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MULTIPLE GAP-, STAND- AND LANDSCAPE-SCALE FACTORS AFFECT REGENERATION IN MANAGED NORTHERN HARDWOOD FORESTS

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MULTIPLE GAP-, STAND- AND LANDSCAPE-SCALE FACTORS AFFECT REGENERATION IN MANAGED NORTHERN HARDWOOD FORESTS

By

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ABSTRACT

MULTIPLE GAP-, STAND- AND LANDSCAPE-SCALE FACTORS AFFECT REGENERATION IN MANAGED NORTHERN HARDWOOD FORESTS

By

Megan Shanahan Matonis

The perpetuation of extensive and economically, socially and ecologically important northern hardwood forests relies largely on natural regeneration below canopy gaps created by selection harvesting. I explored factors affecting the abundance, composition and survival of seedlings and saplings in harvest gaps across northern hardwood stands in the Western Upper Peninsula of Michigan with both a natural experiment and a mesic conifer planting experiment. Sapling abundance was highly variable; nearly fifty percent of harvest gaps were devoid of sugar maple saplings (the dominant overstory species), but abundance was great in other stands (up to 32,100 saplings / ha). Sugar maple sapling abundance was lower on southern stands with rich soil nutrient conditions where estimated winter deer densities were high. Deer browse pressure was high in the study area. Almost all planted hemlock seedlings were browsed, demonstrating the futility of restoring browse preferred coniferous species where winter deer densities are high. Seedling and sapling abundance were positively influenced by canopy openness and negatively by cover of competing vegetation, but effects were weaker than those of Habitat Type and deer density. There was only limited evidence of seed source limitations in these stands. Results illustrate that natural and artificial regeneration in managed northern hardwood forests are affected by multiple interacting and spatially varying factors that need to be considered when planning timber harvests, implementing restoration efforts and modeling regeneration dynamics.

Dedicated to my loving and caring Grandmother, the shining queen of our family. Your presence will be missed but never forgotten.

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INTRODUCTION

Northern hardwood forest (maple-beech-birch type) spans over 53.7 million acres throughout the Great Lakes, North Central and Northeastern United States (Smith et al 2004) and is the predominant forest type in Michigan (Potter-Witter and Lacksen 1993). These forests have high multi-use value because they produce millions of cubic meters of timber each year for pulp, lumber and veneer, they support summer and winter recreation activities and provide habitat for wildlife (Filip 1973; OMNR 1998).

Northern hardwood forests have undergone, and are undergoing changes in structure and composition due in part to the interrelated disturbances of harvesting and deer herbivory (Kraft et al 2004). During the early commercial logging era in the Lake States from the mid 1800's to early 1900's, forests were clear cut and white pine and hemlock were virtually eliminated from many forests (Stearns 1997). As early as the 1920's, industrial forest companies began experimenting with selection harvesting as a sustained yield approach (Stearns 1997). With the publication of long-term studies demonstrating the benefits of this approach (Eyre and Zillgitt 1953) and the development of marking guides (Arbogast 1957), selection harvesting has become common practice in northern hardwood stands. It is advocated as a silvicultural practice that meets ecological and economic objectives by mimicking gap phase dynamics and capitalizing on the ability of these forests to naturally regenerate (Nyland 1998). However, when seedlings and saplings fail to grow into larger size classes, it threatens the ability of these forests to sustain long-term timber production (Nyland 1998) and could destabilize the economy in areas such as the Western Upper Peninsula of Michigan where the timber industry is one of the main economic drivers (Racevskis and Lupi 2006).

Forest harvesting, along with increased agricultural activity, the extirpation of predators, and legislation to regulate hunting has created landscape conditions favorable for white-tailed deer (Rooney 2001; Cote et al 2004). Although a natural herbivore in northern hardwood forests, white-tailed deer populations have reached unprecedented densities and are exerting changes on understory composition in hardwood forests (Rooney 2001). Browsing by white-tailed deer (*Odocoileus virginianus*) can decrease seedling and sapling densities (Stoeckeler et al 1957; Horsley et al 2003; Rooney and Waller 2003; Eschtruth and Battles 2008) by reducing height increments and survivorship (Liang and Seagle 2002; Horsley et al 2003; Eschtruth and Battles 2008). Although intense browse by white-tailed deer (*Odocoileus viriginanus*) is often cited as the major cause of regeneration failure after harvest treatments in hardwood forests (Stoeckeler et al 1957; Shafer et al 1961; Marquis and Brenneman 1981; Cook 2008), seedling and sapling layers are affected by a suite of abiotic and biotic factors throughout their ontogeny, so studying deer density in isolation of other factors produces limited results (Didier and Porter 2003).

Seed source, light availability, competing vegetation, deer density and soil nutrient and moisture conditions were identified from the literature and field observations as key factors limiting regeneration in northern hardwood forests. Chapter 1 describes a study that assesses the relative effect of these factors on seedling and sapling abundance and composition below harvest gaps in 59 northern hardwood stands across the Western Upper Peninsula of Michigan. This natural experiment took advantage of the north to south gradient in winter deer density across this landscape and the variation in gap sizes/light availability within stands created by harvest practices. Although causal

relationships cannot be established from natural experiments, this approach can reveal patterns and associations between variables across their natural range of variation and can be implemented in a more spatially intensive and extensive manner.

Restoring the white pine and eastern hemlock components that were once part of northern hardwood forests are conservation goals across the Great Lakes region in order to increase biodiversity and alter white-tailed deer winter and summer range availability (Herman et al 2004). Chapter 2 describes a study that assesses the efficacy of efforts to plant mesic conifer seedlings in an area of the Western Upper Peninsula with a gradient in snow depth, variation in winter deer densities and variation in landscape contexts related to winter range suitability for deer (i.e. distance to lowland conifer stands used by deer for winter shelter). Results from this study demonstrate a relationship between seedling browse damage and deer density estimated by the fecal pellet technique and can assist with directing restoration efforts.

The two studies in this thesis were performed in managed forests and focus on seedling and sapling populations (natural or artificially planted) in harvest gaps and explore impacts of deer herbivory, as well other factors on seedling and sapling abundance and composition (Chapter 1) and survival (Chapter 2). Results demonstrate that relatively simple mechanisms, such as differences in shade tolerance, cannot be used to explain and predict forest dynamics because various interacting and spatially varying factors act as regeneration filters. Insight into the relative contributions of regeneration limiting factors, provided by my multivariate assessment at multiple stands across a broad geographic area, can assist with predicting future forest structure and composition and with managing northern hardwood forests for the many services they provided.

Chapter 1: Gap-, stand- and landscape-scale factors affect northern hardwood regeneration following selection harvesting

Abstract

The abundance and diversity of saplings regenerating below canopy gaps are affected by a suite of abiotic and biotic variables including seed source, light availability, soil moisture and nutrient regime, competition from understory vegetation and herbivory. Multivariate approaches that explore gap-, stand- and landscape-scale factors across broad geographic areas are necessary to assess the relative effects of these factors and to understand spatial patterns in regeneration success. To this end, I measured seedling and sapling layers and quantified the previously listed factors within 347 canopy gaps created by selection harvesting across 59 northern hardwood stands in the Western Upper Peninsula where winter deer density increases with latitude. A multilevel modeling approach was taken to account for the hierarchical structure of the data (i.e. gaps nested within stands), and parameter estimates from these models were used to simulate sapling abundances under various gap- and stand-level conditions. Sapling abundance of sugar maple (*Acer saccharum* Marsh.) was higher on stands with lower estimated deer densities, higher snow depths, and less nutrient rich Habitat Types underlain with coarser textured substrates. Habitat Type (a proxy for stand soil moisture and nutrient regime) had the greatest effect on sugar maple sapling abundance, followed by deer density, light availability and competing vegetation. Northern hardwood stands have the potential to undergo compositional changes if deer densities are not reduced because unpalatable/browse-tolerant species may replace highly browsed species. Results demonstrate that various factors can interrupt the regeneration of even shade tolerant species following canopy gap formation.

1.1 Introduction

In forests where stand clearing disturbances occur infrequently, sapling regeneration relies on pulses of resource provided by canopy gaps (Runkle 1985; Yamamoto 2000). Canopy gaps form naturally due to mature tree mortality from old age, windfall, lightning, disease and insects (Krasny and Whitmore 1992), but tree removal from selection harvesting has become the primary mode by which these gaps are created in managed northern hardwood forests. The aim of selection harvesting is to sustain the production of high quality timber by mimicking natural gap dynamics to foster regeneration and by maintaining an uneven-aged structure (Arbogast 1957; Guldin 1996; OMNR 1998). This harvest practice is recommended for northern hardwood forests (Arbogast 1957) because of evidence that it promotes the regeneration of economically valuable shade tolerant species such as sugar maple (*Acer saccharum* Marsh.) (Tubbs 1968) and can facilitate regeneration of shade-intolerant and intermediate species if group selection is used to create larger gaps (Leak 1999).

Abundant natural regeneration of desirable species is essential to the success of the selection system (Nyland 1998). Unimodal size-density stand structures considered unsustainable under selection harvesting (Smith et al 1997) may develop when there are insufficient seedling and sapling populations to recruit into larger size classes and replace the pole and saw-log sized trees removed by harvesting (Nyland 1998). Failure of hardwood species such as sugar maple, yellow birch (*Betula alleghaniensis* Britton), black cherry (*Prunus serotina* Ehrh.) and northern red oak (*Quercus rubra* L.) to germinate or grow into taller sapling layers has been observed in many managed hardwood forests for over half a century in the Midwestern and Northeastern United

States (Stoeckeler et al 1957; Marquis and Brenneman 1981; Jenkins 1997; Aldrich et al 2005; Belden and Pallardy 2009), including in the Western Upper Peninsula of Michigan (Graham 1954; Miller 2004; Donovan 2005). Sugar maple is the dominant species in northern hardwood forests, and loss of this species from the understory could dramatically alter future stand composition and structure (Jenkins 1997). Reduced regeneration of commercially important species following selection harvesting causes concern for forest managers who seek to ensure long-term timber production and maintain certification under the Sustainable Forestry Initiative (Donovan 2005). Regeneration failures could jeopardize the sustainability of forest productivity and thus destabilize the economy in areas like the Western Upper Peninsula of Michigan where the timber industry is one of the main economic drivers (Racevskis and Lupi 2006). In addition, loss of seedling and sapling layers in hardwood forests have ecological consequences because they serve as forage for species such as white-tailed deer (*Odocoileus viriginanus* Zimmermann) (Blouch 1984) and provide vertical stand structure necessary for some bird species (Webb et al 1977; DeGraaf et al 1998).

The abundance and species composition of seedling and sapling layers in harvest gaps are affected by many abiotic and biotic factors that reduce or enhance seed availability, germination, growth and survival. Seed production, light availability, soil nutrients and moisture regime, competition from non-tree understory vegetation, and deer herbivory have been identified as key factors influencing regeneration in northern hardwood forests based on previous studies and field observations (Figure 1.1). This list is not all-inclusive, but highlights those factors hypothesized to have the greatest effects on sugar maple and other common northern hardwood species present in the understory.

Densities of seedlings are initially constrained by the production of seeds. Generally positive relationships between tree size, seed production, and seedling densities (Marquis 1975; Tubbs 1977; Hughes and Fahey 1988; Ribbens et al 1994; Garret and Graber 1995; Fei and Steiner 2008) imply that management decisions regarding the retention of large mature seed trees can impact future regeneration. Once seedlings germinate, availability of soil moisture, nutrients and light affect their growth (Canham and Marks 1985; Canham 1988; Walters and Reich 1997; Finzi and Canham 2000; Bigelow and Canham 2002; Webster and Lorimer 2002; Schreeg et al 2005; Kobe 2006), survival (Caspersen and Kobe 2001; Schreeg et al 2005) and species richness (Tubbs 1977; Runkle 1982; Runkle 1984; Burger and Kotar 2003; Schumann et al 2003). Increasing the size of harvest gaps increases understory light availability (Gray et al 2002; Canham et al 1990), seedling and sapling growth rates (Canham and Marks 1985; Kobe 2006) and cover of non-tree understory vegetation (Collins et al 1985; Schumann et al 2003; Shields and Webster 2007). Shrubs, ferns and graminoids can reduce seedling and sapling densities, survival and height growth (Horsley and Marquis 1983; De Steven 1991; Romagosa and Robison 2003; Fei and Steiner 2008) by altering understory microhabitat conditions (e.g. temperature and light availability) and competing for nutrients (George and Bazzaz 1999) and water (Randall 2007).

Intense browse by white-tailed deer is often cited as the major cause of regeneration failure after harvesting treatments in hardwood forests (Graham 1954; Stoeckeler et al 1957; Shafer et al 1961; Marquis and Brenneman 1981; Cook 2008). Selective browsing and differences in species tolerance to browsing (Augustine and McNaughton 1998) affect the abundance and species richness of understory tree layers

(Stoeckeler et al 1957; Liang and Seagle 2002; Horsley et al 2003; Rooney and Waller 2003; Eschtruth and Battles 2008), occasionally causing the near elimination of highly preferred browse species, such as is the case with eastern hemlock (*Tsuga canadensis* (L.) Carrière) and northern white-cedar (*Thuja occidentalis* L.) in the Great Lakes region (Rooney et al 2000; 2002). By removing palatable species, herbivory can permit the dominance of a few unpalatable, browse resistant / tolerant species (Horsley et al 2003; Cote et al 2004) such as ironwood (*Ostrya virginiana* (Mill.) K. Koch) or beech (*Fagus grandifolia* Ehrh.) (Sage et al 2003; Miller 2004).

This study evaluates the relative impacts of deer density and other gap- and stand-level factors on seedling and sapling layers. It takes advantage of a decreasing gradient in winter deer density with increasing latitude in the Western Upper Peninsula of Michigan, caused in part by the southern seasonal migration of deer to avoid deep lake-effect snow (Verme 1973; Doepker et al 1994; VanDeelen et al 1998). The impacts of white-tailed deer on tree regeneration have been the focus of many studies (see reviews- Weisberg and Bugmann 2003; Rooney and Waller 2003; Cote et al 2004), however, few have assessed the relative impact of deer density in conjunction with other gap- and stand-level factors across a large geographic area (Rooney et al 2000; 2002). None have done so for broadly distributed and economically valuable northern hardwood species. Given the suite of factors that affect seedlings and saplings throughout their ontogeny, multivariate assessments at multiple stands across broad geographic areas are critical for determining the relative contributions of different factors and to reduce the risk of assigning significance to factors that are correlated with unmeasured variables.

This study explores the following hypotheses: H1) as winter deer density increases across a landscape-scale gradient, sapling abundance of heavily browsed species such as sugar maple (Swift 1949; Stoeckeler et al 1957) decreases, H2) seedling and sapling abundances, diversity and height growth rates in gaps created by selection harvesting are affected by gap-level seed source availability (+), light availability (+) and cover of competing vegetation (-) and by stand-level soil moisture and nutrient conditions (+) and winter deer density (-) and H3) current understory regeneration may not perpetuate current overstory species composition, due in part to deer browse of palatable species.

1.2 Methods

1.2.1 Study area

Northern hardwood stands included in this study (n=59 stands) were harvested two to fifteen years ago and located across 475,000 contiguous hectares of Dickinson, Iron, Marquette and Menominee counties in the Western Upper Peninsula of Michigan (Figure 1.2; Appendix A, Table A.1). This study area encompasses that for the ongoing Western Upper Peninsula Economic-Ecological Modeling Project that integrates ecology and economics to better understand interactions among deer, tree harvesting and regeneration on managed forest landscapes (Laurent et al 2005; LeBouton et al 2005; Racevskis and Lupi 2006; Millington et al 2009 *in review*). This area was selected for the domination of forest cover, the relative absence of agriculture and urban or suburban developments, and the natural variation in deer densities and snow depth (Doepker et al 1994; Shi et al 2006). All but five stands were dominated by sugar maple in the overstory (43-100% basal area of trees with dbh >20 cm), and had various components of

American basswood (*Tilia americana* L.), red maple (*Acer rubrum* L.), eastern hemlock (*Tsuga canadensis* (L.) Carrière), white ash (*Fraxinus americana* L.), black cherry (*Prunus serotina* Ehrh.), balsam fir (*Abies balsamea* (L.) Mill.), yellow birch (*Betula alleghaniensis* Britton), and other minor coniferous and deciduous species.

Stands ranged in elevation from 283 to 551 m with underlying soils from thirty distinct soil types (Appendix A, Table A.2). Soil drainage varies from very poor to excessive. Annual snow fall varies from 161 cm in the south to 434 cm in the north (National Climatic Data Center 2009) due to lake-effect snow influenced by Lake Superior (Jerome 2006).

1.2.2 Study stand harvest dates

Harvest dates for all stands were estimated with radial increment analysis of stem cross sections taken from saplings growing in harvest gaps. The harvest date was estimated by the year of release from growth suppression (Webster and Lorimer 2005). Harvest dates estimated from release were strongly correlated with the harvest records available for a subset of seventeen stands (Pearson's r= 0.87), with a difference of ± 2 years (average = -0.4 years).

1.2.3 Field methods

1.2.3.a Stand-level variables: Soil moisture and nutrient regime (Habitat Type), deer density, browse pressure and snow depth

Habitat Type, a proxy for soil moisture and nutrient regime, was determined from diagnostic assemblages of understory vegetation at each stand (Burger and Kotar 2003). Northern hardwood stands in the study area fall into five different Habitat Types (listed from lowest to highest soil nutrient availability): TMC, ATM, ATD, ATD-Hp and AOCa

(Table 1.1). Stand classification into one of these types is not based on sapling abundance or diversity.

Winter deer density was estimated with fecal pellet surveys at each stand in spring 2008 (Hill 2001). Fecal pellet surveys are a fairly simple method of assessing relative local deer density (Hill 2001) with reasonable accuracy (Neff 1968; Forsyth et al 2007, but see Fuller 1991). However, it has been criticized because defecation rates are correlated with forage intake, forage moisture content and percentage of young in the herd and estimates can be biased by sampling design and observer error (Neff 1968). Despite these limitations, no other method can be as readily utilized to determine stand-scale variation in deer density across a large geographic area. Pellet groups were counted along ten 50 m by 4 m transects oriented in an hour glass shape (Appendix B, Section B.1). All transects were double counted with different observers to improve accuracy (Jenkins and Manly 2008). The average pellet group counts from all ten transects were used to calculate deer density following the methods of Hill 2001 (Appendix B, Section B.1). Visible pellets were those above leaf litter deposited in November 2007, so the estimate of deer density corresponds to deer presence in the late fall, winter and early spring months. I term the estimate "winter deer density" although deer depositing fecal pellets in northern hardwood stands likely did so while migrating between summer and winter ranges (i.e. in November and April).

Stand-level sugar maple browse index (SMBI), a surrogate for browse pressure, was estimated by counting the number of browsed and unbrowsed terminal twigs 30-200 cm above the ground on 5- 24 sugar maple saplings 1 to 2.5 m tall (Frelich and Lorimer 1985; Rooney et al 2000). Each sapling was assigned to one of five browse categories

based on the percentage of total twigs browsed (0= no browsing, 1 = 1-25%, 2 = 26-50%, 3= 51-75%, and 4 = 76-100%). Average SMBI was calculated for each of the 25 stands where there were more than 5 sugar maple saplings for which browse index could be determined.

Average daily snow depth (cm) for November 2007 to April 2008 was determined from the National Snow and Ice Data Center's Snow Data Assimilation System (SNODAS) snow mass and energy balance model (Barrett 2003; NOHRSC 2004).

1.2.3.b Gap-level variables: gap size, light availability, seed production potential, competing vegetation, seedling and sapling abundance and growth rates

Gap-level variables were quantified within six gaps at each stand, with the exception of five stands where fewer gaps were measured because fewer existed or very high sapling densities made data collection time-intensive. Gaps were defined as canopy openings created by the removal of one or more trees, with the shortest inter-bole diameter of at least ten meters. Gap sizes were estimated using the method of Runkle 1981, i.e. calculated as an ellipse using inter-bole distances between gap edge trees. Gaps were sampled from three size strata (shortest diameter <12.5 m, shortest diameter 12.5-15 m shortest diameter >15 m) when present.

Light availability was estimated from hemispherical photographs (Canham et al 1990; Domke et al 2007) taken at the gap center as well as three meters from the center in each cardinal direction to capture variability in canopy openness. Canopy openness (CO- a proxy for light availability) was estimated from photos converted to binary images using an automatic threshold value (SideLook v. 1.1.01, Nobis 2005) with Gap Light Analyzer software (Frazer et al 1999). The average CO from the usable photos for each

gap was used in analyses. CO was not estimated for ten gaps where three or more of the five photographs were unusable due to sun glare or image obstruction.

Seed production potential (SP) was estimated for each gap by summing the quotient of diameter at breast height (dbh-1.4 m) and the squared distance for each mature tree by species. This method assumes that a tree's contribution to SP increases with diameter and decreases with distance (Ribbens et al 1994). Trees and stumps within 20 meters of the gap plot and with dbh > 5 cm for ironwood (a smaller species at maturity) and > 20 cm for other species were included in this estimate. If the species of a stump could not be determined in the field, it was determined in the laboratory from wood samples (Marx 2005). Stump basal diameter was converted to dbh using relationships developed by Demaerschalk and Omule 1978 (Appendix B, Section B.2). Stumps were not measured at one stand due to the level of decay which made species identification and diameter measurements difficult.

Seed production potential estimates were developed for 2008 (SP_{2008}) based on the current dbh of living trees and for the time of harvest ($SP_{Harvest}$) based on stump dbh and "grown back" dbh of living trees. Mature tree dbh was "grown back" to dbh at the time of harvest using radial growth equations from the USDA Forest Vegetation Simulator Lake States Variant (Bush and Brand 1993) (Appendix B, Section B.3). $SP_{Harvest}$ increases rapidly with the inclusion of large stumps near the gap center.

Percent ground cover of fern, grass and *Carex* spp, *Rubus* spp, and other shrubs was visually estimated in five 1 m^2 quadrats located within each gap. Numbers of tree seedlings (<1 m tall) were tallied by species and height (to the nearest 0.25 m) in two of

the 1 m^2 competing vegetation quadrats located near the gap center. Tree saplings 1-7 m tall were tallied by species and height (to the nearest 0.25 m) in one 154 m^2 gap-centered circular plot (7 m radius). This plot encompassed the entire gap area for smaller gaps, and a large portion of the area for larger gaps. In gaps with extreme sapling densities (> 200 saplings / gap plot), only one forth to three fourths of the gap plot was sampled to improve efficiency, and estimates were scaled up to the entire gap plot.

If saplings were present, stem cross section were taken at 5 cm and breast height from one sugar maple and one ironwood sapling within three different height strata (1-2 m, 2-4 m and >4 m). These species were selected because they were more consistently representated across stands than other species. Sapling age at 5 cm and 1.4 m height was determined (number of rings counted on the cross section plus 0.5 years to account for the current year's growth) in order to estimate height growth rates. Saplings taller than 1.4 m at the time of harvest were excluded from analysis because post-harvest growth rates could not be estimated for them. The average annual height growth rate was determined from 5 cm to the saplings height in 2008 for gap colonizers (saplings with age at 5 cm < time since harvest) and from 1.4 m to the sapling's height for advanced regeneration. A different method was used for advanced regeneration because some height growth below 1.4 m occurred during the period of suppression before harvest. Height growth estimates were adjusted using the method of Carmean 1972 because cross sections did not correspond with terminal bud scars.

1.2.4 Data analysis: independent variables

I sought to explore spatial patterns in seedling and sapling abundances, stocking-levels, growth rates, and gap- and stand-level predictor variables, and to develop models

to explain the impacts of these variables on regeneration. I focus analysis on sugar maple and ironwood because they were the most abundant and consistently represented species in the understory. All other species are pooled together as "other" because infrequent observations within species prohibited separate analyses by species. The "other" category is heavily dominated by red maple, white ash and black cherry with these species representing 55%, 26% and 6% of seedlings in the "other category", 30%, 49% and 12% of saplings 1-2 m tall and 30%, 44% and 15% of saplings 1-7 m tall. Four size categories of regeneration are analyzed: 1) seedlings (< 1 m tall), 2) small saplings that are within the range of deer browse (1-2 m tall), 3) all saplings (1-7 m tall) and 4) a measure of sapling stocking that takes into account densities and heights of saplings.

Comparing sapling abundance alone does not estimate the potential of the sapling pool in a gap to recruit into the overstory because self thinning causes fewer larger saplings to persist over time (Tubbs 1968; Runkle 1984; Kittredge and Ashton 1995; Ray et al 1999). To estimate the stocking level of each gap, I weighted each sapling by the inverse of the maximum observed gap-level density for saplings of that height across all gaps (Figure 1.3) and summed the weights of all saplings in a gap by species. If a gap was at the maximum density for a sapling size class, it had a stocking level of 1 (i.e. 100%), however, many gaps had multiple cohorts of saplings so the stocking level was > 1. One gap with an outlying stocking level (>14) was removed from analyses for sugar maple and another from the analyses of other species (stocking level > 7). Analyses for sapling stocking by species were performed for gaps where the stocking level for that species was > 0.

Shannon Diversity Index (H') was calculated for seedlings, small saplings (1-2 m) and all saplings (1-7 m). Shannon Diversity Index analyses were only performed for gaps where H' was > 0 for that size class.

To improve normality, sapling stocking and sapling post-harvest growth rates were log transformed and H' was square root transformed.

1.2.5 Data analysis: statistical analysis

The data were hierarchically structured, with gaps nested within stands, so a hierarchical multilevel modeling approach was taken for analysis. Ignoring the relatedness between gaps within stands would increase the risk of type I errors because the effective sample size is really less than the total number of gaps (Goldstein 1995; Congdon 2003). Multilevel models incorporate information about the clustering to produce estimates of standard errors that account for non-independence (Goldstein 1995). I used Bayesian inference with Markov chain Monte Carlo (MCMC) sampling to estimate parameter values and obtain credible intervals that average over the uncertainty in fixed- and random-effect parameters (Zhao et al 2006; Bolker et al 2009).

Multilevel models were not used for sapling growth rate analyses because preliminary analyses using the lme4 package (Bates and Maechler 2009) in R 2.9.1 (R Development Core Team 2009) demonstrated that inclusion of a stand-level random intercept did not improve model fit (AIC = 1.68 vs 52.44 for sugar maple and 12.74 vs 62.71 for ironwood linear versus multilevel linear models with all gap- and stand-level covariates). This is likely because variation in growth rates for saplings within the same stand was comparable to variation between all saplings (average within-stand stdev= 0.062 cm vs overall stdev=0.077 cm for sugar maple and 0.086 cm vs 0.099 for

ironwood) and there were many stands (4 of 27 for sugar maple and 10 of 30 for ironwood) where growth rate after harvest could only be determined for one sapling. Non-linear effects in the relationship between sapling height and height growth were not included because it appeared linear over the range of observed heights.

1.2.5.a Assessing spatial patterns in regeneration (H1) and modeling the effect of gap- and stand-level factors (H2)

Spatial trend models (UTM Northing and Easting as covariates), full models (gap- and stand-level covariates) and null models (overall intercept and random stand-level intercepts only) were developed using generalized linear multilevel models for seedling and sapling abundance, linear multilevel models for log transformed sapling stocking level and square root transformed H' and linear models for log transformed sapling growth rates. Seedling and sapling abundances were modeled as negative binomial processes arising from the distribution ~NegBin(p, r) where $p = r / (r + \mu)$ and r (the dispersion parameter) $= \mu^2 / (\sigma^2 - \mu)$. Table 1.2 shows the formulation for the spatial trend, full and null models and lists the covariates used for each analysis.

UTM Easting and Northing were rescaled from 0 to 1 for the spatial trend models, and gap- and stand-level parameters for the full models were standardized to improve convergence. Percent ground cover of fern, grass and *Carex* spp, *Rubus* spp, and other shrubs were added together to create a composite metric, percent cover of competing vegetation, to reduce the number of parameters and because these variables were auto-correlated. SP_{2008} was used in seedling abundance models and H' of overstory trees in seedling H' models because it was unlikely that trees represented by stumps were the seed source for small seedlings except at the most recently harvested stands.

1.2.5.b Model fitting, priors and convergence

Models, including the linear growth rate models, were run with WinBUGS v.1.4.3 (Spiegelhalter et al 2003) (see code Appendix C, Section C.1- C.3) through R v.2.9.1 with the package R2WinBUGS (Sturtz et al 2005) (see code Appendix C, Section C.5). Three parallel chains with dispersed randomly selected starting values were run for 70,000 iterations with a burn-in of 10,000 and a thinning rate of 5 for seedling and sapling abundance and H' models, and for 20,000 iterations with a burn-in of 5,000 and a thinning rate of 1 for stocking level and growth rate models. Some models had to be run for longer iterations and with a higher thinning rate to improve convergence (Appendix D, Tables D.1-D.8). AOCa and ATD-Hp Habitat Types were combined into one group for sugar maple sapling abundance models because low variation within and between these groups affected identifiability (the ability to estimate all parameters in the model).

Deviance Information Criterion (DIC), a method of assessing model performance in terms of fit and complexity based on the posterior mean deviance (-2 × log(likelihood)) and the effective number of parameters (Spiegelhalter et al 2002), was compared for the spatial trend models, full models and null models to determine if predictor variables improved model performance. A decrease in DIC by 5 or more indicates support for better model performance.

In multilevel models, a group's (i.e. stand's) random intercept is adjusted by the group's deviation from the predicted value, so predictions can closely fit observed data. This is especially the case when few observations are made within groups and variation is low within groups. The null model predictions could perfectly fit all gap-level observations at a stand where variation between gaps was zero. Improvements in model

fit over the null model demonstrate the ability of gap- and stand-level covariates to explain variation between and within stands given the deviation of each stand from the mean. If DIC is lower for the null model than a model with covariates, it indicates that relative to other unmeasured differences that might exist between stands, differences cannot be attributable to covariates.

A uniform prior (range 0-50) was used for the standard deviation of the random stand-level intercept for all multilevel models. The random effects standard deviation was insensitive to prior specification (Appendix B; Section B.4). An inverse gamma prior was used for the sapling-level precision in the sapling growth rate linear models. A noninformative prior distribution (Normal~(μ=0, σ^2=10,000)) was used for gap-level and stand-level coefficients (Clark 2007; Bolker et al 2009).

Convergence was diagnosed using the R package coda (Plummer et al 2009) with the Gelman-Rubin diagnostic and the Raferty-Lewis diagnostic. All models showed strong evidence of convergence (Appendex D, Tables D.1-D.8).

1.2.5.c Comparing the effect of significant gap- and stand-level variables

Simulations were used to predict the effect of a one standard deviation increase in gap- and stand-level variables on sugar maple small sapling abundance to determine the relative effect of significant variables, and to aid in the biological interpretation of model parameter values. Predictions were developed using one-to-one simulation draws from the posterior parameter distributions. Simulations for small sugar maple sapling abundance were run for 1) the gap with the greatest observed sugar maple abundance holding all covariates at their observed values and 2) a gap at an unmeasured stand where the covariate values were at the mean level observed across the study area. Method 1

incorporates less uncertainty into the predictions because the posterior distribution for the random stand-level effect for the observed stand can be used (Gelman and Hill 2007).

1.2.5.d Assessing spatial patterns in gap- and stand-level variables

Linear regression with nonparametric pairs bootstrapping was used to explore spatial trends in stand-level variables and stand averages of gap-level variables. Nonparametric Kruskal-Wallis rank sum test was used to determine if Easting and Northing were significantly different between Habitat Types, and compared between Habitat Types with nonparametric Wilcoxon signed-rank test with Bonferroni adjusted p-values.

1.2.5.e Potential species composition changes (H3)

Future forest composition can change if saplings regenerating in harvest gaps are of different species than those that were removed from the gap (Runkle 1981). The potential for species change was assessed with two methods: 1) determining the percentage of gaps where a species was removed by harvesting (i.e. present as a stump in the gap) and also present in the sapling layer and 2) comparing the percentage of gaps where a species was the dominant species removed (highest relative stump basal area) to the percentage of gaps where that species dominated the sapling layer (highest relative sapling stocking level). These analyses only used gaps from stands that had been harvested at least eight years before data collection because younger gap may require more time to accumulate all possible sapling species. The first analysis only included species represented by stumps in at least 5 gaps and the second analysis combines species other than sugar maple and ironwood into the "other" category.

1.3 Results

1.3.1 Characterizing regeneration abundance and composition

A total of 18 species were identified as saplings (1-7m tall) within gaps across the study area, but regeneration was heavily dominated by sugar maple and ironwood (Table 1.3). Only six species occurred in more than 5 percent of the gap plots (ironwood, sugar maple, black cherry, white ash, red maple and balsam fir), and only ironwood and sugar maple occurred in more than 50% of all gap plots. Twelve percent of gap plots were devoid of saplings of any species and 35% had less than five stems of all species combined (< 325 saplings / ha of gap area). Sugar maple was absent from 48% of gap plots and ironwood from 43%.

Species richness and diversity were low, with a median number of two tree species in the seedling layer, two in the sapling layer and three in the overstory layer. The maximum observed number of species was five in the seedling layer, seven in the sapling layer and seven in the overstory layer. Shannon Diversity Index (H') was 0.31 for seedlings with a maximum of 1.46, 0.35 for saplings with a maximum of 1.48 and 0.58 for overstory trees with a maximum of 1.60. The maximum possible H' is 1.61 with five species and 1.95 with seven species.

Percentage of sugar maple and ironwood saplings originating as gap colonizers decreased with increasing height (Table 1.4). The tallest gap colonizer was 2.75 m for sugar maple (7 years old at a stand harvested 7 years ago) and 2.5 m for ironwood (9 years old at a stand harvested 9 years ago). The average age (number of growth rings at 5 cm height) of advanced regeneration at the time of gap formation for sugar maple was 16 years (stdev 14.4 years) and 9 years (stdev 8.0 years) for ironwood.

Average post-harvest growth rates for saplings 1-2 m tall were not significantly different between ironwood (0.19 m / yr, stdev 0.06) and sugar maple (0.18 m / yr, 0.07), but growth rate for ironwood (0.29 m / yr, 0.10) was significantly faster than that for sugar maple saplings 2-4 m tall (0.24 m / yr, 0.07). The growth rate for ironwood 4-7 m tall (0.42 m / yr , 0.07) was higher than the growth rate of the two tall sugar maple saplings for which post-harvest growth could be calculated (0.24 m / yr).

1.3.2 Characterization of gap and stand-level variables

Harvest gaps were created by the removal of three trees (dbh > 20 cm) on average, but as few as one and as many as thirteen, and ranged in extended gap size from 82 to 913 m^2 (Table 1.5). Positive correlations were observed between canopy openness and gap size and cover of competing vegetation (Table 1.6). Canopy openness, cover of competing vegetation and estimated deer density were negatively correlated with time since harvest. Estimated winter deer density was on average 13.9 deer/ km^2, ranging from 0.6 to 61.6 deer/ km^2, and was negatively correlated with snow depth. Stand average sugar maple browse index was positively correlated with time since harvest but not with deer density estimates.

Habitat Types were well represented (n> 10 stands) except for TMC (n= 2). Snow depth was deeper on ATD and ATM types compared to ATD-Hp (Table 1.7). Stand average percent cover of ferns, grass and *Carex* spp and $SP_{Harvest}$ for other species were the only other variables differing between Habitat Types. If TMC was excluded from the Kruskal-Wallis rank sum test due to low sample size, percent cover of *Rubus* spp and sugar maple $SP_{Harvest}$ were significantly different between the remaining four Habitat

Types (χ^2=8.27, *df*=3, p-value=0.04 and χ^2=9.69, *df*=3, p-value=0.02 respectively). However, no pairwise comparisons between Habitat Types were significant for cover of *Rubus* spp. $SP_{Harvest}$ for sugar maple was significantly higher on ATD type stands than on ATD-Hp, even though SP_{2008} was not. This may be due to the larger number of sugar maple stumps harvested from the area around gaps at ATD stands compared to ATD-Hp (9.6 stumps vs 6.5 stumps, Wilcoxon rank sum test W=131.5, p=0.045).

1.3.3 Spatial patterns in regeneration and gap- and stand-level variables (H1)

Spatial trends in abundance were evident for all species groups in either seedling or sapling size classes as well as for seedlings and saplings H' (Table 1.8). Sugar maple showed the most consistent and strongest spatial trends, increasing with UTM Northing for seedling and sapling abundance, sapling stocking levels and growth rates. Sugar maple small sapling abundance was dramatically different between 163 gap plots across 28 stands located south of latitude 46° 6'43" N and 184 gap plots across 31 stands north of this latitude (Figure 1.4). Small sugar maple saplings were present in only 4% of gap plots in southern stands, with a total abundance of eight saplings in the 163 gaps, but were present in 71% of gap plots in the northern stands with abundances as great as 387 saplings in a single gap plot (25,140 saplings / ha of gap area). Consistently low abundance of ironwood (Figure 1.5) and other species (Figure 1.6) were not observed across stands in the southern region. Ironwood and other species small saplings were present in 54% and 39% of southern gap plots with abundances as high as 127 and 242 / gap plot (8,250 and 15,721 / hectare of gap area), respectively.

Although spatial patterns were evident in many models, very few showed signs of improved performance (lower DIC) over the null model (random stand-level intercept

only). Due to few gap observations per stand, the stand-level intercept is able to explain much of the variation in the observations.

Snow depth increased with Northing and marginally decreased with Easting, whereas SMBI and estimated winter deer density decreased with Northing and Easting (Table 1.9). Stand average percent cover of competing vegetation decreased with Easting. Spatial trends were also observed in competing vegetation and seed production potential for sugar maple and ironwood. Sugar maple $SP_{Harvest}$ increased with Northing, even though SP_{2008} did not, because more sugar maple stumps were removed from northern stands in the most recent harvest. Easting was significantly different between Habitat Types (Kruskal-Willis χ^2= 18.07, *df*=4, p-value=0.001) as was Northing (Kruskal-Willis χ^2= 33.63, *df*=4, p-value<0.001), with ATD stands generally located farther east than AOCa, and ATD and ATM located farther north than AOCa and ATD-Hp (Figure 1.7).

1.3.4 Gap- and stand- level variables affecting seedling and sapling abundance, sapling stocking, sapling growth rates and regeneration diversity (H2)

All measured gap- and stand-level factors significantly corresponded with at least one species or species category in the seedling abundance (Figure 1.8), sapling abundance (Figure 1.9) or sapling stocking levels (Figure 1.10) models.

At the gap-level, cover of competing vegetation had a consistent negative association with seedling and sapling abundance and stocking. Canopy openness was positively associated with small sapling abundance and stocking levels of sugar maple and other species. Seed production potential was only positively associated with ironwood seedling abundance.

