

Analysis of white-tailed deer (*Odocoileus virginianus* Zimmerman) browse impacts and implications for forest health across the Lake States region of the United States

A Thesis

SUBMITTED TO THE FACULTY OF THE
UNIVERSITY OF MINNESOTA

BY

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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
MASTER OF SCIENCE

Dr. Matthew Russell

May 2017

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Acknowledgements

I would like to extend a tremendous thanks to my advisor, Matthew Russell, for providing insight, guidance, and support throughout my graduate coursework and thesis. You have challenged me, intellectually, and encouraged a rigorous statistical background to prepare me for my future endeavors in research. I also wish to acknowledge my committee members, Marcella Windmuller-Campione, Lee Frelich, and Meredith Cornett for encouraging and challenging me to think beyond my study and for providing career advice along the way. I also wish to thank my advisor and committee for providing mentorship throughout my time here at the University of Minnesota.

This research would not be possible without the many entities providing the datasets used in this analysis. I would like to extend a thanks to the Michigan State Police, Minnesota Department of Public Safety, and Wisconsin Department of Transportation for recording and providing data on deer-vehicle collisions. Additionally, the Quality Deer Management Association for providing their deer density map. And, the Center for Disease Control for recording and reporting Lyme Disease Cases.

A big thanks to the USDA Forest Service Forest Inventory and Analysis program and all of the field crews for creating a nationally consistent inventory of forests across the US and providing opportunities for researchers to utilize that data to expand our understanding of forested ecosystems.

Most importantly, I wish to thank my parents for their dedicated, unwavering support of me throughout each adventure that has brought me here today.

Finally, a special thanks to the University of Minnesota Office of the Vice President and the Minnesota Department of Natural Resources for supporting this work.

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Chapter 1: Introduction

Since European settlement, people have been managing ungulate populations to best suit societal desires. Historically, caribou, elk, and moose had home ranges across much of the Lake States region, but only small areas of moose populations remain due to anthropogenic changes across the landscape. Much of the Lake States region is now dominated by white-tailed deer (*Odocoileus virginianus* Zimmerman) populations, which did not exist as far north prior to European settlement (MN DNR, 2016).

White-tailed deer provide opportunities for hunting and recreation, but also can become a burden to society with overabundant populations, due to the increase in number of negative deer-human interactions (ie. deer-vehicle collisions, crop browse, Lyme disease cases). Because of this unique mix of stakeholders, there has been a push to create management plans for white-tailed deer. Michigan has updated their deer management plan as of December 2016 and Minnesota is in the process of creating a state wide management plan.

In addition to their societal effects, white-tailed deer can dramatically alter forested ecosystems by severely browsing select species, sometimes to local extirpation. Continual browse of only select species alters natural selection and creates long term changes across the forest (DiTommaso et al. 2014; Frerker et al. 2014). White-tailed deer can also function as an invasive vector by providing growing space for plants such as garlic mustard and buckthorn, which deer rarely consume (Meekins and Mccarthy 1999; Roberts and Anderson 2001).

Many studies have recently aimed to address impacts of continuous deer browse on forested ecosystems, because of their complex direct and indirect effects on the ecosystem. However, estimates of deer populations and population management goals vary greatly across ownerships and state lines. Deer populations are typically estimated by deer harvests each year, which is an incredibly biased estimator and provides no information on population structure (Anderson 2001). These conveniently available data should not be one of the only metrics available for natural resource managers to use to make long term management plans.

The USDA Forest Service Forest Inventory and Analysis (FIA) Program has created a deer browse metric in order to provide a nationally consistent measure of deer browse impacts. This phase of the FIA program (Phase 2-plus) was developed in 2012 and provides on-the-ground measures of white-tailed deer browse impacts in forested plots across the northern US. This is the first nationally-consistent metric ever created to assess deer browse impacts.

Managing natural resources in the face of overabundant white-tailed deer requires appropriate planning, because economic losses can be severe (Switzenberg et al. 1955). Bud capping and tree tubes provide protection from browse for seedlings, but involve significant costs to implement and maintain. Large deer exclosures provide more long-term protection, but are associated with increased economic constraints. Alternatively, accounting for deer browse losses in the long term, without any browse protection, is difficult to predict and risky when managing for timber.

The first research chapter in this study (Chapter 2) aims to utilize the current four years of FIA Phase 2-plus plot data to model browse pressure across the three Lake States: Michigan, Minnesota, and Wisconsin. These models can be used to predict deer browse pressure across the Lake States. Chapter 3 aims to utilize FIA data for the five most palatable species in the Lake States to assess seedling and sapling abundance in the presence of different levels of deer browse. The final chapter (Chapter 4) summarizes conclusions and provides management implications based on these results and suggestions for potential future research.

Chapter 2: Quantifying impacts of white-tailed deer browsing with forest inventory and socio-environmental datasets

2.1. Introduction

Deer browsing can have dramatic direct and indirect effects on the forest habitat, such as changes in the food web, vegetation structure, nutrient cycling (Rooney and Waller 2003; Nuttle et al. 2014), and the spread of invasive plants (Russell et al. 2017). White-tailed deer (*Odocoileus virginianus* Zimmerman) consume buds and twigs of young trees as well as many understory herbaceous plants. Once trees grow large enough to be out of the reach of deer, they can no longer be browsed, which suggests that seedlings and saplings are the most vulnerable to damage (Bradshaw and Waller 2016). A study of vegetation in deer exclosures in Wisconsin showed that deer cause long-term regional shifts in plants, which are typically less diverse than plant communities inside of the exclosures (Frerker et al. 2014) - one of many looking at the effects of deer exclosures on vegetation. Suppression of commercially and ecologically important tree species in these critical stages of growth can alter the forest composition for decades (Alverson et al. 1988). Understanding deer densities and their effects on forest structure and composition can be critical to predicting the health and productivity of forests in the long term (White 2012).

High deer populations affect the entire forest ecosystem, which is detrimental to the ecological functioning as well as the timber industry through loss of merchantable

wood to animal browse (Tilghman 1989). Therefore, understanding how deer affect the health and productivity of forests is important across many disciplines and industries.

In addition to their effects on vegetation, deer have societal influences. Deer carry black-legged ticks (*Ixodes scapularis*) which can potentially transmit Lyme disease to humans. A study of Lyme disease cases before and after a significant deer hunt in Groton, Connecticut showed a significant decline in human Lyme disease infections following the hunt (Kilpatrick et al. 2014), which suggests that this parasitic relationship may help to estimate deer densities. Deer also contribute to vehicle crashes which can result in vehicle damages, injury, and possibly death. This information is publically reported on a regular basis and could be useful when determining the extent to which deer are affecting the forest and society.

Deer populations in the United States (US) Lake States have increased dramatically in recent decades, making them overabundant in many regions and a threat to regenerating tree species (Rooney and Waller 2003). This increase in population is mostly due to habitat modification and reduction in predatory species. For example, expanding urbanization creates a heterogeneous landscape and provides white-tailed deer with optimal habitat (Warren et al. 2017).

Deer population size is difficult to estimate, especially in a consistent fashion across land ownerships and state lines. Therefore, quantifying deer browse impacts is difficult and may require a suite of information including deer density, tree seedling and sapling abundance, and socio-environmental variables. The objective of this study is to

test the use of publicly available socio-environmental datasets in combination with forest inventory data in predicting deer browse pressure in forests of the US Lake States.

2.2. Methods

2.2.1. Study Area

This study was conducted across the US Lake States – in Michigan, Minnesota and Wisconsin. The Lake States contain a mixture of tallgrass prairie, temperate deciduous forests, and mixed boreal forest biomes and are defined by the Laurentian mixed forest, Eastern broadleaf forest, and Prairie parkland ecoregions. Forests of the Lake States region contain diverse forest types and are comparable to many of the world's forests found in cool-to-cold temperate zones (Frelich 2002).

2.2.2. Forest Inventory and Analysis Data

The US Department of Agriculture Forest Service's Forest Inventory and Analysis (FIA) program was the primary source of forest inventory data for this project. The FIA protocols are nationally consistent and provide a basis for comparison across regions of the United States (Bechtold and Patterson 2005). This program divides the US into populations - (typically counties) and subpopulations. Each population and subpopulation has a defined number of plots based on forested area. There are three phases of plots in the FIA program: Phase 1 (P1), Phase 2 (P2), and Phase 3 (P3). Phase 1 stratifies the land into forest- (defined as an area at least 10% stocked with trees) or nonforest using aerial or satellite imagery. Phase 2 uses standard forest inventory

methods to quantify structure, composition, and stand level attributes; plot density is approximately one plot for every 2,428-ha of forested land. Phase 3 plots occur on a subset of P2 plots (one plot every 38,850-ha) with the goal of recording additional measurements addressing forest health concerns (Bechtold & Patterson, 2005).

Each P2 and P3 plot contains four subplots arranged as a central point with three points clustered around the center. The outer points lie 36.58-m from the center at an azimuth of 0, 120, and 240 degrees. Each point denotes the center of a fixed radius plot with a 7.32-m radius in which all trees 12.7-cm and larger in diameter at breast height (DBH) are measured. A microplot, located 3.66-m off center and at an azimuth of 90 degrees, has a 2.07-m radius in which saplings (2.54 to 12.45-cm DBH) and seedlings were measured. Within each microplot all live tree seedlings were tallied, where conifer and hardwood seedlings were at least 15.2 and 30.5-cm in height, respectively, with both having a $DBH \leq 2.5$ -cm.

Collection for yet another FIA category, Phase 2-plus, began in 2012 in the northern US on a subset of P2 plots. One plot was sampled every 19,425-ha of forest. In each plot, browse impact, which was defined as consumption of shoots, twigs, and leaves by animals for food and was recorded on a scale of 1-5 (exclosure, no browse, some browse, high browse, and severe browse, respectively) on seedlings at least 5.08-cm tall (McWilliams et al. 2015). In total, 792 Phase 2-plus plots were available from 2012-2015 (four years of data available from a seven year cycle) in the Lake States, obtained from the PLOT_REGEN tables.

All FIA data were accessed via the “FIA DataMart” (www.fia.fs.fed.us/tools-data, downloaded 20 June 2016). From the P2 FIA plots, the PLOT, TREE, and SEEDLING tables were used to obtain information on live trees.

2.2.3. Socio-environmental Datasets

Socio-environmental datasets were used to determine their predictive power in estimating deer browse effects in forest ecosystems. These freely available datasets included the Centers for Disease Control and Prevention (CDC) Lyme disease surveillance data (Figure 1), deer-motor vehicle crashes (Figure 2), and Quality Deer Management Association (QDMA) deer density estimates (Figure 3, Adams et al. 2009; Walters et al. 2016). Census data were used in the analysis of these datasets (human populations per county) to standardize these population-dependent variables per million residents (<http://www.census.gov/popest/data/index.html>).

Lyme disease is an infectious disease caused by *Borrelia burgdorferi*, a spirochete bacterium, which is carried via *Ixodes scapularis*, the deer tick. Reported CDC Lyme disease cases have been required to be reported since 1991 and are based on county of residence. A case is counted if a physician identifies a patient with *erythema migrans*, which is a type of skin lesion that occurs in 60-80% of patients with Lyme disease (<http://www.cdc.gov/lyme/stats/>). A physician can conclude a case as suspected, plausible, or confirmed based on symptoms and exposure.

Deer-vehicle collision reports were obtained from the Michigan State Police (http://www.mlive.com/news/index.ssf/2013/10/database_see_where_in_michigan.html),

Minnesota Department of Public Safety (<https://dps.mn.gov/divisions/ots/reports-statistics/Pages/Fact-sheets.aspx>), and Wisconsin Department of Transportation (<http://wisconsin.gov/Pages/safety/education/crash-data/crashfacts.aspx>). Total annual deer-vehicle collisions by county were obtained from these sources for 2012 through 2015.

Deer density estimates were obtained from the QDMA spatial map (Walters et al. 2016). There were five categories for deer density, based on deer per square kilometer: rare, less than 5.8 deer km⁻², 5.8 to 11.6 deer km⁻², 11.6 to 17.4 deer km⁻², more than 17.4 deer km⁻² (Adams et al. 2009).

2.2.4. Models of Deer Browse Impacts

R computational software was utilized in creating statistical models (R Core Team 2015). All analyses and comparisons occurred at the county or plot level. Tree stand and stocking information was summarized using FIA data to provide trees per hectare (TPH) for seedlings, saplings, and overstory trees and overstory basal area per hectare (BA m²ha⁻¹) at the plot level.

