Michigan Technological University
Digital Commons @ Michigan Tech

Dissertations, Master's Theses and Master's Reports - Open

Dissertations, Master's Theses and Master's Reports

2010

Patch selection by wintering white-tailed deer : consequences for eastern hemlock regeneration at local and landscape scales

Jill Christine Witt
Michigan Technological University

Follow this and additional works at: https://digitalcommons.mtu.edu/etds

Part of the Forest Sciences Commons

Copyright 2010 Jill Christine Witt

Recommended Citation

Witt, Jill Christine, "Patch selection by wintering white-tailed deer : consequences for eastern hemlock regeneration at local and landscape scales", Dissertation, Michigan Technological University, 2010.
https://doi.org/10.37099/mtu.dc.etds/127

Follow this and additional works at: https://digitalcommons.mtu.edu/etds
Part of the Forest Sciences Commons

PATCH SELECTION BY WINTERING WHITE-TAILED DEER: CONSEQUENCES FOR EASTERN HEMLOCK REGENERATION AT LOCAL AND LANDSCAPE SCALES

By

JILL C. WITT

A DISSERTATION

Submitted in partial fulfillment of the requirements

for the degree of

DOCTOR OF PHILOSOPHY

Forest Science

MICHIGAN TECHNOLOGICAL UNIVERSITY

2010

Copyright©Jill C. Witt 2010

This dissertation, "Patch selection by wintering white-tailed deer: Consequences for eastern hemlock regeneration at local and landscape scales" is hereby approved in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the field of Forest Science.

School of Forest Resources and Environmental Sciences

Michigan Technological University

Signatures:

Dissertation Advisor____
Christopher R. Webster, Ph.D.

Date____

Dean____
Margaret R. Gale, Ph.D.

Date____

I dedicate this dissertation to

my best friend

and constant companion of 16 years.

Thank you for all of the laughs and hugs when I needed them most.

You'll be missed, Tigger.

ACKNOWLEDGEMENTS

I am humbly grateful for the assistance, advice, and encouragement of several people as I worked through the many steps that have gone into the successful completion of this dissertation. Dr. Chris Webster, my advisor, came up with the original idea for this large-scale and intense project, and I thank him for entrusting me with it. Thank you, Chris. You taught me a lot, and I had fun along the way. I would also like to thank my dissertation committee, Drs. Ann Maclean, Tom Drummer, John Vucetich, and Jackie Grant. You have challenged me and encouraged me, and I appreciate your helpful comments and suggestions.

Throughout the majority of this project I was fortunate to have two of the best field technicians a graduate student could ask for: Jesse Provencher and Andy Quinn. Thank you both for your insight, hard work, and excellent work ethic. We hiked a lot of miles and had a lot of fun! Robert Froese, Linda Nagel, Mike Hyslop, Luke Spaete, and Nick Jensen, thank you for your assistance at various stages of this project. I have appreciated your support, friendship, and the occasional KBC moments.

I am grateful for the following for their contribution of resources or financial support: Michigan Department of Natural Resources, USDA Forest Service, Gratiot Lake Conservancy, and Michigan Technological University Ecosystem Science Center, and the Michigan Tech Graduate Student Government.

I have been incredibly fortunate to have such a great group of supportive friends and family: Linda, Amber and Dan, Rachel and Nate, Randy, Doug, Casey and family,

mom and Dad, Ellie and Bill. I am most appreciative, however, for the support of my research partner, fellow graduate student, and close friend, Dr. Stacie Holmes.

Finally, to my husband and best friend, Dr. Steve Bailey, WE DID IT! Thank you for being my biggest fan!

PREFACE

Portions of this dissertation have been submitted as manuscripts for publication in peer-reviewed outlets. The journal, author list, and current status of these manuscripts are acknowledged by a footnote found within the text.

TABLE OF CONTENTS

CHAPTER TWO

CHAPTER THREE

Erosion of patch stability and altered successional trajectories in remnant stands of *Tsuga canadensis*. 68

ABSTRACT

Tsuga canadensis (eastern hemlock) is a highly shade-tolerant, late-successional, and long-lived conifer species found throughout eastern North America. It is most often found in pure or nearly pure stands, because highly acidic and nutrient poor forest floor conditions are thought to favor *T. canadensis* regeneration while simultaneously limiting the establishment of some hardwood species with greater nutrient requirements. Once a common species, *T. canadensis* is currently experiencing widescale declines across its range. The hemlock woolly adelgid (*Adelges tsugae*) is decimating the population across its eastern distribution. Across the Upper Great Lakes region, where the adelgid is currently being held at bay by cold winter temperatures, *T. canadensis* has been experiencing failures in regeneration attributed, in part, to herbivory by white-tailed deer (*Odocoileus virginianus*). Deer utilize *T. canadensis* stands as winter habitat in areas of high snow depth. *Tsuga canadensis*, once a major component of these forests, currently exists at just a fraction of its pre-settlement abundance due to historic logging and contemporary forest management practices, and what remains is found in small remnant patches surrounded by second- and third-growth deciduous forests. The deer population across the region, however, is likely double that of pre-European settlement times. In this dissertation I explore the relationship between white-tailed deer use of *T. canadensis* as winter habitat and the effect this use is having on regeneration and forest succession.

For this research I quantified stand composition and structure and abiotic variables of elevation and snow depth in 39 randomly selected *T. canadensis* stands from across the western Upper Peninsula of Michigan. I also quantified composition and the

configuration of the landscapes surrounding these stands. I measured relative deer use of *T. canadensis* stands as pellet group piles deposited in each stand during each of three consecutive winters, 2005-06, 2006-07, and 2007-08. The results of this research suggest that deer use of *T. canadensis* stands as winter habitat is influenced primarily by snow depth, elevation, and the composition and configuration of the greater landscapes surrounding these stands. Specifically, stands with more heterogeneous landscapes surrounding them (i.e., a patchy mosaic of conifer, deciduous, and open cover) had higher relative deer use than stands surrounded by homogenous deciduous forest cover. Additionally, the intensity of use and the number of stands used was greater in years with higher average snow depth. *Tsuga canadensis* regeneration in these stands was negatively associated with deer use and *Acer saccharum* (sugar maple) basal area. Of the 39 stands, 17 and 22 stands had no *T. canadensis* regeneration in small and large sapling categories, respectively. *Acer saccharum* was the most common understory tree species, and the importance of *A. saccharum* in the understory (stems < 10 cm dbh) of the stands was positively associated with overstory *A. saccharum* dominance. *Tsuga canadensis* establishment was associated with high-decay coarse woody debris and moss, and deciduous leaf litter inputs in these stands may be limiting access to these important microsites. Furthermore, *A. saccharum* is more tolerant to the effects of deer herbivory than *T. canadensis*, giving *A. saccharum* a competitive advantage in stands being utilized as winter habitat by deer. My research suggests that limited microsite availability, in conjunction with deer herbivory, may be leading to an erosion in *T. canadensis* patch stability and an altered successional trajectory toward one of *A. saccharum* dominance, an alternately stable climax species.

INTRODUCTION

Life history traits and current issues affecting Tsuga canadensis

Tsuga canadensis (eastern hemlock), a climax species found throughout the eastern United States, has been referred to as a *foundation* species, one that is profoundly moderating, occupies a low-trophic level, and creates a distinctive microclimate (Ellison *et al.*, 2005). *Tsuga canadensis* is shade tolerant, long-lived, and often exists in pure or nearly pure stands. These stands are unique in that they create forest floor conditions that are cool and humid with slow rates of decomposition and nutrient cycling (Yorks *et al.*, 1999). These conditions are not only important for *T. canadensis* regeneration, but for a wide variety of amphibians, mammals, reptiles, lichens, bryophytes, and stream assemblages (Catovsky and Bazzaz, 2000; Snyder *et al.*, 2002; Ross *et al.*, 2003). Ecologically, *T. canadensis* is an important habitat component for 96 bird and 47 mammal species (Yamasaki *et al.*, 1999), and in northern forests of the Upper Great Lakes region it serves as winter habitat for white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*).

Historically, the primary cover type of the Upper Great Lakes region was a patchy mosaic of hemlock-hardwood forests (Davis *et al.,* 1998). Following the extensive logging and slash fires at the turn of the 20th century, *T. canadensis* was reduced to a fraction of its former abundance, with less than one percent remaining throughout the Upper Peninsula of Michigan (Mladenoff 1996). Contemporary *T. canadensis* is often found in small remnant patches surrounded by second- and third-growth deciduous forest (Alverson et al. 1988).

Throughout its distribution, *T. canadensis* has and is continuing to face a range of perils. In the east, hemlock woolly adelgid (*Adelges tsugae*) is decimating the population (Orwig *et al.*, 2002). In the Upper Great Lakes region, where the woolly adelgid is currently being held at bay, possibly due in part to the lower temperatures associated with long winters, *T. canadensis* is facing other problem. A lack of regeneration has been noted as far back as 1941 (Maissurow, 1941) and as has been a long-term and ongoing problem Crow (1996). Low seed input, poor seedling establishment, and/or limits to recruitment have been the focus of studies trying to identify the underlying mechanisms leading to this deficiency. Hemlock is, however, one of the most frequent cone producers with good seed crops occurring every two to three years in mature stands (Godman and Lancaster, 1990). Moist, well decomposed litter, rotted wood, mineral soil, and moss mats are favorable microsite substrates for seedling establishment (Hough, 1960; Godman and Lancaster, 1990; Collins, 1990); however, absence of these microsite conditions, soil characteristics, low moisture and/or limited light availability are thought to be factors limiting seedling establishment and survival (Rooney *et al.*, 2000). Mladenoff and Stearns (1993) suggest that along with the limited microsites necessary for germination, contemporary climate conditions are limiting seedling survival. In addition, *T. canadensis* is being replaced by *A. saccharum* (*Acer saccharum*) in many locales, an alternative stable climax species, which may further decrease substrate suitability for *T. canadensis* establishment (Frelich *et al.*, 1993; Mladenoff and Stearns, 1993; Davis *et al.*, 1996). In addition to the aforementioned factors, browsing by white-tailed deer is considered to be a bottleneck to *T. canadensis* recruitment throughout the Upper Great

Lakes. The white-tailed deer is often referred to as a keystone herbivore because overbrowsing can have a strong influence on plant community composition, distribution, and abundance throughout an ecosystem (Rooney and Waller, 2003). Hemlock is a common browse species of deer during winter months when deciduous leaves and herbs are unavailable (Dahlberg and Guettinger, 1956). Once the terminal shoot of *T. canadensis* is browsed, however, its potential for re-growth is greatly reduced (Anderson and Loucks, 1979). Sugar maple, on the other hand, re-sprouts readily after browsing, which may lead to *A. saccharum* being the favored competitor in heavily browsed stands (Anderson and Loucks, 1979). Several studies have focused on deer browsing as an impediment to *T. canadensis* recruitment (Anderson and Loucks, 1979; Frelich and Lorimer, 1985; Rooney *et al.*, 2000). Stands with heavy browsing pressure have shown a decrease in the abundance of *T. canadensis* saplings and often exhibit an abnormal size class distribution (Rooney *et al.*, 2000). Since seedling abundance in a specific size class is dependant on seedling abundance in the previous size class (Rooney *et al.*, 2000), persistent heavy browsing, like those found in winter deer yards, could lead to long-term recruitment failure. Frelich and Lorimer (1985) predict that if no action is taken to reduce long-term browse pressure in stands with high deer use, *T. canadensis* dominated stands could undergo a slow conversion to *A. saccharum.*

White-tailed deer of the Upper Great Lakes

Prior to European settlement, the mature forest of the Upper Great Lakes region would have been poor habitat for deer. However, following the extensive logging, the increase in early-successional habitat, lack of predators, and protective hunting laws led to a burgeoning deer population across the region (Alverson et al., 1988). In a habitat suitability model for estimating deer populations in the Upper Peninsula of Michigan for pre- and post-European settlement, Doepker *et al.* (1994) estimated pre-settlement densities to be 5.8 deer/km^2. Post-settlement densities, however, were estimated to be nearly double those of pre-settlement times with the increase being disproportionately in the southern third of the peninsula in areas of relatively lower snow depth (Doepker *et al.*, 1994).

Winter severity and habitat quality are thought to be main factors limiting regional deer populations (Doepker *et al.,* 1996; Xie *et al.,* 1999; Shi *et al.,* 2006). Deer respond to the harsh winter conditions by moving into areas of dense conifer cover (a behavior often referred to as "winter yarding"), like those of mature *T. canadensis* and white-cedar stands. In a study of within-yard habitat use by Morrison et al. (2003), deer selected yards in response to changes in snow depth throughout the winter. Deer selected area of better browse availability, during times of lower snow, as long as it was proximate to conifer cover. However, as snow depths increased, deer began to balance a trade-off between browse and cover, choosing cover over browse at snow depths exceeding 50 cm.

The research presented in this dissertation explores the relationship between white-tailed deer and their use of *T. canadensis* stands as winter habitat. In a region where the deer are thought to be double that of the pre-logging era, this utilization of *T. canadensis* as winter habitat is bound to have some long-term, detrimental effects on a species sensitive to the effects of browsing. This study explores the relationship between deer use of remnant *T. canadensis* stands as winter habitat and the effects that this use is having on *T. canadensis* stand structure and regeneration.

Dissertation overview

My study system is unique; however the issues of an overabundant herbivore population, habitat fragmentation, and altered plant community composition are common. I discuss this study system and current issues affecting it in the terms of contemporary ecological theory. Additionally however, my research highlights some of the underlying processes that have and continue to affect the northern hardwood forest ecosystem. It is my hope that the findings presented in this dissertation can be used to develop creative management solutions that promote the health and diversity of this system. The specific objectives of this study were to:

I. Identify how the composition and structure of *T. canadensis* stands, and the composition and configuration of the landscape surrounding these stands, are influencing winter habitat use by white-tailed deer.

II. Determine how deer use of *T. canadensis* stands as winter habitat is affecting regeneration and recruitment of conspecifics in those stands.

III. Given the current stand structure, in conjunction with natural disturbance, species life history, and contemporary deer use, evaluate stability and successional trajectory of these *T. canadensis* stands.

In *Chapter One* I explore how local- and landscape-scale variables are influencing deer use of *T. canadensis* as winter habitat. Specifically, I hypothesize that, due to the variation in snowfall across our study area, snow depth and elevation will be important predictors of habitat use. At the scale of a *T. canadensis* stand, I expect that the quality of winter cover (i.e., stand size and overstory *T. canadensis* structure) will be most important during winters with higher average snow depth, and forage availability will be more important in low-snow years. The risk-reward trade-off to fitness is influential to habitat selection decisions (Mayor et al. 2009), and therefore, I further hypothesize that the composition and configuration of the greater landscapes surrounding these stands will affect the level of deer use. I use deer fecal pellet groups deposited per winter as a surrogate of the intensity of deer use, and I test my hypotheses at the scale of a *T. canadensis* stand and five increasingly greater areas of landscape surrounding each of these study stands.

In *Chapter Two* I examine how microsites and deer herbivory are influencing the establishment and recruitment of *T. canadensis*. First, I hypothesize that *T. canadensis* establishment is being limited by the availability of important microsites for germination. Specifically, *T. canadensis* is associated with high-decay coarse woody debris, moss, and bare soil, however we hypothesize that broad-leaf litter may be limiting access to these important sites. My second hypothesis is that deer herbivory is acting as a bottleneck to *T. canadensis* recruitment. In this chapter I quantify understory *T. canadensis* and identify important limits to regeneration. I explore how a difference in tolerance to deer herbivory between *T. canadensis* and *A. saccharum*, in conjunction with the limited microsites for *T. canadensis* establishment, may be setting up a scenario that could favor *A. saccharum* regeneration in the understory of these *T. canadensis* stands.

Finally, in *Chapter Three* I further explore this relationship between *Acer spp.* and *T. canadensis*. *Tsuga canadensis* and *A. saccharum* are late succession species in northern hardwood forests. Both form dominant and nearly homogenous patches across the landscape, and both are thought to limit the establishment of the other in these dominant patches (Frelich *et al.,* 1993; Woods, 1984). *Tsuga canadensis* was the dominant overstory species in most of our stands, yet *A. saccharum* was the most abundant understory species. In this chapter I quantify understory stand structure, and given this current structure, I discuss the future of *T. canadensis* patch stability. I also identify variables (e.g., deer herbivory, microsites, nutrient cycling) that may be associated with a loss of *T. canadensis* patch stability. I discuss these in terms of an altered successional trajectory for these stands, one that favors dominance by *A. saccharum*. Finally, I bring this discussion back full circle in this dissertation, and I explore how a change in the successional trajectory of these stands may further alter selection and utilization of winter habitat by white-tailed deer.

CHAPTER ONE

Landscape Heterogeneity as a Driver of Patch Use by *Odocoileus virginianus* Along a Temporal and Spatial Gradient of Snow Depth[1]

Abstract

Anthropogenic changes in landscape composition or configuration have the potential to increase the abundance of generalist species, often resulting in cascading effects on other trophic levels and ecosystem function. The selection or utilization of individual patches of habitat, however, may vary in both time and space, as a result of patch and landscape attributes as well as dynamic abiotic factors, such as snowfall. Given that scale-specific habitat decisions are often an indication of the risk-reward trade-offs to fitness, we hypothesized that the use of high-quality habitat would be most strongly influenced by snow at local scales and by composition and the configuration of the landscape at greater spatial scales. To test this, we examined white-tailed deer (*Odocoileus virginianus*) selection of eastern hemlock (*Tsuga canadensis*) patches as winter habitat. Within-patch habitat structure and patch use were monitored for three consecutive years. The surrounding landscape was characterized using existing spatial data sets. Patch level attributes were poor predictors of patch use in areas with strong gradients in abiotic factors relevant to the energetics of movement or forage acquisition. Additionally, heterogeneity in the greater landscape served to increase use and homogeneity deterred use, suggesting that risk-reward trade-offs may be the greatest at

---

[1] This chapter has been submitted as a manuscript for publication by Witt, JC , Webster, CR, Drummer, TD, Froese, RE, Vucetich, JA, and Peterson, RO and is currently in review at *The Journal of Wildlife Management*.

the coarsest spatial scales (3000 m radius buffer). Decisions regarding habitat modification meant to mitigate the damaging effects of an overabundant species should incorporate knowledge of coarse-scale factors that serve to limit, or encourage, habitat use.

Introduction

Human-influenced changes in landscape composition and configuration have led to locally overabundant or expanding distributions of native generalist species that are able to exploit these conditions (Garrott and White, 1993; Anderson, 1997). For some of these species, expanding populations have, in turn, led to local changes in or simplification of food webs, decreases in diversity, and homogenization of habitat (Garrott and White, 1993). For example, increasing fragmentation or patchiness in the sawgrass (*Cladium jamaicense*) ecosystem of the Florida Everglades has led, in part, to an increase in probability of conversion from sawgrass to a cattail (*Typha* spp.) monoculture, a species that has a strong influence over water chemistry and cascading effects in the Everglades food chain (Wu *et al.*, 1997). Tallmon *et al.* (2003) demonstrated that white-footed mouse (*Peromyscus leucopus*) densities were higher in fragmented versus unfragmented forests, and the increase in seed predation had the potential to lead to reduced recruitment or local extinctions of Pacific trillium (*Trillium ovatum*). Landscapes with a high interspersion of forested and agricultural lands have also been shown to have a positive influence on the density and diversity of avian predator species, leading to an increase in nest predation and declines in songbird abundance (Andren, 1992; Donovan *et al.* 1995; Robinson *et al*., 1995). Similarly, local extinctions of top predators, due to habitat fragmentation and patch isolation, have led to increases in human-tolerant carnivore populations and cascading effects on bird populations (Crooks and Soulé, 1999).

Wildlife species that are able to capitalize on highly fragmented landscapes respond to patchiness in their environment across a wide range of spatial and temporal scales (Wiens, 1976; Senft *et al.* 1987). For ungulates, selection of habitat may begin at the coarser scale of a home range or migration route and be further honed by behaviors at finer spatial scales (Johnson, 1980). Processes that influence habitat selection at one scale, however, are not necessarily the same as those that are influential at another (Senft *et al.*, 1987; Turner, 1989). At the coarser scale of a landscape, an increase in patchiness or edge has been shown to be influential in the selection of both winter and summer ranges for elk (*Cervus elephus* -Jones and Hudson, 2002; Boyce *et al.*, 2003). Home range sizes of mule deer (*Odocoileus hemionus*) tend to be smaller in highly heterogeneous landscapes (Kie *et al.*, 2002). At finer scales, the spatial arrangement of vegetation can influence ungulates as they utilize cover, select forage and avoid predators (Pearson *et al.*, 1995; Rettie and Messier, 2000; Johnson *et al.* 2002). However, habitat selection at one scale may be impeded by limits to selection at another, and these hierarchical constraints, as well as scales of influence, are still being debated (Mayor *et al.*, 2009).

Perhaps one of the best-known examples of a species that has been able to capitalize on forest fragmentation is the white-tailed deer (*Odocoileus virginianus*) as landscapes interspersed with large amounts of forested edge, agriculture, and early-successional habitat provide abundant forage and cover for this generalist species (Dahlberg and Guettinger, 1956; Alverson *et al.*, 1988; Waller and Alverson, 1997). Additionally, a lack of predators and hunting laws geared toward protecting deer populations has contributed to high deer densities and range expansion, and in many locales, deer are thought to be locally overabundant or at densities that exceed social or ecological carrying capacity (McShea *et al.*, 1997; Rooney, 2001)

White-tailed deer, like many ungulates, have the ability to influence plant community distribution and abundance (Alverson *et al.*, 1988; Waller and Alverson 1997; Rooney, 2001; Webster *et al.*, 2008; Rooney, 2009). Throughout their distribution, numerous studies have and continue to document how locally overabundant deer populations are directly or indirectly causing shifts in or homogenization of plant populations and communities, which have, in turn, led to cascading effects on animal species and ecosystem processes (McShea *et al.*, 1997; Russell *et al.*, 2001; Côté *et al.*, 2004).

Adding to the influence of landscape heterogeneity, seasonal weather events also have the potential to modify or decrease the quality or availability of that habitat (Turner, 1989), and the quality of habitat may be of less importance to wintering ungulates than the quantity or distribution of that habitat (Wallace *et al.*, 1995; Boyce *et al.*, 2003). Throughout the Upper Great Lakes region, winter severity is thought to be one of the major factors limiting regional white-tailed deer populations (Xie *et al.*, 1999). Deer respond to harsh winter conditions by congregating in areas of dense conifer cover, which are thought to provide refuge from heavy snow, high winds and radiant heat loss, as well as lower snow for ease of movement and predator avoidance (Blouch, 1984, Nelson and Mech, 2006). Eastern hemlock (*Tsuga canadensis*) is commonly utilized as winter habitat across the region (Verme, 1973). Contemporary hemlock, however, exists at just a fraction of its pre-European settlement abundance (Whitney, 1987), and it is often found in small, remnant patches surrounded by a landscape dominated by second-growth deciduous forests (Alverson *et al.,* 1988). Deer numbers, on the other hand, are thought to be at least double those of pre-European settlement times (Doepker *et al.*, 1994). It is the browsing pressure placed on hemlock during its use as winter deer habitat that is thought to be one of the major factors limiting hemlock recruitment across the region (Frelich and Lorimer, 1985; Alverson *et al.* 1988; Rooney *et al.*, 2000).

The distribution of hemlock is limited and patchy across the landscape, yet despite hemlock's low abundance remnant patches are not being used uniformly by wintering deer. Some patches are experiencing high levels of browse pressure, while others remain untouched. Seasonal and yearly snowfall across the region tends to be high and highly variable, due to the climatic influences of Lake Superior (Eichenlaub, 1970). Since snow depth has been shown to influence habitat selection (Morrison *et al.*, 2003), we expect that variation in snow depth will be an important factor influencing use of these hemlock patches. Additionally, across the region many of these remnant patches are surrounded by a dominant cover of second- and third-growth deciduous forests. At a finer scale, however, the landscape is quite heterogeneous with farm fields, riparian areas and forests at various stages of succession. Since the fitness of the deer population is, in part, linked to this winter habitat, we expect that both the quality of that habitat and its availability within the landscape will be influential to individual patch use.

The objective of this study was to test the importance of scale in identifying how local-scale factors, such as snow, patch structure (i.e. forage availability and the quality of cover), and the landscapes surrounding hemlock patches influence patch use by wintering deer. We hypothesize that quality of winter cover will be more important in high snow years, whereas in lower snow years deer will select for areas of higher forage availability. However, given that scale-specific habitat decisions are often an indication of the risk-reward trade-off to fitness (Mayor *et al.,* 2009), we expect that the composition and the configuration of the greater landscapes surrounding high-quality habitat will also influence habitat use.

