent do spatial and temporal variations in stand structure and understory conditions influence the relative importance of top down and bottom up control? To address this

question, I systematically examined the three major functional response models (Type I, II, and III) across logged, (simulated) insect killed, and intact stands over time in order to better understand the relationships between herbivores and woody plant regeneration across a range of stand structures.

1.3 Materials and Methods

The study was conducted at the Harvard Forest in north-central Massachusetts, (42.478 to 42.488 N, 72.218 to 72.228 W, 215–300 m a.s.l.) in the white pine-hemlock-hardwoods forest region at the transition between maple-birch-beech (*Fagus grandifolia*) forests to the north and oak (*Quercus* spp.)-red maple-white pine forests to the south (Thompson et al. 2013). Exotic forest insects and pathogens including HWA, beech bark disease (*Cryptococcus fagisuga* and *Nectria* spp.), chestnut blight (*Cryphonectria parasitica*), and gypsy moths (*Lymantria dispar*), timber harvesting, and meteorological events (ice and windstorms) are the prevalent disturbances in the region (Foster et al. 2004). Central Massachusetts is close to the southern range limit for moose in eastern North America; moose range as far south as the mixed coniferous and deciduous forests of the elevated plateaus of northern Connecticut (Wattles and DeStefano 2011). In central Massachusetts, moose densities are estimated to be about 0.2 km^{-2} and white-tailed deer densities about 4-6 km^{-2} (McDonald et al. 2007; USGS Massachusetts Cooperative Research Unit, *unpublished data*).

The Harvard Forest Hemlock Removal Experiment (HF-HeRE) includes two canopy manipulations that simulate structural changes caused either by severe HWA infestation or by pre-emptive salvage logging (Ellison et al. 2010). Two types of control plots include either mature hemlock with ≥70% hemlock basal area or younger (~50 year old) mixed hardwood with small hemlocks (Ellison et al. 2010). One block of HF-HeRE occurs on sloping lowland and the

other on a north-south trending ridge; one set of the two treatments and two control plots are sited within each block (Ellison et al. 2010).

Each canopy manipulation replicate was applied in a 90 × 90 m (0.81 ha) forest plot with at least 70% basal area hemlock. In the simulated HWA treatment, all hemlock trees, from small seedlings to mature trees, were girdled using knives or chainsaws in early May 2005 (Ellison et al. 2010). The girdled trees died over the course of the next two and a half years, a rate similar to hemlock mortality from HWA attack in the southern Appalachians, but more rapid than mortality rates from HWA infestations in the Northeast (Orwig et al. 2013). Most of the girdled overstory hemlocks remained standing 8 years later, resulting in structural and environmental (temperature, moisture) changes similar to that from HWA invasion (Orwig and Foster 1998, Lustenhouwer et al. 2012). In the logged treatment, all hemlocks >20 cm in diameter were cut in February-April 2005 and removed along with merchantable white pine and hardwoods such as red oak (*Quercus rubra*) in a fashion similar to hemlock harvests observed in the region (Ellison et al. 2010). Approximately 60-70% of the basal area was removed in each logging plot (Ellison et al. 2010).

In June-July of 2008, I assessed understory woody vegetation and browsing intensity in a 30 × 30 m (900 m^2) plot in the center of each 90 × 90 m treatment and control plot. In each plot, regenerating woody stems ≥0.3 m and < 3 – the approximate height range of stems available to deer and moose (Faison et al. 2010) – were recorded and identified in 56 4-m^2 (224-m^2 total) circular subplots arrayed in a systematic grid. Each stem was assessed for signs of past browsing; twigs were considered browsed if they had a torn, ragged appearance characteristic of ungulates (McInnes et al. 1992). In 2012, the subplots were resampled for woody regeneration and browsing in each treatment. Porcupine (*Erethizon dorsatum*) and lagomorph browsing were readily distinguishable from ungulate browsing by the neat 45 degree angle cut of the stems, and stems browsed by these smaller herbivores were excluded from analysis.

I sampled pellet groups for deer and moose as a comparative index to assess relative variation in impact among my experimental stand types: I did not use it to estimate actual moose and deer density (cf. Van Dyke and Darragh 2007). I sampled pellet groups in each of the 56 4-m^2 (224-m^2) vegetation and browsing subplots in 2008. Pellet groups were defined as having at least 15 individual pellets (Eschtruth and Battles 2008). Despite this relatively large sampling area (cf. Kuijper et al. 2009), I still obtained enough zero values that I decided to double the pellet group sampling area to 450 m^2 in 2012. A 15 × 30-m area was divided into five 3 × 30-m subplots that were systematically searched with two observers walking side by side. Pellet groups in the subplots were pooled for each plot and expressed as number ha^{-1} to standardize values between 2008 and 2012.

In December 2011, I installed a remote camera (Reconyx, Inc., Holmen, Wisconsin) on the edge of each plot in which pellet counts were sampled. The cameras were programmed to take repeated pictures of herbivore movement, which enabled us to document the total time spent by animals in each field of vision. Images were compiled from December 2011-April 2013, and I calculated the total time spent by moose and deer in each treatment per week (seconds wk^{-1}) (Kuijper et al. 2009). I also calculated a weighted total ungulate visitation time (seconds wk^{-1}) by adjusting the time by the mass of the ungulate: (total moose time × 5) + (total deer time × 1).

I used Shapiro-Wilk tests to check all response variables for normality and used square root or log transformations if necessary. Randomized block ANOVAs were performed on tree regeneration density data in 2008 and 2012. Tukey's post hoc tests were used for multiple comparisons. Alpha was set equal to 0.05.

I also compared the three major functional responses of large herbivores to their food supply (Type I, II, and III; Sinclair et al. 2006) using Akaike's Information Criterion (AIC) model selection. I estimated a functional response across all four treatment types (logged, girdled, hemlock, and hardwood) of the experiment to enable sufficient variation in browse density.

Functional responses were not calculated within each treatment type. Because moose and deer browsing generally are indistinguishable and overlap considerably in height, I examined the combined functional response of the animals in the study area, rather than attempting to separate them (cf. Soluk 1993). I used the number of woody stems (0.3-3m in height) in each plot as an estimator of forage density, and the total number of individual woody stems (0.3-3 m in height) browsed in each treatment plot as an estimator of browse consumption rate. Other studies have used similar estimates of browse removal in functional response studies (White et al. 2003).

The Type I functional response is a simple linear regression in which number of stems browsed increases directly with the number of stems available:

$$f(x) = a + bx$$

where *Y* is the number of stems browsed , *x* = woody stem density, and *a* and *b* are intercept and slope parameters, respectively

The Type II response assumes that at a certain density of prey, predator satiation, and limitations of handling time (i.e., searching and consuming) will cause a decrease in consumption rate and a horizontal asymptote (Sinclair et al. 2006). For the Type II response, I used a Michaelis-Menton function (Bolker 2008):

$$F(x) = ax/b + x$$

Here, the fitted parameters x = woody stem density and *a* and *b* refer respectively to the browsing asymptote and the stem density at which browsing intensity reaches half its maximum.

A Type III response is a sigmoidal curve that shows an initially slow increase in consumption rate, followed by a sharp increase in consumption, and finally a slowing down of consumption and a horizontal asymptote similar to the Type II response (Sinclair et al. 2002). For the Type III response, I used the sigmoidal function (Bolker 2008):

$$f(x) = ax^2/b^2 + X\text{^}2$$

Here, the parameters x = woody stem density and a and b refer respectively to the asymptote and the half maximum point (Bolker 2008).

For each model, I estimated the parameters and then calculated an AICc value, the adjusted AIC recommended for small sample sizes (Burnham and Anderson 2004). From this value, I calculated $\Delta i = AICc_i - AICc_{min}$ using the AICtab function in R (package AICmodavg) This transformation results in $\Delta_i = 0$ for the best model, whereas the other models have positive values. Models with Δi values < 2 apart are generally deemed to be similar, whereas those with Δi values >4 are considered distinct (Bolker 2008). Weights (w_i) were then calculated from Δ_i ($\exp(-0.5 \times \Delta_i)$ for each model. The sum of w_i was then normalized to equal 1, and each w_i was reported as a probability that a model was the best fit, given the data and the candidate models (Burnham and Anderson 2004). Functional response models were analyzed and compared using nls2 (non-linear regression with brute force) and AICtab (package AICmodavg) in R (The R Foundation for Statistical Computing 2014; R version 2.15.2).

Lastly, I examined the proportion of stems browsed as a function of stem density (the total response) to further compare among the three functional response models (Sinclair et al. 2006). A Type I functional response should be a flat line showing no increase or decline in per capita consumption with forage density; a Type II functional response should show relatively high proportion of stems consumed at low stem densities, with proportion consumed decreasing linearly with increasing stem densities; a Type III functional response should show an increasing proportions of stems browsed at low stem densities followed by a decline in proportional stem consumption at much higher densities (Sinclair et al. 2006; Fig. 1).

1.4 Results

In 2008, stem densities (0.3-3 m in height) ranged from 89 to 15,700 ha^{-1} across the eight treatment plots. Mean woody stem densities differed by treatment (P = 0.023; Figs. 2 and 3), with

densities highest in logged plots and exceeding those in hemlock controls by a factor of 24. In 2012 stem densities also differed by treatment (P = 0.007; Figs. 2 and 3), but densities were highest in girdled plots. Stem densities in girdled plots exceeded densities in logged plots by a factor of three, hardwood plots by a factor of eight, and hemlock plots by over two orders of magnitude. Densities in logged plots were also significantly higher than those in hemlock plots (Fig. 2 and 3).

Moose and deer pellet groups were only detected in logged and girdled plots in both 2008 and 2012. Moose accounted for 80% of pellet groups sampled in 2008 and 73% of pellet groups in 2012. In 2008, combined moose and deer pellet group densities were highest in the logged ridge plot, corresponding with the highest stem density (Fig. 4a). In 2012, combined pellet group densities remained highest in logged plots, corresponding with intermediate stem densities (Fig. 4b). Total deer time recorded by remote cameras was relatively high in logged (16.7 seconds $week^{-1}$, SD = 0.6), hemlock (19.0 seconds $week^{-1}$, SD = 22.8, and hardwood (13.7 seconds $week^{-1}$, SD = 15.4) plots and low in girdled plots (0.4 seconds per $week^{-1}$, SD = 0.06). Total moose time recorded by remote cameras was highest at intermediate stem densities in logged plots and was low in control and girdled plots (Fig. 5a). Total weighted ungulate time was also highest at intermediate stem densities in logged plots (Fig. 5b).

Browsing intensity (number of stems browsed ha^{-1}) increased in 2008 with increasing stem densities (Fig. 6). Number of browsed stems (10,400 ha^{-1}) peaked in the most densely vegetated logged ridge plot (15,800 stems ha^{-1}). The linear (Type I) functional response model was the best fit for the 2008 data (w_i = 0.996; Table 1). The Type III functional response model was the best fit for the 2012 data (w_i = 0.86; Fig. 6), although the Type II model had limited support (Δi = 3.7, Table 1). Browsing was absent or low in hemlock and hardwood controls, rose sharply with increasing stem densities in logged plots to a peak at ~10,000 stems browsed ha^{-1} in the logged ridge plot, and then reached an asymptote or declined slightly with increasing stem

densities in girdled plots. The proportion of stems browsed as a function of total available stems (the total response) showed a linear relationship with increasing stem densities in 2008 (P = 0.061; Fig. 7). In 2012, the proportion of stems browsed increased initially at low to moderate densities in control and logged plots and then declined sharply at high stem densities in girdled plots (P = 0.049; Fig. 7), revealing a characteristic Type III response (Fig. 1).

1.5 Discussion

Large browsers are strongly associated with young vegetation in regenerating forest openings, utilizing disturbed stands 2-7 times more frequently than ambient, undisturbed areas (Persson et al. 2005, Kuijper et al. 2009, Wattles and DeStefano 2013). Moose, in particular, are associated with logged areas compared to ambient intact forest (Geist 1998, Persson et al. 2005, Wattles and DeStefano 2013). Despite the well-known connection between large browsers and vegetation in regenerating forest openings, relatively little is known about the extent to which ungulate functional responses are influenced across a range of stand structures and recently disturbed patches in northern temperate forests (Schmitz and Sinclair 1997). In this study, I used a range of canopy treatments and tree regeneration densities associated with disturbance by Hemlock Woolly Adelgid (HWA) to estimate the functional response of moose and deer foraging in a heterogeneous forested landscape. My results showed that eastern hemlock stands killed by simulated HWA attack diverged in woody plant regeneration over time from those that were logged, resulting in different relationships between large herbivores and their food supply at different stages of stand regeneration and across different stand structures.

In this experiment, the hemlock canopy died gradually in the simulated HWA (girdled) plots relative to the logged plots. Lustenhouwer et al. (2012) and Orwig et al. (2013) revealed that this difference in timing of canopy death caused initially greater soil and air temperature and solar radiation levels in the logged plots and a lag in plant regeneration in the girdled plots. By

2008, three years after disturbance treatment, woody stem densities (0.3-3 m in height) in the girdled plots had roughly equaled those in the logged and hardwood control plots and had surpassed those in the hemlock control (Fig. 2). Within the range of woody stem densities among treatments in 2008 (89-15,700 stems ha^{-1}), herbivores increased their use and consumption in sites with greater stem densities (Fig. 6a), revealing a Type I functional response Although the Type I functional model was by far the best fit (other models $\Delta i = 12.0, 14.5$), per capita browsing rates revealed that consumption of browse was largely density dependent in 2008 across stand structure and disturbance type, suggesting the lower leg of a Type III functional curve (Figs. 1 and 7a).

By 2012, the environments of the two disturbance treatments converged with respect to soil moisture, available light, and soil and air temperature (Lustenhouwer et al. 2012); but woody stem densities in the girdled plots increased substantially relative to the other treatments (Figs. 2 and 3). A sigmoidal (Type III) functional response developed in which the herbivores apparently ignored or missed woody browse at low densities in the undisturbed stands, or in the case of moose, largely avoided the habitats (cf. Sinclair and Krebs 2002). Deer may also have used the undisturbed stands for other purposes (e.g., thermal shelter, acorn foraging, and herbaceous plant grazing; cf. DeGraaf and Yamasaki 2001); the relatively high use of the undisturbed plots by deer (detected by remote cameras) combined with low browsing pressure in these plots supports this notion. Herbivore use and browse consumption increased sharply with higher stem densities in the logged plots, as moose actively used these plots, and deer perhaps switched from foraging on acorns and herbaceous plants in the hardwood plots to woody browse in the logged plots. Peak browse consumption in 2012 occurred in the logged ridge plot at roughly the same numbers and stem availability as in 2008 (15,000 – 20,000 stems ha^{-1}). However, with a much greater range of stem densities among treatments in 2012 (0-79,000 stems ha^{-1}) than in 2008, herbivore consumption was density dependent across low to moderate stem densities (undisturbed and logged plots) and inversely density dependent from moderate to high stem densities (logged and

girdled) in 2012. In other words for the first three years post disturbance, herbivores exerted top down control over the vegetation, regardless of stem density and structure; but seven years post disturbance, herbivores exerted top down control only at the lower range of stem densities. Regeneration was able to escape the "predator pit" (i.e., the sharply density dependent browsing at low to moderate densities in 2012) presumably because the high density of regeneration in the girdled areas overwhelmed the relatively low density and browsing capacity of the herbivores (cf. Pastor et al. 1988, McLaren and Peterson 1994). In contrast, Healy (1997) reported strong top down effects by deer in both thinned and intact oak stands in a nearby watershed forest where the herd had been protected for decades. Greater densities of ungulates (10-17 km^{-2}) combined with less intensively disturbed stands that supported lower stem densities in Healy's (1997) study may explain the difference between his results and mine.

A contributing factor to the inverse density dependent browsing and Type III functional response in 2012 was that moose and deer appeared to preferentially use the logged stands with intermediate stem densities. This pattern suggests that once a threshold density of stems (~20,000 stems ha^{-1}) was reached, given the density of herbivores in my study area, other food related (e.g., stem palatability) or non-food related (e.g., thermal environment, cover, and topography) factors became more important than additional increases in stem density (Hester et al. 2006, Barret and Schmitz 2013). My results show some parallels with Thompson et al. (1989) who reported preferential foraging by moose in balsam fir stands with 2,000 stems ha^{-1} over stands with 30,000 stems ha^{-1}. Greater use of intermediate forage densities has also been observed by elk (*Cervus elaphus*) foraging on grasses, apparently because energy intake is optimized at intermediate stem densities (Wilmshurst et al. 1995).

A number of characteristics of the vegetation in the logged plots may have resulted in these plots being more heavily used and proportionally impacted by ungulates. Basal sprouting by hardwoods often leads to greater stem palatability (Moore and Johnson 1967), and sprouts on

stumps and trees occurred more frequently in the logged plots than in the girdled and undisturbed plots (Ellison and Barker Plotkin 2009). Sprouts are often thicker in diameter, grow more vigorously, and have more extensive branching than seed-origin stems (Kauppi et al. 1990, Bond and Midgley 2001); these stem characteristics are particularly desirable to moose and other ungulates (Price 1991, Rea and Gillingham 2001, Kuijper et al. 2009). In addition, red maple, a preferred browse species of moose and white-tailed deer (Godin 1977, Faison et al. 2010), was the most prolific sprouter in the logged plots (Ellison and Barker Plotkin 2009). Finally, previous browsing changes chemical and morphological properties (e.g., increased nitrogen, larger diameters) of stems that can make them more likely to be browsed again (Bergstrom and Danell 1987, Makhabu et al. 2006). Because the slowly dying canopy in the girdled plots delayed regeneration relative to the logged plots (Orwig et al. 2013), woody stems in the logged plots were undoubtedly browsed prior to those in the girdled plots, perhaps increasing the desirability of stems in the former in subsequent years relative to the newly emerging stems in the latter.

My results provide evidence that different relationships between large herbivores and their food supply (i.e., both density dependent and inverse density dependent) may develop over small spatial and temporal scales across forest stands of different disturbance histories, structures, and understory characteristics. In other words top down control by large herbivores on forest regeneration is dynamic and context dependent (Hunter and Price 1992, Schmitz and Sinclair 1997). My study also highlights the fact that a system in which the vegetation is controlled, at least in part, from the top down by ungulates is not necessarily synonymous with severe impacts by herbivores (i.e., a "regeneration failure" Strong 1992). The most intensively browsed logged plots still had almost 20,000 stems ha^{-1} in 2012 (seven years after harvest), which is more than enough to regenerate the stand (Oliver and Larson 1996, Bergeron et al. 2011).

Table 1.1 Comparison of functional response models of combined moose and white-tailed deer foraging (number of stems browsed) in relation to woody stem food supply. The lowest AIC_c value (in bold) corresponds with the best model. Δ_i = the difference in AIC_c from the best model. w_i = AIC weights – the probability that a model was the best fit, given the data.

	2008				2012			
Functional Response Model	AICc[a]	Δ_i	*df*	wi	AICc	Δ_i	df	*wi*
Type I[b]	**155.1**	**0**	**3**	1	164.1	9.0	3	0.01
Type II[c]	167.1	12.0	3	0	158.8	3.7	3	0.13
Type III[d]	169.6	14.5	3	0	**155.1**	**0**	**3**	**0.86**

[a] adjusted Akaike's Information Criterion recommended for small sample sizes
[b] $f(x) = a + bx$
[c] $f(x) = ax/b + x$
[d] $f(x) = ax^2/b^2 + x\text{^}2$

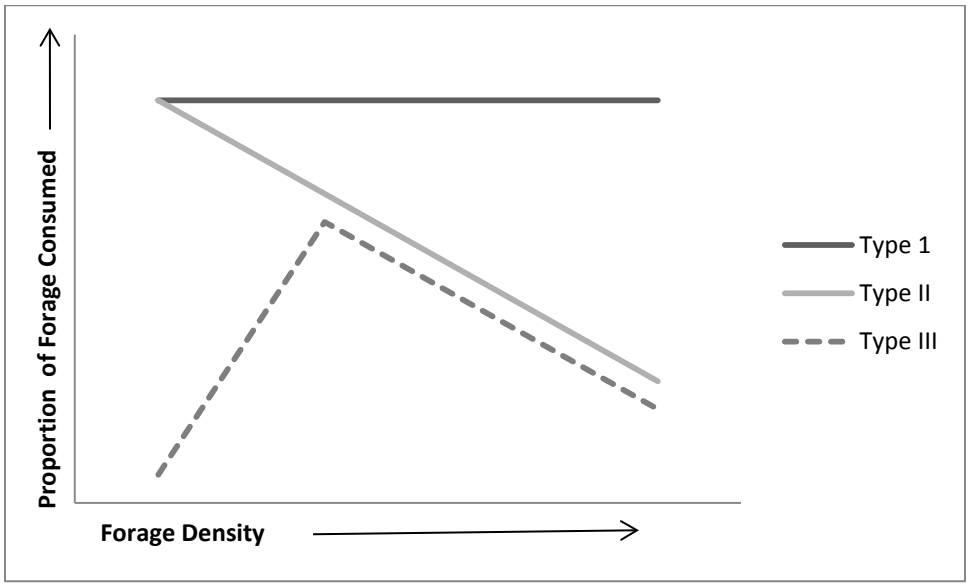


Figure 1.1 Three major functional responses plotted as the proportion of prey eaten relative to forage density. Modified from Sinclair et al. (2006).

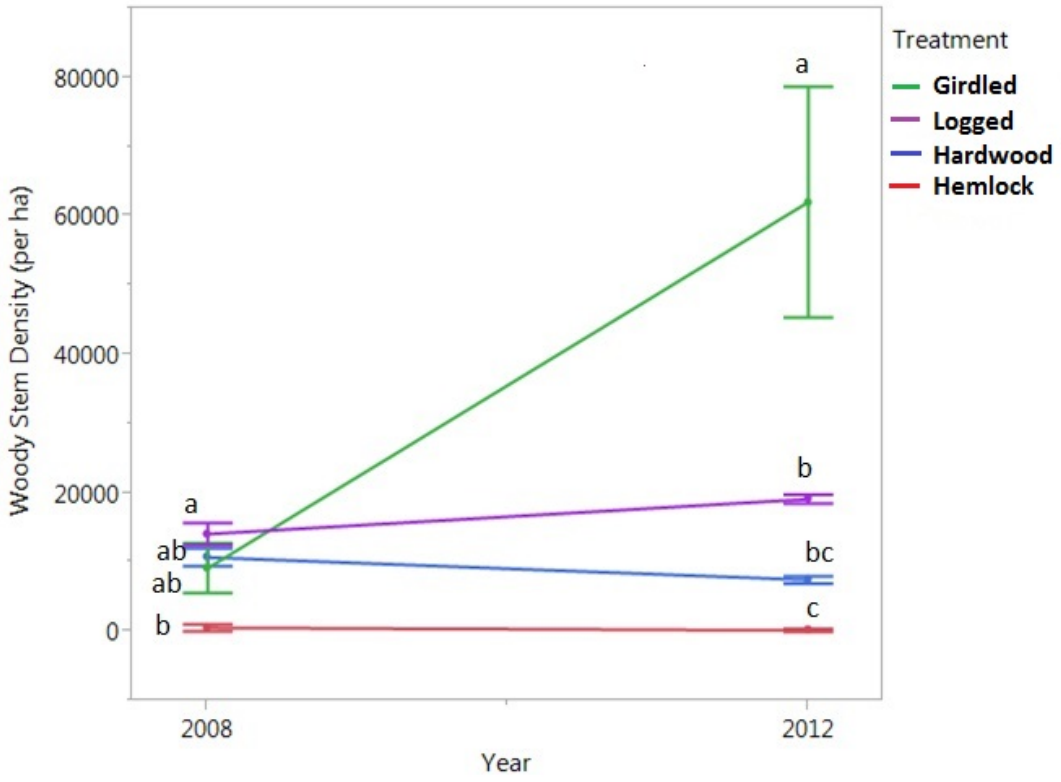


Figure 1.2 Comparison of woody stem densities (0.3-3 m in height) by treatment in 2008 and 2012. Densities differed by treatment in both 2008 ($F_{3,4}$ = 16.56; P = 0.023) and in 2012 ($F_{3,4}$ = 38.95; P = 0.007). Treatment means with the same letter do not differ significantly. Bars represent mean ± SE.

