

REGENERATION DYNAMICS FOLLOWING BEECH REMOVAL IN MICHIGAN'S
NORTHERN HARDWOOD FORESTS IMPACTED BY BEECH BARK DISEASE

By

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ABSTRACT

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Beech Bark Disease (BBD) results in mortality of mature American beech (*Fagus grandifolia* Ehrh.) and increased beech sapling density, resulting in reduced recruitment of desirable species, and economic timber value. To better understand and manage BBD impacted forests, I (1) quantified regeneration structure in beech salvage harvests (partial removal) (2) assessed factors associated with regeneration patterns including winter deer use (pellet count surveys), habitat class (moisture/nutrient regime), geographic region, and post-harvest basal area, and (3) assessed the regeneration potential and likely management outcomes of study stands with a decision support tool I developed.

Throughout my study area, tree regeneration > 1.5 m tall was dominated by beech and ironwood (*Ostrya virginiana* (Mill.) K Koch), which are considered undesirable for management. Region (Northern Lower Peninsula vs. Eastern Upper Peninsula) was more important than habitat class (nutrient/water regime), post-harvest basal area, and winter deer use in predicting tree regeneration composition and density. Despite dominance by undesirable species for stems > 1.5 m tall, most stands had high densities of desirable species (e.g. *Acer saccharum*) in < 1.5 m tall strata indicating potential for regeneration. Results of my decision support tool indicate, 3% of my study stands can regenerate naturally, 83% of stands will require additional treatments for adequate regeneration, and 14% of stands were understocked by desirable stems in all size class and could be targeted for more novel silviculture (e.g. herbicide, scarify or conversion to *Pinus resinosa* plantations).

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Abstract

Beech Bark Disease (BBD) results in mortality of mature American beech (*Fagus grandifolia* Ehrh.) and increased beech sapling density, potentially resulting in reduced recruitment of desirable species, mast production for wildlife, and economic timber value. Changes in forest structure have been quantified in northeastern United States where BBD has been present since 1929. However, these patterns are less understood for managed forests at the western edge of beech distribution where infestations are much more recent. Furthermore, approaches aimed at ameliorating negative impacts to assure the sustainability of managed post-BBD forests are lacking. To better understand and manage BBD impacted forests, I (1) quantified regeneration structure in beech salvage harvests (partial removal) (2) assessed factors associated with regeneration patterns including winter deer use (pellet count surveys), habitat class (moisture/nutrient regime), geographic region, and post-harvest basal area, and (3) assessed the regeneration potential and likely management outcomes of study stands with a decision support tool I developed. Data used to address these goals were collected from multiple plots in 2.02 ha (5 ac) study areas in each of 69 harvested stands in northern Michigan.

Throughout my study area, tree regeneration > 1.5 m tall was dominated by beech and ironwood (*Ostrya virginiana* (Mill.) K Koch), which are considered undesirable for management. Region (Northern Lower Peninsula vs. Eastern Upper Peninsula) was more important than habitat class (nutrient/water regime), post-harvest basal area and current winter deer use in predicting tree regeneration composition and density. Despite dominance by undesirable species for stems > 1.5 m tall, most stands had high densities of desirable species (e.g. *Acer saccharum*) in < 1.5 m tall stratum. My decision support tool is based on regeneration species identity and stocking in different height stratum and the assumption that taller

regeneration will “win” growing space in the near term. Applying this tool, 3% of my stands had adequate desirable regeneration, 83% of stands had undesirable regeneration in taller strata and plentiful desirable regeneration in shorter strata, potentially requiring treatments to decrease undesirable saplings and deer impacts, and 14% of stands were understocked by desirable stems in all size class and could be targeted for other treatments (e.g. conversion *Pinus resinosa* plantations or). In conclusion, most managed stands impacted by BBD will require management aimed at regenerating more diverse and desirable mixtures of species. BBD and harvesting may affect tree regeneration patterns, but 60+ years of selection silviculture and high deer densities may also contribute.

Introduction

BBD Complex

Beach bark disease is a complex between the invasive beech scale insect (*Cryptococcus fagisuga* Lind.) (Hemiptera: Coccoidea) and two separate fungi (*Neonectria faginata* [Lohman, Watson, and Ayers] Castlebury and Rossman and *Neonectria ditissima* [Tulane and C. Tulane] Samuels and Rossman), which infect mature American beech (*Fagus grandifolia* Ehrh.) trees (Jonathan A. Cale et al., 2015; Ehrlich, 1934). The beech scale insect feeds on phloem and phelloderm cells of beech trees, resulting in minute wounds that enable entry of airborne *Neonectria* spp. spores. Upon infection, *Neonectria* spp. kill vascular tissue, and as adjacent infestations coalesce water and nutrient transport is interrupted often resulting in mortality of mature trees (Ehrlich, 1934).

The spread of BBD throughout forested landscapes is characterized by three distinct phases (Shigo, 1972). The first phase, the *advancing front*, is characterized by forests where mature beech trees have been infected by beech scale insects, but *Neonectria* is not present. The

second phase, the *killing front*, occurs when *Neonectria* spp. begin to colonize trees, killing approximately 50% of beech trees over 25 cm diameter at breast height (DBH) (Houston et al., 2005). The third phase, the *aftermath forest*, consists of areas with few residual mature trees and increased beech density in the understory (Houston, 1975). This pattern has been quantified throughout the northeastern United States where BBD first originated in 1929 (Ehrlich, 1934), but it is unknown if similar patterns exist in Michigan. BBD was first found in Michigan in 2000 (O'Brien et al., 2001), and given that Michigan is on the western most edge of American beech's natural range, long-term nature of the disease, and different climactic factors in Michigan compared to the northeastern United States, long term effects of BBD are largely unknown.

BBD in Michigan

Maple/beech/birch is the dominant forest coertype in Michigan covering > 1.4 million hectares, and the 2017 U.S. Department of Agriculture Forest Service Forest Inventory and Analysis (FIA) data estimated 37 million American beech trees greater than 12.7 cm DBH throughout Michigan's forested landscapes (public and private) (Pugh, 2018). This report also estimates a negative net growth that indicates beech mortality has increased by 132% from the 2012-2017 inventory, and estimates current annual mortality at 466,000 m³/yr (Pugh, 2018). BBD has been reported in all counties in the Upper Peninsula that contain American beech, and 18 of 68 counties in the Lower Peninsula, with an expansion rate that varies from <1 to 14.3 km per year (Wieferich, 2013).

Wieferich (2013) continued a long-term experiment beginning in 2005 and tracked progression of the BBD advancing front throughout Michigan. In 62 sites that Wieferich (2013) monitored, spread of the advancing front was faster and resulted in higher mortality rates in the Eastern Upper Peninsula (EUP) in comparison to the Northern Lower Peninsula (NLP), despite

similar introductions of disease agents in both regions (O'Brien et al., 2001). Wieferich (2013) only found one understory that resembled a beech thicket, as has been reported to be common in the Eastern seaboard forests where BBD was first reported (Cale et al., 2013; Guerrier et al., 2003; Houston, 1994). This study highlighted variations in the rate of spread of BBD throughout the advancing front within Michigan, however implications of these patterns to forest dynamics in the killing front and aftermath forests are largely unknown.

Problem

When mature BBD-infected beech dieback, understory beech density may increase resulting in dense competitively dominant regeneration layers (Cale et al., 2013; Houston, 1975; Shigo, 1972). These dense understories may stagnate and become re-infected, potentially resulting in long term beech-dominated understories, decreased density and diversity of other tree regeneration (Cale et al., 2013), and diminished recruitment of non-beech stems (Hane, 2003; Nyland et al., 2006). Over time, this cycle may dramatically alter the structure and composition of forests, and decrease forest productivity, timber value, hard mast production for wildlife, and resiliency to future pests/pathogens. These patterns have been observed throughout the northeastern United States where BBD was first introduced in 1929 (Ehrlich, 1934), but given that BBD was not introduced into Michigan until 2000 (O'Brien et al., 2001), and given differences in forest composition and climate between these regions, patterns could be different. For example, Kearny et al. (2004) found that while mature beech decline was evident throughout BBD impacted forests in Michigan, there was no corresponding increase in beech understory regeneration as is observed in northeastern US forests.

In addition to the potential direct effects of BBD on beech regeneration, other ecological factors may contribute to beech-heavy regeneration outcomes in BBD impacted forests. In

Michigan, American beech grows across a gradient of habitat classes (nutrient/moisture regime) (Burger and Kotar, 2003). Tree species compositions, productivity, and competitive interactions vary among habitat classes, potentially resulting in different tree regeneration dynamics. Selective browse pressure from white-tailed deer (*Odocoileus virginianus* Zimmerman) has also significantly altered regeneration dynamics in northern hardwood forests (Donovan, 2005; Matonis et al., 2011; Stoeckeler et al., 1957). In some cases, deer browsing has nearly eradicated palatable species, such as sugar maple and eastern hemlock (*Tsuga canadensis* (L.) Carr), and resulted in dominance of unpalatable species including American beech and ironwood (*Ostrya virginiana* (Mill.) K Koch) (Rooney and Waller, 2003). Pressure from deer herbivory could contribute to the high proportion of beech regeneration in BBD impacted forests. Supporting this notion, Frigoletto et al. (2017) conducted a long-term experiment in Pennsylvania utilizing deer exclosures and concluded that the absence of deer in BBD impacted forests reduced relative importance of beech root sprouts from 60 to 25%. Acting as herbivores, seed predators, agents of disturbance, or any combination of thereof, deer may exacerbate effects of BBD and further diminish the diversity, resilience, and productivity of northern hardwood forests.

Beech harvests, whether part of a salvage operation or selection harvest, are currently used by the Michigan Department of Natural Resources (MDNR) to capture value of beech timber before mortality. These harvests increase light levels to the forest understory enhancing regeneration growth, but given variable spatial distribution of beech and harvest intensity, I expect beech removal to result in varying residual basal areas (BA) and subcanopy light levels within forest stands.

Characterizing impacts of beech harvests while assessing ecological variables that affect tree regeneration dynamics is an imperative first step in understanding BBD/beechn harvest

impacts. Northern hardwood forests growing on varying habitat classes, experiencing varying levels of browsing pressure, having varied residual basal areas, and located throughout different regions, will have disparate compositions, structures, and growth dynamics requiring unique treatments.

Objectives

My primary research objectives were to (1) quantify regeneration dynamics in stands impacted by BBD following beech harvests in Michigan, (2) assess effects of deer use, habitat class, geographic region and post-harvest basal area on regeneration dynamics, and (3) assess the regeneration potential and likely management outcomes of my study stands through the creation of a decision support tool.

Methods

Study Area

I sampled 69 total stands in this study including 29 located within the NLP and 40 in the EUP of Michigan (44.41 – 46.65° Latitude) under management of the MDNR. On average, the EUP is colder than the NLP across all seasons, and areas along the Great Lakes shorelines experience warmer temperatures and longer growing seasons in comparison to interior areas (Handler et al., 2014). Mean annual temperatures in these regions range from 3.9 – 7.8 °C and precipitation ranges from 73.0 – 95.6 cm (30 year normal, 1981 – 2010 (“PRISM Climate Group,” 2016). Stands in this study occurred over a gradient of soil types ranging from excessively well drained sandy soils on outwash plains, to moderately drained sandy loam soils on end and ground moraines (Burger and Kotar, 2003). Stands within the EUP typically grow within large stretches of continuous forest, while the NLP is more fragmented. Northern hardwood forests in Michigan have predominately been managed since the 1960s by uneven

aged single-tree selection silviculture, resulting in a residual BA ranging from 17-20 m²/ha, with a harvest frequency of 10-20 years (Neumann, 2015).