Stand-level Habitat Type was consistently important in the full multilevel models, especially for sugar maple where higher seedling and sapling abundances and stocking levels were found in gap plots on ATD, ATM and TMC type stands compared to AOCa and ATD-Hp. There was only one sugar maple sapling 1-2 m tall across all 85 gaps measured on ATD-Hp stands. Differences between Habitat Types were not observed for ironwood and other species small saplings, however specific species within the other species group showed variation in sapling abundances between Habitat Types. No white ash saplings (1-7 m tall) were found in gap plots on ATM type stands and only one sapling was found across gap plots on ATD type stands. Stand-level time since harvest was negatively associated with ironwood seedling abundance and estimated deer density was negatively associated with small sugar maple saplings abundance.

The incorporation of gap- and stand-level variables improved model performance (reduced DIC compared to the null model) for all sugar maple models, for ironwood seedling and sapling stocking-level models (marginally), and for the other species sapling abundance model (Table 1.10). Comparison of the observed versus mean posterior predicted values for the sapling abundance models (Figure 1.11) demonstrates that the stand-level intercept explained much of the variation, not the covariates. The stand-level intercept provided the model with the ability to predict gaps with zero seedlings or saplings per gap plot, but incorporation of gap- and stand-level effects improved its ability to predict gaps with higher abundances for sugar maple and other species.

Diversity of seedlings, small saplings and all saplings was mostly insensitive to measured gap- and stand-level variables (Figure 1.12). The Shannon Diversity Index of overstory trees increased seeding diversity, and diversity appeared lower on ATD

compared to AOCa type stands across size classes. The incorporation of gap- and stand-level covariates only improved model performance for the seedling diversity model (Table 1.10).

Sapling post-harvest growth rates increased with height and decreased with time since harvest for both species, but were insensitive to the other gap- and stand-level variables except for marginal increases in ironwood growth rate with canopy openness (Figure 1.13). Sapling growth rates post- harvest for sugar maple and ironwood were lower for advanced regeneration saplings compared to gap colonizers at a given height (Figure 1.14). Model performance was greatly improved with inclusion of sapling-, gap- and stand-level variables (Table 1.10).

1.3.5 Predicting the effect of significant gap- and stand-level variables on sugar maple abundance

Generalized linear mixed model parameter estimates were used to predict sapling abundance for the gap with the highest observed sugar maple small sapling abundance (387 saplings in a gap plot (25,140 / ha of gap area)) and monitor changes in abundance when significant covariates were increased by one standard deviation. With covariates held at their observed values, the median predicted abundance was 146 / gap plot (9,484 / ha of gap area) (95% credible interval for the prediction: 11-731 /gap plot; 715 – 47,487 / ha). The most dramatic change in predicted sapling abundance was elicited by changing the Habitat Type classification from ATM to AOCa/ATD-Hp; predicted sapling abundance declined to 0 / gap plot (0-2 / gap plot; 0-130 / ha) (Figure 1.15). Increasing winter deer density from the observed value by 1 standard deviation (4 to 16 deer/km^2) decreased the prediction to 40 / gap plot (2,598 / ha) (2-315 / gap plot; 130-22,801 / ha),

increasing canopy openness from 5% to 12% increased the prediction to 193 / gap plot (12,538 / ha) (14-972 / gap plot; 909-63,142 / ha), and increasing competing vegetation from 18% to 41% decreased the prediction to 124 / gap plot (8,055 / ha) (6-451 / gap plot; 390 – 29,298 / ha).

Uncertainty in parameter estimates, and the importance of the random stand-level intercept for constraining predictions, reduced the model's ability to predict sapling abundance for gaps at an unmeasured stand (Figure 1.16). Median predictions of sugar maple abundance within a gap at an unmeasured stand were all below 10 / gap plot (650 / ha). Due to similarities between the response of abundance to ATD, ATM and TMC Habitat Types, only results from a simulated gap at an ATD type stand are presented for comparison with predictions of abundance at an AOCa/ATD-Hp type stand. Predictions were consistently higher for ATD compared to AOCa/ATD-Hp, and more variable for ATD. The median predicted sapling abundance for gaps on AOCa/ATD-Hp type stands remained at 0 regardless of changing covariate values.

1.3.6 Potential species composition changes

The percentage of gaps where a species was harvested and at least one sapling of the same species was present varied from 7% for conifer species (n=14 gaps) to 100% for ironwood (n=10) (Figure 1.17). About fifty percent of gaps with sugar maple (n=191), white ash (n=6) or red maple stumps (n=21) had saplings of that species present. Although yellow birch and basswood were removed from 20 and 24 gaps respectively, there were only saplings of these species in about 10% of these gaps.

Sugar maple was the dominant species (highest relative basal area) of stumps removed from 74% of gaps, but only the dominant sapling species (highest relative

stocking level) in 37% of 211 gaps harvested 8-15 years ago (Figure 1.18). Ironwood rarely had the highest relative stump basal area, but was the dominant sapling species in 32% of gaps. Other species were the dominant stump species and the dominant sapling species in about 20% of gaps. Eleven percent of gaps had no regenerating saplings.

1.4 Discussion

Exploring multiple factors across multiple scales is fundamental for elucidating the complexity of ungulate-vegetation interactions (Rooney and Waller 2003; Weisberg and Bugmann 2003) and the causes of regeneration failure (Didier and Porter 2003; Romagosa and Robison 2003; Sage et al 2003). This study responded to this need by characterizing abiotic and biotic variables operating at the landscape-, stand- and gap-scales (Figure 1.1), and their effects on regeneration dynamics in the Western Upper Peninsula of Michigan.

High variation was observed in the abundance of seedlings and saplings in gap plots, with some plots full of saplings but most containing very few. Gap plots were equivalent to the size of the growing space created by the removal of several mature trees, and many sampled gaps were over the minimum size (100-400 m^2) required for the regeneration of shade-intolerant species (Webster and Lorimer 2005). The absence of any sapling species from over ten percent of gap plots, the absence of shade-tolerant sugar maple from fifty percent of gap plots, and the near complete absence of shade-intolerant species from all gap plots implies regeneration failure in many stands.

Sugar maple sapling abundance increased with latitude where snow depth was greater, winter deer densities were lower (H1), and less nutrient rich Habitat Types were more abundant. All measured gap- and stand-level variables were associated with

changes in seedling and/or sapling abundance in selection harvest gaps (H2). I found evidence that shifts in species composition are possible in some northern hardwood stands (H3), potentially due to species sensitivities to gap- and stand-level variables. There was less evidence of gap- and stand-level variables affecting seedling and sapling diversity and sapling growth rates.

1.4.1. Inverse landscape-scale gradients in biotic and abiotic factors and sugar maple sapling abundance (H1)

Snow depth increases with latitude in this region due to lake-effect snow. White-tailed deer avoid areas with deep snow (Tierson et al 1985; Poole and Mowat 2005) and migrate south to winter range where snow depth is lower (Verme 1973; VanDeelen et al 1998). Decreasing winter deer density with UTM Northing and Easting (Figure 1.19) has been documented across the study area for at least half a century (Doepker et al 1994).

Snowfall patterns also help account for the distribution of mesic forest communities in the Great Lakes region, potentially because snow cover impacts soil moisture, nutrient availability and fire history (Henne et al 2007). The landscape-scale gradient in winter deer density and Habitat Types, as influenced by snow depth, may account for the spatial pattern of increasing sugar maple seedling and sapling abundance with Northing and Easting. Sugar maple seed production potential at the time of harvest also increased with Northing, but sugar maple still dominated the overstories of stands in the southern portion of the study area. The sapling spatial trend does not reflect a spatial trend in the range of sugar maple.

Deer density was not correlated with spatial patterns in sugar maple sapling abundance in northern New York State (Didier and Porter 2003), but in the Western

Upper Peninsula of Michigan the spatial pattern in winter deer density is inverse that for sugar maple sapling abundance. Sugar maple saplings are heavily utilized as forage (Swift 1949; Stoeckeler et al 1957) and decline in abundance outside deer exclosures (Stoeckeler et al 1957; Miller 2004). Deer browse in the southern portion of the Western Upper Peninsula may affect the perpetuation of sugar maple following selection harvesting.

Confounding the north to south gradient in deer density is a gradient in Habitat Types. Sugar maple seedling and sapling abundance and sapling stocking levels differ between Habitat Types (Figure 1.20), being more abundant on ATD, ATM and TMC (less-nutrient rich Habitat Types). Abundances of other species and ironwood also differ between Habitat Types, but not to the extent of sugar maple. In the Western Upper Peninsula of Michigan, variation in snow depth between Habitat Types, and the associated impacts of snow on soil moisture-nutrient conditions, may account for some of the abundance of sugar maple saplings observed on ATD, ATM and TMC stands with coarser-textured substrates (Henne et al 2007), but it cannot account for the paucity of saplings on AOCa and ATD-Hp stands with finer-textured substrates. Other evidence also points against the strength of the Habitat Type soil moisture and nutrient regime effect on sugar maple sapling abundance: 1) differences in sapling growth rates between Habitat Types, that could indicate differences in soil moisture and nutrient availability (Walters and Reich 1997), were not observed, 2) the Habitat Types with lowest sugar maple abundance are predicted to be most nutrient-rich and 3) differences in sugar maple seedling abundance between Habitat Types were not as strong as differences in sapling

abundance, potentially because deer browse is interrupting the transition from seedling to sapling.

Quantifying the availability of soil resources previously found to affect sugar maple seedlings (i.e soil moisture, pH, nitrogen, concentrations of exchangeable aluminum and calcium) (Walters and Reich 1997; Kobe et al 2002; Juice et al 2006) between and within Habitat Types in this area could help disentangle the effects of Habitat Types from that of deer. At the same time, habitat-suitability of forest stands for deer has been found to vary among Habitat Types (Felix et al 2004), so interactions between deer and Habitat Type might innately interweave their impacts on regeneration.

1.4.2. Multiple gap- and stand-level factors inhibit or enhance seedling and sapling abundance and stocking levels, but few seem to affect diversity and growth rates (H2)

Seedling abundance appears more sensitive to gap- and stand-level variables than sapling abundance or stocking-levels. Seedlings have experienced less variation in gap and stand-level conditions since germination compared to the older taller saplings, potentially linking their abundance more closely to the condition of variables measured in 2008. Results from the small sapling abundance and stocking-level models were similar because small saplings were also included in the stocking-level model, but they were weighted less than taller saplings. Stocking-level models also did not include gaps with zero saplings. Results of the stocking-level analysis, therefore, indicate variables that affect the recruitment potential of a gap (i.e. Habitat Type, competing vegetation and canopy openness) given there is some regeneration. The sapling abundance models demonstrate impacts to smaller saplings within the range of deer browse, including impacts contributing to instances when no small saplings are present. These instances

represent regeneration failure in the small size class. Many of these saplings germinated after harvest and are directly impacted by silvicultural decisions.

Evidence was found for impacts of abiotic and biotic gap- and stand-scale factors on seedling and sapling abundance. The relative effect of Habitat Type on predicted sugar maple sapling abundance was the greatest, followed by deer density. Habitat Type and deer density are spatially confounded, reducing the model's ability to represent the relative effect of one variable in isolation of the other. Estimated deer density did not differ significantly between Habitat Types, but uncertainty in pellet count estimates could contribute to this.

Gap-level canopy openness and cover of competing vegetation had weaker impacts on sugar maple sapling abundance than stand-level factors, but effects were in the direction predicted. Previous work corroborates my findings that increasing light increases sapling abundance (Schumann et al 2003; Dietze and Clark *in prep*; Runkle 1982), and increasing cover of non-tree vegetation negatively impacts seedling and sapling layers (Horsley and Marquis 1983; De Steven 1991; George and Bazzaz 1999; Romagosa and Robison 2003; Fei and Steiner 2008). The negative association of cover of competing vegetation with seedling and sapling abundance could also be contributed to by the negative effect taller saplings have on non-tree vegetation (Collins et al 1985). However, controlled field experiments have found direct negative impacts of competing vegetation cover on seedling emergence and seedling and sapling survival and growth rates (Yawney and Carl Jr. 1970; Horsley and Marquis 1983; George and Bazzaz 1999; Randall 2007).

Seed production did not appear to limit the abundance of understory regeneration, except for ironwood seedlings. This was surprising given that seed density, and occasionally seedling density, in forest soils show increases with the abundance, size and proximity of mature seed trees in the overstory (Marquis 1975; Ribbens et al 1994; Garret and Graber 1995; Shibata and Nakashizuka 1995; Clark et al 1998). High inter-annual variation in sugar maple seed crop production, seed viability and seed predation (Graber and Leak 1992; Houle 1992; Garret and Graber 1995) may uncouple overstory tree size and distances from gap-level seedling and sapling abundances. Disconnect may also be observed between seed fall and seedling abundance due to different spatial and temporal patterns in mortality factors (e.g. predation, pathogen attack and competition) affecting seeds and seedlings (Houle 1992).

Seedling and sapling diversity and growth rate were not strongly associated with gap- and stand-level factors in these northern hardwood stands. Understory tree layer species diversity did not increase with canopy openness (based on the full H' models). Some studies report similar observation (Shields et al 2007; Dietze and Clark *in prep*) but others report diversity or richness responses to light availability (Runkle 1982; Webster and Lorimer 2002; Schumann et al 2003). The lack of a diversity response to light in this study may be partly attributable to the exclusion of gaps with only 1 species (and therefore H'=0) from analyses to comply with normality assumptions. The correlation between canopy openness in isolation of other gap- and stand-level variables (and ignoring autocorrelation between gaps sampled from the same stand) is positively related to small sapling H' (Kendall's τ=10.9, p-value=0.01) and all sapling H' (τ=14.6, p-value<0.001) for gaps where at least one sapling was present (i.e. including those with

H'=0). Canopy openness remained non-significant for seedling H' (τ=-0.05, p-value= 0.3). Understory seedling diversity appears more limited by overstory diversity than light availability. However, overstory H' did not translate into sapling H', potentially because some species germinate but do not survive and grow into larger size classes (Metzger and Tubbs 1971).

Canopy openness did not affect sugar maple sapling post-harvest growth rates, and only marginally affected ironwood growth rates. Light estimates from 2008 do not approximate light availability at the time of gap formation due to canopy coalescence (Domke et al 2007), which could weaken light vs. growth rate relationships. Extended gap size, which would not change with time since harvest, was not correlated with sugar maple growth (τ=-0.04, p-value=0.56), but it was positively correlated with ironwood growth (τ=0.18, p-value=0.01). Other studies indicate that sapling height growth responses to light saturate beyond relatively low light levels (Canham 1988; Coates 2000; Webster and Lorimer 2002). This causes significant differences to be observed between height growth below a closed canopy and below canopy gaps, but not between gaps of different sizes (Canham 1988; Webster and Lorimer 2002).

Sapling growth rates only responded strongly to time since harvest out of all gap- and stand-level variables. Others have found sugar maple height growth to slow about 23 years after gap formation (McClure et al 2000) but I find evidence of this effect beginning earlier because all sampled gaps were less than 15 years old.

Gap colonizer saplings had faster growth rates than advanced regeneration of the same height, consistent with previous findings (McClure et al 2000; Webster and Lorimer 2005). Physiological differences between gap colonizer and advanced regeneration,

mediated by years of suppression in advanced regeneration saplings, could lead to differences in post-harvest growth rates. However, the differences observed in this study may also be contributed to by differences in the growth rate estimation technique. Post-harvest growth rates obtained using the advanced regeneration method (average growth rate above 1.4 m tall) were slower than those using the method for gap colonizers (height divided by age) by 0.02 to 0.08 m / year (average 0.05 m / yr) for fifteen of the nineteen gap colonizer saplings tall enough to obtain reasonable cross sections at breast height. Growth rates for the remaining four species were faster using the advanced regeneration method by 0.01 to 0.11 m / year (average 0.04).

1.4.3. Potential for species composition changes due to replacement by other species following gap creation

Shade intolerant species like yellow birch, deer browse-preferred species like basswood, and conifers species are not regenerating in gaps where these species were removed by harvesting. Failure of shade intolerant species to regenerate in stands managed with selection silviculture is a common concern in northern hardwood management (Metzger and Tubbs 1971; Shields et al 2007). Loss of conifers (i.e. eastern hemlock, northern white cedar, balsam fir and white spruce) from hardwood forests has implications for forest diversity because conifers provide habitat and food for many songbird species (Kendeigh 1945; Patmos 1995). Others have found negative effects of deer density on sapling H' (Horsley et al 2003; Cote et al 2004; Miller 2004), but I found no evidence of this in the full small sapling H' models. However, when considered in isolation of other variables (and including gaps with only one species), small sapling H' is negatively correlated with estimated deer density (Kendall's τ=-0.17, p-value<0.001).

Shade tolerant sugar maple failed to regenerate in many gaps created by the harvest removal of overstory sugar maple trees, and could be replaced by other species especially in the southern portion of the study area. Ironwood was the most likely successors in many gaps. Although sugar maple trees could potentially overtop ironwood saplings after many years due to the smaller stature of mature ironwood, sugar maple saplings (1-7 m tall) were absent from 88% of gaps where sugar maple was removed and ironwood saplings dominated the gap plot. Ironwood is a small species at maturity, which could account for the infrequency with which it was observed as the dominant stump species. However, it was only removed from 10 gaps so the frequency with which it was the most dominant sapling species is greater than would be expected if species composition were remaining static. Ironwood saplings were unresponsive to gap- and stand-level variables, indicating that this species has the potential to regenerate across all Habitat Types, regardless of seed source, light availability, competing vegetation cover and deer densities. The potential for ironwood to increase in dominance in areas with high winter deer densities is corroborated by evidence from deer exclosure studies (Miller 2004). Replacement of commercially valuable sugar maple by the non-valuable ironwood, and the general loss of species diversity in northern hardwood stands, are concerning to forest managers (Miller 2004).

1.4.4. Management implications

Observations of sugar maple sapling (1-7 m tall) absence from nearly fifty percent of gap plots challenges the notion that "securing some sort of commercially important natural regeneration is usually a simple matter in most northern hardwood stands" (Tubbs 1977), especially for stands located in the southern portion of the Western Upper

Peninsula. Although early work on selection harvesting in the region supports this statement (Eyre and Zillgitt 1953), increasing deer density across the area since the 1970's (Doepker et al 1994) and the potential unsuitability of selection harvesting for securing regeneration on different Habitat Types may affect the ability to apply this technique ubiquitously across northern hardwood stands.

The Michigan Department of Natural Resources is using the Burger and Kotar 2003 Habitat Type system to classify stands and direct management practices. I found significant differences in regeneration abundance between Habitat Types, potentially lending support to stratifying forest management by Habitat Type. Based on the current northern hardwood management recommendations, ATD-Hp type stands are treated equivalent to ATD, but my research suggests that these types should be treated separately because sugar maple regeneration success between these Habitat Types was vastly dissimilar. Specific recommendations may need to be developed for managing AOCa and ATD-Hp type stands in areas with high deer density. Shelterwood cutting has been suggested as a successful alternative to selection harvesting in areas experiencing herbivory-mediate regeneration failure (Sage et al 2003; Marquis and Brenneman 1981). The development of Habitat Type-specific recommendations could facilitate ecosystem management by coordinating appropriate silvicultural techniques with considerations of deer habitat-potential (Felix et al 2004).

Creating larger harvest gaps may produce moderate increases in seedling and sapling abundance, but across the range of gap sizes observed, I find limited evidence that larger gaps increase sapling diversity. Gap size and light availability were positively correlated with cover of competing vegetation, which in turn was negatively associated

with seedling and sapling abundance. I was unable to identify the ideal gap size past which increased light may hinder regeneration by facilitating competing vegetation due to high variation in light availability, sapling abundance and cover of competing vegetation within gaps of the same size class.

The results suggest that removal of competing vegetation may be necessary to ensure successful regeneration (Romagosa and Robison 2003; Horsley and Marquis 1983). Significant increases in height and radial growth were only observed in sugar maple seedlings protected from both competing vegetation and deer herbivory (Yawney and Carl Jr. 1970). Reducing densities of advanced regeneration ironwood may also benefit other species by reducing competition for light and soil nutrients. Results also highlight the importance of avoiding damage to well-formed advanced regeneration sugar maple; few saplings > 2.5 m were gap colonizers, and advanced regeneration has a higher chance of gap capture due to its stature (McClure et al 2000; Cole and Lorimer 2005).

White-tailed deer browsing had stronger effects on sugar maple sapling abundance than light or competing vegetation, so attention should be devoted to quality deer management that maintains populations in balance with their habitat (Frawley 2005). This management approach could strike a balance between deer and forest resources enjoyed by people in the Western Upper Peninsula. Targeted deer harvests that reduce local densities could allow seedlings and saplings an opportunity to outgrow the browse line (Sage et al 2003). Deer harvests may be more successful at improving sugar maple regeneration in the southern portion of the Western Upper Peninsula if regulations are altered to permit hunting during the winter months when deer yard in their winter range.

1.5 Conclusion

Lake Superior may play a strong role in the regeneration failure of sugar maple saplings observed in the southern portion of the study area. Lake-effect snow leads to the southern migration of many deer to their winter range, and may contribute to a gradient in soil moisture and nutrient conditions. Sugar maple abundance was lower in areas with lower snow depth, higher deer densities and less nutrient rich Habitat Types. Habitat Types appear to have the greatest impact on sugar maple small sapling regeneration, followed by deer density, canopy openness and cover of competing vegetation.

Previous studies have found effects of one to several of these gap- and stand-level variables, but few have undertaken a comprehensive assessment of these variables across a large geographic area. Even though these factors were unable to explain much of the variability observed in seedling and sapling abundances, the results suggest that stand-level factors have a larger impact on regeneration than gap-level factors. Temporal and spatial variability in patterns of seed dispersal and seedling establishment (Clark et al 1998), heterogeneity in the suitability and availability of seed bed microhabitats (Houle 1992; Marx and Walters 2008), individual-level variation in sapling growth rates (Dietze and Clark *in prep*) and the chance presence of advanced regeneration saplings in the location of harvest gaps (Brokaw and Busing 2000) all contribute to unpredictability in the abundance and composition of gap-level regeneration.

Studies that focus on multiple factors will provide greater insight into the complexities of the regeneration process, with potential implications for our understanding of the process of succession, the mechanisms that account for species distributions across landscapes, and the maintenance of biodiversity in forest

communities. An integrated, multivariate approach that matches harvest practices to Habitat Types and local deer densities, and considers interactions between light levels and competing vegetation, is also necessary for management practices when the goal is to encourage the success of commercially valuable species, maintain biodiversity, and improve wildlife habitat.

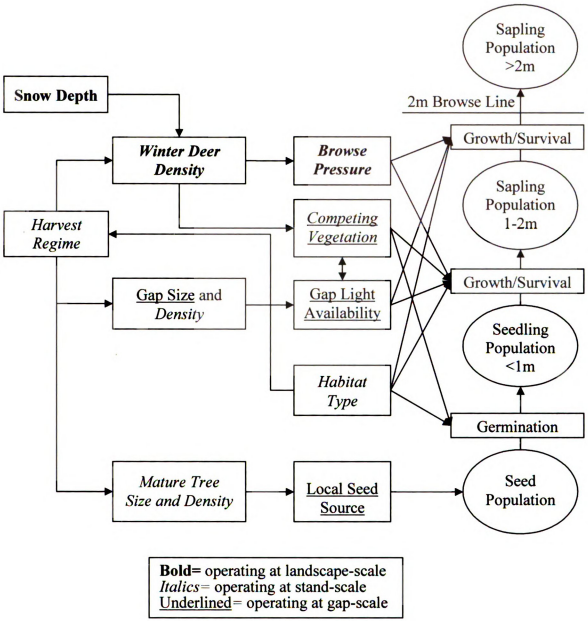


Figure 1.1. Hypothesized factors affecting northern hardwood regeneration throughout seedling and sapling ontogeny and the relationships between them. This is not an all inclusive diagram, but highlights many of the factors the literature and field observations emphasize as important.

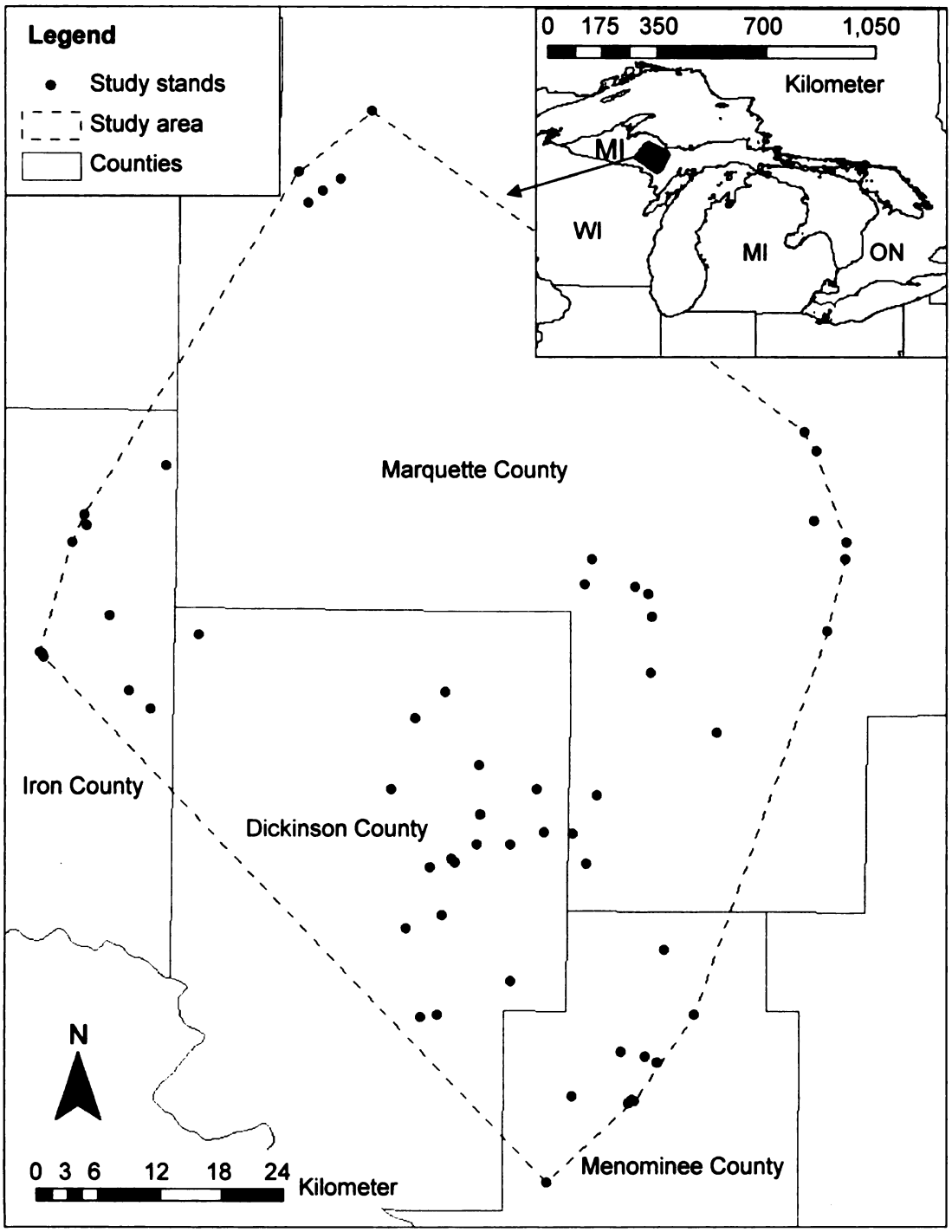


Figure 1.2. Map of study area. MI=Michigan, WI= Wisconsin, ON= Ontario, Canada.

Table 1.1. Northern hardwood Habitat Type descriptions (Burger and Kotar 2003).

Habitat Type	Primary landforms	Primary soils	Soil moisture regime	Soil nutrient regime
AOCa (*Acer saccharum / Osmorhiza claytoni – Caulophyllum thalictroides*)	Moraines, especially ground moraines, and loess deposits	Well to moderately drained silt loam and loam texture soils	Mesic	Rich to very rich
ATD-Hp (*Acer saccharum- Tsuga canadensis / Dryopteris spinulosa- Hepatica* variant)	Medium texture till plains	Well drained and well developed sandy loam soils	Mesic	Medium to rich
ATD (*Acer saccharum- Tsuga canadensis / Dryopteris spinulosa*)	Coarse texture moraines, especially ground moraines, and loess deposits	Moderately well drained podzolized or well developed sandy and loam textured soils	Mesic	Medium to rich
ATM (*Acer saccharum- Tsuga canadensis / Maianthemum canadense*)	End moraines and outwash covered ground moraines	Well to moderately well drained sandy loams and loamy sands	Dry-mesic to mesic	Medium
TMC (*Tsuga canadensis / Maianthemum canadense-Coptis groenlandica*)	Moraines, scattered low-lying areas, along slope bottoms and drainages, and on lake and swamp borders	Poorly drained podzolized sandy loams, loamy sands and loams	Mesic to wet-mesic	Medium

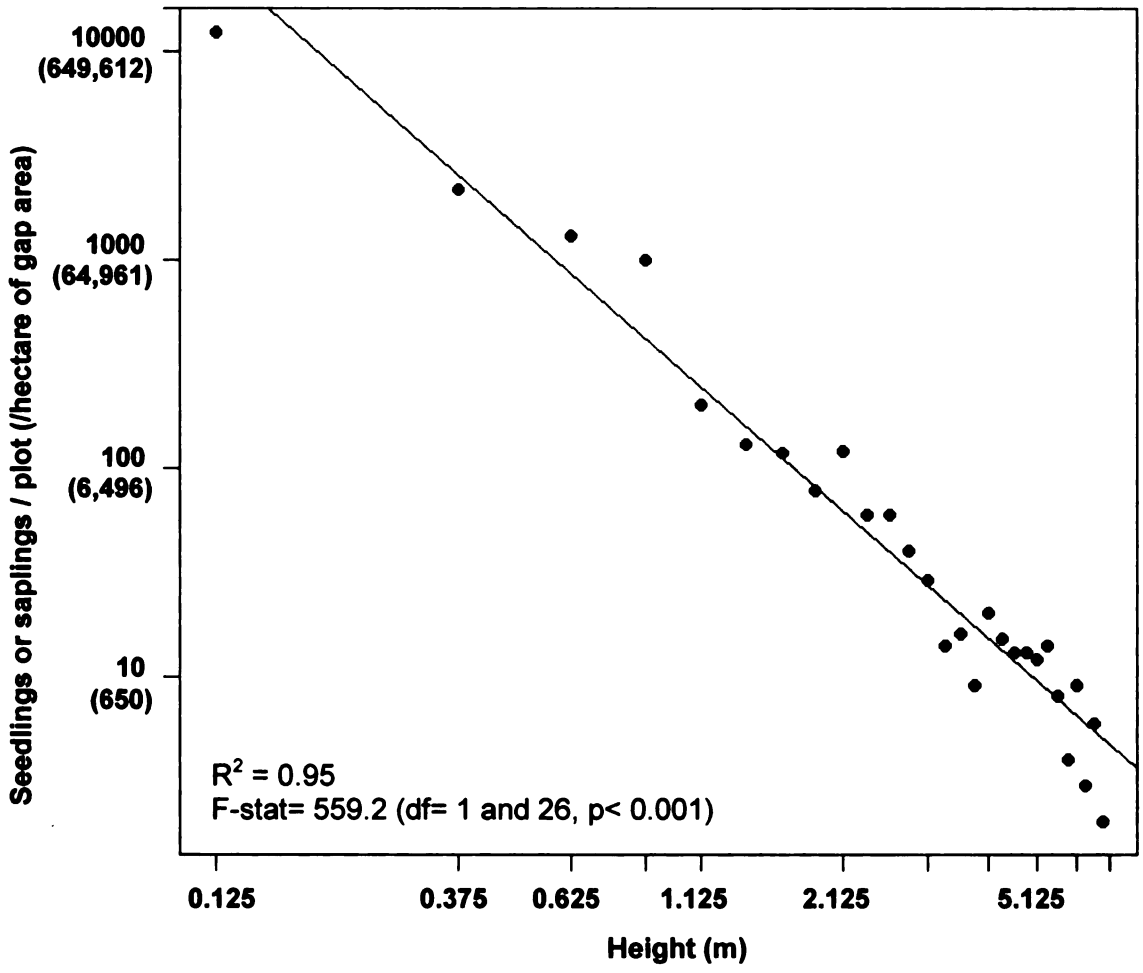


Figure 1.3. Relationship between maximum observed seedling and sapling density in a 154 m^2 gap plot among 347 study gaps versus height. This relationship was used to develop stocking estimates. $Log_e(Density) = -2.316 \times Log_e(Height) + 5.738$.

Table 1.2. Model specification for spatial trend, full and null generalized linear multilevel models (GLMM), linear multilevel models (LMM) and linear models (LM). μij is the predicted value for gap *i* at stand *j*. H'=Shannon diversity index.

Variable	Method	Distribution	Gap-level model (i)	Stand-level model (j)	Gap-level predictors (Xi)	Stand-level predictors (Zj)
Spatial Trend Model						
Seedlings Saplings 1-2 m	GLMM	~NegBin(p, r) $p = r / (r + \mu ij)$	$\log(\mu ij) = \alpha j$	$\alpha j \sim N(\gamma_0 + \gamma Zj, \sigma^2_\alpha)$		N, E
Log(Sapling stocking) Sqrt(H' seedlings) Sqrt(H' saplings 1-2 and 1-7 m)	LMM	$\sim N(\mu ij, \sigma^2 y)$	$\mu ij = \alpha j$	$\alpha j \sim N(\gamma_0 + \gamma Zj, \sigma^2_\alpha)$		N, E
Log(Growth rate)	LM	$\sim N(\mu i, \sigma^2 y)$	$\mu i = \beta_0 + Xi\beta$		N, E	
Full Model						
Seedlings Saplings 1-2 m	GLMM	~NegBin(p, r) $p = r / (r + \mu ij)$	$\log(\mu ij) = \alpha j + Xi\beta$	$\alpha j \sim N(\gamma_0 + \gamma Zj, \sigma^2_\alpha)$	CO, CV, SP_{2008} CO, CV, $SP_{Harvest}$	HT, DD, TSH HT, DD, TSH
Log(Sapling stocking) Sqrt(H' seedlings) Sqrt(H' saplings 1-2 and 1-7 m)	LMM	$\sim N(\mu ij, \sigma^2 y)$	$\mu ij = \alpha j + Xi\beta$	$\alpha j \sim N(\gamma_0 + \gamma Zj, \sigma^2_\alpha)$	CO, CV, $SP_{Harvest}$ CO, CV, H'M CO, CV, H'MS	HT, DD, TSH HT, DD, TSH HT, DD, TSH
Log(Growth rate)	LM	$\sim N(\mu i, \sigma^2 y)$	$\mu i = \beta_0 + Xi\beta$		SapHt, AdR, CO, CV, HT, DD, TSH	
Null Model						
Seedlings Saplings 1-2 m	GLMM	~NegBin(p, r) $p = r / (r + \mu ij)$	$\log(\mu ij) = \alpha j$	$\alpha j \sim N(\gamma_0, \sigma^2_\alpha)$		
Log(Sapling stocking) Sqrt(H' seedlings) Sqrt(H' saplings 1-2 and 1-7 m)	LMM	$\sim N(\mu ij, \sigma^2 y)$	$\mu ij = \alpha j$	$\alpha j \sim N(\gamma_0, \sigma^2_\alpha)$		
Log(Growth rate)	LM	$\sim N(\mu i, \sigma^2 y)$	$\mu i = \beta_0$			

N=UTM Northing, E=UTM Easting, CO= canopy openness, CV= competing vegetation, SP2008= seed production potential in 2008, SPHarvest= seed production potential at the time of harvest, H'M= H' mature trees, H'MS= H' mature trees and stumps, HT= Habitat Type, DD= deer density, TSH= time since harvest, SapHt= sapling height, AdR= dummy variable indicating if sapling is advanced regeneration

Table 1.3. Abundance of saplings 1-7 m tall per 154 m^2 gap plot (per hectare of gap area): Average (Ave), median (Med), standard deviation (Stdev), minimum (Min) and maximum (Max) and percent of gap plots where present (% gaps) (n=347 gaps).

	Ave / plot (/hectare)	Med	Stdev	Min	Max	% gaps
Sugar maple *Acer saccharum* Marsh.	39.3 (2,553)	1 (65)	89.0 (5,782)	0	494 (32,091)	52
Ironwood *Ostrya virginiana* (Mill.) K. Koch	10.5 (6,82)	1 (65)	25.7 (1,670)	0	188 (12,213)	57
White ash *Fraxinus americana* L.	7.3 (474)	0	36.5 (2,371)	0	373 (24,231)	19
Red maple *Acer rubrum* L.	5.0 (325)	0	24.1 (1,566)	0	299 (19,423)	14
Black cherry *Prunus serotina* Ehrh.	2.6 (169)	0	8.5 (552)	0	94 (6,106)	32
Quaking aspen *Populus tremuloides* Michx.	0.7 (45)	0	7.6 (494)	0	132 (8,575)	4
Balsam fir *Abies balsamea* (L.) Mill.	0.6 (39)	0	3.6 (234)	0	42 (2,728)	10
White spruce *Picea glauca* (Moench) Voss	0.1 (6)	0	0.4 (26)	0	4 (260)	5
Balsam poplar *Populus balsamifera* L.	0.1 (6)	0	0.8 (52)	0	11 (715)	2
American elm *Ulmus americana* L.	0.1 (6)	0	0.5 (32)	0	6 (390)	4
Yellow birch *Betula alleghaniensis* Britton	0.1 (6)	0	0.4 (26)	0	5 (325)	3
Bigtooth aspen *Populus grandidentata* Michx.	0.1 (6)	0	1.1 (71)	0	20 (1,299)	1
Northern red oak *Quercus rubra* L.	0.1 (6)	0	0.5 (32)	0	6 (390)	3
American basswood *Tilia americana* L.	<0.1 (<6)	0	0.3 (19)	0	3 (195)	3
American beech *Fagus grandifolia* Ehrh.	<0.1 (<6)	0	0.2 (13)	0	2 (130)	1
Black ash *Fraxinus nigra* Marsh.	<0.1 (<6)	0	0.1 (6)	0	1 (65)	1
Paper birch *Betula papyrifera* Marshall	<0.1 (<6)	0	0.1 (6)	0	1 (65)	1
Tamarack *Larix laricina* (Du Roi) K. Koch	<0.1 (<6)	0	0.1 (6)	0	1 (65)	1
All species	66.5 (4,320)	16 (1,039)	108.8 (7,068)	0	575 (37,353)	88

Table 1.4. Sapling type by species and height. Gap colonizers germinated after gap formation and advanced regeneration saplings were present before harvest.