Methods

Our study area was located in the western Upper Peninsula of Michigan on the south side of Lake Superior in the Laurentian Great Lakes region (Fig. 1). Using U.S. Forest Service and Michigan Department of Natural Resources forest inventory data, we selected randomly 39 remnant eastern hemlock patches from strata defined by four levels of patch area and high or low relative snow depth. Patches ranged in size from 0.4 to 60 hectares. With deer use as our dependant variable, we used a generalized linear modeling framework to explore the relationship between use of remnant hemlock patches and patch- and landscape-scale explanatory variables on an annual (patch-scale only) and multi-year basis.

To quantify the intensity of winter deer use for each of the remnant hemlock patches, we conducted yearly counts of fecal pellet groups for each patch. Study sites contained randomly placed 5, 10, 20 or 30 circular pellet-group plots with a sampling area of 9.29 m^2. Plots were cleared of pellets prior to the first winter, and immediately following snow melt pellet groups were counted by a two-person team employing a system of concurrent rechecks. Deer use was quantified for each study patch for winters 2005-06, 2006-07, and 2007-08.

At the patch scale, we quantified habitat through direct measures of hemlock patch composition and structure. We used hemlock basal area as an indicator of the quality of winter cover (Telfer, 1970). Overstory and mid-story (stems $\geq$ 4 cm dbh) composition and structure were measured on randomly placed 400 m^2 circular plots (3, 5, 7 or 9 plots, depending on patch size). The availability of winter forage for each study patch was quantified on three 1 x 10 meter, randomly oriented, parallel belt transects embedded within each overstory circular sampling plot. Although hemlock is a common browse species of wintering white-tailed deer of the region, it is often missing from sample plots (Frelich and Lorimer, 1985). Therefore, we used maple (*Acer saccharum* and *A. rubrum*) stem density for stems 0.25 cm in height to 0.1 cm dbh (~ 1.5 meters in height) as an indicator of within-patch forage availability.

Additional patch-scale variables of snow depth, elevation and patch area were derived using GIS and remotely sensed data. We calculated average winter snow depth using Snow Data Assimilation System (SNODAS) data, a 1-kilometer snow simulation model data set derived from daily satellite, aerial, and ground-based observations

(National Operational Hydrologic Remote Sensing Center, 2004). Daily snow conditions were averaged for the December 15-March 15 sampling period to calculate a seasonal mean and variance for snow depth at each study site. Patch elevation was derived from a 1:250,000-scale digital elevation model for Michigan. Since study sites selected for this study were initially defined by legal boundaries associated with ownership, in order to obtain a more accurate measurement for patch area independent of ownership we digitized hemlock patches from U.S. Geological Survey Digital Orthophoto Quadrangles (U.S. Geological Survey, 1998) using ArcGIS 9.2 software (ESRI).

To assess the influence of the landscape on hemlock patch use surrounding each study site we established 500, 1000, 3000, 5000, and 7000-meter concentric buffers from the edge of each hemlock patch (Fig. 1-1). Within each of these buffers we reclassified the landscapes into broader categories of *conifer*, *deciduous,* and *open* cover using 30-meter resolution land cover data (Figure 1-1 -Wisconsin Department of Natural Resources, 1998; Michigan Department of Natural Resources, 2001). Forested patches were reclassified as conifer or deciduous dependent on the composition of the overstory. If conifer species occupied more than 40% of the dominant crown cover, it was reclassified as conifer. Areas that contained less than 25% tree cover were considered to be open land, with the exception of aquatic and urban areas, which were classified as inaccessible background. We used FRAGSTATS (McGarigal *et al.*, 2002) to quantify the composition and configuration of the landscapes within each of our five concentric buffers surrounding the study patch (Table 1-1). Metrics were chosen *a priori* as those that are most likely to have biological significance to white-tailed deer winter habitat selection. Specifically, we chose metrics that quantified area, edge, fragmentation, and connectivity of our three cover types as well as the landscape as a whole (Dahlberg and Guettinger, 1956; Alverson *et al.*, 1988; O'Brien *et al.*, 2006).

To identify factors influencing winter use of hemlock patches, we used pellet groups per study patch as our dependant variable and local (snow, cover and browse) and landscape (e.g. edge, fragmentation, and connectivity) variables as our linear predictors in our model-building process (Table 1-1). Because our response variable represented count data, which we assumed followed a Poisson distribution, we used a generalized linear modeling (GLM) framework with a log-link to construct our models (Guisan and Zimmermann, 2000). Since sampling effort was a function of patch size (i.e., larger patches had a greater number of sample plots) it was also necessary to include an offset in our model (offset = log[plots]).

Because our data set included a large number of potential explanatory variables, we chose to carry out model building in a hierarchical process to avoid overfitting. First, using stepwise regression, we identified a *Patch-scale* model from within-patch cover, browse and snow variables (from here on referred to as *Patch-scale* models). Then, we identified alternate *Patch* + *Landscape* models for each of the five buffers.

We hypothesized that patch-scale attributes influencing deer winter use would vary as a function of the mean depth and within season variability in snow. To capture this variation, we modeled patch use both annually and across years for our *Patch-scale* models. To account for the explicit grouping in the *multi-year* model, we included patch as a random effect in the model intercept (Schabenberger and Pierce, 2002). Model parameters were estimated using maximum likelihood (Burnham and Anderson, 2002). We used Akaike Information Criterion (AIC) to identify the most parsimonious and biologically meaningful models (Burnham and Anderson, 2002). For each candidate model we calculated AIC weights (w_i) in order to determine the probability that the model in question was the best among the models being evaluated (Burnham and Anderson, 2002). All model fitting was performed in the R statistical environment, using the lme4 package (R Development Core Team, 2005; Bates and Sarkar, 2006).

Given the large number of potential landscape variables in the candidate *Patch + Landscape* models (Table 1-1), we used the following methods to identify alternate models of patch use for each of our five buffers. Building on our best multi-year *Patch-scale* model, we used a modified forward step-wise regression procedure to evaluate the additional contribution of landscape variables to the base *Patch-scale* model. Variables were added to the model individually and retained if their parameter estimate was significant at $\alpha = 0.05$. Then, since many landscape variables are collinear, we used Pearson's correlation coefficients to identify groups of variables in the resulting models that were highly correlated ($r \geq |0.6|$). Among groups of highly correlated landscape variables, the variable that resulted in the best improvement in model AIC score was retained (Riitters *et al.*. 1995; Woolf *et al.*, 2002; Zuur *et al*., 2009).

Results

Snow conditions across study patches were highly variable both on an inter- and intra-annual basis. Mean annual snow depths across all sites were 0.33, 0.25 and 0.43

meters for the 2005-06, 2006-07, and 2007-08 winters respectively (Table 1-2). Likewise, the number of hemlock patches utilized by wintering white-tailed deer varied between years, with 29, 27 and 32 of the 39 patches being used during consecutive winters, respectively (Fig. 1-2). Relative patch use was quite variable by study site; in some patches in excess of 1,500 pellet groups per hectare were deposited annually (Table 1-3). Within a given year, the relationship between patch use and patch attributes was influenced by year to year variation in snowfall, with patch attributes being less important in high snowfall years (Table 1-4).

For our *multi-year* model of winter patch use, elevation, snow and patch area are the variables most strongly associated with deer use at the patch-scale (Table 1-4). Parameter estimates indicate that patch use was negatively associated with patch elevation. The response to snow depth was parabolic in nature, with patch use increasing with an increase in mean annual snow depth to 38 centimeters before dropping off again (Fig. 1-3). Intra-annual variation in snow depth (standard error of snow depth) was negatively associated with patch use. Additionally, patch use increased with an increase in patch area. *Multi-year* models were greatly improved by the addition of the random effects term ($p \leq 0.001$).

Patch scale variables for cover were not significantly associated with patch use ($p > 0.05$), at least within the range of our data. Patch basal area ranged from 33.8 to 68.7 $m^2\ ha^{-1}$ with hemlock accounting for 21-84 % of the overstory basal area (Table 1-2). Maple browse, as an indicator of forage availability, was a good predictor in two out of three years (2005-06 and 2006-07) in our *annual* models of patch use. Browse, however, was not a good predictor in our *multi-year* model. Patches with browse exceeding 5,000 stems ha^{-1} were found to have high deer use; however, patches depauperate of available forage were also utilized as winter habitat.

For the *multi-year patch* + *landscape* models we were able to identify alternative models of patch use in four out of five buffer distances (Table 1-5). Within each buffer we retained all models within six units of AIC_{min}, because empirical evidence may exist in support for alternative models (Burnaham and Anderson, 2002). Scale of influence was most apparent in 3,000- and 5,000-meter buffers, where there was a decrease in excess of 13 AIC units from the *patch-scale* model (Table 1-4). Landscape attributes proximate to the patch, however, had little or no influence over patch use (i.e. 500- and 1,000-meter buffers).

Snow and elevation variables included in our *multi-year patch-scale* model remained significant predictors ($p \leq 0.05$) in all *patch* + *landscape* models, and patch area was significant in all but two of the retained models (Table 1-5). At the larger extent, greater buffer distances and the addition of measures of habitat fragmentation resulted in models that were better predictors of patch use than the *patch-scale* model. Parameter estimates for division (Div-ALL,DEC) and interspersion and juxtaposition of the open cover (IJI-OPEN) type in the 3,000- and 5,000-meter buffers suggest an increase in patch use with a decrease in patch adjacency or connectivity (Table 1-5). Overall, the two models that best explain our response variable were models 5 and 6 in the 3,000-meter buffer. While both include the IJI-OPEN index, model VI shows a negative association with mean patch size of deciduous cover type (Mn-DEC), an indicator of homogeneity in the landscape. At our coarsest scale, 7,000-meter buffer, hemlock patch use decreases with increasing percentage of the landscape occupied by the largest patch in the landscape (LP-DEC, ALL).

Discussion

Our results suggest that when trying to understand and manage for a highly mobile generalist species on a regional scale, direct measures of underlying behavioral mechanisms, i.e., selection of winter habitat, may provide less information on patch use than measures that also include composition, structure and configuration of the landscape surrounding the patch of interest. Across years, snow depth and elevation were the main drivers of patch use at all scales. However, when we moved to a scale beyond that which would include winter behavior of white-tailed deer, a scale that likely encompasses the summer range of deer, we had a positive accumulation of explanatory information with the inclusion of measures of landscape composition and configuration. Our best-fit models of patch use were found at the 3,000-meter spatial scale, where heterogeneity in the landscape, or the lack thereof, was associated with use of hemlock patches as winter habitat.

Habitat selection takes place at hierarchical-spatial scales (Wiens, 1976; Johnson 1980), but it remains unclear which of these scales is most influential to patch use. Consistent with other landscape-scale studies of ungulate habitat selection, heterogeneity had a positive influence on patch use (Kie *et al.*, 2002; Boyce *et al.*, 2003; Mayor *et al.*, 2007). Our best-fit models, however, were those at the greatest spatial scales, buffer widths in excess of 3,000 meters, and an area of influence that far exceeds what previous studies suggest to be the maximum home range size for white-tailed deer on their wintering grounds (Tierson *et al.*, 1985; Beier and McCullough, 1990; Van Deelen *et al.*, 1998). Conversely, proximate landscapes, those within 1,000 meters of the hemlock patch, had little influence over patch use. While we do know that the composition and structure of the landscape in close proximity to winter conifer cover is important for white-tailed deer (Morrison *et al.*, 2003), our results suggest that habitat selection is being influenced, initially, at a much greater spatial scale.

While habitat characteristics influence habitat selection at all spatial scales, it has been hypothesized that it is the greatest spatial scales that limit the fitness of a population or individual and therefore also limit habitat use (Rettie and Messier, 2000; Dussault *et al.*, 2005). Forest management practices of the region have led to a study area that is dominated by second- and third-growth deciduous forests, which are to varying degrees occupying much of the landscape surrounding these remnant patches of hemlock, and the negative influence of this homogenous cover type was evident, as well as implied, in our three greatest spatial extents. Large expanses of closed-canopy forests, those lacking in edge and therefore available browse, would be poor habitat for deer (Blouch, 1984). Since the greater landscapes surrounding winter habitat likely serve as a source for wintering deer (Nelson and Mech, 2006), we suggest that large expanses of deciduous cover in the landscapes surrounding the patch of interest may be the primary constraint to use of what might otherwise be high-quality winter habitat, and thus supporting the hierarchical scale of limiting factors proposed by Rettie and Messier (2000).

This influence of patch isolation, decreasing patch occupancy with increasing isolation, has been a tenet of landscape ecology for decades, where access to high-quality habitat has been shown to be impeded by a matrix of less than hospitable cover (c.f. Ricketts, 2001; Bradford *et al*. 2003; Bender and Fahrig, 2005). Our results indicate a negative response to an increase in patch size of contiguous deciduous cover in the greater landscape, and we suggest that hemlock habitat embedded in a landscape of mature hardwood cover may be effectively isolated from use by wintering deer, especially in areas of higher snow depth. The composition of the matrix does, to a greater or lesser degree, influence patch occupancy (Gustafson and Gardner, 1996; Ricketts, 2001; Bradford *et al*., 2003; Bender and Fahrig, 2005), and the probability of occupying a patch depends, in part, on the ability of a species to detect it (Olden *et al*., 2004). While vast areas of mature hardwood forest type would be poor habitat for deer during any season, snow conditions have the potential to exacerbate this relationship. Snow cover has the potential to modify and even diminish the availability of forage (Turner *et al.,* 1997; Nordengren *et al*., 2003), while simultaneously increasing the energetic cost to movement (Parker *et al*., 1984; Fancy and White, 1985). Since snow accumulation under hardwood canopies has been shown to be significantly greater than that of adjacent conifer patches (Kirchhoff and Schoen, 1987), large patches of deciduous cover type may effectively limit the detection of or accessibility to high-quality winter habitat.

Across years, mean winter snow depth and elevation were important predictors of patch use at all spatial scales. Our results are consistent with research suggesting that at snow depths of 30-40 cm deer begin to or have already moved into winter habitat (Drolet

1976; Nelson and Mech, 1981; Tierson *et al.,* 1985; Sabine *et al.*, 2002). In response to changes in snow depth, Morrison *et al.* (2003) found that during periods of low snow, white-tailed deer in New Brunswick spent more time in close proximity to browse on their wintering grounds. Conversely, at higher snow depths greater than 0.5 meters, deer were associated with areas of better cover. Our *multi-year* models suggest that deer yarding intensity, as predicted by pellet group counts, increases with increasing mean seasonal snow depth, and relative deer use peaks as mean snow depth approaches 0.4 meters (Fig. 1-3). However, at snow depths beyond 0.4 meters, we saw an inverse in this relationship, suggesting fewer deer are found in the areas of highest snow depth. Additionally, our *annual* models suggest that at a lower mean annual snow depth deer were more closely associated with the availability of within-patch forage. In our highest snow-depth winter (2007-08, 0.43 meter average snow depth) more hemlock patches were utilized by wintering deer than in lower snow-depth years (Fig. 1-2), and our best models of patch use no longer included forage availability.

We found no significant relationship between elevation and snow. Minor increases in elevation along the Lake Superior shoreline often lead to a significant gain in winter precipitation and a resultant snow shadow in areas adjacent to the lake (Stottlemyer and Toczydlowski, 1991). Across the study area a mixture of lake-effect and regional snowfall trends may be masking a more localized relationship between snowfall and elevation found in close proximity to Lake Superior.

In contrast to landscape heterogeneity, deer tended to spend less time in hemlock patches with increasing heterogeneity in snow depth. This was evident both within and between years (Fig. 1-2). The decision to leave a patch is often based on the quality and availability of forage versus the cost of moving to a new patch (Senft et al., 1987). Snow depth and density have been shown to impede ungulate foraging and movement (Parker *et al.*, 1984), therefore leading to an increased cost to movement in higher snow depth winters. While hemlock is a common browse species of deer during winter (Dahlberg and Guettinger, 1956), overbrowsing by deer and other limits to hemlock regeneration and recruitment across the region have led to hemlock patches devoid of available understory browse (c.f. Anderson and Loucks, 1979; Frelich and Lorimer, 1985; Mladenoff and Stearns, 1993; Rooney *et al.*, 2000). Deer must, therefore, find a balance in the trade-off between winter cover and browse acquisition. While our study did not directly measure deer density or time spent in hemlock patches, it was clear that the intensity of winter yarding was lower in low snow and highly variable snow years (Fig. 1-2). Since hemlock patches across the region provide little available browse, our data are congruent with the findings of Morrison et al. (2003) that deer will select for areas of better forage during periods of lower snow depth. Thus, yearly heterogeneity in snow depth, as well as lower snow years, may allow the food-cover trade-off balance to be weighted more toward browse acquisition than in higher snow years.

Processes, and therefore behaviors, underlying habitat selection are dynamic, and among ungulate behaviors, site fidelity and predator avoidance are some of the additional factors that have been shown to have an influence on ungulate winter habitat selection (Nelson, 1998; Van Deelen *et al.,* 1998; Rettie and Messier, 2000; Creel *et al.*, 2005; Nelson and Mech, 2006). After a 30-year absence, the Upper Peninsula of Michigan has experienced a recent re-colonization by grey wolves (*Canis lupus*) and since wolf densities of the region are highly correlated with deer densities (Potvin *et al.*, 2005), this has likely led to shifts in deer winter habitat use. We expect that patch use in highly heterogeneous landscapes is being influenced, to a greater or lesser degree, by the presence of predators. However, we expect that even with a growing predator population, isolated or high-snow region hemlock patches will still likely not be used as winter habitat unless heterogeneity is increased in the landscape surrounding those patches. Further research should explore how land use practices in close proximity to winter habitat, especially those practices that may provide additional forage, influence patch fidelity and the intensity of patch use.

Management Implications

White-tailed deer, like many ungulates, play an important role in ecosystem processes; however, because of their ability to alter successional trajectories and foster the development of alternate stable states with cascading effects on the biota, white-tailed deer are considered by many to be a keystone species (Rooney and Waller, 2003). Previous research suggests the deer densities for our study area are more than double those of pre-European settlement times (Doepker *et al.*, 1994), yet contemporary hemlock is at just a fraction of its historic abundance (Whitney, 1987). It is the browsing pressure exerted by these increased concentrations of wintering deer that are thought to be one of the major factors limiting hemlock recruitment (c.f., Anderson and Loucks, 1979; Frelich and Lorimer, 1985; Mladenoff and Stearns, 1993; Rooney *et al.*, 2000). Thus, balancing the need to provide adequate winter habitat for deer while maintaining healthy and self-perpetuating hemlock patches has become a dilemma. Our research suggests that, while it is clear that the hemlock patch itself is an important resource for wintering deer, the trade-off between risk and reward at the coarse scale of the greater landscapes may be the most influential factor influencing use of these remnant patches of habitat. Management decisions made regarding specific patches would, therefore, likely be ineffective unless the greater landscape was taken into consideration. For example, habitat modifications that lead to increased heterogeneity in the greater landscapes surrounding hemlock have the potential to lead to increased concentrations of wintering deer, thereby increasing within-patch browse pressure. In contrast, modifications made within or proximate to the patch of interest may have little influence over winter deer use if the patch remains isolated in a seemingly homogenous landscape.

Table 1-1. Patch and landscape variables.

Local and landscape scale variable codes, description, units and source of data. Variables were used to model eastern hemlock patch use in a generalized linear mixed effect modeling framework with hemlock patch ID as the random effects term.

Scale	Code	Variable name	Source/description/units
SNOW			
Local	SN	Mean snow depth	NOHRSC-SNODAS 2004 (meters)
Local	SN-SE	Mean snow depth standard error	NOHRSC-SNODAS 2004 (meters)
Local	ELE	Elevation	90-m Digital Elevation Model (DEM) (meters)
COVER			
Local	AREA	Eastern hemlock stand size	Stands selected using USDA Forest Service Forest Type data 1998 and digitized using USGS Digital Orthophotos 1998 (hectares)
Local	HEM_BA	Basal area eastern hemlock	Field measurement (m^2 ha^{-1})
Local	HEM_Pct	Eastern hemlock percent of total basal area	Field measurement (percent)
BROWSE			
Local	BROWSE	*Available browse - Acer spp.* (stems 0.25m in height to 0.1cm dbh)	Field measurement (stems ha^{-1})
LANDSCAPE *			Landscape metrics were calculated in FRAGSTATS (McGarigal 2002) using Michigan IFMAP-GAP land cover data 2001 and WISCLAND land cover data 1998.
Patch area, shape and edge metrics			Metric description
Landscape	Pct	Percent cover	Percent of landscape
Landscape	NP	Number of patches	Number of patches
Landscape	PD	Patch density	Number of patches divided by buffer area
Landscape	LP	Largest patch index	Percent of landscape occupied by the largest patch
Landscape	Edge	Total edge	Length of edge
Landscape	ED	Edge density	Length of edge divided by buffer area
Landscape	Mn	Mean patch size	Average patch size
Landscape	AM	Area weighted mean patch size	Average patch size divided by buffer area
Landscape	Md	Median patch size	Median patch size
Landscape	SD	Patch size standard deviation	Standard deviation of patch size
Landscape	CV	Patch size coefficient of variation	Standard deviation of patch size divided by mean patch size
Landscape	Shape	Landscape shape index	Total length of edge divided by minimum possible total length of edge
Connectivity, fragmentation and heterogeneity metrics			Metric description
Landscape	Adj	Percentage of like adjacencies	Measure of dispersion of cover type. Decreasing values indicate a increasing disaggregation of cover type.
Landscape	Clump	Clumpiness index	Measure of dispersion of cover type scaled for proportion of landscape occupied by patch type. Values range = -1 > Clump < 1, where a value of zero indicates randomly dispersed patches of indicated cover type. Lower values indicate more disaggregated, whereas higher values indicate higher aggregation.
Landscape	Coh	Patch cohesion index	Measure of physical connectedness of indicated cover type. Increasing values of cohesion indicate a more physically connected cover type.
Landscape	Div	Patch division index	Measure of patchiness of cover type. Increase in proportion indicates a decrease in connectedness.
Landscape	Agg	Aggregation index	Measure of dispersion of specified cover type. Higher values indicate a greater level of aggregation.
Landscape	Split	Splitting index	Measure of patchiness of cover type. Split increases as the cover type is divided into smaller pieces.
Landscape	IJI	Interspersion and juxtaposition index	Measure of patch adjacency. Higher values indicate uneven adjacency for indicated cover type, while lower values indicate that all patches are equally adjacent.

* Landscape variables modified by cover type - Conifer (CON), deciduous (DEC), open (OPEN), or patches of all cover types (conifer, deciduous and open) within a buffer (ALL). For a more thorough description of landscape metrics, see McGarigal et al. 2002.

Table 1-2. Descriptive statistics for patch level variables.
Descriptive statistics for patch level variables used to develop Local-base model in generalized linear mixed effects model-building process.

	Code	Variable	Min.	Max.	Mean	St. Dev.
Snow						
	SN	Mean snow depth (meters)				
	Winter 2005-06		0.08	0.51	0.33	0.11
	Winter 2006-07		0.15	0.46	0.25	0.07
	Winter 2007-08		0.28	0.64	0.43	0.09
	SN-SE	Standard error of mean snow depth				
	Winter 2005-06		6.12	22.56	14.51	3.88
	Winter 2006-07		10.17	25.16	17.50	4.44
	Winter 2007-08		9.00	18.39	12.93	2.58
Cover						
	AREA	Stand area (hectares)	0.04	59.6	14.4	14.1
	HEM_BA	Eastern hemlock basal area (m^{2} ha^{-1})	8.0	57.6	24.0	12.1
	HEM_Per	Eastern hemlock percentage of overstory	21.4	85.4	51.9	16.9
	ELE	Elevation (meters)	186.3	555.7	405.3	109.7
Browse						
	BROWSE	Browse available - Acer spp. (stems ha^{-1})	0	31500	3589	6162

Table 1-3. Descriptive statistics of seasonal deer use.
Descriptive statistics of white-tailed deer fecal pellet groups ha^{-1} deposited annually in the 39 eastern hemlock study patches.

Year	Mean pellet groups ha^{-1}	Minimum pellet groups ha^{-1}	Maximum pellet groups ha^{-1}	SD of pellet groups ha^{-1}
2005-06	496	0	2296	614
2006-07	282	0	1722	423
2007-08	504	0	2260	528

Table 1-4. Annual models of patch use.
Parameter estimates and AIC scores for *annual* versus null (intercept-only) models of patch use. Variables in models were significant ($p < 0.05$). Annual models were significant versus the Null model in likelihood ratio tests ($p < 0.05$). Note: See Table 2 for a description of patch-scale variables.