Experimental Design

Sites were established from June-October 2017 using inventory data and local knowledge from MDNR timber specialists. Criteria for study sites included medium-well stocked pole and sawtimber stands with a high pre-harvest beech component where beech was cut between 2006-2016 as part of a salvage, thinning, or ongoing single-tree selection harvest. Salvage harvests are defined as complete removal of beech from the stand with no consideration of post-harvest residual BA. Thinnings focused on beech, but had a target residual BA often resulting in a partial removal of beech. Single-tree selection harvests are the dominant harvest prescription for northern hardwood forests in the study area, are managed to a residual BA of 17-20 m²/ha and beech was targeted heavily for removal. Our stands were first selected from a list of timber sales that were completed from 2011-2013 (65% of study sites). This timeframe was chosen because it was long enough for tree regeneration to respond to harvests, and it coincided with the time frame that MDNR forest managers conduct regeneration surveys (*Forest Certification Work Instructions*, 2005). To bolster sample size, I added stands that fell outside this time period, and these were identified with the help of MDNR forest managers. Stem densities within the regeneration strata were unknown during site selection to avoid bias.

Square 2.02 ha plots (5 ac, 142.24 x 142.24 m) were established within all 69 stands and further divided into a three by three lattice of 0.22 ha subplots (Fig. 2). Locations of plots within stands were mapped prior to site visits to eliminate site selection bias. Plots were then visually inspected to ensure that adequate beech trees, stumps, or snags were present (presence in a minimum of 1/3 plots) due to the heterogenous distribution of beech within stands. If plots did

not meet adequate beech densities, a new plot was mapped in a random location of the stand and the process was repeated until site requirements were met. Sites were stratified post hoc over two regions (NLP and EUP) and three habitat class categories (high, medium, and low moisture/nutrient regime unique to each peninsula) to assess how these predictor variables effect tree species composition and density. Habitat class was determined with a classification system that uses assemblages of herbaceous indicator species whose presence/abundance reflects site nutrient/moisture regimes (Burger and Kotar 2003). Habitat classes fall along a continuum of presumed soil nutrient and water availability and can be used to predict stand characteristics including overstory composition, successional trajectories, and productivity. Habitat classification is currently used by multiple agencies (e.g. MDNR, private timber industry) as a tool to aid development of management, including silvicultural planning. Using habitat class categories as a predictor for understory tree structure in this research project served to both stratify forest stand variation into ecologically/functionally meaningful categories (i.e. productivity, composition, or potential composition) and produce results that can be directly translated and implemented in future management strategies. Habitat classification is also robust in recently disturbed forests, like our study stands, as understory herbaceous indicator species re-establish quickly following disturbance (Coffman and Willis, 1976). Habitat classifications supporting northern hardwood forest with a beech component in the NLP include AFOCa (mesic moisture regime; rich to very rich nutrient regime), AFO (mesic; medium to rich), and ParVVb (dry to dry mesic; poor to medium). Classifications in the EUP include AFOAs (mesic; medium to rich), AFPo (mesic, medium), and ATFD (dry-mesic to mesic; poor to medium) (Fig. 1).

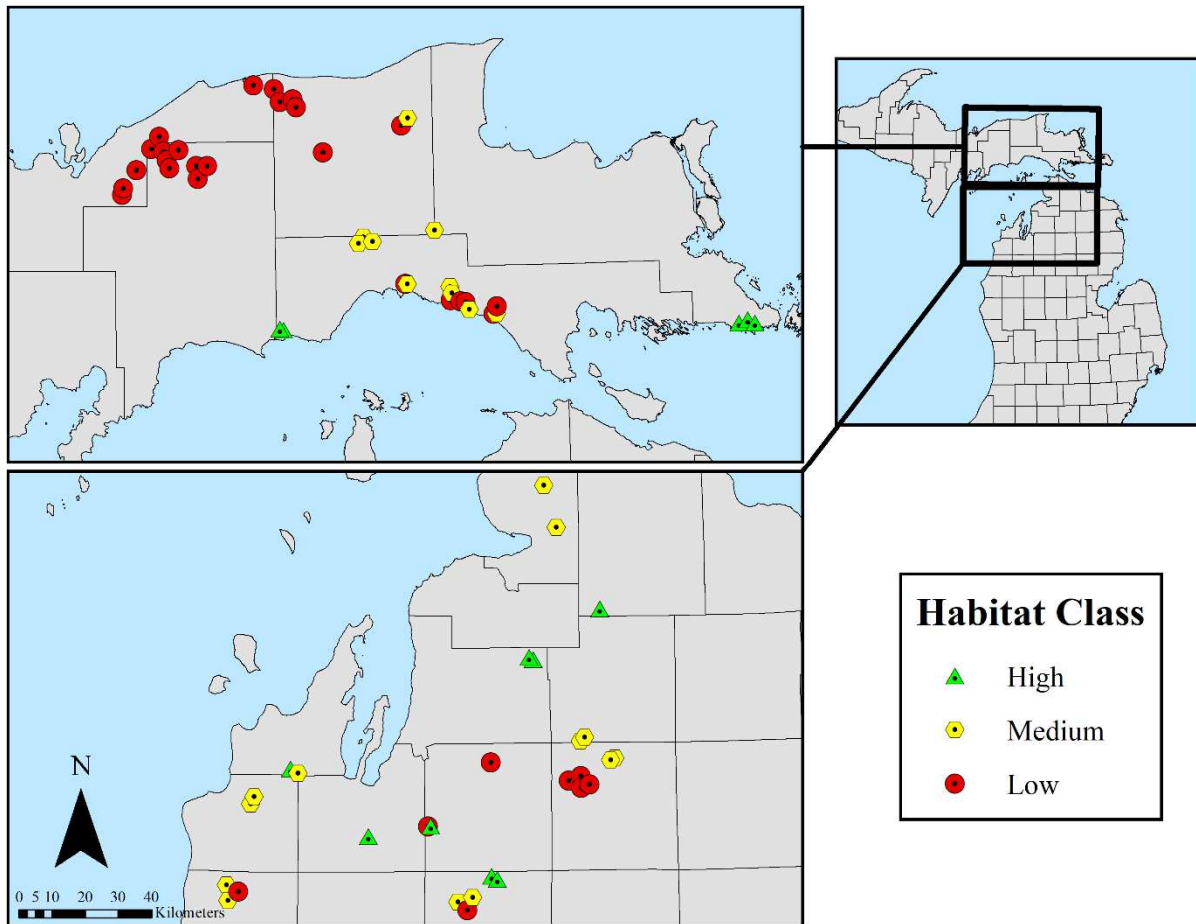


Figure 1. Distribution of 69 sites and associated habitat classes. Classes are unique to EUP and NLP. High classes include AFOCa and AFOAs, medium include AFO and AFPO, and low include PARVVb and ATFD in the NLP and EUP, respectively.

I estimated deer use by collecting fecal pellet count surveys within each site. Pellet counts have inherent limitations including quantification of deer use during winter months, loss of pellet groups due to rain or insects and observer bias. Despite these limitations, pellet count data are reasonably accurate in comparison to other deer density methodologies and can be applied over large landscape level areas (Marques et al., 2003; Neff, 1968). I established six 4 m wide transects ranging from 47-67 m long, throughout the grid system of each stand connecting plot centers in all cardinal and inter-cardinal directions to capture data on overall deer use within study stands (Fig. 3). Distribution of transects resulted in a balanced sampling of both subplots

making up the outer area (outer-most eight sub plots, 89% of transect area, and 88% of total area) and test plots making up the inner square (inner subplot, 11% of transect area, and 12% of total area) of each site. Total transect area was 0.12 ha (6.4% of total site area) per stand. Pellet counts were summed for transects at the site level and transformed to a deer per km² basis following the methods of Hill (2001). This method uses pellet density, defecation rate, and time of defecation deposition (autumn leaf fall to census date) to produce a measure of density per unit area resulting in a site-level measure of deer populations. Given that I only quantified deer use in my study stands (2.02 ha), I recognize these numbers don't necessarily reflect deer use in the surrounding landscape.

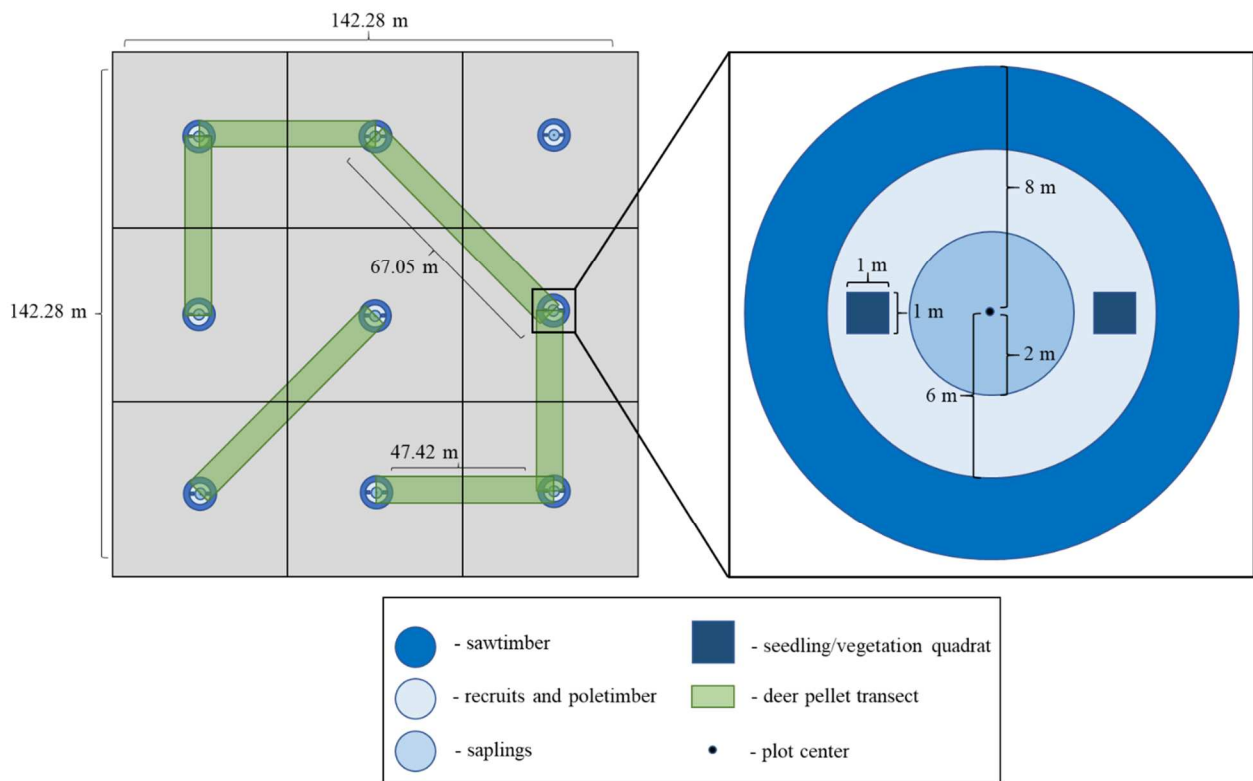


Figure 2. Plot design for vegetation measurements and deer pellet transect layout

Field Methods

Vegetation measurements were taken at the center of all nine subplots using quadrats and nested circular fixed plots designed to efficiently measure stem density (Henttonen and Kangas, 2015). Two 1 m² quadrats were established three meters west (270°) and east (90°) from plot center to avoid sampling vegetation that could be altered due to continued activity at plot center. Three concentric circular fixed radius plots with a common center point were used to collect density data on seedlings, saplings, recruits and canopy trees (Table 1). In quadrats, vegetation density was estimated visually as percent cover. Vegetation categories included grasses and sedges, forbs, ferns, lycophytes, and spring ephemerals as non-species specific groups, and shrubs and tree seedlings (<25 cm tall) were recorded to species. Germination substrate was assessed the same as vegetation with categories including coarse woody debris, humus, bare mineral soil, and hardwood litter.