	Gap colonizers (%)	Advanced regeneration (%)	Number of samples
Sugar maple			
1 - <2 m tall	53	47	118
2 - <4 m tall	9	91	93
4 - <7 m tall	0	100	81
Ironwood			
1 - <2 m tall	34	66	89
2 - <4 m tall	12	88	74
4 - <7 m tall	0	100	50

Table 1.5. Summary of gap and stand-level independent variables: Average (Ave), median (Med), standard deviation (Stdev), minimum (Min), maximum (Max) and number of gap or stand-level observations (N obs).

	Ave	Med	Stdev	Min	Max	N obs
Gap-level						
Competing veg (%)	42	41	23	0	97	347
Gap size (m^2)	191	156	103	82	913	347
Canopy openness (%)	13.4	11.8	7.3	1.7	54.8	337
SP_{2008} sugar maple	6.8	6.5	2.7	0.9	15.9	347
$SP_{Harvest}$ sugar maple	15.9	11.4	13.6	1.7	83.6	341
SP_{2008} ironwood	0.4	0.00	1.5	0.00	16.6	347
$SP_{Harvest}$ ironwood	1.1	0.00	5.4	0.00	67.8	341
SP_{2008} other spp	1.8	0.6	2.8	0.00	22.7	347
$SP_{Harvest}$ other spp	4.6	1.3	8.7	0.00	66.5	341
Stand-level						
Deer density (deer / km^2)	13.9	12.4	11.7	0.6	61.6	59
SMBI	2.2	2.3	0.9	0.4	3.6	25
Snow depth (cm)	26.6	23.3	7.4	15.6	48	59
TSHarvest (years)	9	9	3	2	15	59

Competing veg= % cover of competing vegetation (*Rubus* spp, grass/*Carex* spp, other shrubs and ferns), gap size= extended gap size, SP = seedling production potential (Σdiameter/distance^2) for 2008 and at time of harvest, deer density= estimated deer / km^2 winter 2007-2008, SMBI= stand average sugar maple browse index, snow depth= average snow depth from November 2007-April 2008, TSHarvest= time since harvest.

Table 1.6. Kendall tau rank correlations between gap and stand-level variables. Comparisons between gap-level and stand-level variables use stand-averages for gap-level variables to comply with independence assumptions.

	CV	Gap size	CO	Deer density	SMBI	TSHarvest
Snow depth	0.13	0.06	0.17*	-0.21**	-0.01	-0.03
TSHarvest	-0.23**	-0.05	-0.30**	0.16*	0.34**	
SBMI	0.06	0.17	0.01	0.22		
Deer density	0.06	0.08	-0.04			
CO	0.28**	0.30**				
Gap size	0.18**					

**p-value < 0.05, *p-value < 0.10

CV= % cover of competing vegetation (*Rubus* spp, grass/*Carex* spp, other shrubs and ferns), gap size= extended gap size (m^2), CO = % canopy openness, deer density= estimated deer / km^2 winter 2007-2008, SMBI= stand average sugar maple browse index, snow depth= average snow depth from November 2007-April 2008, TSHarvest= time since harvest.

Table 1.7. Differences in stand-level and stand average gap-level variables by Habitat Type based on Kruskal-Wallis rank sum test. Inter-quartile ranges are listed for those variables that significantly differ between Habitat Types. Significant comparisons ($p < 0.05$) are based on Wilcoxon signed-rank test with Bonferroni adjusted p-values.

Variable	χ^2	*df*	p-value	AOCa	ATD-Hp	ATD	ATM	TMC	Significant Comparisons
N. stand obs (N. obs for SMBI)				19 (4)	15 (0)	12 (10)	11 (10)	2 (1)	
Stand-level and stand average gap-level variables									
Snow depth (cm)	22.09	4	<0.001	20.6-29.4	18.1-22.7	25.4-34.2	23.6-38.4	31.3-31.5	ATD, ATM>ATD-Hp
TSHarvest	3.75	4	0.441						
SMBI	7.54	3	0.057						
Estimated deer density	7.17	4	0.127						
Canopy openness	3.61	4	0.462						
Competing vegetation	2.52	4	0.642						
Grass/*Carex* spp (%)	10.99	4	0.027	5.0-21.5	10.5-30.0	2.0-13.5	4.5-14.0	2.8-3.5[2]	
Rubus spp	9.21	4	0.056[1]						
Other shrubs	8.85	4	0.065						
Ferns (%)	12.38	4	0.015	5.5-20.0	1.0-7.5	5.0-14.3	6.0-13.0	17.3-21.5	AOCa > ATD-Hp
SP_{2008} sugar maple	7.90	4	0.095						
$SP_{Harvest}$ sugar maple	9.38	4	0.052[1]						
SP_{2008} ironwood	5.12	4	0.275						
$SP_{Harvest}$ ironwood	5.92	4	0.205						
SP_{2008} other spp	5.03	4	0.284						
$SP_{Harvest}$ other spp	10.25	4	0.036	0.4-4.1	1.3-11.1	0.6-4.8	4.1-8.3	8.7-12.9[2]	

SMBI= stand average sugar maple browse index, SP = seedling production potential (Σdiameter/distance^2) for 2008 and at time of harvest, TSHarvest=time since harvest

[1] χ^2 was significant when TMC was removed from analysis because of low sample size (see text for details)

[2] Pairwise comparisons were not significant, even when TMC was removed from analysis

Table 1.8. Spatial patterns in sapling abundance 1-2 m tall, stocking levels and Shannon Diversity Index (H'): mean parameter estimates and 95% credible interval from posterior distributions. Positive values indicate increases in that variable with Northing or Easting (UTM position rescaled from 0 to 1). Parameter estimates are on the log or square root scale due to the use of a log-link or transformations (where indicated). Null models include the overall intercept and random stand-level intercepts for multilevel models and the overall intercept for growth rate linear models. A decrease in DIC of 5 or more indicates improved performance for the spatial model over the null model.

Variable	Northing		Easting		N. gaps / stands	DIC (spatial model)	DIC (null model)
	Mean	CI	Mean	CI			
			Seedling Abundance 1-2 m / 2 m^2 gap plot				
Sugar maple	3.44**	2.13 – 4.77	1.16**	0.04 – 2.28	337 / 59	2182.68	2184.88
Ironwood	-3.67**	-6.08 – -1.49	-0.99	-3.06 – 0.94	337 / 59	709.60	714.41
Other spp	0.67	-1.42 – 2.79	1.69*	-0.15 – 3.58	337 / 59	1131.67	1132.46
			Sapling Abundance 1-2 m / 154 m^2 gap plot				
Sugar maple	16.51**	12.21 – 21.76	4.51**	1.37 – 7.79	331 / 58	1216.47	1218.17
Ironwood	-1.25	-4.75 – 2.34	-1.03	-4.04 – 2.05	331 / 58	1297.49	1296.83
Other spp	3.98**	1.02 – 7.12	1.89	-0.75 – 4.56	331 / 58	1487.95	1489.85
			Log(Stocking Saplings 1-7m / 154 m^2 gap plot)				
Sugar maple	3.13**	1.69 – 4.57	2.64**	1.48 – 3.80	164 / 45	538.79	544.32
Ironwood	-0.97	-2.83 – 0.86	-0.46	-1.95 – 1.03	184 / 49	625.80	625.81
Other spp	1.45*	-0.17 – 3.06	2.23**	0.81 – 3.62	193 / 48	675.30	675.80
			Sqrt(H')				
Seedlings	-0.27**	-0.43 – -0.10	-0.08	-0.23 – 0.07	182 / 54	-102.84	-100.26
Saplings 1-2 m	0.03	-0.20 – 0.27	-0.23**	-0.41 – -0.04	180 / 42	-50.73	-50.06
Saplings 1-7m	0.00	-0.21 – 0.21	-0.16*	-0.32 – 0.01	201 / 46	-57.31	-57.47
			Log(Sapling growth rate after harvest m / yr)				
Sugar maple	0.54**	0.19 – 0.89	-0.10	-0.30 – 0.10	127 / 26	105.89	114.86
Ironwood	0.20	-0.13 – 0.54	0.16	-0.14 – 0.45	98 / 30	85.61	84.03

**indicates 95% credible interval does not overlap 0, *indicates 90% CI does not overlap 0

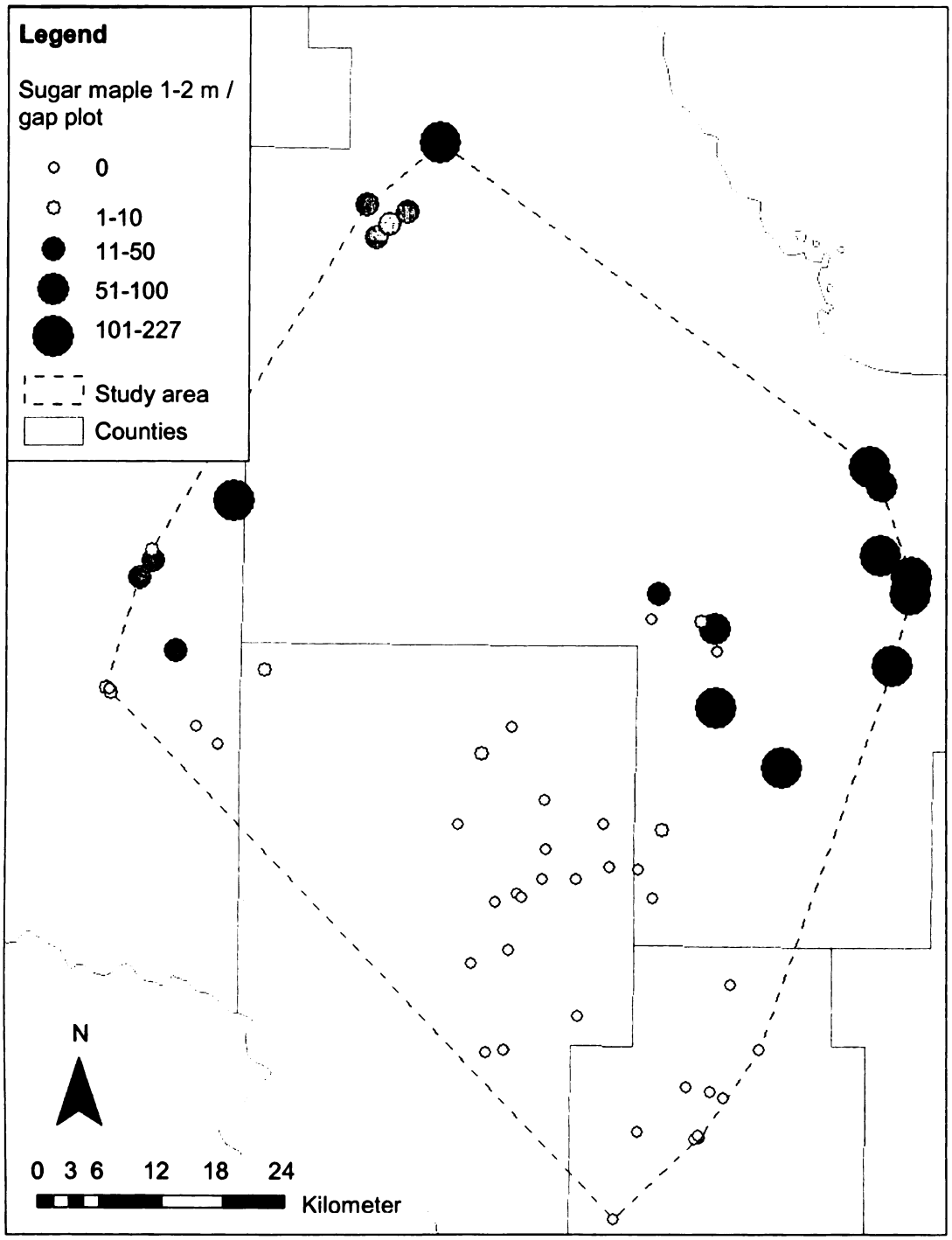


Figure 1.4. Site average sugar maple sapling (1-2 m tall) abundance per gap plot across the study area. For reference, 10 saplings / gap plot is 650 saplings / hectare and 227 saplings / gap plot is 14,746 saplings / hectare of gap area.

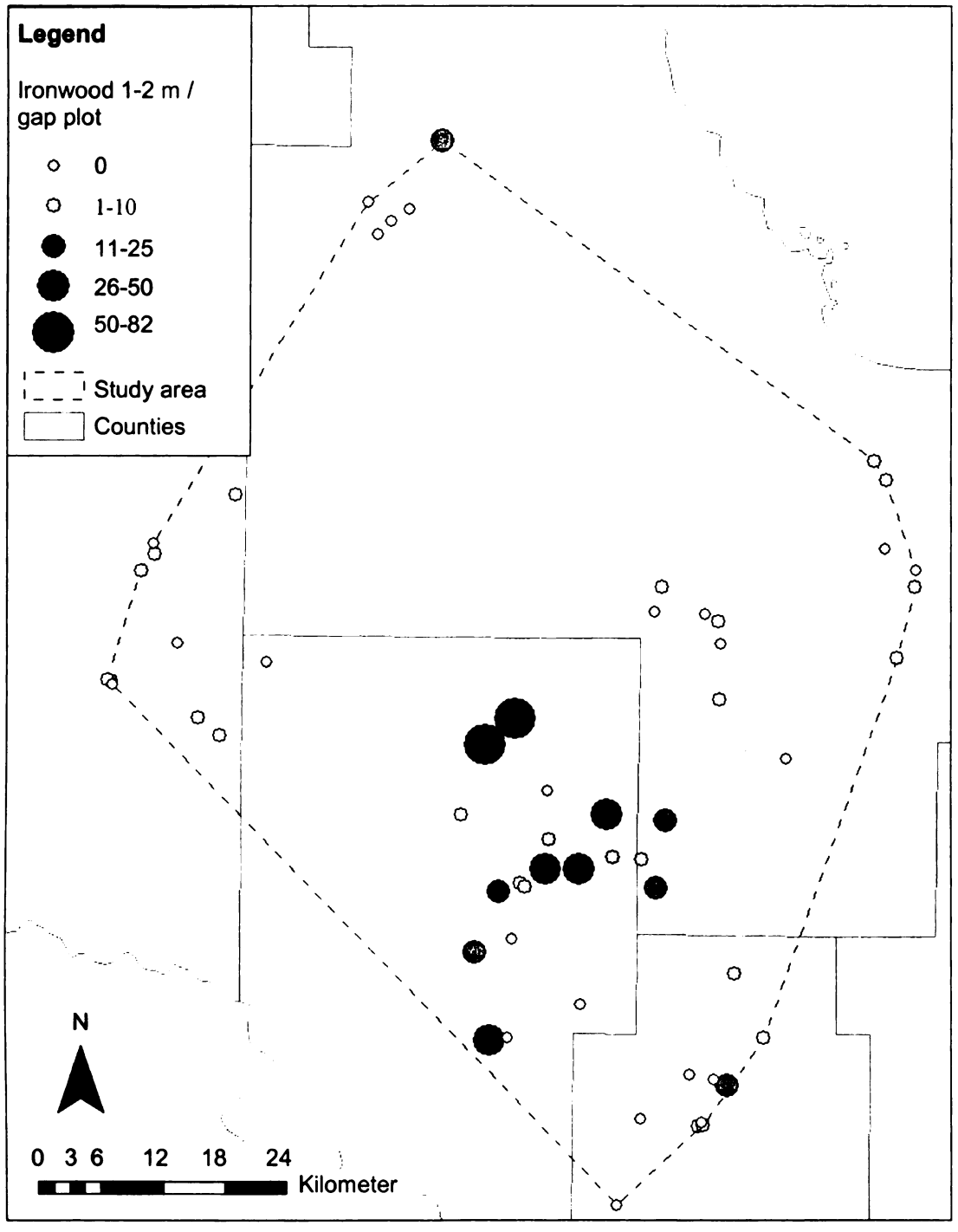


Figure 1.5. Site average ironwood sapling (1-2 m tall) abundance per gap plot across the study area. For reference, 10 saplings / gap plot is 650 saplings / hectare and 82 saplings / gap plot is 5,327 saplings / hectare of gap area.

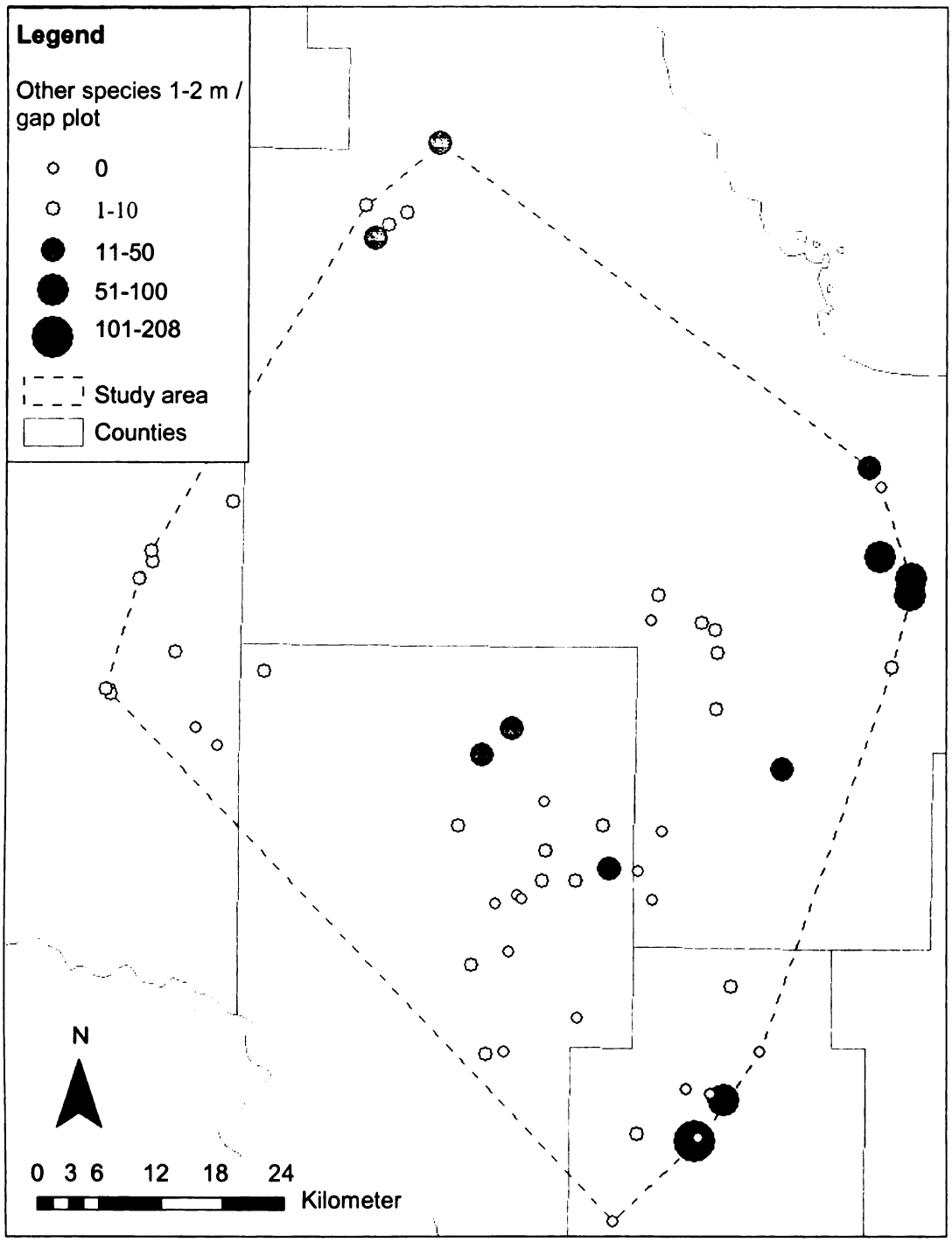


Figure 1.6. Site average other species sapling (1-2 m tall) abundance per gap plot across the study area. For reference, 10 saplings / gap plot is 650 saplings / hectare and 208 saplings / gap plot is 13,512 saplings / hectare of gap area.

Table 1.9. Spatial patterns in gap- and stand-level variables: bootstrap parameter estimate and 95% confidence intervals for stand-level variables or stand averages of gap-level variables. Positive values indicate increases in that variable with Northing or Easting (UTM position rescaled from 0 to 1). Gap- and stand-level variables were not standardized for this analysis.

Variable	Northing		Easting		N. stands
	Estimate	CI	Estimate	CI	
Snow depth	22.24**	16.29 – 28.83	-4.75*	-8.57 – 0.08	59
Time since harvest	-1.43	-4.04 – 1.45	-1.81	-4.89 – 1.39	59
SMBI	-4.03**	-5.26 – -3.02	-1.66**	-2.20 – -1.10	25
Estimated deer density	-17.51**	-26.27 – -9.42	-10.48**	-23.99 – -0.33	59
Canopy openness	4.26	-1.03 – 9.16	1.60	-3.14 – 7.26	59
Competing veg	-5.29	-23.79 – 13.94	-21.28**	-37.23 – -4.51	59
SP_{2008} sugar maple	-0.55	-2.34 – 1.47	0.68	-1.25 – 2.73	59
$SP_{Harvest}$ sugar maple	10.64**	3.76 – 17.56	1.43	-4.93 – 8.18	58
SP_{2008} ironwood	-0.94**	-1.86 – -0.31	-0.38**	-0.95 – -0.04	59
$SP_{Harvest}$ ironwood	-1.65**	-3.40 – -0.45	-0.54	-1.86 – 0.63	58
SP_{2008} other spp	-0.55	-2.64 – 1.32	-1.21	-3.49 – 0.60	59
$SP_{Harvest}$ other spp	-1.51	-7.62 – 4.42	-0.69	-6.84 – 4.26	58

** indicates 95% CI does not overlap 0, * indicates 90% CI does not overlap 0
SMBI= sugar maple browse index.

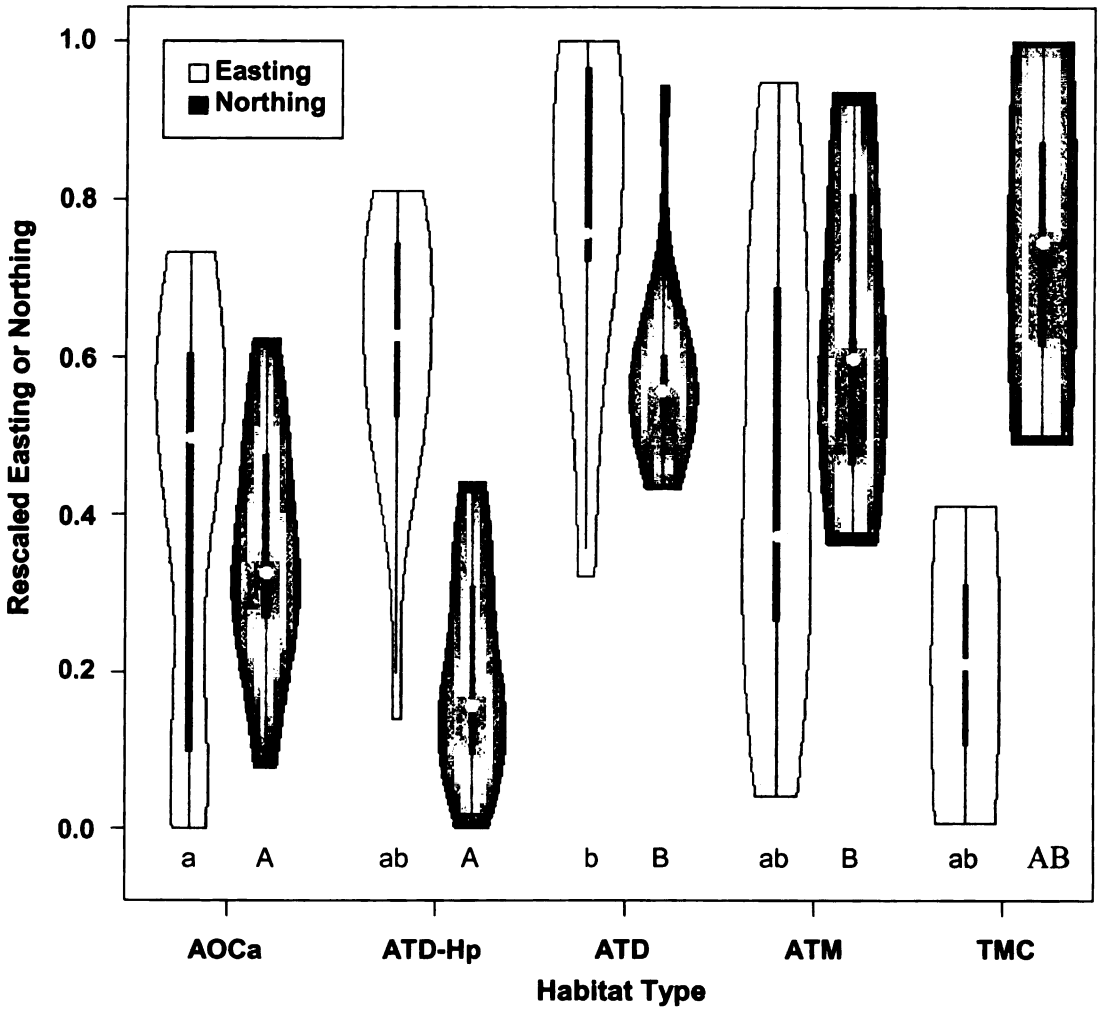
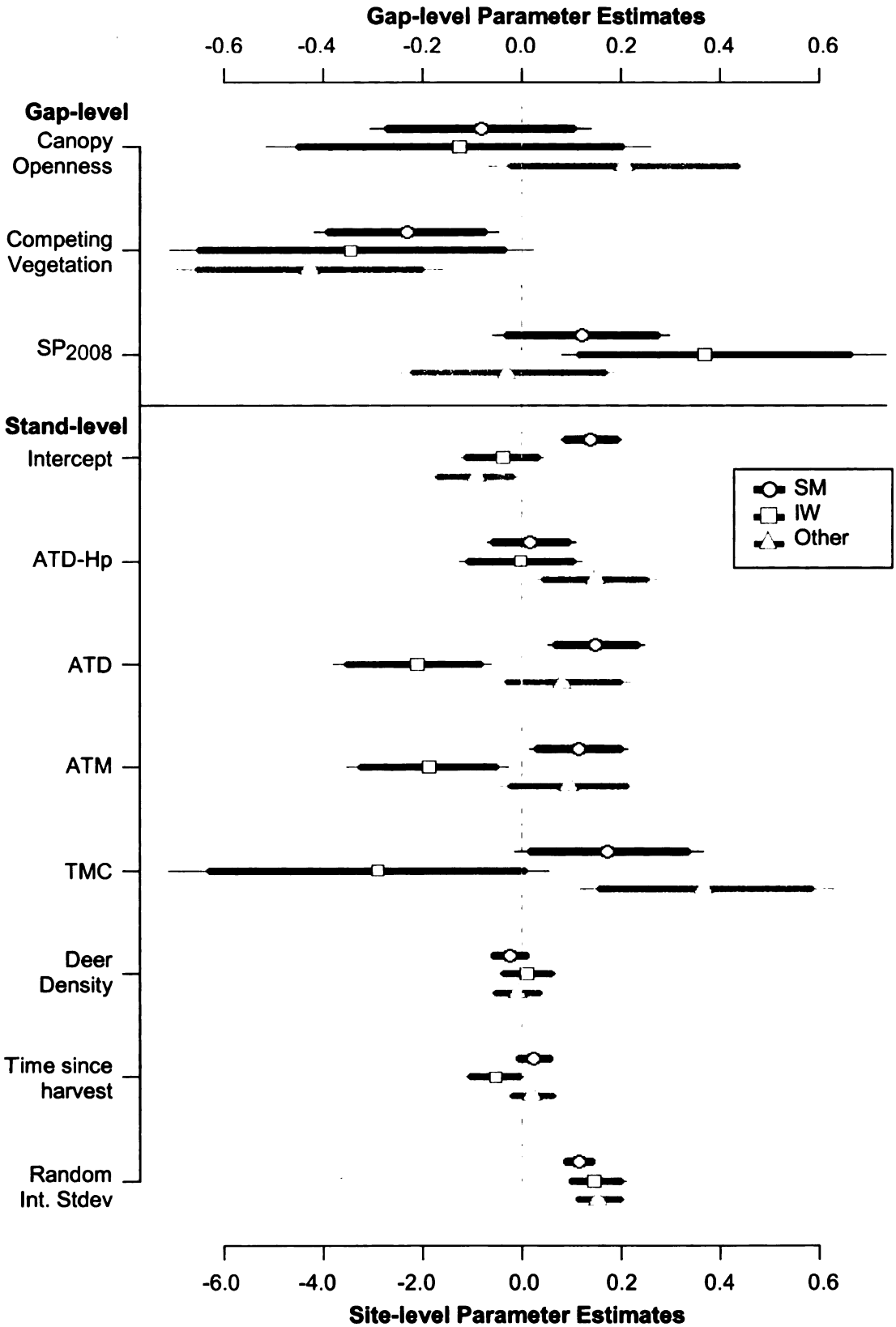


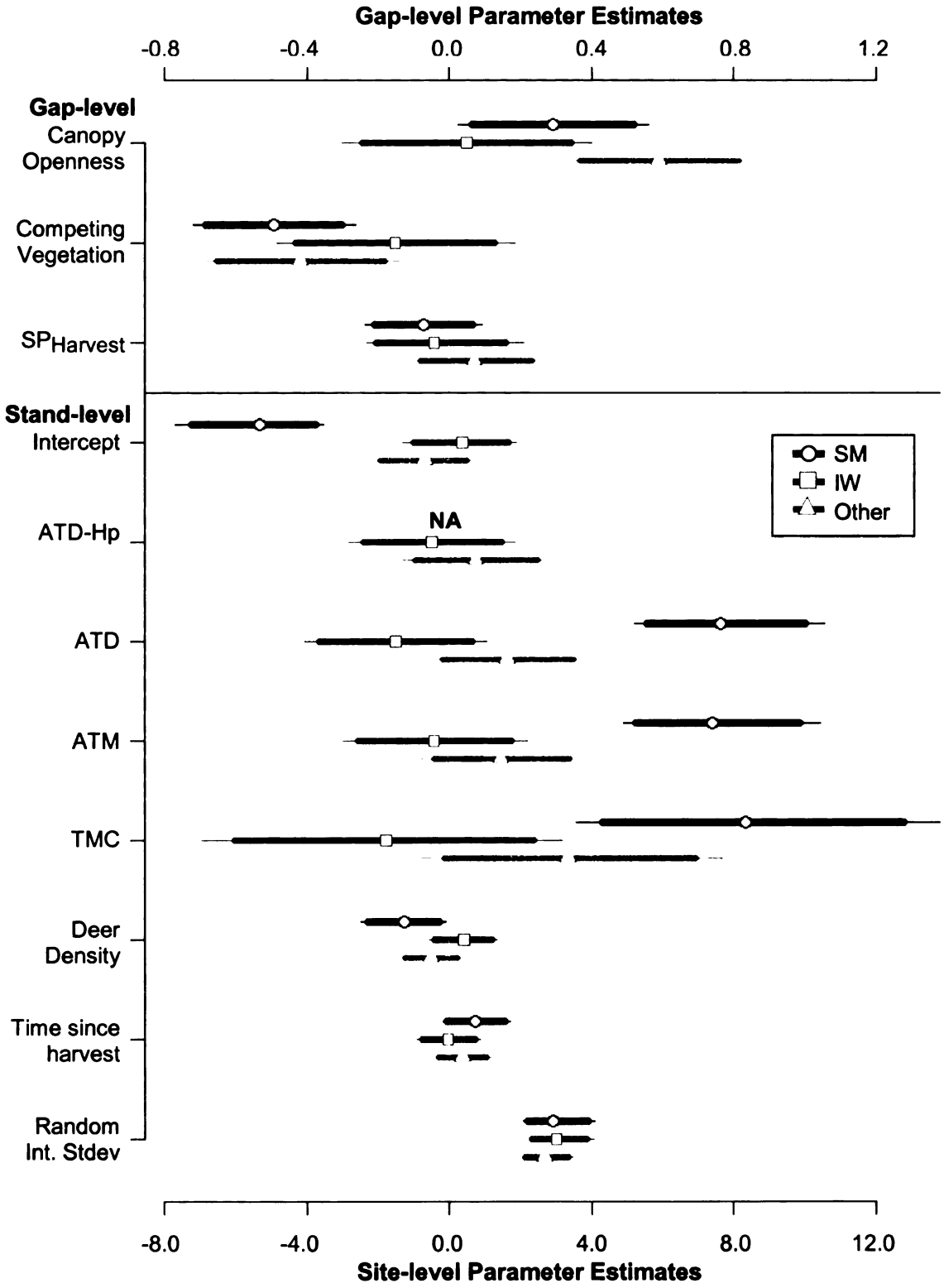
Figure 1.7. Spatial distributions of Habitat Types by UTM Easting and Northing (scaled to 0-1). Letters indicate significant differences between Habitat Types based on Wilcoxon signed-rank test with Bonferroni adjusted p-value. Violin plots show distribution of values and median (white dot), interquartile range (thick vertical line) and range of values 1.5 * IQR (thin vertical line).

Figure 1.8. Effects of gap and stand-level variables on seedling (<1 m tall) abundance: mean parameter estimates, 95% credible interval (thick line), and 90% credible interval (thin line) from posterior distributions. Positive values indicate increases in seedling abundance with a one standard deviation increase in that covariate on the log scale. AOCa is the reference Habitat Type. SM=sugar maple, IW=ironwood, Other=other species, SP_{2008}= seedling production potential (Σdiameter/distance^2) for 2008, Random Int. Stdev= standard deviation for the random stand-level intercept. Exact parameter values can be found in Appendix E, Table E.1.



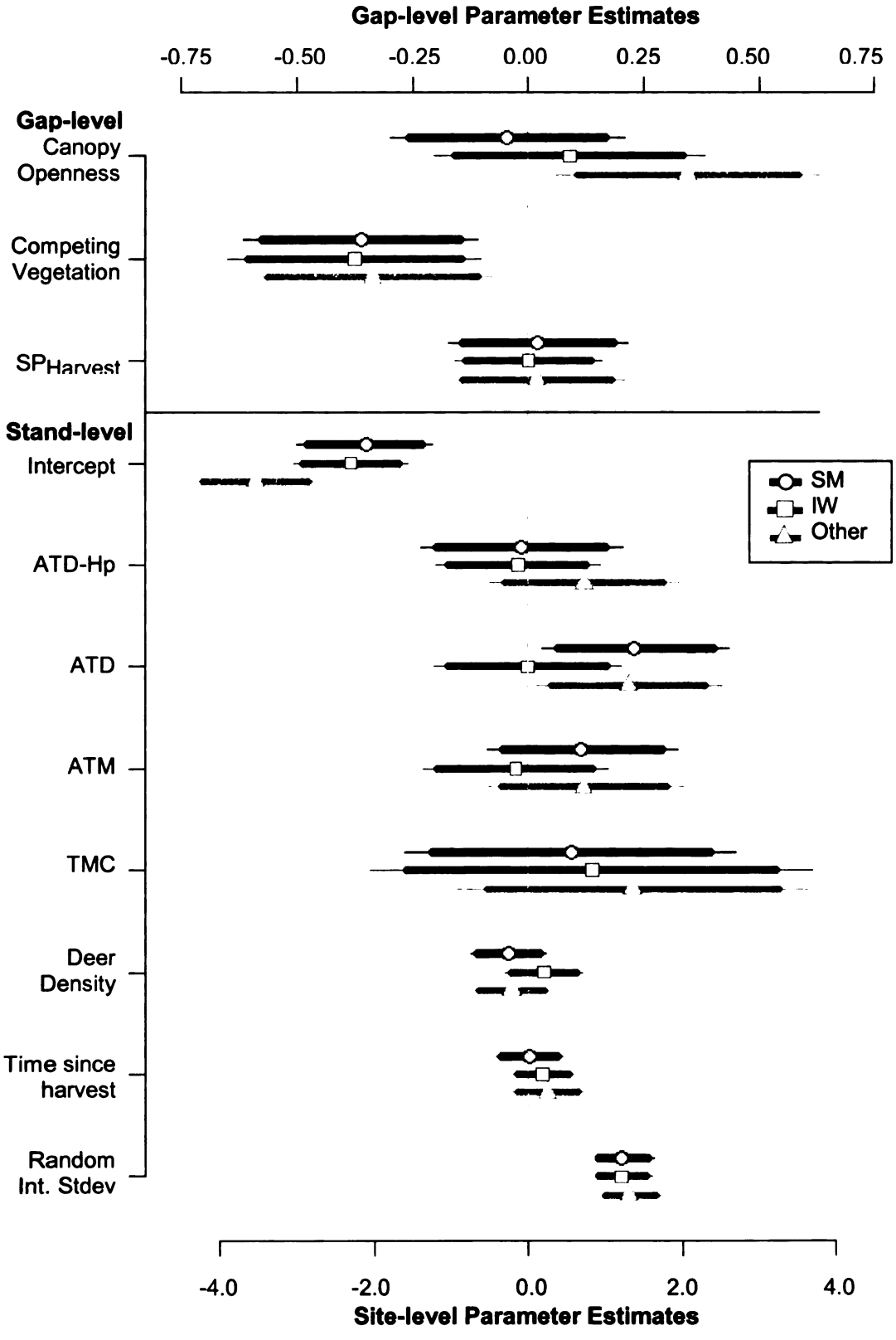
Factors Affecting Seedling Abundance

Figure 1.9. Effects of gap and stand-level variables on small sapling (1-2 m tall) abundance: mean parameter estimates, 95% credible interval (thick line), and 90% credible interval (thin line) from posterior distributions. Positive values indicate increases in sapling abundance with a one standard deviation increase in that covariate on the log scale. AOCa and ATD-Hp are reference Habitat Types for sugar maple and AOCa is the reference Habitat Type for ironwood and other species. SM=sugar maple, IW=ironwood, Other=other species, $SP_{Harvest}$= seedling production potential (Σdiameter/distance^2) at time of harvest, Random Int. Stdev= standard deviation for the random stand-level intercept. Exact parameter values can be found in Appendix E, Table E.2.