All models were created using the randomForest package (Breiman 2001), which was implemented in R and utilizes classification trees of bootstrapped samples to determine variable importance (Liaw and Wiener 2002). Variable importance was used to determine the most important variables in models predicting deer browse for forests across the region based on Lyme disease, deer-vehicle collisions, deer density data, and forest inventory variables (ie. basal area, trees per hectare). Plots from 2012-2015 with

forest inventory data, all socio-environmental datasets, and plots that were not located inside an exclosure were used in the analysis (n=786). With this package, bootstrapped estimates of classification trees were estimated and 20% of the observations from the dataset were used to compare model performance.

Additionally, reduced models were created by eliminating the least important variables and running the model again until the three most important variables were identified. To validate model accuracy, 20% of the plots were randomly sampled and predicted browse score, was compared to the field-assessed browse score. This process was replicated 25 times for each model to determine model accuracy and an estimate of error.

Forest inventory variables utilized in randomForest analysis included seedling TPH, sapling TPH, overstory TPH, and overstory BA. Surrogate dataset variables included collisions per county per 1 million people, Lyme disease cases per county per 1 million people, and QDMA deer density estimates.

The full model, utilizing all of the explanatory variables, was used to predict browse scores for all FIA plots in the Lake States (Phase 2, n=12,386) that were inventoried from 2012-2015. Predicted browse scores for all FIA plots were analyzed in ArcMap to create a map of browse score using inverse distance weighting (IDW; ESRI 2011). The IDW tool in ArcMap weights measured values that are nearest to each other to predict values at unmeasured locations. This interpolation takes into account distance between points as well as spatial arrangement of the measured points. The result is a graphical representation of deer browse severity across the study region.

2.3. Results

2.3.1. Socio-environmental and Deer Density Trends

Forest inventory plots with browse scores were distributed across the forested portions of the Lake States, with less dense areas in northwest and southwest Minnesota, and southeast portions of Wisconsin and Michigan (Figure 2.1). Some level of browsing occurred in more than half of the plots in Michigan and Wisconsin – low browse on 58.0% and 62.0% of plots and high or severe browse on 3.4% and 14.0% of plots, respectively. In Wisconsin, most of the browsed plots occurred in the northern half of the state. Michigan had some areas with high deer browse in the Upper Peninsula as well as in the northern half of the Lower Peninsula. Compared to Michigan and Wisconsin, Minnesota had more plots with no browse (60.8% of plots) and the most plots of all three of the states. Minnesota displayed diverse browse impacts across the landscape, with most of the highly browsed plots located in central and northern Minnesota. The severely browsed FIA plots were only in Minnesota and Wisconsin, one in the north-central part of Minnesota, two in the north, north-west portion of Wisconsin and the final two plots located in the southeast and southwest parts of Minnesota and Wisconsin, respectively (Table 2.1, Figure 2.1).

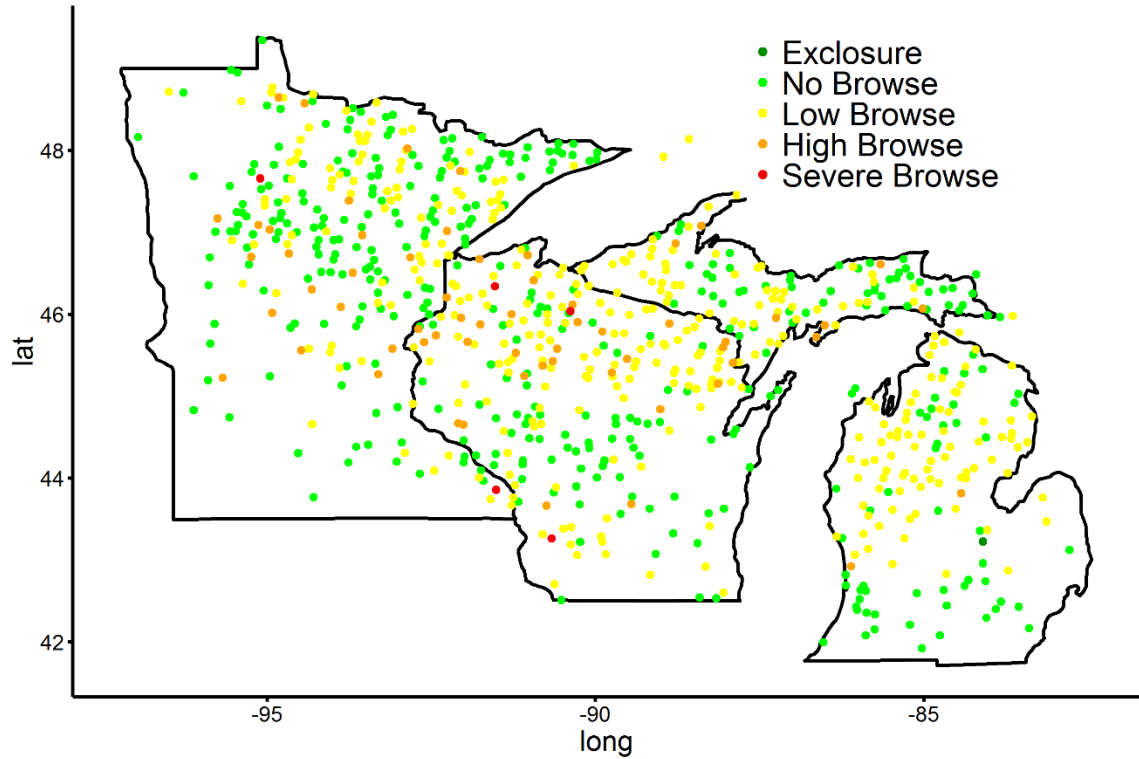


Figure 2.1. Location of FIA Phase 2-plus plots (n=792) within the Lake States with corresponding browse impact score, 2012-2015. Plots located outside the delineated state borders occurred on islands of the Lake States.

Seedling TPH varied more than sapling or overstory TPH for Phase 2 and Phase 2-plus plots (Table 2.1). There was a greater distribution of seedling TPH for Phase 2 versus Phase 2-plus plots, but overall standard deviations were less for Phase 2 plots. Variability for seedling TPH was also the highest across the size classes. The distribution of overstory BA was nearly the same for both phases, where Phase 2 plots showed a slightly higher maximum.

Table 2.1. Summary statistics for forest inventory variables used in randomForest analysis from Phase 2-plus and Phase 2 plots.

Variable	Min	Mean	Max	SD
<i>Phase 2-plus (n=792)</i>				
Seedling TPH	0	7268	55758	7864
Sapling TPH	0	1232	13893	1411
Overstory TPH	0	386	1889	279
Overstory BA (m ² ha ⁻¹)	0	16.78	57.96	11.42
<i>Phase 2 (n=12,386)</i>				
Seedling TPH	0	5608	116703	6614
Sapling TPH	0	1285	13893	1421
Overstory TPH	0	374	1993	264
Overstory BA (m ² ha ⁻¹)	0	16.17	75.63	11.51

Note: TPH, trees per hectare; BA, basal area; SD, standard deviation

One plot from 2012-2015 was located within an enclosure (Table 2.2). The most severe browse occurred on two plots in Minnesota and three plots in Wisconsin. The majority of plots were classified as no browse or low browse (Browse Impact Code 2 or 3, Table 2.2).

Table 2.2. Browse impact criteria for FIA Phase 2-plus plots and number of FIA plots within each state measured between 2012-2015.

Browse Assessment	Browse Impact Code	MI Plots	MN Plots	WI Plots
Within an enclosure	1	1	0	0
No browse; no enclosure	2	109	175	92
Low browse; not affecting seedling abundance	3	143	90	116
High amount of browse; or low seedling abundance	4	9	21	31
Most severe browse	5	0	2	3

Lyme disease cases did not occur in every county across the Lake States from 2012-2015. Many areas in southwest Minnesota (7/87 counties) and across Michigan (28/83 counties) did not have reported cases of Lyme disease. All counties in Wisconsin had at least one reported case of Lyme disease from 2012-2015. The greatest number of Lyme disease cases per one million people was Menominee County (0.24 individuals) in Wisconsin, Cass County (0.17 individuals) in Minnesota, and Menominee County (4.8×10^{-4} individuals) in Michigan. Of the counties with reported Lyme disease cases, Wisconsin counties varied from 7.4×10^{-4} to 0.24, Minnesota counties varied from 1.9×10^{-3} to 0.17, and Michigan counties varied from 5.8×10^{-5} to 0.09 individuals per one million people (Figure 2.2).

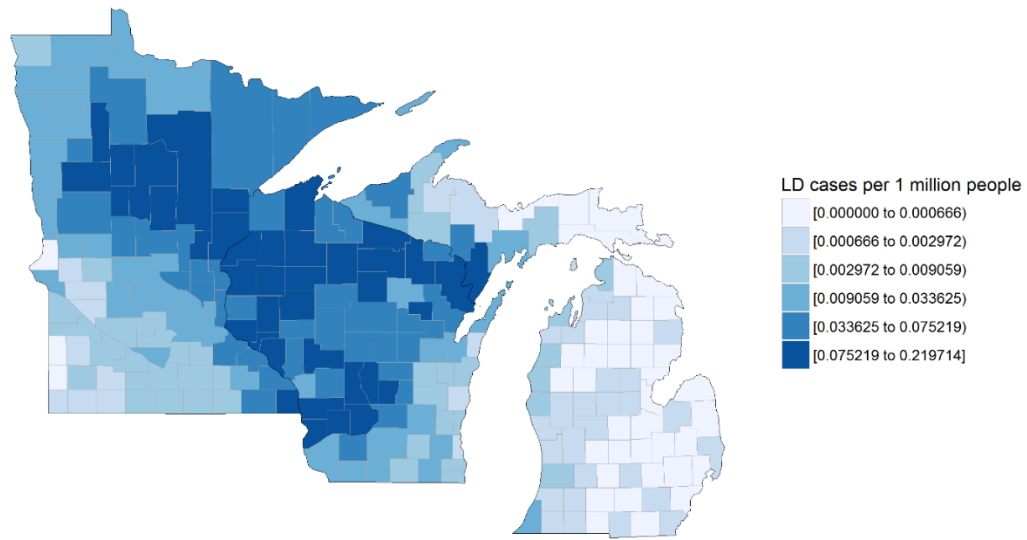


Figure 2.2. Average annual reported cases of Lyme disease per one million people based on county of residence for 2012-2015 in the Lake States.

Each county across the Lake States had at least one reported collision from 2012-2015. The greatest number of collisions per one million people occurred in Alcona County (3.9 individuals) in Michigan, Shawano County (1.8 individuals) in Wisconsin, and Lincoln County (1.5×10^{-3} individuals) in Minnesota and minimums of 2.3×10^{-2} , 1.8×10^{-2} , and 5.6×10^{-3} individuals per one million people in those respective counties. The top 21 counties with the highest number of collisions per one million people all occurred in Michigan (Figure 2.3).

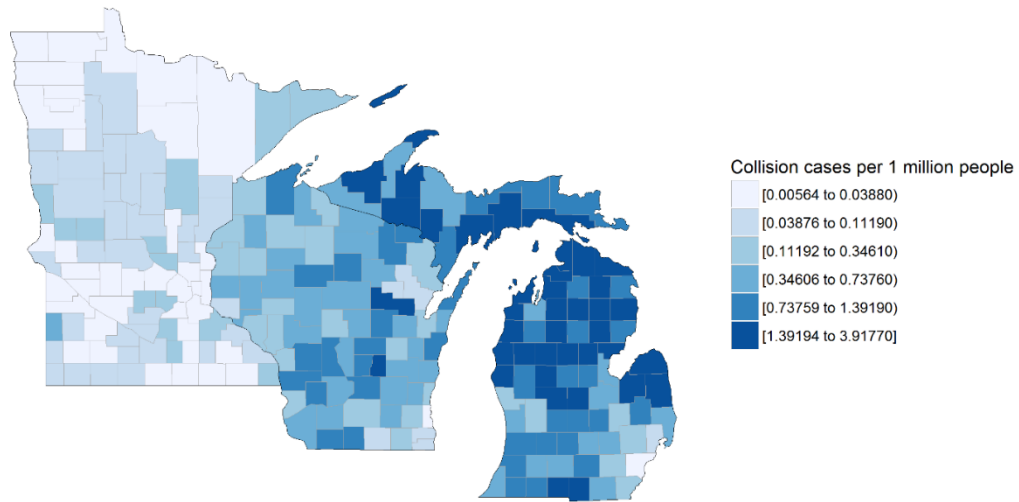


Figure 2.3. Average annual reported cases of deer-vehicle collisions per one million people for 2012-2015 in the Lake States.

From the QDMA deer density map, the maximum possible deer density of >17.4 deer km^{-2} was only observed in Wisconsin (59.7% of counties, 89 FIA plots) and Michigan (9.6% of counties, 17 FIA plots). Minnesota did not have any plots with the highest deer density, >17.4 deer km^{-2} . A rare deer density was only recorded in two plots in Wayne County, Michigan. Wisconsin did not have any plots with rare density or <5.8 deer km^{-2} . Wisconsin generally had the highest deer density, followed by Michigan and Minnesota (Figure 2.4).