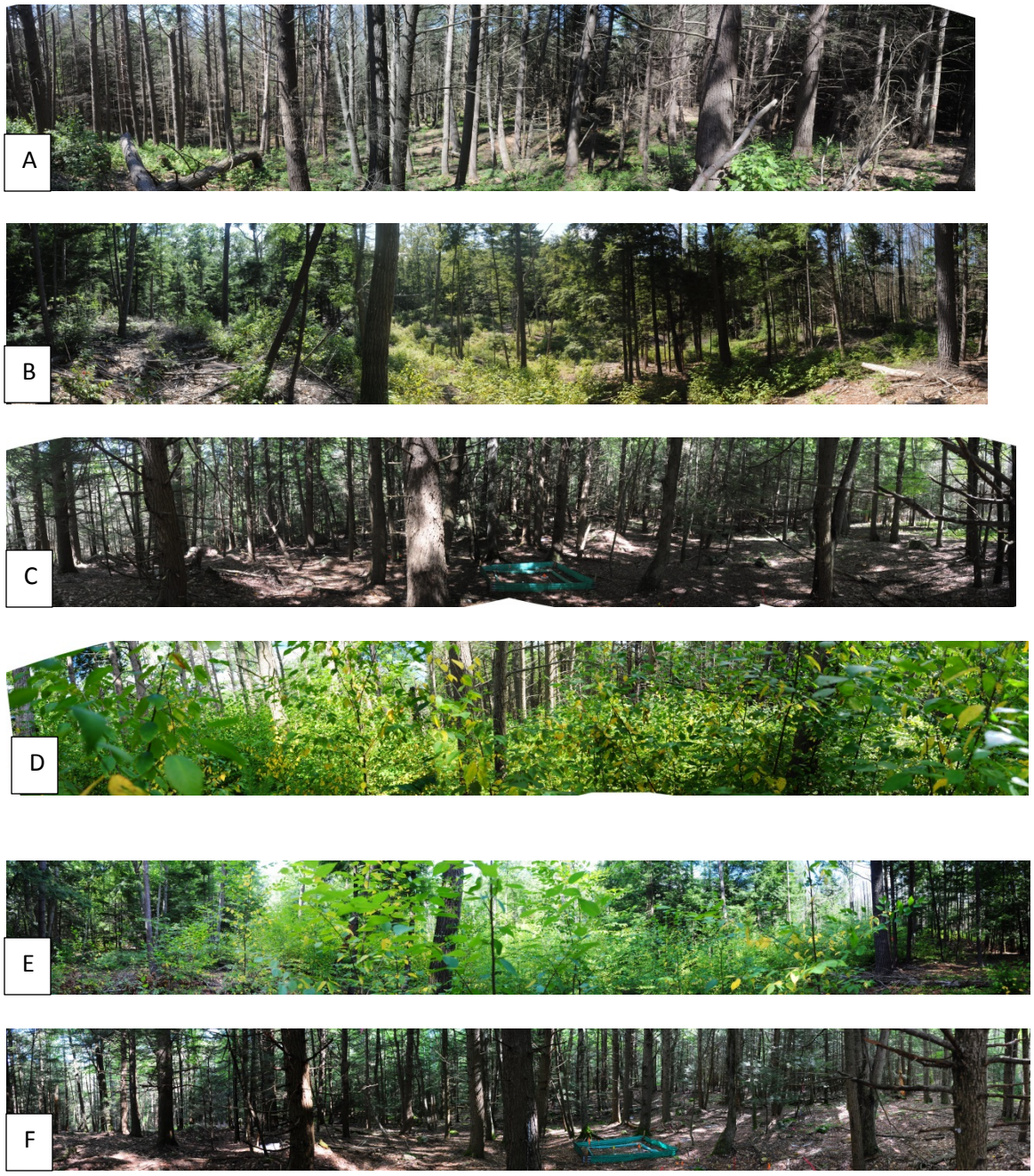
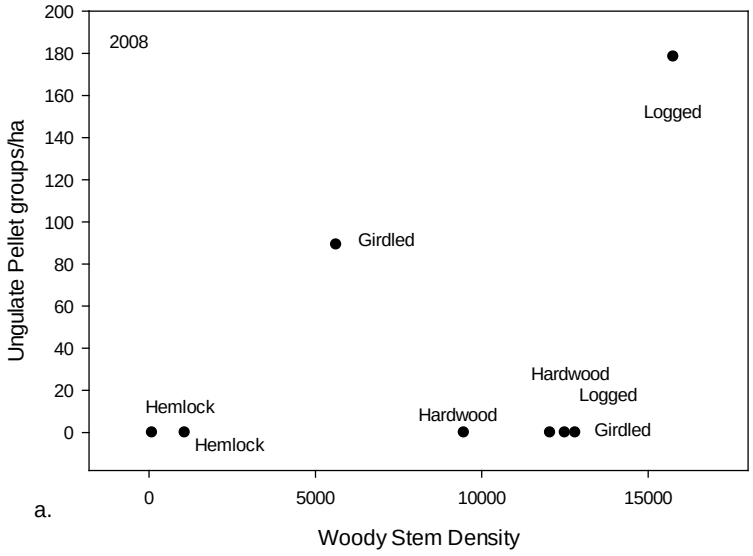
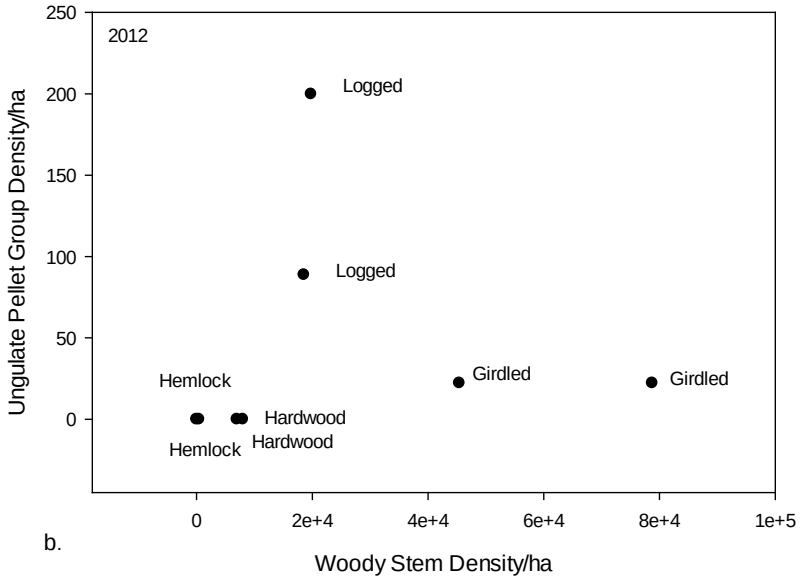


Figure 1.3 Comparative photos of three canopy treatments and understory vegetation response. Photos A-C are of girdled, logged, and hemlock control respectively in 2008. Photos D-F are of the same plots in 2012. Hardwood control photos not shown. Photos by Aaron Ellison



a.



b.

Figure 1.4 Ungulate pellet group densities in relation to woody stem densities in 2008 (a) and 2012 (b). Moose comprised 70-80% of pellet groups in both years.

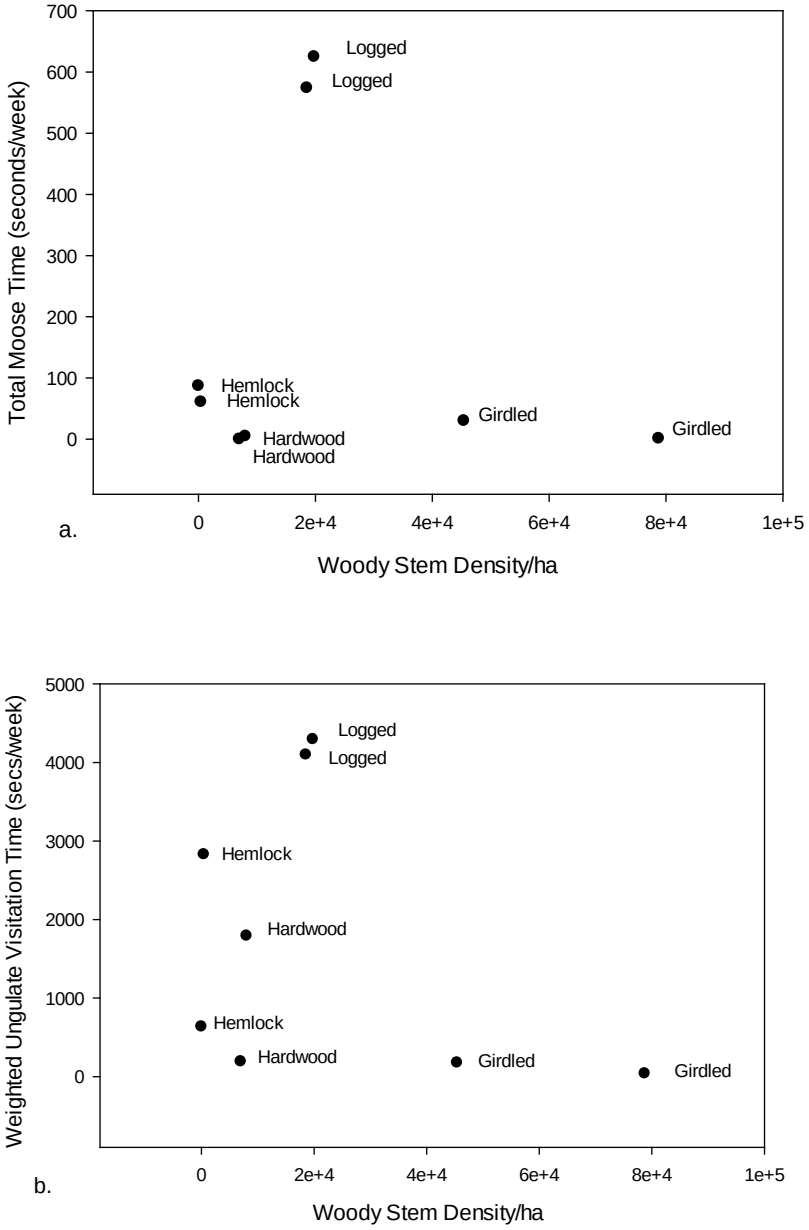


Figure 1.5 Total moose visitation time (a) and weighted ungulate visitation time (b) recorded by remote cameras in the eight treatment plots from Dec 2011-April 2013. Weighted ungulate time = (moose time x 5) + (deer time x 1), which corresponds with the approximate mass and forage consumption ratio of the two animals.

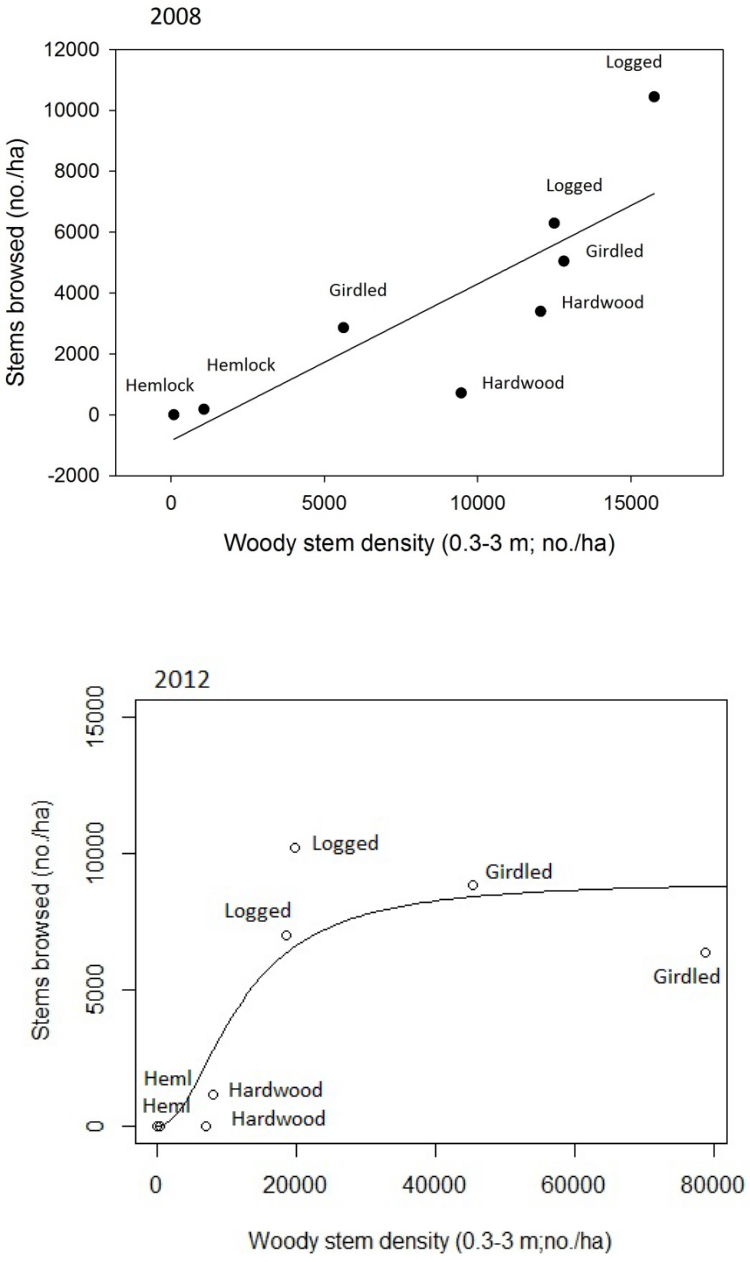


Figure 1.6 Functional response of ungulates in 2008 (top) and 2012 (bottom). In 2008, the Type 1 (linear model) was the best fit. In 2012, the Type III (sigmoidal) model was the best fit when compared with other functional response models with AIC. (see Table 1).

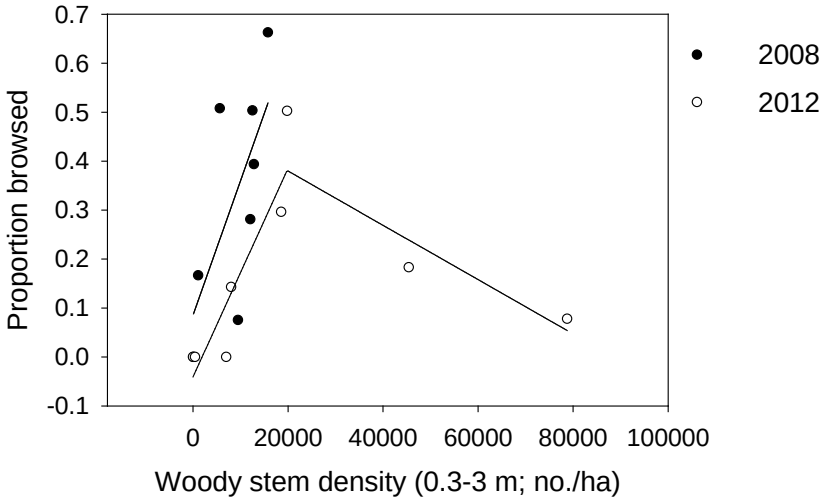


Figure 1.7 Per capita browse consumption by ungulates in 2008 and 2012. 2008 data show a linear increase with increasing stem densities ($R^2 = 0.47$; $P = 0.06$); 2012 data show a linear piecewise response characteristic of a Type III functional response ($R^2 = 0.83$; $P = 0.049$). See Fig. 1 for comparison. Woody stems included all upright woody plants 0.3-3m in height.

CHAPTER 2

TWO UNGULATE BROWSERS DELAY SUCCESSION AND PROMOTE HERBACEOUS LAYER DIVERSITY IN LOGGED TEMPERATE FORESTS

2.1 Abstract

Large herbivores are leading drivers of plant communities in northern forests. Yet, few studies have examined the effect of two ungulate species on forest herbaceous layers where most of the diversity in a forest occurs – particularly in recently disturbed areas. Two or more herbivores can have additive (compounding) or compensatory (opposing) effects on plant communities. I examined the extent to which a recolonizing ungulate (moose [*Alces alces*]) and a long established one (white-tailed deer [*Odocoileus virginianus*]) – both occurring at low densities – influence herbaceous layers (shrubs, herbs, and small trees) in patch cut timber harvests in Massachusetts, USA. I established three combinations of ungulates using fenced exclosures – (none (full exclosure), deer (partial exclosure), and deer + moose (control) – and examined the effect of treatment on herbaceous and woody species composition, abundance, richness, and succession after 5-6 years.

Species composition diverged significantly among browsing treatments, and changes were generally additive. Woody plant abundance above 2 m in height was reduced with the addition of herbivores, and herb and shrubs assemblages characteristic of forests were more abundant in the relatively densely canopied no-ungulate and deer plots than in the more open grown moose + deer plots. In contrast, herb and shrubs characteristic of open/disturbed habitats increases with the addition of browsers. I further documented greater herbaceous species richness (plot scale; 169 m^2) and woody species richness (subplot scale) in deer + moose plots compared to the other treatments. My results suggest that low densities of moose + deer have the capacity to both delay forest succession and increase herbaceous layer richness in young stands following

complete canopy removal from logging. This study highlights the fact that two large browsers at low densities can have unpredictable effects on forest herbaceous layers, stressing the importance of investigating ungulate impacts across the range of herbivore densities and with multiple browser treatments.

2.2 Introduction

Large herbivores are leading drivers of terrestrial plant communities and therefore important determinants of habitat, biodiversity, and a host of ecosystem services (Oliver and Larson 1996, Diaz et al. 2007, Royo et al. 2010, Hegland et al. 2013). Despite their acknowledged importance, the effects of herbivores are notoriously complex and difficult to generalize and may be mediated by disturbance and site productivity, as well as the density and assemblage of herbivores (Ritchie and Olff 1999; Hester et al. 2006, Royo et al. 2010). Until recently, most research on ungulate-forest relationships focused on tree regeneration, with little attention paid to the herbaceous layer flora (shrubs and herbs) where most of the diversity in a forest occurs (Russell et al. 2001, Gilliam 2007, Royo et al. 2010). Even less well studied are ungulate impacts on herbaceous layer floras in stands recovering from recent disturbances such as logging, fire, and insect outbreaks (but see Kraft et al. 2004 and Royo et al. 2010). Because forest ungulates are drawn to disturbed openings, which typically undergo rapid change and witness intense competition in the herbaceous layer in the first several years after disturbance, herbivores would be expected to have strong interactions with shrubs and herbaceous plants in these environments (Oliver and Larson 1996, Eschtruth and Battles 2008, Kuijper et al. 2009, Gilliam 2007, Royo et al. 2010).

Although many ecosystems have more than one ungulate species, few studies have specifically examined the combined direct and indirect effects of multiple herbivore species on vegetation communities (Ritchie and Olff 1999, Wisdom et al. 2006). The effects of two or more

animals on composition may be additive or compensatory, depending on whether the animals consume the same plant species (Ritchie and Olff 1999). Additive effects occur when multiple herbivores consume primarily the same plant species and therefore alter the community in the same direction as a single herbivore (Ritchie and Olff 1999). Compensatory effects occur if the herbivore species consume primarily different plant species so that their individual effects on species' relative abundance balance each other out, resulting in little net effect on community composition (Ritchie and Olff 1999). The extent to which a recolonizing herbivore will join an existing herbivore to have additive or compensatory effects is difficult to predict because the addition of the former can initiate diet shifts in the latter (Hester et al. 2006).

In the late 20th century moose recolonized much of their former southern range in the northeastern deciduous forest region (except for Pennsylvania; Faison et al. 2010, Wattles and DeStefano 2011), creating a two-ungulate system with deer for the first time in almost two centuries in some landscapes. Both animals occur at low densities in Central New England at the moose's southern range limit (moose - 0.2/km^2; deer – 4-5/km^2), suggesting the possibility that their effects on forest understories could differ from areas with higher densities of herbivores (Royo et al. 2010, Goetsch et al. 2011). Because moose and deer are generalist browsers that consume many of the same woody plants they might be expected to have additive effects on plant communities (Boer 1997, Renecker and Schwartz 1997, Ritchie and Olff 1999). For example, during stand initiation additive effects by browsers consuming dominant pioneer trees may retard succession and increase herbaceous layer plant diversity and abundance by reducing competition (Ritchie and Olff 1999). Alternatively, focused herbivory on browse sensitive and inferior competitors can lead to declines in individual species and overall richness (Ritchie and Olff 1999, Hester et al. 2006). Despite broadly similar foraging strategies of the two animals, deer consume a higher proportion of herbaceous plants in their diet (40%) than do moose (10%); and the two animals' woody plant diets are reported to overlap by about 40% with respect to the frequency

with which different plant species are consumed (Ludewig and Bowyer 1985, Renecker and Schwartz 1997). Hence, moose + deer foraging on plant composition could be compensatory in some cases. The paucity of studies on ungulate interactions with herbaceous layers in disturbed forests combined with the uncertainties regarding the effects of foraging by multiple browsers prompted this study. Here I examine the effects of two large browsers occurring at low densities on the composition, succession, and diversity of herbaceous layers 5-6 years after canopy removal from logging.

2.3 Materials and Methods

The physiography of Central Massachusetts is characterized by rolling plateaus with hills, and the climate is humid with warm summers and cold winters (Brouillet and Whetstone 1993, US EPA 2015). Mean annual precipitation ranges from 97 to 127 cm per year, and mean temperature ranges from -12 to -0.5ºC in January and 14 to 28°C in July. Mature forest vegetation is characterized by transition hardwood forests – (mixed oak (*Quercus* spp.), red maple (*Acer rubrum*), black birch (*Betula lenta*), and beech (*Fagus grandifolia*) – with significant components of eastern hemlock (*Tsuga canadensis)* and white pine (*Pinus strobus*; Foster et al. 2004, USDA 2015). In addition to timber harvesting, exotic forest insects and pathogens including hemlock woolly adelgid (*Adelges tsugae*), beech bark disease (*Cryptococcus fagisuga* and *Nectria spp.*), chestnut blight (*Cryphonectria parasitica*) and gypsy moths (*Lymantria dispar*); and meteorological events (ice and windstorms) are the prevalent disturbances in the region (Foster et al. 2004). Patch cuts are a less common form of timber harvest in the region than selective harvests (Kittredge et al. 2003), but are still an important part of many forest management plans (Kyker-Snowman 2007).