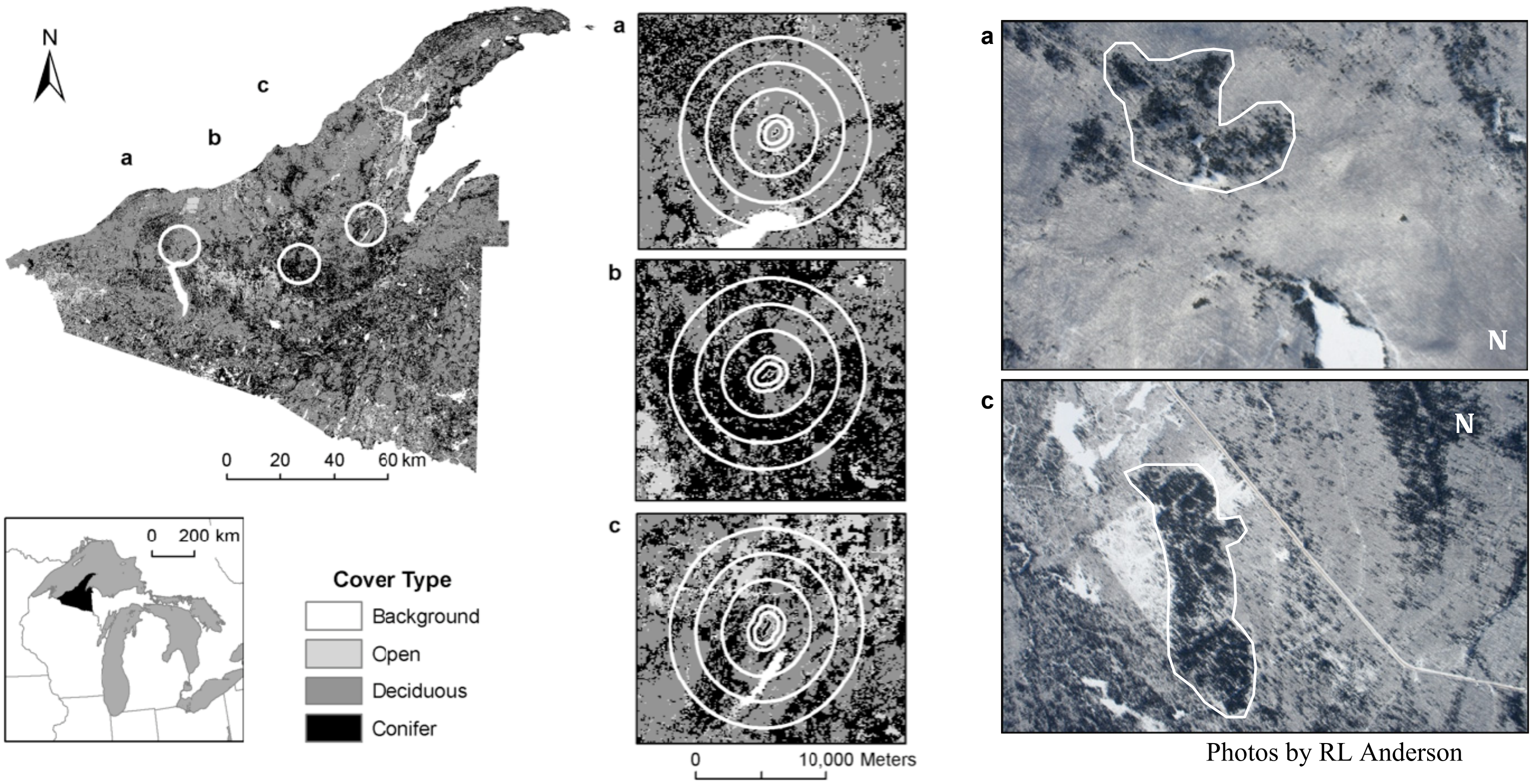
Winter	Model	Parameter estimates					AIC
		Int	**ELE**	**SN**	**Area**	**Browse**	
2005-06	I	0.46	-0.0046		0.022	0.000032	313.5
	Null	-0.52					502.9
2006-07	II	0.49	-0.0060		0.014	0.000044	218.8
	Null	-1.15					345.9
2007-08	III	2.34	-0.0055	-3.2	0.021		242.3
	Null	-0.65					372.1

Table 1-5. Multi-year models of patch use.

Parameter estimates, AIC, ΔAIC, and Akaike weights for *multi-year* patch and patch + landscape scale* models for the 500, 1000, 3000, 5000 and 7000-meter buffer distances using a generalized linear mixed effects modeling framework with hemlock patch ID as the random effect. All variables in models were significant ($p < 0.05$).

Model	Parameter estimates									AIC	ΔAIC	ω_i
Patch-scale												
	Int	**ELE**	**SN**	**$(SN)^2$**	**SN-SE**	**Area**						
I	-1.0	-0.0049	9.75	-13.04	-0.038	0.029				296.7	18.7	0.00
500 meter buffer – patch + landscape												
	Int	**ELE**	**SN**	**$(SN)^2$**	**SN-SE**	**Area**	**CV-DEC**					
II	-1.8	-0.0044	9.80	-13.03	-0.036		0.004			294.8	16.8	0.00
1000 meter buffer - patch + landscape												
	No variables in addition to the Stand-scale model were significant in this buffer.											
3000 meter buffer - patch + landscape												
	Int	**ELE**	**SN**	**$(SN)^2$**	**SN-SE**	**Area**	**Mn-DEC**	**IJI-OPEN**	**Div-ALL**			
III	0.6	-0.0066	9.40	-12.45	-0.035	0.021	-0.077			283.7	5.7	0.03
IV	-3.9	-0.0052	9.53	-12.55	-0.034	0.025			4.13	282.5	4.5	0.04
V	-8.2	-0.0056	9.40	-12.46	-0.036	0.017		0.058	3.09	278.0	0.0	0.51
VI	-5.7	-0.0063	9.29	-12.34	-0.036		-0.057	0.071		279.3	1.3	0.27
5000 meter buffer - patch + landscape												
	Int	**ELE**	**SN**	**$(SN)^2$**	**SN-SE**	**Area**	**Div-DEC**	**Div-ALL**				
VII	-3.9	-0.0070	9.42	-12.43	-0.035	0.025	4.397			281.7	3.7	0.08
IX	-4.3	-0.0058	9.70	-12.74	-0.033	0.023		4.79		282.4	4.4	0.06
7000 meter buffer - patch + landscape												
	Int	**ELE**	**SN**	**$(SN)^2$**	**SN-SE**	**Area**	**LP-DEC**	**LP-ALL**				
X	0.7	-0.0071	9.58	-12.66	-0.035	0.025	-0.028			288.5	10.5	0.00
XI	0.3	-0.0055	9.77	-12.87	-0.034	0.028		-0.03		289.6	11.6	0.00

* Landscape variables modified by cover type: Conifer (CON), deciduous (DEC), open (OPEN), or patches of all cover types (conifer, deciduous and open) within a buffer (ALL). Note: See Table 1 for landscape variable descriptions.



Photos by RL Anderson

Figure 1-1. ***Tsuga canadensis*** **study stands with buffers depicted.**
Western Upper Peninsula of Michigan study area (*left*) with land cover types of conifer, deciduous, open, and background as reclassified from IFMAP and WISCLAND 30 x 30 meter resolution land cover data. Insets (*middle*) are close ups of eastern hemlock study patches with concentric circles representing 500, 1000, 3000, 5000, and 7000-meter buffers surrounding patch. Aerial photos (*Right*; Photographs by R.L. Anderson, 2008) depict hemlock study patches (outlined in white) and the surrounding snow-covered landscape. Letters indicate specific study patches and their locations within the study area.

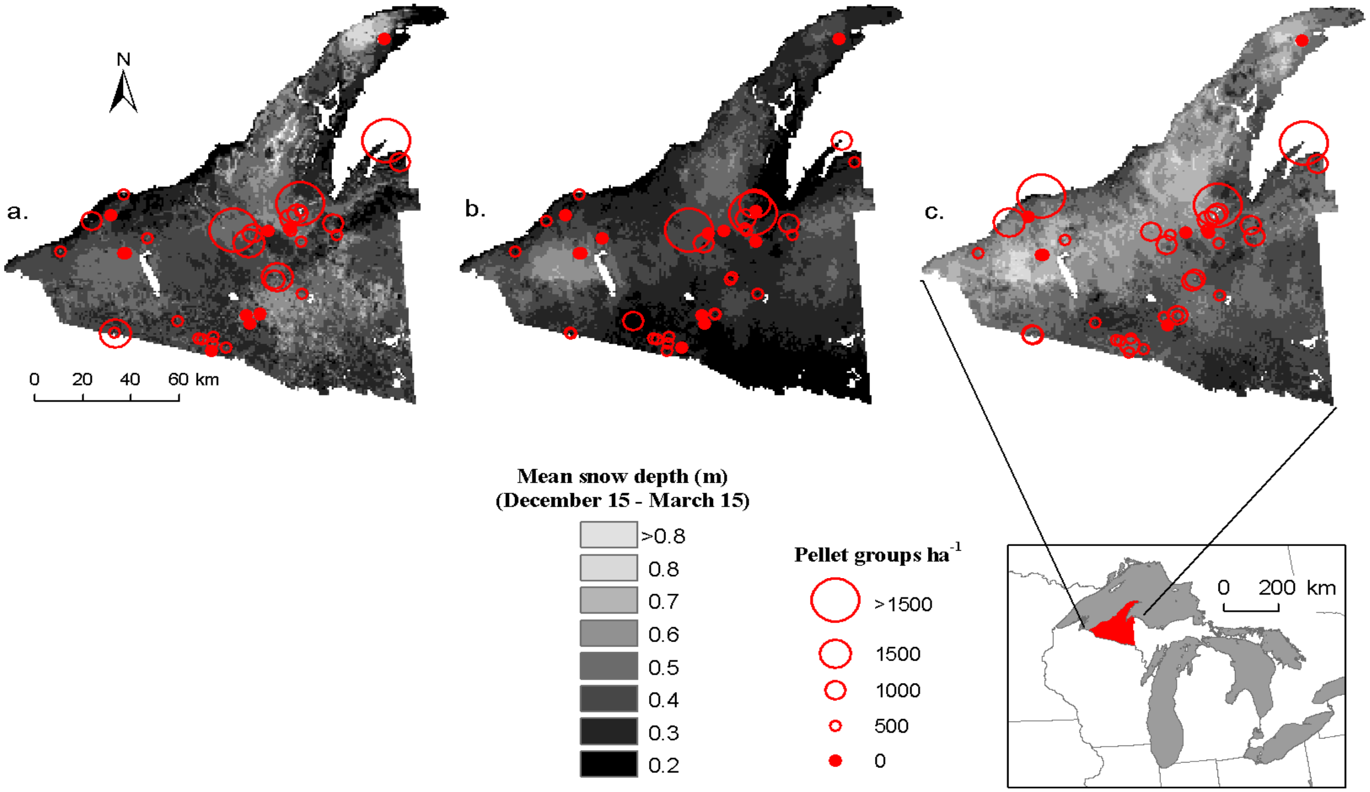


Figure 1-2. Seasonal snow depth and deer use.
Mean seasonal snow depth (December 15 – March 15) for the study periods, winter 2005-06, 2006-07, and 2007-08 (National Operational Hydrologic Remote Sensing Center, 2004). Red circles indicate relative patch use (pellet groups per ha^{-1}) of eastern hemlock patches by wintering white-tailed deer as determined by post-snowmelt pellet group counts.

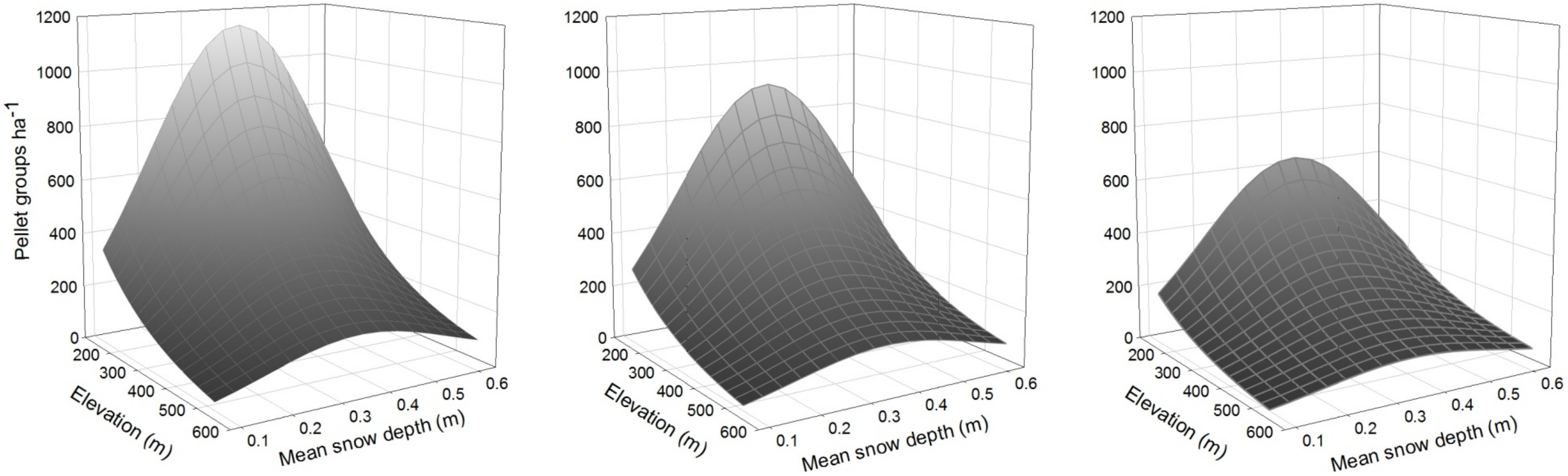


Figure 1-3. Multi-year models predicted patch use.

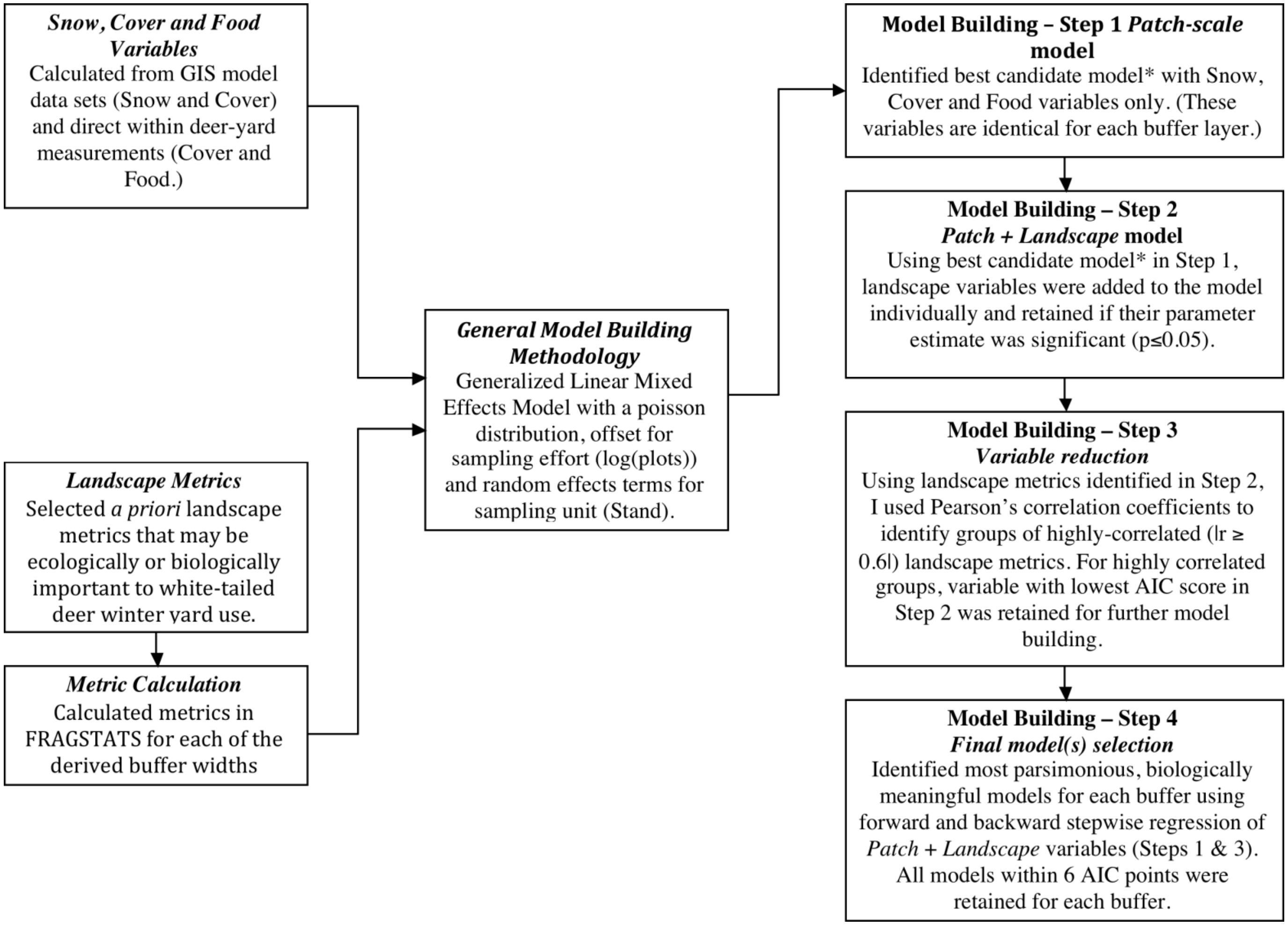
Predicted pellet groups per hectare for *multi-year* patch-scale model as a function of mean snow depth and elevation. Plots depict predicted values at three levels of eastern hemlock patch area as determined by 25, 50 and 75% quartiles within the range of our data: a) patch area equal to 21.5 hectares, b) patch area equal to 14.4 hectares, and c) patch area equal to 2.5 hectares.

APPENDIX 1-1. Land cover reclassification.

Using 30-meter resolution Ifmap and Wiscland land cover data set (Figure 1-1; Wisconsin Department of Natural Resources, 1998; Michigan Department of Natural Resources, 2001), land cover was reclassified into the following four categories: *open, deciduous, conifer* and *background* for each of the five buffer distances used in this analysis.

Land cover classification name	Code	Reclassification category	Reclassification code
Background	-999	background	-999
Low intensity urban	110	background	-999
High intensity urban	123	background	-999
Airports	121	background	-999
Roads/paved	122	open	1
Non-vegetated farmland	2111	open	1
Row crops	2112	open	1
Forage crops/non-tilled herbaceous	2113	open	1
Orchard/vineyard/nursery	222	open	1
Herbaceous openland	310	open	1
Upland shrub/low-density tree	320	open	1
Parks/golf course	350	open	1
Northern hardwood association	411	deciduous	2
Oak association	412	deciduous	2
Aspen association	413	deciduous	2
Other upland deciduous	414	deciduous	2
Mixed upland deciduous	419	deciduous	2
Pines	421	conifer	3
Other upland conifers	423	conifer	3
Mixed upland conifers	429	conifer	3
Upland mixed forest	431	conifer	3
Water	500	background	-999
Lowland deciduous forest	611	deciduous	2
Lowland conifer forest	612	conifer	3
Lowland mixed forest	613	conifer	3
Floating aquatic	621	background	-999
Lowland shrub	622	open	1
emergent wetland	623	background	-999
Mixed non-forested wetland	629	open	1
Sand/soil	710	open	1
Exposed rock	720	open	1
Mud flats	730	open	1
Other bare/sparsely vegetated	790	open	1

APPENDIX 1-2. Flow chart of model building process for *multi-year* models of patch use.



Snow, Cover and Food Variables
Calculated from GIS model data sets (Snow and Cover) and direct within deer-yard measurements (Cover and Food.)

Landscape Metrics
Selected *a priori* landscape metrics that may be ecologically or biologically important to white-tailed deer winter yard use.

Metric Calculation
Calculated metrics in FRAGSTATS for each of the derived buffer widths

General Model Building Methodology
Generalized Linear Mixed Effects Model with a poisson distribution, offset for sampling effort (log(plots)) and random effects terms for sampling unit (Stand).

Model Building – Step 1 *Patch-scale* model
Identified best candidate model* with Snow, Cover and Food variables only. (These variables are identical for each buffer layer.)

Model Building – Step 2
***Patch + Landscape* model**
Using best candidate model* in Step 1, landscape variables were added to the model individually and retained if their parameter estimate was significant ($p \leq 0.05$).

Model Building – Step 3
Variable reduction
Using landscape metrics identified in Step 2, I used Pearson's correlation coefficients to identify groups of highly-correlated ($|r \geq 0.6|$) landscape metrics. For highly correlated groups, variable with lowest AIC score in Step 2 was retained for further model building.

Model Building – Step 4
Final model(s) selection
Identified most parsimonious, biologically meaningful models for each buffer using forward and backward stepwise regression of *Patch + Landscape* variables (Steps 1 & 3). All models within 6 AIC points were retained for each buffer.

* *Best candidate models* were identified as those models with the lowest AIC scores and where all predictors in the model were significant ($p < 0.05$).

APPENDIX 1-3: R Code for Model Building Step 2.

See Appendix 2-1 for model building process. Landscape variables were added to the Patch-scale model individually and retained if their parameter estimate was significant (p ≤ 0.05). All model fitting was performed in the R statistical environment, using the lme4 package (R Development Core Team 2005; Bates & Sarkar, 2006).

```
land <- read.table("land_variables_1000.txt", header=T)

model <- glmer(total.pellet ~  LANDSCAPE VARIABLE + elevation + snow.mean.m +
        snow.mean.sq  + snow.se +  stand.area + offset(log(plots)) + (1|Stand), data =
        land, family=poisson)
        summary(model)
```

APPENDIX 1-4. R Code for Pearson's correlation coefficient calculations.

Coefficients were used to determine correlations between landscape variables for use in variable reduction. See Appendix 2-1 for description of variable reduction.

```
cor.prob <- function(X, dfr = nrow(X) - 2) {
R <- cor(X)
above <- row(R) < col(R)
r2 <- R[above]^2
Fstat <- r2 * dfr / (1 - r2)
R[above] <- 1 - pf(Fstat, 1, dfr)
R
}
cor.land.500 <- cor.prob(land.500)
write.csv(cor.land.500, file="cor_land_500.csv")
```

APPENDIX 1-5. R Code for random effects term test for significance.
Likelihood ratio test was used to compare final model with a random effect term (L0) to model without a random effect term (L1).

```
rt <- function (obj1, obj2) {
L0 <- logLik(obj1)
L1 <- logLik(obj2)
L01 <- as.vector(- 2 * (L0 - L1))
+      df <- attr(L1, "df") - attr(L0, "df")
+      list(L01 = L01, df = df,
+          "p-value" = pchisq(L01, df, lower.tail = FALSE))}
lrt(L0, L1)

L0 <-  glmer(total.pellet ~ offset(log(plots)) + elevation + snow.mean.m + snow.mean.sq
+ snow.se + stand.area + (1|Stand), data = land, family=poisson)

L1 <-  glm(total.pellet ~ offset(log(plots)) + elevation + snow.mean.m + snow.mean.sq +
snow.se + stand.area, data = land, family=poisson)
```

APPENDIX 1-6. Significant variables and AIC scores for landscape variables used in model building step 2.

Significant ($p < 0.05$) landscape variables and associated AIC scores for patch-scale model plus individual landscape variables used in Variable Reduction part 2 (See Appendix 1-2. See Table 1-1 for a list and description of all landscape variables. Correlation code refers to groups of highly correlated variables ($|r \geq 0.60|$). Among groups of highly correlated landscape variables, the variable that resulted in the best improvement in model AIC score was retained for further model comparison. Retained landscape variables are denoted below by an asterisk (*).