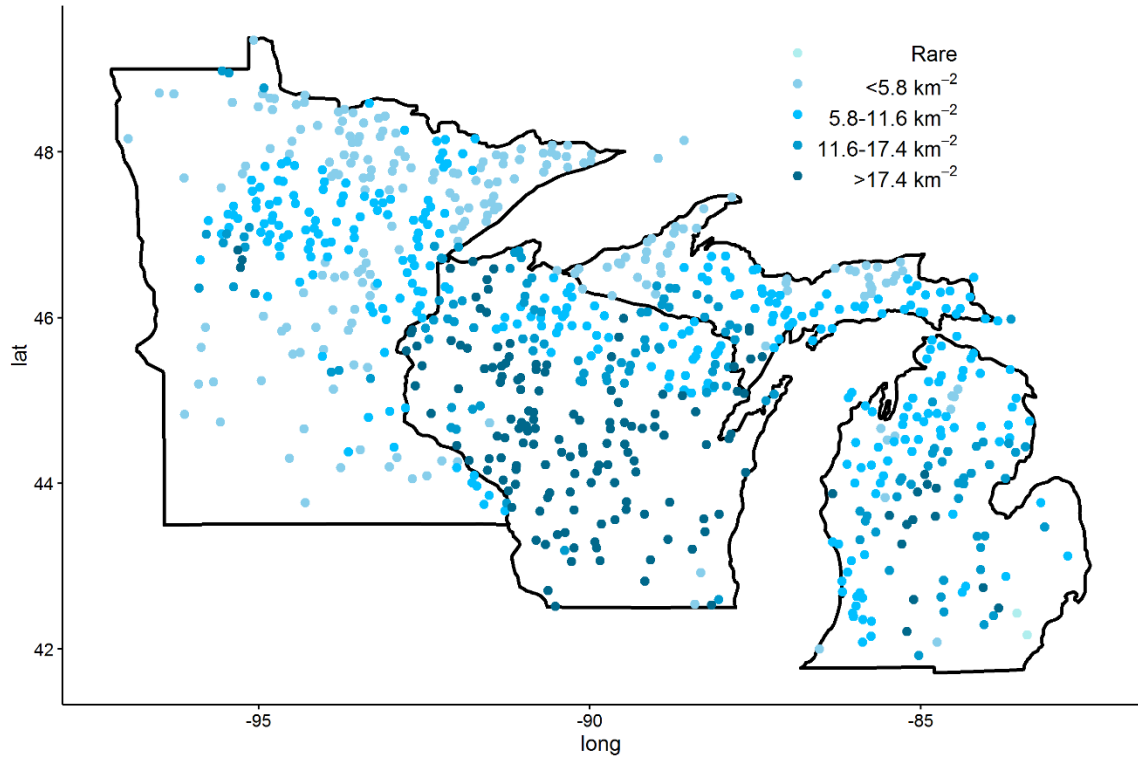


Figure 2.4. Location of FIA Phase 2-plus plots (n=792) within the Lake States measured between 2012-2015 with corresponding deer density provided by QDMA. Plots located outside the delineated state borders occurred on islands of the Lake States.

2.3.2. *Models of Deer Browse Impacts*

The most important variables varied for each of the eight models created (Table 2.3, 2.4). The top three variables for the all states reduced model were deer vehicle collisions, QDMA deer density, and Lyme disease cases with a variable mean decrease accuracy of 34.88%, 26.17%, and 24.31%, respectively.

Table 2.3. Models for Lake States region created using randomForest analysis with explanatory variables listed in order of importance predicted by the models.

State	Model	n	Variable	VarImp ¹
All	Full	786	Car collisions	16.29
			Deer density	10.39
			Lyme disease cases	8.20
			Overstory BA	7.00
			Sapling TPH	5.54
			Overstory TPH	4.16
			Seedling TPH	2.50
All	Reduced	786	Car collisions	34.88
			Deer density	26.17
			Lyme disease cases	24.31

Car collisions and Lyme disease cases are cases per one million people provided by the census.

¹VarImp: variable importance

Deer vehicle collisions ranked high in importance for both Michigan and Minnesota models, but not the Wisconsin models. QDMA deer density estimates ranked high for the Michigan and Wisconsin models, but not the Minnesota models. Sapling TPH was the lowest ranking in importance for all three full models for each of the states (Table 2.4).

Table 2.4. Models for each individual state created using randomForest analysis with explanatory variables listed in order of importance predicted by the models.

State	Model	n	Variable	VarImp ¹
MI	Full	260	Car collisions	16.19
			Overstory BA	6.05
			Deer density	5.47
			Lyme disease cases	4.15
			Overstory TPH	3.96
			Seedling TPH	3.74
			Sapling TPH	0.81
MI	Reduced	260	Car collisions	28.03
			Overstory BA	8.48
			Deer density	6.43
MN	Full	287	Lyme disease cases	13.52
			Seedling TPH	9.26
			Car collisions	7.89
			Overstory BA	5.47
			Overstory TPH	2.69
			Deer density	1.27
			Sapling TPH	-1.12
MN	Reduced	287	Lyme disease cases	28.61
			Car collisions	23.62
			Seedling TPH	9.70
WI	Full	239	Deer density	17.15
			Lyme disease cases	6.69
			Overstory TPH	4.66
			Overstory BA	4.38
			Car Collisions	2.88
			Seedling TPH	2.72
			Sapling TPH	1.54
WI	Reduced	239	Deer density	27.61
			Lyme disease cases	14.83
			Car collisions	7.11

Car collisions and Lyme disease cases are cases per one million people provided by the census.

¹VarImp: variable importance

The full model for all of the Lake States predicted browse score correctly for $87.62 \pm 2.50\%$ (mean \pm SD) of plots and $98.42 \pm 2.40\%$ of plots were within one score from correct (Figure 2.5, Full). The reduced model for combined Lake States predicted browse score correctly for $71.29 \pm 3.04\%$ of plots and was within one score for $96.38 \pm 2.93\%$ of plots (Figure 2.5, Reduced). The full and reduced models were off by more than one 2.05% and 4.14% of the time, respectively. The full model for Minnesota predicted browse score accurately for $90.18 \pm 4.27\%$ of plots and was within one for $98.00 \pm 3.50\%$ of plots (Figure 2.5, MN Full). The reduced model for Minnesota predicted browse score accurately for $88.49 \pm 2.91\%$ of plots and within one for $98.32 \pm 2.91\%$ of plots (Figure 2.5, MN Reduced). The full and reduced models for Minnesota were off by more than one 3.21% and 2.81% of the time, respectively. The full model for Wisconsin predicted browse score accurately for $85.58 \pm 5.83\%$ of plots and was within one for $98.33 \pm 4.63\%$ of plots (Figure 2.5, WI Full). The reduced model for Wisconsin predicted browse score accurately for $70.33 \pm 6.68\%$ of the plots and was within one for $93.58 \pm 6.12\%$ of the plots (Figure 2.5, WI Reduced). Wisconsin full and reduced models were off by more than one score level for 4.58% and 8.42% of predictions, respectively. The full model for Michigan predicted browse score accurately for $87.23 \pm 3.51\%$ of plots and was within one for $98.15 \pm 3.36\%$ of plots (Figure 2.5, MI Full). The reduced model for Michigan predicted browse score accurately for $81.92 \pm 4.15\%$ of plots and was within one for $98.77 \pm 4.55\%$ of plots (Figure 2.5, MI Reduced). The full and reduced models for Michigan predicted browse to be off by more than one level for 4.58% and 8.42% of predictions, respectively.

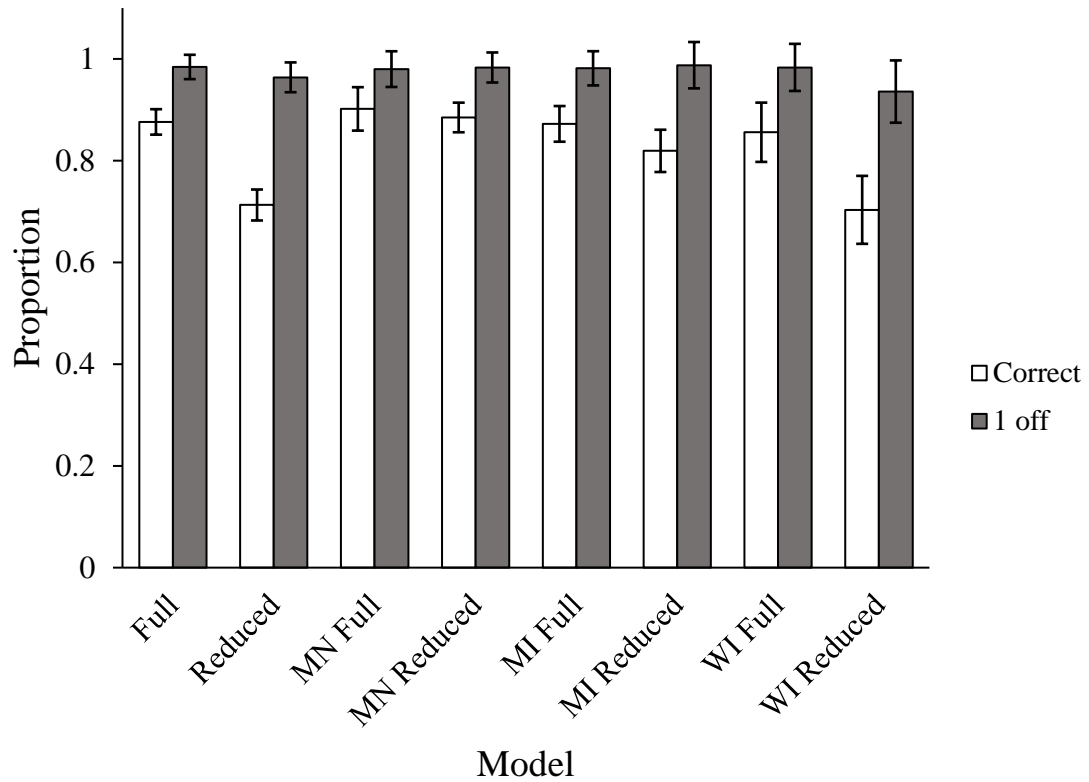


Figure 2.5. Proportion of plots with browse scores predicted correctly based on models created by randomForests for the Lake States, Minnesota (MN), Wisconsin (WI), and Michigan (MI). Correct indicates a correct predicted browse score and 1 Off indicates a browse score that was predicted within one level of the actual browse score.

Corresponding models found in Tables 2.3, 2.4.

The interpolated map of Lake States deer browse indicated most of this region was experiencing some deer browse pressure, based on the full model predictions for all states (Figure 2.6). In Minnesota, the north-central region as well as a region in the northeast displayed high browse pressure. The southern half of the state has some areas with intermediate pressure, but no major continuous high pressure areas. All of northern

Wisconsin displayed a nearly continuous high browse pressure. That high pressure area continued across the border into the Upper Peninsula of Michigan. The Lower Peninsula of Michigan had a medium to high browse pressure across most of the state. Some areas of lower pressure were mixed between areas of very high pressure. This model did not predict the most severe browse (browse score =5) for the Phase 2 plot predictions, therefore no plots are represented as higher than 4 on the browse scale (Figure 2.6).