In a 2 m radius nested plot browse sensitive saplings (25.1-137 cm tall), those that fall beneath the critical height threshold for deer browse (Walters et al. 2018, submitted), were tallied by species. Browse free saplings that exceeded the browse threshold >137 cm tall and <5 cm DBH) were tallied and diameter measured at 137 cm in height (i.e. DBH).

Potential canopy recruits (5.1-10 cm DBH) and poletimber (10.1-25.5 cm DBH) were tallied to species with a DBH measurement within one 6 m radius nested plot, and sawtimber (>25.5 cm DBH) was tallied to species with a DBH measurement within an 8 m radius nested plot. Beech stumps were tallied within each 8 m plot and binned into two separate categories (10.01-25.5 cm diameter for preharvest poletimber and ≥ 25.5 cm diameter for preharvest sawtimber) as a measure of pre-harvest beech density. Sizes of plots were designed to optimize stem count data and are consistent with FIA plot sizes (*Forest Inventory and Analysis*, 2018).

Measurements of BBD agents (beech scale and *Neonectria* spp.) were also recorded and analyzed to quantify the progression of the disease, however these results were not crucial to our objectives so the outcomes of these results can be found in Appendix A.

Table 1. Qualifications of size classes for stem count data

Strata	Height Class	Qualifications	Name
Regeneration	Browse Sensitive	0-25 cm tall	Seedlings
		25.1-137 cm tall	Browse Sensitive Saplings
	Browse Free	<5 cm DBH (>137 cm tall)	Browse Free Saplings
		5.1-10 cm DBH	Recruits
Canopy		10.1-25.5 cm DBH	Poletimber
		>25.5 cm DBH	Sawtimber

Statistical Analysis: Regional Division

Habitat classifications (Burger and Kotar, 2003) are regionally specific due to differences in climatic regimes, bedrock geology, presettlement vegetation and current land use. While overlap in nutrient/moisture regimes occurs between regions, sufficient variation in plant communities exists to warrant regional separation (Burger and Kotar, 2003). To assess if the assumptions of Burger and Kotar (2003) were sufficient to split our analysis into Upper and Lower Peninsula data sets, I used recursive partitioning and nonparametric variance tests to search for evidence of a strong regional split in vegetation data between peninsulas. Recursive partitioning is an exploratory data mining technique that selects optimum splits in data sets through analysis of predictor variables to produce a decision tree (Mulekar and Mauromoustakos, 2002). Decision trees were used to visually assess if habitat classes clustered within regions (unique regional classifications) or by overlapping moisture/nutrient regimes across regions (similar classes across regions). The three dominant tree species (sugar maple, red maple, American beech) were used in this analysis due to their abundance across both regions,

unlike regionally specific associate species, and the three smallest size classes (seedlings, browse sensitive saplings, browse free saplings) were used to avoid confounding factors that management had on species composition and density in larger size classes. Results of recursive partitioning showed clustering of habitat classes within regions as opposed to clustering of moisture/nutrient regimes across regions, suggesting unique regional classifications for tree sapling composition (Appendix B).

Nonparametric variance tests with a Bonferroni adjustment ($p \leq .0019$) were also used to provide further evidence of regionally specific classes. I used nonparametric Wilcoxon exact tests because the distribution of our dataset was non-normal with unequal variance (Lebl, 2016). If regional differences existed, I would expect to see differences between stem count densities in similar habitat classes across regions. Results show 74% of tests (Bonferroni = 41%) were significant, indicating regional differences across similar moisture/nutrient regimes (Appendix C). Results of Recursive partitioning and Nonparametric variance tests, along with the regionally specific habitat classification system in use, led us to separate our data into regionally specific subsets for all further analysis.

Statistical Analysis: Regression Modelling

To standardize measurements of stem counts and reduce variation, all nine subplots were summed for each unique species to produce a single stem count per site value. These measurements were then binned into six separate size classes designed to maintain important trends within the regeneration strata that take size dependency of browsing pressure into consideration, and summarize trends in commercially relevant larger canopy strata (Table 1). Stem count data were often overdispersed and zero-inflated, resulting in the decision to model stem counts using generalized regression with a negative binomial distribution and logarithmic

link function (fit model platform, JMP Pro 13). I began analysis using the maximum likelihood estimation method, however this method often produced estimates with a large and ecologically improbable variance (several hundred thousand stems per hectare) due to a variable spread of continuous predictors (BA and deer use) within our single categorical predictor variable (habitat class). To alleviate this issue, I used the elastic net estimation method, a regularized methodology that avoids overfitting and collinearity among parameters (Crotty and Barker, 2014). Upon comparison of both methods, the elastic net resulted in a more complex final model which more closely satisfied ecological expectations of stem density. In the canopy strata, individual species were modelled by region and size class as a function of habitat class. Other parameters (BA, deer use, etc.) were not included to avoid confounding factors that management has on larger size classes. In the regeneration strata species were modelled individually by region and size class as a function of habitat class, deer use and BA. Other parameters including time since harvest, northing and annual mean temperature were considered during preliminary analysis, but were dropped due to lack of predictive power. For individual species, I restricted modeling to only those species contributing >1% of total composition for the regeneration and canopy strata.

Lastly, individual species in the three smallest size classes (seedlings, browse sensitive saplings, browse free saplings) were pooled into *desirable* and *undesirable* categories (see Appendix D for rationale) to summarize results in a manner better suited for management interpretation. Every iteration of these parameters and their interactions was completed, and model selection was finalized using a backwards elimination process with AICc validation. Models that fell within two AICc units of the lowest AICc score were also considered (Burnham and Anderson, 2002), but were only chosen if the R^2 value increased by >10%.

To isolate individual predictor parameters, I used mean model estimates \pm 95% confidence intervals while keeping all other parameters constant at their mean values. Non-overlap of confidence intervals is interpreted as a conservative test of significant differences between estimated values ($P < 0.01$, Cumming and Finch, 2005). Following analysis area specific expansion factors were applied to present stem densities on a per-hectare basis. For species and size classes where BA or deer use were significant parameters, I explored the magnitude of their effects by reporting model estimates of stem density at a low (10th percentile) vs. high (90th percentile) BA and deer use values, while keeping other parameters constant at their mean values.

Assessing Regeneration Potential for Management

To assess the regeneration potential and likely management outcomes of our study stands (objective 3), I created a decision support tool. This tool is designed to aid managers when making decisions about whether a stand can be maintained (regenerate naturally), restored (require additional treatments for adequate regeneration), or best be managed by conversion to an alternate coertype or more novel silviculture (e.g. herbicide or scarify)

A complete rationale for the decision support tool including its presentation is in Appendix E. Briefly, the system is structured as a dichotomous key with decision points that evaluate (1) minimum stocking densities of *desirable* and *undesirable* species in different regeneration height strata to assess potential for successful regeneration (i.e. free to grow, > 2 m tall) and (2) potential and likely bottlenecks to regeneration. Each decision point is complete with an assessment protocol that guides users through the key until a final treatment point is reached.

For the purpose of this study, I define desirable species as commercially and ecologically valuable species that are capable of being recruited into a canopy position. Undesirable species are primarily understory species, over represented species (beech and ironwood) or species being impacted by pests/pathogens (beech and white ash) (complete list and rationale in Appendix D). Setting minimum stocking thresholds for desirable species is a primary component of the key. Minimum stocking thresholds represent the absolute minimum density of desirable species found in the regeneration strata that can guarantee adequate recruitment of desirable species into the canopy strata in future harvest cycles. I set minimum stocking thresholds in two size classes, browse sensitive saplings (25-137 cm tall) and browse free saplings (>137 tall and < 5 cm DBH). Browse free saplings represent the first sapling size class whose upper canopy is higher than the reach of browsing deer (Walters et al., 2018) and taller than the canopies of most competing non-tree vegetation (e.g. *Rubus* spp.); two of the primary barriers to regeneration of managed northern hardwoods (Donoso and Nyland, 2006; Rooney and Waller, 2003). I propose a density of 950 “free to grow” stems per ha as a minimum stocking threshold for browse free saplings. One 1.82 radius plot (6 ft.) represents the growing space needed by one tree when a stand reaches a merchantable size (large poletimber-small sawtimber, average DBH = 25-28 cm) (Stein, 1992), thus having one free to grow desirable stem in the same plot would expand to roughly 950 stems per hectare. Stocking charts for even aged Allegheny hardwoods and northern hardwoods estimate 741-1,235 stems per ha when a stand reaches merchantable size (Leak, 1969; Stout and Nyland, 1986). Browse sensitive saplings (25-137 cm tall) that do not exceed the browse threshold have the potential to face pressure from deer herbivory and/or competing vegetation. I propose a density of 2,850 stems per ha (3 stems per plot) as a minimum stocking threshold for this size class, to account for these potential barriers to regeneration. I also assessed

likely barriers to regeneration including competing vegetation, deer herbivory, and seed supply (See appendix E for detailed assessment protocols). Following completion of the decision support tool we took the data from our 69 study stands through the key to determine proportion of stands that can be maintained, restored, or best managed through conversion or more novel silviculture.

Results

Forest Characteristics

A total of 25 species (Appendix D) were represented amongst all sites, with sugar maple, red maple and American beech being most abundant in both EUP and NLP regions (Fig. 4 and 5). On average the relative density of these three species combined accounted for 83% (CI: 81-85%) of all species measured across all size classes. Beech dominated the regeneration strata averaging 49% (CI: 42-55%) relative density of browse sensitive saplings, 62% (CI: 56-67%) of browse free saplings, and 46% (CI: 39-52%) of recruits.

Within the canopy strata (pole and sawtimber), stands across both peninsulas are dominated by sugar maple and red maple averaging 73% (CI: 70-77%) relative density, with black cherry (*Prunus serotina* Ehrh.) and eastern hemlock as common associates across regions (Figure 3). Regionally specific associates in the NLP include American basswood (*Tilia americana* L.) and red oak (*Quercus rubra* L.), with basswood being more abundant on higher habitat classes and red oak more abundant on lower habitat classes. With the exception of these two species, overall composition is consistent across habitat classes in the NLP. Within the EUP, diversity of species is higher in lower habitat classes with yellow birch (*Betula alleghaniensis* Britton) and eastern hemlock abundance declining with increasing habitat class. Overall, stands across both regions have a mix of desirable species and are dominated by *Acer*

species (Fig. 3). These results suggest that on average, managed stands impacted by BBD have the potential for adequate regeneration of desirable species given sufficient local seed sources.