Factors Affecting Small Sapling Abundance

Figure 1.10. Effects of gap and stand-level variables on log transformed sapling (1-7 m tall) stocking-level: mean parameter estimates, 95% credible interval (thick line), and 90% credible interval (thin line) from posterior distributions. Positive values indicate increases in sapling stocking on the log scale with a one standard deviation increase in that covariate. AOCa is the reference Habitat Type. SM=sugar maple, IW=ironwood, Other=other species, $SP_{Harvest}$= seedling production potential (Σdiameter/distance^2) at time of harvest, Random Int. Stdev= standard deviation for the random stand-level intercept. Exact parameter values can be found in Appendix E, Table E.3.



Factors Affecting Sapling Stocking-Levels

Table 1.10. Deviance Information Criterion for full models (all gap- and stand-level covariates) and null models (overall intercept and random stand-level intercepts for multilevel models and the overall intercept for growth rate linear models) and number of gaps and stands with observations. A decrease in DIC of 5 or more indicates improved performance for full model over the null model.

Variable	Full model	Null model	N. gaps / stands
Seedling abundance (GLMM)			
Sugar maple	2172.61	2184.88	337 / 59
Ironwood	701.20	714.41	337 / 59
Other species	1132.04	1132.46	337 / 59
Small sapling abundance (GLMM)			
Sugar maple	1197.10	1218.17	331 / 58
Ironwood	1299.96	1296.83	331 / 58
Other species	1468.80	1489.85	331 / 58
Log(Sapling stocking-levels) (LMM)			
Sugar maple	540.62	544.32	164 / 45
Ironwood	622.61	625.81	184 / 49
Other species	674.85	675.80	193 / 48
Sqrt(H') (LMM)			
H' Seedlings	-112.27	-100.26	182 / 54
H' Small Saplings	-46.81	-50.06	180 / 42
H' All Saplings	-54.46	-57.47	201 / 46
Log(Post-harvest growth rate) (LM)			
Sugar maple	2.34	114.86	127 / 26
Ironwood	13.64	84.03	98 / 30

GLMM=generalized linear mixed model, LMM= linear mixed model, LM= linear model, H'=Shannon Diversity Index

Figure 1.11. Observed sapling (1-2 m tall) abundance and mean posterior predicted values and 95% credible intervals per gap plot from generalized linear mixed models with gap- and stand-level covariates (full model) and the null model with an overall intercept and stand-level random effect intercepts.

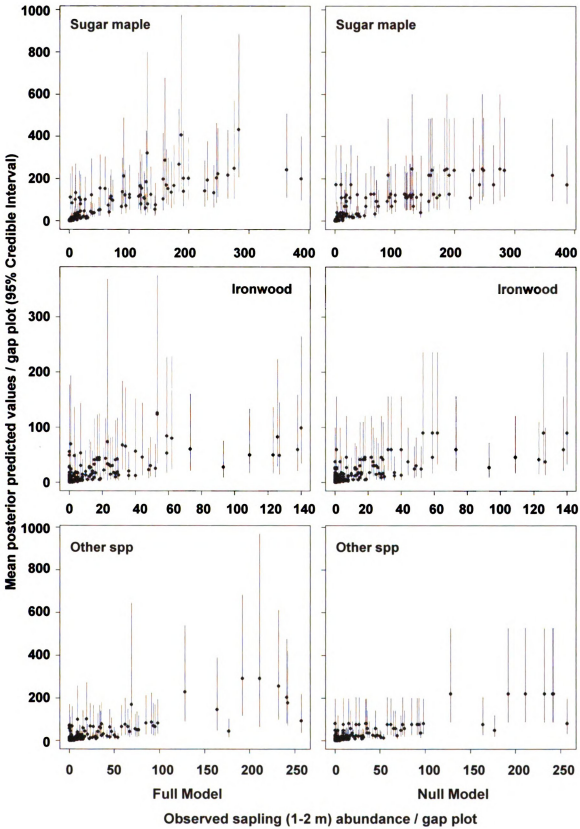
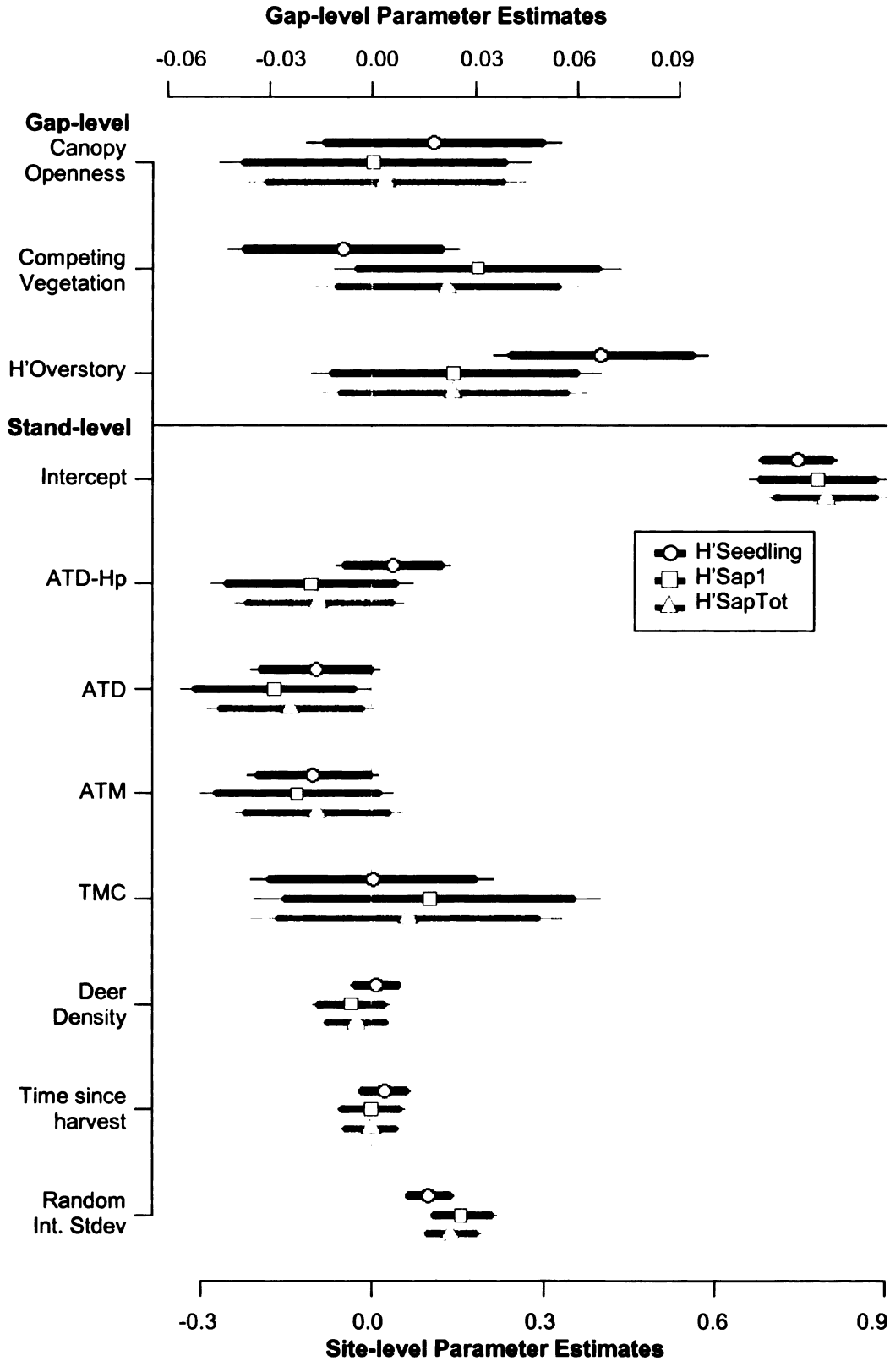
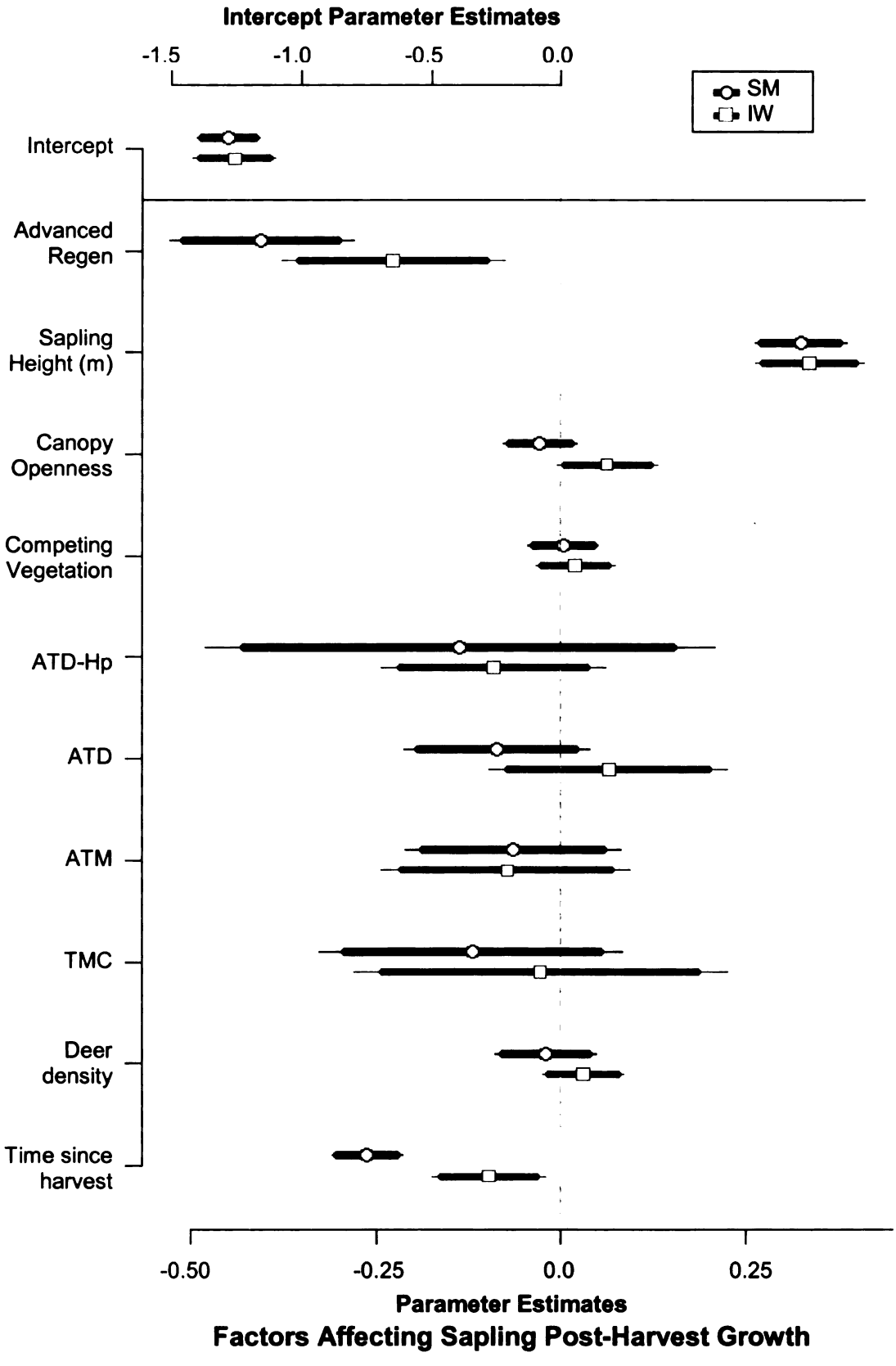

Sugar maple
Sugar maple
Ironwood
Ironwood
Other spp
Other spp
Mean posterior predicted values / gap plot (95% Credible Interval)
Full Model
Null Model
Observed sapling (1-2 m) abundance / gap plot

Figure 1.12. Effects of gap and stand-level variables on square root transformed Shannon Diversity Index (H') for seedling (<1 m tall) (H'seedling), small saplings (1-2 m tall) (H'Sap1) and all saplings (1-7 m tall) (H'SapTot): mean parameter estimates, 95% credible interval (thick line), and 90% credible interval (thin line) from posterior distributions. Positive values indicate increases in H' on the square root scale with a one standard deviation increase in that covariate. AOCa is the reference Habitat Type. H'Overstory = H' of overstory trees for H'Seedling and H' of overstory trees and stumps for H'Sap1 and H'SapTot. Random Int. Stdev= standard deviation for the random stand-level intercept. Exact parameter values can be found in Appendix E, Table E.4.



Factors Affecting Shannon Diversity Index

Figure 1.13. Effects of gap and stand-level variables on log transformed sapling post-harvest growth rates (m/yr mean parameter estimates, 95% credible interval (thick line), and 90% credible interval (thin line) from posterior distributions. Positive values indicate increases in growth rate on the log scale with a one standard deviation increase in that covariate. AOCa is the reference Habitat Type. SM=sugar maple, IW=ironwood, Other=other species, Advanced Regen= bivariate variable indicating if a variable is advanced regeneration. Exact parameter values can be found in Appendix E, Table E.5.



Factors Affecting Sapling Post-Harvest Growth

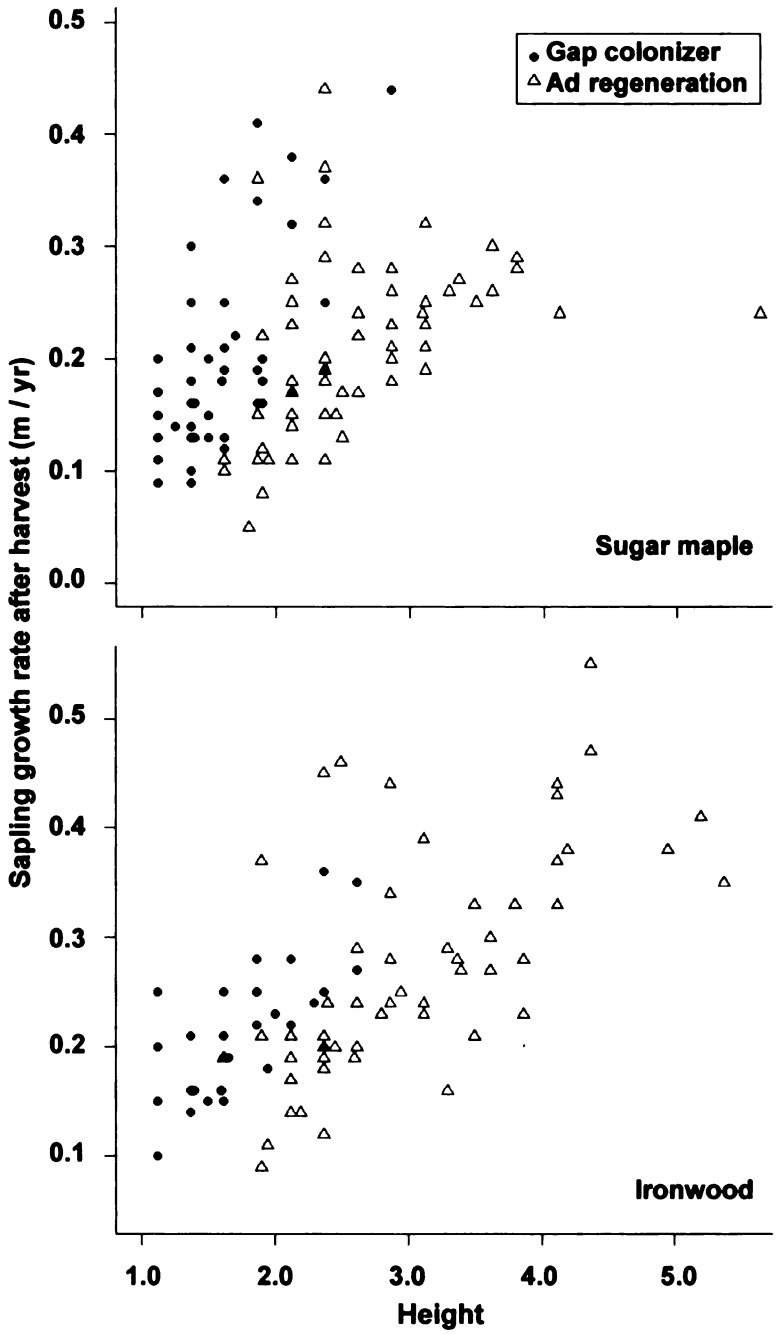


Figure 1.14. Sugar maple and ironwood sapling growth rate after harvest for gap colonizers and advanced regeneration (ad regeneration).

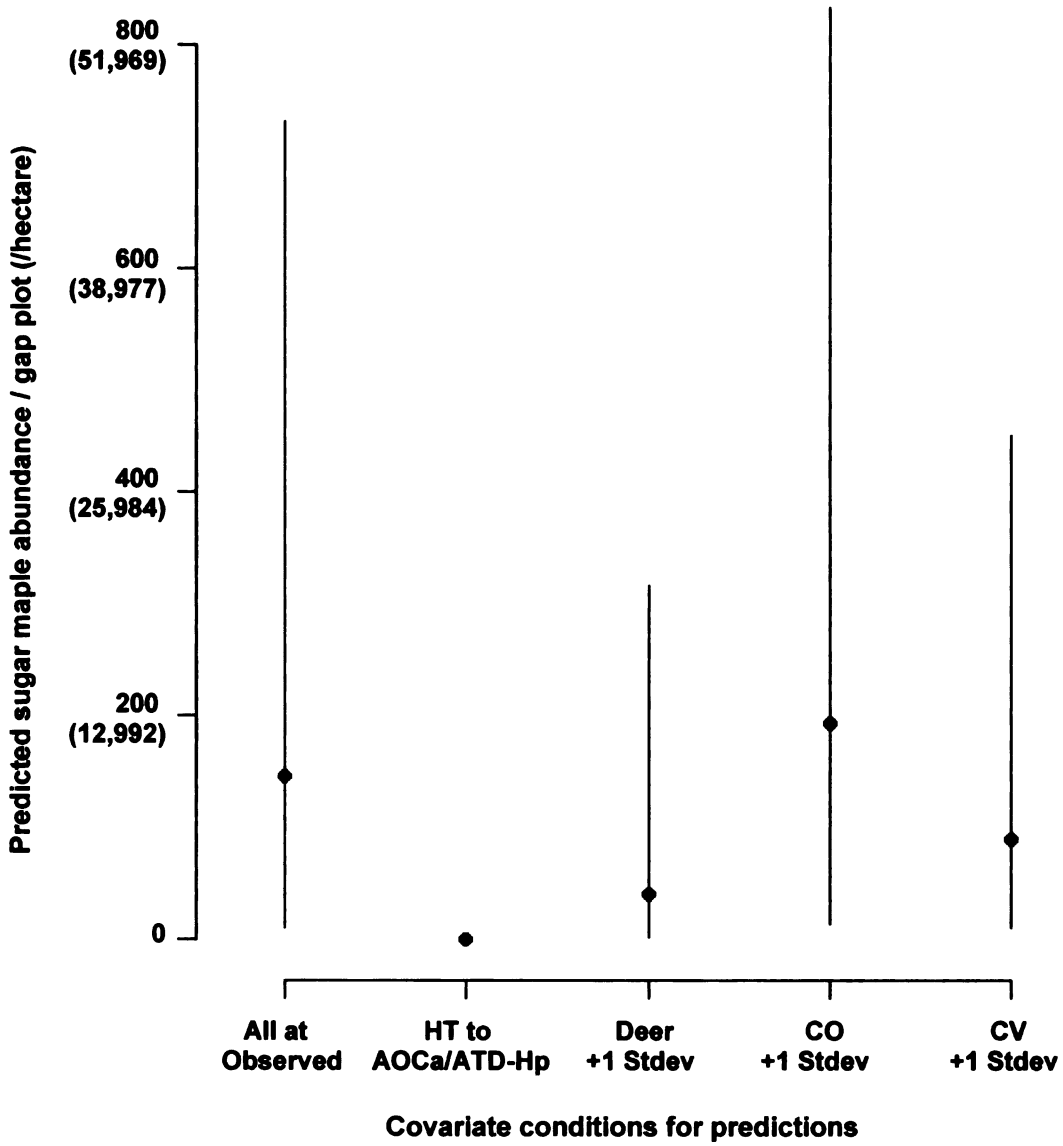


Figure 1.15. Predicting sugar maple abundance / gap plot (or / hectare of gap area) for an observed stand: median and 95% percentile predictions based on one to one simulations drawing from the posterior coefficient distributions and random effects intercept for an observed ATM stand where a gap had 387 saplings in a gap plot (25,140 / ha of gap area). Simulations were run with different covariate conditions (holding all else equal): all at observed covariate values for this gap and stand, changing Habitat Type (HT) to AOCa/ATD-Hp, increasing deer density from 4 to 16 deer/km^2 (observed to observed plus one standard deviation), increasing canopy openness (CO) from 5 to 12% and increasing cover of competing vegetation (CV) from 18 to 41%.

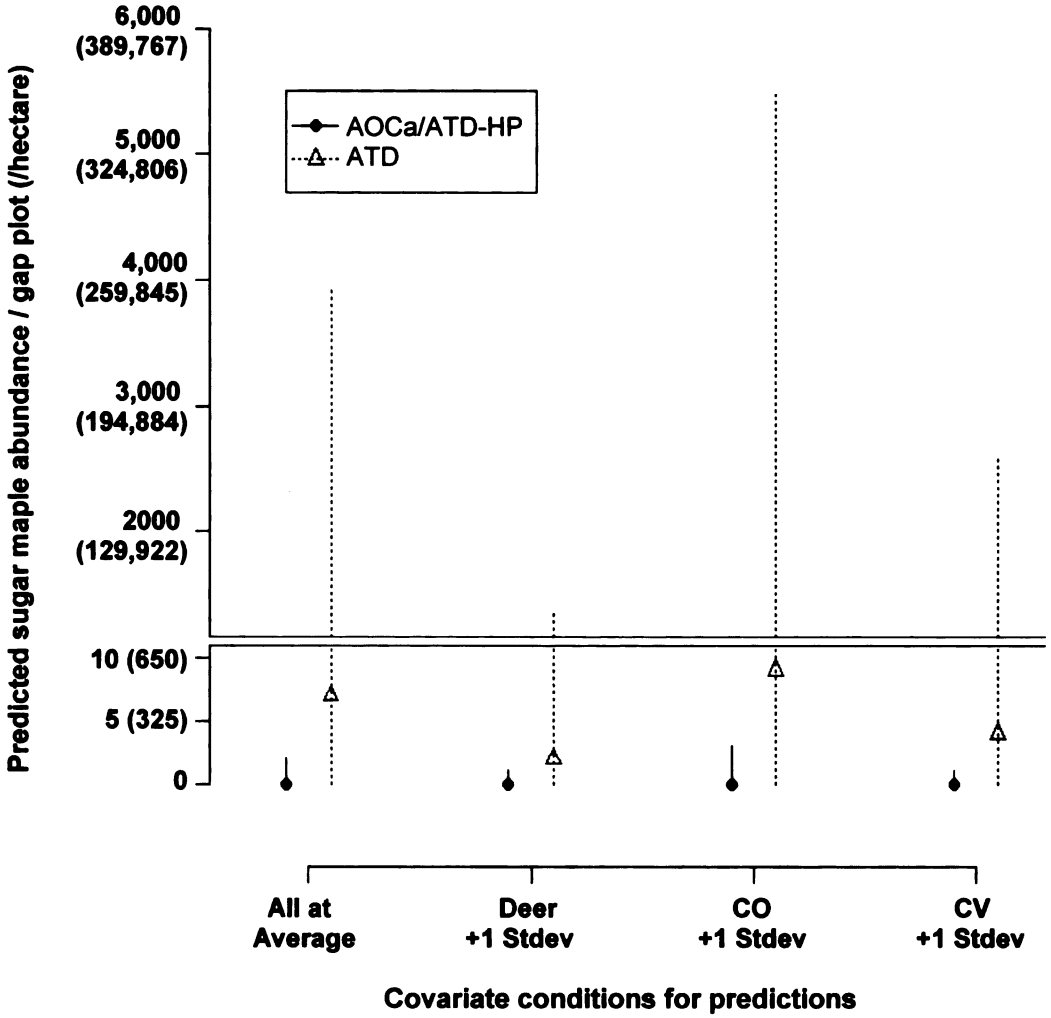


Figure 1.16. Predicting sugar maple abundance / gap plot (or / hectare of gap area) for an unmeasured stand: Median and 95% percentile predictions based on one to one simulations drawing from the posterior coefficient distributions and randomly drawing the stand-level intercept from ~N(μ, σ_α) where μ is defined by the stand-level covariates and σ_α is the random stand-level intercept stand deviation. Simulations were run with different covariate conditions (holding all else equal) for a gap at an AOCa and ATD type stand: all at average observed covariate values, increasing deer density from 14 to 26 deer/km^2 (average observed to average observed plus one standard deviation), increasing canopy openness (CO) from 13 to 20% and increasing cover of competing vegetation (CV) from 42 to 65%. A break was added to the y-axis so changes in the median prediction could be seen.

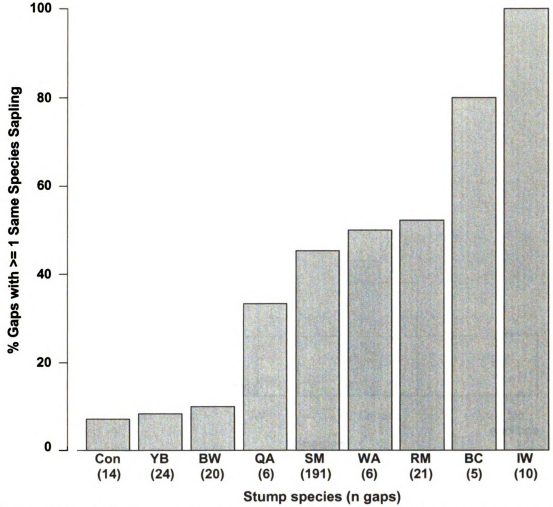


Figure 1.17. Percentage of gaps harvested 8-15 years ago where a species was removed (stump species) and there was at least one sapling of the same in the gap plot. Species codes: Con=conifer (eastern hemlock, northern white cedar, balsam fir and white spruce), YB= yellow birch, BW= American basswood, QA= quaking aspen, SM= sugar maple, RM= red maple, BC= black cherry, IW=ironwood. Numbers below species codes indicate the number of gaps where that species was removed by harvesting.

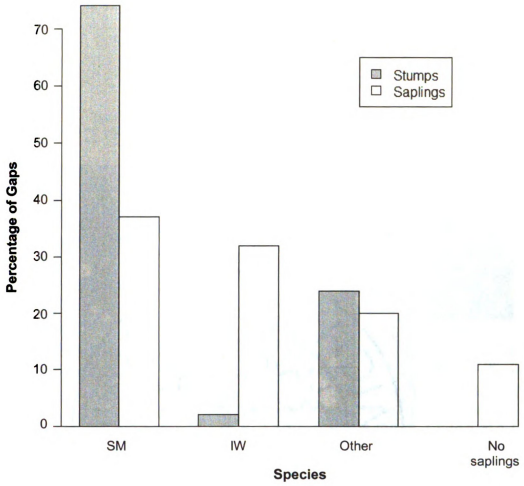


Figure 1.18. Percentage of gaps sugar maple (SM), ironwood (IW) or other species are the dominant stump species (highest relative basal area of stumps removed from gap) and percentage of gaps these species are the dominant sapling species (highest relative stocking level of saplings 1-7 m tall). Percentage of gaps with no saplings is also presented. N= 211 gaps harvested 8-15 years ago.

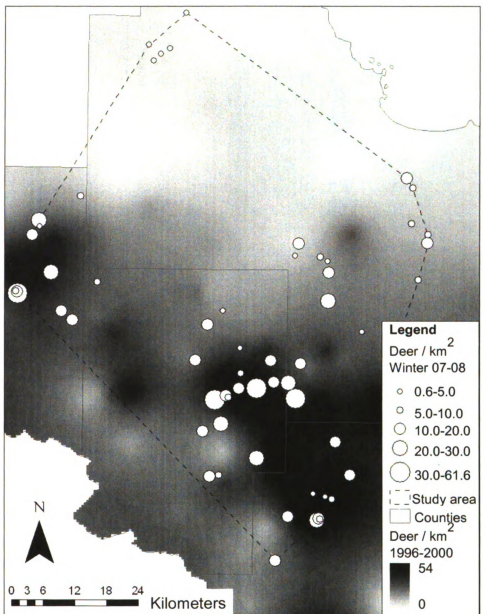
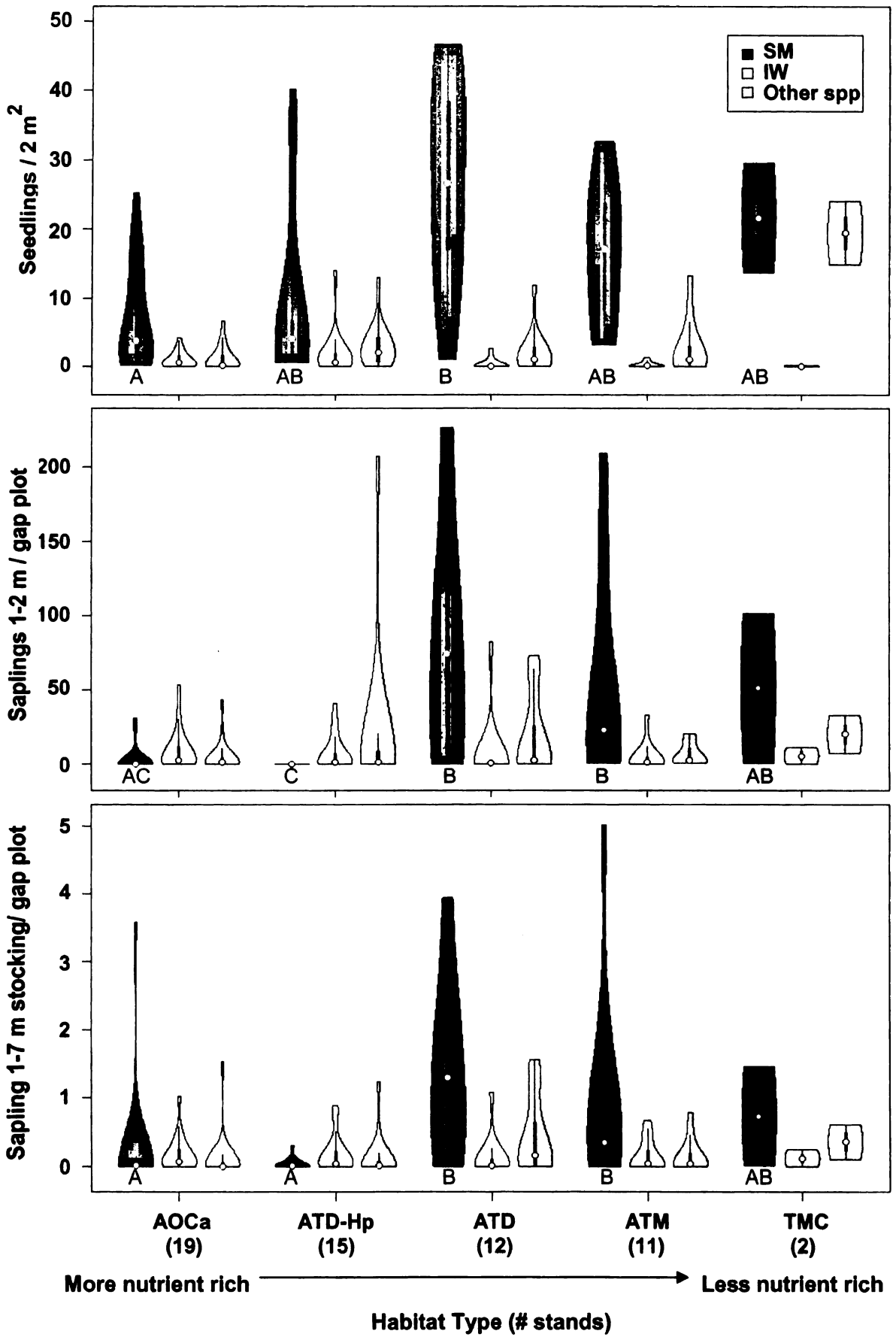


Figure 1.19. Average estimated deer density (deer / km^2) from 1996-2000 created from universal kriging (Appendix B, Section B.5) of 113 observations collected by the Michigan Department of Natural Resources and deer density estimates from winter 2007-2008. Estimates for winter 2007-2008 are positively correlated with the MDNR 1996-2000 estimates (Kendall's τ=0.27, p-value=0.002).

Figure 1.20. Differences in stand average seedling abundance / 2 m^2, small sapling (1-2 m) abundance / gap plot and sapling stocking levels / gap plot by Habitat Type. Gap plots were 154 m^2. Letters indicate significant differences between Habitat Types for sugar maple based on Wilcoxon signed-rank test with Bonferroni adjusted p-value. Kruskal-Wallis rank sum test indicated that sapling abundance and sapling stocking were not significantly different between Habitat Types for ironwood or other species, but it was significant for seedling of both species. However, no pairs of Habitat Types were significantly different based on the Wilcoxon test. Violin plots show distribution of values and median (white dot), interquartile range (thick vertical line) and range of values 1.5 * IQR (thin vertical line).


Seedlings / 2 m2
50
40
30
20
10
0
SM
IW
Other spp
A
AB
B
AB
AB
Saplings 1-2 m / gap plot
200
150
100
50
0
AC
C
B
B
AB
Sapling 1-7 m stocking/ gap plot
5
4
3
2
1
0
A
A
B
B
AB
AOCa
(19)
ATD-Hp
(15)
ATD
(12)
ATM
(11)
TMC
(2)
More nutrient rich
Less nutrient rich
Habitat Type (# stands)

Chapter 2: Snow depth, deciduous-lowland conifer forest edges and deer density affect seedling browse damage

Abstract

Restoration of eastern hemlock (*Tsuga canadensis* (L.) Carrière) and eastern white pine (*Pinus strobus* L.) to forests in the Great Lakes region are priority conservation goals. I planted white pine, hemlock and white spruce (*Picea glauca* (Moench) Voss) seedlings in harvest gaps within northern hardwood stands in the Western Upper Peninsula of Michigan to 1) explore the efficacy of planting efforts in areas with high winter deer densities and 2) improve our understanding of factors affecting deer herbivory at the stand- and gap-level. Results show that white spruce seedlings may successfully reestablish with planting efforts because this species was virtually un-browsed, but white pine and hemlock will not reestablish without protection from deer. Stand-level percentages of seedlings browsed increased with estimated winter deer density and decreased with snow depth and stand-average gap distance to lowland conifer. Non-linearity was observed in the relationship between browse pressure and estimated deer density, emphasizing the importance of maintaining deer densities below a threshold level when the goal is to protect browse-preferred understory vegetation. Snow sheltered seedlings from deer, but relationships between snow depth and estimated stand deer density were not observed. Evidence of deer gap-use corresponded with increased gap-level percentage of seedlings browsed, but contrary to expectations, deer-use within a stand was higher in gaps farther from lowland conifer. The relationship between browse pressure and estimated deer density supports the use of the pellet count technique for estimating deer densities. However, monitoring deer browse directly on seedlings and saplings provides better insight into impacts of herbivory.

2.1 Introduction

Hemlock-white pine-northern hardwood forests in the Great Lake Regions underwent dramatic transformations in the mid 1800s to early 1900s when logging virtually eliminated eastern hemlock (*Tsuga canadensis* (L.) Carrière) and eastern white pine (*Pinus strobus* L.) from the landscape (Whitney 1987; Stearns 1997; MDNR 2006). Hemlock has not been replaced by natural regeneration due to seed source limitations (Mladenoff and Stearns 1993), lack of suitable seed beds (Mladenoff and Stearns 1993; Rooney et al 2000; Marx and Walters 2008), browsing by white-tailed deer (Swift 1949; Graham 1954; Rooney et al 2000), unsuitable climatic conditions (Mladenoff and Stearns 1993) and light limitations (Rooney et al 2000). White pine seedlings and saplings are still found widespread throughout northern hardwood-conifer forests where seed sources are available (Carleton et al 1996) but declines have been observed (MDNR 2006). The absence of a seed source greatly limits the regeneration of this species (Ahlgren 1976; Dovčiak et al 2003), but so does the availability of suitable seed beds (Smith 1951; Dovčiak et al 2003), light availability (Smith 1951; Krueger and Puettmann 2004), browsing by white-tailed deer (Swift 1949; Saunders and Puettmann 1999; Krueger and Puettmann 2004), competition from understory vegetation (Ahlgren 1976; Dovčiak et al 2003; George and Bazzaz 1999) and damage from insects and disease (Ahlgren 1976; Krueger and Puettmann 2004).

Increasing the cover of mesic conifer[1] stands and re-establishing these species as components in hardwood forests are common conservation goals in the Great Lakes Region (Thorne 1992; Crow et al 1994; OMNR 2003; MDNR 2006). On State land in the

[1] Mesic conifers include eastern hemlock, eastern white pine, balsam fir (*Abies balsamea* (L.) P. Mill.) and white spruce (*Picea glauca* (Moench) Voss)

Western Upper Peninsula of Michigan, white pine and hemlock planting efforts are underway (Herman et al 2004). It is predicted that increased cover of pure conifer and mixed deciduous-conifer stands will improve habitat for bird species (Herman et al 2004) like the blackburnian warbler (*Dendroica fusca*) which feeds and nests in hemlock trees (Kendeigh 1945). Increasing the abundance of conifer cover could also reduce suitability of white-tailed deer (*Odocoileus viriginanus* Zimmermann) summer range (Kohn and Mooty 1971; Tierson et al 1985; Felix et al 2004) and increase cover of winter habitat (Graham 1954; Verme 1965; Ozoga 1968; Blouch 1984), resulting in smaller herds dispersed over larger wintering areas (Herman et al 2004).

Heavy deer browsing in the Great Lakes region can impact the efficacy of white pine and hemlock restoration efforts (Rooney et al 2000). Consideration of climatic conditions and landscape contexts that affect deer behavior and local densities could improve restoration success. Snow depth and lowland conifer stands influence deer migration and distribution in the winter months. Many deer in the Upper Peninsula of Michigan migrate on average 10.9-20.3 km (depending on winter severity), and as far as about 50 km, from summer to winter ranges where snow depth is lower and availability of winter habitat is greater (Verme 1973; VanDeelen et al 1998). Winter white-tailed deer densities in northern hardwood stands have been found to decrease with increasing distance to lowland conifer, likely due to the importance of conifers for shelter (Millington et al 2009, *in review*). Within deciduous forests, deer browse on seedlings and saplings may increase with proximity to lowland conifer stands.