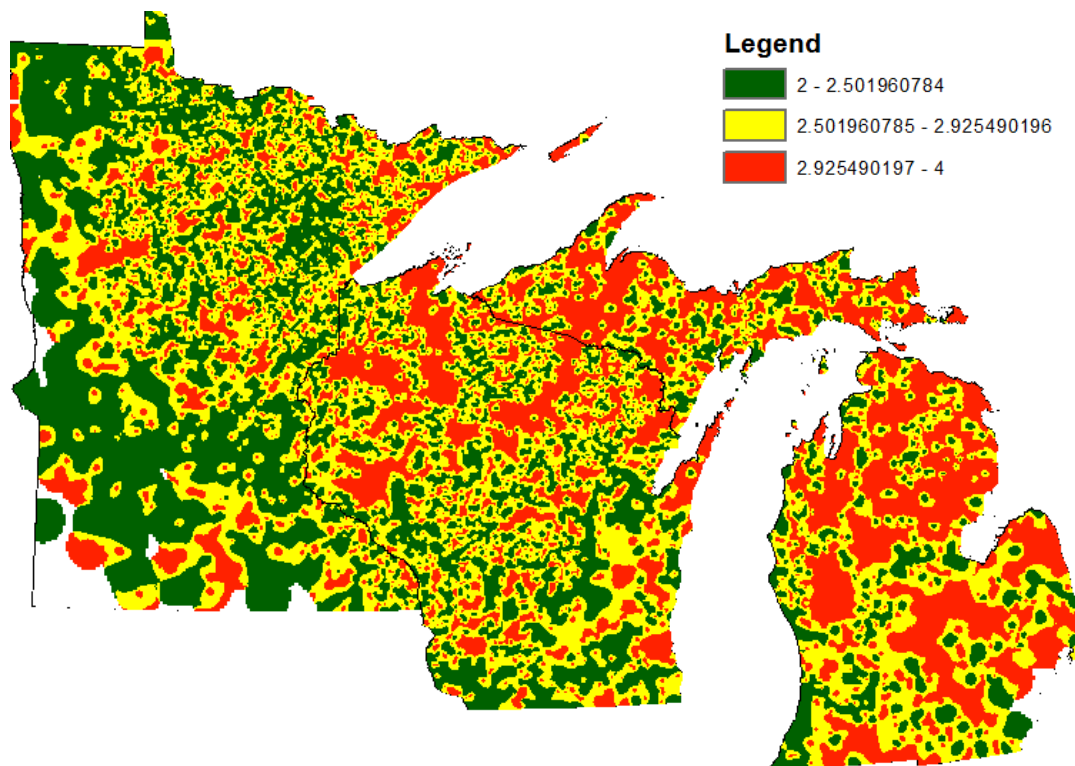


Figure 2.6. Inverse distance weighted interpolation of deer browse pressure based on predicted browse score provided by the full Lake States model. Green indicates lower browse pressure, yellow as intermediate, and red as severe. White areas indicate insufficient forest cover for accurate prediction. Legend cutoffs represent 0.33 and 0.67 quantiles of the data.

2.4. Discussion

White-tailed deer populations have put stress on forested ecosystems across many areas within the Lake States, hence, understanding their impact on our forests is essential to manage forest resources effectively. Natural resource managers need quantitative data on deer impacts in order to effectively manage forests in the face of white-tailed deer. This study utilized the FIA database and selected surrogate datasets (Lyme disease occurrence, deer collisions, QDMA deer density estimates) to predict deer browse pressure across the Lakes States with approximately 88% accuracy. The new deer browse indicator provided by the FIA program provided a nationally consistent method to quantify deer browse pressure across diverse regions and forest types.

The most important variables from the randomForests models varied between states. This is likely due to regional differences in forest types and management strategies across the Lake States as well as significant under reporting such as Lyme disease in Michigan and deer collisions in Minnesota. Additionally, deer density estimates provided by QDMA were based off of state-specific criteria. Deer-vehicle collisions were consistently one of the top predictors for all eight models created. All counties had at least one reported deer-vehicle collision from 2012-2015, hence this consistent coverage likely increased the predictive power of this variable. While deer collisions may be under-reported across all states (e.g. Minnesota had 2,096 reported deer-vehicle collisions in 2014, but State Farm Insurance projected 37,500 total deer-vehicle collisions in that year (State Farm 2015)), the proportion of collisions that are actually reported may be expected to be consistent across the study area.

Lyme disease cases also displayed high importance in most of the random forests models. The full Michigan model placed Lyme disease cases lower than that of the other models, but many counties across Michigan reported little to no cases of Lyme disease from 2012-2015. Without consistent coverage, this may have reduced the variable importance for Lyme disease in Michigan. In contrast, Minnesota and Wisconsin have more cases of Lyme disease than Michigan and are also distributed across most or all of the counties. Possible under-reporting or misclassification of Lyme disease as well as the classification of county of residence, not county of exposure potentially limit the Lyme disease dataset. The vector for this disease, the black-legged tick, has a variety of vertebrate hosts other than white-tailed deer. In the lower peninsula of Michigan and in much of Wisconsin and Minnesota, the white-footed mouse (*Peromyscus leucopus*) may also contribute to the host pool (Anderson and Magnarelli 1984). Populations of *P. leucopus* vary greatly temporally and regionally (Goodwin et al. 2001), which may contribute to some noise in the models. Most research on *P. leucopus* populations contributing to Lyme disease have been in the eastern United States with limited studies in the Lake States, therefore we are assuming it contributes equally as a Lyme disease vector in the Lake States (Anderson and Magnarelli 1984; Donahue et al. 1987; Giardina et al. 2000; Derdákóvá et al. 2004). Our models support the importance of using Lyme disease information when estimating deer browse across regional scales, especially in areas with consistent Lyme disease cases.

The QDMA deer density estimates were important in the full Lake States models, Michigan models, and Wisconsin models, but were low in importance for the Minnesota

models. There are distinct state boundaries in the QDMA map from 2009 due to different approaches the state agencies use in estimating deer density (Walters et al. 2016). These distinctions inspired the individual state modeling and the intra-state differences support a need for modeling at different spatial scales.

The map of estimated browse impacts shows that browse pressure occurs on the majority of regions with forested cover. Southern Minnesota has the area with the lowest predicted browse pressure, but this area is primarily prairie or agricultural land and does not have many FIA plots contributing to the prediction. The primary predator of white-tailed deer today is humans, but wolves (*Canis lupus*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), cougars (*Puma concolor*) and black bears (*Ursus americanus*) can also hunt white-tailed deer. Wolves, bobcats, cougars and bears have migrated away from urban and suburban landscapes. In northeastern Minnesota, northern Wisconsin, and the Upper Peninsula of Michigan, there is a higher predator population contributing to the control of white-tailed deer populations and potentially decreasing the browse pressure in those areas. Even with predation, the predicted deer browse pressure is still high in some areas (Figure 6).

It is important that deer populations are monitored, because they can alter the landscape significantly and affect future forest composition (Frerker et al. 2014; Nuttle et al. 2014; Bradshaw and Waller 2016). Managing these populations can also potentially reduce Lyme disease cases (Kilpatrick et al. 2014), reduce spread of invasive species (Knight et al. 2009; Castellano and Gorchov 2013), and maintain diverse understory herbaceous layer (Jenkins et al. 2014) and soil properties (Shelton et al. 2014). Direct

measurement of ungulate populations is difficult across the landscape, which supports the need for assessment of browse impacts within deer habitat to better understand herbivory pressure in the forests (McWilliams et al. 2015; Bradshaw and Waller 2016).

The financial burden of managing deer populations and their impacts can be significant (Raynor 2016). Properly constructed deer exclosures are effective in excluding deer from a landscape (Shelton et al. 2014), but they can have substantial financial costs in implementation and maintenance. Bud capping is also relatively successful in protecting conifer seedlings and saplings from deer browse, but requires numerous labor hours across multiple years to be effective. For these and other reasons, hunting is an important management tool in the Lake States, particularly in areas with high human populations. Deer hunting also contributes millions of dollars to the economy every year and provides revenue for state agencies to use for conservation. Forested communities have exhibited recovery of preferred browse species following managed deer hunting, which supports its use as an effective management tool (Hothorn and Müller 2010; Jenkins et al. 2014). Understanding deer browse pressure can allow for forest management that can be financially, socially, and ecologically successful.

The map of estimated browse impacts created from this modeling effort (Figure 6) is designed to provide a tool for anyone to utilize as a means of coarsely estimating deer browse pressure within forested landscapes in the Lake States. Clear “hot spots” in the map indicate areas of concern where strategically managing forests with deer may be a financially viable option. In contrast, low browse pressure areas may not need direct management to regenerate trees that are preferred species for deer (e.g., northern white

cedar (*Thuja occidentalis*), yellow birch (*Betula alleghaniensis*), eastern white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), and northern red oak (*Quercus rubra*) in the Lake States, Bradshaw and Waller 2016). With a high accuracy, model predictions that created this map provide a coarse browse pressure estimate that land managers can utilize when determining management strategies. With future data from Phase 2-plus plot measurements from the FIA program, this model can be refined to better quantify browse impacts on forests across the Lake States.

Chapter 3: Analysis of white-tailed deer browse impacts on the abundance and species richness of seedlings and saplings

3.1. Introduction

The ecological effects of white-tailed deer have been studied frequently, due to their overabundance in many regions such as across the northern United States (ie. (Anderson and Loucks 1979, Alverson et al. 1988, Cornett et al. 2000, Bradshaw and Waller 2016). Human expansion has pushed predators out of deer territory and created fragmented landscapes that provide ideal habitat for deer. White-tailed deer consume buds and twigs of young trees as well as many understory herbaceous plants. Once trees grow large enough to be out of the reach of deer, they can no longer be browsed, which suggests that seedlings and young saplings are the most vulnerable to significant damage and death (Bradshaw and Waller 2016). Suppression of tree species in these young stages of growth can alter the forest composition for decades (Anderson and Loucks 1979, Alverson et al. 1988). Understanding ecological effects of deer on the structure and composition of forested ecosystems can be critical to predict the health and productivity of forests over time (White 2012).

These ungulates are selective and will browse “preferred” species until they no longer exist within the reach of deer (Rawinski 2014). In the United States (US) Lake States, eastern hemlock (*Tsuga canadensis*), northern white cedar (*Thuja occidentalis*), yellow birch (*Betula alleghaniensis*), northern red oak (*Quercus rubra*), and eastern white pine (*Pinus strobus*) are all highly palatable species for deer (Bradshaw and Waller

2016). Frelich and Lorimer (1985) have identified white-tailed deer as a major cause of *T. canadensis* decline in the Porcupine Mountains of the Upper Peninsula of Michigan and predicted a long-term decline in *T. canadensis* due to browsing at the seedling and sapling stages. In mixed *Acer saccharum-Tsuga canadensis* forests, like those of the Porcupine Mountains, overbrowsed *T. canadensis* seedlings and saplings cannot resprout as vigorously as their competitors, which limits recruitment into the mid and overstory (Switzenberg et al. 1955; Anderson and Loucks 1979; Salk et al. 2011). *T. occidentalis*, which is a slow growing, long-lived conifer, can survive in a suppressed state for many years. When browsed by deer, *T. occidentalis* can be outcompeted by other nonpalatable species such as balsam fir (*Abies balsamea*), which can cause a severe decline in recruitment of young *T. occidentalis* (Cornett et al. 2000). In both examples, deer browse is creating a competitive advantage for non-preferred browse species, essentially shifting the species composition of these forests (Palik et al. 2015).

The selective pressure of deer will vary based on the surrounding environment. For example, *P. strobus* may not be browsed in certain habitats even if deer numbers are high. However, in northern Minnesota, *P. strobus* is browsed heavily where seedlings are present. Seedlings of *Q. rubra* are browsed preferentially wherever oak are present, but have been shown to be more severely browsed in pine-dominated stands (Buckley et al. 1998). These five woody species have been consistently ranked as highly palatable across the Lake States region.

Browsing by ungulates can cause shifts in overall species composition and abundance. This can include a reduction in regeneration success of desired tree species

and/or an increase in abundance of non-palatable species by reducing competition (Côté et al. 2004). These species that prosper include both native and nonnative nonpalatable species, but invasive species specifically benefit from deer browse, because deer a) disperse invasive seeds, b) disturb the soil to assist in germination, and c) preferentially browse the native species (Williams and Ward 2006; Russell et al. 2017). For example, deer have been shown to assist in dispersal of the invasive amur honeysuckle (*Lonicera maackii*; Castellano and Gorchov 2013) and garlic mustard (*Alliaria petiolata*; Knight et al. 2009).

Deer herbivory can have dramatic indirect effects on the forest ecosystem, such as changes in the food web, vegetation structure, and nutrient cycling (Rooney and Waller 2003; Nuttle et al. 2014). These effects have been understudied mostly due to the long-term data collection needed and complex interacting effects. However, models have been developed which show that deer can cause ecosystem-wide changes through cascading effects. A study of vegetation within deer exclosures in Wisconsin and the Upper Peninsula of Michigan showed that deer cause long-term regional shifts in plants, which are typically less diverse than plant communities inside of the exclosures (Frerker et al. 2014) - one of many looking at the effects of deer exclosures on vegetation. Deer browse affects health and productivity of forests by altering species composition and abundance at the seedling and young sapling stages of development.

Deer populations in the Midwestern US have increased significantly in recent decades, making them overabundant in many regions and a threat to regenerating tree species (Rooney and Waller 2003). This increase in population is mostly due to habitat

modification and reduction in predatory species. The expanding urban landscape creates a heterogeneous landscape and provides white-tailed deer with optimal habitat. Precise deer population measurements are difficult to estimate, especially in a consistent fashion across land ownership and state lines, but the United States Department of Agriculture (USDA) Forest Service Forest Inventory and Analysis (FIA) program has addressed this issue through a deer browse metric. This ‘browse score’ provides a site-specific estimate of deer browse pressure within each FIA plot. This method provides a nationally consistent metric in order to assess implications of deer browse across large regions.