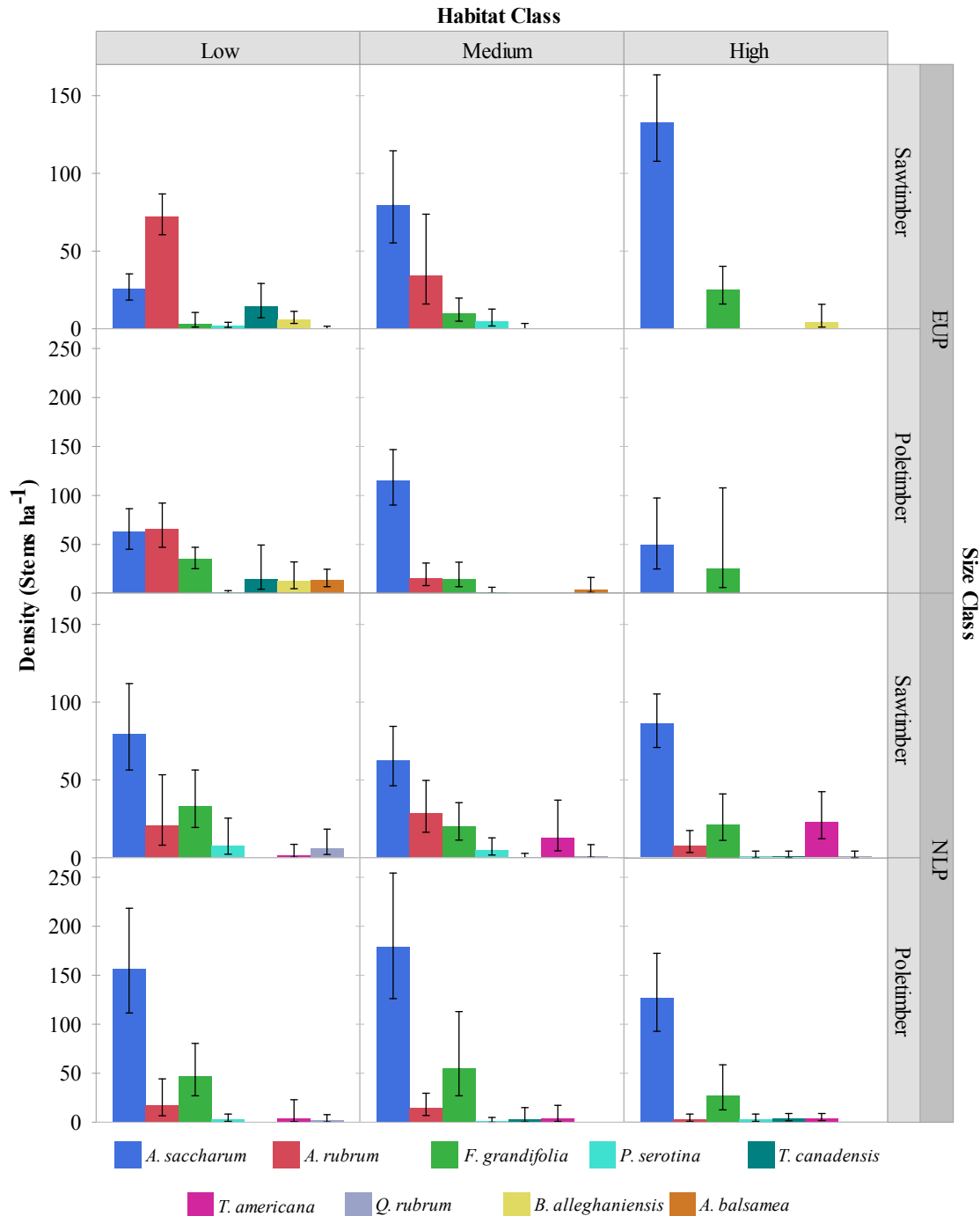


Figure 3. Dominant canopy species and densities across the NLP and EUP. Values represent means \pm 95% confidence intervals by region (peninsula), habitat class and species. Species shown contributed >1 % of the total composition in any one habitat class x size class x peninsula combination.

NLP and EUP forests were similar for many forest characteristics (Table 2). There was a trend of higher pre-harvest canopy beech density and beech harvest density in the EUP than the NLP, but there was considerable variation in both regions such that differences were not significant (i.e. overlapping 95% CI). Forest floor substrate was strongly dominated by hardwood litter at 88% (CI: 87-88%) and tree seedlings were the best represented cover type for forest floor vegetation < 25 cm tall (14%). *Rubus* spp. dominated cover in the woody vegetation category (87% of woody vegetation), but total woody vegetation averaged only 3.5% of total ground cover (Table 2). However, *Rubus* cover at the site level ranged from 0-17%, and ranged from 0-90% at the plot level, indicating high heterogeneity within stands. Additionally, a linear regression of *Rubus* spp. percent cover as a function of BA at the plot scale was significant ($p = .0079$) in the EUP but not significant in the NLP. These results suggest that *Rubus* spp. can be more abundant in areas with a lower BA. However, *Rubus* spp. and other non-tree vegetation was generally low in coverage and likely not major deterrents to seedling regeneration in our stands.

Table 2. Forest stand general characteristics

Region	Habitat Class	Parameter	Mean	SE	95% CI	Range
NLP (n=29)	High (AFOCa, n=8)	Total basal area (m ² /ha)	18	0.2	17.5-18.2	8.9-25.7
	Medium (AFO, n=13)	Time since harvest (year)	5	0.3	4.5-5.7	3-11
	Low (ParVVb, n=8)	Pre-BBD beech density (stems/ha ⁻¹) ¹	45	6.1	32.1-57.1	3.5-153.6
		Beech harvest density (stumps/ha ⁻¹) ²	21	2.9	14.9-36.8	1.7-73.8
		Seedlings (% cover) ³	12	0.0	9-15	2-41
		Competing herbaceous (% cover) ³	7	0.0	6-9	0-23
		Competing woody (% cover) ³	3	0.0	1-4	0-17
		Leaf litter (% cover) ³	87	1.0	85-89	63-95
EUP (n=40)	High (AFOAs, n=5)	Total basal area (m ² /ha)	16	0.2	15.9-16.9	7.6-25.2
	Medium (AFPo, n=10)	Time since harvest (year)	6	0.4	5.0-6.5	1-11
	Low (ATFD, n=25)	Pre BBD beech density (stems/ha ⁻¹) ¹	33	3.0	26.5-38.5	1.7-65.4
		Beech harvest density (stumps/ha ⁻¹) ²	16	2.2	11.4-20.2	0-51.0
		Seedlings (% cover) ³	16	0.0	13-19	5-35
		Competing herbaceous (% cover) ³	6	0.0	4-8	0-18
		Competing woody (% cover) ³	4	0.0	2-6	0-16
		Leaf litter (% cover) ³	89	1.1	87-91	72-97

¹ Pre-BBD beech density is measured as a combination of canopy snags, stumps (pole and sawtimber) and live canopy beech trees.

² Beech harvest density is measured as total stumps tallied within our plots (pole and sawtimber)

³ All forest floor parameters (seedlings, competing herbaceous, competing woody and leaf litter) were measured visually within 1x1m quadrat

Effect of Habitat Class - Regeneration Stratum

NLP - Browse Sensitive Strata

Habitat class was the most important predictor of individual species stem density across all size classes, and was significant in 71% of our regeneration models (Appendix G). The seedling size class (0-25 cm tall) in the NLP is dominated by red and/or sugar maple which comprised 68% (CI: 59-77%) of all stems. Sugar maple occurred at consistent densities across habitat classes (i.e. overlapping 95% confidence intervals) while red maple occurred at higher densities in poorer classes compared to richer classes. There were large changes in composition and density between the seedling and browse sensitive sapling classes with the latter dominated by beech (62% (CI: 53-72%) of all stems). No significant differences occurred for beech stem densities across habitat classes however, mean densities trended towards a decline in density with increasing habitat class. Ironwood was also an important component of the browse sensitive saplings class comprising 16% (CI: 9-23%) of all stems, and beech and ironwood combined comprised 79% (CI: 71-86%) of all stems. In contrast, maple species only represented 6% (CI: 1-10%) of the browse sensitive saplings and occurred at low densities across all habitat classes.

NLP - Browse Free Strata

The browse free saplings size class (0-5 cm DBH, >137 cm tall) was dominated nearly exclusively by beech and ironwood (Fig. 4). Combined, these two species comprised 88% (CI: 82-95%) of total stems. Across habitat classes, no significant differences were found for ironwood stem densities, however beech was found at three times greater densities in the poorest habitat class than the two richer classes. In contrast, red and sugar maple densities combined occurred at extremely low densities in all habitat classes (mean among all sites = 78 ha⁻¹). Within the recruit size class (5-10 cm DBH), sugar maple was the only species in addition to beech that

was well represented at 37% relative density (CI: 27-47%). However, sugar maple occurred at low densities (mean among sites = 47 ha⁻¹) and based on physical appearance many of these stems appeared to be suppressed, low vigor stems and ultimately low-quality trees for timber products (Elenitsky, personal observation).

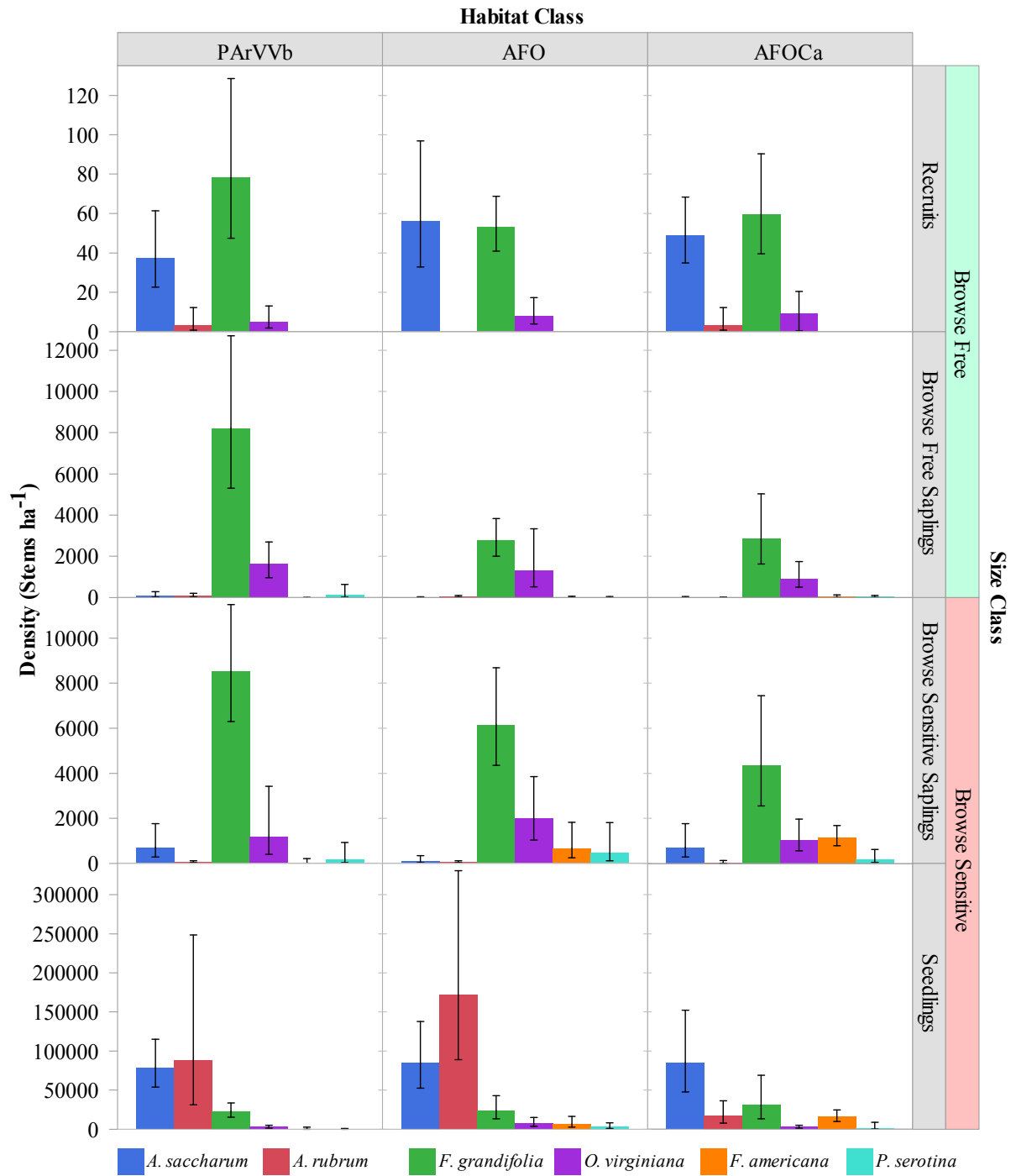


Figure 4. Effects of habitat class on dominant species within the regeneration strata of the NLP. Values are means \pm 95% confidence intervals by region (peninsula), habitat class and species. Species shown contributed >1 % of the total composition in any one habitat class x size class x peninsula combination.