Moose ranged as far south as northwestern Connecticut, southern New York, and Pennsylvania before European settlement (Reeves and McCabe 1997). After being extirpated

from Massachusetts in the early 19th century, moose recolonized central Massachusetts in the late 20th century (Faison et al. 2010), creating a two-ungulate system with deer for the first time in almost two centuries. Today, the southern range limit for moose in the eastern United States is 41.66 degrees latitude in northern Connecticut (Wattles and DeStefano 2011). Densities are estimated to be about 0.2 km^{-2} in north central Massachusetts, which is similar to densities in southern and central Vermont and southern New Hampshire; but much lower than densities in Northern Maine and Northern New Hampshire and Vermont (1-1.7 km^{-2}; USGS Massachusetts Cooperative Research Unit, *unpublished data*, Wattles and DeStefano 2011). White-tailed deer were common in presettlement New England, were extirpated from much of Massachusetts by the mid-19th century, and recovered their former range and abundance during the 20th century (McCabe and McCabe 1984, Foster et al. 2002). Today, deer densities are estimated at ~4.2 km^{-2} for north central Massachusetts, which is on the low end of reported densities of 0.8 to 23+ km^{-2} across the New England and Eastern Deciduous Forest region (Kantar 2007, McDonald et al. 2007, Adams et al. 2009, Kilpatrick 2009).

In 2007-2008, experimental exclosures were established in six mixed conifer-hardwood stands that had been clearcut within the past 3-6 months at the Harvard Forest and the Quabbin and Ware River Watershed forests in Central Massachusetts (Table 1; Fig. 1). At the start of the experiment no woody stems above 1.5 m in height occurred in any of the plots, and virtually all remaining woody stems were less than 1 m. Four of the sites were former conifer plantations [larch (*Larix* spp., red pine (*Pinus resinosa*), or spruce (*Picea* spp.)] with mixed native hardwoods, and the other two were red oak (*Quercus rubra*)-white pine dominated stands with red maple in the understory (Table1). The experimental design was a randomized block with three levels of large herbivores – no-ungulates (full exclosure), deer (partial exclosure), and deer + moose (control). A fourth treatment that excluded deer but was open to moose was not feasible. This inability to utilize a full-factorial design does not pose a problem to the subsequent

analysis and interpretation (Ritchie and Olff 1999, Manier and Hobbs 2007). Blocks were at least 1 km apart from one another. The 2.5-m tall exclosures were made of high-tension wire game fence with 15 cm grid mesh. The full exclosure was a fenced to the ground; the partial exclosure had a 60 cm opening between the bottom of the fence and the ground surface that excluded moose but allowed access to deer and all other wildlife; and the control plot was unfenced and open to both browsers (Fig. 1). The 15 cm wire mesh of the fence enabled access to small mammals including lagomorphs and rodents.

Exclosure and control plots were 20 x 20 m in size and separated by 10-40 m. In 2013, 5-6 years after treatment, I established 13, 1 m^2 grid plots in a systematic grid in the center of each plot. Five rows were established with 3 subplots on the outer and middle rows and two subplots in the second and fourth rows. Subplots were positioned 6 m apart within the same row and 4.5 meters apart between rows. At each 1 x 1 m subplot, all vascular plants in the forest floor layer were recorded by a single observer (original field data collected by Glenn Motzkin archived at Harvard Forest). I defined "herbaceous layer" as all plants (herbs, shrubs, and trees) <2 m in height (Oliver and Larson 1996, Carson et al. 2014). Percent cover was estimated for each species and for each plant group (i.e., woody plants, graminoids, and forbs) in one of 7 cover classes (1 = <1%, 2 = 1-5%, 3 = 6-15%; 4 = 16-25%, 5 = 26-50; 6 = 51-75%, 7 = 76-100%). Because many of the woody stems had recruited above 2 m by the time of sampling, I also estimated the percent cover of woody plants ≥ 2 m in height. In addition I performed a 20 minute "meander" survey throughout the central 13 x 13 m of each plot and recorded the presence of all woody and herbaceous plant species that did not occur in the subplots (Huebner 2007, Goetsch et al. 2011). All data were collected in June and July of 2013, and treatments within a block were sampled in the same week. Nomenclature followed Cullina et al. (2011).

To test the integrity of the experimental design for the presence of the different ungulate species, remote cameras (Reconyx, Inc. [Holmen, Wisconsin] and Cuddeback, Inc. (Greenbay,

Wisconsin) were mounted inside each partial exclosure and toward each control plot between 2008 and 2011 (mention of trade names does not constitute an endorsement from the U. S. Government). Cameras were discontinued after 2011 because the vegetation had grown to a height that effectively blocked the camera's ability to detect animals. All plots in each block had the same type of camera set to the same delay specifications, and were used to calculate the weekly frequency of visits by each species (Augustine and Frelich 1998). A minimum of 5 minutes of elapsed time between each image was used to separate visits. Ungulate pellet groups were counted in 2012 in 25-4m^2 vegetation subplots and again in 2013. Because I encountered a number of 0 values in 2012, I increased the sampling area of pellet counts from 100 m^{-2} to 400 m^{-2} in 2013 and standardized two year mean values by converting counts to number ha^{-1}. Pellet groups were defined as having at least 15 individual pellets to avoid over-counts from scattered individual pellets (Eschtruth and Battles 2008).

I used percent cover as my measure of vegetation abundance. I first converted cover classes to percent cover midpoints, and then calculated the mean percent cover for species and growth form groups (i.e., ferns, forbs, graminoids, woody plants) across the 13, 1 x 1 m subplots in each plot. To examine the potential effects of ungulate browsing on forest succession I calculated the combined abundance of herb and shrub species characteristic of forest habitats in each plots and the combined abundance of herb and shrub species characteristic of open/disturbed habitats. Forest and open species were selected from 51 species that occurred in at least two of the 18 study plots. I used habitat descriptions from the New England Wildflower Society (2015) and Haines (2011) to categorize species into different habitat/successional groups (Table 2). *Forest indicator species* were: (1) required to be listed as occurring in forests, and (2) could not be listed as occurring in anthropogenic or disturbed habitats, marshes, or meadows and fields. *Open/disturbed habitat species* (1) could not be listed as occurring in forests; and were (2)

required to be listed as occurring in anthropogenic or disturbed habitats, marshes, or meadows and fields (Table 2).

I examined species richness for herbs and woody plants at two scales in each plot: subplot scale (mean number of species per 13, $1m^{-2}$ quadrats) and plot scale (number of species $169m^{-2}$). Although these measurements are technically species density (Gotelli and Colwell 2001), I hereafter refer to species density as "species richness" for the sake of clarity. I used linear mixed effects models (package lmer, R Statistical software) with ungulate treatment as fixed effect and block as random effect to examine species richness, abundance of forest and open indicator species, and abundance of different growth form groups to three levels of browsers. I also examined models including variation in herbivore abundances across the blocks (using pellet count indices) as a covariate, but in no instance did these models fit the data better than the basic treatment model when compared by AIC. I used either a Gaussian or Gaussian with log link (log normal) distribution for each response variable after examining the residuals to determine the best fit. For hypothesis tests of treatment effects, I used likelihood ratio tests (LRTs). For significant results ($P < 0.05$) of treatment, I performed pairwise comparisons between the three treatment pairs by simulating the posterior distribution 10000 times to calculate 95% confidence intervals and approximate P-values for the fixed effects (Bagchi et al. 2011, Rapp et al. 2013). This test further validated the results obtained from the LRT. Alpha was set = 0.05.

Lastly to test for significant differences in community composition among treatments I used adonis (package vegan), the analysis of variance of distance measures (Bray), grouped by block (1000 permutations; Oksanen et al. 2015) Species abundances (% cover) were entered into the multivariate test. Rare species that occurred in only 1 of the 18 treatment plots (5.5%) were removed prior to analysis (McCune and Grace 2002). Data were analyzed using R (The R Foundation for Statistical Computing 2014; R version 2.15.2).

2.4 Results

Two year mean deer pellet groups were similar in partial exclosure (216.7 groups ha^{-1}; SE = 94.4) and control plots (187.5 group ha^{-1}; SE = 70.0; Wilcoxon signed rank test: V = 13, P = 0.67). Moose pellet groups (two year mean: 202.1 groups ha^{-1}; SE = 82.9) were detected only in control plots. Remote cameras detected deer in partial exclosures (0.31 visits wk^{-1}; SE = 0.13); and control plots (0.61 visits wk^{-1}; SE = 0.20; Wilcoxon signed rank test: V = 12, P = 0.31) at each block; and moose were detected only in control plots (0.56 visits wk^{-1}; SE = 0.18).

Browsing by deer + moose significantly reduced woody plant abundance above 2 m in h eight (P <0.0001; Fig. 2) and simultaneously increased woody plant cover below 2 m in height rel ative to deer browsing alone and ungulate exclusion (P = 0.001; Fig. 2). Across the 18 plots in 6 blocks, 124 native vascular plant taxa were recorded to species or genus below 2 m in height, incl uding 8 ferns, 31 forbs, 25 graminoids, and 60 woody plants (tree, shrubs, and lianas). Exotic spe cies comprised 12 species (10% of the flora) and occurred in 7 of the 18 plots. Sixty three species of trees, shrubs, and herbs were common, occurring in at least two of the 18 plots. Analysis of ec ological distance revealed a significant difference among treatments (F = 0.68; R^2 = 0.08; P = 0.0 24).

Forb abundance and graminoid abundance did not differ among treatments (Table 3), but fern abundance (mostly eastern hay-scented fern [*Dennstaedtia punctilobula*]; 50%) and evergree n wood fern [*Dryopteris intermedia*]*;* 44%) was higher in deer plots and no-ungulate plots than in deer + moose plots (LRT χ^2 = 7.1; df = 2; P = 0.028; Table 3). Deer and no-ungulate plots did not differ in fern cover. Total *Rubus* abundance was greater in deer + moose plots than in no ungulat e plots (LRT χ^2 = 8.98; df = 2; P = 0.01; Table 3). Other treatment combination did not differ sig nificantly. Deer + moose plots supported less than half the abundance of forest herb and shrub in dicator species, on average, than did no-ungulate and deer plots (LRT = χ^2 = 9.81; df = 2 ; P = 0.

007; Fig. 3). In contrast, abundance of herb and shrub species characteristic of open/disturbed ha bitats was almost twice as high in deer + moose plots compared to no-ungulate plots (LRT χ^2 = 9. 20; df = 2; P = 0.010; Fig. 3). Open/disturbed indicator species were also significantly more abun dant in deer than in no ungulate plots (Fig. 3).

Deer + moose significantly increased woody species richness relative to areas with just deer or no-ungulates (P = 0.006; Fig. 4A). The presence of deer alone had little effect on woody richness relative to areas without ungulates. Total native species averaged about one species fewer in no-ungulate (7.1 species m^{-2}; SE = 0.70) and deer (7.3 species $m^{-2;}$ SE = 0.4) than in deer + moose plots (8.2 species m^{-2}; SE = 0.48; LRT χ^2 = 4.59; df = 2; P = 0.10). Native herbaceous and forb density were similar among treatment plots.

Plots browsed by deer + moose had three more native species (combined woody and herbaceous) on average than plots without ungulates and one more species than plots browsed by deer; but these differences were not significant (LRT = 4.25, df = 2, P = 0.119) Native herbaceous plant richness (combined number of forbs, ferns, and graminoid species) was greater by 3 and 4 species, on average, in deer + moose plots than in deer and no-ungulate plots respectively (P = 0.013; Fig. 4B). Graminoid species richness was higher in deer + moose plots (7.5 species; SE = 1.8) and deer plots (5.2 species; SE = 0.79) than in no-ungulate plots (4.5 species; SE = 1.8; LRT χ^2 = 11.99; df = 2; P <0.002). Neither forb nor woody species richness differed among treatments.

2.5 Discussion

Two ungulate browsers had strong additive effects on the structure and composition of temperate forest herbaceous layers 5-6 years after complete canopy removal from logging. The addition of a second large herbivore species (moose) reduced the abundance of tall woody plants, altered species composition, and promoted woody richness (subplot scale) and herbaceous

richness (plot scale). Plots browsed by low densities of white-tailed deer ($\leq$4 km^{-2}) were generally more similar to ungulate excluded plots (cf. Holladay et al. 2006), but frequently diverged from plots browsed by moose + deer. My results highlight the straightforward and unpredictable effects that large browsers at low densities can have on forest herbaceous layers in disturbed habitats (cf. Royo et al. 2010).

The divergence of species composition among browser treatments reveals the important role that ungulates play in the initial stages of forest succession following clearcut logging when much of the vegetation is within the browsing zone of the animals (cf. Oliver and Larson 1996). A suite of 13 herbs and shrubs characteristic of undisturbed forest habitats had more than twice the combined abundance in the relatively densely canopied no-ungulate and deer plots than in the more open grown deer + moose plots. At the same time, herbs and low shrubs (< 2m in height) associated with open/disturbed habitats had almost twice the abundance in moose + deer plots compared to no-ungulate plots. Herbivory-induced reductions of dominant woody plants (above 2 m in height) were likely one mechanism driving these divergent herb and low shrub communities (Fig. 2; cf. Persson et al. 2000, Royo et al. 2010, Roberts and Gilliam 2014). Additionally, much greater trampling effects by the heavier moose along with deer in the control plots may have resulted in greater soil compaction and damage to some of the more delicate forest herbs and shrubs, furthering altering composition (Persson et al. 2000, Hester et al. 2006, Heckel et al. 2010). Direct effects of herbivory by deer in the control plots may also have contributed to the shift in composition, as at least three of the forest indicator herb species – partridge-berry (*Mitchella repens*), Indian cucumber root (*Medeola virginiana*), and sessile-leaved bellwort (*Uvularia sessilifolia*) – are sensitive to herbivory by deer (Webster et al. 2005, Frerker et al. 2014).

Interestingly, fern abundance was significantly lower in plots browsed by moose + deer than in the other two treatments, which contrasts with a number of studies linking increased deer

browsing intensity with fern abundance in recently disturbed stands (Horsley et al. 2003, Royo et al. 2010). A number of factors may have contributed to the different pattern in my study area. First, one of the co-dominant fern species, evergreen wood fern, along with the less abundant New York fern (*Parathelypteris noveboracensis*) are indicators of undisturbed primary forests and thus would be expected to be associated with more developed tree canopies found in the deer and no-ungulate plots (Flinn 2014). Second, evergreen wood fern has declined in heavily browsed forests relative to less browsed areas (Rooney 2009, Frerker et al. 2013), suggesting some sensitivity to ungulate activity, whether by trampling or herbivory. Third, eastern hay-scented fern, the other co-dominant species in my study area, tends to decline with increased abundance of *Rubus* spp. in clearcuts (Horsley and Marquis 1983). *Rubus* abundance was highest in deer + moose plots, perhaps limiting fern cover. Deer at high densities typically reduce *Rubus*, allowing hay-scented fern to proliferate (Horsley and Marquis 1983). In my study area, however, where deer occurred at low densities and moose generally avoided *Rubus* (cf. Telfer 1967), this light-demanding taxon thrived in the relatively open grown control plots.

Browsing by deer + moose resulted in higher (native) herbaceous plant richness at the plot scale than in all six no-ungulate plots and five of the six deer plots. Graminoids, which are relatively resistant to herbivory because of their basal meristems and often thrive in high-light environments (Haines 2011, Waller 2014), were particularly species-rich in deer + moose plots. An increase in graminoid richness and cover with browsing has been noted by several other authors (e.g., Putman et al. 1989, Rooney 2009, Waller 2014). Graminoid abundance was generally higher in deer + moose plots in my study, but did not differ significantly among treatments ($P = 0.14$). The increase in herb richness by moose + deer foraging also points to overall additive effects by the two browsers on community composition (i.e., the two herbivores generally selected the same dominant woody competitors, thereby "rescuing" shorter statured herbaceous plants from competitive exclusion; Ritchie and Olff 1999, Hester et al. 2006). In

addition to reductions of tall woody plants, other contributing factors to increased herbaceous species richness may have been increased soil disturbance, spatial heterogeneity, and germination sites resulting from additional trampling by the larger moose (Olff and Ritchie 1998, Hester et al. 2006).

Increased herbaceous richness and diversity with herbivory has been documented in other temperate forest habitats ranging from disturbed open to woodland to old growth forest (Schreiner et al. 1996, Royo et al. 2010, Perrin et al. 2011, Hegland et al. 2013). These authors also pointed to the reduction of tall woody plant layers by browsing as important drivers of increased herbaceous diversity. Declines in herbaceous richness with deer herbivory have also been reported in undisturbed temperate forests in regions with long histories of high deer densities (Rooney et al. 2003, Webster et al. 2005, Goetsch et al. 2011). To what extent my results differed from these studies because of lower ungulate densities, the addition of moose, or logging disturbance is unclear.

Reductions in tall woody plant cover by browsers was also associated with significant increases in woody plant cover and woody species richness below 2 meters in height (at the subplot scale) in deer + moose plots. Woody richness changed little in response to foraging by deer alone, but increased sharply in response to foraging by deer + moose. Increased diversity and cover of low woody plants resulting from browsing has been noted by other authors in northern forests (e.g., Risenhoover and Maass 1987). Because my study sites were in clearcuts with abundant light, woody plants in the herbaceous layer were generally not eliminated by browsing – as often occurs in shaded environments – but rather became reduced in height (cf. Tilghman 1989, Gill 2006).

Two important and related questions emerged from these results. (1) To what extent were effects by moose + deer in the control plots influenced by the larger herbivore? (2) What explains the strong compounding effect on tree recruitment by the addition of very low densities

of moose (~0.2 km^{-2}) that typically have unimportant effects on forest regeneration (Abaturov and Smirnov 2002, Bergeron et al. 2011)? Remote camera visitation rates and pellet group densities suggest similar rates of visitation by the two herbivores in the control plots. Hence moose appeared to play a very important role – perhaps 5-6X that of deer given that moose are heavier than deer by that factor (Godin 1977, Forsythe 1985, Renecker and Schwartz 1997) – in areas exposed to both herbivores. The similar visitation rates recorded by the indices was surprising given that reported densities of deer (~4.5 km^{-2}) exceed those of moose (0.2 km^{-2}) by over 20-fold in central Massachusetts (Massachusetts Cooperative Fish and Wildlife Research Unit *Unpublished Data*, McDonald et al. 2007). However, estimated regional densities of moose likely underestimate the local densities that occurred in these patch clearcuts. My indices (cameras and pellet counts) and studies of moose movements suggest that local densities of moose in logged areas are at least twice the ambient densities in uncut forests (Faison et al. Unpublished Data; Wattles and DeStefano 2013). In contrast deer tend to use logged and unlogged forests more evenly (Degraaf and Yamasaki 2001).

The current study reveals the ecological and conservation effects of a recolonizing browser on temperate forest herbaceous layers during the first 5-6 years after complete canopy removal. In a region where existing deer densities are low, the addition of low densities of moose resulted in largely additive effects on the vegetation: delaying succession of tall woody plants and maintaining open habitat shrub and herb communities (e.g., *Rubus* spp.). By slowing down succession, moose and deer reduced competition from tall woody plants, resulting in greater richness of herbaceous and woody plant species below 2 m in height. Hence, the arrival of moose to areas where deer densities are relatively low may slow forest growth but prove beneficial, in some cases, to plant diversity during the initial stages of stand development following logging.

Table 2.1 Characteristics of study site blocks in central Massachusetts, USA.

Block	Location	Previous overstory composition	Exclosures Built	Age of Plot (yrs.)
Dana	Quabbin Reservation	oak-red maple-black birch	Nov. 2007	5.6
Fisher	Harvard Forest	red pine-white pine, black birch-red maple	July 2008	4.9
Locust	Harvard Forest	red pine-red maple-red oak	June 2008	5.1
Prescott	Quabbin Reservation	oak-red maple-black birch	Nov.2007	5.7
Prospect	Harvard Forest	spruce-black cherry-red maple	October 2008	4.8
Ware	Ware River Reservation	pine-larch-hardwoods	December 2007	5.6

Table 2.2 Herb and shrub species associated with forest and open/disturbed habitats used in species composition analysis. Species selected from 51 common species that occurred in at least two treatment plots. Habitat associations determined from Haines (2011) and New England Wildflower Society (https://gobotany.newenglandwild.org/).

Forest herbs	Open/disturbed herbs	Forest shrubs	Open/disturbed shrubs
Aralia nudicaulis	*Aralia hispida*	*Corylus cornuta*	*Comptonia peregrina*
Carex swanii	*Carex vestita*	*Sambucus racemosa*	*Prunus virginiana*
Dryopteris intermedia	*Carex normalis*	*Swida alternifolia*	*Rhus hirta*
Lysimachia borealis	*Carex lurida*	*Vaccinium corymbosum*	*Rubus* allegheniensis
Medeola virginiana	*Carex scoparia*	*Viburnum nudum*	*Rubus flagellaris*
Mitchella repens	*Danthonia compressa*		*Rubus hispidus*
Parathelypteris noveboracensis,	*Fragaria virginiana*		
Uvularia sessilifolia.	*Juncus effusus*		
	Lysimachia quadrifolia		
	Potentilla simplex		
	Solidago rugosa.		

Table 2.3 Mean abundance of common plant species and growth form groups in the herbaceous layer (<2m in height) by ungulate browser treatment in 2013. Only species that occurred in at least 4 of the 18 treatment plots were included. Standard errors are in parentheses. Total growth form groups were compared among treatments using Likelihood Ratio Tests. See Fig. 2 for results of woody plants. * P <0.05.