500-meter buffer	AIC	Correlation Code	100- meter buffer	3000-meter buffer	AIC	Correlation Code	5000-meter buffer	AIC	Correlation Code	7000-meter buffer	AIC	Correlation Code
dec.area.cv*	295.3	1	no significant variables	con.area.cv*	294.6	6	con.area.cv*	293.3	5	dec.pland	290.5	1
con.nlsi*	295.5	2		con.iji*	294.9	7	con.cohesion	293.0	1	dec.lpi*	288.5	1
open.split*	301.0	3		con.cohesion	290.1	3	con.nlsi	294.6	1	dec.area.am	288.5	1
				con.split*	288.9	3	dec.pland	290.1	2	dec.area.sd	293.6	1
				con.nlsi	291.3	3	dec.lpi	284.5	1,2	dec.area.cv	293.5	1
				dec.pland	290.9	2	dec.area.mn	294.0	1,2	dec.division	287.7	1,2
				dec.lpi	288.1	2	dec.area.sd	288.1	1,2	dec.mesh	287.8	1,2
				dec.area.mn*	283.7	2	dec.area.cv*	292.9	6	dec.ai	292.7	1,2
				dec.area.am	288.0	2	dec.pladj	293.4	2	open.lpi*	294.4	3
				dec.area.sd	284.9	2	dec.division*	281.7	1,2	open.area.mn	294.7	3
				dec.pladj	294.7	2	dec.mesh	282.3	1,2	open.area.sd	294.4	3
				dec.division*	285.5	2	dec.ai	293.4	2	land.lpi*	289.6	2,4
				dec.mesh	286.1	2	dec.nlsi*	292.3	7	land.area.am	292.9	2,4
				dec.nlsi*	290.5	1	land.lpi	282.5	3	land.area.sd	292.2	2,4
				open.iji	286.8	8	land.area.am	284.6	3	land.area.cv	292.4	4
				open.division*	294.4	5	land.area.sd	286.7	3	land.contagion	293.3	2,4
				open.mesh	294.4	5	land.area.cv	283.5	3	land.cohesion	293.1	4
				land.lpi	284.1	1	land.contagion	291.0	3	land.division	291.6	2,4
				land.area.am	282.5	1	land.cohesion	286.8	3	land.mesh	293.9	2,4
				land.area.sd	283.7	1	land.division*	282.4	3	land.ai	294.7	2,4
				land.area.cv	287.1	1	land.mesh	283.2	3			
				land.contagion	285.0	1,4						
				land.pladj	293.5	4						
				land.cohesion	286.9	1						
				land.division*	282.5	1						
				land.mesh	282.8	1						
				land.split*	294.1	9						
				land.ai	293.7	4						

CHAPTER TWO

Regeneration dynamics in remnant *Tsuga canadensis* stands in the northern Lake States: potential direct and indirect effects of herbivory[2]

Abstract

We examined the effects of white-tailed deer (*Odocoileus virginianus*) use of hemlock as winter habitat and microsite limitation on *Tsuga canadensis* regeneration in 39 randomly-selected remnant *T. canadensis* stands in Michigan's Upper Peninsula. Deer of the region migrate to and congregate in *T. canadensis* stands in winter resulting in strong seasonal habitat use patterns. In each study stand, we quantified vegetation, microsite availability, and deer use (via pellet counts). While some stands contained high densities of *T. canadensis* regeneration (stems < 4.0 cm dbh), we found complete *T. canadensis* regeneration failures in 6 out of 39 stands. Additionally, 17 and 22 stands respectively, had complete failures in the small and large sapling categories. Data suggested that deer use was associated with low values of small saplings, even at relatively low levels of deer use. *Tsuga canadensis* seedling density was positively associated with the availability of high-decay coarse woody debris and negatively associated with basal area of *Acer saccharum* in the overstory. This latter association may be due, at least in part, to negative effects of broad-leaf litter on *T. canadensis* establishment and a general trend toward increasing *Acer* abundance in the regeneration layer. Our results suggest that differential tolerance to browsing (*Tsuga v. Acer*) in conjunction with reduced germination substrate availability may set up a scenario where

---

[2] This chapter has been accepted, as a manuscript by Witt, JC and Webster, CR, for publication pending minor revisions in *Forest Ecology and Management*.

successful *T. canadensis* establishments is more limited by legacy and indirect effects, than direct effects given contemporary levels of deer use.

Introduction

Plant species most susceptible to the negative effects of herbivory are often those that are either more palatable, and therefore more commonly browsed by ungulates, or less resilient to the effects of browsing than equally palatable species (Augustine and McNaughton, 1998). In the case of an overabundant herbivore population, this difference in tolerance or palatability can directly lead to the suppression or elimination of more susceptible species (Brandner *et al.*, 1990; Horsley *et al.*, 2003; Holmes *et al.*, 2009), as well as an increase in abundance or dominance of more tolerant (Van Hees *et al.*, 1996; Horsley *et al.*, 2003), less palatable (Horsley *et al.*, 2003; Husheer *et al.*, 2003; Côté *et al.*, 2004), or even invasive species (Kellogg and Bridgham, 2004). Once species that are better adapted to environments with higher levels of herbivory become established, factors such as life history traits (Schmitz and Sinclair, 1997), disturbance interactions (Dublin *et al.*, 1990; Webster *et al.*, 2008), and changes in soil or nutrient composition (Hobbs, 1996; Hulme, 1996) may interact with herbivory to further hinder establishment or growth of more palatable or less tolerant species, even in the event of reduced herbivory (Augustine and McNaughton, 1998; Webster *et al.*, 2008).

Failures in the regeneration of *Tsuga canadensis* (eastern hemlock) throughout the Upper Great Lakes region have been noted as far back as the 1940s (Maissurow, 1941), and white-tailed deer (*Odocoileus virginianus*) herbivory is often cited as the main limitation to recruitment (Anderson and Loucks, 1979; Frelich and Lorimer, 1985;

Alverson *et al.*, 1988; Waller and Alverson, 1997; Rooney *et al.*, 2000). In addition to localized herbivory, an absence of appropriate microsites for establishment (e.g., high-decay coarse woody debris, bare soil of tip-up mounds, moss) may be prohibiting *T. canadensis* establishment in some stands (Goder, 1961; Frelich and Lorimer, 1985; Rooney and Waller, 1998; Rooney *et al.*, 2000; Marx and Walters, 2008). At the regional scale, regeneration may be episodic and depend, in part, on periodic climate or disturbance events (Stearns, 1951; Mladenoff and Stearns, 1993). Currently, *T. canadensis*, once a major component of northern forests, is at a mere fraction of its former abundance due, in part, to historic and contemporary land use practices (Whitney, 1987; Mladenoff and Stearns, 1993). What remains is found in small, remnant patches surrounded to varying degrees by second- and third-growth deciduous forest (Alverson *et al.*, 1988). Across the region, many of these remnant stands appear to be experiencing little or no *T. canadensis* regeneration, while others seem to have adequate and even copious amounts.

Across the northern portion of their range, white-tailed deer respond to harsh winter conditions (i.e, high snow depth) by migrating to and congregating in areas of dense conifer, which are thought to provide lower snow depths for ease of movement and predator avoidance in addition to refuge from harsh winter conditions (Blouch, 1984; Nelson and Mech, 2006). Throughout the Upper Great Lakes region where seasonal snowfall can exceed six meters, deer utilize remnant stands of *T. canadensis* as winter habitat. Selection of winter habitat is thought to be driven by a trade-off between habitat providing for better cover and habitat providing for greater forage availability, i.e. during winters with higher snow depths deer will use *T. canadensis* stands as habitat regardless of forage availability (Morrison *et al.*, 2003; Witt *et al.*, 2010). In addition to *T. canadensis*, understory *Acer saccharum* (sugar maple) buds are common winter forage for deer, and several studies have used a maple browsing index as a surrogate for the intensity of within-stand winter deer herbivory (Frelich and Lorimer, 1985; Rooney *et al.*, 2000). Like *T. canadensis*, however, densities of *A. saccharum* saplings are highly variable. In stands lacking this species component, an *Acer* browse index would be a poor indicator of the intensity of herbivory, whereas direct measure of deer use may provide insights into browsing impacts that may otherwise be obscured by the lack of an indicator species.

Acer saccharum and *T. canadensis*, both late-successional species, show a negative reciprocal association between overstory tree species and understory regeneration, giving these two late-successional species the potential to form nearly homogenous patches across the landscape (Frelich *et al.*, 1993). However, even small inclusions of *A. saccharum* in the overstory of *T. canadensis* stands may be setting up a scenario where seedbed conditions could favor *A. saccharum* regeneration. The input of deciduous litter in a primarily *T. canadensis* stand could lead to an increase in nutrient cycling and altered soil properties, which may, in turn, create a micro-mosaic of seedbed conditions, some of which could favor *A. saccharum* establishment (Pastor and Mladenoff, 1992). Deciduous litter also has the potential to cover important microsites for *T. canadensis* seedling establishment, while simultaneously increasing the potential for seedling desiccation (Mladenoff and Stearns, 1993).

In this paper, we examine the effects of deer herbivory and microsite limitation on *T. canadensis* regeneration and recruitment. We hypothesize that white-tailed deer herbivory presents a direct bottleneck to *T. canadensis* recruitment, especially in larger regeneration size classes. In smaller seedling and sapling size classes, however, we hypothesize that indirect effects should predominate. We suspect that deer herbivory is indirectly leading to a positive feedback with *A. saccharum*, a species more tolerant of herbivory than *T. canadensis* (see also Anderson and Loucks, 1979). This in turn, may have cascading effects on the establishment of *T. canadensis* via microsite limitations (e.g., swamping of microsites by broad-leaf litter) and enhanced competitive environments.

Methods

We examined stand-scale *T. canadensis* recruitment in 39 remnant *T. canadensis* stands from across the western Upper Peninsula of Michigan (Figure 2-1). Potential stands, described as having a primarily *T. canadensis* overstory, were identified from across four ownerships: U. S. Forest Service, Michigan Department of Natural Resources, Michigan Technological University, and Gratiot Lake Conservancy. Stands were selected using a stratified random sampling design with four levels of stand area and average winter snow depth. Categories for stand area were as follows: < 1 ha, 1 - 10 ha, 10 – 20 ha, and 20 – 50 ha. Average snow depth was categorized as low or high. Because of its proximity to Lake Superior, our study area experiences enhanced precipitation in the form of winter snowfall. Cold air systems moving over a warmer Lake Superior pick up moisture, and cooling as this moisture moves inland, these systems can produce locally-heavy, “lake-effect” snowfall events. Snowfall totals vary across the study area, and average 200 cm per year in some locations to in excess of 600 cm per year in others, with areas closest to Lake Superior receiving the highest snow (Norton and Bolsenga, 1993).

Tsuga canadensis stands of the region tend to be found in mesic to wet/mesic conditions and most often occur on medium nutrient, acidic, loamy-sand to sand-loams soils (Albert 1994). All *T. canadensis* stands sampled fell within one of the following three habitat type classifications: *Acer-Tsuga-Maianthemum*, *Acer-Tsuga-Dryopteris*, or *Tsuga-Maianthemum-Coptis* (Burger and Kotar, 2003).

We quantified overstory *T. canadensis* stand structure (stems $\geq$ 4.0 cm dbh) during the summer of 2006 and understory regeneration (stems < 4.0cm dbh) during summer of 2007. *Tsuga canadensis* stand structure and composition were quantified using a nested sampling plot design. A series of 400 m^2 circular sampling plots were randomly placed at random coordinates in each *T. canadensis* stand (1, 3, 5, 7 or 9 plots, dependent on stand size) using Arcview 3.3 Random Point Generator extension (Jennes, 2001). All plot centers were located no closer than one plot radius distance (11.28 m) from the stand boundary. Within these plots we measured the composition and structure of overstory and midstory trees (stems $\geq$ 4.0 cm dbh). To quantify understory *T. canadensis* recruitment and competition we used three size categories (seedlings, small saplings, and large saplings), which were chosen based on their winter availability to white-tailed deer. Large saplings (stems 1.4 m height - 4.0 cm dbh), those likely to have outgrown the height level of deer browsing, were quantified on three 2 x 10 meter randomly oriented parallel belt transects nested within the greater 400 m^2 sampling plot. Small saplings (stems 0.25 ~ 1.4 m height), those stems within reach of winter deer browsing, were quantified on 1 x 10 m transects nested within the larger sampling transects. Seedlings (stems 0.04 - 0.24 m height), stems that likely were hidden below the surface of the snow and not available to deer for browsing, were quantified on a 0.1 x 10 m transect nested within each 1 x 10 m transect. All understory vegetation sampling took place during June – August 2007. However, due to the inconsistencies caused by various factors that can affect *T. canadensis* seedling establishment during the first year (i.e., desiccation, etc.) and the three months over which the sampling took place across all sites, we opted to include only seedlings that were likely in their second year of growth and older (stems ≥ 0.04 m height; Goerlich and Nyland, 2000).

Probable substrate of establishment was identified for each of the *T. canadensis* seedlings and saplings measured. We categorized substrate of establishment for the seedling size class as follows: moss, bare soil, and leaf litter – needle, deciduous, or mixed, low- or high-decayed wood (low = decay class 1 – 3; high = decay class 4 – 5; (Rooney *et al.*, 2000; Jenkins *et al.*, 2004). For small and large saplings, where transient substrates of establishment would be less apparent (i.e., leaf litter, bare soil, moss), we used broader categories of decayed wood (DW), tip-up mound (TM), and forest floor (FF; Rooney *et al.*, 2000). We quantified the availability of substrate on each 0.1 x 10 m seedling transect based on percent cover. Light availability within each sampling plot was quantified using 180^{o} fisheye lens canopy photos. Photos were analyzed for gap fraction, in WinSCANOPY image analysis software (Regent Instruments, Inc., Quebec, Canada).

White-tailed deer use of *T. canadensis* stands as winter habitat was measured using yearly counts of fecal pellet groups. Each stand contained 3, 5, 10, 20 or 30 randomly located (as described above) circular sampling plots (9.29 m^2) dependent on stand area. During the first year we cleared plots of pellets. Following snowmelt in subsequent years, plots were checked for pellet piles using a two-person system of concurrent rechecks and then re-cleared (re-set) for the subsequent year. Winter deer use was quantified for each *T. canadensis* stand as pellet groups ha^{-1} for each winter (2005 - 2008) and averaged across all three winters (Witt *et al.*, 2010).

Additional stand-scale variables of stand area and elevation were derived from remotely sensed data using ArcGIS 9.2 (ESRI). Initially, stand area used for random stand selection was based on delineations provided by ownership entities. These stand boundaries were often constrained by ownership boundaries and, therefore, did not necessarily reflect the actual area of each hemlock stand. In order to obtain a more accurate measurement of stand size, we digitized stand boundaries on U.S. Geological Survey Digital Orthophoto Quadrangles (U.S. Geological Survey, 1998) and calculated stand area. To derive stand elevation, we used a 1:250,000-scale digital elevation model for Michigan.

To identify potential impediments to *T. canadensis* seedling establishment and recruitment, we conduct our analyses at both a plot-scale and a stand-scale. Since *T. canadensis* abundance tends to be patchy and often clumped within a particular site (Rooney and Waller, 1998), we used a plot-scale analysis to identify factors influencing *T. canadensis* seedling establishment (Table 2-1). However, since limits to *T. canadensis* recruitment may be functioning at a much larger scale than those that affect *T. canadensis* establishment (Table 2-1), we chose to analyze small and large sapling recruitment at the scale of the *T. canadensis* stand (n=39).

Count of *T. canadensis* seedlings was used as our dependent variable to identify factors influencing *T. canadensis* abundance at the establishment and early recruitment stages as a function of plot-scale measures for light, competition, and substrate for establishment. Because our response variable was count data, which we assumed followed a Poisson distribution, we used a generalized linear mixed-effect modeling framework with a log-link function. It was also necessary to include an offset for sampling effort in our model (offset = log[plots]), since sampling was a function of patch size. To account for the nested nature of our data (plots within stand), we also included stand as a random effect in the model intercept (Zuur *et al.*, 2009).

All three size classes of *T. canadensis* seedlings and saplings were analyzed at the stand scale. We evaluated *T. canadensis* recruitment as a function of demographic inertia (density of seedlings or saplings in the next smallest size class), biotic and abiotic habitat variables, and relative deer use of each *T. canadensis* stand (Table 2-1). We used a generalized linear modeling framework (GLM) with a Poisson error distribution and a log-link function. Often, however, count data in ecological studies are overdispersed and the variance of the distribution exceeds the mean (Ver Hoef and Boveng, 2007). If overdispersion was detected in any of our final GLM-Poisson models, models were fit using a quasi-Poisson error distribution (Ver Hoef and Boveng, 2007; Zuur *et al.*, 2009). Deviance residual plots of models and predictor variables were examined for fit, and we used a square root or natural log transformed predictors as needed to meet assumptions and improve model fit (Zuur *et al.*, 2009).

Model parameters for all models were estimated using maximum likelihood. To avoid overfitting our model, we used a series of regression models and Akaike Information Criterion (AIC) to select the model that best (most parsimonious) explained *T. canadensis* seedling establishment and recruitment (Burnham and Anderson, 2002).

We used the R statistical environment to perform model fitting (R Development Core Team, 2005). Mixed effect modeling was conducted using the lme4 package (Bates and Sarkar, 2006).

To determine if *T. canadensis* seedlings showed greater affinity for a substrate of establishment than would be found by chance alone, we used a *G*-test for association with an $\alpha = 0.05$.

Means are reported plus or minus one standard deviation.

Results

Tsuga canadensis stand area ranged from that of a single sampling plot (0.04 ha) to 60 ha. Stand basal area ranged from 30.1 to 68.7 $m^2 ha^{-1}$. *T. canadensis* and *A. saccharum* occupied 21-84% and 0-30% of this overstory basal area respectively (Table 2-1). Out of the 223 subplots across the 39 stands, 56 contained *T. canadensis* seedlings (freq. = 0.25) with an average of 0.6 ± 1.7 stems per plot. Stand-scale *T. canadensis* densities by size class averaged 1244 ± 1565 stems ha^{-1} for *T. canadensis* seedlings, 607 ± 1030 for small saplings, and 87 ± 143 stems ha^{-1} for large saplings. Failures in *T. canadensis* recruitment were also found in both our small and large sapling size classes, where we found no *T. canadensis* in 17 and 22 out of 39 stands respectively. Of the 39 stands, 15% contained no *T. canadensis* regeneration in any of the three size classes.

Tsuga canadensis seedlings did not establish equally across all substrates (G-test statistic = 205.5; $p < 0.001$). We found strong seedling substrate associations with percentage of moss, high-decay coarse woody debris, and *A. saccharum* basal area (*T. canadensis* seedlings $plot^{-1}$ = -1.25 + 0.026*moss + 0.062*high-decay coarse woody debris – 4.191**A. saccharum* basal area; AIC = 282.5, with $p < 0.001$ for all parameters) in our best-fit (most-parsimonious) Poisson GLM model of seedling abundance versus plot-level environmental variables. Across all stands, moss cover ranged from 0-24.9% with a mean of 4.7 ± 5.8%, while the availability (% cover) of high-decay coarse woody debris ranged from 1.5-25.4% with an average of 7.0 ± 4.6%. Broad-leaf litter, which was not significant in our best-fit model of *T. canadensis* seedling establishment, but was significantly correlated with *A. saccharum* basal area ($r = 0.37$, $p < 0.001$), was the most dominant substrate with 40 ± 37% cover (Table 2-1).

White-tailed deer use of *T. canadensis* stands as winter habitat was quite variable by study site (Witt *et al.*, Unpublished results). In some stands, in excess of 2,200 pellet groups ha^{-1} were deposited annually, and across sites, our three-year average of relative deer use was 457 ± 486 pellet groups ha^{-1}.

Tsuga canadensis establishment and recruitment was best modeled using a Poisson distribution error structure (large sapling category) or Poisson with an estimate of dispersion in the variance structures (seedling and small sapling categories). Our models suggest that failures in hemlock regeneration are occurring at both the seedling and sapling stages, and may be driven by a combination of deer herbivory and stand composition (Table 2-1). At the seedling stage, *T. canadensis* was negatively associated with stand basal area and *A. saccharum* basal area and positively associated with stand elevation (Table 2-2). The correlation between stand basal area and *A. saccharum* basal area was not significant ($r^2 = 0.13$, $p = 0.43$).

At the small sapling stage, our best-fit model of *T. canadensis* recruitment included measures of demographic inertia, stand basal area, and white-tailed deer use

(Table 2-2). Stem density of small saplings was positively correlated with *T. canadensis* seedling density. However, stand basal area and white-tailed deer pellet groups ha^{-1} had a negative association with *T. canadensis* recruitment. Like small saplings, large saplings were positively correlated with the density of *T. canadensis* stems in the next smallest size class, small saplings ha^{-1} (Table 2-2). Large saplings also showed significant negative and positive relationships, respectively, with stand area and elevation (Table 2-2). In all three size classes of stand-scale *T. canadensis* establishment and recruitment, there was no significant relationship between *T. canadensis* seedlings and saplings and stem density of *A. saccharum* seedlings and saplings suggesting that direct competition with maple saplings may not be a major driver of hemlock recruitment at the sites we examined.

Discussion

Our research suggests that failures in regeneration may be occurring at multiple points throughout *T. canadensis'* establishment and recruitment (Figure 2-2), and these findings are consistent with studies implicating microsite limitations and deer herbivory as the primary cause of failure (Anderson and Loucks, 1979; Frelich and Lorimer, 1985; Alverson *et al.*, 1988; Rooney *et al.*, 2000; Marx and Walters, 2008). Furthering this research, however, our models suggest that a wide range of deer use and basal area combinations are having a substantial negative effect on *T. canadensis* regeneration (Figure 2-3). Yet, relative to other areas where overpopulated white-tailed deer populations are thought to be influencing plant populations and communities, deer densities are low and not necessarily considered to be overabundant at the landscape scale (c.f., Doepker *et al.*, 1994; Horsley *et al.*, 2003). However, seasonal concentrations in winter in conjunction with the limited availability of winter habitat may lead to novel densities and associated interactions with habitat resilience.

Ungulate species do not have to be overabundant to have an effect on sensitive species. For example, Brandner *et al.* (Brandner *et al.*, 1990) concluded that the relative effect of moose browsing on the suppression of *Abies balsamea* (balsam fir) was not necessarily due to an overabundance of moose. It was more likely an interaction between *A. balsamea* density and moose abundance. Areas with low *A. balsamea* abundance remained suppressed regardless of moose population levels, whereas areas with high relative abundance that were previously suppressed were able to recover under lower moose densities. Across our study site, historic and contemporary land-use and forest management practices have created a system where a once plentiful *T. canadensis* cover type has been reduced to a fraction of its historic abundance, while deer densities are thought to have at least doubled since pre-European settlement times (Doepker *et al.*, 1994).

The combination of land use history, seasonal weather events, and contemporary population levels of white-tailed deer and *T. canadensis* have likely set up a scenario where once infrequent and episodic overbrowsing events are now common or even sustained from season to season. In a related study, Witt *et al*. (2010) found that, in years with higher average snow depths, a greater number of *T. canadensis* stands were utilized as winter habitat, and the intensity of deer use increased in stands that were already being utilized by deer. Furthermore, at a coarse spatial scale (3,000-meter buffer) *T. canadensis* stands in highly heterogeneous landscapes were used significantly more than stands surrounded by large patches of deciduous forest. Across our study area, remnant *T.*

canadensis stands are surrounded, to varying degrees, by a dominant cover type of mature second- and third-growth deciduous forest interspersed with conifer and a few open areas. Vast areas of mature hardwoods would be poor habitat for deer during any season (Blouch, 1984), and the high snow depths of the region would only exacerbate this situation by further reducing forage availability while simultaneously increasing the energetic cost to movement (Parker *et al.*, 1984; Fancy and White, 1985; Turner *et al.*, 1997; Nordengren *et al.*, 2003). On the other hand, landscapes that are highly heterogeneous could support higher deer densities during non-winter months, and are likely serving as a source of deer for those *T. canadensis* stands that are experiencing failures in regeneration. Consequently, since use of remnant *T. canadensis* stands as winter habitat ultimately depends on winter snow conditions and the position of that stand within the context of the greater landscape, management decisions regarding deer populations need to consider local and landscape scales.

Stand-scale failures in *T. canadensis* recruitment were most prevalent in the largest sapling size class (Figure 2-4). Shade-tolerant *T. canadensis* saplings are slow growing, often spending up to 60 - 70 years in the understory before a canopy gap allows for recruitment (Hibbs, 1982). Based on height-age equations for *T. canadensis* found in the *Acer-Tsuga-Myanthemum* habitat type in northern Wisconsin, small *T. canadensis* saplings (0.25 to 1.37 m in height) could remain within reach of deer for up to 10 years (CR Webster, *unpublished data*). Furthermore, given the wide range of heights in our largest size class (1.37 - 4.98 m; mean = 2.55 m), the age of this cohort could easily range from 20 to 50 years, placing them within the range of deer herbivory anytime within the last two to four decades.

We suspect that, while deer use was not a significant factor in our model of large sapling recruitment, stand area and elevation may be latent variables coding for the legacy effect of deer use (Table 2-2). In the study by Witt *et al.* (2010) snow, elevation, stand area, and the composition and configuration of the landscape were important predictors of deer use of *T. canadensis* stands as winter habitat. Deer of the region exhibit strong site fidelity to winter yarding areas, and during winter they tend to concentrate activities in conifer stands at lower elevations (Beier and McCullough, 1990). Evidence of demographic inertia, or overlaps in the absence of small and large *T. canadensis* recruitment, may be suggestive of these consistencies in habitat use across the study area (Figure 2-4). However, the few inconsistencies in the presence and absence of small and large saplings across a few sites may be suggestive of changes in deer population levels or shifts in habitat use over time (Figure 2-4).