The most direct method of assessing the impact of deer herbivory on seedlings and saplings is to monitor browse damage, but it is also important to establish reliable

estimates of deer density for informing deer management and modeling the relationships between deer density and herbivory. Fecal pellet surveys are a relatively simple and inexpensive method of assessing relative local deer density (Hill 2001; Langdon 2001) and positive relationships between pellet count metrics and deer density have been empirically supported (Neff 1968; Bailey and Putman 1981; Forsyth et al 2007). However, others have found poor performance of the pellet count method compared to population estimates from aerial surveys (Fuller 1991) and higher variability in pellet count population estimates compared to mark-resighting and distance sampling techniques (Langdon 2001). Deer density estimates derived from pellet counts can be biased because defecation rates are correlated with forage intake, forage moisture content and percentage of young in the herd, and they can be affected by sampling design and observer error (Neff 1968). Regardless, they remain the cheapest and most implementable method available for assessing relative differences between deer density at the stand-scale across a large geographic area.

I planted mesic conifer seedlings within northern hardwood stands in the Western Upper Peninsula of Michigan to test the following hypotheses: H1) seedling browse damage will be higher at stands with lower snow depth, shorter distance to lowland conifer and higher winter deer density and H2) within a stand, seedling browse damage will increase with proximity to lowland conifer where winter deer-use is higher. The results of this study can aid in the development of effective mesic conifer restoration efforts and provide insights into the relationship between estimated deer densities and browse pressure.

2.2 Methods

2.2.1 Study area

This study occurred within 34 northern hardwood stands across Dickinson, Iron, Marquette and Menominee counties in the Western Upper Peninsula of Michigan (Figure 2.1). Stands were owned by Plum Creek Timber Company Inc. (PCT), GMO Renewable Resources Inc. (managed by American Forest Management Inc. (AFM)), and the State of Michigan and had been selection harvested from 2003 to 2007. The study area corresponds with that for the ongoing Western Upper Peninsula Economic-Ecological Modeling Project (Laurent et al 2005; LeBouton et al 2005; Racevskis and Lupi 2006; Millington et al 2009 *in review*). This area was selected for the domination of forest cover, the relative absence of agriculture and urban or suburban developments, and the natural variation in deer densities and snow depth (Doepker et al 1994; Shi et al 2006).

Northern hardwood forests are found throughout the area on upland topography, such as drumlins, created by glacial activity and coniferous forests are prevalent in lowland areas. Aspen and mixed upland cover types are also present. Coniferous forests are composed of mixes of northern white cedar (*Thuja occidentalis* L.), black spruce (*Picea mariana* (Mill.) Britten & et al.), tamarack (*Larix laricina* (Du Roi) K. Koch) and balsam fir (*Abies balsamea* (L.) Mill.) and northern hardwood forests are dominated by sugar maple (*Acer saccharum* Marsh), with various components of American basswood (*Tilia americana* L.), yellow birch (*Betula alleghaniensis* Britton), red maple (*Acer rubrum* L.), white ash (*Fraxinus americana* L.) and other minor species including eastern hemlock and white pine.

Stands were located within ecoregion sub-sections VIII.3.1 (loamy ground moraines and drumlin ridges), VIII.3.2 (poorly drained outwash plains), IX.1 (steep bedrock knobs, outwash plains and sandy ground moraines) and IX.3.2 (irregular ice-disintegration topography) (Albert 1995). Section VIII is underlain by Cambrian-age sandstone and Paleozoic limestone, shale and dolomite whereas section IX is underlain by highly resistant igneous and metamorphic bedrock of the Precambrian Shield.

Annual snow fall varies from 161 cm in the southern portion of the Western Upper Peninsula to 434 cm in the northern portion (National Climatic Data Center 2009). Snowfall is higher in the northern parts of the Upper Peninsula due to lake-effect snow that develops when cooler air masses from the north move over the warmer waters of Lake Superior (Jerome 2006).

2.2.2 Field methods

Six seedlings of hemlock, white pine and white spruce were planted in ten harvest gaps at each stand for a total of 2,040 seedlings per species in November 2007. Hemlock seedlings were the tallest (mean 34.3 cm, stdev 7.1 cm) followed by white pine (26.7 cm, 7 cm) and white spruce (20.8 cm, 4.9 cm). Hemlock and white spruce were two year old containerized seedlings and white pines were two year old bare root seedlings. If lowland conifer stands could be identified in the surrounding landscape, gaps were selected at various distances from the hardwood-conifer edge. The planted seedlings were not individually marked so as not to attract or deter deer, but within gaps they were planted in straight lines and maps were made of the orientation of gaps within stands to facilitate relocation.

Stands were revisited to monitor browse damage and perform pellet surveys from late April to early May 2008 after snow melted and before cover of spring ephemerals would hinder relocation of planted seedlings. Browse damage for each hemlock seedling was qualitatively classified into one of five categories: no browsing (0), light browsing (1), moderate browsing (2), heavy browsing (3) and complete removal of needles (4). White pine and white spruce seedlings were marked as browsed or unbrowsed because natural variation in the size and branching patterns of the seedlings made it difficult to consistently categorize browse damage. Browse damage caused by cottontail rabbits (*Sylvilagus floridanus* J. A. Allen) or snowshoe hares (*Lepus americanus* Erxleben) was possible, but likely negligible. Rabbits browse minimally on hemlock (Todd 1927; Hough 1949), white pine and spruce (Swihart and Yahner 1983), and hare browse preference is only moderate for white pine and low for spruce and hemlock (Telfer 1972).

To estimate stand-level winter deer density, pellet groups were counted within ten 50 m by 4 m transects oriented in an hour glass shape (LeBouton et al 2005) (Appendix B, Section B.1). A handheld GPS unit was used to determine the UTM Northing and Easting for the center of the pellet surveys. Transects were double counted with different observers to improve accuracy (Jenkins and Manly 2008). The mean pellet group counts from all ten transects were used to calculate deer density following the methods of Hill 2001 (Appendix B, Section B.1). Visible pellets were those above leaf litter deposited in November 2007, so the estimate of deer density corresponds to deer presence in the late fall, winter and early spring months. I term the estimate "winter deer density" although deer depositing fecal pellets in northern hardwood stands likely did so while migrating between summer and winter ranges (i.e. in November and April).

Pellet groups were also counted within one 10 m by 4 m transect located parallel to the planting lines through the center of each planted gap. Pellet groups counted along these transects were not incorporated into the stand-level deer density estimate. Gap pellet group counts (PGC) were used as estimates of fine-scale differences in deer-use of the planted gaps. A deer has a higher chance of defecating in an area where it spends more time; however, the absence of pellet groups does not necessarily correspond to the absence of deer-use. Gap-PGC were not converted into deer densities because they were quantified in such small areas that they could not reasonably be scaled up to a larger area.

A subset of 19 stands was revisited in late April and early May 2009 to reassess browse damage. Eleven stands were selected because percentage of hemlock seedlings severely browsed (category 3 or 4) was <50% in 2008 and eight stands were selected because distance to lowland conifer (DLC) estimates could be obtained for them (DLC could also be found at three stands selected for hemlock browse criteria). Hemlock seedlings were only reassessed at stands with low 2008 browse pressure because severe browse damage made relocation difficult elsewhere. Seedlings with completely desiccated foliage were noted as was their browse status. White spruce seedling browse status was not reassessed in 2009 because browse was infrequent the first year.

Distance to lowland conifer (DLC) could only be determined for thirteen stands due to incomplete stand-level data across the study area. At these stands a Trimble® Asset Surveyor™ model TSC1 GPS receiver and datalogger system with built in real-time differential correction capabilities was used to determine the location of each planted gap. GPS locations were not determined for four gaps at one stand due to battery failure. Distance to lowland conifer for each gap was determined using ERSI ArcMap

v9.2 and digitized stand-level data provided by MDNR, AFM and PCT. Although the Integrated Forest Monitoring, Assessment and Prescription (IFMAP) project provides forest classification for the entire Upper Peninsula (Donovan 2005), its accuracy has been challenged even for distinguishing conifer and deciduous cover types (Linden 2006).

The number of weeks from November 1st 2007 to April 30th 2008 when the snow depth at each stand was deeper than 40 cm was found from daily 1-km resolution maps created by the National Snow and Ice Data Center's Snow Data Assimilation System (SNODAS) (Barrett 2003; NOHRSC 2004). Deer often avoid areas with snow depths greater than 40 cm (Poole and Mowat 2005) because it hinders their movement (Kelsall 1969), and snow depths approaching this threshold can initiate their migration to winter range (Tierson et al 1985). This depth also corresponds closely with the 90th percentile height of planted hemlock seedlings (41.5 cm). The estimate represents the number of weeks when snow depth was prohibitive to deer movement and provided cover for planted seedlings.

2.2.3 Statistical analysis

The goals of this study were to determine browse damage on planted conifer seedlings, quantify relationships between deer densities, deep snow weeks (DSW) and DLC and determine their effects on browse pressure. Variation in the percentage of browsed white spruce was low within and between stands, so analysis focused on the percentage of white pine and hemlock seedlings browsed at the stand-level and at the gap level. Since almost all hemlock seedlings showed signs of browse, hemlock seedlings were classified into two categories: un-browsed / minimally browsed (browse category 0,

1 or 2) and severely browsed (category 3 or 4). Hereafter, "browsed" is used to refer to browsed white pine and severely browse hemlock seedlings.

To test hypothesis 1, non-parametric Kendall's tau correlations were calculated between stand-level percentage of seedlings browsed in 2008 and stand-mean gap-DLC, stand-mean gap-PGC, stand deer density and stand deep snow weeks (DSW). Correlation between percent browsed in 2009 was only found with stand-mean gap-DLC because gap-PGC, deer density and DSW were only found for winter 2007-2008.

To address hypotheses 1 and 2, multilevel logistic regression models were developed for hemlock and white pine to predict the gap-level percentage of seedlings browsed in 2008 based on stand and gap-level characteristics. Models included a random stand-level intercept to account for the hierarchical structure of the data (gaps nested within stands) and to incorporate information about the clustering to produce estimates of standard errors that account for non-independence (Goldstein 1995). In order to determine the effects of differences in gap-level PGC and DLC within stands on gap-level percentage of seedlings browsed (i.e. to isolate the effects of variation in gap-level PGC and DLC within stands instead of between stands), these variables were centered on the stand-mean (Enders and Tofighi 2007).

The number of seedlings browsed in gap *i* at stand *j* (y_{ij}), out of n_{ij} seedlings relocated in 2008 was modeled as a binomial process $y_{ij} \sim \text{Bin}(p_{ij}, n_{ij})$. The percentage of browsed seedlings (p_{ij}) was a function of the inverse logit of $X_i\beta + \alpha_j$, where X_i's were gap-level covariates. The random stand-level intercept (α_j) came from a normal distribution $\sim N(\gamma_0 + Z_j\gamma, \sigma^2_\alpha)$ where Z_j's were stand-level covariates. Five models were

developed with different gap-level (Xi's) and stand-level (Zj's) covariates (Table 2.1): 1) null model (stand-level random intercept only), 2) stand deer density and DSW, 3) stand-mean centered gap-PGC and DSW, 4) stand-mean centered gap-PGC, gap-DLC and DSW and 5) stand-mean centered gap-DLC only. Variables were put on more comparable scales to improve convergence; deer density was rescaled to 10's of deer / km^2, gap-DLC was rescaled to 10's of meters and stand deer density and DSW were grand mean centered.

Models were run with WinBUGS v.1.4.3 (Spiegelhalter et al 2003) (see code Appendix C, Section C.4) through R v.2.9.1 with the package R2WinBUGS (Sturtz et al 2005) (see code Appendix C, Section C.5). Three parallel chains with dispersed randomly selected starting values were run for 40,000 iterations with a burn-in of 10,000 and a thinning rate of 5. Models were run with a uniform prior (range 0-100) for the standard deviation of the random stand-level intercept. The random intercept standard deviation was insensitive to prior specification (Appendix B; Section B.4). A noninformative prior distribution (Normal~(μ=0, σ^2=10,000)) was used for gap-level and stand-level coefficients (Clark 2007; Bolker et al 2009).

Gap-level percentages of seedlings browsed were overdispersed as is often the case with count data used in logistic regression (i.e. variance is greater than explained by the model) (Gelman and Hill 2007). However, the random stand-level intercept helped account for the overdispersion in the data. Pearson residuals were closer to a standard normal distribution N~(μ=0, σ^2=1) with the inclusion of a stand-level random effect (N~(-0.01, 1.37) vs ~N(0.00, 2.66) without stand-level random effect for pine and N~(0.01, 1.64) vs N~(0.02, 2.99) for hemlock null models).

Deviance Information Criterion (DIC), a method of assessing model performance in terms of fit and complexity based on the posterior mean deviance (-2 × log(likelihood)) and the effective number of parameters (Spiegelhalter et al 2002), was compared between models to determine if predictor variables improved model performance. A decrease in DIC by 5 or more indicates support for better model performance.

Convergence was diagnosed using the R package coda (Plummer et al 2009) with the Gelman-Rubin diagnostic and the Raferty-Lewis diagnostic. All models showed strong evidence of convergence (Appendix D, Tables D.9 and D.10).

2.3 Results

2.3.1 Summary of gap- and stand-level variables

The number of deep snow weeks (DSW) varied from 0 to 12.6 (Table 2.2) and was negatively correlated with stand-mean gap-PGC and positively with Northing (Table 2.3). Stand-mean centered gap-PGC varied from 4.1 pellet groups less than the stand mean to 10.9 groups more than the stand mean. Stand-mean centered gap-DLC varied from 161 m less than the stand mean to 156 m more than the stand mean. Non-centered gap-PGC and DLC were not significantly correlated, but stand-mean centered gap-PGC and DLC were positively correlated (Figure 2.2). Stand-level deer density estimates ranged from 4.1 to 64.5 deer / km^2 and were not correlated with Northing or DSW.

2.3.2 Percentage browsed varied between species and increased over time

Over 97% of planted seedlings for each species were relocated in 2008 (Table 2.4). Two spruce, eight white pine and 15 hemlock seedlings were found pulled out of the ground, so some seedlings may have been completely removed from the gaps by deer.

Percentage of seedlings browsed varied by species (Kruskal-Wallis $\chi^2 = 86.8$, p-value < 0.001), with browsing lowest on white spruce, intermediate on white pine and highest on hemlock (Figure 2.3). Over winter 2007-2008, 92% of hemlock, 30% of white pine and 2% of white spruce seedlings were browsed (Table 2.4). Sixty percent of hemlock seedlings were severely browsed (category 3 or 4).

In 2009, relocation of seedlings was more difficult, likely due to increased incidence of browse and death from apparent desiccation (Table 2.5). In 2009, 9% of hemlock and 21% of white pine relocated had completely desiccated foliage. Percentage of seedlings browsed for both white pine and hemlock increased at all resurveyed stands from 2008 to 2009. Percentage of hemlock seedlings severely browsed increased from less than 50% to over 50% for all but one resurveyed stand between spring 2008 and spring 2009, and increased to as high as 96% at one stand.

2.3.3 Deer density, deep snow weeks, deer gap-use and distance to lowland conifer affect stand-level percentages of browsed seedlings (H1)

Stand deer density estimates were positively correlated with the percentage of hemlock seedlings browsed ($p<0.10$) (Figure 2.4), but not with percentage of pine seedlings browsed (Figure 2.5). The impact of deer on percentage of severely browsed hemlock was nonlinear, with percentage browsed rising rapidly with increasing deer density. One stand was the exception with high estimated deer density (38 deer / km^2) and low browse pressure (13%), potentially because there were 9 weeks of deep snow at this stand. Stand average gap-PGC (related to deer gap-use) was not correlated with hemlock browse, but showed a similar pattern to the relationship between deer density and percent severely browsed hemlock. Stand average gap-PGC was positively correlated

with white pine percent browsed. Percentages of planted hemlock and white pine browsed were negatively correlated with DSW. Hemlock browsing was greater than 45% at all stands where DSW was less than 8, but as low as 3% where DSW was greater. Stand-level percentages of seedlings browsed for both species were negatively correlated with stand average gap-DLC. This relationship strengthened between 2008 and 2009 for white pine.

2.3.4 Deep snow weeks, deer gap-use and distance to lowland conifer affect gap-level percentages of browsed seedlings (H1 and H2)

Stand deer density did not affect gap-level percentages of seedlings browsed for either species (Model 2, Table 2.6). In contrast, the gap-level percentage of hemlock and white pine seedlings browsed decreased with increasing DSW and increased with increasing stand-mean centered gap-PGC (Model 3). Compared to the null model (Model 1), inclusion of snow and gap-PGC improved model performance for hemlock and marginally for white pine. However, differences in predicted percentages between Model 3 and the null model (Model 1) were very minor for both species (Figure 2.6).

Distance to lowland conifer and DSW for both species, and gap-PGC for pine, were unrelated to percentage of seedlings browsed for the subset of stands where DLC could be quantified (Model 4, Table 2.7). In the univariate model with DLC (Model 5), increasing stand mean-centered gap-DLC corresponded to increased gap-level percentages of seedlings browsed for hemlock, but not for pine.

Based on simulations using parameters from the model with mean-centered gap-DLC and stand DSW (Model 3), increasing the number of DSW from 6.6 (the average observed) to 7.6 decreased the mean predicted percentage of severely browsed hemlock

seedlings in a gap by 2%, and the percentage of browsed white pine by 1% (Table 2.8). Larger decreases in the percentages were predicted (15% for hemlock and 8% for white pine) when number of DSW increased from 6.6 to 12.6 (the maximum observed). Increasing the gap-PGC by one over the stand-mean increased the predicted percentage of severely browsed hemlock by 4% and the percentage of browsed white pine by 1%. Larger increases in the percentage (24% for hemlock and 14% for pine) were predicted when the gap-PGC increased by eleven over the stand-mean. For all simulations, the 95% quantiles for the predictions were large due to uncertainty in the stand-level random intercept.

Based on simulations using parameters from the model with only DLC (Model 5) for hemlock, the mean gap-level percentage of severely browsed seedlings showed no significant increase if gap-DLC increased 10 m from the stand-mean. If gap-DLC increased 150 m from the stand-mean, the probability of severe browse increased from 56% (95% quantiles for the predictions: 3-99%) to 66% (5-99%).

2.4 Discussion

A high percentage of planted hemlock and white pine seedlings, both deer browse-preferred winter foods (Blouch 1984), were browsed over a two year period in northern hardwood forests. White spruce, a last resort forage species for deer (Blouch 1984; Dumont et al 2005), was only minimally browsed. Percentages of browsed seedling were negatively related to abiotic stand characteristics (i.e. length of time when snow depth prohibits deer movement and shelters seedlings) and local landscape context (i.e. distance to lowland conifer).

2.4.1 Hypothesis 1: the percentage of browsed seedlings will be higher at stands where snow depth and distance to lowland conifer are lower and winter deer density is greater

Stand-level percentage of hemlock seedlings severely browsed was positively, but non-linearly, related to estimated deer density. Non-linear relationships between deer density and browse impacts have been reported for hemlock and some hardwood species (Rooney and Waller 2003; Eschtruth and Battles 2008). Variability in deer density estimates from the pellet count technique (Langdon 2001) may contribute to the relative weakness in the relationship between browse pressure and deer density. The relationship between stand-level percentage of white pine browsed and deer appears sensitive to pellet-count transect location and length; it was not significant with stand-level deer density estimated from pellet counts observed along long transects radiating from a random center but was positive with stand-average gap-pellet group counts observed along short transects in areas with expected deer use. Both transect length and distribution of transects are important considerations when designing fecal pellet surveys (Neff 1968). Counting pellets in patches where deer use may be higher (i.e. in harvest gaps with greater forage availability) would likely over-estimate stand deer densities, but might assist with monitoring relationships between relative deer density and herbivory at a finer spatial scale.

Stand-level percentages of white pine and hemlock seedlings browsed decreased with increasing length of deep snow weeks and stand-average gap-distance to lowland conifer. Browse pressure could be lower at stands where snow depth is > 40 cm for a longer portion of the winter because: 1) snow provides cover to seedlings from deer, 2) many deer migrate south to winter range where snow depth is lower (Verme 1973;

Tierson et al 1985; Blouch 1984; VanDeelen 1998) and 3) deep snow and winter severity cause deer to alter their foraging behavior and habitat selection to conserve energy (Ozoga and Verme 1970; Pauley et al 1993; Dumont et al 2005; Poole and Mowat 2005).

Both deep snow weeks and deer density varied across northern hardwood stands and had the anticipated relationships with stand-level percentage of seedlings browsed, but were not negatively correlated with each other as was expected. I found a negative relationship between deer density and snow depth in this region across a larger study area that included more stands and extended farther north (Chapter 1). The latitudinal gradient of the stands for this planting study and the number of stands measured may not be great enough to capture the inverse relationship between deer density and snow fall, given high variability in pellet count derived estimates of deer density (Langdon 2001).

Unlike deer density, stand-average gap-pellet group counts (i.e. deer gap-use) were negatively correlated with deep snow weeks. It is possible that the relationship between snow and deer was captured by counting pellet groups in gaps because deer might avoid gaps where snow depth is greater due to lower interception of snow by tree branches.

The observed relationship between stand-level browse and distance to lowland conifer support previous findings that deer density is lower in stands farther from lowland conifer stands (Millington et al 2009 *in review*). The correlation between deer density estimates and stand-average gap-distance to lowland conifer was not significant in this study, likely because distance to lowland conifer could only be determined for thirteen stands.

2.4.3 Hypothesis 2: percentage of seedlings browsed will increase with proximity to lowland conifer where deer-use is higher

Browsing of hemlock and white pine seedlings increased with deer gap-use (stand-mean centered gap-pellet group counts) and with gap distance to lowland conifer (stand-mean centered gap-level distance to lowland conifer) for hemlock, but not pine. Deer gap-use was positively correlated with gap distance to lowland conifer. The later findings are contrary to the hypothesis that deer browse would be lower in gaps farther from lowland conifer. Deer confinement to conifer stands increases with winter severity (Ozoga and Gysel 1972), so deer foraging may not have been limited to gaps near conifer stands during this fairly average winter (MDNR 2008). Also, deer disperse farther from habitat edges when highly-browse preferred species are available (Williamson and Hirth 1985). Within stands, planted gaps may not have been located sufficiently far from each other to infer small-scale difference in deer use of a stand. Daily winter movement for a deer can be 341 to 1,650 meters (Heezen and Tester 1967) and the farthest distance between gaps within a stand was 730 m (average maximum distance was 370 m). Within one day, one deer could have visited all gaps at a stand.

The relationships between browse, gap distance to lowland conifer and deer gap-use could also be an artifact of the uncertainty in the gap pellet group counts and the small sample size for gap distance to lowland conifer. Gap pellet group counts were quantified in small areas and was not a perfect estimate of deer use of a gap (i.e. there were no gap-pellet groups in 40% of gaps where there was evidence of deer browse).

2.4.4 Management implications

The efficacy of efforts to restore hemlock and white pine in northern hardwood stands with replanting may be minimal in areas with high deer densities (> 15 deer / km^2). Hemlock seedlings will not grow into larger size classes unless protected from white-tailed deer. White pine browse was relatively low the first year of planting, but increased to fifty percent at re-surveyed stands after the second year. Many white pine seedlings desiccated after two winters and one growing seasons, often independent of browse damage, so planting containerized seedlings or taller saplings may increase white pine survival. Planting more seedlings per acre may also satiate deer browse, however, this comes at a higher cost and risk. Last-resort browse species, such as white spruce or balsam fir (Blouch 1984; Dumont et al 2005) may be the only mesic conifers that can successfully reestablish in areas with high deer density.

Seedling browse was lower at stands with lower deer densities (< 15 deer / km^2) that were farther from lowland conifer (>150 m) and covered by deep snow for a longer portion of the winter (> 6 weeks). Using these criteria to select planting sites may improve success. Snow cover will only confer protection to small seedlings, so it may also be necessary to plant seedlings on microsites that serve as refugia from deer, such as slash piles or tip-up mounds (Grisez 1960; Krueger and Peterson 2006), to use plastic tree shelters (Ward and Stephens 1995), or to plant larger seedlings with bud caps (Saunders and Puettmann 1999). Seedlings may need protection until they reach 125 cm, past which point terminal leader browsing by deer decreases (Saunders and Puettmann 1999).

Quality deer management that maintains populations in balance with their habitat (Frawley 2005) could benefit mesic conifer restoration efforts and increase the abundance

of naturally regenerating saplings (Chapter 1). This management approach could strike a balance between deer and forest resources enjoyed by people in the Western Upper Peninsula, and improve habitat for other species such as birds that associate with conifer species and require vertical stand structure provided by seedlings and saplings. The percentage of severely browsed hemlock seedlings rose rapidly with estimated deer densities, suggesting that if the goal is to restore browse-preferred conifer species to the landscape, intensive hunting may be necessary to reduce deer populations below 15 deer / km^2. Hunting may be more effective at reducing deer densities in the southern portion of the Western Upper Peninsula if permitted during the winter when deer yard together.

2.5 Conclusion

Mesic conifers are important sources of biodiversity in northern hardwood forests, providing food and habitat structure for birds, especially warbler species, and white-tailed deer (Kendeigh 1945; Blouch 1984; Green 1992; Patmos 1995). Intense logging and poor regeneration have reduced the representation of mesic conifers across the Great Lakes Region. The acreage of hemlock-dominated mixed forests and white pine-mixed forests are estimated to have declined over eighty five percent from circa 1800 to 2000 in the Western Upper Peninsula of Michigan (MDNR 2006). Unfortunately, restoration of white pine and hemlock in areas with high deer density seems unlikely.

Browse pressure on seedlings in northern hardwoods stands was affected by deer density, local landscape context (i.e. distance to lowland conifer) and snow depth. The percentage of hemlock seedlings browsed rose rapidly with stand deer density, highlighting the importance of maintaining deer densities below a threshold level if the goal is to restore browse preferred species. The relationship between browse pressure and

estimated deer density provides evidence that the pellet-count method can be used to predict relative browse pressure based off relative estimates of deer density. Variability was observed in the relationships of the pellet count estimation techniques (deer density vs deer gap-use) with browse pressure, distance to lowland conifer and deep snow weeks, indicating that the ability of the pellet count method to estimate deer densities, or relative deer densities, is sensitive to sample method.

Deer herbivory can eliminate browse-preferred species from seedling and sapling layers established by natural regeneration or planting. An understanding of factors that affect deer distributions and browse habits are important for developing methods to restore browse-preferred species to landscapes with high deer densities. When studying the effects of deer on seedling and sapling layers, using fecal pellet counts in conjunction with observations of browse on planted or naturally regenerating seedlings may improve the inferences made.

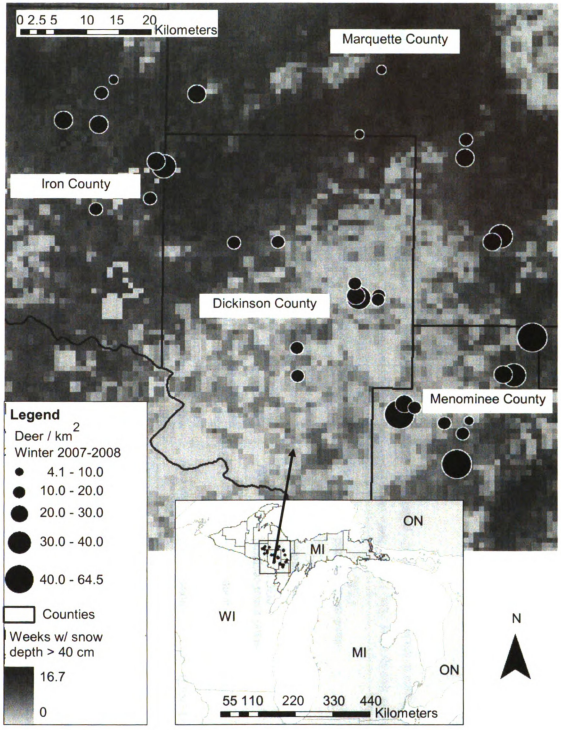


Figure 2.1. Location of stands and estimated winter 2007-2008 deer density overlaid the number of weeks from November 2007 to April 2008 predicted to have snow depth > 40 cm. MI=Michigan, WI=Wisconsin, USA. ON=Ontario, Canada.

Table 2.1. Multilevel logistic regression models used to explore the effects of gap- and stand-level variables on percentage (p_{ij}) of white pine or hemlock seedlings browsed in gap *i* at stand *j* in 2008. The number of seedlings browsed is y_{ij}, the number of seedlings relocated is n_{ij}, and the random stand-level intercept is α_j.

Model specification	Model	Gap-level variables (Xi)	Stand-level variables (Zj)	Explanation
$y_{ij} \sim Bin(p_{ij}, n_{ij})$ $p_{ij} = logit^{-1}(X_i\beta + \alpha_j)$	1 (Null)	none	γ_0 only	Null model used as baseline for comparison of model fit. Separate null models were developed with all gap observations and for the subset of observations with gap-DLC measurements.
$\alpha_j \sim N(\gamma_0 + Z_j\gamma, \sigma^2_\alpha)$	2	none	Deer and DSW	Explores the impact of stand deer density and deep snow weeks on percentage of seedlings browsed (H1)
	3	stand-mean centered PGC	DSW	Explores the impact of deer gap-use within a stand and stand deep snow weeks on percentage of seedlings browsed (H1 and 2)
	4	stand-mean centered PGC and DLC	DSW	Explores the impact of deer gap-use and distance to lowland conifer within a stand and stand deep snow weeks on percentage of seedlings browsed (H1 and 2)
	5	stand-mean centered DLC	γ_0 only	Explores the impact of DLC within a stand without consideration of PGC with which stand-centered DLC was correlated (H2). DSW was not included in Model 5 because it was not significant in Model 4.

Deer = estimated stand deer density (deer / km^2) winter 2007-2008; DSW=deep snow weeks (number of weeks from November 2007 to April 2008 with snow depth > 40 cm); DLC= distance to lowland conifer; PGC= pellet group count (the number of deer fecal pellets found within a 40 m^2 area in a planted harvest gap).

Table 2.2. Summary of gap- and stand-level variables: Average (Ave), median (Med), standard deviation (Stdev), minimum (Min), maximum (Max) and number of gap or stand-level observations (N obs).

	Ave	Med	Stdev	Min	Max	N obs
Gap-level						
DLC (m)	245.2	187.3	187.5	63.24	886.0	126
Stand-mean centered gap-DLC	0.0	3.7	52.7	-161.3	156.4	126
PGC (pellets groups / gap transect)	1.5	1	2.1	0	16	338
Stand-mean centered gap-PGC	0.0	-0.2	1.7	-4.1	10.9	338
Stand-level						
Deer density (deer/km^2)	22.1	17.7	14.0	4.1	64.5	34
DSW (weeks)	6.6	8.3	4.9	0	12.6	34

DLC= distance to lowland conifer in meters, PGC= pellet group count (the number of deer fecal pellets found within a 40 m^2 area in a planted harvest gap), DSW=deep snow weeks (number of weeks from November 2007 to April 2008 with snow depth > 40 cm).

Table 2.3. Kendall's tau rank correlation between gap- and stand-level variables. Comparisons between gap-level and stand-level variables use stand-averages for non-centered gap-level variables to comply with independence assumptions. UTM Easting and Northing values were taken from the center of the deer pellet transects.

	Northing	Easting	DSW	Deer density	Gap-PGC
Gap-DLC	0.31	-0.51**	0.12	-0.28	0.06§
Gap-PGC	-0.16	0.04	-0.32**	0.16	
Deer density	-0.09	0.10	-0.07		
DSW	0.56**	-0.18			
Easting	-0.40**				

**p-value < 0.05, *p-value < 0.10

§stand-mean centered gap-PGC and stand-mean gap-DLC are significantly positively correlated (Kendall's τ=0.24, p-value < 0.001).

Gap-DLC= distance to lowland conifer from gap centers, DSW=deep snow weeks (number of weeks from November 2007 to April 2008 with snow depth > 40 cm), gap-PGC= pellet group count (the number of deer fecal pellets found within a 40 m^2 area in a planted harvest gap).

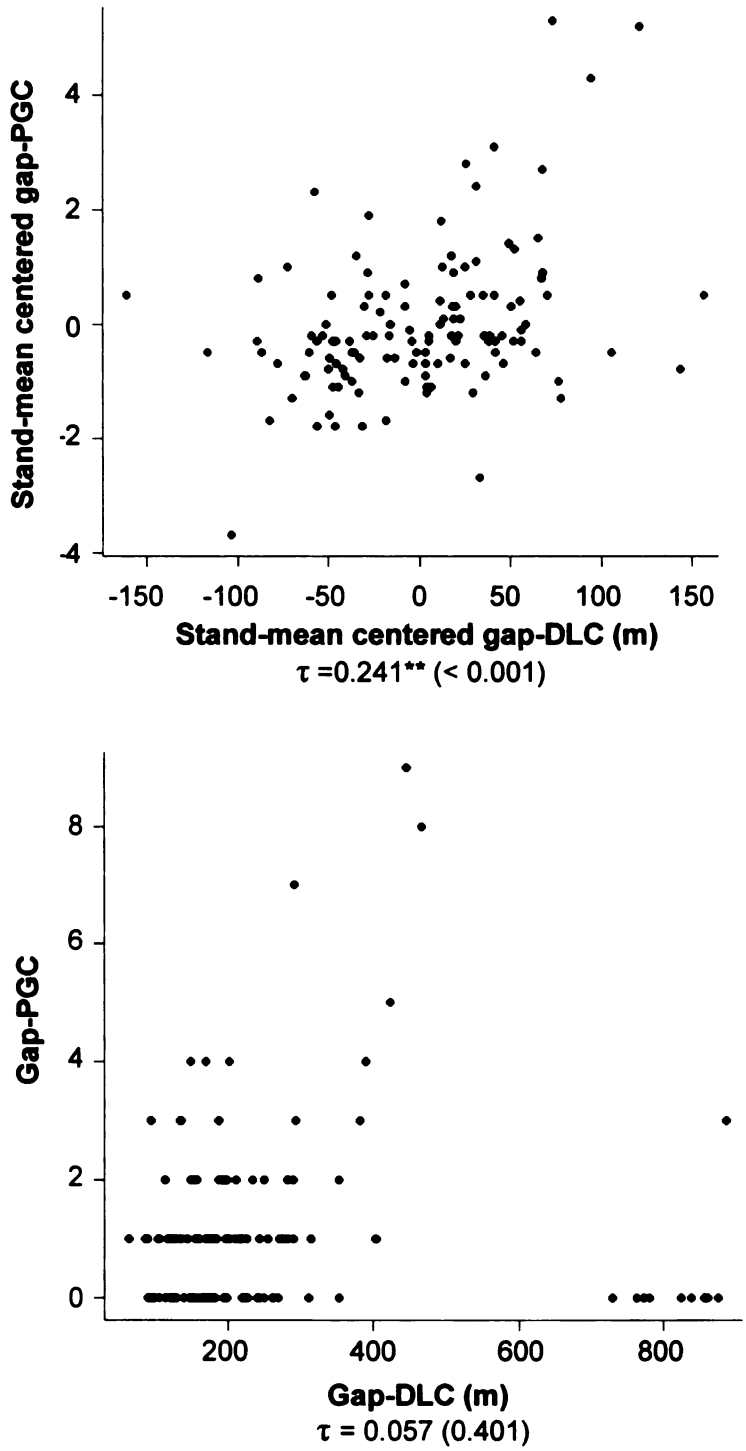


Figure 2.2. Correlation between stand-mean centered gap distance to lowland conifer (DLC) and stand-mean centered gap pellet group counts (PGC). Lower image shows the correlation between the non-centered estimates. Non-parametric Kendall's tau rank correlations (τ (p-value)) are presented.

Table 2.4. Average height (stdev), number seedlings found (N.found), percent found (of 2040 seedlings / species planted), browsed and severely browsed (browse category 3 or 4 for hemlock only) for planted seedlings across all gaps and stands in spring 2008.

Species	Average height (cm)	N. found	% found	% browsed	% severely browsed
Hemlock	34.3 (7.1)	1982	97.2	92.4	60.3
White pine	26.7 (7.0)	2014	98.7	29.5	
White spruce	20.8 (4.9)	2018	98.9	1.8	

Table 2.5. Number of seedlings found (N.found) and percent found, browsed, severely browsed (hemlock only), desiccated and percentage of desiccated seedlings showing evidence of browse for hemlock at the same 11 stands and for pine at the same 19 stands visited in both spring 2008 and 2009. Hemlock seedlings were only resurveyed in 2009 at stands where more than 50% of the seedlings had not been severely browsed in 2008.

	2008	2009
Hemlock		
N. found	652	609
% found	98.8	92.3
% browsed	81.7	95.6
% severely browsed	28.7	75.9
% desiccated	0	9.2
% desiccated browsed		85.7
White pine		
N. found	1126	1015
% found	98.8	89.0
% browsed	19.0	51.6
% desiccated	0	20.6
% desiccated browsed		30.2

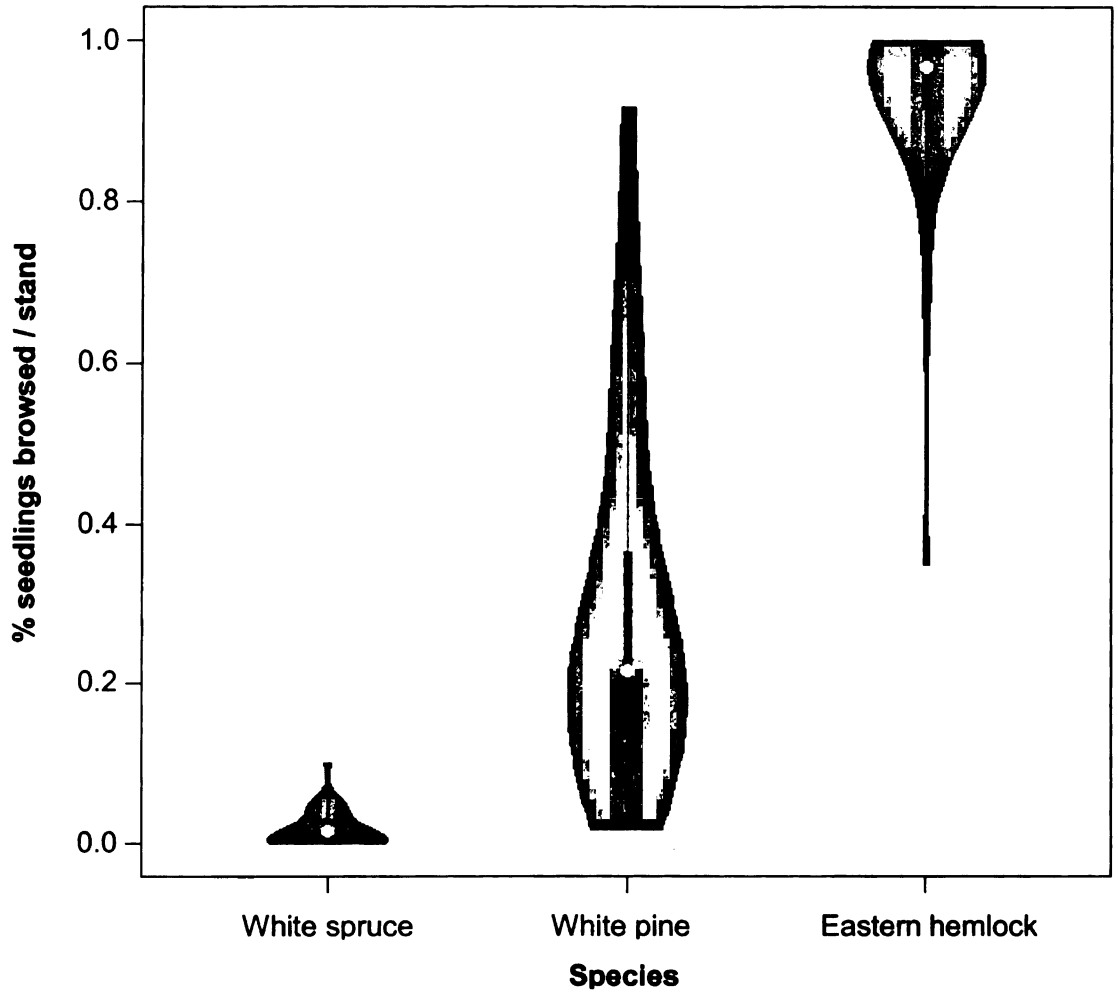


Figure 2.3. Percentage of seedlings browsed by species / stand based on browsed vs not-browsed categorization. Distributions were all significantly different from each other based on Wilcoxon signed-rank test with bonferroni adjusted p-value. Violin plots show distribution of values and median (white dot), interquartile range (thick vertical line) and range of values 1.5 * IQR (thin vertical line).