Species	No-ungulates	Deer	Deer + Moose
Trees			
Acer rubrum	3.50 (0.42)	4.0 (1.35)	5.43 (1.10)
Betula lenta	0.29 (0.18)	1.40 (0.70)	3.0 (1.67)
Betula papyrifera	0.31 (0.21)	0.17 (0.17)	0.49 (0.32)
Fraxinus americana	0.13 (0.15)	0	0.99 (0.59)
Pinus strobus	0.88 (0.62)	0.15 (0.13)	1.00 (0.83)
Prunus pensylvanica	0.59 (0.55)	1.14 (0.42)	0.81 (0.39)
Prunus serotina	0.82 (0.41)	0.54 (0.31)	1.88 (1.0)
Quercus rubra	0.97 (0.41)	2.18 (1.64)	1.20 (0.57)
Quercus velutina	1.05 (0.54)	0.17 (0.13)	0.04 (0.04)
Shrubs and lianas			
Amelanchier spp.	0.17 (0.14)	0.27 (0.17)	0.14 (0.13)
Comptonia peregrina	0.26 (0.29)	0.63 (0.49)	2.55 (1.61)
Gaylussacia baccata	1.36 (1.44)	0.66 (0.66)	2.16 (1.62)
Ilex verticillata	0.17	0	0.60 (0.38)
Rubus allegheniensis	10.51 (6.32)	17.31 (4.39)	23.06 (8.7)
Rubus flagellaris	0	0.66 (0.52)	3.91 (3.86)
Rubus hispidus	10.82 (7.0)	17.47 (10.11)	12.31 (8.16)
Rubus idaeus	7.07 (4.0)	4.22 (1.68)	7.28 (2.66)
*Rubus total**	28.41 (5.02)	39.66 (6.64)	46.55 (6.73)
Vaccinium angustifolium	3.70 (2.17)	2.28 (1.46)	2.1 (1.73)
Vaccinium carymbosum	1.15 (0.59)	0.97 (0.62)	0.30 (0.26)
Vaccinium pallidum	1.49 (1.58)	0.02 (0.02)	1.99 (1.83)
Vitis labrusca	0.17 (0.14)	0.01 (0.01)	0.01 (0.01)
Forbs	14.93 (0.74)	18.67 (3.81)	13.21 (2.97)
Aralia hispida	0.01 (0.01)	0.74 (0.74)	0.40 (0.35)
Aralia nudicaulis	1.36 (1.01)	5.0 (2.89)	0.59 (0.54)
Lysimachia borealis	0.83 (0.70)	0.68 (0.38)	0.45 (0.20)
Lysimachia quadrifolia	0.43 (0.27)	1.12 (0.70)	0.95 (0.66)
Maianthemum canadense	5.30 (0.93)	3.66 (0.79)	3.24 (2.17)
Medeola virginiana	0.04 (0.04)	0.01 (0.01)	0.05 (0.04)
Mitchella repens	0.13 (0.09)	0.04 (0.04)	0.04 (0.03)
Potentilla simplex	0.15 (0.17)	0.33 (0.29)	1.41 (1.05)
Rumex acetosella	0.01 (0.01)	0.06 (0.04)	0.01 (0.01)
Solidago rugosa	0.26 (0.29)	0.14 (0.13)	0.19 (0.19)
Uvularia sessilifolia	0.23 (0.15)	0.16 (0.14)	0.02 (0.02)
Graminoids	4.9 (2.01)	2.56 (0.56)	7.59 (3.0)
Carex debilis	0.08 (0.06)	0.23 (0.17)	0.64 (0.60)
Carex pensylvanica	2.35 (2.42)	1.0 (0.33)	5.36 (3.02)
Carex scoparia	0.32 (0.35)	0.01 (0.01)	0.46 (0.33)
Carex swanii	0.28 (0.28)	0.31 (0.31)	0.47 (0.31)

Carex vestita	1.43 (1.04)	0.03 (0.03)	1.15 (1.15)
Danthonia compressa	0.01 (0.01)	0.04 (0.04)	0.06 (0.05)
Ferns*	7.0 (1.96)	9.19 (4.31)	5.27 (3.35)
Dennstaedtia punctilobula	5.55 (2.75)	6.78 (4.65)	4.37 (3.38)
Dryopteris intermedia	1.39 (0.61)	2.28 (1.36)	0.74 (0.55)

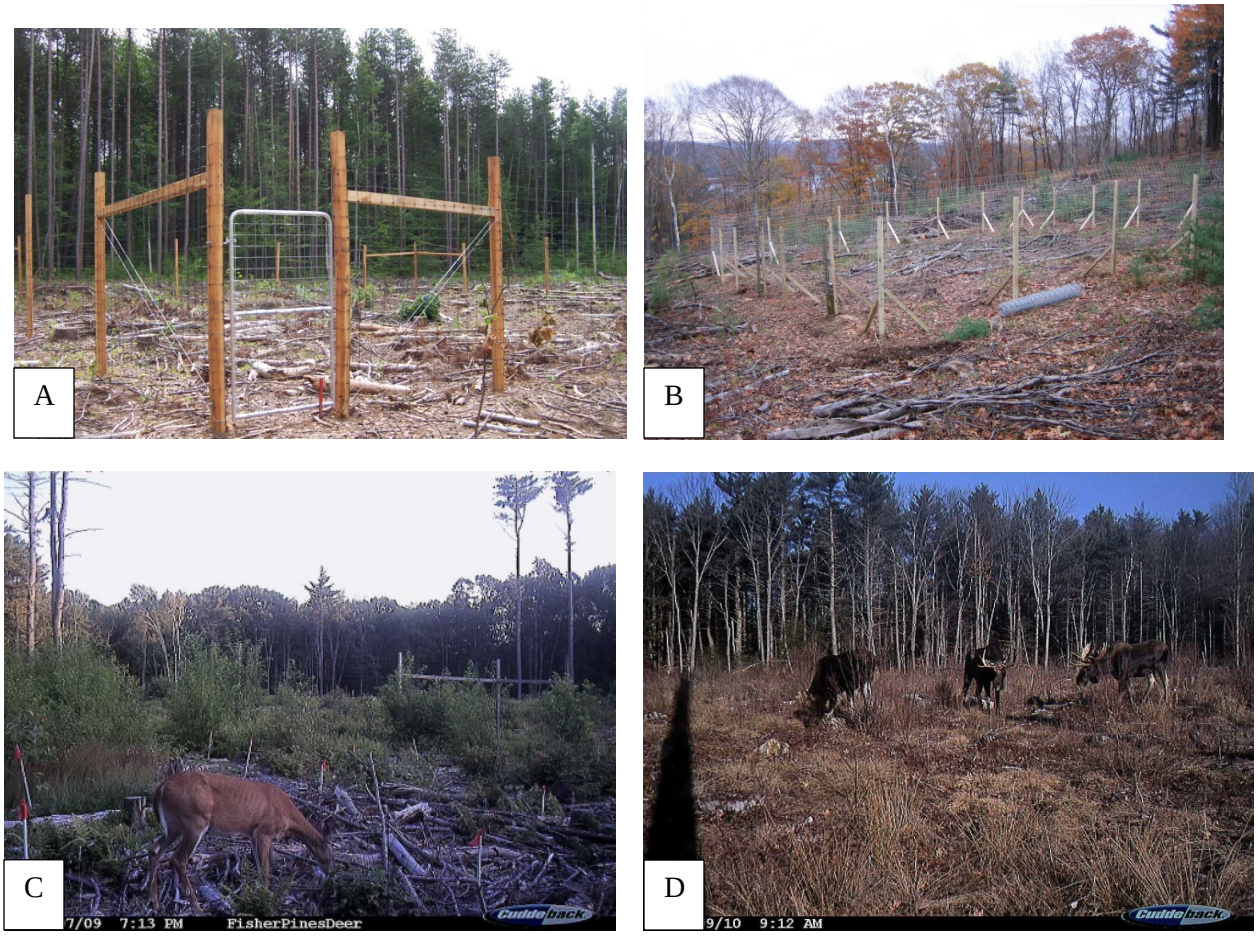


Figure 2.1 Photos of experimental treatments. (A) Full exclosure plot, Locust Block 2008; (B) partial exclosure plot, Prescott Block 2007; (C) deer foraging inside partial exclosure, Fisher Block 2009; (D) moose foraging in control plot, Locust Block 2010. Photo credits: A by Audrey Barker-Plotkin; B by Justin Compton

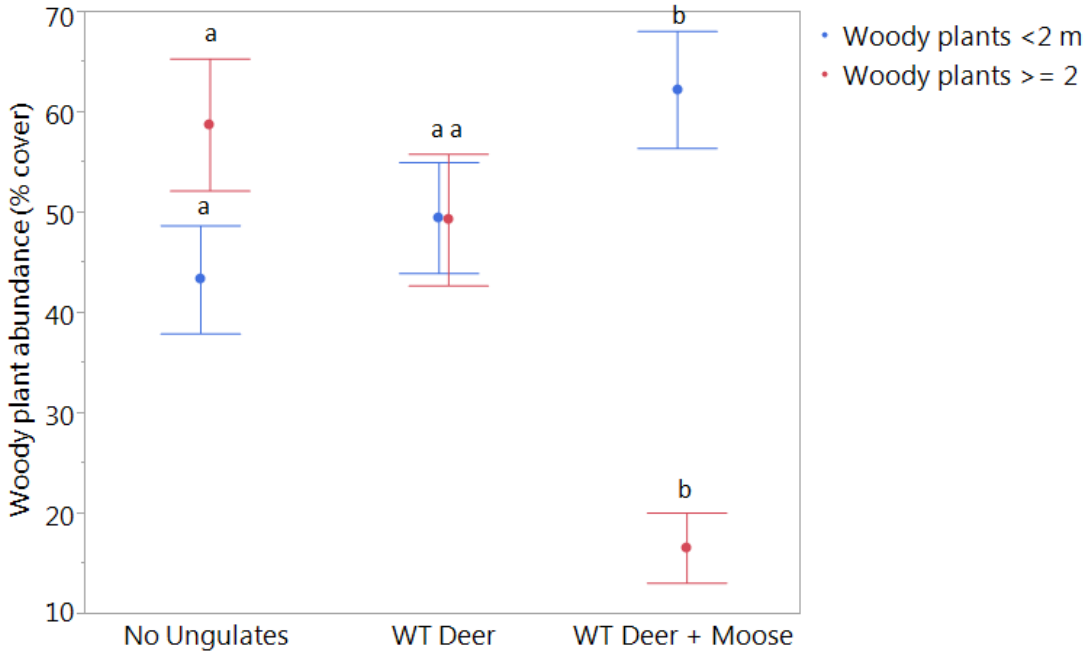


Figure 2.2 Effect of browsers on the abundance of woody plants above the herbaceous layer (≥ 2 m in height; LRT χ^2 = 23.2; df= 2; P <0.0001) and within the herbaceous layer (<2 m in height; LRT χ^2 = 13.78; df = 2; P = 0.001). Bars represent mean ± SE. Treatment means with the same letter do not differ significantly.

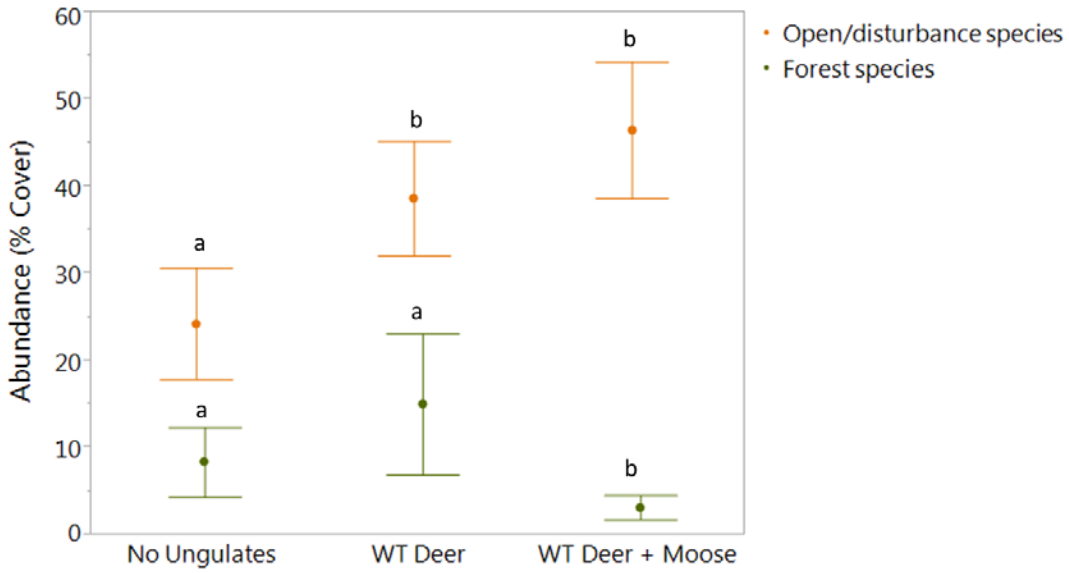


Figure 2.3 Effect of browsers on the combined abundance of 13 herb and shrub species affiliated with undisturbed/forest habitat (P = 0.007) and 18 herb and shrub species associated with disturbed/open habitats (P = 0.010). Bars represent mean ± SE. Treatment means with the same letter do not differ significantly. *Aralia nudicaulis* was the dominant forest species (26% of total abundance), and *Rubus allegheniensis* the dominant open species (47% of total abundance). See Table 2 for complete list of indicator species.

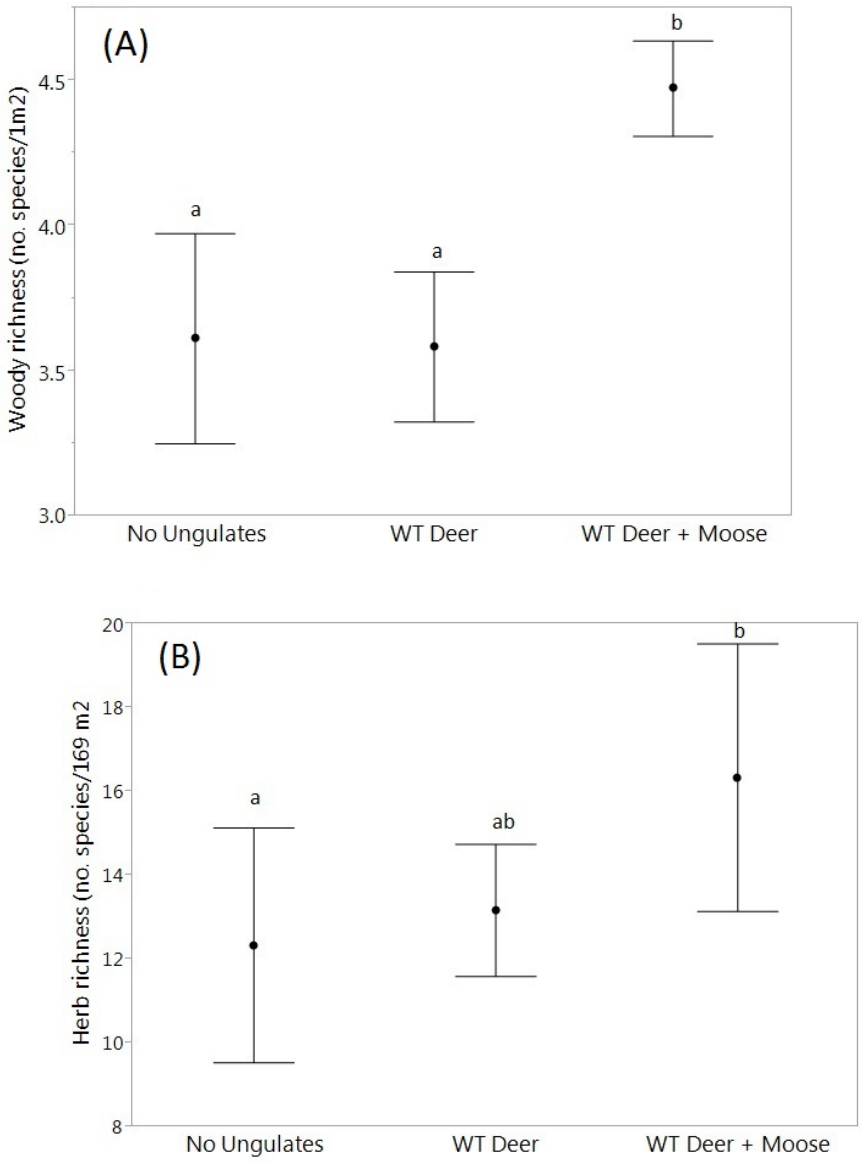


Figure 2.4 Effect of browsers on (A) native woody plant richness at the subplot scale (mean no. of species of trees, shrubs, and lianas in 13, 1m^2 in each plot (LRT $\chi 2 = 10.21$; df = 2; P = 0.006); and (B) native herbaceous species richness at the plot scale (no. species of forbs, graminoids, and ferns 169 m^{-2}; LRT = $\chi^2 = 8.6$; DF = 2; P = 0.013). Bars = mean ± SE. Treatment means with the same letter do not differ significantly.

CHAPTER 3

EFFECTS OF UNGULATE BROWSERS ON TREE RECRUITMENT IN LOGGED TEMPERATE FORESTS

3.1 Abstract

Large herbivores at high densities are major drivers of tree recruitment in northern forests. However, few studies have examined the combined effects of multiple ungulate species at low densities in structuring temperate forests. Low densities of herbivores may alter the vegetation in unexpected ways, and the effects of two or more herbivore species are difficult to predict because their combined foraging may be compensatory (opposing) or additive (compounding). I explored the effects of two ungulates (moose [*Alces alces*] and white-tailed deer [*Odocoileus virginianus*]) occurring at low densities on tree recruitment over 6-7 years in recently logged patch cuts of Massachusetts, USA. I established three combinations of ungulates using two types of fenced exclosures – (none (full exclosure), deer (partial exclosure), and deer + moose (control) -- and examined the response of tree density, basal area, species composition, and diversity (≥2 m in height) to browser treatments in 2011 and 2014.

The addition of browsers had strong additive effects on tree recruitment. Stem densities and basal area in deer + moose plots were reduced by 2-3-fold in 2014 relative to no-ungulate plots. Deer alone had relatively minor effects on density and basal area that did not differ significantly from ungulate exclusion. Moose + deer reduced the density of *Prunus pensylvanica* and *Acer rubrum* in 2011 and *P. pensylvanica* and *Quercus* spp. in 2014. The addition of browsers initially suppressed species richness and diversity in 2011, but moose + deer increased or maintained diversity and richness in 2014. In contrast, less intensive but more selective browsing by deer alone reduced richness in both time periods. My results revealed that low

densities of two ungulate species had both straightforward and complex effects on regenerating forests in the first several years following canopy removal from logging. Examining browsing impacts at low densities of herbivores and by multiple levels of browsers is a critical piece in understanding ungulate-forest interactions.

3.2 Introduction

Numerous recolonizations and population increases of previously extirpated or depleted forest ungulates occurred in the 20th century as a result of conservation efforts and changes in land use (Foster et al. 2002, Cote et al. 2004, Kuijper et al. 2010a). Over the past several decades, a large body of research has documented that ungulates (primarily cervids) dramatically reduce the density, height, composition and species richness of regenerating trees (Tilghman 1989, McInnes et al. 1992, Thompson et al. 1992, Russell et al. 2001, Horsley et al. 2003, Gill 2006, Nuttle et al. 2013). However, most of these studies occurred in landscapes with elevated cervid densities (i.e, >8 deer km^{-2}; or ≥1.5 moose km^{-2}). The extent to which lower cervid densities (i.e., ≤6-7 deer km^{-2} and <1 moose km^{-2}) – characteristic of large parts of North America's Eastern Deciduous Forests (Adams et al. 2009, Bergeron et al. 2011, Wattles and DeStefano 2011) – alter tree regeneration is less understood and may differ substantially from areas with high densities of cervids (Royo et al. 2010, Bergeron et al. 2011). For instance, low to moderate densities of browsers could potentially enhance tree diversity in forest openings by controlling dominant woody plants within reach of the browsers and "rescuing" inferior competitors from competitive exclusion (Gill 2006, Hester et al. 2006, Borer et al. 2014). This hypothesis however remains largely untested for tree regeneration. Understanding herbivory impacts across the range of ungulate densities is essential to accurately assessing and generalizing vegetation changes that are critical for habitat and ecosystem services.

In addition to the paucity of studies capturing the lower end of cervid density gradients, few studies have examined the combined effects of multiple ungulate species on forest regeneration (Ritchie and Olff 1999, Wisdom et al. 2006). The effects of two or more herbivores on plant communities may either compound (additive) or offset (compensatory) the effects of a single herbivore species, although vegetation biomass is generally reduced in either scenario (Ritchie and Olff 1999). Additive effects occur when multiple herbivores consume primarily the same plant species and therefore alter the community in the same direction as a single herbivore (Ritchie and Olff 1999). Compensatory effects occur if the herbivore species consume primarily different plant species so that their individual effects on plant species balance each other out (Ritchie and Olff 1999). The extent to which a recolonizing herbivore will join an existing herbivore to have additive or compensatory effects is difficult to predict because the addition of the former can initiate diet shifts in the latter (Hester et al. 2006).

In the late 20th century moose (*Alces alces*) recolonized much of their former southern range in the northeastern deciduous forest region (Faison et al. 2010, Wattles and DeStefano 2011), creating a two-ungulate system with white-tailed deer (*Odocoileus virginianus*) for the first time in almost two centuries in some landscapes. Almost nothing is known about how low densities of moose (<0.5 km^{-2}) interact with other browsers to shape the structure and composition of temperate forests (but see Kuijper et al. 2010b). Because moose and deer are generalist browsers that consume many of the same woody plants, they might be expected to have additive effects on plant communities (Boer 1997, Renecker and Schwartz 1997; Ritchie and Olff 1999). However, deer consume a higher proportion of herbaceous plants (40%) than do moose (10%), and the two animals' woody plant diets are reported to overlap by only about 40% with respect to the frequency with which different plant species are consumed (Ludewig and Bowyer 1985, Renecker and Schwartz 1997). Hence, deer + moose foraging could be compensatory in some cases.

Foraging by moose and deer at low densities could have implications for one of the most important and enigmatic dynamics across the temperate forest: the long-term recruitment failure of oaks *(Quercus*) – a valuable timber tree, and critical source of food for wildlife (McShea and Healy 2002) – and replacement by maple (*Acer),* birch (*Betula),* and other shade tolerant hardwoods (Gill 2006, Vera et al. 2006, McEwan et al. 2011). Oaks are generally reduced by deer browsing (Gill 2006), but some evidence suggests that low to moderate browsing may benefit oaks via competitive release (Eschtruth and Battles 2008). Moreover, deer sometimes have even greater effects on red maple (*Acer rubrum)* than on oaks (Abrams and Johnson 2012, Nuttle et al. 2013). Moose appear to prefer red maple over oaks, but are still known to suppress oaks in some areas (Godin 1977, Abaturov and Smirnov 2002, Faison et al. 2010). Thus uncertainty exists about the extent to which the recent addition of moose and low densities of deer have influenced oak-red maple dynamics in northeastern temperate forests.

Here I explore the role of moose + deer in structuring temperate forest communities in the first 6-7 years following canopy removal from logging. Ungulates are drawn to disturbed openings and often exert strong interactions in these sites where most or all of the vegetation must pass through the ungulate browsing zone (Eschtruth and Battles 2008, Kuijper et al. 2009). Specifically, I asked: (1) To what extent would low densities of moose + deer browsing have significant additive (negative) effects on stem density and basal area? (2) Would the addition of moose have additive or compensatory effects on species composition, and how would these interactions affect species richness and diversity? (3) How would the addition of moose influence oak-maple-birch dynamics? (4) Finally, to what extent would low densities of deer alone alter stem density, species composition, and diversity?

3.3 Materials and Methods

The physiography of Central Massachusetts is characterized by rolling plateaus with hills, and the climate is permanently humid with warm summers and cold winters (Brouillet and Whetstone 1993, US EPA 2015). Mean annual precipitation ranges from 97-127 cm per year, and mean temperature ranges from -12 – -0.5ºC in January and 14-28°C in July. Mature forest vegetation is characterized by transition hardwood forests – (mixed oak, red maple, black birch (*Betula lenta*), and beech (*Fagus grandifolia*) – with significant components of eastern hemlock (*Tsuga canadensis)* and white pine (*Pinus strobus*; Foster et al. 2004, USDA 2015). In addition to timber harvesting, exotic forest insects and pathogens including hemlock woolly adelgid (*Adelges tsugae*), beech bark disease (*Cryptococcus fagisuga* and *Nectria* spp.), chestnut blight (*Cryphonectria parasitica*) and gypsy moths (*Lymantria dispar*); and meteorological events (ice and windstorms) are the prevalent disturbances in the region (Foster et al. 2004). Patch cuts are a less common form of timber harvest in the region than selective harvests (Kittredge et al. 2003), but patch cuts are still an important part of some forest management plans on public land and timber company lands (Kyker-Snowman 2007).

Moose historically ranged as far south as northwestern Connecticut, southern New York, and Pennsylvania before European settlement (Reeves and McCabe 1997). After being extirpated from Massachusetts in the early 19th century, moose recolonized central Massachusetts in the late 20th century (Faison et al. 2010). Today, the southern range limit for moose in the eastern United States is in northern Connecticut (Wattles and DeStefano 2011). Densities are estimated to be about 0.2 km^{-2} in central Massachusetts (USGS Massachusetts Cooperative Research Unit, *unpublished data*). White-tailed deer were common in presettlement New England, were extirpated from much of the state of Massachusetts by the mid-19th century, and recovered their former range and abundance during the mid to late 20th century (McCabe and McCabe 1984, Foster et al. 2002). Today, deer densities are estimated at 3.9-5.8 km^{-2} for north-central Massachusetts (McDonald et al. 2007, D. Stainbrook pers. comm).