Under low to moderate levels of deer use, our small-sapling model predicts little or no *T. canadensis* recruitment (Figure 2-3). *Acer saccharum*, however, was a common understory component in most stands, even those with highest levels of deer use (Table 2-1). In stands where herbivory is suppressing *T. canadensis* recruitment, we expect that *A. saccharum* saplings may have a competitive advantage over *T. canadensis*. The effects of selective overbrowsing by generalist herbivores can lead to an increase in the dominance of less palatable or more browse tolerant species and has the potential to alter successional trajectories (as reviewed by Augustine and McNaughton, 1998). Both *A. saccharum* and *T. canadensis* are utilized by deer as winter forage, and deer preferentially select winter habitat containing a large component of available understory browse, especially under lower relative snow-depth conditions (Morrison *et al.*, 2003;

Witt *et al.*, 2010). *Acer saccharum*, however, is a more browse tolerant species and has the ability to re-sprout following damage to the terminal bud, whereas conifers, especially *T. canadensis*, are less adept at this trait (Anderson and Loucks, 1979). Given the differential tolerance to herbivory between these two species, we suspect that *T. canadensis* stands with an understory *A. saccharum* component may follow divergent successional trajectories than those that perpetuated the patch mosaic of *T. canadensis* and *A. saccharum* stands in the presettlement landscape (Woods, 1984; Frelich et al., 1993). This tendency may be particularly strong if they are experiencing sustained or periodically high levels of browsing.

Our results suggest that the increasing importance of *Acer* spp. in hemlock-northern hardwood stands (Webster and Lorimer, 2005) may be a more important player in the regeneration dynamics of *T. canadensis* than previously suspected. The traditional view has long been that *T. canadensis* canopies discourage establishment of hardwoods, particularly *A. saccharum*, and vice versa (Woods, 1984). Our findings clearly lend support to the latter half of this adage, but not the former. As expected, *T. canadensis* seedlings were not associated with broadleaf-litter microsites and a general trend of declining *T. canadensis* seedling and sapling abundance was observed with increasing *A. saccharum* overstory basal area. Broadleaf litter is likely limiting access to important microsites for *T. canadensis* establishment (e.g., bare mineral soil, moss, and the surface of highly-decay CWD; Collins, 1990) and may present an "ecological trap" for germinating *T. canadensis*. The slow developing radicals of *T. canadensis* germinants are often unable to penetrate broadleaf-litter mats and reach mineral soil before they dry out, resulting in moisture stress, desiccation and death (Mladenoff and Stearns, 1993).

Furthermore, relative to needle-leaf, broadleaf litter increases soil nutrient availability and provides seedbed conditions that favor hardwood succession (Pastor and Mladenoff, 1992), potentially furthering *A. saccharum*'s competitive edge over *T. canadensis* in stands containing even small inclusions of *A. saccharum* in the overstory. *Acer saccharum* sapling density, however, was not a significant predictor of *T. canadensis* seedling or sapling density in our models, which may suggest that direct competition in the sapling layer was not a major limiting factor or that this effect was largely captured by the relationship between *A. saccharum* sapling density and overstory basal area. That said the regeneration layer in these stands is largely dominated by *A. saccharum,* which is on average an order of magnitude more abundant than *T. canadensis*, suggesting little to weak interference with *A. saccharum* regeneration by the overstory dominant *T. canadensis*. Further research is needed to clarify the causal mechanisms underlying these interactions and potential feedbacks with herbivory.

Conclusion

Our research corroborates findings that suggest white-tailed deer are a major factor limiting *T. canadensis* recruitment. However, given *A. saccharum's* relative tolerance to herbivory, we believe that, even at relatively low levels of deer use, herbivory may be giving a competitive advantage to *A. saccharum*. In stands containing inclusions of overstory *A. saccharum,* deer herbivory may be perpetuating a positive feedback with cascading effects on the establishment of *T. canadensis*. Furthermore, in the absence of proactive management of the deer population, the success of *T. canadensis* may rest simply on *T. canadensis*' location within the context of the greater landscape surrounding it.

Table 2-1. Descriptive statistics for plot- and stand-scale variables.
Descriptive statistics for variables used to model understory *Tsuga canadensis* establishment and recruitment at the plot and stand scale and across three size classes: Seedlings (stems 0.04 - 0.24 m height), small saplings (stems 0.25 ~ 1.4 m height), and large saplings (stems ~1.4 m height - 4.0 cm dbh).

Variable	***MIN***	***MAX***	***MEAN***	***SD***
Plot-scale				
Gap fraction (percent)	3.7	17.9	8.8	1.8
Needle-leaf litter (percent cover)	0	95	24	30
Mixed-leaf litter (percent cover)	0	85	15	21
Broad-leaf cover (percent cover)	0	99	40	37
Moss (percent cover)	0	78	5	11
Coarse woody debris - high decay (percent cover)	0	50	7	7
Coarse woody debris - low decay (percent cover)	0	30	2	3
Bare mineral soil (percent cover)	0	25	1	3
Acer spp. seedlings (stem m^{-2} - stems < 0.25 m height)	0	57.3	7.5	10.2
Acer saccharum basal area (m^{2} ha^{-1})	0	1.48	0.19	0.26
Stand-scale				
Tsuga canadensis seedlings (stem ha^{-1} - stems 0.04 - 0.24 m height)	0	7407	1244	1565
Tsuga canadensis small saplings (stem ha^{-1}- 0.25 ~ 1.4 m height)	0	4857	607	1030
Acer saccharum basal area (m^{2} ha^{-1})	0	13.8	4.3	3.9
Stand basal area (m^{2} ha^{-1})	30.1	68.6	43	10.1
Acer spp. seedlings (stem ha^{-1} - stems 0.04 - 0.24 m height)	4.7x10^{4}	2.6x10^{5}	7.4x10^{4}	6.7x10^{4}
Acer spp. small saplings (stem ha^{-1} -stems 0.04 - 0.24 m height)	0	2.7x10^{4}	2.9x10^{3}	4.9x10^{3}
White-tailed deer relative winter use (pellet groups ha^{-1})	0	1907	457	486
Elevation (msl)	186	555	405	110
Stand area (ha)	0.1	59.6	14.4	14.1

Table 2-2. Model parameter estimates for *Tsuga canadensis* seedling, small sapling, and large sapling abundance.

Parameter estimates and 95% confidence interval (in parentheses) for our best-fit model of *Tsuga canadensis* abundance for seedling, small sapling, and large sapling size classes using a generalized linear modeling framework. All variables in models were significant ($p < 0.05$).

Model covariates	***Tsuga canadensis*** **Seedlings** (0.04 - 0.24 m height)	***Tsuga canadensis*** **Small saplings** (0.25 ~ 1.4 m height)	***Tsuga canadensis*** **Large saplings** (~1.4 m height - 4.0 cm dbh)
Intercept	1.211 (0.832)	8.690 (2.588)	-5.026 (1.047)
Tsuga canadensis seedlings		0.012 (0.005)†	
Tsuga canadensis small saplings			0.475 (0.002) ‡
Acer saccharum basal area	-0.804 (0.133)†		
Stand basal area	-0.045 (0.015)	-1.256 (0.403)†	
White-tailed deer pellet groups ha^{-1}		-0.056 (0.018)†	
Stand area			-0.036 (0.012)
Stand elevation	0.003 (0.001)		0.005 (0.002)

† variable was square root transformed; ‡ variable was natural log transformed

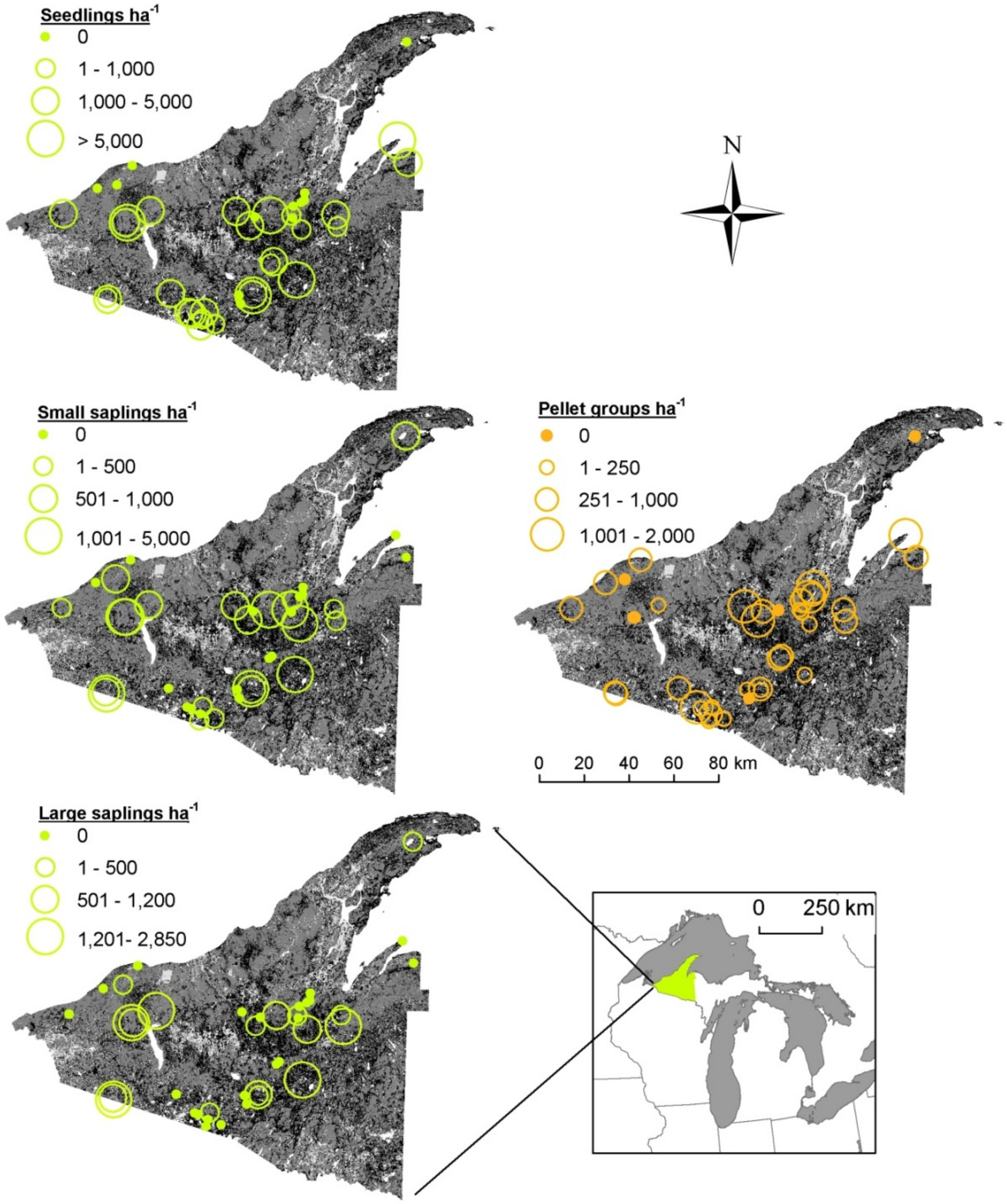


Figure 2-1. Tsuga canadensis abundance and relative white-tailed deer use. Stem density of *Tsuga canadensis* (green circles) for seedlings (stems 0.04 - 0.24 m height), small saplings (stems 0.25 ~ 1.4 m height), and large saplings (stems ~1.4 m height - 4.0 cm dbh) along with relative use of each stand by white-tailed deer (orange circles; pellet groups per ha^{-1}) averaged over three winters (2005-06, 2006-07, 2007-08). Shades of gray on base map indicate cover type as follows: conifer forest (black), dark gray (deciduous forest), and light gray (open areas).

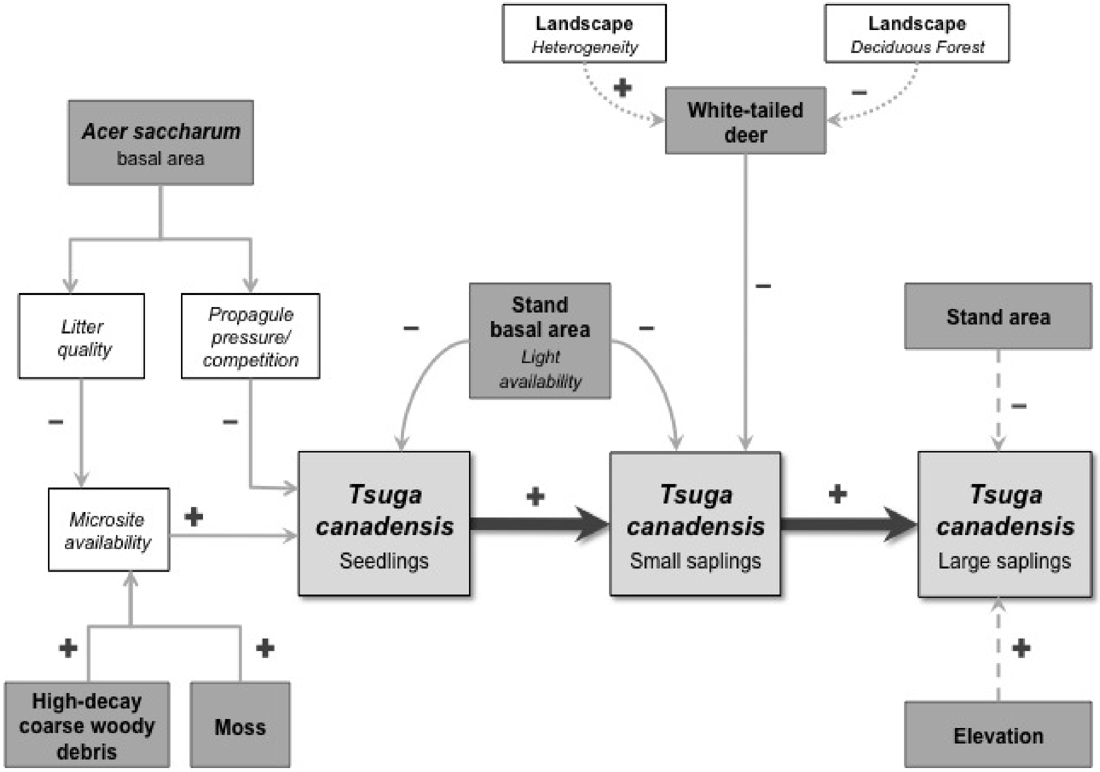


Figure 2-2. Conceptual diagram of relationships between *Tsuga canadensis* and variables predicted to influence its regeneration and recruitment.
Conceptual diagram of relationships between *Tsuga canadensis* and variables predicted to influence its regeneration and recruitment, as predicted by generalized linear models of eastern *T. canadensis* abundance. Direction and sign of arrows indicated direct (solid arrows) and indirect (dashed arrows) relationships between covariates (dark gray boxes) and *Tsuga canadensis* size class categories (light gray boxes). Dotted arrows signify hypothesized relationships between the greater landscape surrounding eastern *T. canadensis* stands and winter use by white-tailed deer (from Witt *et al.*, 2010). *Tsuga canadensis* size classes: Seedlings (0.04 - 0.24 m height), small saplings (0.25 ~ 1.4 m height), and large saplings (~1.4 m height - 4.0 cm dbh).

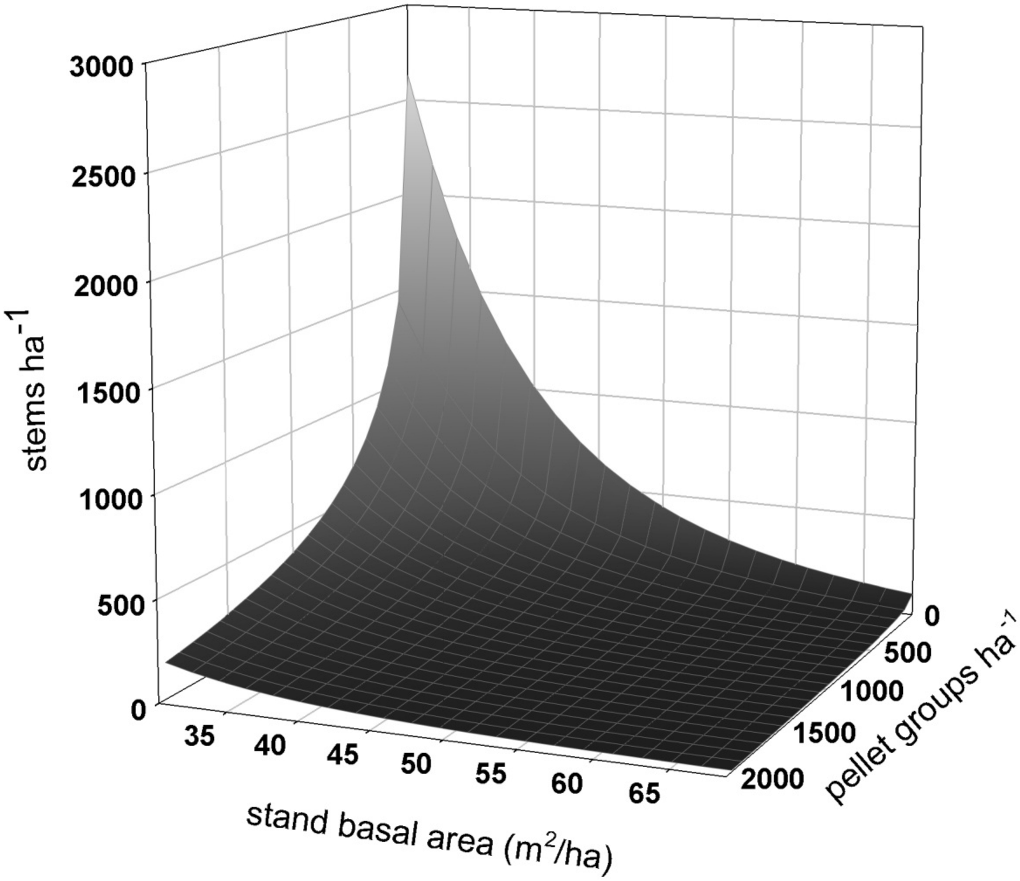


Figure 2-3. Predicted stems ha^{-1} for *Tsuga canadensis* small saplings.
Predicted stems ha^{-1} for stand-scale model of *Tsuga canadensis* small saplings size class (~0.25m in height to 0.1 cm dbh) as a function of stand basal area and relative deer use. For display purposes, *T. canadensis* seedling density has been held constant at a mean value of 1175 stems ha^{-1} across all study sites.

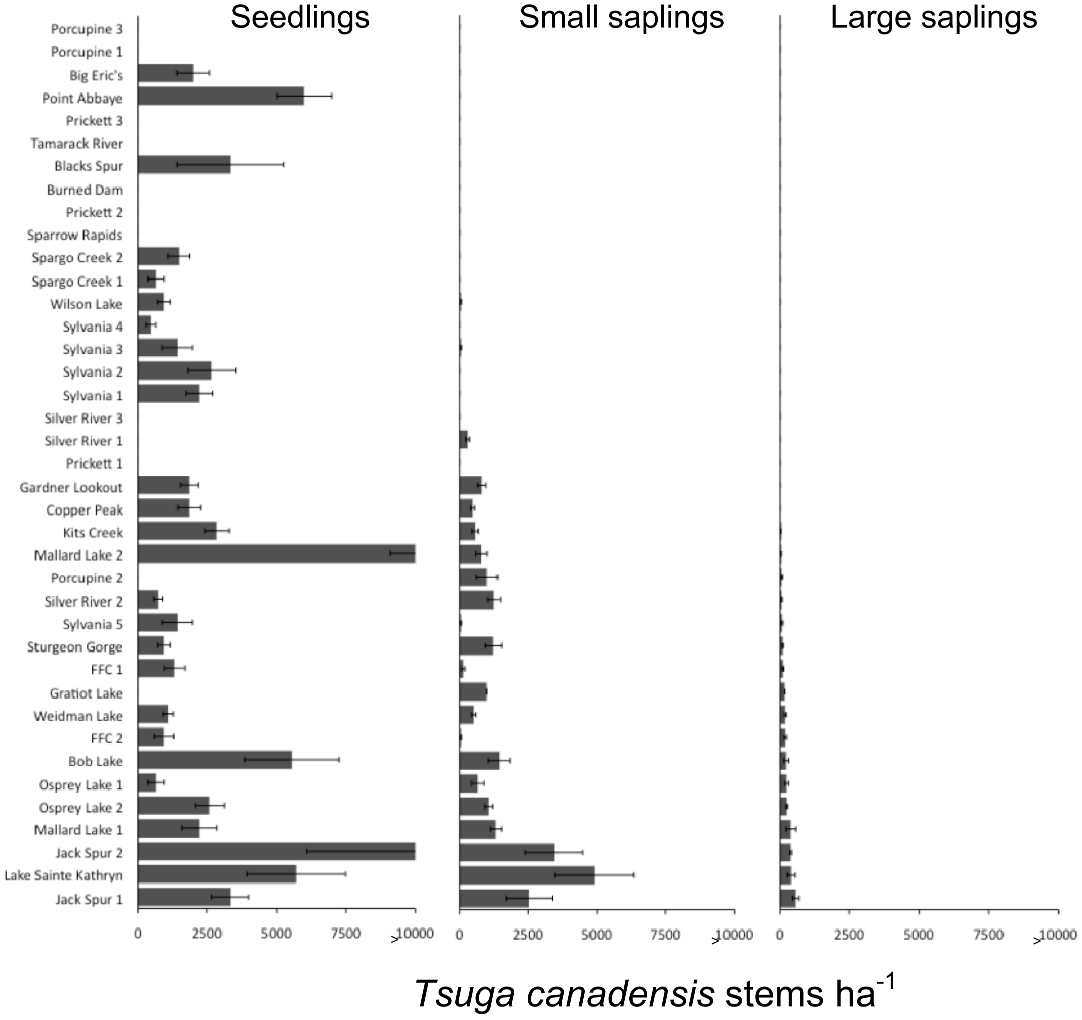


Figure 2-4. *Tsuga canadensis* stem density by size class.

Stem density and standard errors of *Tsuga canadensis* regeneration listed by size class for each of the 39 study stands. Size classes: Seedlings (stems 0.04 - 0.24 m height), small saplings (stems 0.25 ~ 1.4 m height), and large saplings (stems ~1.4 m in height – 3.9 cm dbh).

CHAPTER THREE

Erosion of patch stability and altered successional trajectories in remnant stands of *Tsuga canadensis*.

Abstract

Loss of habitat resiliency in ungulate grazing/browsing systems can occur gradually over time, due to habitat fragmentation, loss of diversity, or other ecosystem eroding events. Once system resiliency is lost, even small perturbations to the system could lead to catastrophic shifts in plant community composition. *Tsuga canadensis*, a species that was once common throughout eastern North America, is experiencing wide-scale declines in abundance throughout its distribution. Across the Upper Great Lakes region, where *T. canadensis* exists at just a fraction of its former abundance, white-tailed deer (*Odocoileus virginianus*) herbivory, microsite limitations, and climate are contributing to a paucity of regeneration. *Tsuga canadensis* and *Acer saccharum*, an alternately stable climax species, form dominant patches across the landscape and, through leaf-litter inputs and soil nutrient availability, each has the ability to limit establishment of the other. Yet *A. saccharum* appears to be replacing *T. canadensis* in some locations. In this study we quantify stand structure and understory regeneration in 39 randomly selected remnant *T. canadensis* stands from across the western Upper Peninsula of Michigan. Using understory species importance values (IV), a measure of species dominance, as our dependent variable, we identify factors influencing understory regeneration (e.g., microsite, deer herbivory, and dominance of overstory species). *Tsuga*

canadensis was the dominant overstory species, yet *A. saccharum* was the most common understory species in these stands (261 ± 320 stems ha^{-1} for stems $0.1 < 10$ cm dbh), and of the 39 stands, only 14 exhibited *T. canadensis* diameter distributions indicative of a self-replacing stand. Understory *A. saccharum* IV was positively associated with the dominance of *A. saccharum* in the overstory, while understory *T. canadensis* was negatively associated with both *A. saccharum* overstory dominance and white-tailed deer. Our findings suggest that we may be seeing an erosion of *T. canadensis* patch stability in stands containing an overstory component of *A. saccharum*, and given contemporary levels of deer herbivory, this could be leading to an altered successional trajectory and a shift to dominance by *A. saccharum*.