Our study aims to assess the effects of white-tailed deer on the health of forests in the Lake States, particularly palatable species, using the FIA browse impact scores. Specifically, I (1) quantified the abundance of seedlings and saplings at the plot level, (2) quantified species richness at the plot level, and (3) determined seedling and sapling abundance for the most palatable woody winter browse for white-tailed deer at different levels of browse pressure.

3.2. Methods

3.2.1. Study Area

This study was conducted across the Lake States, USA – in Michigan, Minnesota and Wisconsin. The Lake States contain a mixture of tallgrass prairie, temperate deciduous forests, and mixed boreal forest biomes and are defined by the Laurentian mixed forest, Eastern broadleaf forest, and Prairie parkland ecoregions. Forests of the

Lake States region contain diverse forest types and are comparable to many of the world's forests found in cool-to-cold temperate zones (Frelich 2002).

3.2.2. Forest Inventory and Analysis Data

The US Department of Agriculture Forest Service's Forest Inventory and Analysis (FIA) program was the primary source of forest inventory data for this project. The FIA protocols are nationally consistent and provide a basis for comparison across regions of the United States (Bechtold and Patterson 2005). This program divides the US into populations- (typically counties) and subpopulations. Each population and subpopulation has a defined number of plots based on forested area. There are three phases of plots in the FIA program: Phase 1 (P1), Phase 2 (P2), and Phase 3 (P3). Phase 1 stratifies the land into forest- (defined as an area at least 10% stocked with trees) or nonforest using aerial or satellite imagery. Phase 2 uses standard forest inventory methods to quantify structure, composition, and stand level attributes; plot density is approximately one plot for every 2,428-ha of forested land. Phase 3 plots occur on a subset of P2 plots (one plot every 38,850 ha) with the goal of recording additional measurements addressing forest health concerns. (Bechtold & Patterson, 2005).

Each P2 and P3 plot is arranged as a central point and three points clustered around the center. The outer points lie 36.58-m from the center at the following azimuths: 0, 120, and 240 degrees. Each point denotes the center of a fixed radius plot with a 7.32-m radius in which all trees 12.7-cm and larger diameter in breast height (DBH) are measured. A microplot, located 3.66-m off center and at an azimuth of 90 degrees, has a

2.07-m radius in which saplings (2.54 to 12.45-cm DBH) and seedlings were measured. Within each microplot all live tree seedlings were tallied, where conifer and hardwood seedlings were at least 15.2 and 30.5-cm in height, respectively, with both having a DBH \leq 2.5-cm.

Phase 2-plus plots were collected beginning in 2012 in the northern US on a subset of P2 plots. One plot was sampled every 19,425-ha of forest. In each plot, browse impact, which was defined as consumption of shoots, twigs, and leaves by animals for food and was recorded on a scale of 1-5 (exclosure, no browse, some browse, high browse, and severe browse, respectively) on seedlings at least 5.08-cm tall (McWilliams et al. 2015). In total, 792 Phase 2-plus plots were available from 2012-2015 (four years of data available from a seven year cycle) in the Lake States, obtained from the PLOT_REGEN tables. One plot, marked as within an exclosure, was removed from the modeling dataset. Six additional plots were removed from the modeling dataset, because they were assigned a browse score and have no other forest inventory data recorded for those plots (N=786).

All FIA data were accessed via the “FIA DataMart” (www.fia.fs.fed.us/tools-data, downloaded 20 June 2016). From the P2 FIA plots, the PLOT, TREE, and SEEDLING tables were used to obtain information on live trees. Trees per hectare and basal area per hectare were summarized for each plot by size class (overstory trees or saplings). Trees per hectare were summarized for each plot for seedlings.

3.2.3. *Study Species*

T. canadensis, *T. occidentalis*, *B. alleghaniensis*, *Q. rubra*, and *P. strobus* were identified as the most palatable species in northern Wisconsin by Bradshaw and Waller (2016). In their study, eleven common tree species were classified into palatability classes ranging from least to most palatable based on previous studies in the region in combination with expertise on deer impacts. The five species chosen for our study were assigned a 3 or 4 on the palatability scale. Due to close proximity and similar ecotypes, examining these species is appropriate for an analysis of white-tailed deer impacts across the Lake States.

3.2.4. *Models of Seedling and Sapling Abundance*

R computational software was utilized in creating statistical models (R Core Team, 2015). All analyses and comparisons occurred at the plot level. Tree stand and stocking information was summarized using FIA data to provide trees per hectare (TPH) for seedlings, saplings, and overstory trees and overstory basal area per hectare by species ($BA\ m^2ha^{-1}$) at the plot level.

Generalized linear models were created with the Poisson and negative binomial distributions. Models were created to predict abundance and species richness of all FIA 2-plus plots ($n=786$). Browse impact and overstory BA were used to create one overall model for seedling and sapling abundance, separately. Browse impact and species-specific overstory BA were used as predictors for species models. A dummy variable (0,1) was created to describe two levels of deer browse: none to low deer browse (browse score 2 and 3) and medium to high deer browse (browse score of 4 and 5). If a predictor

was not significant (i.e., $\alpha > 0.05$), it was removed from the model to increase predictive power. Comparison between Akaike's information criterion (AIC) values were used to determine the best fit models.

3.3. Results

Across all species, the variability was high for seedling and sapling abundance with severe deer browse, due to limited sample size (five plots). Seedling abundance and diversity increased significantly with some browse compared to no browse. On average, seedling TPH outnumbered sapling TPH by about an order of magnitude. Sapling species richness was only 50% that of seedlings, on average (Figure 3.1).

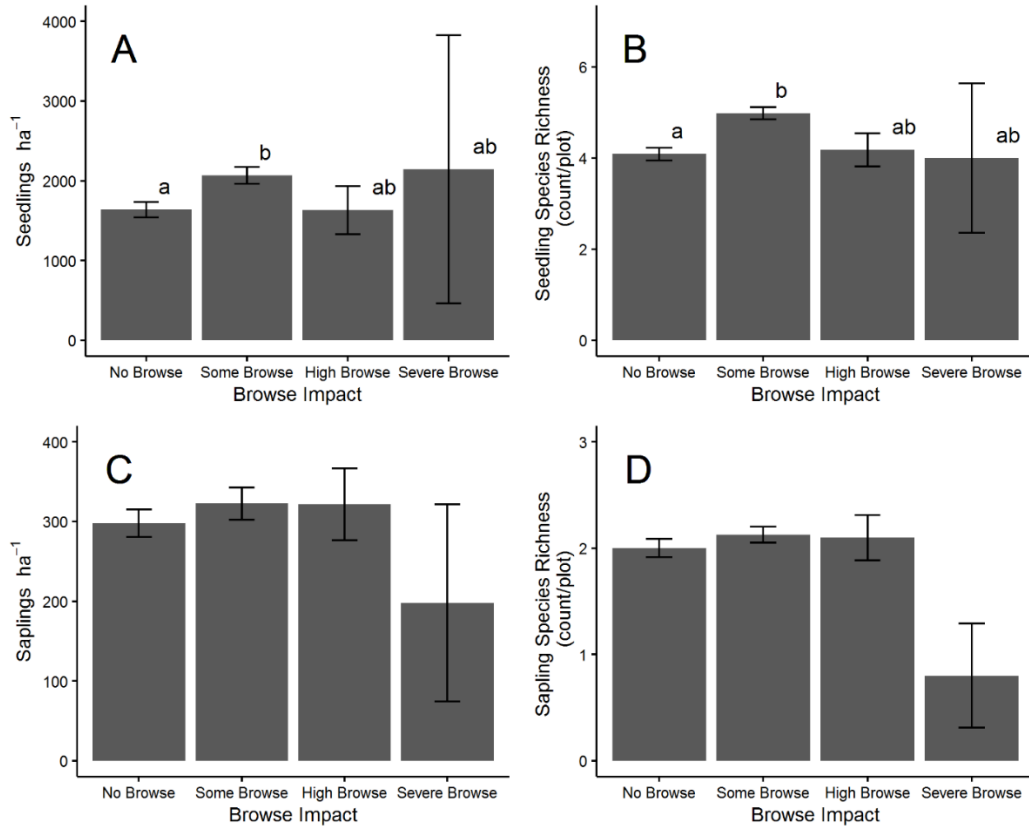


Figure 3.1. Average seedling TPH (A), seedling species per plot (B), sapling TPH (C), and sapling species per plot (D) for all Phase 2-plus plots from 2012-2015. Error bars represent +/- 1 SE. Lowercase letters denote significant differences between deer browse intensity.

The five palatable species used in this analysis displayed different distributions across the Lake States, according to the FIA plots measured between 2012-2015. *T. canadensis* did not occur on Phase 2 plots within Minnesota, but did occur in Wisconsin and Michigan. *T. occidentalis* occurred across the northeast region of each of the Lake States. The majority of *B. alleghaniensis* observations occurred in northern Wisconsin and the Upper Peninsula of Michigan, with scattered individuals in the Lower Peninsula

of Michigan and the northern region of Minnesota. The Phase 2 plots represented the species ranges recorded by the FIA program from 2012-2015. There were fewer plots that also had a recorded browse score from the FIA Phase 2-plus plots, for each species. The Phase 2-plus plots for *T. canadensis* (n=12), *T. occidentalis* (N=19), *B. alleghaniensis* (n=20), *Q. rubra* (n=38), and *P. strobus* (n=27) were approximately evenly distributed across the range of each species. Minnesota had one Phase 2-plus plot with recorded *B. alleghaniensis*, within its range. The Upper Peninsula of Michigan had no Phase 2-plus plots for *Q. rubra*, but did record individuals in several Phase 2 plots (Figure 3.2).

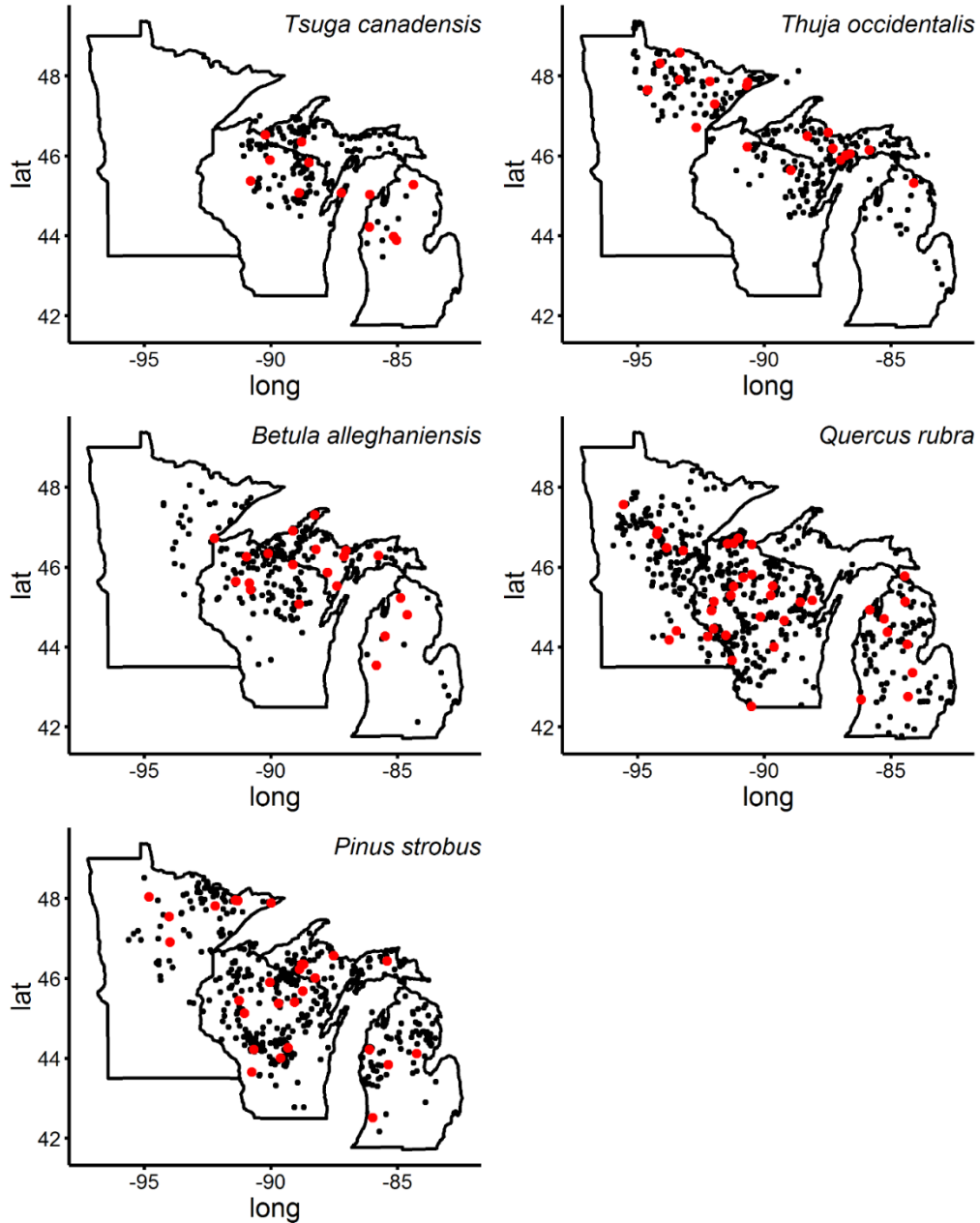


Figure 3.2. Distribution of *Tsuga canadensis*, *Thuja occidentalis*, *Betula alleghaniensis*, *Quercus rubra*, and *Pinus strobus* species across the Lake States. Black dots indicate plots where at least one individual of that species was recorded on a FIA Phase 2 plot between 2012-2015. Red dots indicate plots with seedlings, saplings, or overstory individuals recorded that were also assigned a browse score from FIA 2-plus plots.