In 2007-2008, experimental exclosures were established in six mixed conifer-hardwood stands (≤6 ha in size) 3-6 months after being clearcut at the Harvard Forest and the Quabbin and Ware River Watershed forests in Central Massachusetts (Table 1). Four of the sites were former conifer plantations with mixed native hardwoods, and the other two were naturally grown oak-pine-hardwood stands (Table 1). The experimental design was a randomized block with three levels of large herbivores – complete ungulate exclusion (hereafter no-ungulate plots), moose exclusion (hereafter deer plots), and no exclusion (hereafter deer + moose plots). A fourth treatment that excluded the smaller deer but was open to moose was not feasible, but other studies have successfully utilized similar additive, non-factorial designs (Ritchie and Olff 1999, Manier and Hobbs 2007). Blocks were at least 1 km apart from one another. The exclosures were made of high tension wire game fence with 15 cm grid mesh and 2.5 m in height. The full exclosure was fenced to the ground, the partial exclosure had a 60 cm opening around the bottom of the fence that excluded moose but allowed access to deer and other wildlife, and the control plot was unfenced and open to both browsers. The 15cm wire mesh of the full exclosure fence enabled access to small mammals, including lagomorphs and rodents.

Exclosure and control plots were 20 x 20 m in size and located at least 10 m apart from each other. In 2008, a 5 x 5 sampling grid of 4 m^2 circular subplots was established in the center of each plot, (4 m from plot edge and 3 m from each other), totaling a 100 m^2 sampling area. At each of the subplots, tree seedlings were sampled and measured for height. At the start of the experiment, no residual trees were present in the three treatments, and virtually all advance regeneration or sprouts were < 1m in height; no woody regeneration was >2 m in height. Baseline sampling revealed there were no significant initial differences in species composition or stem density among treatments. In 2012, stems 0.5-2 m in height were assessed for past browsing on the leading shoot in each treatment plot (Kuijper et al. 2010a).

Tree regeneration data presented in this paper were collected in June-August of 2011 (3-4 years after treatment) and again in July 2014, 6-7 years after treatment. Twenty-five of the subplots were sampled in 2011 ($100m^{-2}$), and 13 of the original subplots were resampled (i.e., every other subplot, totaling a 52 m^2 sampling area) in 2014 because the stem density of the plots had grown enormously. To standardize comparisons between the two time periods, I analyzed only the 13 subplots from 2011 that were also sampled in 2014. At each of the subplots, all tree and shrub species ≥2 m in height were recorded, and in 2014 the diameter at breast height (DBH) of each stem was measured. I chose the 2 m height minimum because it corresponded with the upper limit of the herbaceous or forest floor layer (Oliver and Larson 1996, Gilliam 2014), as well as the upper limit of the predominant browsing zone for eastern North American forest ungulates (Frerker et al. 2013). My study therefore focused on the composition, diversity, and density of tree recruitment that was able to successfully pass through the browsing filter into the next forest stratum (cf. Kuijper et al. 2010b)

To test the integrity of the experimental design for maintaining different diversities of herbivores, Reconyx, Inc. (Holmen, Wisconsin) and Cuddeback, Inc. (Greenbay, Wisconsin) remote cameras were mounted inside each partial exclosure and toward each control plot between 2008 and 2011 (mention of trade names does not constitute an endorsement from the U. S. Government). Cameras were discontinued after 2011 because the vegetation had grown to a height that effectively blocked the camera's ability to detect animals. Control and partial exclosure plots in each block had the same type of camera set to the same delay specifications, and I calculated the frequency of visits by deer and moose ($week^{-1}$; Augustine and Frelich 1998). A minimum of 5 minutes of elapsed time between the last image taken of an animal and the arrival of a new animal (or the same animal returning at a later time) was used to separate visits. Ungulate pellet groups were counted in 2012 in 25 4-m^2 vegetation subplots and again in 2013. Because I encountered a number of 0 values in 2012, I increased the sampling area of pellet group

counts from 100 m^{-2} to 400 m^{-2} in 2013 and standardized two year mean values by converting counts to number ha^{-1}. Pellet groups were defined as having at least 15 individual pellets to avoid over-counts from scattered individual pellets (Eschtruth and Battles 2008).

I used linear mixed effects models (package lmer, the R Foundation for Statistical Computing 2014; R version 2.15.2) with ungulate treatment as fixed effect and block as random effect to determine the response of tree recruitment density, basal area, species richness, and diversity to three levels of ungulate browsers. I also examined models that included variation in herbivore abundance (from pellet count indices) across the blocks as a covariate, but in no instance did these models fit the data better than the basic treatment model when compared with AIC. Because my study sites were logged at slightly different times (age since harvest ranged from 5.8-6.7 years), I also examined the effects of time since harvest on tree regeneration characteristics and found time to be an unimportant factor.

For species richness I examined both species density (no. species/52 m^2) and rarefied species richness (Gotelli and Colwell 2001). Hereafter I refer to species density as "species richness" to avoid confusion with stem density and herbivore density. For rarefied richness I constructed individual based rarefaction curves and used non-overlapping 95% confidence bounds as the criterion for significant differences among treatments (Gotelli and Ellison 2013). For diversity, I used effective number of species defined as exp(Shannon diversity Index) (Jost 2006, Nuttle et al. 2013).

I used either a Gaussian or Gaussian with log link (log normal) distribution for all response variables after examining the residuals to determine the best fit. For hypothesis tests of treatment effects, I used likelihood ratio tests on nested null and treatment models. For significant effects ($P \leq 0.05$) of treatment, I performed pairwise comparisons between treatment pairs by simulating the posterior distribution 10,000 times to calculate 95% confidence intervals and approximate P-values for the fixed effects (Bagchi et al. 2011, Rapp et al. 2013). To

compare individual species density among treatments, I used Friedman tests with post hoc tests (package agricolae), because the data were frequently heterogenous. To test for significant differences in community composition among treatments I used adonis (package vegan), the analysis of variance of distance measures (Bray), grouped by block (1,000 permutations; Oksanen et al. 2015) The stem density for each species was entered into the multivariate test, and rare species that occurred in only 1 of the 18 treatment plots (5.5%) were removed prior to analysis (McCune and Grace 2002).

I examined browsing preferences and overall selectivity by deer in the partial exclosure and by moose + deer in the control plot. I analyzed the 10 most common tree species using IVLEV's electivity index (Ivlev 1961, Tanentzap et al. 2009) using the equation:

$$I_{i=}\frac{r_i - p_i}{r_{i+P_i}}$$

where r = the frequency of browsed stems of a species/the total number of browsed stems of all tree species, and p = the frequency of available stems of a species/the total number of available stems of all tree species. I values range from -1 to 1, with positive values denoting species browsed in greater proportion to their availability and negative values species browsed in lower proportion to their availability.

3.4 Results

Two year mean deer pellet groups were similar in partial exclosure (216.7 groups ha^{-1}; SE = 94.4) and control plots (187.5 group ha^{-1}; SE = 70.0; Wilcoxon signed rank test: V = 13, P = 0.67). Moose pellet groups (two year mean: 202.1 groups ha^{-1}; SE = 82.9) were detected only in control plots. Remote cameras detected deer in partial exclosures (0.31 visits wk^{-1}; SE = 0.13) and control plots (0.61 visits wk^{-1}; SE = 0.20; Wilcoxon signed rank test: V = 12, P = 0.31) at each block; and moose were detected only in control plots (0.56 visits wk^{-1}; SE = 0.18).

Percentage of stems with leading shoot browsed was much higher in moose + deer plots (58%; SE = 8) than in deer only plots (16%; SE = 3).

Nine of 10 tree species had higher electivity indexes in deer-only plots compared to deer + moose plots (Table 2). Pin cherry (*Prunus pensylvanica*) and white ash (*Fraxinus Americana*) had the highest electivity index in deer plots, and red maple had the highest electivity index in deer + moose plots. White pine had the lowest electivity index in both plots.

Deer + moose browsing in control plots reduced stem density (≥2 m in height) by almost 5-fold in 2011 (LRT $\chi^2 = 17.04$; df = 2; P = 0.0002) and by almost half in 2014 relative to ungulate excluded areas (LRT $\chi^2 = 8.48$; df = 2; P = 0.014; Figs. 1 and 2). Deer alone caused relatively minor reductions in stem density that did not differ significantly from ungulate exclusion in either time period (P> 0.10). Results were similar but more pronounced for basal area in 2014, as deer + moose reduced the cross sectional area of stems above 2 m by 2.5-3-fold relative to no-ungulate and deer plots (LRT $\chi^2 = 21.91$; df = 2; P<0.0001; Figs. 1 and 2). Again, deer alone had relatively minor and non-significant effects on basal area.

A total of 34 tree and shrub species ≥2 m were recorded in the 18 plots of the six blocks; 92% of the stems sampled were tree species. Four species (12%) were exotic, including glossy false buckthorn (*Frangula alnus*), Morrow's honeysuckle (*Lonicera morrowii*), and European buckthorn *Rhamnus cathartica*, and European mountain-ash (*Sorbus accuparia*), which occurred in three (one of each of the three treatments) of the 18 plots. Community composition did not differ significantly among treatments in 2011 (Adonis F = 0.94; $R^2 = 0.11$; P = 0.255) or in 2014 (Adonis F = 0.57; $R^2 = 0.07$; P = 0.294), as the same three species – pin cherry, red maple, and black birch – dominated the three treatment plots in both time periods. In 2011, two species declined significantly with the addition of browsers: pin cherry (Friedman $\chi2 = 8.59$; df = 2; P = 0.014), and red maple (Friedman $\chi2 = 5.83$; df = 2; P = 0.054; Figs. 1 and 3). Pin cherry declined

in both deer and deer + moose treatments relative to ungulate exclusion, whereas red maple declined only in moose + deer plots relative to ungulate exclusion.

In 2014, pin cherry (Friedman $\chi^2 = 8.67$; df = 2; P = 0.013) and oaks (combined red [*Quercus rubra*, white [*Q. alba*], and black [*Q. velutina*]; Friedman $\chi^2 = 6.64$; df = 2; P = 0.036; Fig. 3) differed significantly among treatments. Both taxa were reduced in deer + moose plots relative to the other treatments, which did not differ from one another (Fig. 3). Red maple recovered to some extent in the control plot in 2014 and no longer differed significantly among treatments (P = 0.11). Black birch increased sharply in the deer + moose plot compared to 2011, becoming the only taxa with a higher density of stems in the control plot than the other treatments. Both red maple and black birch became more dominant in terms of relative abundance with the addition of browsers, and oaks became less abundant.

Species richness (LRT $\chi^2 = 16.56$; df = 2; P = 0.0003) and diversity (LRT $\chi^2 = 12.23$; df = 2; P = 0.002) differed significantly by ungulate treatment in 2011 (Fig. 3). All treatment combinations differed significantly in richness, whereas deer + moose plots differed from the other two treatments with respect to diversity (Fig. 4). In 2014, species richness still differed by treatment ($\chi^2 = 8.18$; df = 2; P = 0.017), with deer effects lower than in no-ungulate plots, but moose + deer plots no longer differed significantly from the other treatments (P = 0.06; Fig. 4). Diversity did not differ by treatment in 2014 (Friedman $\chi^2 = 2.87$; df = 2; P = 0.238). In 2011, rarefied richness was lowest in deer + moose plots, and this treatment diverged from deer plots at approximately 35 stems (Fig. 5). In 2014 rarefied richness was highest in deer + moose plots and diverged from deer plots at approximately 190 stems (Fig. 5).

3.5 Discussion

My results revealed both straightforward and complex effects by two ungulate browsers at low densities on regenerating temperate forests, 6-7 years after canopy removal from logging.

The addition of moose reduced tree recruitment and individual tree taxa to a much greater extent than deer alone, but foraging by deer + moose had fluctuating and complex effects on diversity and richness. Deer browsing alone had relatively minor effects on stem density and basal area, but browsing by the smaller herbivore more consistently reduced measures of diversity than did more intensive browsing by moose + deer.

Greater consumption of woody plants by two generalist browsers had additive (negative) effects on density and basal area of stems ≥ 2 meters in height. Moose + deer plots diverged quickly from the other treatments with respect to stem density after the first 3-4 years and remained different after 6-7 years. By 2014, stem densities in deer + moose plots had equaled densities in no-ungulate plots in 2011, suggesting a three year delay in recruitment by the two herbivores. Consistent with other studies examining impacts by low to moderate densities (3.7-7.0 km^{-2}) of deer (Tilghman 1989, Holladay et al. 2006), browsing by deer (~4-5 km^{-2}) alone had relatively minor effects on stem density and basal area that did not differ from ungulate excluded plots. What explains the strong compounding effect on tree recruitment by the addition of very low densities of moose (~0.2 km^{-2}) – densities that typically have unimportant effects on forest regeneration (Abaturov and Smirnov 2002, Bergeron et al. 2011)? First, reported regional densities of moose probably underestimate the local densities of moose that occurred in these patch clearcuts. My indices (cameras and pellet counts) along with studies of moose movements suggest that local moose densities in logged areas may be at least twice the ambient densities in uncut forests (Faison et al. *Unpublished Data*; Wattles and DeStefano 2013). A second possible explanation is the relatively small size of the patch clearcuts in my study area (≤6 ha), which tend to concentrate browsing impacts by moose (Faison et al. 2010). Very large clearcuts and burns in boreal forests that are several orders of magnitude larger than my study sites can overwhelm moose with available forage, rendering browsing impacts relatively unimportant (McLaren and Peterson 1994, Pastor et al. 1988, Delong and Tanner 1996, Hunter 1996). A third reason is that

moose browsing could result in greater per capita impact by deer than when deer forage alone. By reducing the height of vegetation, a larger herbivore can maintain the vegetation within the browsing zone of a smaller herbivore for a longer period of time; and previous browsing often increases the palatability of shoots and therefore the probability that they will be browsed again (Bergstrom and Danell 1987, Makhabu et al. 2006).

Early reductions in stem density by deer + moose coincided with reduced species richness and diversity in 2011, as would be expected, given the close relationship between species richness and number of individuals sampled (Gotelli and Colwell 2011). However reductions in species richness appeared to exceed that which would be expected by stem densities alone, as rarefied richness in deer + moose plots diverged from deer plots and perhaps from no-ungulate plots (Fig. 4). That deer alone reduced species richness relative to no-ungulate plots (Fig. 4), revealed that even low densities and browsing intensities by deer can reduce the number of species recruiting above the browsing zone (Alverson and Waller 1988). Thus, in the first 3-4 years, ungulate browsing (at all levels) appeared to act mainly as a filter through which only a limited number of individual species could pass (cf. Kuijper et al. 2010b).

In 2014, patterns of richness and diversity among treatments changed markedly, as all diversity and richness metrics increased sharply in deer + moose plots. Diversity no longer differed significantly among treatments. Richness remained significantly lower in deer plots, but the addition of moose had no additional effect; in fact, deer + moose plots no longer differed significantly from no-ungulate plots ($P > 0.05$). Rarefied richness in deer + moose plots was highest and diverged significantly from deer plots, but not from no-ungulate plots, suggesting compensatory effects by the two browsers (Ritchie and Olff 1999, Hester et al. 2006). After 6-7 years of growth, deer + moose browsing appeared to change from a suppressive filter to a process reducing competition via the reduction of dominant plants (Hester et al. 2006, Borer et al. 2014). Divergence in (rarefied) richness between deer and moose + deer plots can perhaps be explained

by the vegetation in deer plots exposed to two important limiting factors: competition from a dominant overstory left mostly intact by deer (Fig. 2) and relatively selective browsing (Table 2). In contrast, the vegetation in no-ungulate plots was exposed to only competition. By 2014, deer + moose plots appeared to have neither limiting factor, with competition significantly reduced by browsing and relatively unselective foraging dispersing browsing impacts more evenly across many species (Edenius 1991, Ritchie and Olff 1999).

Moose + deer browsing had clear additive effects on oaks, reducing this important tree taxon sharply compared to the other treatments. Reductions in plant competition by moose + deer revealed no detectable benefits for oaks, failing to offset the suppressive effects of browsing. Relatively high abundance of thorny *Rubus* spp. in the control plots compared to the other treatments also appeared to provide little benefit or protection to oaks (cf. Vera et al. 2006; Faison et al. *unpublished data*). Oaks did show some tolerance to low intensity browsing by deer alone (cf. Healy 1997), as they remained unchanged in stem density in deer plots relative to ungulate excluded plots. Red maple and black birch, however, showed greater resilience to browsing by deer + moose. Black birch recruitment was suppressed early by browsing in 2011, but recovered strongly in 2014. Red maple, despite being the most preferred browse species by moose + deer and reduced in 2011, still increased in relative abundance that year. In other words red maple benefitted from intensive herbivory by being more browse tolerant than other taxa such as oaks., pin cherry, and paper birch (*Betula papyrifera*). My results at this stage of forest development (6-7 years post treatment), though admittedly limited in scope, suggest that deer + moose foraging in harvested areas favors the continued long-term transition of oak to maple-dominated composition in the region (Fei et al. 2011, McEwan et al. 2011). Still, it is important to consider the transient nature of these developing stands and the changes that could occur to oaks and other tree taxa as stems grow above the reach of ungulates. For instance, mature red oaks develop larger diameters

in heavily browsed, open grown environments with reduced stem competition than in areas protected from browsing (Lucas et al. 2013).

Browsing induced declines in stem density, basal area, and individual taxa also revealed relatively short-term successional dynamics. Pin cherry, which declined sharply with the addition of browsers in both 2011 and 2014, is often the dominant species for the first 10-15 years after major disturbances in northern and transition hardwood forests of northeastern North America (Marks 1974; Hibbs 1983). Thus the response of this pioneer species to browsing in my study area suggests that deer + moose may reduce the duration of its dominance and accelerate the transition of tree species toward more shade tolerant red maple and black birch. However, the much reduced stem density and basal area in deer + moose plots, resulting in a more open-grown structure, suggests an overall slowing down of forest succession from browsing (Oliver and Larson 1996).

The current study reveals the ecological and conservation effects of a recolonizing large herbivore on tree recruitment in temperate forest communities during the first 6-7 years after canopy removal from logging. Effects by moose + deer appeared to be additive, in terms of reducing the density and basal area of tree recruitment and the density of important pioneer (pin cherry) and later successional (oak) tree taxa. In contrast, browser effects on species richness and diversity were more complex over time, initially showing additive reductive effects in 2011 and later showing compensatory effects in 2014. My results highlight the predictable and complex effects of two large herbivores at low densities on regenerating temperate forests and stress the importance of investigating ungulate impacts across the range of herbivore densities and (when feasible) with multiple browser treatments.

Table 3.1 Characteristics of study site blocks in central Massachusetts, USA

Block	Location	Previous Overstory Composition	Dominant Regeneration Species	Exclosures Built	Age of Plot (yrs.)
Dana	Quabbin Reservation	oak-red maple-black birch	*Acer rubrum Betula lenta, Pinus strobus*	Nov. 2007	6.7
Fisher	Harvard Forest	red pine-white pine, black birch-red maple	*Prunus pensylvanica, Acer rubrum, Betula lenta*	July 2008	6.0
Locust	Harvard Forest	red pine-red maple-red oak	*Acer rubrum, Betula papyrifera, Prunus pensylvanica*	June 2008	6.1
Prospect	Harvard Forest	spruce-black cherry- red maple	*Prunus pensylvanica, Prunus serotina, Acer rubrum*	October 2008	5.8
Prescott	Quabbin Reservation	oak-red maple-black birch	*Acer rubrum Betula lenta, Quercus rubra*	Nov.2007	6.7
Ware	Ware River Reservation	pine-larch-hardwoods	*Acer rubrum, Prunus serotina, Quercus rubra, Fraxinus americana*	December 2007	6.6

Table 3.2. Browsing selectivity by deer alone and moose + deer combined on the 10 most common tree species. The Ivlev index (Ivlev 1961) ranges from -1 to 1. Species with positive values were browsed in greater proportion to their availability and those with negative values in lesser proportion to their availability.

Species	Deer	Moose + Deer
Acer rubrum	-0.015	0.12
Amelanchier spp.	-0.18	-0.01
Betula lenta	-0.347	-0.03
Betula papyrifera	-0.18	-0.04
Fraxinus americana	0.297	-0.14
Pinus strobus	-1.0	-0.81
Populus tremuloides	0.16	0.03
Prunus pensylvanica	0.35	-0.02
Prunus serotina	-0.52	-0.19
Quercus rubra	-0.5	-0.09

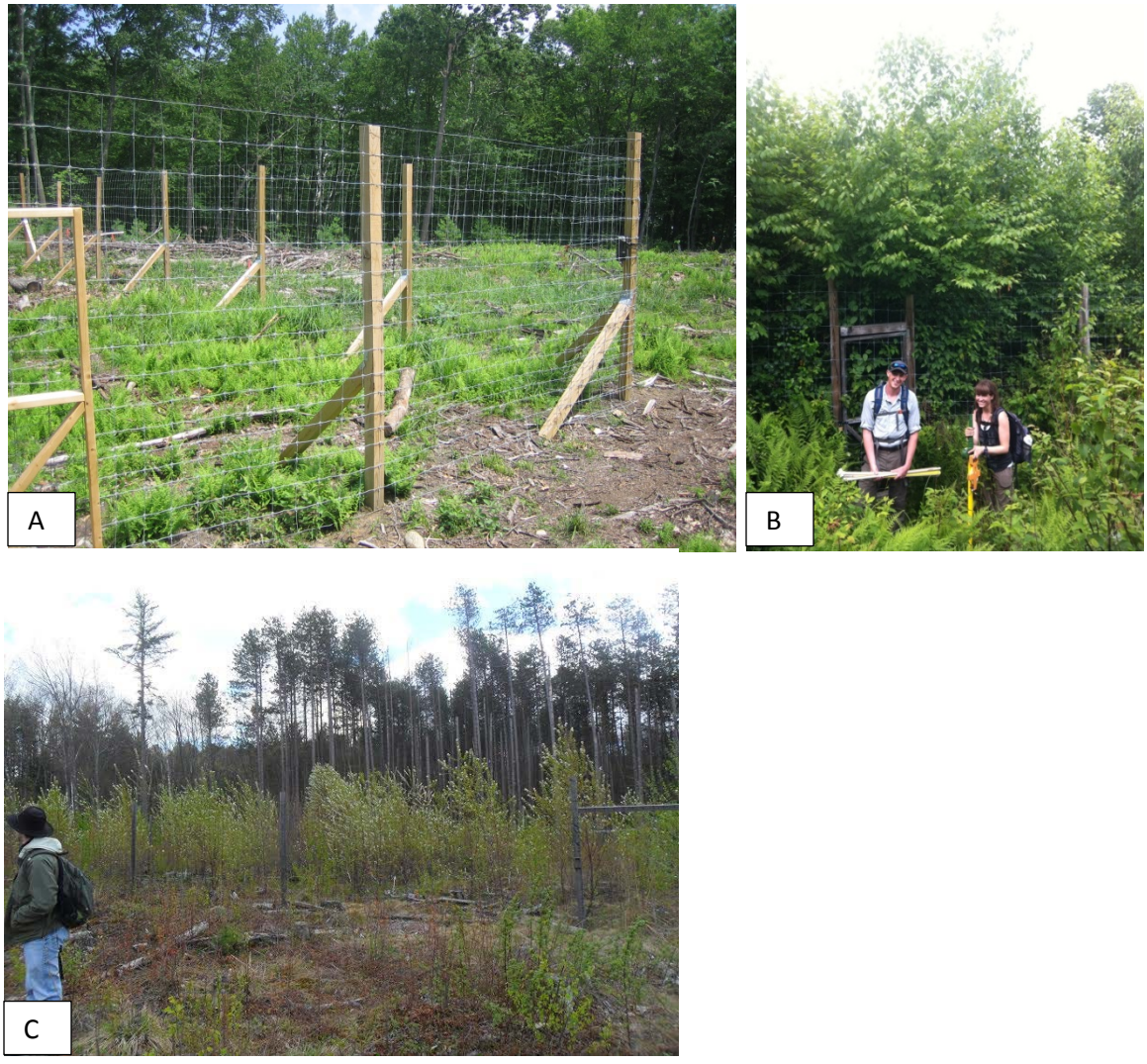


Figure 3.1 . Photos of tree recruitment. (A) full exclosure plot in 2008; and (B) the same plot 6 years later in 2014, with moose + deer browsed area in foreground; (C) Dominant *Prunus pensylvanica* in bloom inside full exclosure plot (in background) and largely suppressed or absent in foreground area browsed by moose + deer in 2012.