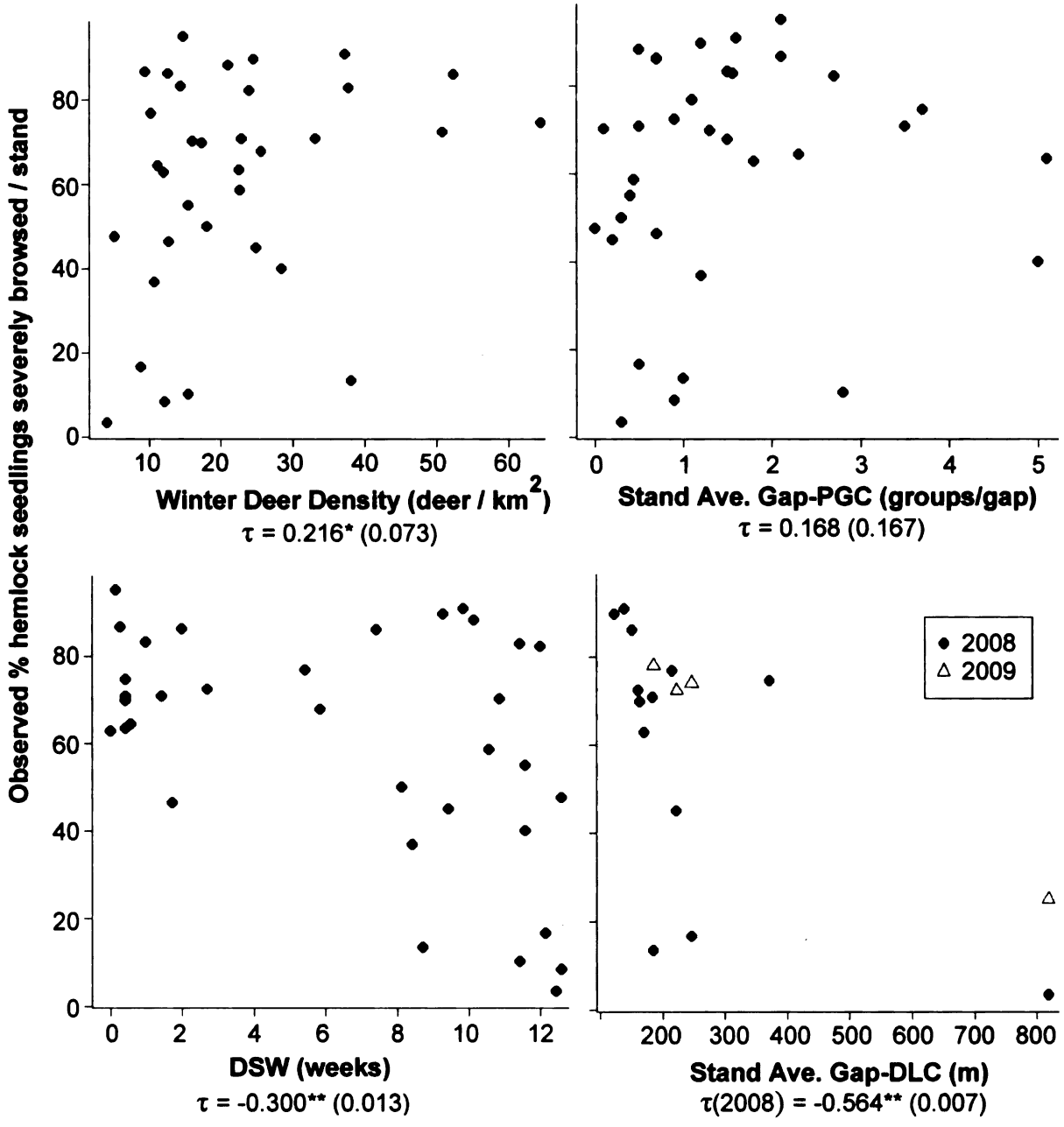


Figure 2.4. Observed percentages of hemlock seedlings severely browsed / stand in 2008 (and 2009 in the distance to lowland conifer (DLC) plot only) versus estimated winter deer density, stand average pellet group count (PGC), deep snow weeks (DSW), and stand average gap-DLC. Non-parametric Kendall's tau rank correlations (τ (p-value)) are presented. τ was not calculated for 2009 observed percentage browsed versus DLC due to low sample size (n=4).
**p-value < 0.05, * p-value < 0.10

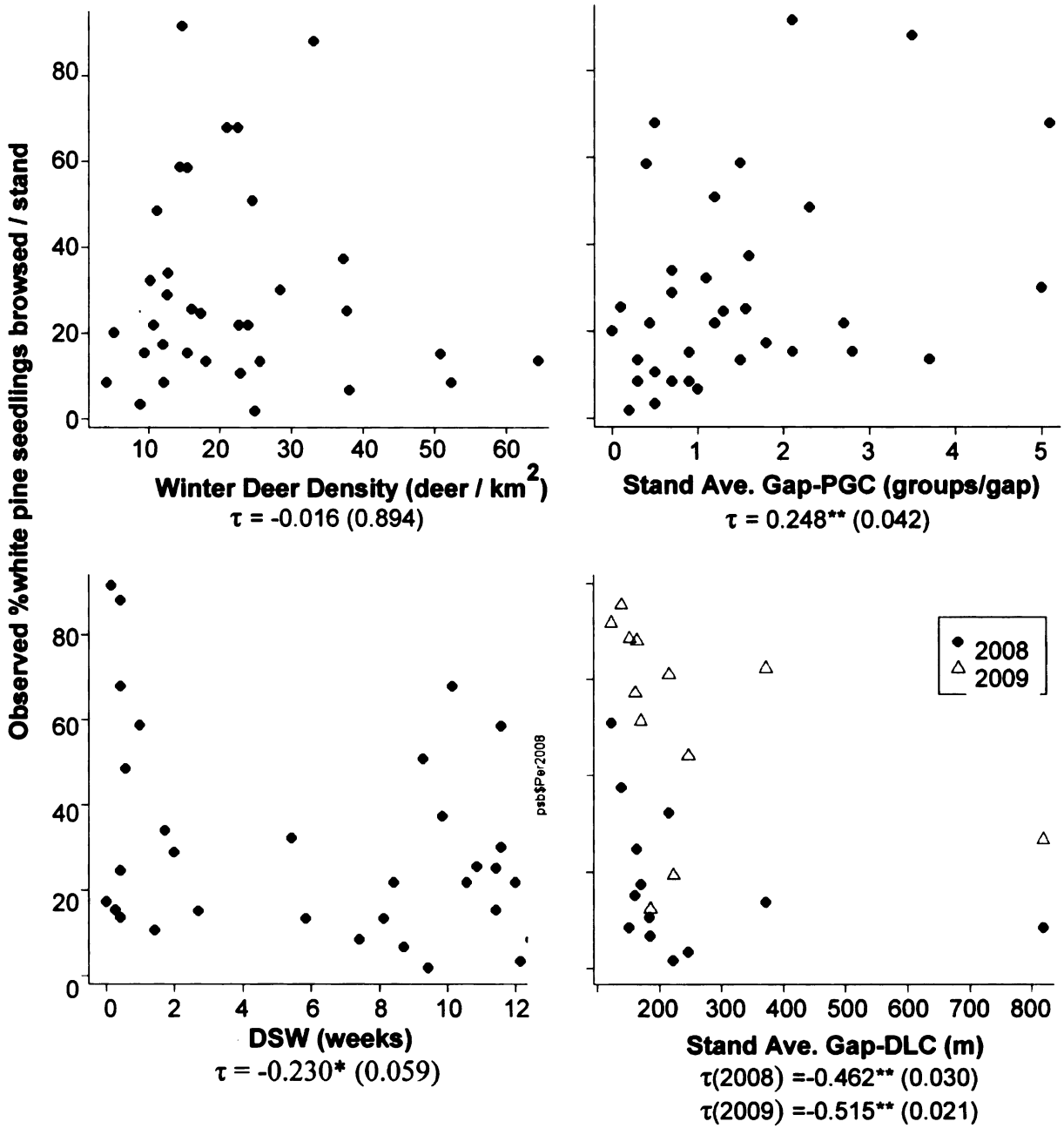


Figure 2.5. Observed percentages of pine seedlings browsed / stand in 2008 (and 2009 in the distance to lowland conifer (DLC) plot only) versus estimated winter deer density, stand average pellet group count (PGC), deep snow weeks (DSW), and stand average gap-DLC. Non-parametric Kendall's tau rank correlations (τ (p-value)) are presented.
**p-value < 0.05, * p-value < 0.10

Table 2.6. Multilevel logistic regression models predicting the gap-level percentage of hemlock seedlings severely browsed or a white pine seedling browsed in 2008: mean parameter estimates and 95% credible interval from posterior distributions. Deer and DSW were grand mean centered and pellets were group (i.e. stand) mean centered. Estimates are on the logistic scale, so a change of one unit in the independent variables corresponds to a change of at most β/4 on the probability scale. A decrease in DIC of 5 or more indicates improved performance for full model over the null model.

	Hemlock			White pine		
	Mean	95% CI	DIC	Mean	95% CI	DIC
Model 1: Null model			1159.84			1018.37
Intercept	0.49	-0.02 – 0.99		-1.09	-1.58 – -0.62	
Stand Stdev	1.43	1.09 – 1.89		1.35	1.02 – 1.79	
Model 2: DSW + Deer			1159.38			1017.76
Intercept	0.49*	0.03 – 0.95		-1.10*	-1.56 – -0.64	
Deer	0.24	-0.08 – 0.58		-0.13	-0.47 – 0.21	
DSW	-0.12*	-0.22 – -0.03		-0.10*	-0.20 – -0.01	
Stand Stdev	1.27	0.96 – 1.70		1.30	0.97 – 1.74	
Model 3: DSW + PGC			1133.83			1014.59
Intercept	0.50*	0.04 – 0.96		-1.10*	-1.56 – -0.64	
Pellets	0.18*	0.11 – 0.26		0.08*	0.01 – 0.14	
DSW	-0.14*	-0.23 – -0.04		-0.10*	-0.20 – -0.003	
Stand Stdev	1.31	0.99 – 1.73		1.29	0.97 – 1.71	
N gaps		338			338	
N stands		34			34	

Deer= estimated winter deer density in 10's of deer / km^2, DSW=deep snow weeks (number of weeks from November 2007 to April 2008 with snow depth > 40 cm), PGC= pellet group count (the number of deer fecal pellets found within a 40 m^2 area in a planted harvest gap).

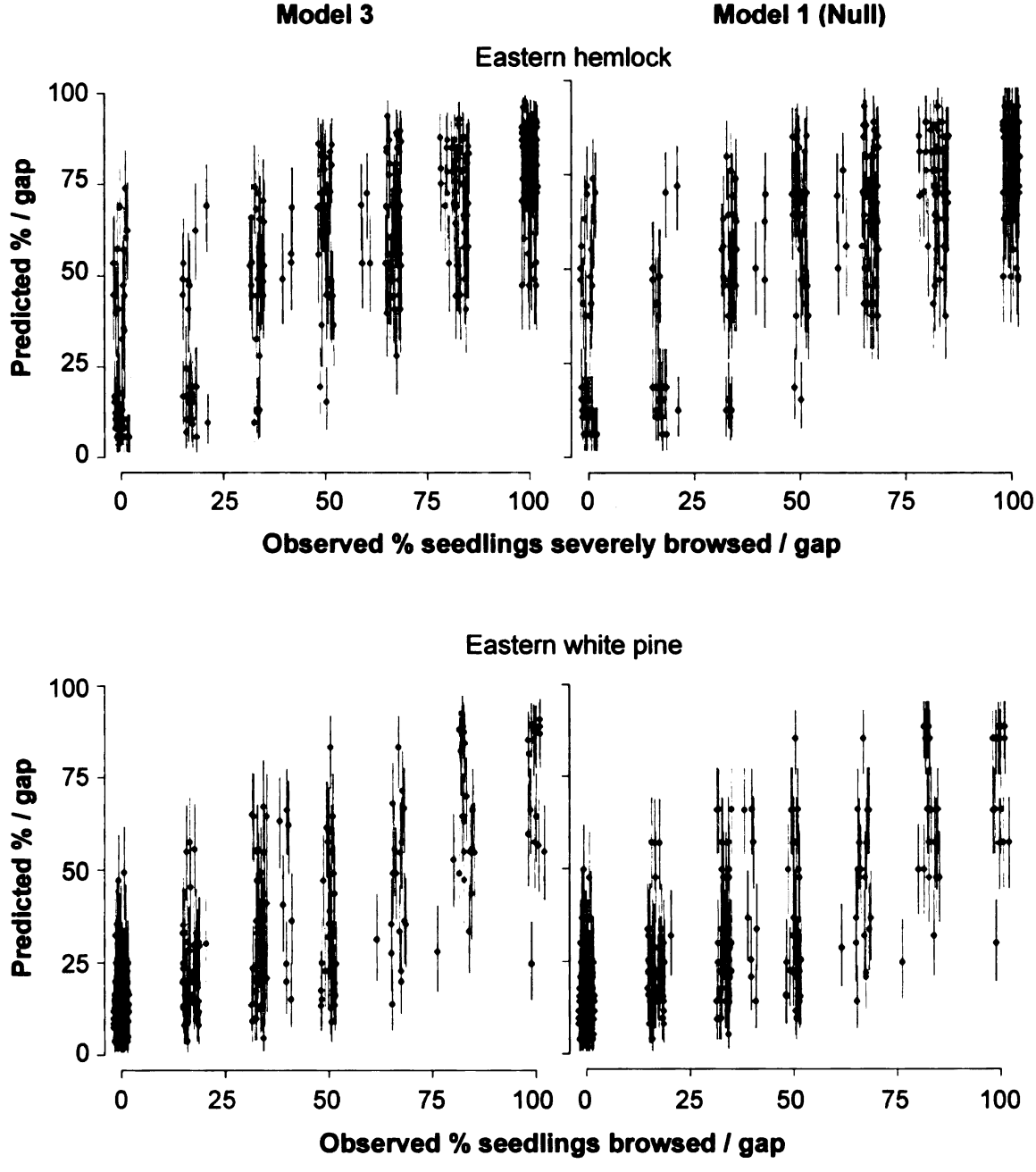


Figure 2.6. Observed percentage of hemlock seedlings severely browsed and white pine seedlings browsed / gap in 2008 versus mean posterior predicted percentages per gap and 95% credible intervals from logistic mixed models. Model 3 includes deep snow weeks and stand-centered gap-level pellet group counts as covariates and model 1 (null model) includes only an overall intercept and stand-level random effect intercept. Observed percentage on the x-axis has been jittered for visualization (random jitter is equivalent for Model 3 and Model 1 plots within species).

Table 2.7. Multilevel logistic regression models predicting the probability that a hemlock seedling was severely browsed or a white pine seedling was browsed in 2008 for thirteen stands where distance to lowland conifer was determined: mean parameter estimates and 95% credible interval from posterior distribution. DSW was grand mean centered and pellets and DLC were group (i.e. stand) mean centered. Estimates are on the logistic scale, so a change of one unit in the independent variables corresponds to a change of at most β/4 on the probability scale. A decrease in DIC of 5 or more indicates improved performance for full model over the null model.

	Hemlock			White pine		
	Mean	95% CI	DIC	Mean	95% CI	DIC
Model 1: Null model			397.18			325.29
Intercept	0.37	-0.71 – 1.42		-1.87	-2.60 – -1.19	
Stand Stdev	1.84	1.15 – 2.97		1.16	0.69 – 1.95	
Model 4: DSW + PGC + DLC			374.76			326.83
Intercept	0.36	-0.70 – 1.42		-1.92*	-2.71 – -1.18	
DLC	0.02	-0.02 – 0.05		0.02	-0.03 – 0.07	
Pellets	0.42*	0.22 – 0.63		0.06	-0.11 – 0.22	
DSW	-0.18	-0.43 – 0.06		-0.05	-0.23 – 0.12	
Stand Stdev	1.81	1.11 – 2.99		1.23	0.72 – 2.12	
Model 5: DLC			392.10			325.32
Intercept	0.37	-0.73 – 1.47		-1.88*	-2.63 – -1.18	
DLC	0.05*	0.01 – 0.08		0.03	-0.01 – 0.07	
Stand Stdev	1.87	1.16 – 3.04		1.17	0.69 – 1.96	
N gaps		126			126	
N stands		13			13	

DSW=deep snow weeks (number of weeks from November 2007 to April 2008 with snow depth > 40 cm), PGC= pellet group count (the number of deer fecal pellets found within a 40 m^2 area in a planted harvest gap), DLC= distance to lowland conifer in 10s of m.

Table 2.8. Mean predicted probability (Pr.) (95% prediction quantiles) of severe browse for hemlock seedlings and probability of browse for white pine seedlings under different gap pellet count (stand centered) and deep snow week conditions. Predictions are for an unmeasured stand based on one-to-one simulations using the posterior distribution for Model 3 parameters.

Gap pellet count (stand centered)	Deep snow weeks	Pr. of severe browse hemlock	Pr. of browse white pine
At stand mean	6.6 weeks (ave obs)	59% (10-96%)	30% (2-81%)
At stand mean	7.6 weeks (+1 week)	57% (9-95%)	29% (2-80%)
At stand mean	12.6 weeks (max obs)	44% (4-92%)	22% (1-72%)
+1 from stand mean	6.6 weeks (ave obs)	63% (12-97%)	31% (3-83%)
+11 from stand mean (max obs)	6.6 weeks (ave obs)	87% (44-99%)	45% (5-92%)

APPENDICES

APPENDIX A: Descriptions of Study Stands

Table A.1. Description of 59 study stands including average snow depth November 2007 – April 2008 (cm), county, ownership, Habitat Type, relative densities (RD) of the three most abundant overstory tree species and average stand diameter at breast height (DBH) of mature trees with dbh >20 cm, and year of harvest entry (YOE).

Stand ID	Snow Depth[a]	County[b]	Owership[c]	Habitat Type	RD[d,e]	DBH (Stdev)[d]	YOE
4	16.3	MN	PCTC	ATD-Hp	SM 93% BA 4% HM 2%	30.4 (6.4)	2005
20	18.7	DI	S. MI	ATD-Hp	SM 92% BA 5% AR 2%	27.8 (5.2)	2004
27	33.9	MA	S. MI	ATD	SM 99% BC 1% IW <1%	35.3 (10.2)	2006
34	31.1	IR	KLA	ATD-Hp	SM 85% BA 14% AR 1%	30.7 (6.9)	2002
38	31.5	IR	GMO	ATM	SM 96% YB 2% IW 2%	29.6 (6.4)	2006
803	23.3	MN	S. MI	ATD-Hp	SM 97% BP 2% YB 1%	28.5 (5.2)	2000
806	20.4	DI	GMO	AOCa	SM 97% BA 3% IW <1%	28.9 (5.2)	1999
807	22.6	MN	GMO	ATD-Hp	SM 67% BA 33% IW <1%	29.6 (6.2)	2001
808	22.2	MN	GMO	ATD-Hp	BA 54% SM 22% WA 20%	28.6 (5.9)	2000
814	19.2	DI	S. MI	AOCa	SM 79% BA 20% YB 1%	31.9 (7.6)	1999
815	33.5	DI	S. MI	ATM	SM 81% PB 10% BA 4%	30.5 (8.1)	1995
816	22.8	DI	S. MI	AOCa	SM 45% BA 37% WA 14%	29.8 (7.1)	2001
817	21.3	DI	GMO	AOCa	SM 83% BA 13% YB 4%	30.8 (7.2)	2001
818	23.1	MA	PCTC	AOCa	SM 94% BA 6% IW <1%	34.0 (7.0)	2002
819	21.2	MA	PCTC	AOCa	SM 100%	29.9 (5.7)	1999
820	48.0	MA	GMO	ATD	SM 86% YB 9% AR 4%	27.9 (5.8)	2001
821	40.5	MA	GMO	ATM	SM 85% YB 7% QA 4%	29.5 (8.6)	2002
822	43.9	MA	GMO	ATM	SM 59% BF 12% WS 10%	27.1 (5.6)	2002
823	40.8	MA	GMO	ATM	SM 79% BF 14% AR 6%	29.9 (8.7)	2003
824	31.1	MA	GMO	TMC	SM 78% YB 13% AR 4%	32.7 (9.4)	1999
825	22.6	MA	PCTC	ATD	SM 92% YB 5% RO 3%	29.3 (7.0)	2003

Table A.1. continued

Stand ID	Snow Depth	County	Owership	Habitat Type	RD	DBH (Stdev)	YOE
826	22.6	MA	PCTC	ATM	SM 97% AR 3%	26.5 (5.4)	1999
829	24.5	MA	PCTC	ATD	SM 85% BC 6% AR 6%	32.5 (6.2)	1998
832	22.4	MA	PCTC	ATM	SM 84% BA 9% AR 4%	30.8 (5.9)	2003
834	37.0	MA	S. MI	ATD	SM 81% AR 18% IW 1%	30.7 (9.1)	1993
837	35.2	IR	S. MI	AOCa	SM 69% AR 17% AE 8%	29.5 (7.8)	1998
842	28.8	MA	S. MI	ATD	SM 78% AR 20% HM 1%	33.4 (11.1)	1997
844	25.7	MA	PCTC	ATD	SM 92% AR 4% BC 4%	28.3 (5.9)	2001
847	32.2	MA	S. MI	ATD	SM 79% BC 8% BA 8%	33.6 (11.8)	2002
851	24.6	DI	S. MI	ATD	BA 65% SM 24% QA 9%	32.1 (7.0)	2000
852	22.6	DI	KLA	ATD-Hp	SM 78% BA 19% IW 3%	30.3 (8.0)	2001
1042	31.9	IR	S. MI	TMC	SM 36% AR 36% HM 22%	30.9 (9.0)	1996
1043	31.9	IR	S. MI	AOCa	SM 94% AR 3% NC 2%	30.9 (6.6)	1998
1044	30.4	IR	S. MI	AOCa	SM 95% BA 5% IW <1%	31.8 (8.8)	1995
1081	24.5	IR	S. MI	ATM	SM 77% AR 18% BA 5%	29.6 (8.0)	1996
1133	22.2	DI	KLA	AOCa	SM 78% BA 12% YB 8%	28.8 (6.4)	1999
1272	17.5	DI	GMO	ATD-Hp	SM 59% BA 33% WA 8%	32.6 (8.2)	1998
1603	37.2	IR	S. MI	AOCa	SM 43% AR 29% BC 18%	33.6 (10.9)	2002
4024	19.4	MN	PCTC	ATD-Hp	SM 79% HM 11% BA 9%	35.5 (10.3)	2000
4042	20.3	MN	PCTC	AOCa	SM 84% BA 11% NC 4%	34.6 (10.6)	1999
4052	20.5	MN	PCTC	ATD-Hp	BA 43% SM 40% WA 9%	30.3 (9.0)	2002
4082	20.6	DI	S. MI	AOCa	BA 52% SM 47% BL 1%	31.6 (6.1)	2001
4102	20.5	DI	GMO	AOCa	SM 97% BA 2% WA 1%	27.5 (6.3)	1996
4162	23.8	DI	S. MI	AOCa	SM 98% BA 2% IW <1%	33.5 (6.8)	1998
4172	16.9	DI	S. MI	ATD-Hp	SM 96% BA 4% IW <1%	32.4 (7.8)	1994
4232	29.5	MA	S. MI	ATM	SM 69% AR 18% QA 7%	30.4 (8.8)	1995

Table A.1. continued

Stand ID	Snow Depth	County	Owership	Habitat Type	RD	DBH (Stdev)	YOE
4324	35.1	MA	S. MI	ATD	SM 91% RO 6% BA 3%	29.0 (6.2)	2002
4332	36.2	MA	S. MI	ATM	SM 94% BC 4% YB 2%	33.8 (8.8)	1998
4342	29.4	MA	S. MI	ATD	SM 98% AR 1% YB 1%	32.3 (6.6)	1998
4422	22.9	MN	PCTC	ATD-Hp	SM 84% HM 8% AB 6%	27.8 (7.0)	2000
4423	22.8	MN	PCTC	ATD-Hp	SM 95% WA 4% HM <1%	29.9 (6.0)	1997
4429	22.9	MN	PCTC	AOCa	SM 84% HM 5% AB 4%	29.1 (8.1)	1999
4524	22.0	DI	KLA	ATD-Hp	SM 83% BA 15% AR 1%	30.9 (6.8)	1998
5032	15.6	DI	S. MI	ATD-Hp	SM 88% BA 11% IW 1%	34.6 (7.5)	1997
5052	16.9	DI	S. MI	AOCa	SM 94% BA 6% IW <1%	32.1 (7.3)	1995
5104	30.3	MA	S. MI	ATD	SM 97% AR 3% IW <1%	31.1 (6.7)	1998
5292	34.6	IR	S. MI	AOCa	SM 95% AR 4% BA 1%	29.1 (6.4)	1997
5314	28.4	IR	S. MI	AOCa	SM 80% BA 19% YB 1%	28.0 (5.3)	1995
5342	22.3	DI	Private owners	ATM	SM 63% BA 36% QA 1%	28.5 (5.6)	2001

[a]Snow Data Assimilation System (SNODAS) from the National Snow and Ice Data Center (NSIDC)

[b]DI=Dickinson, IR=Iron, MA=Marquette, MN=Menominee

[c]GMO = GMO Renewable Resources (managed by American Forest Management, Inc); KLA= Keweenaw Land Association, Ltd.; PCTC= Plum Creek Timber Co., Inc.; S. MI = State of Michigan

[d]Calculated for all trees with dbh >20 cm within 20 m from 2-5 non-overlapping gaps at each staqbd randomly selected from the list of all possible combinations with the most non-overlapping gaps.

[e]**AB**= American beech (*Fagus grandifolia* Ehrh.), **AE**= American elm (*Ulmus americana* L.), **AR**= red maple (*Acer rubrum* L.), **BA**= American basswood (*Tilia americana* L.), **BC**= black cherry (*Prunus serotina* Ehrh.), **BF**= balsam fir (*Abies balsamea* (L.) Mill.), **BL**= black ash (*Fraxinus nigra* Marsh.), **BP**= balsam poplar (*Populus balsamifera* L.), **HM**= eastern hemlock (*Tsuga Canadensis* (L.) Carrière), **IW**= ironwood (*Ostrya virginiana* (Mill.) K. Koch), **NC**= northern white-cedar (*Thuja occidentalis* L.), **PB**= paper birch (*Betula papyrifera* Marshall), **SM**= sugar maple (*Acer saccharum* Marsh.), **QA**= quaking aspen (*Populus tremuloides* Michx.), **RO**= northern red oak (*Quercus rubra* L.), **WA**= white ash (*Fraxinus americana* L.), **WS**= white spruce (*Picea glauca* (Moench) Voss), **YB**= yellow birch (*Betula alleghaniensis* Britton)

Table A.2. Geological characteristics for each stand, including landform type, soil type, upper layer soil texture and sugar maple site index at age 50 (SI_{50}) in meters estimated for each soil type and soil series.

Stand ID	Landform[a]	Soil type[b]	Soil texture[b,c]	SI_{50}[b]	Soil series[b]
4	Drumlinized ground moraine	Onaway fine sandy loam, 3-9% slopes	fsal	19.8	Onaway
20	Ground moraine	Emmet fine sandy loam, 6-18% slope	fsal	20.1	Emmet
27	Disintegration moraine	Karlin sandy loam, 1-6 % slopes	sal	NA	Keewaydin-Michigamme-Rock Outcrop Association
34	Ground moraine	Trenary fine sandy-loam, 6-18% slopes, stony	fsal	18.6	Trenary
38	Disintegration moraine	Sundog very fine sandy loam, 6-18% slopes	vfsal	NA	Sundog
803	Drumlinized ground moraine	Onaway fine sandy loam, 3-9% slopes	fsal	19.8	Onaway
806	Drumlinized ground moraine	Emmet fine sandy loam, 0-6% slope	fsal	20.1	Emmet
807	Bedrock-controlled ground moraine	Onaway fine sandy loam, 3-9% slopes	fsal	19.8	Onaway
808	Drumlinized ground moraine	Onaway fine sandy loam, 3-9% slopes	fsal	19.8	Onaway
814	Ground moraine	Emmet fine sandy loam, 6-18% slope	fsal	20.1	Emmet
815	Disintegration moraine	Pemene fine sandy loam, 6-18% slope	fsal	18.3	Pemene
816	Ground moraine	Emmet-Pemene fine sandy loams, 0-6% slope	fsal	20.1 / 18.3	Emmet-Pemene
817	Ground moraine	Emmet fine sandy loam, 6-18% slope	fsal	20.1	Emmet
818	Drumlinized ground moraine	Onaway fine sandy loam, 6-18% slopes	fsal	19.8	Cunard-Nahma Association
819	Drumlinized ground moraine	Emmet fine sandy loam, 6-18% slopes	fsal	20.1	Kalkaska-Ishpeming-Rock Outcrop Association
820	Bedrock-controlled ground moraine	Keewaydin-Dishno complex, 6-18% slopes, rocky, bouldery	cfsal / csl	18.6 / 18.3	Sundog-Minocqua-Channing Association
821	Bedrock-controlled ground moraine	Keewaydin-Dishno complex, 6-18% slopes, rocky, bouldery	cfsal / csl	18.6 / 18.3	Sundog-Minocqua-Channing Association
822	Bedrock-controlled ground moraine	Keewaydin-Michigamme-Rock outcrop complex, 6-25% slopes, very bouldery	cfsal	18.6 / 18.3	Kalkaska-Carbondale-Deford Association
823	Bedrock-controlled ground moraine	Keewaydin-Michigamme-Rock outcrop complex, 6-25% slopes, very bouldery	cfsal	18.6 / 18.3	Kalkaska-Carbondale-Deford Association

Table A.2. continued.

Stand ID	Landform	Soil type	Soil texture	SI_{50}	Soil series
824	Bedrock-controlled ground moraine	Keewaydin-Dishno complex, 6-18% slopes, rocky, bouldery	cfsal / csl	18.6 / 18.3	Sundog-Minocqua-Channing Association
825	Dissected moraine	Garlic-Alcona-Voelker complex, 15-70% slopes	fsa / lvfsa / fsa	18.9 / 18.6 / 18.6	Kalkaska-Ishpeming-Rock Outcrop Association
826	Dissected moraine	Garlic-Alcona-Voelker complex, 15-70% slopes	fsa / lvfsa / fsa	18.9 / 18.6 / 18.6	Kalkaska-Ishpeming-Rock Outcrop Association
829	Dissected moraine	Garlic-Alcona-Voelker complex, 8-35% slopes	fsa / lvfsa / fsa	18.9 / 18.6 / 18.6	Kalkaska-Ishpeming-Rock Outcrop Association
832	Drumlinized ground moraine	Onaway fine sandy loam, 6-18% slopes	fsal	19.8	Cunard-Nahma Association
834	Disintegration moraine	Amasa very fine sandy loam, 1-6% slopes	vfsal	18.6	Cunard-Nahma Association
837	Ground moraine	Petticoat-Wabeno silt loams, 6-8% slopes, very stony	sl	20.1 / 20.4	Petticoat-Wabeno
842	Till-floored lake plain	Munising-Yalmer complex, 6-18% slopes	fsal / fsa	19.2 / 18.6	Zeba-Jacobsville Association
844	Till-floored lake plain	Munising-Yalmer complex, 1-6% slopes	fsal / fsa	19.2 / 18.6	Zeba-Jacobsville Association
847	Ground moraine	Shoepac-Trenary silt loams, 1-6% slopes	sl	19.8 / 18.6	Shoepac-Carbondale Association
851	Ground moraine	Emmet-Pemene fine sandy loams, 6-18\% slope	fsal	20.1 / 18.3	Emmet-Pemene
852	Ground moraine	Emmet fine sandy loam, 6-18% slope	fsal	20.1	Emmet
1042	Bedrock-controlled ground moraine	Wabeno silt loam, 1-6% slopes, very stony	sl	20.4	Wabeno
1043	Bedrock-controlled ground moraine	Wabeno silt loam, 1-6% slopes, very stony	sl	20.4	Wabeno
1044	Bedrock-controlled ground moraine	Wabeno silt loam, 1-6% slopes, very stony	sl	20.4	Wabeno
1081	Disintegration moraine	Goodman-Wabeno-Sundog sandy substratum complex, 6-18% slopes, stony	sl / sl / vfsal	21.0 / 20.4 / NA	Goodman-Wabeno-Sundog
1133	Bedrock-controlled ground moraine	Emmet fine sandy loam, 6-18% slope	fsal	20.1	Emmet
1272	Drumlinized ground moraine	Emmet fine sandy loam, 0-6% slope	fsal	20.1	Emmet
1603	Ground moraine	Petticoat-Wabeno silt loams, 1-6% slopes, very stony	sl	20.1 / 20.4	Petticoat-Wabeno
4024	Drumlinized ground moraine	Onaway fine sandy loam, 3-9% slopes	fsal	19.8	Onaway
4042	Drumlinized ground moraine	Onaway fine sandy loam, 3-9% slopes	fsal	19.8	Onaway

Table A.2. continued.

Stand ID	Landform	Soil type	Soil texture	SI_{50}	Soil series
4052	Drumlinized ground moraine	Onaway fine sandy loam, 12-35% slopes	fsal	19.8	Onaway
4082	Bedrock-controlled ground moraine	Emmet-Rock outcrop complex, 6-18% slope	fsal	20.1	Emmet
4102	Drumlinized ground moraine	Emmet fine sandy loam, 0-6% slope	fsal	20.1	Emmet
4162	Ground moraine	Emmet fine sandy loam, 0-6% slope	fsal	20.1	Emmet
4172	Ground moraine	Emmet fine sandy loam, 0-6% slope	fsal	20.1	Emmet
4232	Drumlinized ground moraine	Emmet-Escanaba complex, 1-6% slopes	fsal / lfsa	20.1 / 18.3	Rubicon-Sayner Association
4324	Disintegration moraine	Keweenaw-Kalkaska complex, 6-18% slopes	lsa / sa	18.6 / 19.5	Rubicon-Sayner Association
4332	Disintegration moraine	Keweenaw-Kalkaska complex, 6-18% slopes	lsa / sa	18.6 / 19.5	Rubicon-Sayner Association
4342	Disintegration moraine	Keweenaw loamy sand, 6-18% slopes	lsa	18.6	Zeba-Jacobsville Association
4422	Drumlinized ground moraine	Onaway fine sandy loam, 3-9% slopes	fsal	19.8	Onaway
4423	Drumlinized ground moraine	Onaway fine sandy loam, 3-9% slopes	fsal	19.8	Onaway
4429	Drumlinized ground moraine	Onaway fine sandy loam, 3-9% slopes	fsal	19.8	Onaway
4524	Ground moraine	Longrie fine sandy loam, 0-6% slope	fsal	18.6	Longrie
5032	Bedrock-controlled ground moraine	Emmet fine sandy loam, 6-18% slope	fsal	20.1	Emmet
5052	Ground moraine	Emmet fine sandy loam, 0-6% slope	fsal	20.1	Emmet
5104	Disintegration moraine	Emmet fine sandy loam, 6-18% slopes	fsal	20.1	Kalkaska-Ishpeming-Rock Outcrop Association
5292	Bedrock-controlled ground moraine	Petticoat-Wabeno silt loams, 6-8% slopes, very stony	sl	20.1 / 20.4	Petticoat-Wabeno
5314	Disintegration moraine	Stambaugh silt loam, 2-6% slopes, stony	sl	18.6	Stambaugh
5342	Drumlinized ground moraine	Emmet fine sandy loam, 0-6% slope	fsal	20.1	Emmet

[a] Jerome, Dwight S. and Upper Peninsula, Michigan Soil Survey Staff. 2006 draft. Landforms of the Upper Peninsula of Michigan. USDA NRCS.

[b] Linsemier, Lyle H. 1997. Soil survey of Iron County, Michigan. USDA NRCS and USFS. Washington, D.C.; Schwenner, Chalres. 1989. Soil survey of Menominee County, Michigan. USDA NRCS. Washington, D.C.; Schwenner, Chalres. 2007. Soil survey of Marquette County, Michigan. USDA NRCS. Washington, D.C.; USDA. 1989. Soil survey of Dickinson County, Michigan. USDA NRCS. Washintgon, D.C.

[c] Abbreviations: cfsal= cobbly fine sandy loam; csl= cobbly silt loam; fsa= fine sand; lfsa= loamy fine sand; fsal= fine sandy loam; lsa= loamy sand; lvfsa= loamy very fine sand; sa= sand; sal= sandy loam; sl= silt loam; vfsal= very fine sandy loam

APPENDIX B: Additional Details on Methodology

B.1. Pellet count layout and conversion of pellet counts to deer density

Pellet groups were double counted within ten 50 m by 4 m transects oriented in an hour glass shape (LeBouton et al 2005) (Figure B.1).