Mean seedlings per hectare for the five palatable species varied from 0.47 to 10.84 TPH. Mean sapling per hectare for the five palatable species varied from 0.47 to 1.00 TPH. The range and standard deviation of seedling TPH was much wider than that for sapling TPH on Phase 2-plus plots (Table 3.1). Most Phase 2-plus FIA plots in the Lake States counted zero individuals of one of these palatable species.

Table 3.1. Summary statistics for trees per hectare of all species on Phase 2-plus FIA plots from 2012-2015 (n=786).

Species	Prop 0s ¹	Min	Mean	Max	SD
Trees per hectare					
<i>Seedling</i>					
All species	0.055	0	1829.6	14021	1978.02
<i>Tsuga canadensis</i>	0.996	0	0.47	279.49	10.21
<i>Thuja occidentalis</i>	0.992	0	10.84	5170.53	196.62
<i>Betula alleghaniensis</i>	0.994	0	0.53	139.74	7.58
<i>Quercus rubra</i>	0.973	0	4.00	745.30	39.92
<i>Pinus strobus</i>	0.977	0	5.89	2142.74	82.39
<i>Sapling</i>					
All species	0.165	0	310.2	3494.00	354.89
<i>Tsuga canadensis</i>	0.997	0	0.24	139.74	5.24
<i>Thuja occidentalis</i>	0.992	0	1.00	372.65	15.43
<i>Betula alleghaniensis</i>	0.994	0	0.47	186.32	7.4
<i>Quercus rubra</i>	0.995	0	0.29	93.16	4.37
<i>Pinus strobus</i>	0.992	0	0.59	139.74	7.39

¹Prop 0s indicates the proportion of plots with 0 seedlings or saplings recorded of the respective species

Seedling TPH for *T. occidentalis* and *B. alleghaniensis* decreased with each increase in browse pressure. Seedling TPH did not differ across browse levels for the other three species. There were no differences in sapling TPH across the five palatable

species with increased browse. *B. alleghaniensis* saplings had two plots with high browse recorded (Figure 3.3).

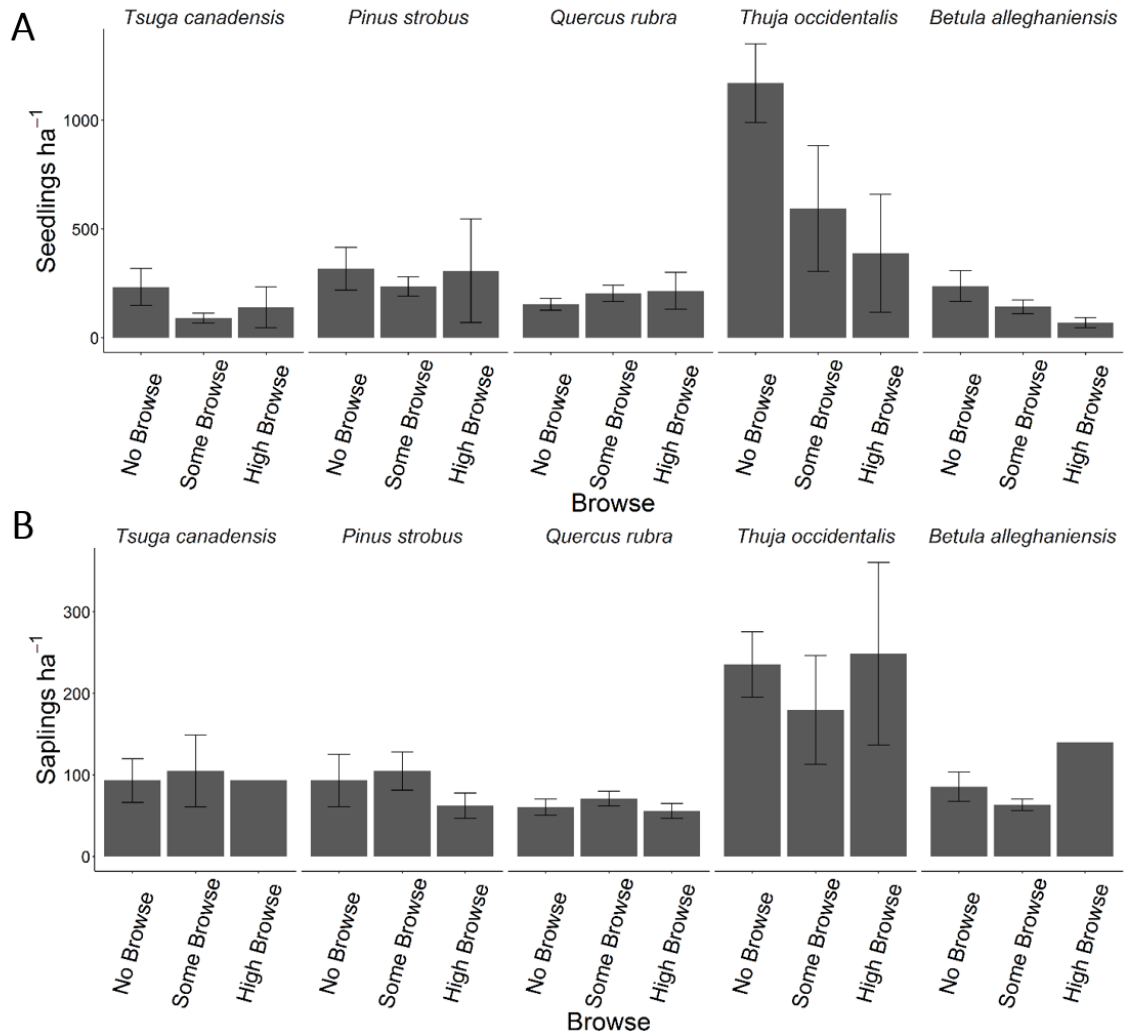


Figure 3.3. Seedling (A) and sapling (B) TPH for each level of browse for Phase 2-plus plots in the Lake States. The distribution was divided into the five most palatable species in the region. Error bars represent +/- 1 SE.

Species-specific overstory basal area was significant in all of the models ($p < 0.05$). Browse was significant for the majority of the species, with the exception for predicting *T. canadensis* seedling or sapling abundance. Low browse (browse impact = 3) for *T. occidentalis* exhibited a significant decrease in predicted seedling and sapling abundance compared to no browse. Low and medium browse (browse impact = 4) for *Q. rubra* exhibited a significant increase in predicted seedling abundance. Medium browse for *Q. rubra* exhibited a significant increase in predicted sapling abundance. Low browse for *B. alleghaniensis* exhibited a significant decrease in predicted sapling abundance. Low and medium browse for *P. strobus* exhibited a significant decrease in predicted seedling abundance. Low browse for *P. strobus* exhibited a significant decrease in predicted sapling abundance. High browse impact was not significant for any of the models created. All results were consistent assuming a Poisson or negative binomial distribution and denoted as significant if $p < 0.05$. AIC values for total seedling or sapling abundance were much higher than any of the individual species (Table 3.2).

Table 3.2. AIC values for models predicting seedling or sapling abundance (TPH). All models predicted either seedling or sapling abundance for one species assuming a Poisson or negative binomial distribution.

Model	Distribution			
	Poisson		Negative binomial	
	Browse	Browse + Overstory BA ^b	Browse	Browse + Overstory BA ^b
<i>Seedling</i>				
All Species	Inf ^a	Inf	13271.4	13265.7
<i>Tsuga canadensis</i>	4306.0	2255.3	4306.5	2256.5
<i>Thuja occidentalis</i>	92226.3	40272.1	92128.5	40234.9
<i>Betula alleghaniensis</i>	3733.8	2914.1	3734.9	2915.4
<i>Quercus rubra</i>	23313.0	22045.0	23304.1	22039.4
<i>Pinus strobus</i>	42933.4	34324.4	431.7	34295.3
<i>Sapling</i>				
All Species	Inf	Inf	10186.7	10183.4
<i>Tsuga canadensis</i>	2231.1	1315.0	2232.4	1316.4
<i>Thuja occidentalis</i>	8158.4	2918.4	8156.1	2919.3
<i>Betula alleghaniensis</i>	3841.2	3697.2	3841.9	3697.7
<i>Quercus rubra</i>	2111.6	2082.6	2112.6	1965.4
<i>Pinus strobus</i>	4561.9	3661.4	4561.9	3662.1

^aInf represents infinity

^bOverstory BA is species-specific for species models

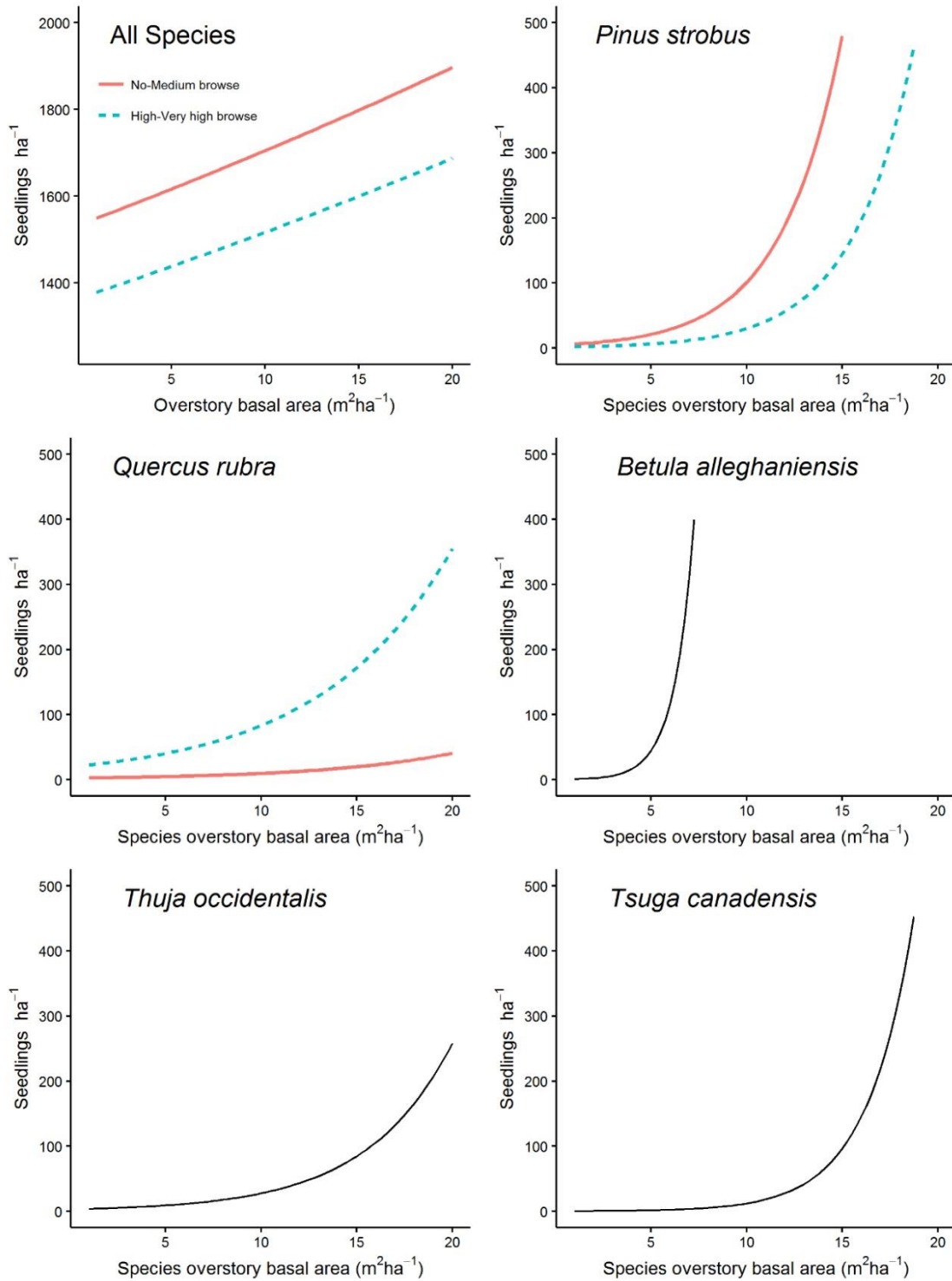


Figure 3.4. Predicted seedlings per hectare by overstory BA and browse impact for *Pinus strobus*, *Quercus rubra*, *Betula alleghaniensis*, *Thuja occidentalis*, and *Tsuga canadensis*.