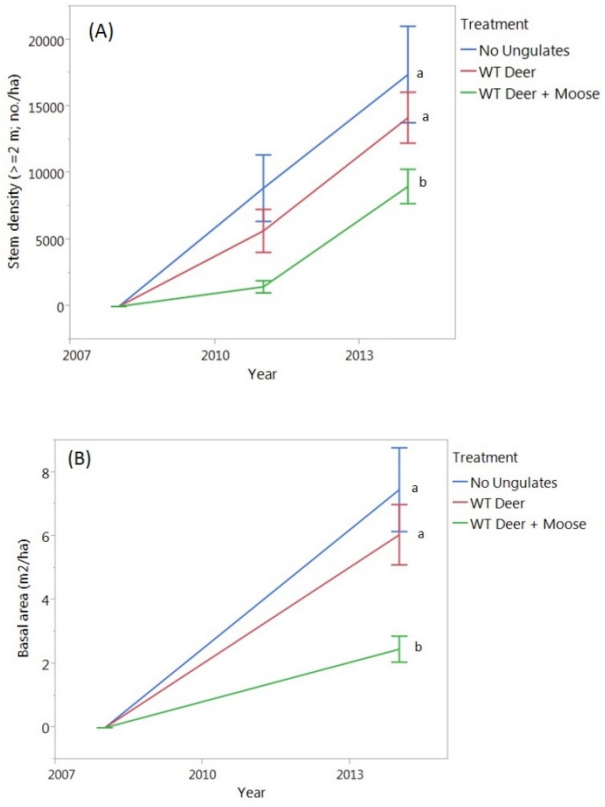


Figure 3.2. Effects of browsers on (A) woody stem density and (B) basal area for stems ≥ 2 m in height from 2008 to 2014. Differences among treatments were significant for density in both 201 1 (P = 0.0002) and 2014 (P = 0.014) and for basal area (only measured in 2014; P < 0.0001) as de termined by likelihood ratio tests. Treatment means with the same letter do not differ significantl y. Pairwise comparisons for density were the same in 2011 and 2014. Bars represent mean ± SE.

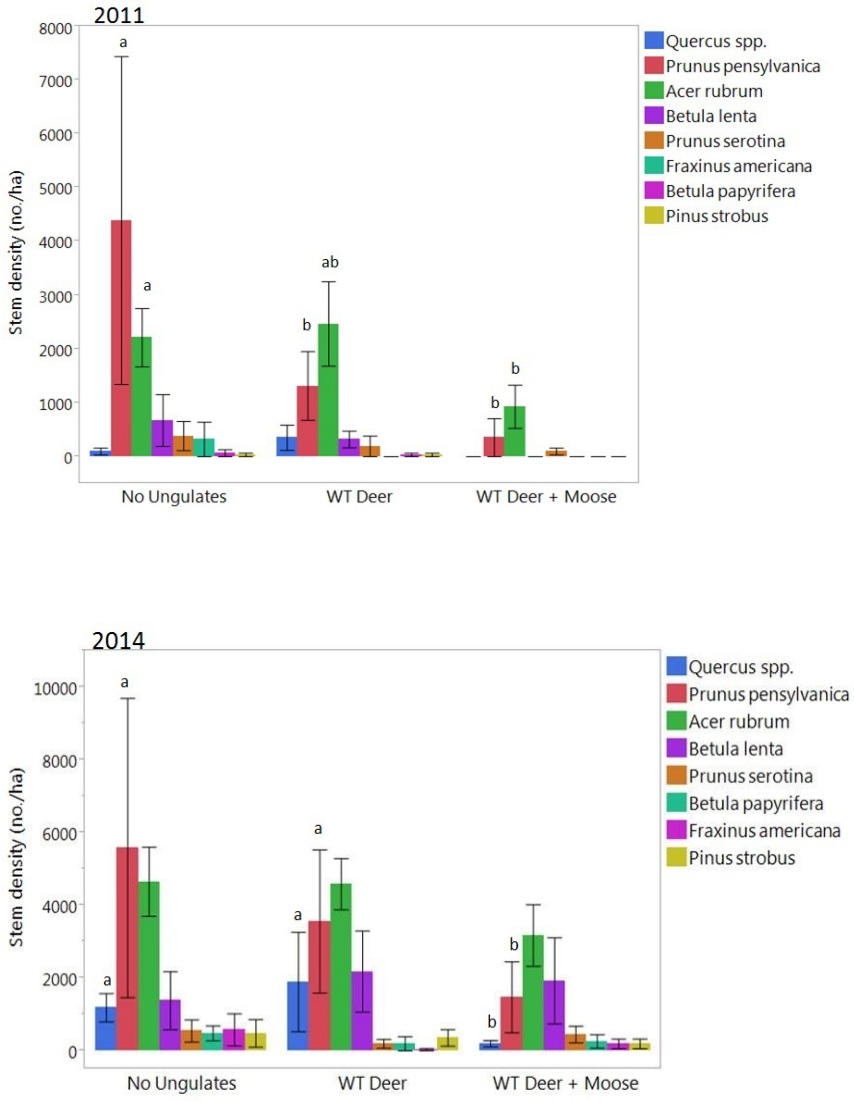


Figure 3.3 Effect of browsers on the recruitment density of common tree taxa above 2 m in height in 2011 (top) and 2014 (bottom). *Prunus pensylvanica* differed significantly by treatment in both years (P = 0.01), *Acer rubrum* differed significantly in 2011 (P = 0.05) and *Quercus* spp. (combined *Q. rubra*, *Q. velutina*, and *Q. alba*) differed significantly in 2014 (P = 0.04) as determined by Friedman rank tests. Bars represent mean ± SE. Treat ment means with the same letter do not differ significantly.

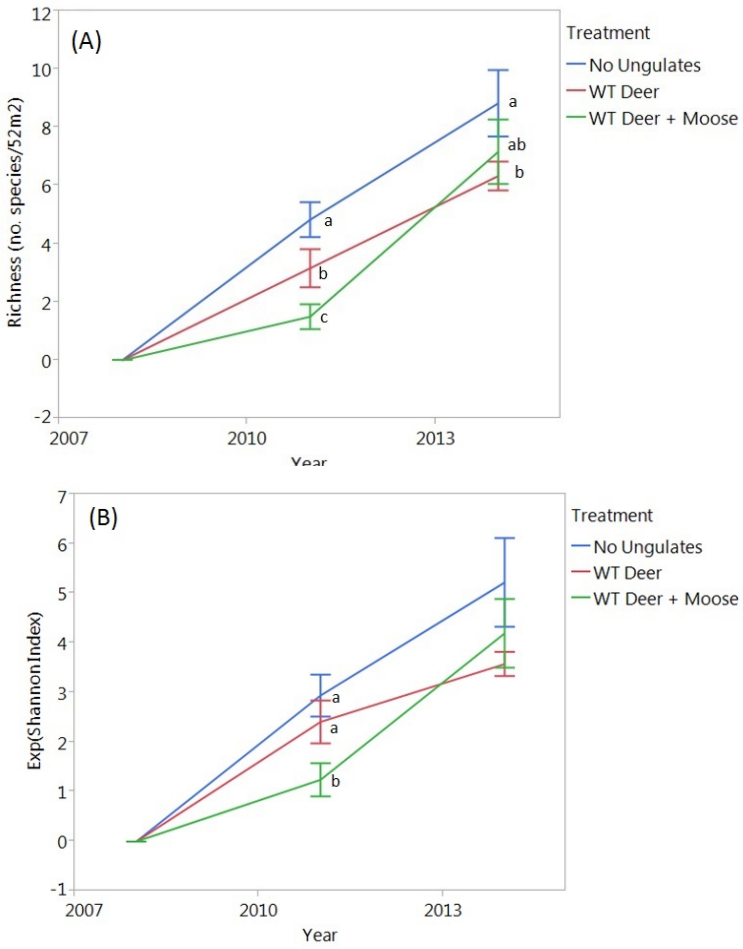


Figure 3.4 Effect of browsers on (A) species richness and (B) diversity of tall woody stems (≥2 m) in 2011 and in 2014. Richness differed significantly by treatment in 2011 (P = 0.0003) and in 2014 (P = 0.04), and diversity differed by treatment only in 2011 (P = 0.002). Bars represent mean ± SE. Treatment means with the same letter do not differ significantly.

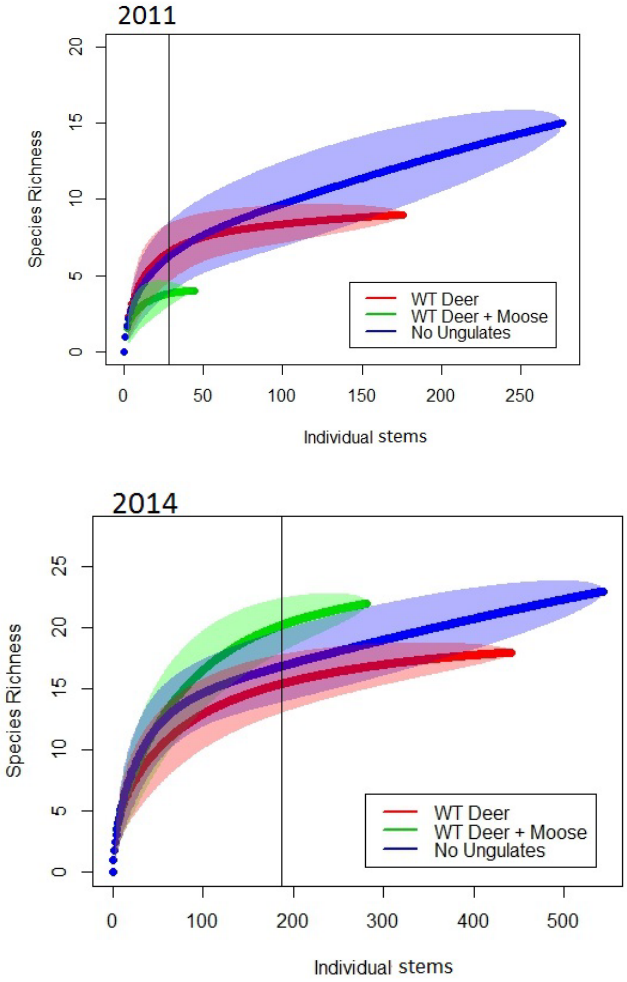


Figure 3.5 Individual based rarefaction curves (rarefied richness) by browser treatment in 2011 (l eft) and 2014 (right). Vertical lines represent number of individual stems at which one treatment diverged from another as determined by non-overlapping 95% confidence intervals (Gotelli and E llison 2013).

CHAPTER 4

LONG-TERM DEER EXCLUSION HAS COMPLEX EFFECTS ON DIVERSITY AND COMPOSITION IN A SUBURBAN HARDWOOD FOREST

4.1 Abstract

Deer herbivory is one of the leading biotic disturbances on forest herbaceous layers (i.e. herbs, small shrubs, and small tree seedlings). A large body of research has reported declines in height, abundance, and reproductive capacity of forbs and woody plants coupled with increases in abundance of graminoids, ferns, and exotic species from deer herbivory. Less clear is the extent to which (and the direction in which) deer alter herbaceous layer diversity, where much of the plant diversity in a forest occurs. We examined the effect of 15 years of deer exclusion on the understory of a suburban hardwood forest in Connecticut exposed to decades of intensive herbivory by white-tailed deer (*Odocoileus virginianus*). We used a block design with two treatments (fenced and unfenced) to compare species richness (at subplot and plot scale), abundance, structure, and composition between browsed and unbrowsed plots.

Forbs were more than twice as abundant in fenced than in unfenced plots, whereas sedges were 28 times more abundant and total exotic cover generally higher in unfenced than exclosure plots. Native and exotic species richness were both higher in grazed than ungrazed plots at the subplot scale, and native herbaceous richness was higher in grazed plots at both spatial scales; in contrast, native shrub richness increased with deer exclusion at the plot scale. My results suggest that deer exclusion has contrasting effects on species richness depending on plant functional group (i.e. low herbs vs taller shrubs), but that overall richness of both exotic and native plants declined with deer exclusion in this suburban hardwood forest. Neither high densities of deer,

nor the absence of deer, can be assumed to have uniformly “negative” or “positive” effects on forest understories.

4.2 Introduction

It is well established that intensive herbivory by cervids has powerful effects on herbaceous layers (i.e. herbs, small shrubs, and small tree seedlings) in northern forests (Cote et al. 2004; Waller 2014). Browsing induced declines in height, abundance, and reproductive capacity of forbs and woody plants coupled with increases in abundance of graminoids, ferns, and exotic species have been reported by many authors (Cote et al. 2004, Eschtruth and Battles 2009, Rooney 2009, Frerker et al. 2014, Nuttle et al. 2014). Less clear is the extent to which (and the direction in which) deer alter herbaceous layer diversity, where much of the plant diversity in forests occur (Gilliam 2007). This uncertainty is due in part to the relatively few studies that have examined cervid effects on herbaceous plants (Royo et al. 2010, Roberts and Gilliam 2014), but also to the varied results that have been reported. Studies from regions with long histories of high deer densities reported declines in diversity from herbivory (Putman et al. 1989, Rooney et al. 2003, Webster et al. 2005, Goetsch et al. 2011). Other authors reported increases in diversity with cervid herbivory (Royo et al. 2010, Perrin et al. 2011, Hegland et al. 2013, Roberts and Gilliam 2014). Still others reported no significant effect by white-tailed deer on diversity or richness (Webb et al. 1956, Kraft et al. 2004, Rooney 2009). Given that global loss of biodiversity is of critical concern today and that herbivory by large herbivores is one of the most important biotic disturbances influencing vegetation composition and structure (Hegland et al. 2013, Borer et al. 2014), a better understanding of how forest herbaceous layer diversity is shaped by cervids is needed.

The direction in which cervids drive diversity appears in some cases to be determined by animal density and forest disturbance. Low to moderate deer densities (5-8 deer km^{-2}) interacting

with forest disturbance (treefall gaps and ground fire) resulted in greater herbaceous plant diversity (Royo et al. 2010), whereas high deer densities (≥10-15 deer km^{-2}) in intact forests resulted in declines in diversity (Goetsch et al. 2011). However, in other intact forests exposed to even greater animal densities (18-82 deer km^{-2}), herbaceous layer diversity increased with browsing (Perrin et al. 2011). Other studies suggest that the direction in which diversity is altered by herbivory depends on plant functional group and height. Ungulates may reduce the diversity of relatively tall woody plants (i.e., shrubs and tree saplings), but increase the diversity of small herbs and small tree seedlings by reducing competition, creating spatial heterogeneity through trampling and excreta, and dispersing seeds (Risenhoover and Maass 1987, Hester et al. 2006, Kuijper et al. 2010, Hegland et al. 2013). Although deer are known to facilitate the invasion of certain exotic species and increase overall exotic plant abundance (Eschtruth and Battles 2009, Frerker et al. 2014), the extent to which deer impact exotic plant diversity either directly or indirectly (e.g., by reducing native diversity) is not well documented. Collectively these results suggest that the direction in which cervids are apt to drive native and exotic diversity in a particular forest is complex and difficult to predict.

Here we examine the effects of 15 years of white-tailed deer (*Odocoileus virginianus*) exclusion on the herbaceous layer of a small suburban forest patch in southwestern, CT, USA. Severe browse lines have been noted for several decades in this landscape, suggesting strong reductive effects by deer on the understory flora. Because significant reductions in plant biomass from browsing do not necessarily correspond with a decline in diversity (Ritchie and Olff 1999) – indeed diversity and woody plant biomass are often inversely related (Royo et al. 2010, Roberts and Gilliam 2014) – we asked the following questions: (1) has long-term exclusion of deer reduced or increased the diversity of native and exotic species in this temperate forest patch; (2) has deer exclusion had opposing effects on native diversity in which shorter plant functional

groups declined and larger functional groups increased (Hegland et al. 2013)? (3) How has deer exclusion altered overall herbaceous layer composition, structure, and abundance?

4.3 Materials and Methods

The study was conducted at Highstead, a 60 hectare woodland preserve in southwestern Connecticut. Deer densities in southwestern CT (SWCT) have been high since the mid to late 1980s, and for the past three decades SWCT has supported the highest deer densities in the state and among the highest densities in Southern New England (Gregonis 2000, Adams et al. 2009, Kilpatrick 2009, SCWDS 1982). Estimates of 21-24 deer km^{-2} were reported near Highstead between 2009 and 2013 (Kilpatrick 2013). Observations by preserve staff members from 1998-2009 suggest that local deer densities at Highstead may have previously been higher, with crude estimates ranging from 33-49 deer km^{-2}.

The study was located in a red maple (*Acer rubrum*)-white ash (*Fraxinus americana*) forest with the shrub and herb layer dominated by Japanese barberry (*Berberis thunbergii*), northern spicebush (*Lindera benzoin*), and various graminoid species including sweet wood-reed (*Cinna arundinacea*), white cut grass (*Leersia virginica*), and sedges (*Carex* spp.). Over the past 8-10 years the exotic Japanese stiltgrass (*Microstegium vimineum*) has rapidly invaded the woodland and has become one of the dominant herbaceous species. Tree sapling recruitment above 30 cm in height is very sparse from decades of herbivory, but very small tree seedlings below this height remain common, especially white ash. The site is positioned below a prominent drumlin that rises 35-40 m in elevation approximately 400 m to the east. The topography is gently sloping, and the fine sandy loam soils range from wet to mesic (poorly to moderately well-drained) and are acidic (pH: 4.5-5; Faber 2008). This forest was cleared historically for pasture in the 18th and 19th centuries, and the land reverted back to forest in the early to mid-20th century.

The combination of past land use history, moist soils, and proximity to residential development has resulted in a forest heavily invaded by exotic species (cf. DeGasperis and Motzkin 2007).

One large deer exclosure, 2.1 meters high, 0.40 ha in size (120 x 35 m) was erected in 1998. The upslope half of the exclosure and adjacent unfenced area were located on level ground with poorly drained soils (hereafter "wet" block), whereas the lower half of the fence and control plot were positioned on gently sloping and moderately well drained soils (hereafter "mesic block"). The two blocks have distinct forest ages, due to different timing of pasture abandonment. The wet block stand is about 50-55 years old and the mesic block stand approximately 80-90 years old. The wet block is located approximately 50-75 meters from the edge of a large meadow on the drumlin. Because the exclosure was originally constructed for demonstration purposes, no baseline herbaceous layer data were gathered. Given the size of the exclosure and the discrete environments at opposite ends of the fence, we decided to use a two-replicate block design with deer exclusion as treatment and soil type/forest age as block to examine the vegetation in the fenced and unfenced area after 15 years of deer exclusion. Although technically this constituted pseudoreplication because replicates within the single large exclosure were not independent (Hurlburt 1984), my plots in the two blocks were located 75-100 m apart and thus functioned more as independent replicates. We chose to apply a relatively conservative approach using an N = 2 rather than treating many subplots from the single exclosure as replicates (cf., Goetsch et al. 2011).

In 2013, we established 13 1-m^2 subplots along five successive parallel transect lines within larger 20 x 20 m treatment plots (cf. Frerker et al. 2014). Plots (both exclosure and control) were positioned 5-6 meters from the fence edge at the upper and lower ends of the exclosure. Three subplots were positioned on the two outer and middle rows, and two subplots in the 2^{nd} and 4^{th} rows. Subplots were 6 m apart within the same row and 4.5 meters apart between rows. At each 1 x 1 m subplot, all vascular plants in the herbaceous layer were recorded by the

first author and a botanical expert in the region, William Moorhead. We defined "herbaceous layer" as all plants <2 m in height (Oliver and Larson 1996; Carson et al. 2014). Percent aerial cover was estimated for each species and for each plant group (i.e., woody plants, graminoids, and forbs) in one of 7 cover classes (1 = <1%, 2 = 1-5%, 3 = 6-15%; 4 = 16-25%, 5 = 26-50; 6 = 51-75%, 7 = 76-100%). In addition we performed a 15 minute "meander" survey throughout the entire 400 m^2 area of each plot and recorded the presence of all woody and herbaceous plant species that did not occur in the subplots (Huebner et al. 2007, Goetsch et al. 2011). Nomenclature followed Haines (2011).

We used linear mixed effects models (package lmer, R Statistical software) with ungulate treatment as fixed effect and block as random effect to examine the response of species richness, composition, and abundance to deer herbivory. Before analysis, we converted cover classes to percent cover midpoints, and then calculated the mean percent cover for species and species group across the 13 1-m^2 subplots in each plot as my measure of abundance. We examined species richness at two scales in each plot: subplot (mean number of species per 13 1-m^2 quadrat) and plot (number of species 400 m^{-2}). Although these measurements are technically species density (Gotelli and Colwell 2001), we hereafter refer to species density as "species richness."

For each response variable we examined the residuals for normal and log normal models and selected the model that fit the data best (Zuur 2009). For hypothesis tests of treatment effects, we simulated the posterior distribution 10,000 times to calculate 95% confidence intervals and approximate P-values for the fixed effects (Bagchi et al. 2011, Rapp et al. 2013). To test for significant differences in community composition between treatments we used adonis (package vegan), the analysis of variance of distance measures (Bray), grouped by block (1000 permutations; Oksanen et al. 2015) Percent cover abundance for each species was entered into the multivariate test, and rare species that occurred in only 1 of the 4 treatment plots

were removed prior to analysis (McCune and Grace 2002). Data were analyzed using R statistical software, and alpha was set = 0.05.

4.4 Results

Across the four plots in two blocks, 112 native vascular plant species were recorded, of which 85 were native and 27 exotic. Growth forms included 6 ferns, 37 forbs, 28 graminoids, 15 trees, 20 shrubs, and 6 lianas. Fifty-four species were common to both treatments; 27 species were found only in the fenced plots and 31 species were found only in the unfenced plots. Species composition did not differ significantly by treatment as determined by multivariate analysis (Adonis: $F = 1.412$ $R^2 = 0.41$; $P = 0.5$). Still, important compositional and structural differences emerged between treatments after 15 years. Forbs were more than twice as abundant in fenced than unfenced plots (Treatment = -0.06; 95% CI = -0.103 to -0.015; P = 0.031), and ferns were 12 times more abundant in fenced than unfenced plots. Ferns only occurred in the mesic block, precluding statistical comparison. White wood-aster (*Eurybia divaricata*) and jewelweed (*Impatiens capensis*) were dominant forbs in the wet block exclosure plot, and broad-leaved enchanter's-nightshade (*Circaea canadensis*) was the dominant forb in the mesic block exclosure plot. In contrast, sedges (*Carex* spp.) were 28 times more abundant in grazed than exclosure plots (Treatment = 3.78; 95% CI = 1.2 to 6.48; P = 0.023). Graceful sedge (*Carex gracillima*) was the dominant sedge in the lower block control plot, and eastern star sedge (*C. radiata*) the dominant sedge in the wet block control plot. Total graminoid abundance also trended higher in unfenced plots (by a factor of 8; P = 0.12). Total woody plant abundance (combined native and exotic) was similar between treatments (Table 1), but native woody abundance (P = 0.13) was almost twice as high in fenced compared to grazed plots. Tree seedling abundance was also more than twice as high, on average, in exclosure plots compared to grazed

plots (P = 0.15; Table 1). Total native plant abundance remained similar between the two treatments (Table 1).