EUP - Browse Sensitive Strata

In the EUP, the seedling size class (0-25 cm tall) was dominated by sugar maple and red maple, comprising 91% of all stems and occurring at high densities (Fig. 5). Red maple was better represented in the poorest habitat class and sugar maple was better represented in the two richer habitat classes. However, with increasing size class both maple species steadily decline. Beech becomes better represented in the browse sensitive sapling class (25-137 cm tall) with a relative density of 39% (CI: 32-46%) across all habitat classes. However, unlike the NLP, beech representation does not outnumber the combined relative density of sugar and red maple (45%, (CI: 36-53%) for ATFD, 66% (CI: 54-78%) for AFPo, and 41% (CI: 12-70%) for AFOAs) (Fig. 5).

EUP - Browse Free Strata

Beech continues to become more dominant with increasing size and makes up 59% (CI: 52-66%) of all stems in the browse sensitive sapling class (>137 cm tall, 0-5cm DBH). Sugar maple and red maple are present in this size class, but at low densities with a combined relative density of 24% (CI: 18-31%). Additionally, ironwood and pin cherry become better represented in the browse sensitive saplings class with a combined relative density of 8% (CI: 4-12%). Within the recruits size class (5-10 cm DBH), beech dominates the ATFD habitat class representing 52% (CI: 43-60%) of all stems. Sugar maple is better represented in the higher habitat classes comprising 36% (CI: 17-56%) of all stems, but occurring at low densities of 30 stems/ha⁻¹. Overall, beech makes up a smaller proportion and maple species make up a larger proportion of the regeneration stratum in comparison to the NLP (Fig. 4 and 5).

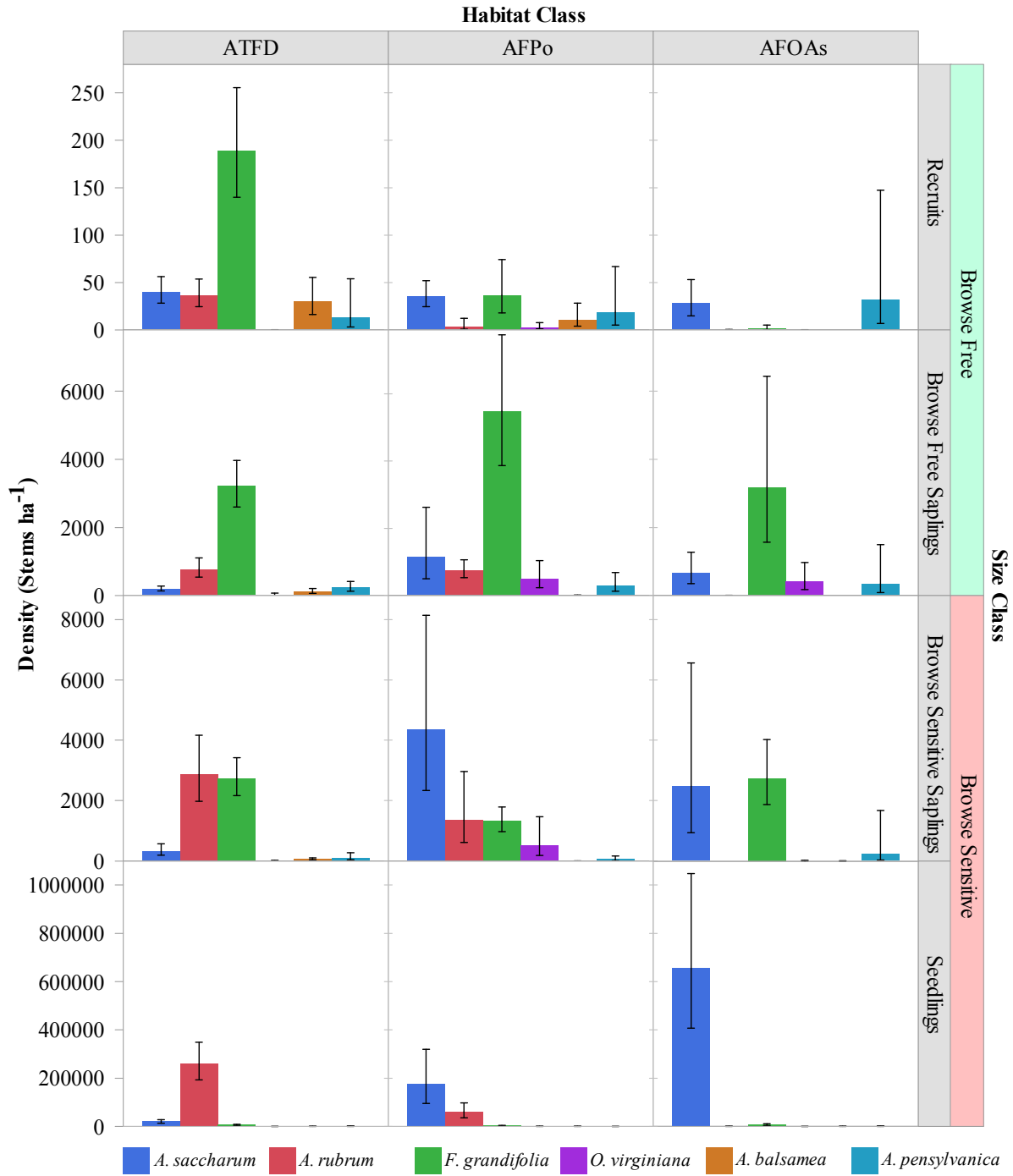


Figure 5. Effects of habitat class on dominant species within the regeneration strata of the EUP. Values are means \pm 95% confidence intervals by region (peninsula), habitat class and species. Species shown are those that contributed >1 % of total composition in any one habitat class x size class x peninsula combination.

Desirable and Undesirable categories

To illustrate problems regeneration patterns pose for forest management I combined individual species into *desirable* and *undesirable* categories based on commercial value, potential for growing into saw log sized tree and pests/pathogen impacts (Appendix D). Within the seedling strata, desirable species were found at higher densities (85% of all stems), when compared to undesirable species (15% of all stems), irrespective of region or habitat class (Figure 6). This pattern demonstrates that, on average, these stands all show the potential for successful regeneration recruitment, however with increasing size class, this promise dissipates with dominance of undesirable species and low densities of desirable species (Figure 6). Within the sapling size classes this pattern varied little among habitat classes, however I found distinct patterns between regions.

In the NLP, desirable species occurred at low densities in both the browse sensitive (638 ha⁻¹, 11% of all stems) and browse free saplings class (345 ha⁻¹, 6% of all stems), resulting in a complete dominance of undesirable species (6,189 ha⁻¹, 93% of all stems) in sapling classes that exceed the browse threshold. By contrast, sapling size classes in the EUP had a higher relative and absolute density of desirable species compared to the NLP. In the browse sensitive sapling class, desirable species were found at higher densities (4,610 ha⁻¹, 53% of all stems) when compared to undesirable stems (2,911 ha⁻¹, 46% of all stems), showing potential for adequate regeneration. However, dominance of desirable species declined when reaching the browse free sapling class (crossing browse threshold, 1,669 ha⁻¹, 28% of all stems) and undesirable species represented a higher proportion of total stems (5,134 ha⁻¹, 71% of all stems).

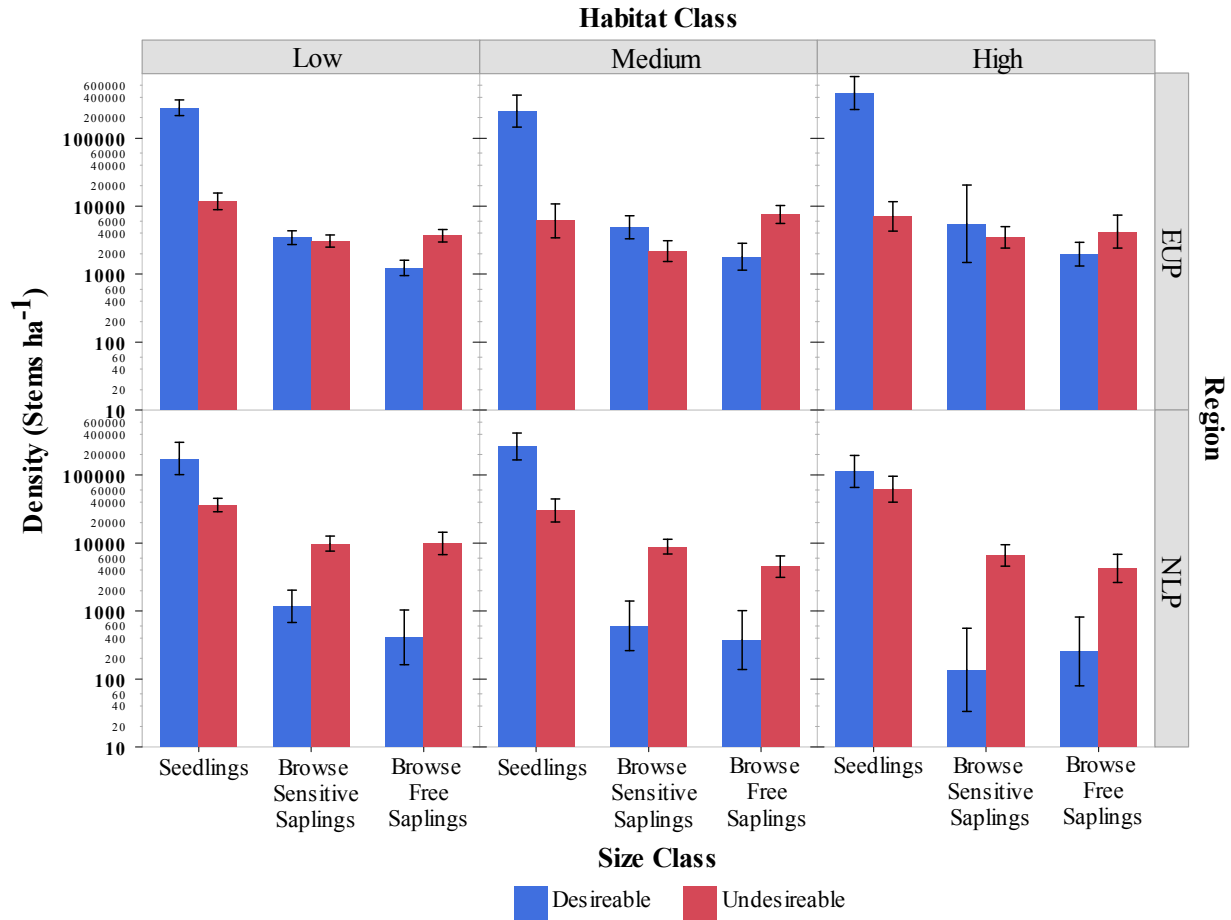


Figure 6. Stem densities of desirable and undesirable categories across both regions and all habitat classes. Values represent means \pm 95% confidence intervals by region and habitat class. High classes include AFOCa and AFOAs, medium include AFO and AFPO, and low include PArVVb and ATFD in the NLP and EUP, respectively. Results are presented on a log scale to compare highly variable densities between size classes.