All models for seedling and sapling abundance predicted an increase in seedling or saplings, respectively, with an increase in overstory basal area (Figure 3.4, 3.5). For all species, *P. strobus*, and *Q. rubra* seedling and sapling models, browse impact (none-low or med-high) was significant in predicting seedling or sapling abundance. For *B. alleghaniensis*, *T. occidentalis*, and *T. canadensis*, browse score was not significant. Total species and *P. strobus* seedling abundance decreased with a higher level of browse. *Q. rubra* seedling abundance was significantly higher with a higher level of deer browse (Figure 3.4). For all species, *Q. rubra*, and *P. strobus* sapling abundance increased with browse (Figure 3.5).

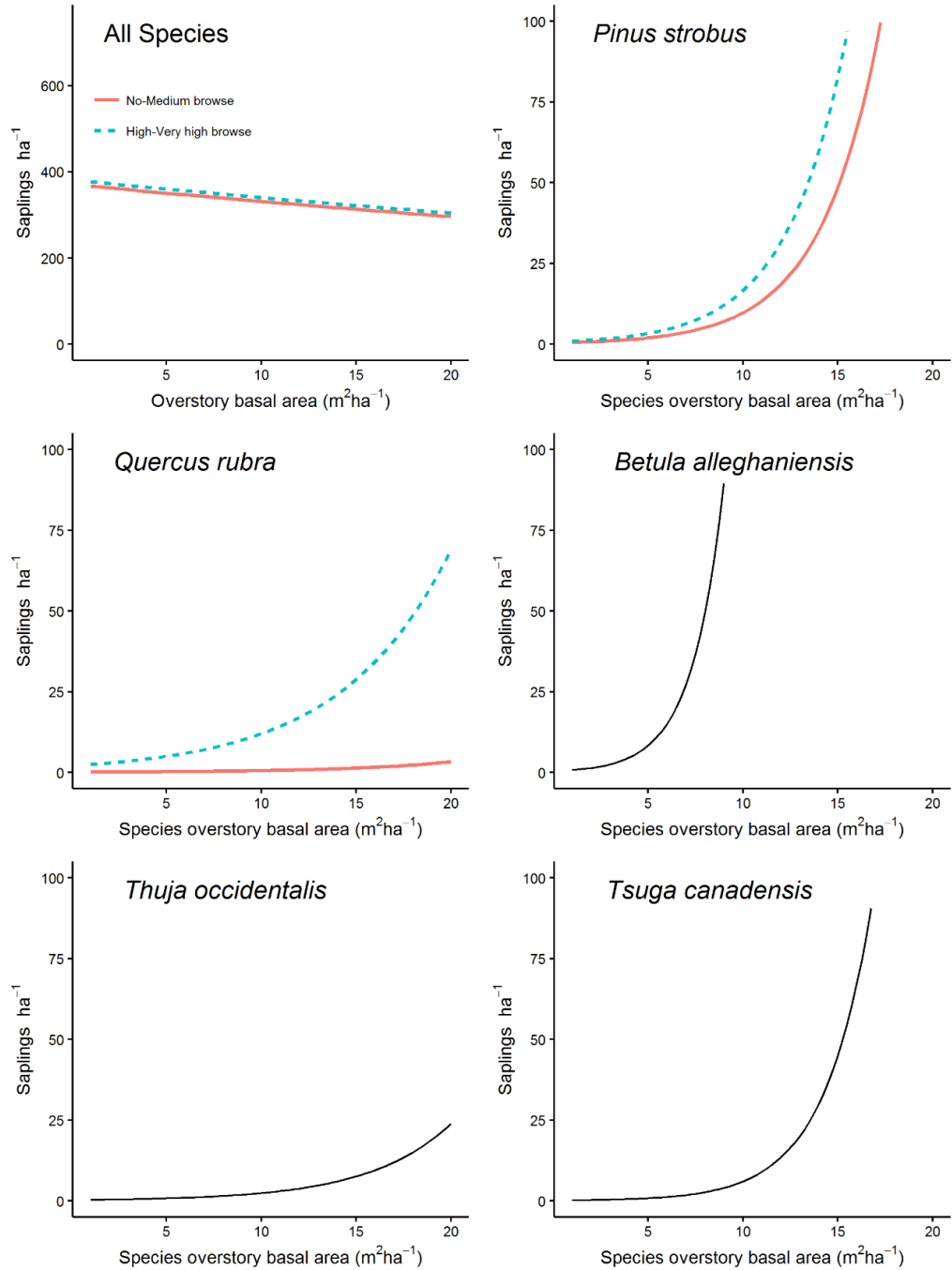


Figure 3.5. Predicted saplings per hectare by overstory BA and browse impact for *Pinus strobus*, *Quercus rubra*, *Betula alleghaniensis*, *Thuja occidentalis*, and *Tsuga canadensis*.

3.4. Discussion

We modeled seedling and sapling abundance by using browse impacts and species-specific overstory BA. Models for seedling abundance across all species showed a nonlinear increase in seedlings and saplings with increased overstory BA of that species. This indicates, as expected, that if there is a sufficient seed source, there will be more individuals regenerating in the understory. *B. alleghaniensis*, *T. occidentalis*, and *T. canadensis* exhibited no significant effect of deer browse on seedling or sapling abundance. These models were created for plots that recorded browse with seedlings or saplings present, therefore it is impossible to determine if an absence of seedlings or saplings is due to lack of regeneration or severe overbrowsing to local extinction.

T. occidentalis can survive decades within the understory under moderate to intense deer browse. This slow-growing shade tolerant species will allocate limited resources to diameter growth until a canopy gap allows suppressed trees to establish in the overstory. This delay in recruitment is not quantified through the FIA program, but is common where *T. occidentalis* is present. The USDA Forest Service recommends a height of 3m before *T. occidentalis* are considered out of deer browse range (Bouffroy et al. 2012). This unique growing strategy may suggest why impacts of browse were not significant for *T. occidentalis* with four years of FIA data.

Several studies have addressed issues with *T. canadensis* regeneration, in general. While deer may be contributing to *T. canadensis* seedling loss, the unique site characteristics required for *T. canadensis* to establish (i.e. 60 days of cold stratification, high moisture) may not be present, regardless of deer abundance (Mladenoff and Stearns

1993). Additionally, climate change is potentially affecting regeneration of many species due to drier, warmer conditions, especially those that occur at their southern range (Salk et al. 2011).

In contrast, browse pressure was significant for *P. strobus*, *Q. rubra*, and overall seedling abundance. Total seedling abundance decreased with higher browse and increased with overstory BA (Figure 3.4). In our models, overstory BA functions as a proxy for seed source abundance. *P. strobus* seedling abundance decreased with higher browse, given presence of individuals in the overstory. This suggests that selective deer browsing reduces *P. strobus* seedling regeneration in areas where natural regeneration would otherwise be expected – a relationship observed in other studies on seedling abundance (Matonis et al. 2011). *Q. rubra* seedlings showed an inverse relationship in which a higher browse level predicted greater seedling abundance. This may be partially due to the fact that *Quercus* species, in general, are not regenerating as expected throughout most of the eastern United States for many reasons in addition to deer browse (Crow 1988). This regeneration issue limits our conclusions about deer browse pressure on *Q. rubra* seedlings. *Quercus* species are moderately shade tolerant, but can survive on acorn reserves for the first several years following germination. This acorn effect could make seedlings more resilient to deer browse for a couple of years, due to underground energy reserves.

In the sapling size class, overall abundance decreased with an increase in overstory basal area. This illustrates how competition in the overstory limits resources available for individuals in the mid- and understory. *P. strobus* and *Q. rubra* sapling

abundance were both predicted to increase with higher deer browse levels. According to the FIA sampling protocol, saplings include trees from 2.54 to 12.7-cm DBH and many of the trees classified as saplings are likely out of browse range. In this case, elevated browsing pressure may create growing space for saplings to grow past browse height, therefore allowing more palatable species to mature into the sapling age class (Windmueller-Campione, personal communication, March 20, 2017). Total sapling abundance was higher with more deer browse pressure, thus supporting the species-specific results (Figure 3.5).

Long term deer browsing causes reduced species richness within forested landscapes (Anderson and Loucks 1979; Frelich and Lorimer 1985; Waller and Alvenson 1997; Russell et al. 2001). Changes in the vegetation have cascading effects on wildlife, which are dependent on particular ecosystems (e.g. DeCalesta 1994). Our results do not show a decrease in diversity with increasing browse pressure, but there may be a significant decrease in diversity with severe browsing. There were a limited number of Phase 2-plus plots marked as severe browse from 2012-2015, indicating a relatively small sample observed as medium-high browse for comparison to the none-low browse. With more samples in the future, analyses could be conducted to investigate woody species diversity at extreme deer browse impacts. Overabundance is site-specific and relative to the community at each site. There may be regions where deer populations are high, but so is their food source such that the community can survive sustainably. In contrast, areas with lower deer populations may still be considered overabundant if available browse is low and causes local extirpation of palatable species in that area. Therefore, a steep drop

in plot-level diversity may be expected beyond a certain threshold of deer abundance. In addition, overall plot diversity may not decrease immediately, but a more detrimental shift in which species are present is likely with more severe deer browse. Over 50 years of deer browse outside of exclosures in the Upper Peninsula of Michigan and northern Wisconsin exhibited a shift to ferns grasses, and exotics, compared to forbs, shrubs, and woody understory regeneration found inside of exclosures (Frerker et al. 2014).

The current abundance of seedlings and saplings represents the effects of past deer populations and may not reflect current deer browse pressure. The FIA Phase 2-plus dataset provides deer browse values of only the past four years of the current FIA cycle. In the Lake States, there has been deer overabundance and severe browse pressure in some areas for decades. The current state of the forest today is the legacy of these recent decades of browse, hence, the current browse score may not be representative of how deer have been browsing in recent years. Bradshaw and Waller (2016) utilized a browse metric for 10 years prior to the forest inventory data to account for this delay in browse effects. Continual recording of deer browse pressure in a nationally-consistent manner is necessary to assess deer browse legacy effects on current forest conditions.

The Lake States region of the US is reasonably similar across the landscape, but there are variations in regional browse preference. For example, white pine is selectively browsed more in northern Minnesota compared to southern Minnesota (Lee Frelich, personal communication, March 23, 2017). In addition, deer overabundance or harsh winters can cause deer to browse less 'ideal' species. These inconsistencies cannot be effectively quantified with the data available, but provide noise to the results, which

cannot be eliminated based on four years of forest inventory data. Regeneration following disturbances such as harvest and fire can also be greatly affected by deer browsing, which was not considered in this analysis. Deer browse can suppress advanced regeneration and when canopy openings occur, these growing spaces are either not filled or not occupied by the expected successional species (Stromayer and Warren 1997).

A historical effort to increase game populations in addition to a decrease in predator populations has created a unique niche for white-tailed deer across the northern US. Deer can alter the natural succession of forests by severely browsing and potentially eliminating palatable woody and herbaceous species, and have been rightfully deemed keystone herbivores (Waller and Alverson 1997). Regenerating tree species are in a relentless battle to find nutrients, light, and space to germinate and then grow into the mid and overstory. Ungulate browse provides an additional stressor that alters the natural competition between species and favors some species over others. Understanding the impacts of deer on our forests is essential to predict ecosystem and community-level shifts and effectively manage for healthy and productive forests.

Chapter 4: Conclusions and Management Implications

Estimates of deer populations and browse impacts are difficult to assess, particularly across ownerships and state lines. Through the FIA Phase 2-plus program, categorization of deer browse provides the first nationally consistent metric to quantify deer browse pressure across the eastern United States (McWilliams et al. 2015). In combination with the other FIA forest inventory variables from Phase 2, these data provide numerous opportunities to explore forest health risks in order to adapt management appropriately.