Introduction

Noy-Meir (1975) showed that simple models of predator-prey systems could be applied to ungulate grazing systems, and the stability within these systems is dependant on both plant species abundance and herbivore densities. Loss of habitat resiliency often takes place gradually (e.g. climate change, nutrient loss or input, loss of diversity, or habitat fragmentation), and with that loss of resiliency, even small perturbations, such as stochastic disturbance events can lead to dramatic shifts of plant community composition (Scheffer *et al.*, 2001). In the case of a highly-abundant plant populations, herbivore density may have little impact on the population, however, if the plant population is rare or low in abundance an increase in the rate of herbivory could lead to declines in or complete loss of a population (Tilghman, 1989; Brandner *et al.*, 1990; Augustine and McNaughton, 1998). Further, if an alternate or degraded system becomes established, feedbacks between biotic and abiotic factors may lead to long-term persistence and reticence to restoration or change, regardless of a reduction in the rate of herbivory (Scheffer *et al.*, 2001).

Tsuga canadensis (eastern hemlock) has been described as a “foundation” species, one that is abundant across the landscape and has a profound effect on ecosystem function and stability (Ellison *et al.*, 2005). Historically, this species commonly occurred in nearly mono-dominant stands throughout the northern hardwoods region of North America (Frelich *et al.,* 1993). Forest floor conditions of *T. canadensis* dominated stands tend to be moist and highly shaded, with acidic, highly-tanic, nutrient-poor soils and slow rates of decomposition and nutrient cycling (Pastor and Mladenoff, 1992; Jenkins *et al.*, 1999). These conditions result in relatively species poor understory plant communities, but because the environment is consistently shaded and cool with moderated soil moisture conditions, it provides important habitat for stream and amphibian assemblages (Snyder *et al.*, 2002). These dense patches are also important to a unique assemblage of songbird and small mammal species, and in areas of high winter snow depth, they an important seasonally as habitat for white-tailed deer and moose (*Alces alces*; Wydeven and Hay, 1996; Yamasaki *et al.*, 2000).

Prior to European settlement, forests of the upper Great Lakes region would have been dominated by *T. canadensis* or *Acer saccharum* (sugar maple), both late-successional species that have the ability to form relatively stable patches across the landscape (Frelich *et al.*, 1993). In contrast to *T. canadensis*, forest floors conditions in *A. saccharum* dominated stands are generally less limited by nitrogen, and they undergo higher rates of decomposition and nutrient cycling (Pastor and Mladenoff, 1992). Both are highly shade-tolerant species and do not require canopy disturbance for seedling establishment, and both are thought to facilitate their own regeneration while simultaneously inhibiting establishment of the other (Woods, 1984; Frelich *et al.*, 1993).

Throughout its distribution, *T. canadensis* has been facing a range of perils. Across the Eastern U. S. and the Appalachian Mountains, the hemlock woolly adelgid (*Adelges tsugae*) has been spreading largely unimpeded, and this infestation has led to wide-scale decline in *T. canadensis* abundance (Orwig *et al.*, 2002). In northern New England, the advancement of the adelgid has been slower, likely due to the colder winter temperatures (Paradis *et al.*, 2008). Similarly, across the western range of its distribution, throughout the Upper Great Lakes region, the adelgid is currently not a factor influencing the *T. canadensis* population. Region-wide failures in the establishment and recruitment of *T. canadensis*, however, have been documented as far back as the early 1940s (Maissurow, 1941; Crow, 1996). The extensive early twentieth-century logging and slash fires reduced the population of *T. canadensis* to a fraction of its former abundance (Whitney, 1987), and this, in conjunction with contemporary forest management practices, have resulted in the remaining remnant stands of *T. canadensis* being surrounded, to a greater or lesser degree, by a landscape of second- and third-growth deciduous forests (Alverson *et al.*, 1988). Further, the resulting increase in early-successional habitat led to an increase in the abundance of white-tailed deer (*Odocoileus virginianus*), and across the western Upper Peninsula of Michigan, the population has been estimated to be at least double that of the pre-logging era landscape (Doepker *et al.*, 1994). Deer utilize *T. canadensis* as winter habitat across this region, because dense, closed canopy forests are thought to provide lower snow depth and shelter from the harsh winter conditions found on the leeward side of Lake Superior (Blouch, 1984; Nelson and Mech, 2006). Deer herbivory has been implicated as one of the main causal factors in the region-wide failure of *T. canadensis* recruitment (Anderson and Loucks, 1979; Frelich and Lorimer, 1985; Alverson *et al.*, 1988; Rooney *et al.*, 2000; Witt and Webster, 2010).

In addition to deer, a variety of factors may be limiting *T. canadensis* at the point of establishment, and as suggested by Mladenoff and Stearns (1993), in a landscape where *T. canadensis* population is at mere fraction of its former abundance, these may be acting in concert to limit *T. canadensis* regeneration. Warm and moist conditions are needed for germination and establishment, and seedlings are especially prone to desiccation (Godman and Lancaster, 1990). Seedling establishment is associated with moss, and high decay coarse woody debris (CWD), and organic soil exposed by tip-up mound or light ground fire disturbances (Collins, 1990). In a landscape with relatively few remaining *T. canadensis* patches, the occurrence of these necessary disturbance events in conjunctions with suitably moist climate conditions may be rarer than is needed to produce adequate *T. canadensis* regeneration (Mladenoff and Stearns, 1993). The volume of high-decay *T. canadensis* CWD, a preferred substrate for germination, that is found in younger *T. canadensis* stands (<250 years) is lower than that of other early successional species (Tyrrell and Crow, 1994; Marx and Walters, 2008), and may be another factor leading to the poor showing in *T. canadensis* regeneration in some stands. In addition to the lack of suitable substrate, broad-leaf litter may be covering these important microsites for establishment. Broad-leaf litter likely inhibits access of the developing *T. canadensis* radicals to microsites with more stable moisture conditions, leading to desiccation and death of new germinants (Mladenoff and Stearns, 1993).

Further, these inputs of deciduous litter have been shown to create patches of increased soil nutrient availability within a primarily acidic, nutrient-limited conifer litter environment, a microenvironment that has the potential to favor hardwood seedling establishment (Pastor and Mladenoff, 1992).

In a preliminary survey of *T. canadensis* across the western upper peninsula of Michigan, we observed that the understories of many stands are dominated by thick mats of *Acer spp.* seedlings and saplings. If these stands are experiencing a sustained influx of *Acer* regeneration, then it would likely follow that a reduction in the resistance of *T. canadensis* to hardwood invasion and an erosion of the hypothesized long-term patch stability between these two species is underway (Woods, 1984; Frelich *et al.*, 1993; Davis *et al.*, 1998). The objectives of this study were to, 1) quantify understory regeneration in remnant *T. canadensis* stand for use as an indicator of future overstory composition under disturbance regimes natural to the northern hardwoods region, and 2) identify variables that may be important indictors of *T. canadensis*' susceptibility to *Acer spp.* invasion. We hypothesize that the loss of important microsites for establishment and growth, in conjunction with deer herbivory, may be lowering *T. canadensis*' resistance to invasion by hardwood species. Further, microsites conditions created by deciduous litter inputs may be creating a positive feedback in *Acer spp.* regeneration and recruitment in stands containing an overstory *Acer spp.* component, which could be leading to the erosion of *T. canadensis* patch stability and a successional trajectory that could eventually lead to overstory dominance by *A. saccharum*.

Methods

Study area

We examined overstory and understory composition and the potential for an altered successional trajectory in remnant stands of *T. canadensis* in the northern hardwood's region of the western Upper Peninsula of Michigan, USA. Due to its location on the south side of Lake Superior, areas of upper Michigan experience locally heavy "lake-effect" snowfall. Moisture is picked up by cold air or storm systems moving out of Canada and over Lake Superior and is deposited in the form of snow as it moves onshore and inland. Areas closest to the lake generally receive the greatest snowfall, and range, on average, from 200 to 600 cm annually (Norton and Bolsenga, 1993). Across our study area *T. canadensis* stands tend to be found on medium nutrient, acidic soils and in wet-mesic to mesic conditions, and they most often occur in one of three habitat type classifications, *Acer-Tsuga-Maianthemum*, *Acer-Tsuga-Dryopteris*, or *Tsuga-Maianthemum-Coptis* (Burger and Kotar, 2003).

Stands described as being primarily *T. canadensis* were identified from four ownerships across six counties in the western Upper Peninsula of Michigan. Our target for these stands was ≥ 50% basal area occupied by *T. canadensis*, as described by forest inventory data. Using a stratified random sampling design we selected 39 *T. canadensis* stands by two categories of snow depth (low and high) and four classes of stand area (< 1 ha, 1 - 10 ha, 10 – 20 ha, and 20 – 50 ha) for use in this study. Study stands were located in Ottawa National Forest, Copper Country State Forest, Michigan Technological University's Ford Forestry Center, Porcupine Mountains Wilderness State Park, Sylvania Wilderness Area, Sturgeon River Gorge Wilderness Area, and Gratiot Lake Conservancy.

Field methods

We quantified *Tsuga canadensis* stand composition and structure on randomly-placed sampling plots during the summers of 2005 and 2006. Using GIS maps and a random points generator extension (Jenness Enterprises, Flagstaff, AZ) in Arcview 3.3 (ESRI, Redlands, CA), 400 m^2 circular plots were located *a priori* within each stand with the criteria that all plots fell no less than one plot radius from the edge of the stand or another sampling plot (n = 1, 3, 5, 7, or 9 plots– dependant on stand size). In stands where no GIS data were available, plots were placed at the time of sampling using a table of random compass direction and distance. For all stems ≥ 4.0 cm dbh found within these 400 m^2 sampling plots, we identified species and measured dbh, height, and crown length. Stems < 4.0 cm dbh were divided into three size categories and quantified by species on transects nested within the 400 m^2 circular plot. We measured height and dbh of large saplings (stems 0.1 < 4.0 cm dbh) on three, 2 x 10 m, randomly-oriented, parallel belt transects. Trees were tallied as individuals if stems split below dbh. Small saplings (stems 0.25 ~ 1.4 m in height) were identified and height was measured on 1 x 10 m transects nested within the large sapling transects, and seedlings (stems 0.04 < 0.25 cm in height) were counted by species on 0.1 x 10 m transects nested within the small sapling transects.

In order to quantify relative use of *T. canadensis* stands by deer as winter habitat, we used fecal pellet group counts. Using the random plot placement methods described above, we placed 3, 5, 10, 20, or 30 – 9.29 m^2 circular sampling plots within each stand. Prior to the first winter, plots were cleared of pellets. In May of the following year and after snowmelt, we used a two-person team to concurrently check each plot. Pellet group piles were located, marked with a flag, and counted, and then plots were reset (cleared of pellets) for the following year. Relative deer use was expressed as pellet groups per hectare for each stand and averaged across three winters: 2005-06, 2006-07, and 2007-08.

Since additional factors may be interacting with herbivory to influence the importance of *Acer spp.* within a stand, we included variables of forest floor composition, stand area, and elevation in our analysis. Within each of the small sapling transects described above, we quantified the percent cover of three classes of forest floor litter: primarily needle-leaf, primarily broad-leaf, and mixed-leaf litter (Rooney et al. 2000). Stand area was calculated from polygons representing stand boundaries that were digitized in ArcGIS 9.2 (ESRI, Redlands, CA) using U. S. Geological Survey Digital Orthophoto Quadrangles (USGS). Stand elevation was derived for each stand using a 1:250,000 digital elevation model for the Upper Peninsula of Michigan.

Data analysis

Diameter distributions plot the number of trees by diameter class, and the shapes of these distributions can be used to describe stand structure and stocking levels as well as elicit structural deficiencies (Goff and West, 1975; Leak, 1996). Using 2 cm diameter classes, we calculated diameter distributions for stems ≥ 0.1 cm dbh for all species, *Tsuga canadensis*-only, and a combined *Acer spp.* class composed of *Acer saccharum* and *Acer rubrum*. With $\log_{10}$ trees per hectare as our dependent variable and dbh, dbh^2, and dbh^3, as our independent variables, we used multiple linear regression to identify shape category for our diameter distributions (Leak, 1996; Schwartz *et al.*, 2005; Janowiak *et al.*, 2008). For statistically significant models ($p < 0.05$), we used adjusted-R^2 and root mean square error (RMSE) values to determine the best-fitting model. The significance of ($p < 0.05$) and sign of predictor variables (dbh, dbh^2, and dbh^3) were used to determine the shape of the diameter distribution (Janowiak *et al.*, 2008). The following have been identified as potential diameter distribution shapes in managed and unmanaged northern hardwood stands: rotated sigmoid (RS), increasing *q* (IQ), negative exponential (NE), binomial (BI), and unimodal (UNI; Janowiak *et al.* 2008). In northern hardwood forests, NE, IQ, and RS would be considered stable populations or populations that are in structural equilibrium (Goff and West, 1975), whereas diameter distributions that are BI or UNI likely contain deficits in the small or intermediate size classes (Janowiak *et al.*, 2008).

In order to ascertain how deer herbivory in conjunction with stand composition and structure may be influencing the successional trajectories for *T. canadensis* stands across northern portions of *T. canadensis'* range, we modeled the relative dominance of understory *T. canadensis* and *Acer spp.* We divided trees into two structural classes, understory (stems 0.1 < 10 cm dbh) and overstory (stems ≥ 10 cm dbh). Within these two structural classes we determined the relative dominance of each species or species group by calculating a species importance value (IV), where $IV = (R_{ba} + R_{den})/2$ (Neuendorff *et al.*, 2007). For a given species or species group, R_{ba} is the relative basal area ($m^2\ ha^{-1}$) and R_{den} is the relative density (trees ha^{-1}). Species IV values range from zero to one. Values close to zero indicate that the species is absent or of low importance relative to other species, whereas a value approaching one would indicate near complete dominance within the specified structural class. Species groups were identified as being *Tsuga canadensis*, *Acer saccharum*, *Acer rubrum*, other hardwood, other conifer, or shrub species. We used understory IV as our dependant variable in a multiple linear regression for the following species: *Acer saccharum*, *Acer rubrum*, and *Tsuga canadensis.* Predictor variables used in analysis were as follows: overstory IV (*A. saccharum*, *A. rubrum*, and *T. canadensis*), stand BA (basal area), stand area, deer use, and leaf litter (% cover – needle-, broad-, and mixed-leaf). Important predictors of understory dominance were identified in these models using forward and backward stepwise selection procedure. Among models with significant predictors ($p < 0.05$), the best fitting model was chosen as one that maximized adjusted-R^2 and minimized RMSE.

Means are reported plus or minus one standard deviation.

Results

Stand Structure

Across the 39 study sites, *T. canadensis* stands ranged in sizes from 0.04 – 60 ha, with an average of 14.6 ± 14.1 ha. Stand basal area averaged 43.0 ± 10.1 m^2 ha^1 with a range of 30.1 – 68.6 m^2 ha^{-1}. Average overstory (stems ≥10 cm dbh) basal area for *T. canadensis*, *A. saccharum*, and *A. rubrum* was 24.0 ± 12.1, 4.3 ± 3.9, 4.6 ± 4.1 m^2 ha^{-1}, respectively. Percentagewise *Acer saccharum* accounted 0 – 30% while *A. rubrum* accounted 0 – 46% of stand basal area. For understory trees (stems 0.1 < 10 cm dbh), total stem density averaged 970 ± 866 stems ha^{-1} across all stands. Understory stem density varied by species with averages of 141 ± 199, 261 ± 320, and 64 ± 98 stems ha^{-1} respectively for *T. canadensis*, *A. saccharum*, and *A. rubrum*, respectively.

In our regression analysis of diameter distributions, we identified the following four distinct shapes in our 39 stands: NE (n = 16), BI (n = 7), RS (n = 10), and UNI (n =

4). We were able to identify significant patterns of diameter distributions for *Acer spp.* in 36 of these stands. These consisted of NE (n = 14), BI (n = 10), RS (n = 10), and UNI (n = 2; Figure 3-1). For *T. canadensis*, 34 out of the 39 stands had diameter distribution shapes consisting of the following: NE (n = 7), RS (n = 7), BI (n = 7), and UNI (n = 15; Figure 3-1).

Species Importance

Tsuga canadensis was the dominant overstory species in 27 out of 39 stands, with an average IV of 0.47 ± 0.18 across all sites (Table 3-1, Figure 3-2). Understory *T. canadensis* IV averaged only 0.16 ± 0.20 across sites, and 20 out of the 39 stands had an IV value of ≤ 0.05 (Figure 3-2). *Acer saccharum*, however, dominated the understory of our study sites with an average IV of 0.32 ± 0.31 and values ranging from absent in the stand to complete understory dominance (Table 3-1, Figure 3-2). Similarly, *A. rubrum*, while not dominant in the overstory, was an important understory species (Table 3-1, Figure 3-2). However, given the propensity for coppice regeneration, and the methodology used to tally stems, we believe that importance values presented here may be leading to an over-inflation of the importance of *A. rubrum* in the understory of some of these stands.

Understory *A. saccharum* dominance was positively associated with both overstory *A. saccharum* and *T. canadensis* dominance and negatively associated with stand basal area ($R^2_{adj} = 0.68$; $F = 27.6$, $p < 0.001$), and we found an increase in *A. rubrum* with increasing white-tailed deer use and *A. rubrum* overstory IV ($R^2_{adj} = 0.25$; $F = 7.23$, $p = 0.002$; Table 3-2). Understory *T. canadensis* decreased with an increase in deer use and overstory *A. saccharum* dominance ($R^2_{adj} = 0.25$; $F = 10.13$, $p < 0.001$; Table 3-2).

Discussion

Ungulates have the potential to directly and indirectly modify ecosystems, and under certain scenarios, they have the ability to affect plant community composition to the point of altered succession (Hobbs, 1996; Augustine and McNaughton, 1998). Often however, it is a combination of triggers that lead to lowered system resilience, and herbivory may just be the catalyst to promoting a change in species composition (Dublin *et al.*, 1990; Webster *et al.*, 2008; Royo *et al.*, 2010). Our findings suggest that we may be seeing an erosion of *T. canadensis* patch stability in stands containing an overstory component of *A. saccharum*, and given contemporary levels of deer herbivory, this could be leading to an altered successional trajectory and a shift to dominance by *A. saccharum*. *T. canadensis* was the dominant overstory species across most of our sites, yet in many of these stands, the subcanopy and sapling layers were dominated by *A. saccharum* (Figure 3-2). The absence of *T. canadensis* regeneration has been linked to herbivory by white-tailed deer (Anderson and Loucks, 1979; Frelich and Lorimer, 1985; Rooney *et al.*, 2000), and our results support these findings (Table 3-2). However, as suggested by Mladenoff (1993), we also agree that a variety of causes may be directly and indirectly limiting *T. canadensis* establishment and recruitment, and further perpetuating *A. saccharum* understory dominance.

Small gaps associated with the death of a single overstory tree are the most common canopy disturbance in these late-successional species forests, as opposed to the large-scale wind throws, which happen on a >1,000 year return cycle (Canham and

Loucks, 1984; Tyrrell and Crow, 1994). It is likely that these small gaps will perpetuate the growth of more advanced shade-tolerant species found in the understory (Dahir and Lorimer, 1996; McClure *et al.*, 2000; Webster and Lorimer, 2005), and *T. canadensis* is expected be the most competitive in the smallest gaps (< 100 m^2; Webster and Lorimer, 2005). However, out of the 39 study stands, 16 showed no advanced *T. canadensis* regeneration in the smallest diameter classes (stems < 4 cm dbh), and of these, 13 were completely devoid of *T. canadensis* under 10 cm dbh (Figure 3-1). In contrast, *Acer spp.* dominated the understory in more than half of the study stands (Figure 3-1). Unimodal diameter distributions for *T. canadensis* may be suggestive of an even-aged stand or a stand that has had so little recruitment for so long that several size classes are missing from the distribution. Similar to previous studies of *T. canadensis* of the region, our results suggest that the truncated distribution in the lower size classes of many of these stands may, in part, be attributed to deer herbivory (Frelich and Lorimer, 1985; Tyrrell and Crow, 1994).

Across our study area, deer herbivory is directly influencing this dearth of *T. canadensis* (Frelich and Lorimer, 1985; Witt and Webster, 2010). Post-logging era increases in early-successional forests, along with contemporary forest management practices, have led to an increase in forage availability and a doubling of the deer population across the region (Doepker *et al.*, 1994). This in conjunction with a 99% decline in mature *T. canadensis* (Mladenoff *et al.*, 1996), an important winter habitat for deer, have created a situation where, in some stands, frequent or even sustained browsing events are common in winter (Witt *et al.*, 2010), whereas historically, with half as many deer, these browsing events would likely have been more diffuse and transient.

Acer spp. and *T. canadensis* are common forage for wintering deer. *Acer saccharum*, however, is a more browse tolerant species relative to *T. canadensis*, because it has the ability to resprout following browsing of the terminal bud (Anderson and Loucks, 1979). Tolerance to herbivory has been linked to an increase in dominance of more browse tolerant species (as reviewed by Augustine and McNaughton, 1998). Therefore, in stands with frequent browsing events, we would expect *A. saccharum* to have a competitive edge over *T. canadensis*, and indeed, we are seeing a pulse of *A. saccharum* seedlings and saplings in the understory of many of these stands (Figure 3-1).

Further supporting this, overstory *T. canadensis* had a positive influence on the importance of *A. saccharum*, which we believe may be a latent variable coding for deer use. In areas of seasonally high snow depth, deer will vary habitat selection favoring areas of higher browse availability during times of lower snow and areas of better cover (i.e., stands dominated by *T. canadensis*) during higher snow (Morrison *et al.*, 2003). Similarly, in a concurrent study by Witt *et al.* (2010), a greater number of remnant *T. canadensis* stands were utilized as habitat during winters with higher average snow depth, regardless of the availability of browse, and *T. canadensis* seedlings and saplings were absent or minimal at best in these stands, even in the event of low or episodic deer use , (Witt and Webster, 2010). Given their difference in tolerance to herbivory and the length of time that these two shade tolerant species can remain as subcanopy trees, it is not surprising that, even in the presence of low or episodic browsing, over time *A. saccharum* could become the dominant understory species. We saw a similar trend with *A. rubrum* in these stands (Figure 3-3). This self-perpetuating relationship is not as strong as that of *A. saccharum*, however, possibly due to the competitive advantage held by *A. saccharum* on the more mesic sites (Table 3-2; Abrams, 1998).

Our research also supports a hypothesized feedback that promotes the potential for conversion of *T. canadensis* stands to *A. saccharum* dominance, as proposed by Mladenoff *et al*. (1993). The historic loss in *T. canadensis* population followed by contemporary logging practices that served to promote *Populus spp.* and *A. saccharum*, have created a landscape where the relatively few remaining hemlock patches are surrounded to varying degrees by second- and third-growth deciduous forests. For *T. canadensis* and *A. saccharum*, it has long been the view that canopy and forest floor conditions work to suppress establishment of the other (Woods, 1984; Frelich *et al.*, 1993) and in essence, both should be able to maintain dominant patches on the landscape. Our data, however, suggest that *T. canadensis* stands may be undergoing erosion in that patch stability, as across our study sites *A. saccharum* was the dominant understory species (Table 3-2, Figure 3-2). The remnant stands used for this study were relatively small (≤ 60 ha), and while stand area was not a significant predictor in our models, at least within the range of sizes studied here, these stands may be seeing an erosion in stability from pressure exerted by the surrounding deciduous landscapes.

Even with only a small portion of the overstory being comprised of *A. saccharum*, we saw a strong positive association with the dominance of conspecifics in the understory (Figure 3-3). Overstory *A. saccharum* IV alone accounted for 64% of the explained variation in understory dominance across sites, as opposed to 68% when the model included overstory *T. canadensis* IV and stand area (Table 3-2). *Acer saccharum* was also associated with lower importance values for understory *T. canadensis* (Table 3-2). For *T.*

canadensis stands containing a significant proportion of deciduous species in the overstory, seasonal broad-leaf litter inputs may be limiting these important microsites and creating an "ecological trap" for germinating *T. canadensis*. Further, quickly decomposing deciduous litter has also been shown to increase soil nitrogen mineralization, and within what are generally nutrient-poor understories, there likely exists a micro-mosaic of relatively nutrient rich soil conditions (Pastor and Mladenoff, 1992). Given this relationship, and the competitive advantage of *A. saccharum* relative to *T. canadensis* in nutrient rich environments, it is not surprising that our models predict such a strong positive association, and a potential feedback, between overstory and understory *A. saccharum*. Further exacerbating this feedback, ungulates, through urine and fecal inputs, can accelerate decomposition and the rate of nutrient turnover in a system (Hobbs, 1996). By preferentially selecting areas of higher browse availability, like the *A. saccharum* seedling and sapling mats found in our study sites, the rapid rate of nitrogen return could be leading to an accelerated rate of *A. saccharum* succession in and around these *A. saccharum* inclusions (Pastor and Naiman, 1992; Hobbs, 1996; Augustine and McNaughton, 1998). This relationship and the underlying mechanisms clearly warrant further research.