Effect of Deer

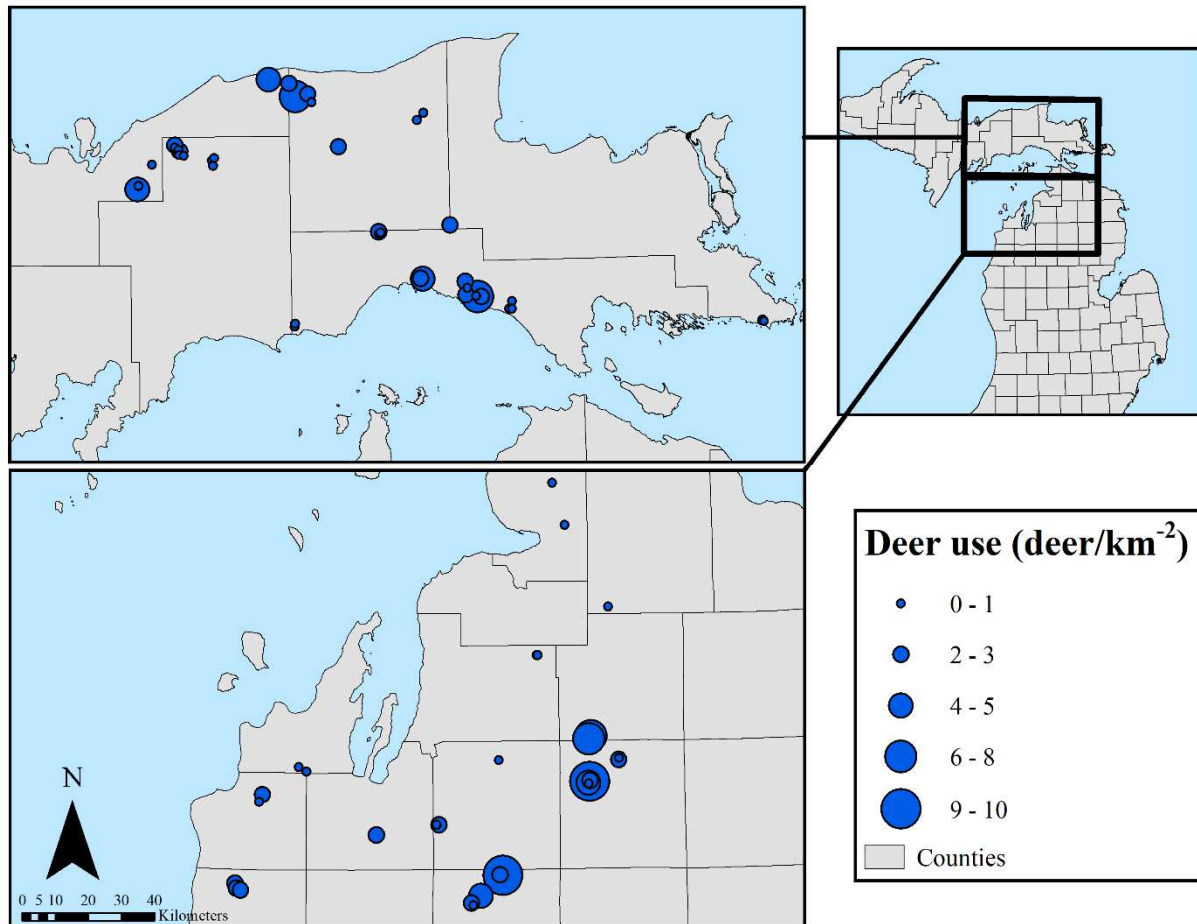


Figure 7. Spatial distribution of deer use (deer/km²) across study sites (n=69).

On average winter deer use in the stands was low (2.5 deer/km²), but ranged from 0 to 10.4 deer/km². I expected deer use to be low in the northern half of the EUP due to greater winter snow depth, but found no spatial trend. In the NLP, deer use appears generally lower in areas of deep lake effect snow near Lake Michigan. Among tree species in the three smallest size classes, deer use was a significant predictor of stem density in 28% of our final models (Appendix G). In the NLP, ironwood was the only species in the seedling class correlated with pellet counts resulting in a negative relationship. No species in the browse sensitive saplings

class showed a significant relationship to deer use, but white ash (*Fraxinus americana* L.) and black cherry density in the browse free saplings class had a positive relationship to deer use.

In the EUP, as deer use increased, densities of browse sensitive classes (0-135 cm tall) increased for sugar maple, balsam fir and striped maple (*Acer pensylvanicum* L.) and decreased for ironwood and yellow birch. In the browse free sapling class pin cherry, yellow birch, and balsam fir density were all negatively related to deer use (Table 3).

Table 3. Summary of modeling results for deer use (D) and basal area (BA). Areas within parenthesis represent models where the interaction of a parameter and a specific habitat class (AFPo, ATFD, AFOAs, AFOCa) were significant. “+” and “-” indicate the direction of the effect. *= p < 0.05; **= p < 0.01; ***= p < 0.001; ****= p < 0.0001.

Parameter	Region	Size Class		
		Seedlings	Browse sensitive Saplings	Browse Free Saplings
Deer Use	EUP	<i>A. saccharum</i> ,***, + <i>O. virginiana</i> ,***, - <i>A. pensylvanicum</i> ,****, +	<i>B. alleghaniensis</i> ,(AFPo*D),***, - <i>A. balsamea</i> ,(ATFD*D),***, + <i>A. pensylvanicum</i> , D = ****, +	<i>P. pensylvanica</i> ,****, - <i>B. alleghaniensis</i> ,**, - <i>A. balsamea</i> ,(AFPo*D),**, -
	NLP	<i>O. virginiana</i> ,**,-		<i>F. americana</i> ,(AFOCa*D),****, + <i>P. serotina</i> ,**, +
Basal Area	EUP	<i>T. canadensis</i> ,**,+	<i>A. rubrum</i> ,****, - <i>F. grandifolia</i> ,**, - <i>O. virginiana</i> ,(AFOAs*BA)****, + <i>B. alleghaniensis</i> ,*, +	<i>F. grandifolia</i> ,****, - <i>P. pensylvanica</i> ,****, - <i>B. alleghaniensis</i> ,***, + <i>T. canadensis</i> ,*, +
	NLP		<i>F. grandifolia</i> ,**,-	<i>P. pensylvanica</i> , (AFOCa *BA)****,+

Effect of Basal Area

For the three smallest regeneration size classes across the eleven most dominant species, mean site basal area (i.e. canopy tree density) was a significant predictor of stem density in 30% of our models (Appendix G). Beech was the only species where BA significantly predicted stem density across regions and size classes, always resulting in increasing stem density with decreasing BA in all sapling size classes. In the EUP significant differences occurred in the AFPO habitat class (10th percentile BA = 8,287, 90th percentile BA = 3,613 stems ha⁻¹) and AFOAs habitat class (10th percentile BA = 4,860, 90th percentile BA = 2,119 stems ha⁻¹) for browse free saplings. In the NLP significant differences occurred in the PArVVb habitat class (10th percentile BA = 24,726, 90th percentile BA = 728 stems ha⁻¹) for browse free saplings. Beech density was also significantly different for both the PArVVb (10th percentile BA = 19,424, 90th percentile BA = 2,377 stems ha⁻¹) and AFOCA (10th percentile BA = 14,258, 90th percentile BA = 1,744 stems ha⁻¹) classes in the browse sensitive sapling class in the NLP.

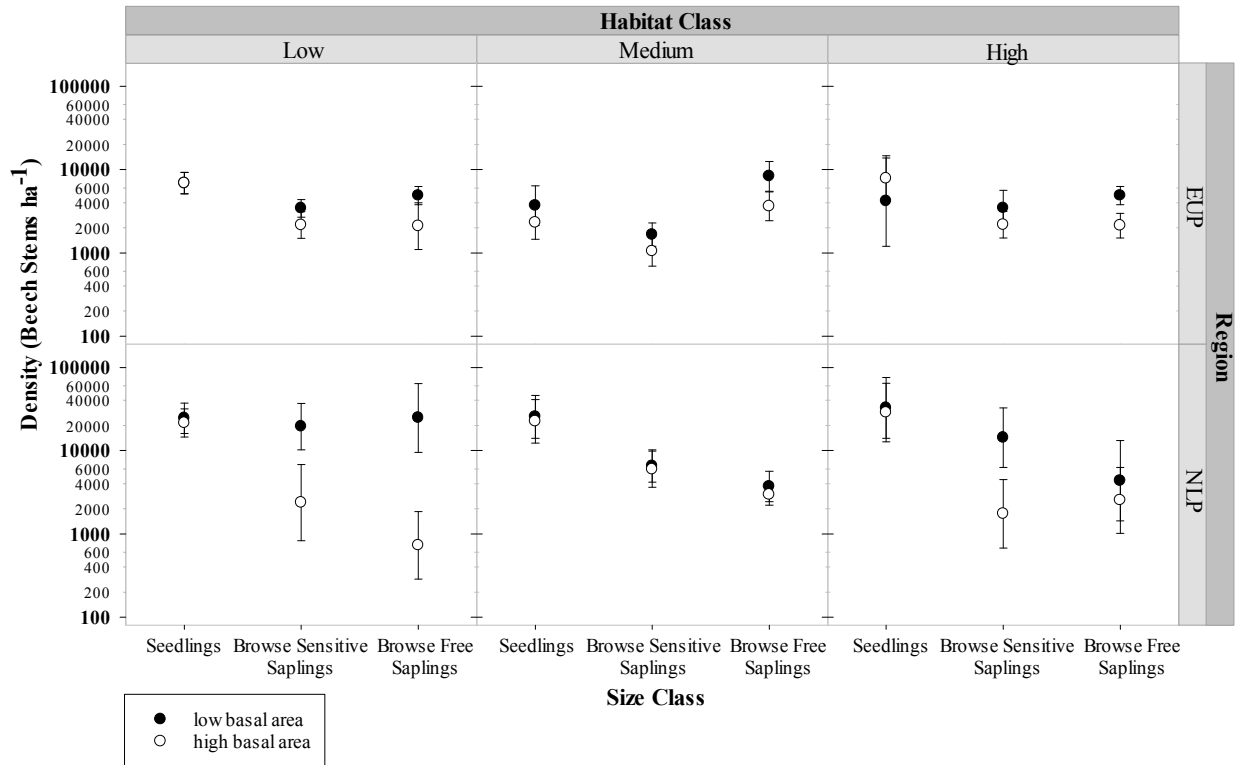


Figure 8. Effects of basal area on American beech in the regeneration strata. 10th percentile BA = 11.7 m²/ha, 90th percentile BA = 22.4 m²/ha. Values are model estimates, and error bars represent 95% confidence intervals. High classes include AFOCa and AFOAs, medium include AFO and AFPo, and low include PARVVb and ATFD in the NLP and EUP, respectively.

In the NLP, the only other species significantly impacted by BA was white ash in the browse free sapling class, resulting in a positive relationship. In the EUP, eastern hemlock had a positive relationship with BA in the seedlings class. In the browse free sapling class red maple had a negative relationship, while ironwood and yellow birch had positive relationships with BA. In the browse free sapling class yellow birch and hemlock had a positive relationship with BA (Table 3).

Regeneration Potential: Results of Decision Support Tool

Using the data collected from our study stands, I took the 57 stands that met the underlying assumptions of our decision support tool (BA<16m²/ha) (see Appendix E for

rationale) through the decision points to identify trends in both evenness of regeneration within stands, as well as proportions of stands that would regenerate naturally, require additional treatments for adequate regeneration, or be candidates for conversion or more novel silviculture.