Total exotic plant abundance was marginally higher in unfenced than fenced plots (P = 0.06). Over 70% of exotic species abundance was comprised of Japanese barberry, which was approximately three times more abundant in grazed than fenced plots (P = 0.08). Japanese stilt grass was the second most important exotic in the grazed plots, comprising 14% of the exotic flora abundance; this species was absent from exclosure plots. Two major exotic species trended higher inside the fences. Asian bittersweet (*Celastrus orbiculatus;* P = 0.15), was almost four times more abundant and burning-bush (*Euonymus alatus;* P = 0.095) approximately 12 times more abundant in plots protected from browsing (Table 1).

Effect on species richness- plot scale (400m^2)

Total species richness trended higher in unfenced (62 species; SE = 4) than fenced plots (54.5 species; SE = 9.5), but the difference was not significant (P = 0.318). Almost 10 more native species, on average, were sampled in unfenced than fenced plots, a marginally significant difference (P = 0.066; Fig. 2). Native herbaceous richness was significantly higher in unfenced plots, with 12 more species on average, than in fenced plots (Treatment = 12; 95% CI = 7.54 to 16.58; P = 0.007; Fig. 2). In contrast, native shrub richness was lower in grazed plots by almost 3 species, on average, compared to exclosure plots (Treatment = -0.25; 95% CI = -4.71 to -0.42; P = 0.036; Fig. 2). Exotic species richness, native forb richness and native woody richness did not differ between treatments (P> 0.10; Fig. 2).

Effect on species richness-subplot scale (1m^2)

Total species richness was lower in deer excluded plots (7.7 species; SE = 0.43) than in unfenced plots (10.8 species; SE = 0.31; Treatment = 0.33; 95% CI = 0.06 to 0.59; P = 0.031). Both native species (Treatment = 2.27; 95% CI = -0.11 to 4.52; P = 0.053) and exotic species richness (Treatment = 0.615; 95% CI = 0.22 to 1.01; P = 0.020) were significantly greater in

unfenced than fenced plots (Fig. 3). Grazed plots had over two more native herbaceous species, on average, than did deer excluded plots (Treatment = 0.55; 95% CI = 0.38 to 0.715; P = 0.004; Fig. 3). Native forb richness also trended higher in unfenced than fenced plots (P = 0.094). Neither native woody nor native shrub richness differed between treatments. P>0.10; Fig. 3).

4.5 Discussion

Fifteen years of white-tailed deer exclusion resulted in both predictable and complex effects on plant diversity, composition, abundance, and exotic plant dynamics in the herbaceous layer of a red maple-white ash forest. Overall, species richness of native and exotic plants was lower in deer excluded plots; however, deer exclusion had opposing effects on the richness of different plant functional groups (cf. Hegland et al. 2013). Native herbaceous richness was lower with deer exclusion at both the plot ($400m^2$) and subplot ($1m^2$) scale, whereas native shrub richness increased with deer exclusion at the plot scale. My results suggest that relatively diverse communities of both native and exotic plants may coexist under high deer densities ($\geq$21-24 km^{-2}) in this suburban forest, and that native herb richness may decline (and shrub richness increase) when herbivory is removed (cf. Perrin et al. 2011, Goetsch et al. 2011, Hegland et al. 2013).

Many of my results from this local study corroborated broad-scale and well documented deer-forest relationships. Long-term exclusion of deer resulted in greater forb abundance and much lower sedge abundance compared to areas intensively grazed by deer (cf. Rooney 2009, Waller 2014). Deer exclusion also resulted in reduced exotic species richness at the subplot scale and perhaps reduced exotic abundance at the plot scale (P = 0.06), including a three-fold reduction in abundance of the shrub, Japanese barberry, and the absence of the grass, Japanese stiltgrass, relative to grazed plots (Fig. 1; cf. Eschtruth and Battles 2009, Frerker et al. 2014).

Interestingly, however, greatly reduced sedge abundance and exotic species richness with deer exclusion were associated with lower richness of native herbaceous plants compared to

grazed areas. Greater exotic species and graminoids are generally assumed to result in lower herbaceous richness (Baiser et al. 2008, Waller 2014); however, my results corroborate recent studies that show little negative effect by graminoids, Japanese barberry, and other exotic plants on native plant richness (Rooney 2009, Flinn et al. 2014, Thomas and Palmer 2015). Indeed, native and exotic plant richness may simultaneously increase in response to similar environmental gradients (Gilbert and Lechowitz 2005). In my study area, heavy grazing and activity by deer appeared to create the open niches, reduced competition, and disturbed soil – and perhaps disperse the seeds – for a relatively high number of both native herbaceous and exotic plant species to germinate and become established (Olff and Ritchie 1998, Myers et al. 2004, Hester et al. 2006). Although deer exclusion seems more apt to reduce herbaceous layer richness in areas with low to moderate cervid densities in disturbed (e.g., logging, fire, and treefall gaps) habitats – and promote richness in landscapes with high deer densities in undisturbed habitats (Royo et al. 2010; Nuttle et al. 2014, Goetsch et al. 2011) – my results suggest that under certain conditions deer exclusion can also reduce plant richness in intact stands with high deer densities (cf. Perrin et al. 2011).

One of the reasons for the relatively high herbaceous richness in the grazed plots was the presence of a large diversity of sedge species rather than a single dominant species. Nine species of *Carex* occurred in grazed plots that did not occur in fenced plots. Sedges are generally resistant to herbivory and trampling by ungulates because of continuous growth from basal meristems; they are also less preferred forage for deer than are forbs, and many sedge species thrive in high-light environments (Renecker and Schwartz 1997, Haines 2011, Waller 2014). Indeed, sedges were almost completely absent below the densely shaded spicebush subcanop*y* in the mesic block fenced plot. Reduced native herb richness with deer exclusion did not appear to be driven exclusively by sedges, however, as native forb richness also trended lower with deer exclusion at the subplot scale ($P = 0.09$).

In contrast to reduced native herbaceous richness in deer excluded plots was greater native shrub richness (~3-fold) at the plot scale with deer exclusion. Uncommon species such as round-leaved dogwood (*Swida rugosa*), gray dogwood (*Swida racemosa*), black elderberry (*Sambucus nigra*), and nannyberry (*Viburnum lentago*) were found only inside the exclosures. This result is consistent with the literature that intensive cervid herbivory may have opposing effects on the richness of different plant functional groups (i.e., small herbs and tall shrubs; Hegland et al. 2013). Tree species richness below 2 m was notably unaffected by deer exclusion in my study area and may be explained by the fact that my sampling lumped tree seedlings of all sizes < 2m together. Opposing effects on tree richness can occur on different size classes (i.e., richness or diversity of larger tree saplings is reduced and richness of smaller tree seedlings sometimes increases (Kuijper et al. 2010, Hegland et al. 2013). Additional sampling that we conducted on tree sapling recruitment (stems 30 cm–2 m in height) appeared to support this notion, as deer excluded plots contained 2.5X the number of tree species, on average, as grazed plots (Faison et al. *Unpublished Data*).

Despite the reductive effects of deer exclusion on exotic species richness and perhaps abundance, the relationship between deer exclusion and exotic species was not straightforward. Two dominant exotic shrubs/lianas, burning-bush and Asian bittersweet, had much higher (though non-significant) abundances inside exclosures than in grazed plots (Table 1); in fact, these two species were the dominant woody plants in the wet block exclosure plot. Thus, some palatable exotic species appear to benefit from deer exclusion, while other unpalatable/browse tolerant ones such as Japanese barberry, Japanese stiltgrass, and garlic mustard (*Alliaria petiolata*) tend to benefit from deer grazing (Eschtruth and Battles 2009). Exotic richness was clearly reduced by deer exclusion at the subplot scale but was unaffected at the plot scale. The latter result can be explained by a number of uncommon and apparently browse-sensitive exotic woody plants that were found only in the exclosure plots, including sweet cherry (*Prunus avium*),

Norway maple (*Acer platanoides*), and autumn-olive (*Eleagnus umbellata*). These results suggest that deer exclusion can provide protection for some exotic species in heavily browsed forests that would otherwise be eliminated or greatly reduced by herbivory. In contrast, herbivore exclusion – perhaps by reducing small scale soil disturbance, niche openings, and seed dispersal on the forest floor by deer – can reduce exotic richness at smaller spatial scales.

My results revealed the powerful ecological effects of 15 years of deer exclusion on the herbaceous layer of a suburban forest exposed to decades of intensive deer herbivory. Deer exclusion generally reduced species richness of both exotic and native species, but increased native shrub richness, revealing contrasting effects of herbivore exclusion on the richness of different plant functional groups. Deer exclusion also had predictable and complex effects on composition, structure, and exotic species dynamics at different spatial scales in this woodland. In other words the effects of deer exclusion were both "positive" and "negative" on this plant community; and therefore deer, even at high densities, cannot be assumed to have uniformly negative impacts on forest understories.

Table 4.1 Mean abundance of common plant species and growth form groups in the herbaceous layer (<2m in height) by treatment in 2013. Only species that occurred in at least 2 of the 4 treatment plots are included. Standard errors are in parentheses. *P ≤0.05

Species	Native	Fenced	Unfenced
Woody plants		36.1 (2.6)	32.3 (0.02)
Trees		5.6 (2.9)	2.1 (1.4)
Acer rubrum	N	0	0.10 (0.02)
Fraxinus americana	N	2.73 (0.27)	1.94 (1.4)
Liriodendron tulipifera	N	0.79 (0.79)	0.02 (0.02)
Prunus serotina	N	1.44 (1.2)	0
Shrubs and lianas			
Berberis thunbergii	E	6.4 (0.73)	20.8 (4.2)
Celastrus orbiculatus	E	8.2 (3.88)	2.1 (0.5)
Euonymus alatus	E	4.5 (2.1)	0.42 (0.38)
Ilex verticillata	N	0.25 (0.02)	0.06 (0.06)
Lindera benzoin	N	8.1 (7.9)	4.0 (3.96)
Parthenocissus quinquifolia	N	0.56 (0.29)	1.36 (1.3)
Rosa multiflora	E	0.13 (0.10)	0.37 (0.14)
Rubus flagellaris	N	0.64 (0.64)	0.52 (0.29)
Rubus phoenicolasius	E	0.56 (0.25)	0.12 (0.12)
Toxicodendron radicans	N	0.56 (0.52)	0.11 (0.04)
Vitis nova angliae	N	0.12 (0.12)	0.17 (0.10)
Graminoids		3.0 (2.97)	24.3 (17.3)
*Carex total**		0.6 (0.54)	16.8 (10.7)
Carex gracillima	N	0	1.1 (0.67)
Carex intumescens	N	0	0.42 (0.38)
Carex laxiculmis	N	0	0.77 (0.27)
Carex radiata	N	0.54 (0.54)	12.8 (11.7)
Carex swanii	N	0.02 (0.01)	0.69 (0.12)
Cinna arundinacea	N	1.2 (1.2)	2.1 (1.62)
Dactylis glomerata	E	0.12 (0.12)	0.02 (0.02)
Glyceria striata	N	0.14 (0.14)	0.40 (0.40)
Leersia virginica	N	0.40 (0.40)	0.12 (0.12)
Microstegium vimineum	E	0	3.94 (3.9)
Forbs*		11.0 (1.42)	5.1 (0.39)
Arisaema triphyllum	N	0.63	0.50 (0.46)
Circaea canadensis	N	2.1 (2.1)	0.12 (0.12)
Eurybia divaricata	N	3.1 (3.0)	0.6 (0.1)
Galium triflorum	N	0	0.15 (0.08)
Geum spp.	N	0	0.13 (0.10)
Impatiens capensis	N	1.8 (1.8)	0.14 (0.14)
Maianthemum canadense	N	0.52 (0.52)	0.65 (0.04)
Mitchella repens	N	0	0.13 (0.10)
Oxalis stricta	N	0.08 (0)	0.06 (0.06)
Persicaria longiseta	E	0.06 (0.06)	0.11 (0.08)
Persicaria sagittata	N	0.06 (0.06)	0.93 (0.93)
Ranunculus recurvatus	N	0.02 (0.02)	0.04 (0.02)
Trillium erectum	N	0.27 (0.27)	0.02 (0.02)
Viola sororia	N	0.02 (0.02)	0.68 (0.67)

Ferns		6.3 (6.3)	0.52 (0.52)
Polystichum acrostichoides	N	2.25 (2.25)	0.5 (0.52)
Exotic total		21.4 (6.9)	28.7 (8.8)
Native total		35.1 (6.25)	33.4 (8.35)

Figure 4.1 Photos of the four treatment plots in 2013. (A) Wet block unfenced plot dominated by graminoids (*Microstegium vimineum* and *Carex radiata*) and *Berberis thunbergii*; (B) wet block fenced plot dominated by *Eurybia divaricata-Impatiens capensis* and shrub layer of *Celastrus orbiculatus* and *Euonymus alatus* (C) Mesic block unfenced plot with sparse herb layer and *Berberis thunbergii-Lindera benzoin* shrub layer; and (D) mesic fenced plot dominated by dense *Lindera benzoin* shrub layer.

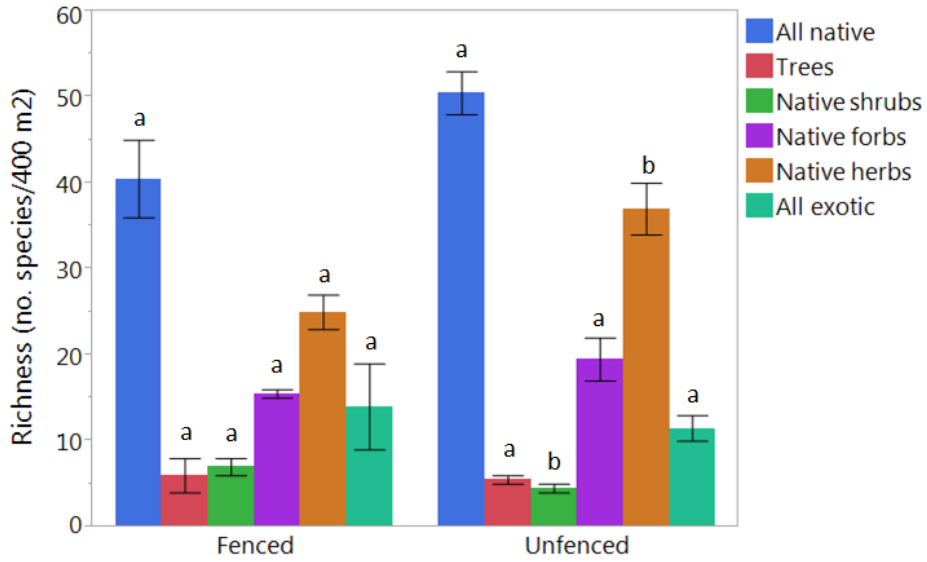


Figure 4.2 Contrasting effects of deer exclusion on species richness <2 m in height at the plot scale (no. species/400m^2). Native herbaceous richness was higher in unfenced plots, and native shrub richness was higher in fenced plots. Bars represent mean ± SE. Treatment means with the same letter do not differ significantly at P ≤0.05.

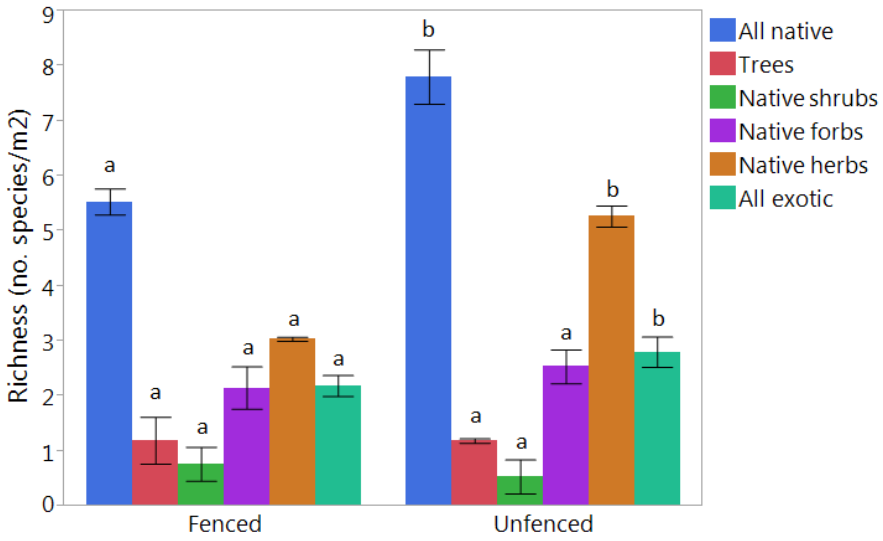


Figure 4.3 Effects of deer exclusion on native and exotic species richness <2 m in height at the subplot scale (mean no. of species in 13, $1m^2$ subplots in each plot). Bars represent mean ± SE. Treatment means with the same letter do not differ significantly at $P \leq 0.05$.

CONCLUSION

Ungulate browsers had both predictable and complex effects on the regeneration and composition of New England temperate forests. Herbivores, regardless of density or number of species, generally reduced tree regeneration abundance and recruitment (Chs. 3 and 4; cf. Gill 2006). However, large variations in tree densities that developed over time in different stand disturbance types (simulated HWA attack, logging, intact forest), altered the functional response of herbivores and mitigated browsing effects (Ch.1; cf. McLaren et al. 1994, Schmitz and Sinclair 1997). The effects of herbivores on tree richness were complex and depended on the timing and growth stage of the regeneration and the number and selectivity of the browser species (Chs. 3 and 4).

In logged forests, moose + deer reduced the abundance of a dominant pioneer species (pin cherry [*Prunus pensylvanica*]) and a later successional dominant taxon (oaks [*Quercus* spp.]; Ch. 3). By reducing the former species, browsers appeared to accelerate the transition of pioneer toward more shade tolerant tree species (Ch. 3). By reducing the latter taxon, moose + deer appeared to favor more browse tolerant species such as black birch (*Betula lenta*) and red maple (*Acer rubrum*). Overall, browsers, by reducing tree recruitment, slowed down succession in logged stands, reducing the abundance of herbs and shrubs associated with forest habitat and maintaining shrubs and herbs associated with open/disturbed habitats (Ch. 2).

Browsers generally increased herbaceous plant richness in both logged and unlogged forest, although low levels of herbivory by deer ($\leq$4-5 deer km^{-2}) in logged forests had little effect (Chs. 2 and 4; cf. Olff and Ritchie 1999). Forb cover declined significantly with high deer densities in intact forest, but remained unchanged in response to low densities of deer + moose in recently logged forest. Sedge abundance and richness generally increased with browsing across all stand and herbivore assemblages. Somewhat unexpectedly, fern abundance was generally higher with protection from herbivores in both logged and intact stands (Chs. 2 and 4), although

this pattern has been noted by other authors (Rooney 2009). Shrub richness and abundance (<2 m in height) increased with the addition of a second herbivore in disturbed patch cuts, but native shrub richness declined with intensive herbivory in intact forest (Chs. 2 and 4). The direction in which species richness was altered by browsing in the intact forest depended on the plant functional group (i.e., shrub richness declined, but herb richness increased; cf. Hegland et al. 2013). Exotic species richness and abundance was also higher in areas exposed to deer in the intact forest, but certain exotic shrubs appeared to benefit from protection by browsers (Ch. 4). Probable mechanisms driving increased plant richness in the presence of herbivores include reduced plant competition and increased available light from browsing along with increased soil disturbance, spatial heterogeneity, and germination sites from herbivory and trampling (Olff and Ritchie 1998, Hester et al. 2006. Royo et al. 2010).

My results highlight the importance of examining browsing impacts across a broad range of ungulate densities, and (when feasible) with multiple browser treatments, in order to accurately assess and generalize vegetation changes that are important for habitat and ecosystem services (Oliver and Larson 1996, Diaz et al. 2007). Effects of ungulates on certain aspects of vegetation composition (e.g., increased sedge abundance, reduced tree recruitment, decline in oak regeneration) appear to be predictable and generalizable under most circumstances. However, complex and unexpected effects of browsing occurred on other aspects of the vegetation (e.g., species richness, fern, and *Rubus* abundance) making broad generalizations about certain ungulate-vegetation relationships problematic. A broad range of "positive" and "negative" outcomes on plant communities should be expected by large browsers at low densities in temperate forests.

BIBLIOGRAPHY

Abrams, M. D., and S. E. Johnson. 2012. Long-term impacts of deer exclosures on mixed-oak forest composition at the Valley Forge National Historical Park, Pennsylvania, USA. Journal of the Torrey Botanical Society 139:167–180.

Abaturov, B. D., and K. A. Smirnov. 2002. Effects of moose population density on development of forest stands in Central European Russia. Alces Supplement 2:1–5.

Adams, K., J. Hamilton, and M. Ross. 2009. QDMA's whitetail report 2009. Quality Deer Management Association, Bogart, USA.

Alverson, W. S., and D. M. Waller. 1988. Forests too deer: edge effects in northern Wisconsin. Conservation Biology 2:348–358.

Augustine, D. J., and L. E. Frelich. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. Conservation Biology 12:995–1004.

Bagchi, R., C. D. Philipson, E. M. Slade, A. Hector, S. Phillips, J. F. Villanueva, O. T. Lewis, C. H. C. Lyal, R. Nilus, A. Madran, J. D. Scholes, and M. C. Press. 2011. Impacts of logging on density-dependent predation of dipterocarp seeds in a South East Asian rainforest. Philosophical Transactions of the Royal Society B-Biological Sciences 366:3246–3255.

Baiser B., J. L. Lockwood, D. La Puma, and M. F. J. Aronson. 2008. A perfect storm: two ecosystem engineers interact to degrade deciduous forests of New Jersey. Biological Invasions 10:785–795.

Barrett, K. J., and O. J. Schmitz. 2013. Effects of deer settling stimulus and deer density on regeneration in a harvested southern New England forest. International Journal of Forestry Research. http://dx.doi.org/10.1155/2013/690213.

Bergeron, D. H., P. J. Pekins, H. F. Jones, and W. B. Leak. 2011. Moose browsing and forest regeneration: a case study in northern New Hampshire. Alces 47:39–51.

Bergstrom, R., and K. Danell. 1987. Effects of simulated winter browsing by moose on morphology and biomass of two birch species. Journal of Ecology 75:533–544.

Boer, A. H. 1997. Interspecific relationships. Pages 337–349 *in* A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American moose. Smithsonian Institution, Washington, D.C., USA.

Bolker, B. M. 2008. Ecological models and data in R. Princeton University Press, Princeton, USA.

Bond, W. J., and J. J. Midgley. 2001. Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology and Evolution 16:45–51.

Borer, E. T., E. W. Seabloom, D. S. Gruner et al. 2014. Herbivores and nutrients control grassland plant diversity via light limitation. Nature 508:517–520.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods and Research 33:261–304.