Our results suggest that we may indeed be seeing erosion of *T. canadensis* patch stability and a shift toward *Acer* dominance, but what does the future hold for these stands? Clearly, some areas do contain *T. canadensis* regeneration; fourteen out of 39 stands showed distributions which may be adequate to maintain healthy and self-perpetuating stands (Figures 3-2 & 3-3). However, for those stands containing an *A. saccharum* overstory component, herbivory may just be the catalyst to this altered succession. If these stands are not given adequate time for *T. canadensis* to establish and recruit to the point where it is competitive in capturing small gaps formed by toppled overstory trees, we will, over time, see acceleration in dominance and stand scale conversions to *A. saccharum*, a species that is currently dominating understories and also able to capitalize on these small gaps. Further, we predict that decreasing *T. canadensis* dominance could lead to a decrease in winter habitat for deer, which, in turn, could further facilitate and accelerate conversion to *A. saccharum* in areas commonly used as winter habitat by deer (Figure 3-4). For example, we found that deer utilized *T. canadensis* stands as winter habitat throughout the range of *T. canadensis* basal area used in this study (Witt *et al.*, in review). However, during lower relative snow depth years, deer tend to select for areas of higher browse availability (Morrison *et al.*, 2003; Witt *et al.*, 2010). For this reason, we initially expect to see a positive feedback between increasing understory *A. saccharum* abundance and the intensity of use of that habitat, as stands slowly convert to *A. saccharum* dominance. However, as stands drop below a point where functionally *T. canadensis* is no longer serving as winter cover we expect to see a shift in winter habitat selection (Figure 3-4), thus leading to increased browse pressure and the potential for further erosion of stability in neighboring stands of *T. canadensis*.

Table 3-1. Stand attributes and species importance values.
Stand attributes and species importance values (IV) used in multiple linear regression models to identify important predictors of understory dominance for *Tsuga canadensis*, *Acer saccharum*, and *Acer rubrum*. Species IV = $(R_v + R_t)/2$, where for a given species or species group, R_v is the relative basal area (m^2 ha^{-1}) and R_t is the relative density (trees ha^{-1}).

	Min	Max	Mean ± 1 St. Dev.
Stand Attributes			
Stand BA (m^2 ha^{-1})	30.1	68.6	43.1 ± 10.1
Stand area (ha)	0.04	59.6	14.4 ± 14.1
Leaf litter (% cover)			
Broad leaf	0	83.7	38.5 ± 23.5
Needle leaf	0	84.6	23.7 ± 19.3
Mixed leaf	0	55.7	17.0 ± 12.9
Deer use (pellet groups ha^{-1})	0	1950	456 ± 486
Overstory Species Importance Values (stems $\geq$ 10 cm dbh)			
Tsuga canadensis	0.16	0.87	0.47 ± 0.18
Acer saccharum	0	0.43	0.13 ± 0.11
Acer rubrum	0	0.50	0.14 ± 0.12
Understory Species Importance Values (stems 0.1 < 10 cm dbh)			
Tsuga canadensis	0	0.86	0.16 ± 0.20
Acer saccharum	0	1	0.32 ± 0.31
Acer rubrum	0	1	0.12 ± 0.17

Table 3-2. Model parameter estimates for understory *Acer saccharum*, *Acer rubrum*, and *Tsuga canadensis* species importance values.

Model	Model covariates	Parameter estimate	p-value	F-stat	df	R^2(adj)
Understory *Acer saccharum* IV*				27.6	35	0.68
	Constant	0.1777	0.227			
	Overstory *Acer saccharum* IV*	1.4660	<0.001			
	Overstory *Tsuga canadensis* IV*	0.4679	0.036			
	Stand basal area	-0.0089	0.024			
Understory *Acer rubrum* IV*				7.2	36	0.25
	Constant	0.0516	0.439			
	Overstory *Acer rubrum* IV*	0.4990	0.003			
	White-tailed deer average pellet groups ha^{-1}	0.0001	0.025			
Understory *Tsuga canadensis* IV*				7.2	36	0.25
	Constant	0.6143	<0.001			
	Overstory *Acer saccharum* IV*	-0.5825	0.011			
	White-tailed deer average pellet groups ha^{-1}*	-0.0079	0.017			

* Variable was square root transformed.

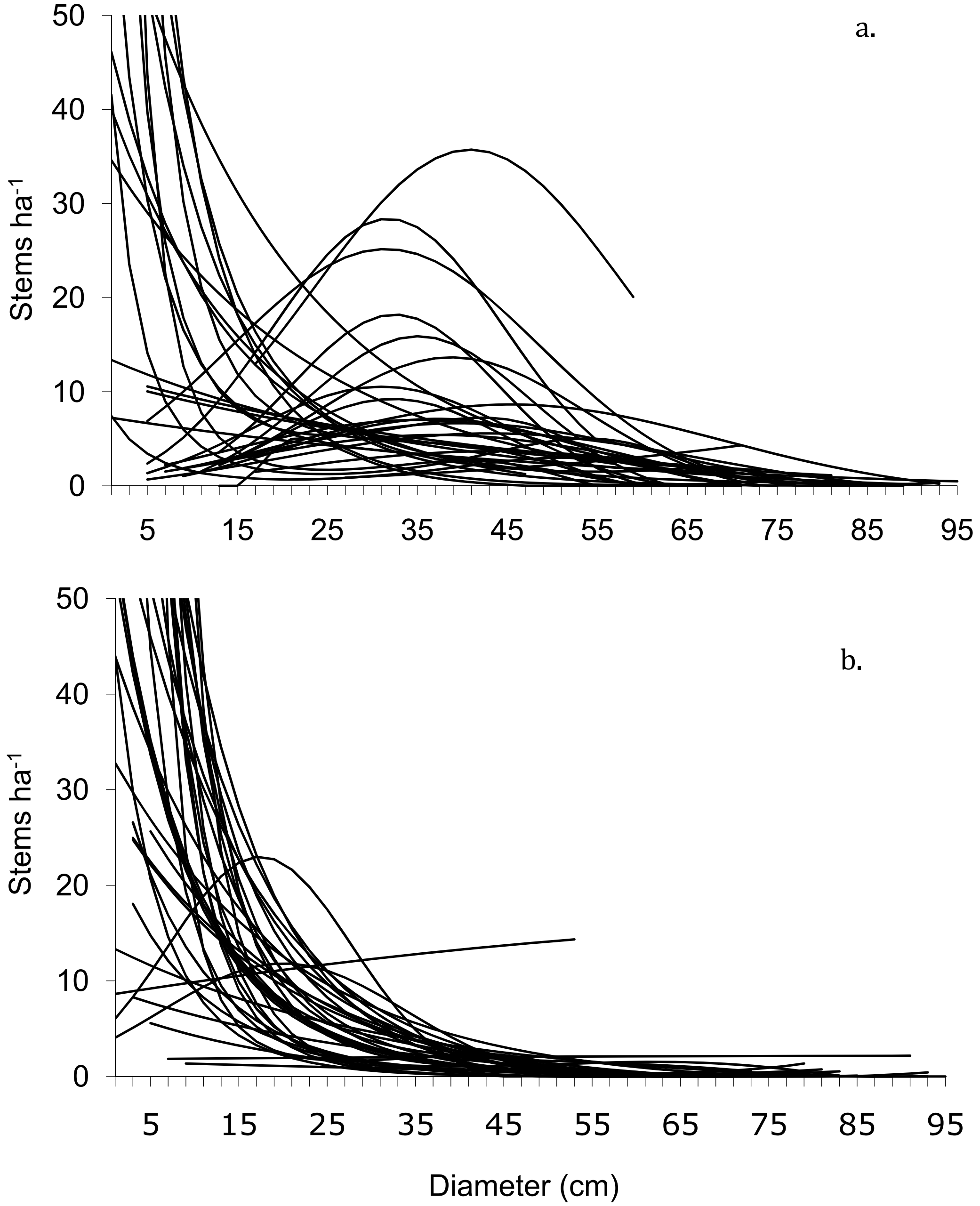


Figure 3-1. Diameter distributions by species for each study stand. Diameter distributions by species for study stands, a) *Acer spp.* and b) *Tsuga canadensis*. Distributions presented here have been truncated based on the range of the data.

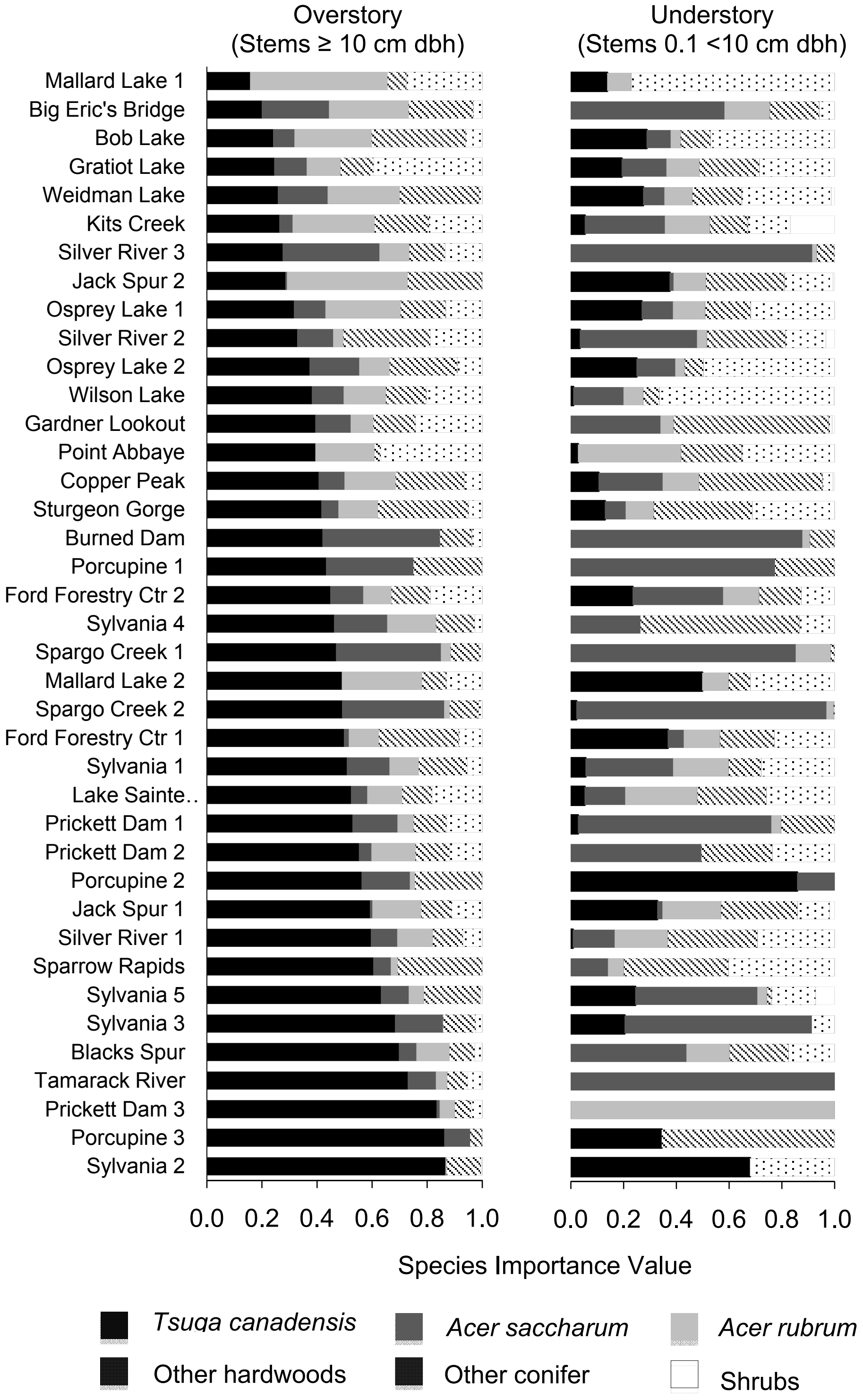


Figure 3-2. Species importance values (IV) for overstory and understory species or species groups listed by study site.

Species IV = $(R_a + R_t)/2$, where for a given species or species group, R_a is the relative basal area ($m^2\ ha^{-1}$) and R_t is the relative density (trees ha^{-1}).

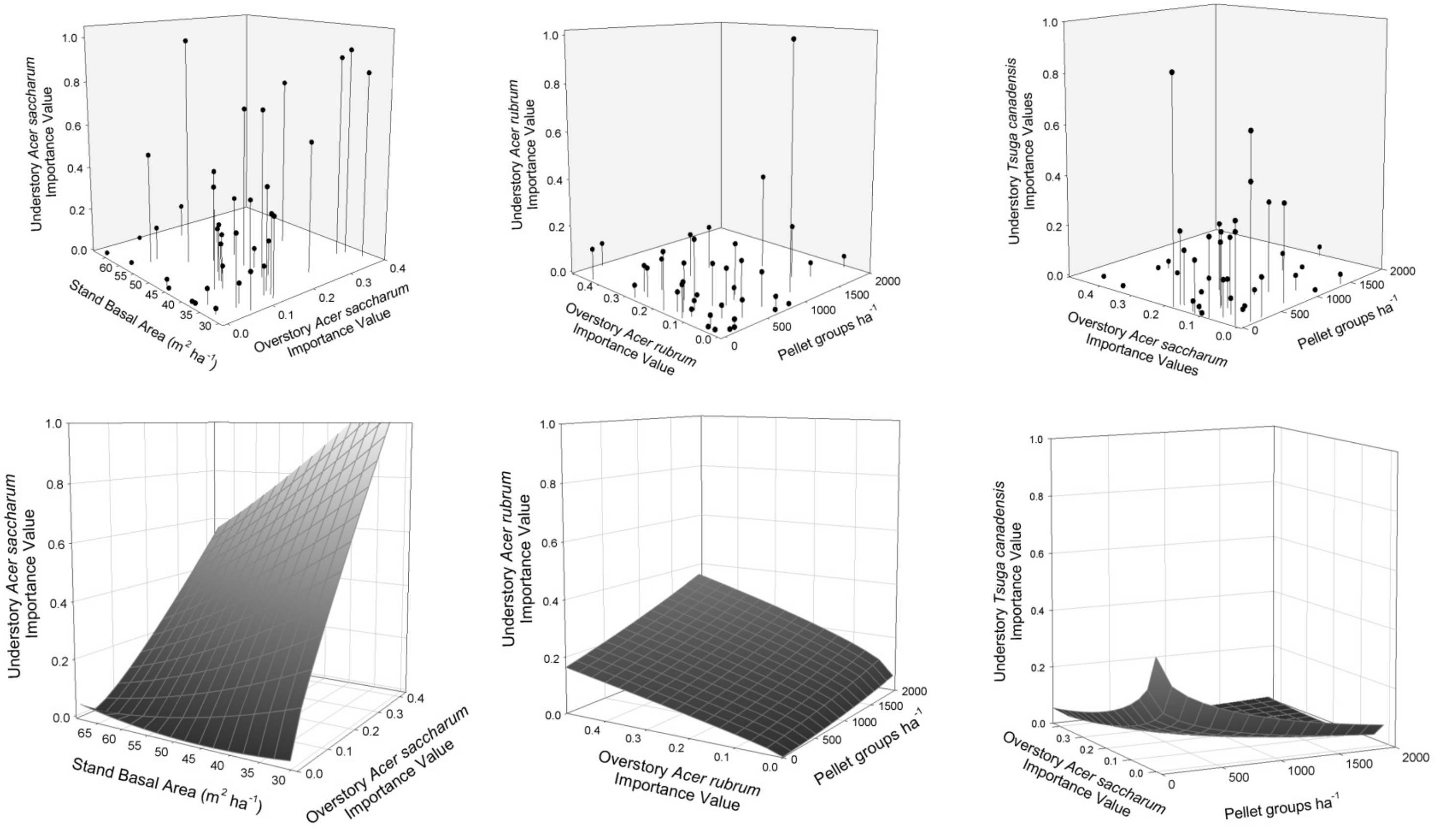


Figure 3-3. Predicted and observed understory species importance values.
Understory (stems 0.1 < 10 cm dbh) importance values (IV): actual (top row) and predicted (bottom row) for a) *Acer saccharum*, b) *Acer rubrum*, and c) *Tsuga canadensis* as a function of model covariates. For display purposes, overstory *T. canadensis* IV has been held constant at the mean (IV = 0.47) for predicted understory *A. saccharum* IV.

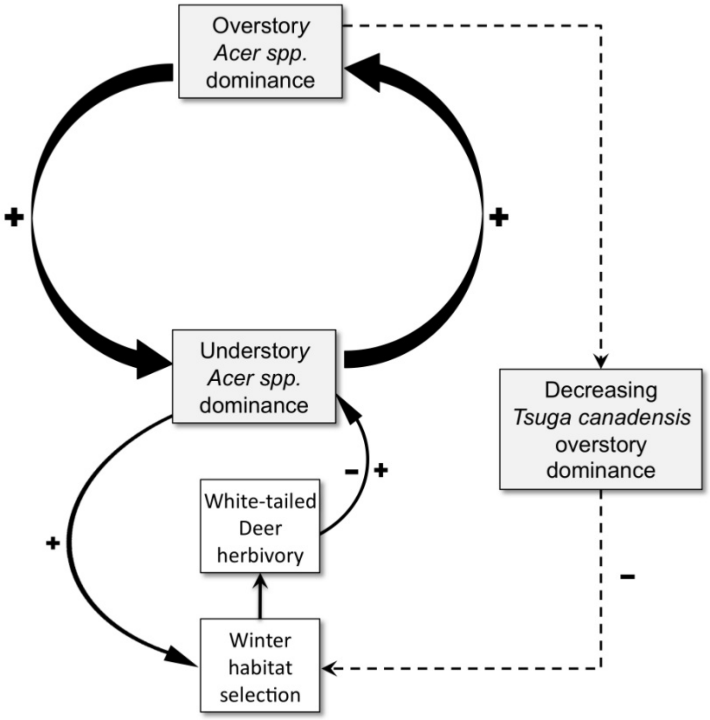


Figure 3-4. Hypothesized *Acer saccharum* feedback.
Pathways by which the interaction between white-tailed deer herbivory and the relative dominance of Acer species may alter successional trajectories and the availability of winter habitat.

APPENDIX 3-1. Diameter distribution shape classifications.

Shape category was identified by sign of the parameter estimate in a multiple linear regression analysis of log10 trees ha-1 as a function of dbh, dbh2, and dbh3 (Leak, 1996; Schwartz et al., 2005; Janowiak et al., 2008).

	Tsuga canadensis					*Acer spp.*					All species				
STAND	**DBH**	**DBH^2**	**DBH^3**	**Shape**	**$R^2_{(adj)}$**	**DBH**	**DBH^2**	**DBH^3**	**Shape**	**$R^2_{(adj)}$**	**DBH**	**DBH^2**	**DBH^3**	**Shape**	**$R^2_{(adj)}$**
Copper Peak	-			NE	19.3	-	+		BI	78	-			NE	80.6
Jack Spur 1	-			NE	73.4	-	+	-	RS	81.5	-	+		BI	85.7
Jack Spur 2	-	+		BI	66.4	-			NE	55.4	-	+		BI	83.1
Weidman Lake	-	+	-	RS	69	-			NE*	51.5	-			NE	90.4
Gardner Lookout	+	-		UNI	77.3	-	+	-	RS	72.4	-	+	-	RS	84.6
Kits Creek	*NS*			-	-	-	+		BI	79.1	-			NE	78.4
Bob Lake	-			NE	30.5	+	-		UNI	42.9	-			NE	73.1
Prickett Dam 1	+	-		UNI	60.2	-	+	-	RS	84	-	+	-	RS	84.4
Silver River 1	+	-		UNI	27.6	-	+		BI	82.6	-	+	-	RS	76.4
Silver River 2	-	+	-	RS	7.5	-	+	-	RS	84	-	+	-	RS	73.5
Silver River 3	*NS*			-	-	-	+		BI	72.1	-	+		BI	67.5
Sturgeon Gorge	-	+		BI	68.6	-	+		BI	74.3	-	+		BI	85.4
Osprey Lake 1	-	+	-	RS	69.8	-			NE*	83.9	-			NE	85.5
Osprey Lake 2	-	+	-	RS	51.9	-			NE	83.8	-	+	-	RS	87.5
Sylvania 1	+	-		UNI*	54.3	-	+		BI	73	-			NE	80.4
Sylvania 2	+	-		UNI	43.5	*NS*					+	-		UNI	28.1
Sylvania 3	-			NE	18.3	-	+		BI	45.3	-			NE	35
Sylvania 4	*NS*			-	-	-			NE	58.4	-			NE	59.4
Sylvania 5	-			NE	18.8	-	+	-	RS	73.4	-	+	-	RS	50.7
Wilson Lake	+	-		UNI	42.4	-			NE	52.2	-			NE	76.1
Mallard Lake 2	-			NE	24.3	+	-		UNI*	43.6	-			NE	70.6
Spargo Creek 1	+	-		UNI	49.5	-			NE	75.3	-			NE	68.2
Spargo Creek 2	+	-		UNI	43.6	-	+	-	RS	81.5	-	+	-	RS	79.6
Lake Sainte Kathryn	-	+	-	RS	20	-	+	-	RS	92.6	-	+	-	RS	83.1
Ford Forestry Center 1	-	+		BI	60.9	-	+		BI	60.7	-	+		BI	83.9
Ford Forestry Center 2	-	+		BI	70.9	-	+	-	RS	90.5	-	+		BI	87.4
Sparrow Rapids	-	+	-	RS	43.8	-			NE*	24.6	-	+	-	RS	45.9
Prickett Dam 2	+	-		UNI	47.6	-			NE	13.3	+	-		UNI	43.4
Burned Dam	+			?	16.8	-			NE	45.5	-			NE	16.7
Blacks Spur	+	-		UNI	19.2	-	+	-	RS	73.9	-	+	-	RS	53.1
Mallard Lake 1	-	+	-	RS	51.2	-			NE	25.6	-	+		BI	75.2
Tamarack River	+	-		UNI*	24.2	-			NE	7.4	+	-		UNI*	33.1
Prickett Dam 3	+	-		UNI	43.2	*NS*					+	-		UNI	44.4
Point Abbaye	+	-		UNI	15.4	-	+		BI	57.8	-			NE	77.4
Big Eric's Bridge	*NS*					-			NE*	64.1	-			NE*	55
Porcupine Mountains 1	+	-		UNI	17.6	-	+	-	RS	57.9	-			NE	44.5
Porcupine Mountains 2	-			NE	28	-			NE	7.2	-			NE	24.2
Porcupine Mountains 3	+	-		UNI	26.8	*NS*					+	-		UNI	18.7
Gratiot Lake	*NS*					-			NE	15.9	-			NE	17.9

* When distribution shapes were determined to be variable (+-+), the next best-fitting significant model was used (Janowiak et al. 2008). *NS* = not significant.

CONCLUSION

My goal for this dissertation was to explore the links between white-tailed deer winter habitat selection, limits to *Tsuga canadensis* regeneration, and the stability of remnant *T. canadensis* stands. In chapter one, I identified important stand and landscape variables associated with winter deer use. Stand use was associated with the availability of browse during lower relative snow depth years. *Tsuga canadensis* stands found in more heterogeneous landscapes, as opposed to being surrounded by primarily deciduous forests, had higher levels of winter use. However, the influence of snow on the intensity of habitat use was probably the most influential and directly contributed to my next two chapters. The intensity of use, as well as the number of stands used as winter habitat, increased during the highest snow years. *Tsuga canadensis* likely did not evolve under high levels of deer herbivory. Therefore, one of the most interesting adaptive characteristics of *T. canadensis*, the ability to remain suppressed for decades in a densely shaded understory until a gap allows for additional recruitment, turns out to be its Achilles heel. A single episodic browsing event occurring during an exceptionally snowy winter could result in the decimation of understory *T. canadensis* regeneration.

Further, as I discuss in chapters two and three, the adaptive ability of *Acer saccharum*, resprouting after a browsing event, may be giving this species a competitive advantage over *T. canadensis* under contemporary levels of deer herbivory. When found in nearly pure stands, both of these late-successional species modify understory conditions, preventing the establishment of the other and favoring their own succession. However, in many of these *T. canadensis* stands, the understory is dominated by *A.*

saccharum, and this input of deciduous litter in concert with deer herbivory may be lowering the resiliency of *T. canadensis* and allowing for continued *Acer* invasion. While speculative at best, the continuation of this positive feedback has the potential to further reduce forest ecosystem biodiversity in favor of a hardwood-dominant landscape.