Applying the decision support tool to all 57 stands, I found that 3% of stands (all in the EUP) supported adequate regeneration of desirable species in taller strata and need no further treatment, 83% of stands had undesirable regeneration in taller strata and plentiful regeneration in shorter strata and might require treatments to control undesirable saplings and diminish deer impacts, and 14% of stands had little regeneration of desirable stems in any size class and could be targeted for conversion to other cover types (e.g. *Pinus resinosa* plantations) or be ideal candidates for more novel silviculture options (herbicide/scarify) (see results of Appendix E for a more detailed breakdown).

Discussion

Regional Effect

Our results indicate that the EUP and NLP differ markedly in tree regeneration composition and structure. There are likely several reasons for this, but contributing factors may include differences in the dynamics of beech harvests, landscape context, climate and differences in stages of BBD progression. Wieferich (2013) found varying rates of advancing front spread, beech scale density, and overstory beech mortality between the NLP and EUP, indicating distinct differences in BBD progression between regions. I collected supplementary data on BBD agents (Appendix A) and my results also indicate unique stages of BBD progression between peninsulas. BBD progression is more advanced in the EUP, as indicated by higher rates of overstory beech mortality and lower densities of beech scale, aligning with descriptions of aftermath forests (J. A. Cale et al., 2015). Forests in the NLP maintained higher proportions of

live canopy beech and higher densities of beech scale, more closely resembling stands from the killing front (Houston et al., 2005; Mielke, 1990). Varying stages of BBD progression will result in varying regeneration dynamics, making BBD progression an important consideration for management objectives.

Considering broader-scale differences between my Michigan data and studies from the Eastern United States beech sapling density in Michigan is generally lower than beech “thickets” found in the Eastern United States. In New York, Cale et al. (2013) defined a beech thicket density (stems <5 cm DBH and >1.4 m tall) as > 10,000 stems/ ha⁻¹. Average density of the same size class (browse free saplings) in my study stands was 4,250 stems/ ha⁻¹ (CI: 3313-5187) in the EUP and 4,295 (CI: 2751-5840) in the NLP. At the tree scale (individual subplots) only 13% of my plots exceeded 10,000 beech stems/ ha⁻¹. In Maine, Farrar and Ostrotsky (2006) found beech stem (< 2.5 cm DBH and >139 cm tall) densities ranging from 27,181- 44,478 stems/ ha⁻¹ ten years following partial harvests. Average density of beech stems (browse sensitive saplings and seedlings) in my study stands were 4,471 stems/ ha⁻¹ (CI: 3,448-5,495) in the EUP and 14,305 (CI: 9,977-18,633) in the NLP.

Regeneration Dynamics

High *Acer* spp. seedling densities across both regions and all habitat classes indicate adequate seed availability and germination/establishment conditions for these key species. However, *Acer* spp. and other deer browsing preferred species became small proportions of taller size classes that exceed the deer browse threshold (Walters et al., 2018). The near absence of browsing preferred species in stratum taller than seedlings suggests that pressure from deer herbivory is strongly limiting recruitment from seedlings to saplings that exceed the browse threshold, especially in the NLP. Overall, deer use had a larger effect on species in the EUP than

the NLP, and had a larger negative effect on palatable species in comparison to unpalatable species. There were some cases where deer use had a positive effect on palatable species (sugar maple seedlings), which in both peninsulas may be explained by deer being more attracted to stands with higher densities of food in their reach. Overall, results of our direct measure of deer effects (pellet counts) were modest, perhaps because our data only captured winter deer densities in 2018 and fail to characterize legacies of past deer densities. Our pellet count data represent a snap shot in time of what deer use looks like five years post-harvest. However, the shift from a dominance of palatable species in the seedling size class to unpalatable species in size classes that exceed the browse threshold is not a direct measure of deer herbivory, but offers convincing evidence for the effects of past browsing pressure (figure 4 and 5).

In addition to deer browse competing vegetation is a common barrier to regeneration in northern hardwood forests. Competing vegetation often occurs at higher densities in recently harvested northern hardwood forests (Donoso and Nyland, 2006; Donovan, 2005, Walters et al. 2016) and can affect the probability of recruitment from seedlings to browse free saplings, but our BBD impacted forests are characterized by a low density of competitive non-tree vegetation (e.g. *Rubus*, Walters et al. 2016, Widen et al., 2018). Low densities of non-tree vegetation could be explained by low light availability from relatively dense understories, thick persistent beech leaf litter layers inhibiting germinations and establishment of non-tree vegetation (Cale et al., 2013) or heavy deer browsing impacts on non-tree vegetation (Walters et al. 2016).

Management history may also influence predominance of beech dominated understories. Studies have shown that repeated single-tree selection harvests can result in low diversity sapling layers with high proportions of beech saplings (Angers et al., 2005; Nolet et al., 2008) and or ironwood (Matonis et al., 2011). Beech dominated understories have also been found in managed

northern hardwood stands prior to BBD infection (Roy and Nolet, 2018), indicating that BBD may not be a necessary trigger for beech understory establishment.

Management Implications

In stands managed by selection silviculture, beech removal harvests (salvage) are not considered a regeneration cut however, these treatments sometimes result in basal areas low enough to trigger regeneration. My study indicated beech removal harvests largely resulted in beech dominated understories, demonstrating this technique's inability to be considered a regeneration technique. Managers often rely on natural regeneration and advanced regeneration to ensure recruitment of desirable species, however more resource-intensive treatments (i.e., herbicide, scarify) aimed at removing beech dominated understories and silviculture techniques aimed at reducing pressure from deer herbivory are needed to promote adequate regeneration of desirable species in managed northern hardwoods impacted by BBD.

Regardless of the intention of the previous harvest (selection silviculture, salvage, thinning) most of my study stands have been managed in the longer term (50 years plus) by selection silviculture, and fail to meet the regeneration standards expected from this technique. Results of our decision support tool suggest that none of the stands in the NLP and only 4% of stands in the EUP can regenerate naturally in their current state. 16% of our stands failed regeneration requirements in both sapling stratum and were dominated by undesirable species in the canopy making them ideal candidates for conversion or more novel silviculture. The vast majority of our stands (80%) however are dominated by desirable stems in the canopy and seedling strata and will require additional treatments to recruit adequate densities of seedlings to browse free sapling size classes in order to meet regeneration requirements (i.e. herbicide and/or scarify).

Presently, northern hardwood management in Michigan focuses on overstory harvesting patterns to promote adequate stocking of desirable natural regeneration. Understory treatments are rarely used to foster regeneration, and guidelines informing managers when to use understory treatments are not well developed. Nyland et al. (2006) suggested understory management if 30-40% of the stand is dominated by undesirable stems. Hannah (1987) recommended site preparation when beech or other undesirable species comprise >50% of advanced regeneration, and Bohn and Nyland (2003) indicate regeneration failure when any undesirable stem reaches tallest of plot status in milacre plots. Our results, and the findings of these studies, suggest that understory management is a necessary component of strategies aimed at promoting adequate regeneration. Currently, mechanical means of removing undesirable species in smaller size classes include spec cutting and mowing of saplings using feller-bunchers during overstory harvest. These practices may result in short term reduction of undesirable stems, however in the long run may actually increase beech sapling density through promotion of root sprouting (Mallik et al., 1997). Harvests are usually completed during winter to reduce damage to shallow root systems, however cutting of understory stems during dormant seasons may actually increase root suckering due to reserve carbohydrates in root systems (Farrar and Ostrocsky, 2006; Mallett, 2002).

Other techniques of reducing undesirable stems in small classes include girdling, stem injections, and basal sprays (Nyland et al., 2006), however these treatments are not applicable at landscape levels. Techniques that can effectively be carried out at a landscape level include prescribed burning and broadcast foliar herbicide applications. There are few studies that have tested the effects of fire on beech dominated understories, however there is some evidence suggesting prescribed burning is largely ineffective at killing beech saplings (Johnson, 1996;

Swan, 1970). Foliar herbicide application has been well documented and several studies have reported successful removal of beech dominated understories and successive recruitment of desirable stems (Nyland et al. 2006). Glyphosate and triclopyr based herbicides are effective and can be applied with a tractor mounted mist blower, allowing managers to effectively treat large landscape level areas.

In addition to understory management, deer herbivory is an important factor that needs to be considered when assessing the potential for regeneration. Most studies advocate the use of deer fencing or increased hunting of does, however both techniques are often not viable economically and/or socially. I instead advocate use of novel silviculture treatments that aim to reduce deer herbivory within stands while maintaining populations of deer in the surrounding landscape. Walters et al. (2016) found that reducing residual BA (large patch cuts) in a stand can deter herbivory through increased levels of non-tree vegetation that overwhelm browsing deer, act as physical deterrents, and/or make desirable seedlings more difficult to find.

Use of salvage harvests may be an effective overstory technique to capture commercial value of diseased trees, however our results indicate that salvage harvests largely result in beech dominated understories. Our results illustrate the importance of regeneration monitoring, adequate regeneration protocols, and novel management techniques that address modern barriers to regeneration (deer herbivory, pests/pathogens, legacies of past management). Traditional overstory management techniques that rely on natural regeneration and advanced regeneration will likely not be effective in restoring BBD impacted forests. Northern hardwoods are the dominant coverteype in Michigan and currently cover around two million hectares, making it imperative for forest managers to implement novel management techniques aimed at ensuring adequate regeneration.

APPENDICES

APPENDIX A: MEASUREMENT AND ANALYSIS OF BBD AGENTS

Methods

American beech in the canopy strata were assessed for beech scale wax density and bark condition to assess progression and outcomes of BBD throughout both regions. Beech scale wax density was visually estimated as a proxy for beech scale density and placed into four ordinal categories (Wieferich, 2013):

1. Absent or Trace – scale wax completely absent or miniscule amounts present
2. Light – small patches of scale wax present, <10% coverage
3. Patchy – large patches of scale wax present, 10 – 60% coverage
4. White-washed – one or more aspect heavily infested, $\geq 60\%$

Beech bark condition was visually estimated as a proxy for *Neonectria* spp. density and tree's individual response to BBD. These estimations were placed into four ordinal categories.

1. Smooth – healthy bark, no signs of cankers
2. Light – Small cankers and bark distortion present, <10 %
3. Patchy – patches of cankers and bark distortion present, 10-60%
4. Heavy – Cankers and bark distortion cover the majority of the bole, $\geq 60\%$

Beech snags were tallied within all nine subplots and as an additional measure, tallied as total snags visible from plot center to quantify beech mortality within stands. Snags were not limited to fixed area plots to obtain measurements at a broader scale and capture more data on beech mortality.