Using socio-environmental datasets along with forest inventory data provided an approach that approximates deer browse pressure in the Lake States to at least 80% accuracy (see Chapter 2). Our map of estimated browse impacts provides a coarse assessment of browse pressure across the Lake States, which can be used to identify hot spots within forested landscapes where deer browse is high. The strength of this model could continue to increase with more years of FIA data, particularly with a complete cycle of the FIA program. This model also highlights the importance of other freely available datasets for use in better understanding how we can predict deer populations and browse pressure.

This map can be an effective tool when determining strategic forest management actions. The economic impacts of choosing to manage for deer, or not, can be a major factor when planting or naturally regenerating tree species. Other factors to consider include, changes in the food web, vegetation structure, and nutrient cycling (Rooney and Waller 2003; Nuttle et al. 2014). Forested ecosystems are slow growing and require

management considerations for the long term, regardless of the management goals. Legacy effects of white-tailed deer can significantly alter forest composition over the lifetime of a forested stand (Cornett et al. 2000). Our analysis highlights the negative effects of deer browse on white pine seedling abundance and suggests – in parallel with other studies – that woody species diversity declines with severe browse. The deer browse map in Chapter 2 is designed to provide a coarse estimate of deer browse across forested areas in the Lake States such that land managers can create management plans based on level of browse, desired species, and desired ecosystem services. The ecological effects in Chapter 3 provide insights into the potential effects of ungulate browse on seedlings and saplings.

Analysis of individual species in Chapter 3 suggests that browse at the seedling size class is reflected in the composition of the larger saplings. While terminal buds of saplings are typically out of reach of deer, lateral browsing and seedling browsing may open up space for saplings to grow in the understory.

Our data support the use of an ungulate browse metric to quantify deer browse pressure within forests. Because immediate impacts of deer browse are not usually obvious, these metrics are needed over long time scales in order to better quantify the legacy effects that deer can have on tree regeneration.

With additional years of the FIA Phase 2-plus program, future analyses can aim to better understand the impacts of deer browse. Additionally, this consistent metric provides more opportunities to research the long-term impacts of deer browse on larger scales than have been attempted before. Finally, the effects of increasing or decreasing

white-tailed deer populations can be easily quantified with continual cycles of recorded browse pressure. The lag time between overabundant deer populations and significant effects on the landscape level are not fully quantified, but this metric provides an opportunity to address that question with more years of data.

Bibliography

- Adams K, Hamilton J, Ross M (2009) Quality Deer Management Association's Whitetail Report 2009.
- Alverson WS, Waller DM, Solheim SL (1988) Forests Too Deer : Edge Effects in Northern Wisconsin. *Conserv Biol* 2:348–358.
- Anderson DR (2001) The need to get the basics right in wildlife field studies. *Wildl Soc Bull* 29:1294–1297.
- Anderson JF, Magnarelli LA (1984) Avian and Mammalian Hosts For Spirochete-Infected Ticks and Insects in a Lyme Disease Focus in Connecticut. *Yale J Biol Med* 57:627–641.
- Anderson RC, Loucks OL (1979) White Tail Deer Influence on the Structure and Composition of *Tsuga canadensis* Forests. *J. Appl. Ecol.* 16:855–861.
- Bechtold W a., Patterson PL (2005) The Enhanced Forest Inventory and Analysis Program - National Sampling Design and Estimation Procedures.
- Bouffroy E, Forget E, Hofmeyer P V, et al (2012) Silvicultural Guide for Northern White-Cedar (Eastern White Cedar).
- Bradshaw L, Waller DM (2016) Impacts of White-Tailed Deer on Regional Patterns of Forest Tree Recruitment. *For Ecol Manage* 375:1–11. doi: 10.1016/j.foreco.2016.05.019
- Breiman L (2001) Random Forests. *Mach Learn* 45:5–32.
- Buckley DS, Sharik TL, Isebrands JG (1998) Regeneration of Northern Red Oak : Positive and Negative Effects of Competitor Removal. *Ecology* 79:65–78.
- Castellano SM, Gorchoff DL (2013) White-tailed Deer (*Odocoileus virginianus*) Disperse Seeds of the Invasive Shrub , Amur Honeysuckle (*Lonicera maackii*). *Nat Areas J* 33:78–80. doi: 10.3375/043.033.0109
- Cornett MW, Frelich LE, Puettmann KJ, Reich PB (2000) Conservation Implications of Browsing by *Odocoileus virginianus* in Remnant Upland *Thuja occidentalis* Forests. *Biol Conserv* 93:359–369. doi: 10.1016/S0006-3207(99)00129-9
- Côté SD, Rooney TP, Tremblay J, et al (2004) Ecological Impacts of Deer Overabundance. *Annu Rev Ecol Evol Syst* 35:113–147. doi: 10.2307/annurev.ecolsys.35.021103.30000006
- Crow TR (1988) Reproductive Mode and Mechanisms for Self-Replacement of Northern Red Oak (*Quercus rubra*) - A Review. *For Sci* 34:19–40.
- DeCalesta D (1994) Effect of White-Tailed Deer on Songbirds within Managed Forests in Pennsylvania. *J Wildl Manage* 58:711–718.
- Derdáková M, Dudišák V, Brei B, et al (2004) Interaction and Transmission of Two *Borrelia burgdorferi* Sensu Stricto Strains in a Tick-Rodent Maintenance System. *Appl Environ Microbiol* 70:6783–6788. doi: 10.1128/AEM.70.11.6783
- DiTommaso A, Morris SH, Parker JD, et al (2014) Deer Browsing Delays Succession by Altering Aboveground Vegetation and Belowground Seed Banks. *PLoS One*. doi: 10.1371/journal.pone.0091155
- Donahue JG, Piesman J, Spielman A (1987) Reservoir Competence of White-Footed Mice for Lyme Disease Spirochetes. *Am J Trop Med Hyg* 36:92–96.

- ESRI (2011) ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.
- Frelich LE (2002) Forest Dynamics and Disturbance Regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press, Cambridge, England
- Frelich LE, Lorimer CG (1985) Current and Predicted Long-Term Effects of Deer Browsing in Hemlock Forests in Michigan, USA. *Biol Conserv* 34:99–120. doi: 10.1016/0006-3207(85)90103-X
- Frerker K, Sabo A, Waller D (2014) Long-Term Regional Shifts in Plant Community Composition Are Largely Explained by Local Deer Impact Experiments. *PLoSone* 9:1–17. doi: 10.1371/journal.pone.0115843
- Giardina AR, Schmidt K a, Schaubert EM, Ostfeld RS (2000) Modeling the Role of Songbirds and Rodents in the Ecology of Lyme Disease. *Can J Zool* 78:2184–2197. doi: 10.1139/z00-162
- Goodwin BJ, Ostfeld RS, Schaubert EM (2001) Spatiotemporal Variation in a Lyme Disease Host and Vector: Black-Legged Ticks on White-Footed Mice. *Vector Borne Zoonotic Dis* 1:30–35. doi: 10.1089/ast.2007.0153
- Hothorn T, Müller J (2010) Large-Scale Reduction of Ungulate Browsing by Managed Sport Hunting. *For Ecol Manage* 260:1416–1423. doi: 10.1016/j.foreco.2010.07.019
- Jenkins LH, Jenkins MA, Webster CR, et al (2014) Herbaceous Layer Response to 17 Years of Controlled Deer Hunting in Forested Natural Areas. *Biol Conserv* 175:119–128. doi: 10.1016/j.biocon.2014.04.022
- Kilpatrick HJ, Labonte AM, Stafford KC (2014) The Relationship Between Deer Density, Tick Abundance, and Human Cases of Lyme Disease in a Residential Community. *J Med Entomol* 51:777–784.
- Knight TM, Dunn JL, Smith LA, et al (2009) Deer Facilitate Invasive Plant Success in a Pennsylvania Forest Understory. *Nat Areas Assoc* 29:110–116.
- Liaw A, Wiener M (2002) Classification and Regression by randomForest. *R news* 2:18–22. doi: 10.1177/154405910408300516
- Matonis MS, Walters MB, Millington JDA (2011) Gap-, Stand-, and Landscape-Scale Factors Contribute to Poor Sugar Maple Regeneration After Timber Harvest. *For Ecol Manage* 262:286–298. doi: 10.1016/j.foreco.2011.03.034
- McWilliams WH, Westfall JA, Brose PH, et al (2015) A Regeneration Indicator for Forest Inventory and Analysis : History, Sampling, Estimation, Analytics, and Potential Use in the Midwest and Northeast United States.
- Meekins JF, Mccarthy BC (1999) Competitive Ability of *Alliaria petiolata* (Garlic Mustard, Brassicaceae), an Invasive Nonindigenous Forest Herb. *Int J Plant Sci* 160:743–752. doi: 10.1086/314156
- Mladenoff DJ, Stearns F (1993) Eastern Hemlock Regeneration and Deer Browsing in the Northern Great Lakes Region: A Re-examination and Model Simulation. *Conserv Biol* 7:889–900.
- Nuttle T, Ristau TE, Royo AA (2014) Long-Term Biological Legacies of Herbivore Density in a Landscape-Scale Experiment: Forest Understoreys Reflect Past Deer Density Treatments for at Least 20 Years. *J Ecol* 102:221–228. doi: 10.1111/1365-2745.12175

- Palik BJ, Haworth BK, David AJ, Kolka RK (2015) Survival and Growth of Northern White-Cedar and Balsam Fir Seedlings in Riparian Management Zones in Northern Minnesota, USA. For Ecol Manage 337:20–27. doi: 10.1016/j.foreco.2014.10.033
- R Core Team (2015) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org>.
- Rawinski TJ (2014) White-tailed Deer in Northeastern Forests: Understanding and Assessing Impacts. Newtown Square, PA
- Raynor JL (2016) The causal impact of increased deer abundance on vehicle collisions.
- Roberts KJ, Anderson RC (2001) Effect of Garlic Mustard [*Alliaria petiolata* (Beib. Cavara & Grande)] Extracts on Plants and Arbuscular Mycorrhizal (AM) Fungi. Am Midl Nat 146:146–152. doi: 10.1674/0003-0031(2001)146[0146:EOGMAP]2.0.CO;2
- Rooney TP, Waller DM (2003) Direct and Indirect Effects of White-Tailed Deer in Forest Ecosystems. For Ecol Manage 181:165–176. doi: 10.1016/S0378-1127(03)00130-0
- Russell FL, Zippin DB, Fowler NL (2001) Effects of White-tailed Deer (*Odocoileus Virginianus*) Plants, Plant Populations and Communities: A Review. Am Midl Nat 146:1–26.
- Russell MB, Woodall CW, Potter KM, et al (2017) Interactions Between White-Tailed Deer Density and the Composition of Forest Understories in the Northern United States. For Ecol Manage 384:26–33. doi: 10.1016/j.foreco.2016.10.038
- Salk TT, Frelich LE, Sugita S, et al (2011) Poor Recruitment is Changing the Structure and Species Composition of an Old-Growth Hemlock-Hardwood Forest. For Ecol Manage 261:1998–2006. doi: 10.1016/j.foreco.2011.02.026
- Shelton AL, Henning JA, Schultz P, Clay K (2014) Effects of Abundant White-Tailed Deer on Vegetation, Animals, Mycorrhizal Fungi, and Soils. For Ecol Manage 320:39–49. doi: 10.1016/j.foreco.2014.02.026
- Stromayer KAK, Warren RJ (1997) Are Overabundant Deer Herds in the Eastern United States Creating Alternate Stable States in Forest Plant Communities? Wildl Soc Bull 25:227–234.
- Switzenberg DF, Nelson TC, Jenkins BC (1955) Effect of Deer Browsing on Quality of Hardwood Timber in Northern Michigan. For Sci 1:61–67.
- Tilghman NG (1989) Impacts of White-Tailed Deer on Forest Regeneration in Northwestern Pennsylvania. J Wildl Manage 53:524–532. doi: 10.1002/jwmg.192
- Waller DM, Alvenson WS (1997) The White-Tailed Deer: A Keystone Herbivore. Wildl Soc Bull 25:217–226.
- Walters BF, Woodall CW, Russell MB (2016) White-tailed deer density estimates across the eastern United States, 2008 [dataset].
- Warren RJ, Warren RJ, Editor SI (2017) Editor's Page: The Challenge of Deer Overabundance in the 21st Century The challenge of deer overabundance in the 21st century. 25:213–214.
- White MA (2012) Long-Term Effects of Deer Browsing: Composition, Structure and Productivity in a Northeastern Minnesota Old-Growth Forest. For Ecol Manage 269:222–228. doi: 10.1016/j.foreco.2011.12.043

Williams S, Ward J (2006) Exotic Seed Dispersal by White-Tailed Deer in Southern Connecticut. *Nat Areas J* 26:383–390. doi: 10.3375/0885-8608(2006)26[383:ESDBWD]2.0.CO;2