The research I present in this dissertation is unique; however, the underlying themes are, unfortunately, being echoed globally as we struggle to comprehend the cascading effects of landscape fragmentation and biotic homogenization (McKinney and Lockwood, 1999; Rooney et al. 2004; Garrott and White, 1993). As I wrestled with some of the concepts associated with this research, I kept coming back to one overarching question. If indeed much of the *T. canadensis* population of the Upper Great Lakes region is undergoing a slow shift to *Acer* dominance, can we reverse what has been set in motion? Could we come close to restoring this majestic species to a level where it once again becomes that functional "foundation" species that it once was? As with all good ecological questions, the answer begins with "It depends…"

It depends. Will the re-colonization of wolves across the region begin to exert top-down pressure or alter deer habitat selection enough to allow *T. canadensis* adequate time reach a height where herbivory no longer impedes growth? Would a reduction in the amount of early successional habitat or an increase in hunting effort work to lower the deer population? Would a reduction in the deer population alone be enough? Or, have we already crossed some unknown threshold of ecosystem stability? Has the influx of *A. saccharum* already set in motion the erosion and altered successional trajectory of some of these remaining *T. canadensis* patches? What about hemlock woolly adelgid? Global climate change?

Mostly, however, where we go from here depends on our values, goals, and interests. So, what’s next? With *T. canadensis* facing so many perils across its distribution, is it worth it to us to continue to invest time and resources into a rapidly declining species? My answer, as an ecologist, a Michigander, and a member of the human race, is *Yes*. We have only touched the tip of the iceberg in our ecological understanding, and time and resources invested into answering these questions, no matter which system we are studying or trying to restore, will only further our knowledge of ecosystem processes and the cascading effects of fragmentation, species invasions, exploitation, and a host of other factors. Plus, *T. canadensis* is just a really interesting species!

REFERENCES

Abrams, M.D., 1998. The red maple paradox. BioScience 48, 355-364.

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

Anderson, R.C., 1997 Native pests: the impact of deer in highly fragmented habitats. In: Schwartz, M.D. (Ed.), Conservation in highly fragmented landscapes. Chapman and Hall, New York, NY, pp. 117-134.

Anderson, R.C., Loucks, O.L., 1979. White-tailed deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. Journal of Applied Ecology 16, 855-861.

Anderson, R.L., 2008. Skypixs Aerial Photography, Lake Linden, MI.

Andren, H., 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73, 794-804.

Augustine, D.J., McNaughton, S.J., 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. The Journal of Wildlife Management 62, 1165-1183.

Bates, D., Sarkar, D., 2006. lme4: Linear mixed-effects models using S4 classes. R package version 0.995-2 3.

Beier, P., McCullough, D.R., 1990. Factors influencing white-tailed deer activity patterns and habitat use. Wildlife Monographs 109, 3-51.

Bender, D.J., Fahrig, L., 2005. Matrix structure obscures the relationship between interpatch movement and patch size and isolation. Ecology 86, 1023-1033.

Blouch, R.I., 1984. Northern Great Lakes states and Ontario forests. In: Halls, L.K. (Ed.), White-tailed deer ecology and management. Stackpole Books, Harrisburg, PA, USA, pp. 391-410.

Boyce, M.S., Mao, J.S., Merrill, E.H., Fortin, D., Turner, M.G., Fryxell, J., Turchin, P., 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Ecoscience 10, 421-431.

Bradford, D.F., Neale, A.C., Nash, M.S., Sada, D.W., Jaeger, J.R., 2003. Habitat patch occupancy by toads (*Bufo punctatus*) in a naturally fragmented desert landscape. Ecology 84, 1012-1023.

Brandner, T.A., Peterson, R.O., Risenhoover, K.L., 1990. Balsam fir on Isle Royale: effects of moose herbivory and population density. Ecology 71, 155-164.

Burger, T.L., Kotar, J., 2003. A guide to forest communities and habitat types of Michigan. The University of Wisconsin, Madison.

Burnham, K., Anderson, D., 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer, New York, NY.

Canham, C.D., Loucks, O.L., 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. Ecology 65, 803-809.

Catovsky, S., Bazzaz, F., 2000. The role of resource interactions and seedling regeneration in maintaining a positive feedback in hemlock stands. Journal of Ecology 88, 100-112.

Collins, S.L., 1990. Habitat relationships and survivorship of tree seedlings in hemlock-hardwood forest. Canadian Journal of Botany 68, 790-797.

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

Creel, S., Winnie Jr, J., Maxwell, B., Hamlin, K., Creel, M., 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86, 3387-3397.

Crooks, K.R., Soulé, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400, 563-566.

Crow, T.R., 1996. The social, economic, and ecoogic significance of hemlock in the Lake States. In: Mroz, G., Martin, A.J. (Eds.), Hemlock ecology and management. Department of Forestry, University of Wisconsin, Iron Mountain, MI, pp. 11-17.

Dahir, S.E., Lorimer, C.G., 1996. Variation in canopy gap formation among developmental stages of northern hardwood stands. Canadian Journal of Forest Research 26, 1875-1892.

Dahlberg, B.L., Guettinger, R.C., 1956. The white-tailed deer in Wisconsin. Game Management Division, Wisconsin Conservation Department.

Davis, M., Sugita, S., Calcote, R., Parshall, T., Ferrari, J., 1996. 3000 years of abundant hemlock in Upper Michigan. . In: Mroz, G., Martin, A. (Eds.), Hemlock Ecology and Management. Department of Forestry, University of Wisconsin, Madison, Iron Mountain, MI.

Davis, M.B., Calcote, R.R., Sugita, S., Takahara, H., 1998. Patchy invasion and the origin of a hemlock-hardwoods forest mosaic. Ecology 79, 2641-2659.

Doepker, R.V., Beyer, D.E., Donovan, M.L., Wildlife, D., 1994. Deer population trends in Michigan's Upper Peninsula. Michigan Dept. of Natural Resources, Wildlife Division.

Donovan, T.M., Thompson, F.R., Faaborg, J., Probst, J.R., 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9, 1380-1395.

Drolet, C.A., 1976. Distribution and movements of white-tailed deer in southern New Brunswick in relation to environmental factors. Canadian Field-Naturalist 90, 123-136.

Dublin, H.T., Sinclair, A.R.E., McGlade, J., 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. The Journal of Animal Ecology, 1147-1164.

Dussault, C., Ouellet, J.P., Courtois, R., Huot, J., Breton, L., Jolicoeur, H., 2005. Linking moose habitat selection to limiting factors. Ecography 28, 619-628.

Eichenlaub, V.L., 1970. Lake effect snowfall to the lee of the Great Lakes: Its role in Michigan. Bulletin of the American Meteorological Society 51, 403-412.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3, 479-486.

Fancy, S.G., White, R.G., 1985. Energy expenditures by caribou while cratering in snow. The Journal of Wildlife Management 49, 987-993.

Frelich, L.E., Calcote, R.R., Davis, M.B., Pastor, J., 1993. Patch formation and maintenance in an old-growth hemlock-hardwood forest. Ecology, 513-527.

Frelich, L.E., Lorimer, C.G., 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. Biological Conservation 34, 99-120.

Garrott, R.A., White, P.J., 1993. Overabundance: an issue for conservation biologists? Conservation Biology 7, 946-949.

Goder, H.A., 1961. Hemlock reproduction and survival on its border in Wisconsin. Wisconsin Academy of Sciences, Arts and Letters 50, 175-181.

Godman, R.M., Lancaster, K., 1990. *Tsuga canadensis* (L.) Carr. eastern hemlock. Silvics of North America 1, 604-612.

Goerlich, D.L., Nyland, R.D., 2000. Natural regeneration of eastern hemlock: a review. In: McManus, K.A. et al. (Eds.), Proc. Symp. on Sustainable Management of Hemlock Ecosystems in Eastern north America, U.S. Department of Agriculture Forest Service General Technical Report NE-267, pp. 14–22. Goff, F.G., West, D., 1975. Canopy-understory interaction effects on forest population structure. Forest Science 21, 98-108.

Guisan, A., Zimmermann, NE, 2000. Predictive habitat distribution models in ecology. Ecological modelling 135, 147-186.

Gustafson, E.J., Gardner, R.H., 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77, 94-107.

Hibbs, D.E., 1982. Gap dynamics in a hemlock-hardwood forest. Canadian Journal of Forest Research 12, 538-544.

Hobbs, N.T., 1996. Modification of ecosystems by ungulates. The Journal of Wildlife Management 60, 695-713.

Holmes, S.A., Webster, C.R., Flaspohler, D.J., Froese, R.E., 2009. Death and Taxus: the high cost of palatability for a declining evergreen shrub, Taxus canadensis. Canadian Journal of Forest Research 39, 1366-1374.

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

Hough, A.F., 1960. Silvical characteristics of eastern hemlock (Tsuga canadensis). U.S. Forest Service Northeastern Experiment Station Paper 132.

Hulme, P.E., 1996. Herbivory, plant regeneration, and species coexistence. Journal of Ecology, 609-615.

Husheer, S.W., Coomes, D.A., Robertson, A.W., 2003. Long-term influences of introduced deer on the composition and structure of New Zealand Nothofagus forests. Forest Ecology and Management 181, 99-117.

Janowiak, M.K., Nagel, L.M., Webster, C.R., 2008. Spatial scale and stand structure in northern hardwood forests: implications for quantifying diameter distributions. Forest Science 54, 497-506.

Jenkins, J.C., Aber, J.D., Canham, C.D., 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. Canadian Journal of Forest Research 29, 630-645.

Jenkins, M., A., Webster, C., R., Parker, G., R., Spetich, M., A., 2004. Coarse woody debris in managed central hardwood forests of Indiana, USA. Forest Science 50, 781-792.

Johnson, C.J., Parker, K.L., Heard, D.C., Gillingham, M.P., 2002. Movement parameters of ungulates and scale-specific responses to the environment. Journal of Animal Ecology 71, 225-235.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65-71.

Jones, P.F., Hudson, R.J., 2002. Winter habitat selection at three spatial scales by American elk, *Cervus elaphus*, in west-central Alberta. Canadian Field-Naturalist 116, 183-191.

Kellogg, C.H., Bridgham, S.D., 2004. Disturbance, herbivory, and propagule dispersal control dominance of an invasive grass. Biological Invasions 6, 319-329.

Kie, J.G., Bowyer, R.T., Nicholson, M.C., Boroski, B.B., Loft, E.R., 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology 83, 530-544.

Kirchhoff, M.D., Schoen, J.W., 1987. Forest cover and snow: implications for deer habitat in southeast Alaska. The Journal of Wildlife Management 51, 28-33.

Leak, W.B., 1996. Long-term structural change in uneven-aged northern hardwoods. Forest Science 42, 160-165.

Maissurow, D.K., 1941. The role of fire in the perpetuation of virgin forests of northern Wisconsin. Journal of Forestry 39, 201-207.

Marx, L., Walters, M.B., 2008. Survival of tree seedlings on different species of decaying wood maintains tree distribution in Michigan hemlock-hardwood forests. Journal of Ecology 96, 505-513.

Mayor, S., Schaefer, J., Schneider, D., Mahoney, S., 2007. Spectrum of selection: New approaches to detecting the scale-dependent response to habitat. Ecology 88, 1634-1640.

Mayor, S.J., Schneider, D.C., Schaefer, J.A., Mahoney, S.P., 2009. Habitat Selection at Multiple Scales. Ecoscience 16, 238-247.

McClure, J.W., Lee, T.D., Leak, W.B., 2000. Gap capture in northern hardwoods: patterns of establishment and height growth in four species. Forest Ecology and Management 127, 181-189.

McGarigal, K., Cushman, S.A., Neel, M.C., Ene, E., 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst, Massachusetts, USA.

McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution 14, 450-453.

McShea, W.J., Underwood, H.B., Rappole, J.H., 1997. The science of overabundance: deer ecology and population management. Smithsonian Institution Press.

Michigan Department of Natural Resources, 2001. IFMAP/GAP Upper Peninsula Land Cover data with 30-m resolution, Michigan Department of Natural Resources. Lansing, MI.

Mladenoff, D., 1996. The role of eastern hemlock across scales in the northern Lake States. In: Mroz, G., Martin, A. (Eds.), Hemlock Ecology and Management. Department of Forestry, University of Wisconsin, Madison, Iron Mountain, MI.

Mladenoff, D.J., Stearns, F., 1993. Eastern hemlock regeneration and deer browsing in the northern Great Lakes region: A re-examination and model simulation. Conservation Biology 7, 889-900.

Morrison, S.F., Forbes, G.J., Young, S.J., Lusk, S., 2003. Within-yard habitat use by white-tailed deer at varying winter severity. Forest Ecology and Management 172, 173-182.

Nelson, M.E., 1998. Development of migratory behavior in northern white-tailed deer. Canadian Journal of Zoology 76, 426-432.

Nelson, M.E., Mech, L.D., 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildlife Monographs, 3-53.

Nelson, M.E., Mech, L.D., 2006. A 3-decade dearth of deer (*Odocoileus virginianus*) in a wolf (*Canis lupus*)-dominated ecosystem. American Midland Naturalist 155, 373-382.

National Operational Hydrologic Remote Sensing Center, 2004. Snow Data Assimilation System (SNODAS) data products at NSIDC. National Snow and Ice Data Center., Boulder, CO.

Neuendorff, J.K, Nagel, L.M., Webster, C.R., Janowiak, M.K., 2007. Stand structure and composition in a northern hardwood forest after 40 years of single-tree selection. Northern Journal of Applied Forestry 24 (3) 197-202.

Nordengren, C., Hofgaard, A., Ball, J.P., 2003. Availability and quality of herbivore winter browse in relation to tree height and snow depth. Annales Zoologici Fennici 40, 305-314.

Norton, D.C., Bolsenga, S.J., 1993. Spatiotemporal trends in lake effect and continental snowfall in the Laurentian Great Lakes 1951-1980. Journal of Climate 6, 1943-1956.

Noy-Meir, I., 1975. Stability of grazing systems: an application of predator-prey graphs. Journal of Ecology 63, 459-481.

O'Brien, D., Manseau, M., Fall, A., Fortin, M.J., 2006. Testing the importance of spatial configuration of winter habitat for woodland caribou: an application of graph theory. Biological Conservation 130, 70-83.

Olden, J.D., Schooley, R.L., Monroe, J.B., Poff, N.L., 2004. Context-dependent perceptual ranges and their relevance to animal movements in landscapes. Ecology 73, 1190-1194.

Orwig, D.A., Foster, D.R., Mausel, D.L., 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. Journal of Biogeography 29, 1475-1487.

Paradis, A., Elkinton, J., Hayhoe, K., Buonaccorsi, J., 2008. Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. Mitigation and Adaptation Strategies for Global Change 13, 541-554.

Parker, K.L., Robbins, C.T., Hanley, T.A., 1984. Energy expenditures for locomotion by mule deer and elk. The Journal of Wildlife Management, 474-488.

Pastor, J., Mladenoff, D.J., 1992. The southern boreal-northern hardwood forest border. In: Shugart, H.H., Leemans, R., Bonan, G.B. (Eds.), A systems analysis of the global boreal forest. Cambridge University Press, Cambridge, England, pp. 216-240.

Pastor, J., Naiman, R.J., 1992. Selective foraging and ecosystem processes in boreal forests. The American Naturalist 139, 690-705.

Pearson, S.M., Turner, M.G., Wallace, L.L., Romme, W.H., 1995. Winter habitat use by large ungulates following fire in northern Yellowstone National Park. Ecological Applications 5, 744-755.

Potvin, M.J., Drummer, T.D., Vucetich, J.A., Beyer Jr, D.E., Peterson, R.O., Hammill, J.H., 2005. Monitoring and habitat analysis for wolves in Upper Michigan. Journal of Wildlife Management 69, 1660-1669.

R Development Core Team, 2005. R: A language and environment for statistical computing, reference index version 2.8.0. R Foundation for Statistical Computing, Vienna, Austria.

Rettie, W.J., Messier, F., 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23, 466-478.

Ricketts, T.H., 2001. The matrix matters: effective isolation in fragmented landscapes. The American Naturalist 158, 87-99.

Riitters, K., O'Neill, R., Hunsaker, C., Wickham, D., Yankee, D., Timmins, S., Jones, K., Jackson, B., 1995. A factor analysis of landscape pattern and structure metrics. Landscape Ecology 10, 23-39.

Robinson, S.K., Thompson, F.R., Donovan, T.M., Whitehead, D.R., Faaborg, J., 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267, 1987-1990.

Rooney, T.P., 2001. Deer impacts on forest ecosystems: a North American Perspective. Forestry 74, 201-208.

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.

Rooney, T.P., Wiegmann, S.M., Rogers, D.A., Waller, D.M., 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. Conservation Biology 18, 787-798.

Rooney, T.P., McCormick, R.J., Solheim, S.L., Waller, D.M., 2000. Regional variation in recruitment of hemlock seedlings and saplings in the Upper Great Lakes, USA. Ecological Applications 10, 1119-1132.

Rooney, T.P., Waller, D.M., 1998. Local and regional variation in hemlock seedling establishment in forests of the upper Great Lakes region, USA. Forest Ecology and Management 111, 211-224.

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

Ross, R.M., Bennett, R.M., Snyder, C.D., Young, J.A., Smith, D.R., Lemarie, D.P., 2003. Influence of eastern hemlock(*Tsuga canadensis* L.) on fish community structure and function in headwater streams of the Delaware River basin. Ecology of Freshwater Fish 12, 60-65.

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

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

Sabine, D.L., Morrison, S.F., Whitlaw, H.A., Ballard, W.B., Forbes, G.J., Bowman, J., 2002. Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick. The Journal of Wildlife Management, 718-728.

Schabenberger, O., Pierce, F., 2002. Contemporary statistical models for the plant and soil sciences. . CRC Press, Boca Raton, FL.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591-596.

Schmitz, O.J., Sinclair, A.R.E., 1997. Rethinking the role of deer in forest ecosystem dynamics. In: McShea, W.J., Underwood, H.B., Rappole, J.H. (Eds.), The science of overabundance; deer ecology and population management Smithsonian Institution Press, Washington D.C., pp. 201-223.

Schwartz, J.W., Nagel, L.M., Webster, C.R., 2005. Effects of uneven-aged management on diameter distribution and species composition of northern hardwoods in Upper Michigan. Forest Ecology and Management 211, 356-370.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E., Swift, D.M., 1987. Large herbivore foraging and ecological hierarchies. BioScience 37, 789-799.

Shi, H., Laurent, E.J., LeBouton, J., Racevskis, L., Hall, K.R., Donovan, M., Doepker, R.V., Walters, M.B., Lupi, F., Liu, J., 2006. Local spatial modeling of white-tailed deer distribution. Ecological Modelling 190, 171-189.

Snyder, C.D., Young, J.A., Lemarie, D.P., Smith, D.R., 2002. Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams.

Stearns, F., 1951. The composition of the sugar maple-hemlock-yellow birch association in northern Wisconsin. Ecology 32, 245-265.

Stottlemyer, R., Toczydlowski, D., 1991. Stream chemistry and hydrologic pathways during snowmelt in a small watershed adjacent Lake Superior. Biogeochemistry 13, 177-197.

Stottlemyer, R., Toczydlowski, D., 1999. Seasonal change in precipitation, snowpack, snowmelt, soil water and streamwater chemistry, northern Michigan. Hydrological Processes 13.

Tallmon, D.A., Jules, E.S., Radke, N.J., Mills, L.S., 2003. Of mice and men and trillium: cascading effects of forest fragmentation. Ecological Applications 13, 1193-1203.

Telfer, E.S., 1970. Winter habitat selection by moose and white-tailed deer. The Journal of Wildlife Management 34, 553-559.

Tierson, W., Mattfeld, G., Sage, R., Behrend, D., 1985. Seasonal movements and home ranges of white-tailed deer in the Adirondacks. Journal of Wildlife Management 49, 760-769.

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

Turner, M., Pearson, S., Romme, W., Wallace, L., 1997. Landscape heterogeneity and ungulate dynamics: What spatial scales are important? In: Bissonette, J. (Ed.), Wildlife and Landscape Ecology: Effects of Pattern and Scale. Springer-Verlag, New York, NY, pp. 331-348.

Turner, M.G., 1989. Landscape ecology: the effect of pattern on process. Annual review of ecology and systematics 20, 171-197.

Tyrrell, L.E., Crow, T.R., 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. Ecology 75, 370-386.

US Geological Service, 1998. 1998 Series USGS Digital Orthophoto Quadrangles.

Van Deelen, T.R., Campa III, H., Hamady, M., Haufler, J., B, 1998. Migration and seasonal range dynamics of deer using adjacent deeryards in Northern Michigan. Journal of Wildlife Management 62, 205-213.

Van Hees, A.F.M., Kuiters, A.T., Slim, P.A., 1996. Growth and development of silver birch, pedunculate oak and beech as affected by deer browsing. Forest Ecology and Management 88, 55-63.

Ver Hoef, J.M., Boveng, P.L., 2007. Quasi-poisson vs. negative binomial regression: How should we model overdispersed count data? Ecology 88, 2766-2772.

Verme, L.J., 1973. Movements of white-tailed deer in upper Michigan. The Journal of Wildlife Management 37, 545-552.

Wallace, L.L., Turner, M.G., Romme, W.H., O'Neill, R.V., Wu, Y., 1995. Scale of heterogeneity of forage production and winter foraging by elk and bison. Landscape Ecology 10, 75-83.

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

Webster, C.R., Lorimer, C.G., 2005. Minimum opening sizes for canopy recruitment of midtolerant tree species: a retrospective approach. Ecological Applications 15, 1245-1262.

Webster, C.R., Rock, J.H., Froese, R.E., Jenkins, M.A., 2008. Drought–herbivory interaction disrupts competitive displacement of native plants by Microstegium vimineum, 10-year results. Oecologia 157, 497-508.

Whitney, G.G., 1987. An ecological history of the Great Lakes forest of Michigan. Journal of Ecology 75, 667-684.

Wisconsin Department of Natural Resources, 1998. WISCLAND Land Cover (WLCGW930). Madison, WI.

Wiens, J.A., 1976. Population responses to patchy environments. Annual review of ecology and systematics 7, 81-120.

Witt, J.C., Webster, C.R., Accepted for publication pending minor revision. Regeneration dynamics in remnant *Tsuga canadensis* stands in the northern Lake States: potential direct and indirect effects of herbivory. Forest Ecology and Management.

Witt, J.C., Webster, C.R., Drummer, T.D., Froese, R.E., Vucetich, J.A., Peterson, R.O., In review. Landscape deterogeneity as a driver of patch use by *Odocoileus virginianus* along a temporal and spatial gradient of snow depth. The Journal of Wildlife Management.

Woods, K.D., 1984. Patterns of tree replacement: canopy effects on understory pattern in hemlock-northern hardwood forests. Plant Ecology 56, 87-107.

Woolf, A., Nielsen, C., Weber, T., Gibbs-Kieninger, T., 2002. Statewide modeling of bobcat, *Lynx rufus,* habitat in Illinois. Biological Conservation 104, 191-198.

Wu, Y., Sklar, F.H., Rutchey, K., 1997. Analysis and simulations of fragmentation patterns in the Everglades. Ecological Applications 7, 268-276.

Wydeven, A.P., Hay, R.W., 1996. Mammals, amphibians, and reptiles of hemlock forest in the Lake Superior region. In: Mroz, G., Martin, A.J. (Eds.), Hemlock ecology and management. Department of Forestry, University of Wisconsin, Iron Mountain, MI, pp. 115-123.

Xie, J., Hill, H.R., Winterstein, S.R., Campa Iii, H., Doepker, R.V., Van Deelen, T.R., Liu, J., 1999. White-tailed deer management options model (DeerMOM): design, quantification, and application. Ecological Modelling 124, 121-130.

Yamasaki, M., DeGraff, R.M., Lanier, J.W., 2000. Wildlife habitat associations in eastern hemlock - birds, smaller mammals, and forest carnivores. In: McManus, K., Shields, K.S., Souto, D.R. (Eds.), Proceedings of the symposium on sustainable management of hemlock ecosystems in eastern North America. USDA Forest Service, Northeastern Research Station, Newton Square, PA, pp. 135-143.

Yorks, T.E., Jenkins, J.C., Leopold, D.J., Raynal, D.J., Orwig,D.A., 2000. Influences of eastern hemlock mortality on nutrient cycling. In: McManus, K., Shields, K.S., Souto, D.R. (Eds.), Proceedings of the symposium on sustainable management of hemlock ecosystems in eastern North America. USDA Forest Service, Northeastern Research Station, Newton Square, PA, pp. 126–133.

Zuur, A.F., Ieno, E.N., Walker, N., Smith, G.M., Saveliev, A.A., 2009a. Mixed Effects Models and Extensions in Ecology With R. Springer Science+Business Media, LLC, New York, NY.