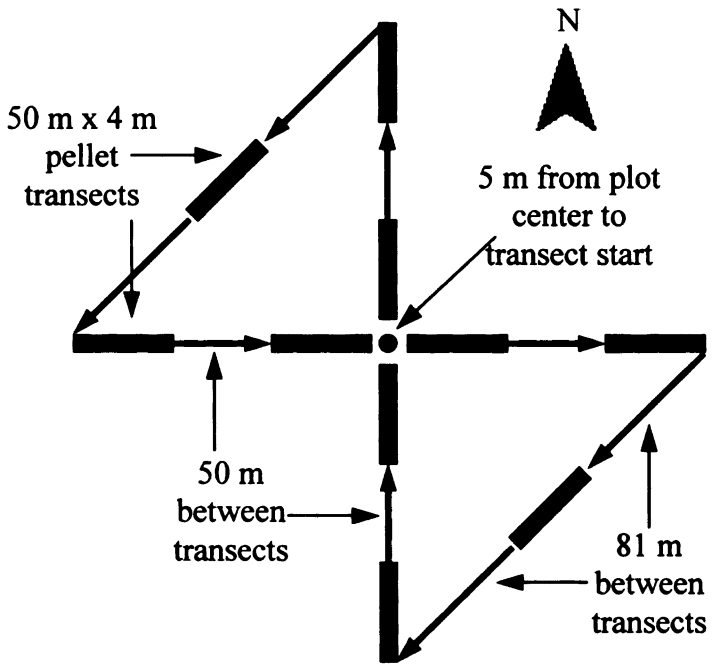


Figure B.1. Layout of pellet count transects.

Average pellet group counts from all ten transects were used to calculate deer density (equation 1). The pellet deposition rate estimated for the Upper Peninsula is 13.4 times per deer in a 24-h period (Hill 2001) and the period of deposition was the number of days from November 1 (assumed date of leaf-off) to the date of the pellet surveys in April and May (180 to 200 days). A constant was required to convert to deer / km^2.

$$\text{Estimated deer density / km}^2 = \frac{\textit{average pellet group count} \times 5000}{\textit{period of deposition} \times 13.4} \qquad (1)$$

B.2. Predicting diameter at breast height from stump basal diameter and measurement height

Stump basal diameter was converted to diameter at breast height using the equation below developed by Demaerschalk and Omule 1978 for merchantable tree species in British Columbia:

$$DBH = StDiam + b \times StDiam \times \ln \frac{StHt + 1}{2.3}$$

StDiam is the stump diameter outside bark in centimeters, StHt is the ht of the diameter measurement in meters and b is a species specific constant. Values for the constant "b" from the southern central forest inventory zones in British Columbia were instead of the higher latitude or coastal regions because this region is more similar to the Western Upper Peninsula in terms of climatic conditions. Constant values were available for balsam fir, quaking aspen, birch species and spruce species. Values for western hemlock (*Tsuga heterophylla*) were used for eastern hemlock (*Tsuga canadensis*), western red-cedar (*Thuja plicata*) for northern white-cedar (*Thuja occidentalis*), and bigleaf maple (*Acer macrophyllum*) for sugar maple and all other hardwood species (Table B.1).

Table B.1. Species-specific parameter values for "b" in equation estimating dbh from stump diameter (equation 2) and standard error of estimated dbh (Demaerschalk and Omule 1978). "Species" refers to the species from this study and "Equivalent species" refers to the species from Demaerschalk and Omule 1978.

Species	Equivalent species	b	Standard error (cm)
Balsam fir		0.301495	2.26
Birch species		0.297892	2.07
Spruce species		0.415792	3.65
Quaking aspen		0.281240	1.68
Northern white-cedar	Western red-cedar	0.486935	4.53
Eastern hemlock	Western hemlock	0.264130	3.02
Other hardwoods	Bigleaf maple	0.285892	0.91

B.3. FVS diameter growth simulations to "grow back" diameter of mature seed trees to their diameter at the time of harvest

I wanted to predict seed production potential at the time of harvest because some saplings present in harvest gaps may have come from seeds produced by trees that were removed by the harvest. USDA Forest Vegetation Simulator Lake States Variant (Bush and Brand 1993) diameter growth equations were implemented in NetLogo (Wilensky 1999) to "grow back" the diameter at breast height (dbh) of living trees to dbh at harvest ($dbh_{Harvest}$). Observed stand conditions were simulated and annual diameter growth for each measured tree of a given dbh and species were estimated. For each time step: 1) predicted diameter growth from the current year was subtracted from the diameter, 2) stand basal area and quadratic mean diameter were re-calibrated, and 3) annual diameter growth was recalculated. This process was reiterated for the number of years since harvest.

Species-specific FVS diameter growth equations require Site Index (obtained from soil survey data) and stand basal area (BA) and quadratic mean diameter (QMD) of trees with dbh > 2.54 cm. However, I only measured trees with dbh >= 20 cm. In order to predict the basal area of trees with dbh < 20 cm (BAu) and the quadratic mean diameter of trees with dbh > 2.54 cm (QMDt) in Netlogo, linear regression models were developed with covariates that could produced from my data set (i.e. variables involving trees with dbh > 20 cm). Models were calibrated with stand BA and dbh data from 55 managed northern hardwood stands in the study area collected using prism point-sampling (Millington et al 2009 *in review*). Twelve of these stands coincide with those sampled for gap regeneration.

Variables included in regression models were BA (BAo), quadratic mean diameter (QMDo), the percentage of trees per hectare not sugar maple (PerNotSM) and the species richness (SR) for trees with dbh > 20 cm. Time since harvest (TSHarvest) was also included, but only known for 23 stands. AIC values were compared in order to determine the model that best predicted BAu and QMDt (i.e. lower AIC values by 2 indicate better model performance). BAu and species richness (SR) were log transformed to comply with normality assumptions. Two stands where no saplings < 20 cm were sampled were removed because they were outliers. The best model for both variables (i.e. lowest AIC of models tested) included BAo and PerNotSM (Tables B.2 and B.3). TSHarvest and SR were not significant predictors.

I decided that incorporating stochasticity into the BAu and QMDt predictions was unnecessary. This was determined based on twenty 15 year simulations for one randomly selected stand for which the average standard deviation of the predicted $dbh_{Harvest}$ for all 183 trees at this stand was monitored. For each simulation, β-values for the BAu and QMDt regression models were randomly selected from a uniform distribution bounded by the β point-estimate plus or minus one standard error. The average standard deviation stabilized after 10 simulations at around 0.052-0.059 cm. Diameter estimates in the field were measured to the nearest tenth of a centimeter, so a difference of ~ 1 cm in $dbh_{Harvest}$ estimates was insignificant.

Sensitivity analysis were also run to determine the effect of BAu and QMDt on one year diameter growth estimates for trees with the average dbh for sugar maple (30.1 cm), basswood (34.0 cm) and ironwood (24.0 cm). BAo and site index equal were set to the average from the 59 sites (19.5 m^2/ha and 19.7 m respectively). For baseline diameter

Table B.2. Parameter estimates (β), standard errors (SE), AIC and adjusted R^2 values from linear regression models to predict log transformed basal area (BAu) of trees with dbh < 20 cm.

Log(BAu)			
Model predictors	β (SE)	AIC	Adj R^2
Models using all stand (n=53)			
Intercept	3.634 (0.291)***	100.3	0.484
BAo	-0.017 (0.004)***		
PerNotSM	1.360 (0.327)***		
Intercept	4.237 (0.291)***	114.0	0.319
BAo	-0.021 (0.004)***		
Intercept	4.053 (0.347)***	115.1	0.319
BAo	-0.021 (0.004)***		
Log(SR)	0.155 (0.160) NS		
Intercept (null)	2.851 (0.114)***	133.5	
Models using stands with known time since harvest (n=25)			
Intercept	3.511 (0.474)***	45.8	0.409
BAo	-0.017 (0.006)*		
PerNotAcesac	1.229 (0.643) NS		
Intercept	3.686 (0.433)***	46.0	0.403
BAo	-0.022 (0.006)**		
TSHarvest	0.067 (0.036) NS		
Intercept	4.022 (0.415)***	47.6	0.334
BAo	-0.022 (0.006)**		
Intercept (null)	2.655 (0.160)***	56.1	
Intercept	2.328 (0.312)***	56.5	0.021
TSHarvest	0.057 (0.047) NS		

***p < 0.001 **p < 0.01 *p < 0.05 NS p > 0.05

BAo= basal area of trees with dbh > 20 cm, PerNotSM= percentage of trees with dbh > 20 not sugar maple, SR= species richness of trees with dbh > 20 cm, TSHarvest=time since harvest.

growth estimates, BAu was set to 2.62 m^2/ha and QMDt to 22.8 cm (the estimates predicted from the average BAo and PerNot_SM (17.8%)). BAu was varied from the average estimate to the average estimate plus the first quartile residual from the

Table B.3. Parameter estimates (β), standard errors (SE), AIC and adjusted R^2 values from linear regression models to predict quadratic mean diameter (QMDt) of trees with dbh > 2.54 cm.

	QMDt		
Model predictors	β (SE)	AIC	Adj R^2
Models using all stand (n=53)			
Intercept	5.296 (0.948)***	225.3	0.363
BAo	0.050 (0.012)***		
PerNotSM	-2.908 (1.064)**		
Intercept	4.008 (0.873)***	230.7	0.282
BAo	0.058 (0.013)***		
Intercept	4.753 (1.035)***	230.9	0.293
BAo	0.057 (0.013)***		
Log(SR)	-0.628 (0.477) NS		
Intercept	-0.163 (0.962) NS	243.9	0.080
QMDo	0.683 (0.290)*		
Intercept (null)	7.837 (0.333)***	247.3	
Models using stands with known time since harvest (n=25)			
Intercept	6.156 (1.442)***	97.0	0.383
BAo	0.042 (0.019)*		
PerNotSM	-4.327 (1.959)*		
Intercept	4.357 (1.295)**	100.0	0.269
BAo	0.059 (0.019)**		
Intercept	4.153 (1.459)**	101.9	0.237
BAo	0.058 (0.020)**		
TSHarvest	0.041 (0.123)		
Intercept (null)	8.066 (0.477)***	106.3	
Intercept	3.930 (6.500) NS	107.9	-0.028
QMDo	0.342 (0.535) NS		
Intercept	7.670 (0.958)***	108.1	-0.036
TSHarvest	0.068 (0.143) NS		

***p < 0.001, **p < 0.01, *p < 0.05, NS p > 0.05

BAo= basal area of trees with dbh > 20 cm, PerNotSM= percentage of trees with dbh > 20 not sugar maple, SR= species richness of trees with dbh > 20 cm, QMDo=quadratic mean diameter of trees with dbh > 20 cm, TSHarvest=time since harvest.

predictive equations (-1.02 m^2/ha), plus the third quartile residual (2.38 m^2/ha) and plus the maximum observed residual (9.33 m^2/ha). Subtracting the third quartile residual and maximum residual produced unrealistic negative estimates of BAu. QMDt was varied from the average estimate to the average plus the first quartile residual (-2.5 cm), and plus or minus the third quartile (3.6 cm) and maximum residual (9.3 cm).

The sensitivity index (the percent change in diameter growth divided by the percent change in BAu or QMDt) was on average 0.055 for BAu and 0.279 for QMDt, well under the 1.5 threshold indicating significant sensitivity to a variable (Table B.4). A 356% increase in BAu (adding the maximum residual) only decreased diameter growth by 17.8 - 19.6 % and a 41% increase in QMDt (adding the maximum residual) only decreased diameter growth by 3.8 - 21.1% for the three species. The maximum differences in growth rate was a 0.36 cm decrease in annual sugar maple growth rate with a 41% increase in QMDt and a 0.30 cm decrease in annual basswood growth rate with a 356% increase in BAu (adding the maximum residual). Over fifteen years, this would translate into at most a 5.3 and 4.6 cm bias in $dbh_{Harvest}$. However, this represents a worst case scenario in which the stand-level BAu and QMDt are most poorly predicted. Fifty percent of the residuals (the interquartile range) lie within a much narrower range for BAu (-1.02 and +2.38 m2 / ha) and QMD (-2.45 and +3.55 cm), and over- or under-predictions within this range only results in a maximum change of 0.11 cm diameter growth/yr, or a biased $dbh_{Harvest}$ estimation of 1.65 cm over 15 years. This error is acceptable given the error already inherent to FVS growth estimates (Canavan and Ramm 2000; Pokharel and Froese 2008).

Table B.4. Sensitivity analysis: percent change in diameter growth (DG) with given percent change in BAu or QMDt and sensitivity index (absolute percent change in diameter growth divided by absolute percent change in BAu or QMDt).

Species	% Change DG	% Change BAu	Sensitivity Index
BAu average (2.62 m^2/ha) + max residual (9.33 m^2/ha)			
Basswood	-17.77	356.13	0.050
Sugar maple	-19.64	356.13	0.055
Ironwood	-18.97	356.13	0.053
BAu average (2.62 m^2/ha) + 3rd quartile residual (2.38 m^2/ha)			
Basswood	-4.62	90.65	0.051
Sugar maple	-5.24	90.65	0.058
Ironwood	-5.18	90.65	0.057
BAu average (2.62 m^2/ha) + 1st quartile residual (-1.02 m^2/ha)			
Basswood	2.03	-39.07	0.052
Sugar maple	2.34	-39.07	0.060
Ironwood	2.33	-39.07	0.060
	Average Sensitivity Index BAu		0.055
Species	% Change DG	% Change QMDt	Sensitivity Index
QMDt average (22.8 cm) + max residual (9.3 cm)			
Basswood	-21.11	40.90	0.516
Sugar maple	-3.78	40.90	0.092
Ironwood	-15.02	40.90	0.367
QMDt average (22.8 cm) - max residual (9.3 cm)			
Basswood	3.74	-40.9	0.091
Sugar maple	-11.59	-40.9	0.283
Ironwood	15.85	-40.9	0.387
QMDt average (22.8 cm) + 3rd quartile residual (3.6 cm)			
Basswood	-6.37	15.57	0.409
Sugar maple	0.45	15.57	0.029
Ironwood	-6.01	15.57	0.386
QMDt average (22.8 cm) – 3rd quartile residual (3.6 cm)			
Basswood	3.53	-15.57	0.226
Sugar maple	-2.80	-15.57	0.180
Ironwood	6.22	-15.57	0.400
QMDt average (22.8 cm) + 1st quartile residual (-2.5 cm)			
Basswood	2.74	-10.74	0.255
Sugar maple	-1.70	-10.74	0.158
Ironwood	4.29	-10.74	0.399
	Average Sensitivity Index QMDt		0.279

B.4. Determining the sensitivity of the random stand-level effect standard deviation to prior specification

Multilevel model estimates with Bayesian inference can be sensitive to the prior specification on the random-effect variance component because of its impact on fixed-effect coefficients and random effect estimates (Natarajan and Kass 2000; Spiegelhalter et al 2004; Browne and Draper 2006). To test the robustness of the posterior distribution of the random effect variance to different priors, I ran the full generalized linear multilevel model for sugar maple 1-2 m sapling abundance (Chapter 1) and the Model 4 logistic multilevel model for the gap-level percentage of hemlock seedlings browsed (Chapter 2) with three commonly recommended priors: inverse gamma for the precision ($1/\sigma^2$) (Browne and Draper 2006), half-normal for the standard deviation (σ) (Spiegelhalter et al 2004; Gelman 2006), and uniform for σ on a wide range (Clayton 1996; Spiegelhalter et al 2004; Gelman 2006). The standard deviation for the stand-level random intercept was insensitive to prior specification (i.e. all 95% credible intervals overlapped) for the sapling abundance model (Figure B.2) and percentage of seedlings browsed model (Figure B.3).

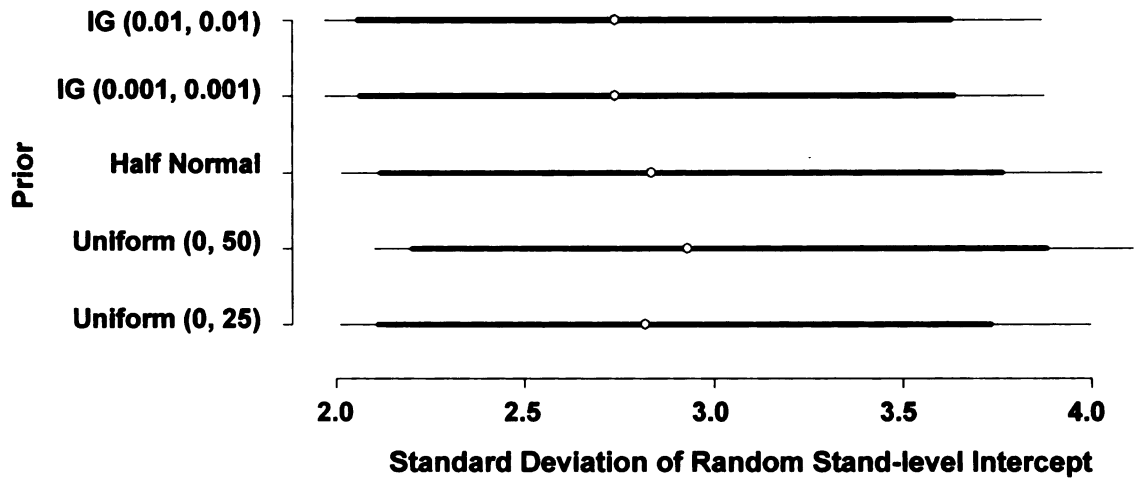


Figure B.2. Effect of the prior on the standard deviation (σ) of the random stand-level intercept in the sugar maple sapling abundance generalized linear multilevel model: mean, 90% credible interval (thick black line), and 95% credible interval (thin black line) of the posterior distribution. IG (inverse gamma) prior was on the precision ($1/\sigma^2$) and half normal and uniform density priors were on σ. The half normal distribution was ~N(0, 10,000), bounded above 0.

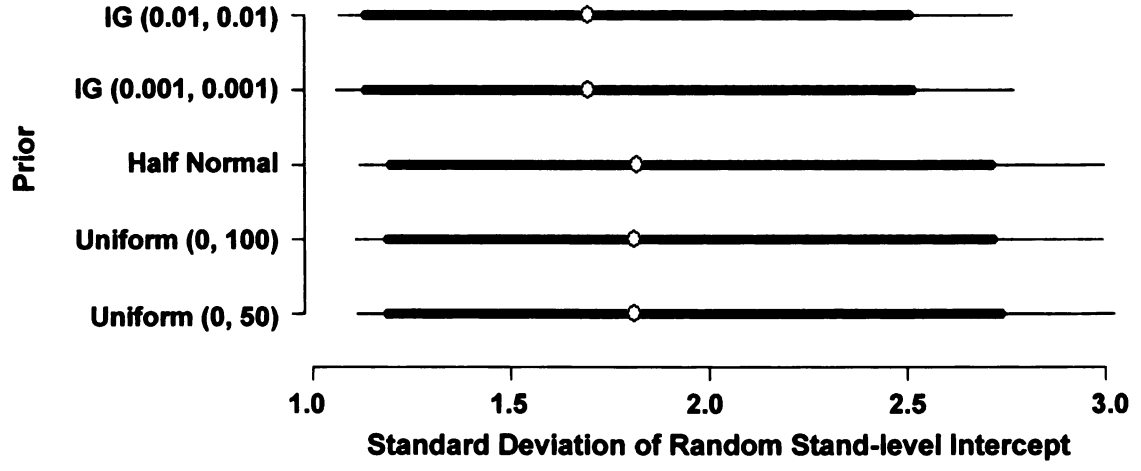


Figure B.3. Effect of the prior on the standard deviation (σ) of the random stand-level intercept in the gap-level percentage browsed hemlock seedlings logistic multilevel model: mean, 90% credible interval (thick black line), and 95% credible interval (thin black line) of the posterior distribution. IG (inverse gamma) prior was on the precision ($1/\sigma^2$) and half normal and uniform density priors were on σ. The half normal distribution was ~N(0, 10,000), bounded above 0.

B.5. Creating image of deer density across the study area using DNR pellet count data collected from 1996-2000 and Universal Kriging

The Wildlife Division within the Michigan Department of Natural Resources collected deer pellet count data across the Upper Peninsula of Michigan from 1981 to 2000 (Doepker et al 1994; Hill 2001). I developed an interpolated map from this dataset for comparison with deer density estimates at my northern hardwood study stands to validate the spatial pattern observed in deer densities.

I used a subset of the DNR data collected from 1996-2000 within 113 Public Land Survey sections within the four study area counties (Iron, Dickinson, Marquette and Menominee). The DNR randomly selected sections from three strata and surveyed deer pellets within five randomly selected 1/50-acre (81 m^2) rectangular plots (3.7 m by 22.1 m) (Hill 2001). The average pellet count from these five plots was converted into deer density (deer / km^2) (Appendix B, Section B.1). The years 1996 to 2000 were selected because pellet count surveys were consistently made in more sections during these years than they were during other years. Only sections where pellet surveys were performed more than four years during the five year timeframe were included in analysis.

An empirical semivariogram was developed to describe the spatial correlation between deer densities estimates from sections. Deer density estimates were $\log_{10} +1$ transformed to comply with normality assumptions. The spatial coordinates for the deer density estimates were the UTM Northing and Easting for the center of the section. Deer density generally decreased with increasing UTM Northing (Figure B.4) so a semivariogram was developed using residuals from the relationship between transformed deer density and UTM Northing. Generalized Least Squared (GLS) estimation was used

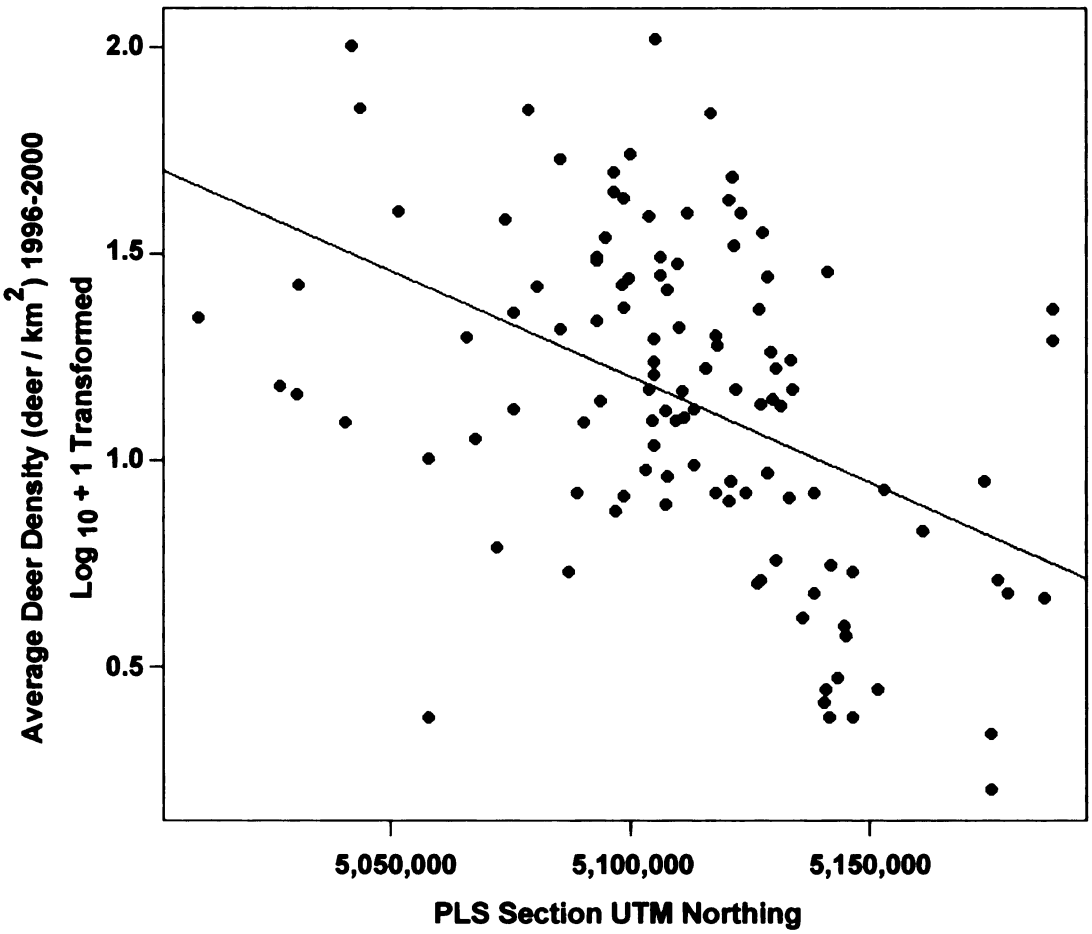


Figure B.4. Average estimated deer density (deer/km^2) from DNR pellet count surveys 1996-2000 within Iron, Dickinson, Marquette and Menominee counties versus UTM Northing for the Public Land Survey section. Log transformed deer density = 23.8518 – 4.0e-06 × UTM Northing based on GLS-estimation. AIC is 107.7 compared to 85.7 for the null model.

to take into account the correlation between observations. Residuals from the Ordinary Least Squared estimated linear regression between log transformed deer density and UTM Northing were first used to estimate the nugget, partial sill and range for the semivariogram. The semivariogram values were used to develop the correlation matrix necessary for GLS-estimation. GLS residuals were used to develop the final semivariogram which was best approximated with an exponential model in the form

$\gamma(h) = c_0 + c(1 - \exp\left(-\frac{3h}{a}\right))$ where c_0 (the nugget) is 0.04, c (the partial sill) is 0.10, a (the range) is 20,000 m and h (the lag distance) is 2,000 m (Figure B.5). There were very few points separated by a distance less than 1,600 m (Table B.5), but the sample size was adequate for the other size bins.

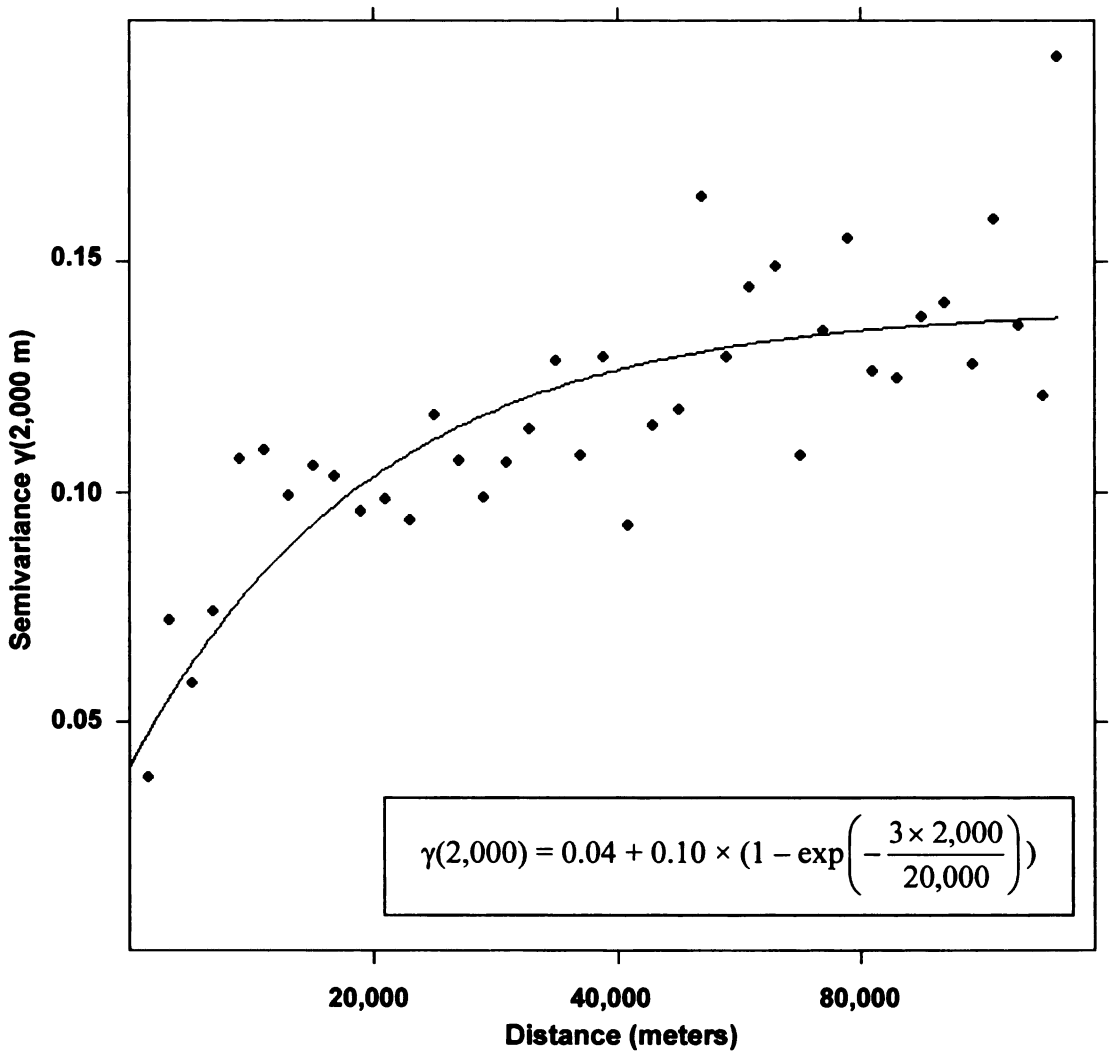


Figure B.5. Semivariogram of the residuals from the GLS-estimated relationship between estimated average deer density (deer/km^2) and UTM Northing. A lag distance of 2,000 m and an exponential model form were used.

The semivariogram was used to perform universal kriging (Goovaerts 1997) and develop an interpolated map of back-transformed deer density across the study area counties using geostatistical analyst in ERSI ArcMap v 9.2. The average standard error between the observed deer density and predicted from cross validation (Figure B.6) was 0.35 and the root-mean-square error was 0.32.

Table B.5. Number of section (N. sections) centers separated by different distances. The average of the semivariance values from the points in the different distance bins was used to develop the semivariogram (Figure B.3).

N. sections	Distance (m)	N. sections	Distance (m)
6	1610	134	40967
24	3258	140	42999
25	5108	142	45057
28	6854	146	46933
52	9049	145	48994
64	11096	154	50940
92	13104	134	53045
92	15068	128	55027
97	16895	145	56908
101	19012	120	58948
94	21079	116	60972
98	23027	108	62994
120	25008	117	64984
131	27059	155	66887
125	29070	147	69137
134	30938	117	70963
131	32907	110	72946
157	35056	128	74979
129	37014	11	76084
149	38918		

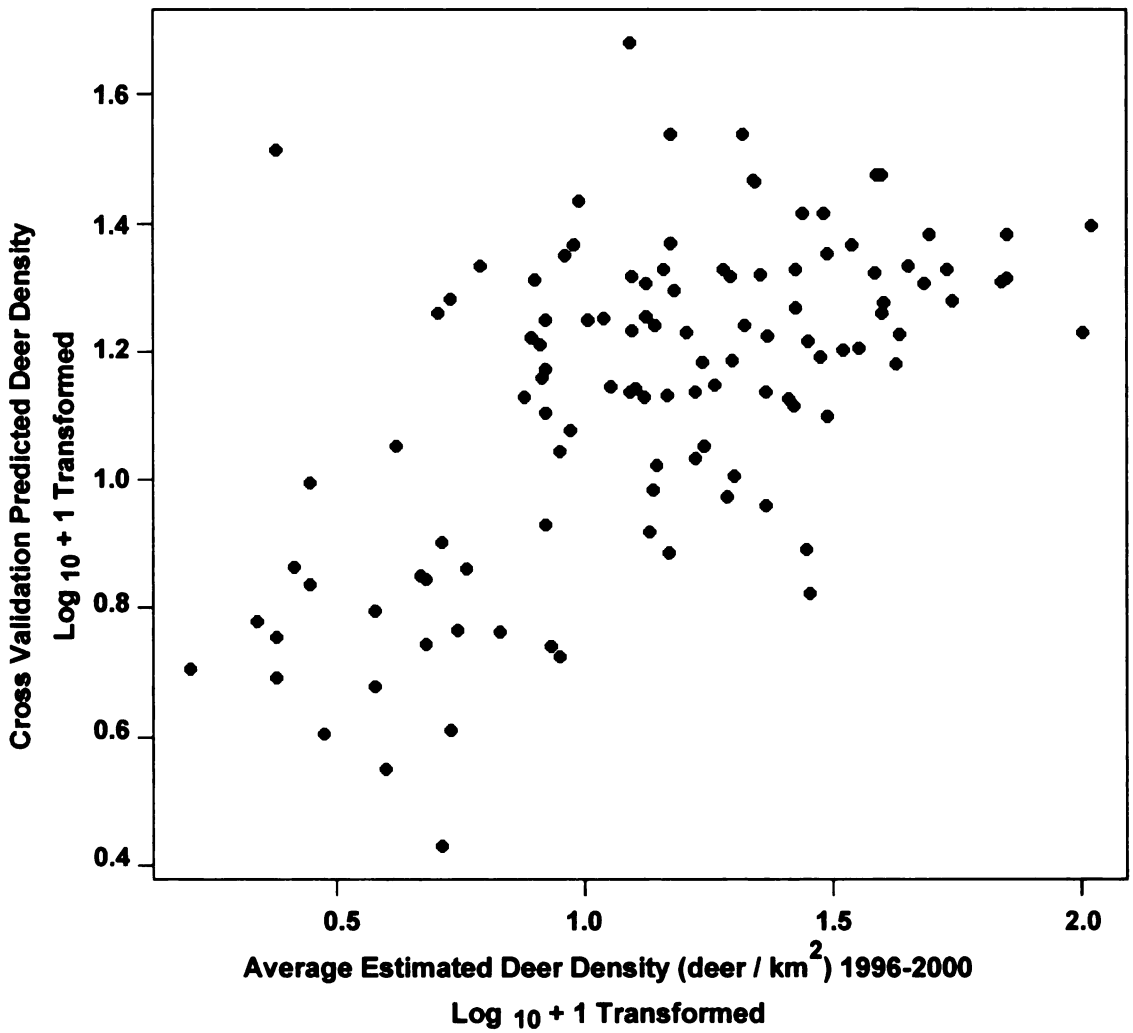


Figure B.6. Observed deer density estimates versus values predicted from cross validation.

APPENDIX C: Sample R2WinBUGS code and WinBUGS models

Models were run with WinBUGS v.1.4.3 (Spiegelhalter et al 2003) through R v.2.9.1 with the package R2WinBUGS (Sturtz et al 2005). Below are WinBUGS models for Chapter 1 seedling and sapling abundance generalized linear multilevel models (GLMM) (Section C.1), log transformed sapling stocking levels and square root transformed Shannon Diversity Index linear multilevel models (LMM) (Section C.2), log transformed sapling growth rates linear models (LM) (Section C.3) and Chapter 2 percentage of seedlings browsed multilevel logistic regression models (Section C.4). WinBUGS model code was derived from examples in Ntzoufras 2009 and Gelman and Hill 2007. Code is also provided for running the sugar maple seedling model with R2WinBUGS, with R code modified from Qian and Shen 2007 (Section C.5).