Brouillet, L., and R. D. Whetstone. 1993. Climate and physiography. Pages 15-46 *in* Flora of North America Editorial Committee, editors. Flora of North America north of Mexico.Volume 1, Introduction. Oxford University Press, New York, USA.

Carson, W. P., A. A. Royo, and C. J. Peterson. 2014. A pox on our land: a case study of chronic deer overbrowsing throughout the Allegheny National Forest region of Pennsylvania. Pages 400-411 *in* F.S. Gilliam, editor. The herbaceous layer in forests of eastern North America. Oxford University Press, New York, USA.

Cote, S. D., T. P. Rooney, J. P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113–47.

Cullina, M. D., B. Connolly, B. Sorrie, and P. Somers, 2011. The vascular plants of Massachusetts: A county checklist, first revision. Massachusetts Natural Heritage &

Endangered Species, Massachusetts Division of Fisheries and Wildlife. Westborough, USA.

DeGasperis, B.G., and G. Motzkin. 2007. Windows of opportunity: historical and ecological controls on *Berberis thunbergii* invasions. Ecology 88:3115–3125.

DeGraaf, R. M., and M. Yamasaki. 2001. New England wildlife: habitat, natural history, and distribution. University Press of New England, Hanover, USA.

Delong, S. C., and D. Tanner. 1996. Managing the pattern of forest harvest: lessons from wildfire. Biodiversity and Conservation 5:1191–1205.

Diaz, S., S. Lavorel, F. deBello, F. Quetier, K. Grigulis, and T. M. Robson. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. PNAS 104:20684–20689.

Edenius, L. 1991. The effect of resource depletion on the feeding behaviour of a browser: winter foraging by moose on Scots pine. Journal of Applied Ecology 28:318–328.

Ellison, A., and A. Barker Plotkin. 2005. Overstory vegetation in hemlock removal experiment at Harvard Forest since 2003. Harvard Forest Data Archive: HF126, Petersham, Massachusetts, USA.

Ellison, A., and A. Barker Plotkin. 2009. Coarse woody debris in hemlock removal experiment at Harvard Forest since 2005. Harvard Forest Data Archive: HF125, Petersham, Massachusetts, USA.

Ellison, A. M., A. Barker Plotkin, D. R. Foster, and D. A. Orwig. 2010. Experimentally testing the role of foundation species in forests: the Harvard Forest Hemlock Removal Experiment. Methods in Ecology & Evolution 1:168–179.

Eschtruth, A. K., and J. J. Battles. 2008. Deer herbivory alters forest response to canopy decline caused by an exotic insect pest. Ecological Applications 18:360–376.

Eschtruth, A. K. and J. J. Battles. 2009. A generalist herbivore accelerates exotic

plant invasion in a forested ecosystem. Conservation Biology 23:388–399.

Estes, J. A., J. Terborgh, J. S. Brashares et al. 2011. Trophic downgrading of planet Earth. Science 333:301-306.

Faber, M. 2008. Soil survey of the state of Connecticut. USDA Natural Resources Conservation Service.

Faison, E. K., G. Motzkin, D. R. Foster, and J. E. McDonald. 2010. Moose foraging in the temperate forests of southern New England. Northeastern Naturalist 17:1–18.

Fei, S, N. Kong, K. C. Steiner, W. K. Moser, and E. B. Steiner. 2011. Change in oak abundance in the eastern United States from 1980 to 2008. Forest Ecology and Management 262:1370–1377.

Flinn, K. M. 2014. Agricultural legacies in forest herb communities. Pages 438-444 *in* F. S. Gilliam, editor. The herbaceous layer in forests of eastern North America, 2nd edition. Oxford University, UK.

Flinn, K. M., J. L. Bechhofer and M. Malcolm. 2014. Little impact of the invasive shrub Japanese barberry (Berberis thunbergii DC) on forest understory plant communities. Journal of the Torrey Botanical Society 141:217-224.

Foster, D. R., G. Motzkin, D. Bernardos, and J. Cardoza. 2002. Wildlife dynamics in a changing landscape. Journal of Biogeography 29:1337–1357.

Foster, D., G. Motzkin, J. O'Keefe, E. Boose, D. Orwig, J. Fuller, and B. Hall. 2004. The environmental and human history of New England. Pages 43-100 *in* D. R. Foster and J.D. Aber, editors. Forests in time: the environmental consequences of 1000 years of change in New England. Yale University Press, New Haven, USA.

Forsythe, A. 1985. Mammals of the American north. Camden House, Ontario, Canada.

Frerker, K., G. Sonnier, and D. Waller. 2013. Browsing rates and ratios provide reliable indices of ungulate impacts on forest plant communities. Forest Ecology and Management 291:55–64.

Frerker, K. A. Sabo, and D. Waller. 2014. Long-term regional shifts in plant community composition are largely explained by local deer impact experiments. PLOS one DOI: 10.1371/journal.pone.0115843.

Geist, V. 1998. Deer of the world: their evolution, behavior, and ecology. Stackpole Books.

Gilbert, B. and M. J. Lechowitz. 2005. Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. Ecology 86:1848–1855.

Gill, R. 2006. The influence of large herbivores on tree recruitment and forest dynamics, Pages 170–202 *in* K. Danell, R. Bergstrom, P. Duncan, and J. Pastor, editors. Large herbivore ecology, ecosystem dynamics and conservation. Cambridge University Press, Cambridge, UK.

Gilliam, F. S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience 57:845–858.

Gilliam, F. S. 2014. Introduction: the herbaceous layer – the forest between the trees. Pages 1-9 *in* F. S. Gilliam, editor. The herbaceous layer in forests of eastern North America. Oxford University Press, New York, USA.

Godin, A. J. 1977. Wild mammals of New England. John Hopkins University Press, Baltimore, USA.

Goetsch, C., J. Wigg, A. A. Royo, T. Ristau, and W. P. Carson. 2011. Chronic over browsing and biodiversity collapse in a forest understory in Pennsylvania: results from a 60 year-old deer exclusion plot. Journal of the Torrey Botanical Society 138:220–224.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379–391.

Gotelli, N. J., and A. M. Ellison. 2013. A primer of ecological statistics, 2nd edition. Sinauer Associates, Sunderland, USA.

Gregonis. M. 2000. Aerial deer survey results indicate population is increasing. Connecticut Wildlife May/June:12.

Haines, A. 2011. New England Wild Flower Society's flora novae angliae: a manual for the identification of native and naturalized higher vascular plants of New England. New England Wild Flower Society, Framingham, USA.

Healy, W. M. 1997. Influence of deer on the structure and composition of oak forests in central Massachusetts. Pages 249–266 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance. Smithsonian Institution, Washington, D.C., USA.

Heckel, C. D., N. A. Bourg, W. J. McShea, and S. Kalisz. 2010. Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. Ecology 91:319–326.

Hegland, S. J., M. S. Leleeng, and S. R. Moe. 2013. Old-growth forest floor richness increases with red deer herbivory intensity. Forest Ecology and Management 310:267–274.

Hester, A. J., M. Bergman, G. R. Iason, and J. Moen. 2006. Impacts of large herbivores on plant community structure and dynamics, Pages 97-141 *in* K. Danell, R. Bergstrom, P. Duncan, and J. Pastor, editors. Large herbivore ecology, ecosystem dynamics and conservation. Cambridge University, Cambridge, UK.

Hibbs, D. E. 1983. Forty years of forest succession in central New England. Ecology 64:1394–1401.

Holladay, C. A., C. Kwit, and B. Collins. 2006. Woody regeneration in and around aging southern bottomland hardwood forest gaps: Effects of herbivory and gap size. Forest Ecology and Management 223:218–225.

Horsley, S. B., and D. A. Marquis. 1983. Interference by weeds and deer with Allegheny hardwood reproduction. Canadian Journal of Forest Research 13:61–69.

Horsley S. B., S. L. Stout, and D. S. deCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications 13:98–118.

Huebner, C. D. 2007. Detection and monitoring of invasive exotic plants: a comparison of four sampling methods. Northeastern Naturalist 14:183–206.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187–211.

Hunter, M. D. and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724–732.

Hunter, M. L. 1993. Natural fire regimes as spatial models for managing boreal forests. Biological Conservation 65:115–120.

Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. New Haven: Yale University Press, USA.

Jost, L. 2006. Entropy and diversity. Oikos 113:363–375.

Kantar, L. 2007. State of the Maine deer herd in Maine's working forest: a changing dynamic. Maine Department of Inland Fisheries and Widlife. http://umaine.edu/cfru/Events/Munsungan_DWA_12.07/Kantar_StatusofDeerHerd.pdf. Accessed 15 April 2015.

Kauppi, A., M. Kiviniitty, and A. Ferm. 1990. Leaf morphology and photosynthetic rate in birch seedlings and stump sprouts. Canadian Journal of Forest Research 20:952–960.

Kilpatrick, H. 2009. New estimates for deer densities in Fairfield County. Connecticut Wildlife May/June:3.

Kilpatrick, H. 2013. Hunting is lowering deer densities in Fairfield County. Connecticut Wildlife. May/June.

Kittredge, D. B., A. O. Finley, and D. R. Foster, 2003. Timber harvesting as ongoing disturbance in a landscape of diverse ownership. Forest Ecology and Management 180: 425–442.

Kohn, B. E., and J. J. Mooty. 1971. Summer habitat of white-tailed deer in north-central Minnesota. Journal of Wildlife Management 35:476–487.

Kraft, L. S., T. R. Crow, D. S. Buckley, E. A. Nauertz, and J. C. Zasada. 2004. Effects of harvesting and deer browsing on attributes of understory plants in northern hardwood forests, Upper Michigan, USA. Forest Ecology and Management 199:219–230.

Kuijper, D. P. J., J. P. G. M. Cromsigt, M. Churski, B. Adam, B. Jędrzejewska, and W. Jędrzejewski. 2009. Do ungulates preferentially feed in forest gaps in European temperate forests? Forest Ecology and Management 258:1528–1535.

Kuijper, D. P. J, J. Bogumił, B. Brzeziecki,M. Churski, W. Jędrzejewski, and H. Żybura. 2010a. Fluctuating ungulate density shapes tree recruitment in natural stands of the Białowieża Primeval Forest, Poland. Journal of Vegetation Science 21:1082–1098.

Kuijper, D. P. J., J. P. G. M. Cromsigt, B. Jedrzejewska, S. Miscicki, M. Churski, W. Jedrzejewski, and I. Kweczlich. 2010b. Bottom-up versus top-down control of tree regeneration in the Białowieza Primeval Forest, Poland. Journal of Ecology 98:888–899.

Kyker-Snowman, T., D. Clark, H. Eck, J. French, D. Morin, R. Stone, M. Fluet, S. Campbell, D. Small, P. Lyons, and J. Zimmerman. 2007. Quabbin reservoir watershed system: land management plan. 2007–2017. Massachusetts Department of Conservation and Recreation Division of Water Supply Protection, Office of Watershed Management. Boston, USA.

Lucas, R. W., R. Salguero-Gómez, R., D. B. Cobb, B. G. Waring, F. Anderson, W. J. McShea, and B. B. Casper. 2013. White-tailed deer (*Odocoileus virginianus*) positively affect the

growth of mature northern red oak (*Quercus rubra*) trees. Ecosphere 4:art84. http://dx.doi.org/10.1890/ES13-00036.1.

Ludewig, H. A. and R. T. Bowyer. 1985. Overlap in winter diets of sympatric moose and white-tailed deer in Maine. Journal of Mammalogy 66:390–392.

Lustenhouwer, M. N., L. Nicoll, and A. M. Ellison. 2012. Microclimatic effects of the loss of a foundation species from New England forests. Ecosphere 3:1–16.

Makhabu, S. W., C. Skarpe, and H. Hytteborn. 2006. Elephant impact on shoot distribution on trees and on rebrowsing by smaller browsers. Acta Oecologia 30:136–146.

Manier, D. J., and N. T. Hobbs. 2007. Large herbivores in sagebrush steppe ecosystems: livestock and wild ungulates influence structure and function. Oecologia 152:739–750.

Marks, P. L. 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. Ecological Monographs 44:73–88.

Marquis, D. A. 1974. Impact of deer browsing on Allegheny hardwood regeneration. USDA Forest Service Research Paper. NE-308.

McCabe, R. E., and T. R. McCabe. 1984. Of slings and arrows: An historical perspective. Pages19–72 *in* L. K. Halls, editor. White-tailed deer: ecology and management. Stackpole Books, Harrisburg, USA.

McCune, B., J. B. Grace, and D. L. Urban. 2002. Analysis of ecological communities. MJM Software Design, Gleneden Beach, USA.

McDonald, J. E., D. E. Clark, and W. A. Woytek. 2007. Reduction and maintenance of a white-tailed deer herd in central Massachusetts. Journal of Wildlife Management 71:1585–1593.

McEwan, R. W., J. M. Dyer, and N. Pederson. 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. Ecography 34:244–256.

McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology 73: 2059–2075.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose, and tree rings on Isle Royale. Science 266:1555–1558.

McShea, W. J., and W. M. Healy. 2002. Oaks and acorns as a foundation for ecosystem management. Pages 1–9 *in* W. J. McShea and W. M. Healy, editors. Oak forest ecosystems: ecology and management for wildlife. The Johns Hopkins University Press, Baltimore, USA.

Moore, W. H., and F. M. Johnson. 1967. Nature of deer browsing on hardwood seedlings and sprouts. Journal of Wildlife and Management 31:351–353.

Myers, J. A., M. Vellend, S. Gardescu, and P. L. Marks. 2004. Seed dispersal by white-tailed deer: implications for long-distance dispersal and migration of plants in eastern North America. Oecologia 139:35–44.

New England Wildflower Society. 2015. Go botany. https://gobotany.newenglandwild.org/. Accessed 10 April 2015.

Nuttle, T., A. A. Royo, M. B. Adams, and W. P. Carson. 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. Ecological Monographs 83:3–17.

Nuttle, T., T. E. Ristau, and A. A. Royo. 2014. Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understoreys reflect past deer density treatments for at least 20 years. Journal of Ecology doi: 10.1111/1365-2745.12175.

Oksanen, J. et al. 2015. Package vegan: community ecology package in R. http://cran.ism.ac.jp/web/packages/vegan/vegan.pdf.

Olff, H., and M. E. Ritchie**.** 1998. Herbivore effects on grassland plant diversity. Trends in Ecology and Evolution 13:261–265.

Oliver, C. D., and B. C. Larson. 1996. Forest stand dynamics. John Wiley Sons, Hoboken, USA.

Orwig, D. A., and D. R. Foster. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. Journal of the Torrey Botanical Society 125:59–72.

Orwig, D. A., J. R. Thompson, N. A. Povak, M. Manner, D. Niebyl, and D. R. Foster. 2012. A foundation tree at the precipice: *Tsuga canadensis* health after the arrival of *Adelges tsugae* in central New England. Ecosphere 3:1–16.

Orwig, D. A., A. Barker Plotkin, E. A. Davidson, H. Lux, K. E. Savage, and A. M. Ellison. 2013. Foundation species loss affects vegetation structure more than ecosystem function in a northeastern USA forest. PeerJ 1:e41 http://dx.doi.org/10.7717/peerj.41.

Pastor, J., R. J. Naiman, B. Dewey, and P. McInnes. 1988. Moose, microbes, and the boreal forest. Bioscience 38:770–777.

Peek, J. M. 1997. Habitat relationship Pages 351–375 *in* A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American moose. Smithsonian Institution, Washington, D.C., USA.

Perrin, P. M, F. J. G Mitchell, and D. L. Kelly. 2011. Long-term deer exclusion in yew-wood and oakwood habitats in southwest Ireland: changes in ground flora and species diversity. Forest Ecology and Management 262: 2328–2337.

Persson, I. L., K. Danell, and R. Bergstrom. 2000. Disturbance by large herbivores in boreal forests with special reference to moose. Annales Zoologici Fennici 37:251–263.

Persson, I. L., K. Danell, and R. Bergstrom. 2005. Different moose densities and accompanied changes in tree morphology and browse production. Ecological Applications 15:1296–1305.

Price, P. W. 1991. The plant vigor hypothesis and herbivore attack. Oikos 62:244–251.

Putman, R. J., P. J. Edwards, J. C. E. Mann, R. C. How, and S. D. Hill. 1989. Vegetational and faunal changes in an area of heavily grazed woodland following relief of grazing. Biological Conservation 47:13–32.

Rapp, J. M., E. J. B. McIntire, and E. E. Crone. 2013. Sex allocation, pollen limitation and masting in whitebark pine. Journal of Ecology doi: 10.1111/1365-2745.12115.

Rea, R. V., and M. P. Gillingham. 2001. The impact of the timing of brush management on the nutritional value of woody browse for moose *Alces alces.* Journal of Applied Ecology 38:710–719.

Reeves, H. M., and R. E. McCabe. 1997. Of moose and man. Pages 1–75 *in* A. W. Franzmann, and C. C. Schwartz, editors. Ecology and Management of the North American Moose. Smithsonian Institution, Washington, D.C.

Renecker, L. A., and C. C. Schwartz. 1997. Food habits and feeding behavior. Pages 403–439 *in* A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American moose. Smithsonian Institution, Washington, D.C., USA.

Ritchie, M. E., and H. Olff, H.1999. Herbivore diversity and plant dynamics: compensatory and additive effects. Pages 175–204 in H. Olff, V. K. Brown, and R. H. Drent, editors. Herbivores: between plants and predators. The 38th Symposium of the British Ecological Society. Blackwell Scientific Publications, Oxford, UK.

Roberts, M. R., and F. S. Gilliam. 2014. Response of the herbaceous layer to disturbance in eastern forests. Pages 321–339 *in* F. S. Gilliam, editor. The herbaceous layer in forests of eastern North America. Oxford University Press, New York, USA.

Rooney, T. P. and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management 181:165–176.

Rooney, T. P. 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecology 202:103–111.

Royo, A. A., R. Collins, M. B. Adams, C. Kirschbaum, and W. P. Carson. 2010. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. Ecology 91:93–105.

Russell, L. F., D. B. Zippin, and N. L. Fowler. 2001. Effects of white-tailed deer (Odocoileus virginianus) on plants, plant populations and communities: a review. American Midland Naturalist 146:1–26.

Schmitz, O. J., and A. R. E Sinclair. 1997. Rethinking the role of deer in forest ecosystem dynamics. Pages 201-223 *in* W. J. McShea, H. Brian Underwood, and J. H. Rappole editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Books, Washington, D.C. USA.

Schreiner, E. G., K. A. Krueger, P. J. Happe, and D. B. Houston. 1996. Understory patch dynamics and ungulate herbivory in old-growth forests of Olympic National Park, Washington. Canadian Journal of Forest Research 26:255–265.

Sinclair, A. R. E., and C. J. Krebs. 2002. Complex numerical responses to top-down and bottom-up processes in vertebrate populations. Philosophical Transactions of the Royal Society 357:1221–123.

Sinclair, A. R. E., J. M. Fryxell, and G. Caughley, 2006. Wildlife ecology, conservation, and management. Blackwell Publishing, Malden, USA.

Soluk, D. A. 1993. Multiple predator effects: predicting combined functional response of stream fish and invertebrate predators. Ecology 74:219–225.

Soule, M. 2003. The role of large mammals in US forests. Pages 73–83 *in* Towards forest sustainability. D. B. Lindenmayer and J. F. Franklin, editors. Island Press, Washington, DC, USA.

Stormer, F. A., and W. A. Bauer. 1980. Summer forage use by tame deer in Northern Michigan. Journal of Wildlife Management 44:98–106.

Strong, D. R. 1992. Are trophic cascades all wet? differentiation and donor control in speciose ecosystems. Ecology 73:747–754.

Struhsaker, T. T., J. S. Lwanga, and J. M. Kasenene. Elephants, selective logging and forest regeneration in the Kibale Forest, Uganda. Journal of Tropical Ecology 12:45–64.

Tanentzap, A. J. J. N. Bee, W. G. Lee, R. B. Lavers, J. A. Mills, A. F. Mark, and D. A. Coomes. 2009. The reliability of palatability estimates obtained from rumen contents analysis and a field-based index of diet selection. Journal of Zoology 278:243–248.

Thompson, I. D., W. J. Curran., J. A. Hancock, and C. E. Butler. 1992. Influence of moose browsing on successional forest growth on black spruce sites in Newfoundland. Forest Ecology and Management 47:29 –37.

Telfer, E. S. 1967. Comparison of moose and deer winter range in Nova Scotia. Journal of Wildlife Management 31:418–425.

Thomas, C. D. and G. Palmer. 2015. Non-native plants add to the British flora without negative consequences for native diversity. Proceedings of the National Academy of Sciences 112: 4387–4392.

Thompson, I. D., R. E. McQueen, P. B. Reichardt, D. G. Trenholm, and W. J. Curran. 1989. Factors influencing choice of balsam fir twigs from thinned and unthinned stands by moose. Oecologia 8:506–509.

Thompson, J. R., D. N. Carpenter, C. V. Cogbill, and D. R. Foster. 2013. Four centuries of change in northeastern United States forests. PLoS ONE 8: e72540.

Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. Journal of Wildlife Management 53:524–532.

University of Georgia. 2015. Historic wildlife range maps. White-tailed deer populations 1982. http://vet.uga.edu/scwds/range-maps. Accessed 15 April 2015.

USA EPA. 2015. Ecoregions of New England.

http://www.epa.gov/wed/pages/ecoregions/new_eng_eco.htm. Accessed 15 April 2015.

USDA 2015. FIA data mart. Htt p://apps.fs.fed.us/fiadb-downloads/datamart.html Accessed 15 April 2015.

Van Dyke, F., and J. A. Darragh. 2007. Response of elk to changes in plant production and nutrition following prescribed burning. Journal of Wildlife Management 71:23–29.

Vera, F. W. M., E. S. Barker, and H. Olff. 2006. Large herbivores: missing partners of western European light-demanding tree and shrub species? Pages 203–231 *in* K. Danell, R. Bergstrom, P. Duncan, and J. Pastor, editors. Large herbivore ecology, ecosystem dynamics and conservation. Cambridge University Press, Cambridge, UK.

Waller, D. M. 2014. Effects of deer on forest herb layers. Pages 369-399 *in* F.S. Gilliam, editor. The herbaceous layer in forests of eastern North America. Oxford University Press, New York, USA.

Wattles, D. W., and S. DeStefano. 2011. Status and management of moose in the northeastern United States. Alces 47:53–68.

Wattles, D. W., and S. DeStefano. 2013. Moose habitat use in Massachusetts: assessing use at the southern edge of the range. Alces 49:133–147.

Webster, C. R., M. A. Jenkins, and J. H. Rock. 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smok**y** Mountains National Park, USA**.** Biological Conservation 125:29–307.

White, C. A., M. C. Feller, and S. Bayley. 2003. Predation risk and the functional response of elk–aspen herbivory. Forest Ecology and Management 181:77–97.

Wilmshurst, J. F., J. M. Fryxell, and R. J. Hudson. 1995. Forage quality and patch choice by wapiti (*Cervus elaphus*). Behavioral Ecology 6:209–217.

Wisdom, M. J., M. Vavra, J. M. Boyd, M. A. Hemstrom, A. A. Ager, and B. K. Johnson. 2006.

Understanding ungulate herbivory-episodic disturbance effects on vegetation dynamics: knowledge gaps and management needs. Wildlife Society Bulletin 34:283–292.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effect models and extensions in R. Springer Publishing, UK.