Section C.1. WinBUGS code: Seedling and sapling GLMM

```
model{
    for (i in 1:n){
        y[i] ~ dnegbin(p[i], r2)
        p[i]<- r2/(r2+mu[i])
        log(mu[i])<-a[site[i]] + b.cv*cv[i] + b.co*co[i] + b.ss*ss[i]
 }
 b.cv~dnorm(0,0.0001)   #prior for cv (competing vegetation) β
 b.co~dnorm(0,0.0001)   #co = canopy openness
 b.ss~dnorm(0,0.0001)   #ss= seed production potential
 r2~dgamma(0.1,0.1)
    for (j in 1:J){
```

```
        a[j] ~ dnorm(a.hat[j], tau.a)
        a.hat[j] <- g.0 + g.atdhp*atdhp[j] + g.atd*atd[j] + g.atm*atm[j] + g.tmc*tmc[j] +
                    g.d*d[j] + g.tsh*tsh[j]
    }
    g.0 ~ dnorm(0, 0.0001)          #g0= overall intercept (AOCa is reference Habitat Type)
    g.atdhp ~ dnorm(0, 0.0001)      #adthp= ATD-Hp Habitat Type
    g.atd ~ dnorm(0, 0.0001)        #atd= ATD
    g.atm ~ dnorm(0, 0.0001)        #atm= ATM
    g.tmc ~ dnorm(0, 0.0001)        #tmc= TMC
    g.d ~ dnorm(0, 0.0001)          #d= deer density
    g.tsh ~ dnorm(0, 0.0001)        #tsh= time since harvest
    tau.a <- pow(sigma.a, -2)       #random stand-level intercept precision
    sigma.a ~ dunif (0, 50)         #prior on random stand-level intercept stdev
}
```

Section C.2. WinBUGS code: Log transformed sapling stocking level and square root transformed Shannon Diversity Index LMM

```
model{
    for (i in 1:n){
        y[i] ~ dnorm(mu[i], tau.b)
        mu[i]<- a[site[i]] + b.cv*cv[i] + b.co*co[i] + b.hm*hm[i]
    }
    b.cv~dnorm(0,0.0001)
    b.co~dnorm(0,0.0001)
```

```
b.hm~dnorm(0,0.0001)        #hm= overstory diversity
tau.b<-pow(sigma.b, -2)
sigma.b~dunif (0, 50)
   for (j in 1:J){
        a[j] ~ dnorm(a.hat[j], tau.a)
        a.hat[j] <- g.0 + g.atdhp*atdhp[j] + g.atd*atd[j] + g.atm*atm[j] + g.tmc*tmc[j] +
                    g.d*d[j] + g.tsh*tsh[j]
}
g.0 ~ dnorm(0, 0.0001)
g.atdhp ~ dnorm(0, 0.0001)
g.atd ~ dnorm(0, 0.0001)
g.atm ~ dnorm(0, 0.0001)
g.tmc ~ dnorm(0, 0.0001)
g.d ~ dnorm(0, 0.0001)
g.tsh ~ dnorm(0, 0.0001)
tau.a <- pow(sigma.a, -2)
sigma.a ~ dunif (0, 50)
}
```

Section C.3. WinBUGS code: Log transformed sapling growth rates LM

```
model{
   for (i in 1:n){
        y[i] ~ dnorm(mu[i], tau.b)
```

```
        mu[i]<- b.0 + b.ht*ht[i] + b.ar*ar[i] + b.cv*cv[i] + b.co*co[i] + b.atdhp*atdhp[i]
                + b.atd*atd[i] + b.atm*atm[i] + b.tmc*tmc[i] + b.d*d[i] + b.tsh*tsh[i]
    }
    b.0 ~ dnorm(0, 0.0001)
    b.ht~dnorm(0,0.0001)        #ht=sapling height
    b.ar~dnorm(0,0.0001)        #ar= advanced regeneration
    b.cv~dnorm(0,0.0001)
    b.co~dnorm(0,0.0001)
    b.atdhp ~ dnorm(0, 0.0001)
    b.atd ~ dnorm(0, 0.0001)
    b.atm ~ dnorm(0, 0.0001)
    b.tmc ~ dnorm(0, 0.0001)
    b.d ~ dnorm(0, 0.0001)
    b.tsh ~ dnorm(0, 0.0001)
    tau.b~dgamma(0.001,0.001)        #prior on sapling-level precision
    sigma.b<- 1/sqrt(tau.b)          #sapling-level standard deviation
}
```

Section C.4. WinBUGS code: Gap-level percentage of seedlings browsed or severe browsed multilevel logistic regression model

```
model{
    for(i in 1:n.gaps){
        r[i]~ dbin(p.bound[i],n[i])    #r[i] = predicted number browsed of n[i] seedlings
        p.bound[i] <- max(0, min(1, p[i]))  #constrains probability estimates btwn 0 and 1
```

```
        logit(p[i]) <- a.stand[stand[i]] + b.pel*pel[i] + b.dlc*dlc[i]
}
b.pel~ dnorm(0, 0.0001)      #pel= pellet counts / gap transect
b.dlc~ dnorm(0, 0.0001)      #dlc= gap distance to lowland conifer
   for(k in 1:n.stands){
        a.stand[k]~dnorm(a.hat[k], tau.a)
        a.hat[k]<- g.0 + g.dsd*dsd[k]
}
g.0~ dnorm(0, 0.0001)        #g.0= overall intercept
g.dsw~ dnorm(0, 0.0001)      #dsw= deep snow weeks
tau.a<-pow(sigma.a, -2)
sigma.a~dunif(0,100)
}
```

Section C.5: Code for running sugar maple seedling code with R2WinBUGS

```
AcesacGLMM1 <- function(infile=AS, infile2=ASsite){
y <- infile$AcesacSeedTot
n <- length(y)
cv<-infile$CompetingS
co<- infile$CO
ss<-infile$RibbensAcesac
tsh<-infile2$TSHarvest
d<-infile2$DeerDen
atdhp=infile2$ATDHp
```

```
atd=infile2$ATD

atm=infile2$ATM

tmc=infile2$TMC

J<- length(tsh)

site <- as.numeric(ordered(infile$Site))

bugs.dat <- list(n=n, y=y, J=J, cv=cv, co=co, ss=ss, tsh=tsh, d=d,

            atdhp=atdhp, atd=atd, atm=atm, tmc=tmc, site=site)

 ## input data needed to run the WinBUGS program

inits1 <- list(a=rnorm(length(infile2$Site)), g.atdhp=rnorm(1), g.atd=rnorm(1),

            g.atm=rnorm(1), g.tmc=rnorm(1), g.tsh=rnorm(1), g.d=rnorm(1),

            g.0=rnorm(1), sigma.a=runif(1), r2=1, b.cv=rnorm(1), b.co=rnorm(1),

            b.ss=rnorm(1))

inits2 <- list(a=rnorm(length(infile2$Site)), g.atdhp=rnorm(1), g.atd=rnorm(1),

            g.atm=rnorm(1), g.tmc=rnorm(1), g.tsh=rnorm(1), g.d=rnorm(1),

            g.0=rnorm(1), sigma.a=runif(1), r2=2, b.cv=rnorm(1), b.co=rnorm(1),

            b.ss=rnorm(1))

inits3 <- list(a=rnorm(length(infile2$Site)), g.atdhp= rnorm(1), g.atd=rnorm(1), g.atm=

            rnorm(1), g.tmc=rnorm(1), g.tsh=rnorm(1), g.d=rnorm(1), g.0=rnorm(1),

            sigma.a=runif(1), r2=5, b.cv=rnorm(1), b.co=rnorm(1), b.ss=rnorm(1))

inits <- list (inits1, inits2, inits3)

## variables to be monitored
```

```
parameters <- c("g.0", "g.atdhp", "g.atd", "g.atm", "g.tmc", "g.tsh", "g.d", "sigma.a",
            "b.cv", "b.co", "b.ss", "r2", "mu") return(list(para=parameters, data=bugs.dat,
            inits=inits))
}
input.to.bugs <- AcesacGLMM1()
AcesacGLMM1 <- bugs(input.to.bugs$data, input.to.bugs$inits,
            input.to.bugs$para, model.file="Seedling_GLMM.txt", n.chains=3,
            n.iter=70000, n.burnin=10000, n.thin=5, DIC=T,  bugs.directory="
            C:/Program Files/WinBUGS14", debug=TRUE)
```

APPENDIX D: Assessing Convergence

Seedling and sapling abundance generalized linear multilevel models (GLMM), log transformed stocking-level linear multilevel models (LMM), square root transformed Shannon Diversity Index linear multilevel models (LMM), log transformed sapling growth rate linear models (LM) (Chapter 1) and percentage of seedlings browsed multilevel logistic models (Chapter 2) were fit using Markov Chain Monte Carlo sampling in WinBugs. Three parallel chains were run with dispersed randomly selected starting values. Model convergence was assessed using the R package coda (Plummer et al 2009). If the Raftery-Lewis diagnostic for a model indicated that an insufficient number of iterations had been run to have a 95% probability of estimating the 2.5% quantile with a tolerance of +/-0.5%, it was rerun with an increased number of iterations and an increased thinning factor. *I* is the proportional increase in *N* attributable to autocorrelation and indicates poor mixing of the MCMC chains if values are > 5.

Based on both diagnostics, the chains converged for all variables across all analyses. All *Rhat* values (potential scale reduction factor) from the Gelman-Rubin diagnostic were 1.0 (Gelman and Hill 2007) and the number of iterations run were greater than *N* from the Raftery-Lewis diagnostic and *I* was less 5 (Table D.1 - D.10)

Table D.1. Convergence in models of spatial trends in seedling and sapling abundance and log transformed stocking-level: sample size (N obs.), burn-in length (N.burnin), iterations after burn-in (N.iter), thinning factor (T.factor) and maximum Raftery-Lewis diagnostic *N* (number of iterations required to have a 95% probability of estimating the 2.5% quantile with a tolerance of +/-0.5%) and *I* (Dependence Factor) from three parallel MCMC chains.

Species	Sugar maple	Ironwood	Other species
Seedling abundance GLMM			
N obs. gaps /stands	337 / 59	337 / 59	337 / 59
N.burnin	10,000	15,000	10,000
N.iter	60,000	85,000	60,000
T.factor	5	5	5
Variable	Raftery-Lewis Diagnostics (*N* / *I*)		
Intercept	4001 / 1.07	3945 / 1.05	4140 / 1.11
Northing	3940 / 1.05	4338 / 1.16	3972 / 1.06
Easting	3787 / 1.01	4290 / 1.15	3839 / 1.02
Stand Stdev	4344 / 1.16	10550 / 2.82	4487 / 1.20
Dispersion parameter	3881 / 1.04	4150 / 1.11	3903 / 1.04
Sapling abundance GLMM			
N obs. gaps/stands	331 / 58	331 / 58	331 / 58
N.burnin	10,000	10,000	10,000
N.iter	60,000	60,000	60,000
T.factor	5	5	5
Variable	Raftery-Lewis Diagnostics (*N* / *I*)		
Intercept	9786 / 2.61	4001 / 1.07	4151 / 1.11
Northing	4275 / 1.14	3892 / 1.04	3865 / 1.03
Easting	3865 / 1.03	3865 / 1.03	3972 / 1.06
Stand Stdev	9364 / 2.50	4384 / 1.17	4340 / 1.16
Dispersion parameter	3881 / 1.04	3839 / 1.02	4067 / 1.09
Sapling stocking LMM			
N obs. gaps/stands	164 / 45	184 / 49	192 / 48
N.burnin	5,000	5,000	5,000
N.iter	15,000	15,000	15,000
T.factor	1	1	1
Variable	Raftery-Lewis Diagnostics (*N* / *I*)		
Intercept	4845 / 1.29	4307 / 1.15	4290 / 1.15
Northing	4713 / 1.26	4394 / 1.17	4508 / 1.20
Easting	4346 / 1.16	4299 / 1.15	4361 / 1.16
Stand Stdev	11360 / 3.03	9518 / 2.54	9024 / 2.41
Gap Stdev	5007 / 1.34	5257 / 1.4	5045 / 1.35

Stand Stdev= standard deviation for the random stand-level intercept.

Table D.2. Convergence in LMM of spatial trends in square root transformed Shannon Diversity Index (H'): Sample size (N obs.), burn-in length (N.burnin), iterations after burn-in (N.iter), thinning factor (T.factor) and maximum Raftery-Lewis diagnostic *N* (number of iterations required to have a 95% probability of estimating the 2.5% quantile with a tolerance of +/-0.5%) and *I* (Dependence Factor) from three parallel MCMC chains.

Species	H' Seedlings	H' Saplings 1-2 m	H' Saplings 1-7 m
N obs. gaps/stands	182 / 54	180 / 42	201 / 46
N.burnin	10,000	5,000	10,000
N.iter	60,000	15,000	60,000
T.factor	1	1	1
Variable	Raftery-Lewis Diagnostics (*N* / *I*)		
Intercept	3918 / 1.05	4583 / 1.22	3918 / 1.05
Northing	3839 / 1.02	4541 / 1.21	3978 / 1.06
Easting	3892 / 1.04	4338 / 1.16	3761 / 1.00
Stand Stdev	6609 / 1.76	11274 / 3.01	4527 / 1.21
Gap Stdev	3952 / 1.05	4939 / 1.32	3836 / 1.02

Stand Stdev= standard deviation for the random stand-level intercept.

Table D.3. Convergence in LM of spatial trends in log transformed sapling growth rate after harvest: Sample size (N obs.), burn-in length (N.burnin), iterations after burn-in (N.iter), thinning factor (T.factor) and maximum Raftery-Lewis diagnostic *N* (number of iterations required to have a 95% probability of estimating the 2.5% quantile with a tolerance of +/-0.5%) and *I* (Dependence Factor) from three parallel MCMC chains.

Species	Sugar maple	Ironwood
N obs. gaps/stands	127 / 26	98 / 30
N.burnin	5,000	5,000
N.iter	15,000	15,000
T.factor	1	1
Variable	Raftery-Lewis Diagnostics (*N* / *I*)	
Intercept	3803 / 1.02	3879 / 1.04
Northing	3908 / 1.04	3908 / 1.04
Easting	3802 / 1.01	3823 / 1.02
Sapling Stdev	3846 / 1.03	3946 / 1.05

Table D.4. Convergence in GLMM of seedling abundance with gap- and stand-level covariates: Sample size (N obs.), burn-in length (N.burnin), iterations after burn-in (N.iter), thinning factor (T.factor) and maximum Raftery-Lewis diagnostic *N* (number of iterations required to have a 95% probability of estimating the 2.5% quantile with a tolerance of +/-0.5%) and *I* (Dependence Factor) from three parallel MCMC chains.

Species	Sugar maple	Ironwood	Other spp
N obs. gaps/stands	337 / 59	337 / 59	337 / 59
N.burnin	10,000	15,000	15,000
N.iter	60,000	84,000	1,600,000
T.factor	5	7	20
Variable	Raftery-Lewis Diagnostics (*N* / *I*)		
	Full model		
Canopy openness	7615 / 2.03	5593 / 1.49	7217 / 1.93
Competing veg	6796 / 1.81	5705 / 1.52	6852 / 1.83
SP_{2008}	6138 / 1.64	4886 / 1.30	6273 / 1.67
Intercept	3933 / 1.05	4067 / 1.09	4404 / 1.18
ATD-Hp	3945 / 1.05	4028 / 1.08	3918 / 1.05
ATD	3761 / 1.00	8242 / 2.20	3918 / 1.05
ATM	3945 / 1.05	4284 / 1.14	3945 / 1.05
TMC	3918 / 1.05	10480 / 2.80	3865 / 1.03
Deer density	3945 / 1.05	4001 / 1.07	3945 / 1.05
TSHarvest	3839 / 1.02	4547 / 1.21	3918 / 1.05
Dispersion parameter	3972 / 1.06	4151 / 1.11	4011 / 1.07
Stand Stdev	4226 / 1.13	11494 / 3.07	9284 / 2.48
	Null model		
Intercept	3865 / 1.03	4272 / 1.14	4056 / 1.08
Dispersion parameter	3956 / 1.06	3888 / 1.04	3945 / 1.05
Stand Stdev	4167 / 1.11	8066 / 2.15	4665 / 1.25

SP_{2008}= seedling production potential (Σdiameter/distance^2) in 2008, TSHarvest=time since harvest, Stand Stdev= standard deviation for the random stand-level intercept.

Table D.5. Convergence in GLMM of sapling (1-2 m) abundance with gap- and stand-level covariates: Sample size (N obs.), burn-in length (N.burnin), iterations after burn-in (N.iter), thinning factor (T.factor) and maimum Raftery-Lewis diagnostic *N* (number of iterations required to have a 95% probability of estimating the 2.5% quantile with a tolerance of +/-0.5%) and *I* (Dependence Factor) from three parallel MCMC chains.

Species	Sugar maple	Ironwood	Other spp
N obs. gaps/stands	331 / 58	331 / 58	331 / 58
N.burnin	15,000	15,000	10,000
N.iter	84,000	84,000	60,000
T.factor	5	5	5
Variable	Raftery-Lewis Diagnostics (*N* / *I*)		
	Full model		
Canopy openness	9812 / 2.62	6500 / 1.74	6898 / 1.84
Competing veg	9216 / 2.46	9008 / 2.40	9369 / 2.50
$SP_{Harvest}$	4768 / 1.27	5130 / 1.37	5341 / 1.43
Intercept	9940 / 2.65	3972 / 1.06	4140 / 1.11
ATD-Hp	NA	3685 / 0.98	3839 / 1.02
ATD	4151 / 1.11	3735 / 1.00	3972 / 1.06
ATM	3967 / 1.06	3721 / 0.99	3813 / 1.02
TMC	4028 / 1.08	3787 / 1.01	3813 / 1.02
Deer density	4496 / 1.20	3787 / 1.01	3929 / 1.05
TSHarvest	3813 / 1.02	3761 / 1.00	3839 / 1.02
Dispersion parameter	4021 / 1.07	3819 / 1.02	3972 / 1.06
Stand Stdev	9612 / 2.57	4094 / 1.09	4190 / 1.12
	Null model		
Intercept	8576 / 2.29	4098 / 1.09	3945 / 1.05
Dispersion parameter	3892 / 1.04	3929 / 1.05	4011 / 1.07
Stand Stdev	9858 / 2.63	4295 / 1.15	4255 / 1.14

$SP_{Harvest}$= seedling production potential (Σdiameter/distance^2) at time of harvest, TSHarvest=time since harvest, Stand Stdev= standard deviation for the random stand-level intercept.

Table D.6. Convergence in LMM of log transformed sapling 1-7 m tall stocking with gap- and stand-level covariates: Sample size (N obs.), burn-in length (N.burnin), iterations after burn-in (N.iter), thinning factor (T.factor) and maximum Raftery-Lewis diagnostic *N* (number of iterations required to have a 95% probability of estimating the 2.5% quantile with a tolerance of +/-0.5%) and *I* (Dependence Factor) from three parallel MCMC chains.

Species	Sugar maple	Ironwood	Other Spp
N obs. gaps/stands	164 / 45	184 / 49	192 / 48
N.burnin	5,000	5,000	5,000
N.iter	15,000	15,000	15,000
T.factor	1	1	1
Variable	Raftery-Lewis Diagnostics (*N* / *I*)		
	Full model		
Canopy openness	5094 / 1.36	9618 / 2.57	7610 / 2.03
Competing veg	5835 / 1.56	9182 / 2.45	8618 / 2.30
$SP_{Harvest}$	4267 / 1.14	4661 / 1.24	4643 / 1.24
Intercept	7652 / 2.04	4508 / 1.20	4677 / 1.25
ATD-Hp	4479 / 1.20	4558 / 1.22	4583 / 1.22
ATD	4410 / 1.18	4508 / 1.20	4290 / 1.15
ATM	4385 / 1.17	4387 / 1.17	4338 / 1.16
TMC	5152 / 1.38	8032 / 2.14	4533 / 1.21
Deer density	4267 / 1.14	4252 / 1.14	4410 / 1.18
TSHarvest	4299 / 1.15	4338 / 1.16	4129 / 1.10
Stand Stdev	10438 / 2.79	10440 / 2.79	10152 / 2.71
Gap Stdev	5094 / 1.36	5343 / 1.43	5044 / 1.35
	Null model		
Intercept	4402 / 1.18	4418 / 1.18	4229 / 1.13
Stand Stdev	5825 / 1.55	9988 / 2.67	5770 / 1.54
Gap Stdev	5021 / 1.34	5021 / 1.34	5094 / 1.36

$SP_{Harvest}$= seedling production potential (Σdiameter/distance^2) at time of harvest, TSHarvest=time since harvest, Stand Stdev= standard deviation for the random stand-level intercept.

Table D.7. Convergence in LMM of square root transformed of Shannon Diversity Index (H') with gap- and stand-level covariates: Sample size (N obs.), burn-in length (N.burnin), iterations after burn-in (N.iter), thinning factor (T.factor) and Raftery-Lewis diagnostic *N* (number of iterations required to have a 95% probability of estimating the 2.5% quantile with a tolerance of +/-0.5%) and *I* (Dependence Factor) from three parallel MCMC chains.

Species	H' Seedlings	H' Saplings 1-2 m	H' Saplings 1-7 m
N obs. gaps/stands	182 / 54	180 / 42	201 / 46
N.burnin	20,000	5,000	5,000
N.iter	200,000	15,000	15,000
T.factor	10	1	1
Variable	Raftery-Lewis Diagnostics (*N* / *I*)		
	Full model		
Canopy openness	3740 / 1.00	5010 / 1.34	9214 / 2.46
Competing veg	3834 / 1.02	9784 / 2.61	8990 / 2.40
H' Overstory[1]	3872 / 1.03	9120 / 2.43	5038 / 1.34
Intercept	3818 / 1.02	4800 / 1.28	8762 / 2.34
ATD-Hp	3740 / 1.00	4687 / 1.25	4765 / 1.27
ATD	3787 / 1.01	4299 / 1.15	8800 / 2.35
ATM	3818 / 1.02	4669 / 1.25	4982 / 1.33
TMC	3802 / 1.01	7864 / 2.10	8752 / 2.34
Deer density	3802 / 1.01	4660 / 1.24	4765 / 1.27
TSHarvest	3802 / 1.01	4483 / 1.20	4661 / 1.24
Stand Stdev	9650 / 2.58	14559 / 3.89	12726 / 3.40
Gap Stdev	3845 / 1.03	5103 / 1.36	4997 / 1.33
	Null model		
Intercept	3853 / 1.03	4385 / 1.17	4687 / 1.25
Stand Stdev	4095 / 1.09	9358 / 2.50	12498 / 3.34
Gap Stdev	3978 / 1.06	4970 / 1.33	5048 / 1.35

TSHarvest=time since harvest, Stand Stdev= standard deviation for the random stand-level intercept.

[1] H'Overstory for H'Seedlings is Shannon Diversity of overstory trees, H'Overstory for H'Saplings 1-2 and 1-7 m tall is Shannon Diversity of overstory trees and stumps

Table D.8. Convergence in LM of log transformed sapling growth rates with gap- and stand-level covariates: Sample size (N obs.), burn-in length (N.burnin), iterations after burn-in (N.iter), thinning factor (T.factor) and Raftery-Lewis diagnostic *N* (number of iterations required to have a 95% probability of estimating the 2.5% quantile with a tolerance of +/-0.5%) and *I* (Dependence Factor) from three parallel MCMC chains.

Species	Sugar maple	Ironwood
N obs. gaps/stands	127 / 26	98 / 30
N.burnin	5,000	5,000
N.iter	15,000	15,000
T.factor	1	1
Variable	Raftery-Lewis Diagnostics (*N* / *I*)	
	Full model	
Intercept	4043 / 1.08	3913 / 1.04
Advanced regen	3832 / 1.02	3802 / 1.01
Sapling height	3740 / 1.00	3802 / 1.01
Canopy openness	3844 / 1.03	3823 / 1.02
Competing veg	3782 / 1.01	3908 / 1.04
ATD-Hp	3844 / 1.03	3811 / 1.02
ATD	3938 / 1.05	3782 / 1.01
ATM	3799 / 1.01	3782 / 1.01
TMC	3802 / 1.01	3761 / 1.00
Deer density	3938 / 1.05	3865 / 1.03
TSHarvest	3746 / 1.00	3770 / 1.01
Sapling Stdev	3860 / 1.03	3959 / 1.06
	Null model	
Intercept	3841 / 1.03	3834 / 1.02
Sapling Stdev	3841 / 1.03	3782 / 1.01

Advanced regen= bivariate variable indicating if a variable is advanced regeneration, TSHarvest=time since harvest.

Table D.9. Convergence in multilevel logistic models of gap-level percentage of seedlings browsed within gaps with gap- and stand-level covariates: Sample size (N obs.), burn-in length (N.burnin), iterations after burn-in (N.iter), thinning factor (T.factor) and Raftery-Lewis diagnostic *N* (number of iterations required to have a 95% probability of estimating the 2.5% quantile with a tolerance of +/-0.5%) and *I* (Dependence Factor) from three parallel MCMC chains.

Species	Hemlock	White pine
N obs. gaps/stands	338 / 34	338 / 34
N.burnin	10,000	10,000
N.iter	30,000	30,000
T.factor	5	5
Variable	Raftery-Lewis Diagnostics (*N* / *I*)	
	Model 1 (null)	
Intercept	3887 / 1.04	3761 / 1.00
Stand Stdev	3962 / 1.06	3900 / 1.04
	Model 2 (Deer + DSW)	
Intercept	4084 / 1.09	3710 / 0.99
Deer density	4028 / 1.08	3973 / 1.06
DSW	3973 / 1.06	3866 / 1.03
Stand Stdev	4028 / 1.08	4028 / 1.08
	Model 3 (PGC + DSW)	
Intercept	3973 / 1.06	3710 / 0.99
Centered PGC	3973 / 1.06	3710 / 0.99
DSW	3866 / 1.03	3761 / 1.00
Stand Stdev	3973 / 1.06	4084 / 1.09

Deer= winter deer density in 10's of deer / km^2, DSW=deep snow weeks (number of weeks from November 2007 to April 2008 with snow depth > 40 cm), PGC= pellet group count (the number of deer fecal pellets found within a 40 m^2 area in a planted harvest gap), Stand Stdev= standard deviation for the random stand-level intercept.

Table D.10. Convergence in multilevel logistic models of gap-level percentage of seedlings browsed within gaps with gap- and stand-level covariates for stands where DLC could be determined: Sample size (N obs.), burn-in length (N.burnin), iterations after burn-in (N.iter), thinning factor (T.factor) and Raftery-Lewis diagnostic *N* (number of iterations required to have a 95% probability of estimating the 2.5% quantile with a tolerance of +/-0.5%) and *I* (Dependence Factor) from three parallel MCMC chains.

Species	Hemlock	White pine
N obs. gaps/stands	126 / 13	126 / 13
N.burnin	10,000	10,000
N.iter	30,000	30,000
T.factor	5	5
Variable	Raftery-Lewis Diagnostics (*N* / *I*)	
Model 1 (null)		
Intercept	3973 / 1.06	3866 / 1.03
Stand Stdev	4084 / 1.09	3973 / 1.06
Model 4 (DLC + PGC + DSW)		
Intercept	4050 / 1.08	3973 / 1.06
Centered DLC	4558 / 1.22	5485 / 1.46
Centered PGC	5408 / 1.44	5705 / 1.52
DSW	3866 / 1.03	3866 / 1.03
Stand Stdev	3973 / 1.06	3866 / 1.03
Model 5 (DLC)		
Intercept	4084 / 1.09	3761 / 1.00
Centered DLC	5095 / 1.36	4623 / 1.23
Stand Stdev	4028 / 1.08	4028 / 1.08

DSW=deep snow weeks (number of weeks from November 2007 to April 2008 with snow depth > 40 cm), PGC= pellet group count (the number of deer fecal pellets found within a 40 m^2 area in a planted harvest gap), DLC= distance to lowland conifer in 10s of m, Stand Stdev= standard deviation for the random stand-level intercept.

APPENDIX E: Model Parameters

Bayesian inference was used with Markov chain Monte Carlo (MCMC) sampling to estimate parameter values and obtain credible intervals for generalized linear mixed models (GLMM), linear mixed models (LMM) and linear models (LM).

Table E.1. Effects of gap and stand-level variables on seedling abundance <1 m tall: mean parameter estimates and 95% credible interval from posterior distributions. Positive values indicate increases in seedling abundance with a one standard deviation increase in that covariate on the log scale. AOCa is the reference Habitat Type. A decrease in DIC of 5 or more indicates improved performance for full model over the null model.

Variable	Sugar maple		Ironwood		Other Spp	
	Mean	CI	Mean	CI	Mean	CI
GLMM full model						
Gap level						
Canopy openness	-0.08	-0.31 – 0.14	-0.13	-0.52 – 0.26	0.21	-0.07 – 0.48
Competing veg	-0.23**	-0.42 – -0.05	-0.34*	-0.71 – 0.02	-0.43**	-0.70 – -0.16
SP_{2008}	0.12	-0.06 – 0.30	0.37**	0.08 – 0.74	-0.03	-0.25 – 0.21
Stand level						
Intercept	1.40**	0.80 – 2.00	-0.37	-1.23 – 0.43	-0.90**	-1.82 – -0.08
ATD-Hp	0.18	-0.70 – 1.08	-0.02	-1.27 – 1.21	1.49**	0.30 – 2.75
ATD	1.50**	0.55 – 2.48	-2.11**	-3.81 – -0.61	0.83	-0.49 – 2.19
ATM	1.15**	0.16 – 2.15	-1.86**	-3.53 – -0.29	0.94	-0.44 – 2.35
TMC	1.74*	-0.13 – 3.65	-2.91	-7.14 – 0.55	3.68**	1.18 – 6.31
Deer density	-0.24	-0.61 – 0.12	0.11	-0.43 – 0.68	-0.08	-0.61 – 0.42
Time since harvest	0.24	-0.10 – 0.58	-0.53*	-1.11 – 0.04	0.21	-0.27 – 0.70
Variance components						
r	0.94	0.76 – 1.16	0.50	0.32 – 0.75	0.78	0.56 – 1.06
Stand-level Stdev	1.14	0.88 – 1.45	1.45	0.94 – 2.10	1.52	1.11 – 2.06
DIC		2172.61		701.20		1132.04
GLMM null model						
Intercept	2.06**	1.69 – 2.42	-0.99**	-1.58 – -0.47	-0.02*	-0.57 – 0.48
r	0.90	0.73 – 1.09	0.45	0.29 – 0.68	0.77	0.56 – 1.05
Stand-level Stdev	1.32	1.05 – 1.66	1.54	1.06 – 2.15	1.74	1.33 – 2.28
DIC		2184.88		714.41		1132.46
N. gaps / stands		337 / 59		337 / 59		337 / 59

**indicates 95% credible interval does not overlap 0, * indicate 90% CI does not overlap 0

r= negative binomial gap-level dispersion parameter, SP_{2008}= seedling production potential (Σdiameter/distance^2) for 2008, Stand-level Stdev= standard deviation for the random stand-level intercept.

Table E.2. Effects of gap and stand-level variables on sapling abundance 1-2 m tall: mean parameter estimates and 95% credible interval from posterior distributions. Positive values indicate increases in sapling abundance with a one standard deviation increase in that covariate on the log scale. AOCa is the reference Habitat Type for ironwood and other species. ATD-Hp and AOCa were combined as the reference Habitat Types to improve convergence of the sugar maple model. A decrease in DIC of 5 or more indicates improved performance for full model over the null model.

Variable	Sugar maple		Ironwood		Other Spp	
	Mean	CI	Mean	CI	Mean	CI
			GLMM full model			
Gap level						
Canopy openness	0.29**	0.03 – 0.56	0.05	-0.30 – 0.40	0.59**	0.33 – 0.86
Competing veg	-0.49**	-0.72 – -0.26	-0.15	-0.48 – 0.19	-0.42**	-0.70 – -0.14
$SP_{Harvest}$	-0.07	-0.23 – 0.09	-0.04	-0.23 – 0.21	0.07	-0.10 – 0.27
Stand level						
Intercept	-5.32**	-7.70 – -3.53	0.38	-1.30 – 1.91	-0.67	-2.18 – 0.71
ATD-Hp	NA	NA	-0.48	-2.80 – 1.86	0.76	-1.30 – 2.85
ATD	7.63**	5.23 – 10.58	-1.48	-4.06 – 1.08	1.64	-0.51 – 3.89
ATM	7.40**	4.90 – 10.46	-0.41	-2.96 – 2.23	1.47	-0.78 – 3.78
TMC	8.34**	3.59 – 13.80	-1.75	-6.93 – 3.19	3.35	-0.80 – 7.71
Deer density	-1.24**	-2.47 – -0.08	0.42	-0.55 – 1.37	-0.49	-1.34 – 0.36
Time since harvest	0.75	-0.17 – 1.73	-0.02	-0.90 – 0.88	0.39	-0.40 – 1.19
Variance components						
r	1.49	1.06 – 2.01	0.64	0.48 – 0.82	0.84	0.64 – 1.07
Stand-level Stdev	2.93	2.10 – 4.11	3.03	2.25 – 4.08	2.68	2.05 – 3.50
DIC		1197.10		1299.96		1468.80
			GLMM null model			
Intercept	-2.05**	-4.10 – -0.41	-0.08	-0.95 – 0.70	0.44	-0.35 – 1.18
r	1.28	0.94 – 1.72	0.64	0.49 – 0.82	0.74	0.58 – 0.94
Stand-level Stdev	5.46	3.99 – 7.55	2.78	2.12 – 3.65	2.64	2.05 – 3.41
DIC		1218.17		1296.83		1489.85
N. gaps / stands		331 / 58		331 / 58		331 / 58

**indicates 95% credible interval does not overlap 0

r= negative binomial gap-level dispersion parameter, $SP_{Harvest}$= seedling production potential (Σdiameter/distance^2) at the time of harvest, Stand-level Stdev= standard deviation for the random stand-level intercept.

Table E.3. Effects of gap and stand-level variables on log transformed sapling 1-7m tall: mean parameter estimates and 95% credible interval from posterior distributions. Only gaps with stocking-levels > 0 by species were used in these analyses. Positive values indicate increases in stocking-levels on the log scale with a one standard deviation increase in that covariate. AOCa is the reference Habitat Type. A decrease in DIC of 5 or more indicates improved performance for full model over the null model.

Variable	Sugar maple		Ironwood		Other Spp	
	Mean	CI	Mean	CI	Mean	CI
LMM full model						
Gap level						
Canopy openness	-0.05	-0.30 – 0.21	0.09	-0.20 – 0.38	0.31**	0.02 – 0.61
Competing veg	-0.36**	-0.61 – -0.11	-0.38**	-0.65 – -0.10	-0.36**	-0.64 – -0.08
$SP_{Harvest}$	0.02	-0.17 – 0.22	0.00	-0.16 – 0.16	0.02	-0.17 – 0.23
Stand level						
Intercept	-2.10**	-2.99 – -1.24	-2.30**	-3.04 – -1.57	-3.43**	-4.26 – -2.63
ATD-Hp	-0.09	-1.40 – 1.22	-0.14	-1.21 – 0.93	0.63	-0.61 – 1.87
ATD	1.39**	0.18 – 2.60	0.00	-1.22 – 1.21	1.21**	0.01 – 2.42
ATM	0.69	-0.53 – 1.93	-0.16	-1.37 – 1.04	0.61	-0.65 – 1.89
TMC	0.56	-1.59 – 2.70	0.83	-2.05 – 3.70	1.28	-1.02 – 3.59
Deer density	-0.26	-0.74 – 0.22	0.20	-0.29 – 0.70	-0.23	-0.74 – 0.28
Time since harvest	0.02	-0.40 – 0.43	0.18	-0.20 – 0.57	0.24	-0.23 – 0.72
Variance components						
Stand-level Stdev	1.20	0.86 – 1.62	1.20	0.88 – 1.60	1.30	0.94 – 1.73
Gap-level Stdev	1.12	0.99 – 1.28	1.18	1.04 – 1.33	1.25	1.12 – 1.41
DIC		540.62		622.61		674.85
LMM null model						
Intercept	-1.50**	-1.96 – -1.05	-2.34**	-2.72 – -1.96	-2.73**	-3.17 – -2.30
Stand-level Stdev	1.35	1.03 – 1.75	1.14	0.84 – 1.50	1.34	1.02 – 1.74
Gap-level Stdev	1.14	1.01 – 1.30	1.20	1.07 – 1.36	1.27	1.13 – 1.42
DIC		544.32		625.81		675.80
N. gaps / stands		164 / 45		184 / 49		193 / 48

**indicates 95% credible interval does not overlap 0

$SP_{Harvest}$= seedling production potential (Σdiameter/distance^2) at the time of harvest, Stand-level Stdev= standard deviation for the random stand-level intercept.

Table E.4. Effects of gap and stand-level variables on square root transformed Shannon Diversity Index (H') for seedlings, saplings 1-2 m and saplings 1-7 m tall: mean parameter estimates and 95% credible interval from posterior distributions. Only gaps with H' > 0 by size class were used in these analyses. Positive values indicate increases in H' on the square root scale with a one standard deviation increase in that covariate. AOCa is the reference Habitat Type. A decrease in DIC of 5 or more indicates improved performance for full model over the null model.

Variable	H' Seedlings		H' Saplings 1-2 m		H' Saplings 1-7 m	
	Mean	CI	Mean	CI	Mean	CI
			LMM full model			
Gap level						
Canopy openness	0.02	-0.02 – 0.05	0.00	-0.04 – 0.05	0.00	-0.04 – 0.04
Competing veg	-0.01	-0.04 – 0.03	0.03	-0.01 – 0.07	0.02	-0.02 – 0.06
H' Overstory[1]	0.07**	0.04 – 0.10	0.02	-0.02 – 0.07	0.02	-0.02 – 0.06
Stand level						
Intercept	0.75**	0.68 – 0.82	0.78**	0.66 – 0.90	0.80**	0.69 – 0.90
ATD-Hp	0.04	-0.06 – 0.14	-0.11	-0.28 – 0.07	-0.09	-0.24 – 0.06
ATD	-0.10*	-0.21 – 0.01	-0.17**	-0.34 – -0.005	-0.14*	-0.29 – 0.01
ATM	-0.10*	-0.22 – 0.01	-0.13	-0.30 – 0.04	-0.10	-0.25 – 0.05
TMC	0.00	-0.21 – 0.21	0.10	-0.21 – 0.40	0.06	-0.21 – 0.33
Deer density	0.01	-0.04 – 0.05	-0.04	-0.10 – 0.03	-0.03	-0.09 – 0.03
Time since harvest	0.02	-0.02 – 0.06	0.00	-0.06 – 0.06	0.00	-0.05 – 0.05
Variance components						
Stand-level Stdev	0.10	0.06 – 0.14	0.16	0.10 – 0.22	0.14	0.09 – 0.19
Gap-level Stdev	0.16	0.14 – 0.18	0.19	0.17 – 0.22	0.19	0.17 – 0.22
DIC	-112.27		-46.81		-54.46	
			LMM null model			
Intercept	0.73*	0.69 – 0.77	0.69*	0.63 – 0.75	0.72*	0.67 – 0.77
Stand-level Stdev	0.12	0.08 – 0.17	0.16	0.12 – 0.21	0.14	0.10 – 0.18
Gap-level Stdev	0.17	0.15 – 0.19	0.19	0.17 – 0.22	0.19	0.17 – 0.22
DIC	-100.26		-50.06		-57.47	
N. gaps / stands	182 / 54		180 / 42		201 / 46	

**indicates 95% credible interval does not overlap 0, * indicates 90% CI does not overlap 0
Stand-level Stdev= standard deviation for the random stand-level intercept

[1] H'Overstory for H'Seedlings is Shannon Diversity of overstory trees, H'Overstory for H'Saplings 1-2 and 1-7 m tall is Shannon Diversity of overstory trees and stumps

Table E.5. Effects of gap and stand-level variables on log transformed sapling after harvest growth rates (m/yr): mean parameter estimates and 95% credible interval from posterior distributions. Positive values indicate increases in growth rate on the log scale with a one standard deviation increase in that covariate. AOCa is the reference Habitat Type. A decrease in DIC of 5 or more indicates improved performance for full model over the null model.

Variable	Sugar maple		Ironwood	
	Mean	CI	Mean	CI
	LM full model			
Intercept	-1.28**	-1.40 – -1.16	-1.26**	-1.42 – -1.10
Advanced regen	-0.40**	-0.53 – -0.28	-0.23**	-0.38 – -0.08
Sapling height	0.32**	0.26 – 0.38	0.34**	0.26 – 0.41
Canopy openness	-0.03	-0.08 – 0.02	0.06*	-0.01 – 0.13
Competing veg	0.00	-0.04 – 0.05	0.02	-0.03 – 0.07
ATD-Hp	-0.14	-0.48 – 0.21	-0.09	-0.24 – 0.06
ATD	-0.09	-0.21 – 0.04	0.06	-0.10 – 0.23
ATM	-0.06	-0.21 – 0.08	-0.07	-0.24 – 0.09
TMC	-0.12	-0.33 – 0.08	-0.03	-0.28 – 0.23
Deer density	-0.02	-0.09 – 0.05	0.03	-0.03 – 0.08
Time since harvest	-0.26**	-0.31 – -0.21	-0.10**	-0.17 – -0.02
Variance components				
Sapling Stdev	0.23	0.21 – 0.27	0.24	0.21 – 0.28
DIC	2.34		13.64	
	LM null model			
Intercept	-1.64**	-1.70 – -1.57	-1.46*	-1.53 – -1.38
Sapling Stdev	0.38	0.34 – 0.43	0.37	0.32 – 0.43
DIC	114.86		84.03	
N. gaps / stands	127 / 26		98 / 30	

**indicates 95% credible interval does not overlap 0, * indicates 90% CI does not overlap 0

Advanced regen= bivariate variable indicating if a variable is advanced regeneration.

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