Statistical Analysis

Disease agent densities (beech scale and *Neonectria* spp.) were estimated by ordinal categorization and I used ordinal logistic regression models for analysis. Scale density and bark

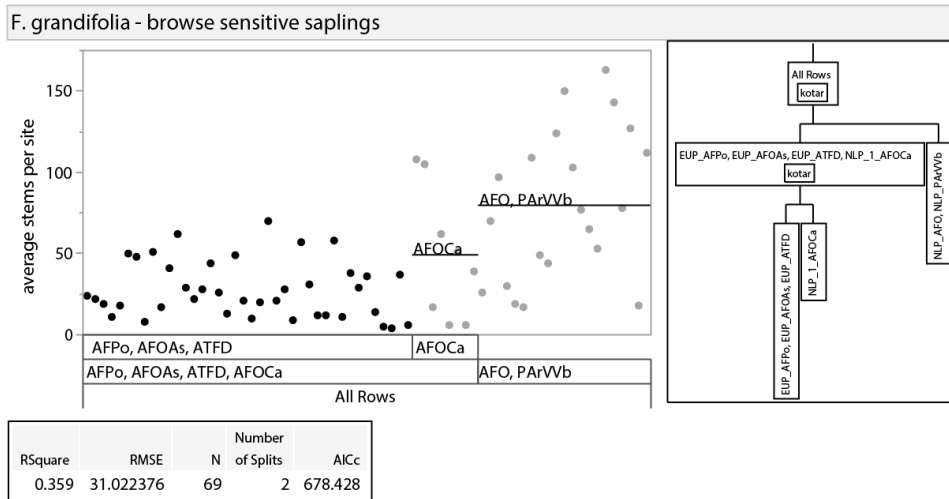
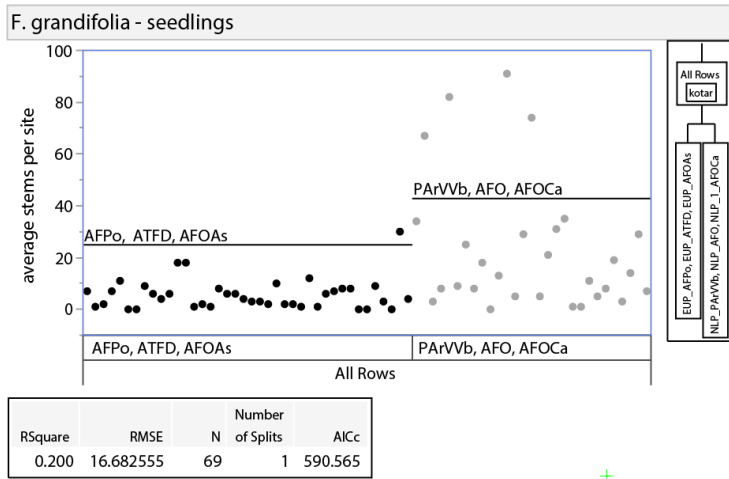
condition were used as response variables and modelled as a function of region to interpret regional differences between disease progression.

Results

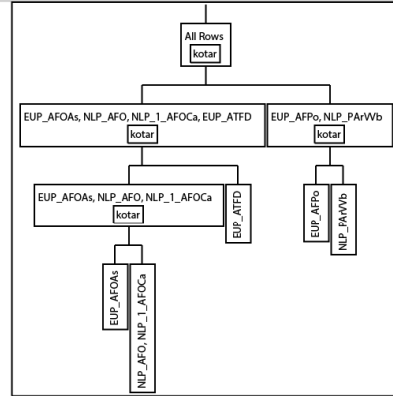
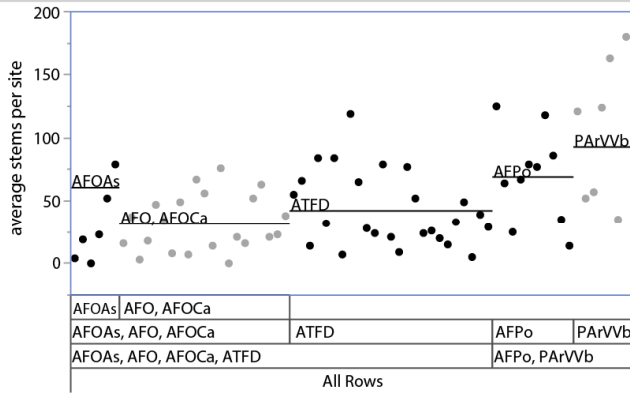
Metrics of disease progression included scale wax density and beech bark condition (beech response to *Neonectria* spp.) analyzed at the tree-level, and overstory beech mortality analyzed at the site-level. Canopy beech in the NLP predominately had “light” or “patchy” scale densities (category 2-3 = 80%), in contrast to “absent or trace” densities in the EUP (category 1 = 64%). Conversely, bark condition in the NLP was categorized as “smooth” or “light” (category 1-2 = 82%) while bark vigor in the EUP had higher instances of “patchy” and “heavy” classifications (category 3-4 = 57%). Both scale density and bark vigor of canopy beech trees, were significantly different ($p = <.0001$) between regions and indicate that stands in the EUP are in a more advanced stage of BBD (aftermath forest) than stands in the NLP (killing front). Additionally, we observed an average of 1.58 (CI: 0.12-3.05) snags per site (nine plots within five acres) in the NLP while stands in the EUP had an average of 8.75 (CI: 5.01-12.48), indicating higher unsalvaged beech mortality in the EUP. We recognize these results are likely confounded by the history of management practices within stands, however they support the notion that the NLP and EUP are in distinctly different phases of the BBD progression (Wieferich, 2013).

APPENDIX B: RESULTS OF RECURSIVE PARTITIONING

Recursive partitioning trees were used to visually compare stem densities of the three smallest size classes of the three most dominant species (sugar maple, red maple, American beech) to assess regional separation. Black dots represent data points from EUP and grey dots represent data points from NLP.

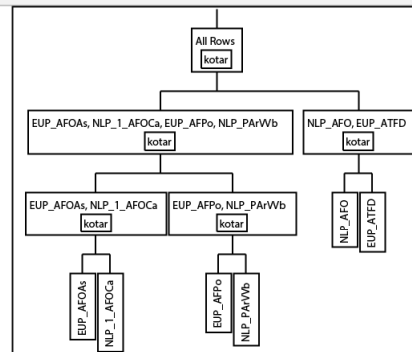
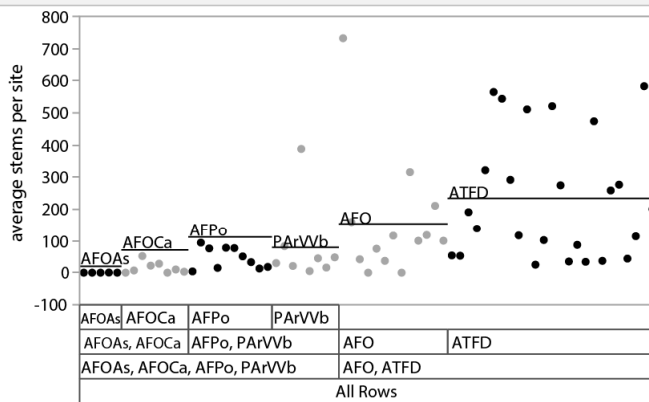


F. grandifolia - small saplings above browse



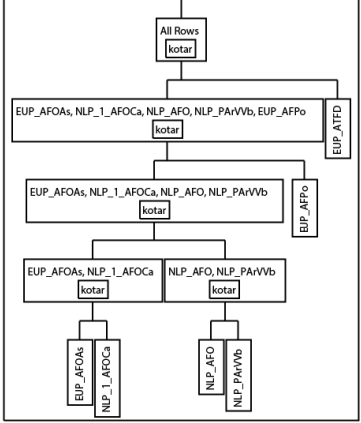
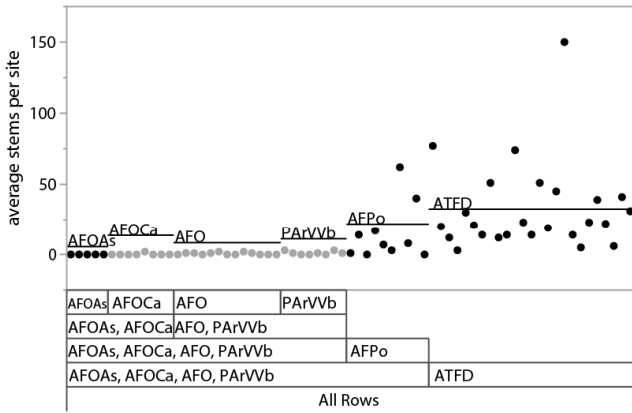
RSquare	RMSE	N	Number of Splits	AICc
0.278	32.774821	69	4	700.537

A. rubrum - seedlings



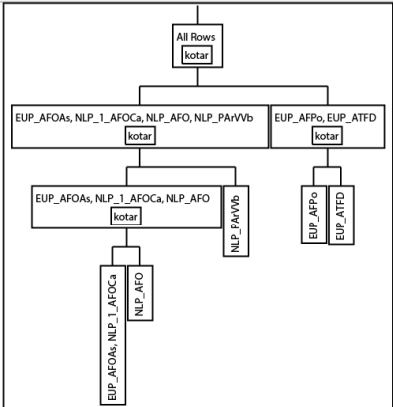
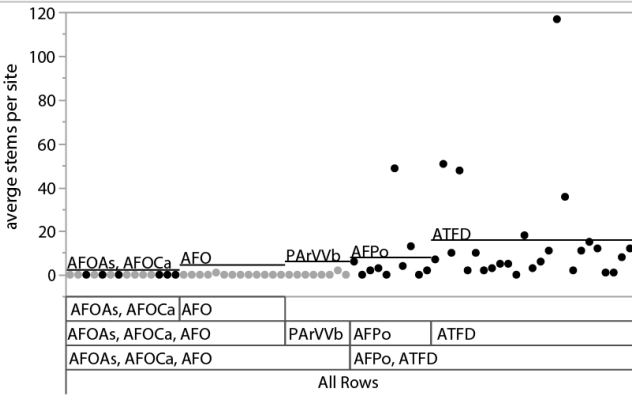
RSquare	RMSE	N	Number of Splits	AICc
0.275	146.40726	69	5	899.772

A. rubrum - browse sensitive saplings



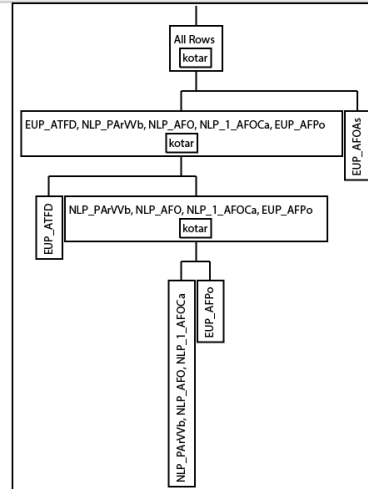
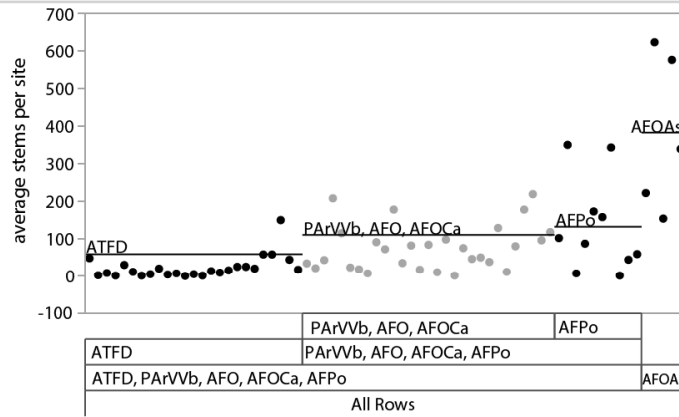
RSquare	RMSE	Number of Splits	N	AICc
0.347	19.976512	5	69	624.898

A. rubrum - small saplings above browse



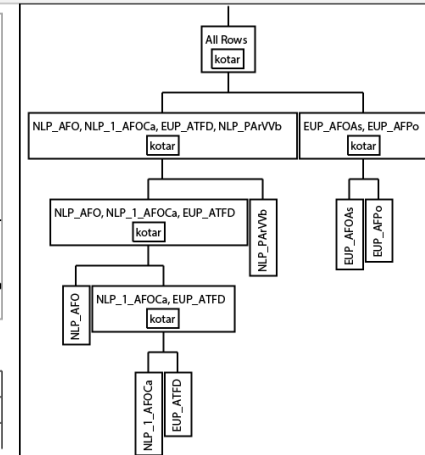
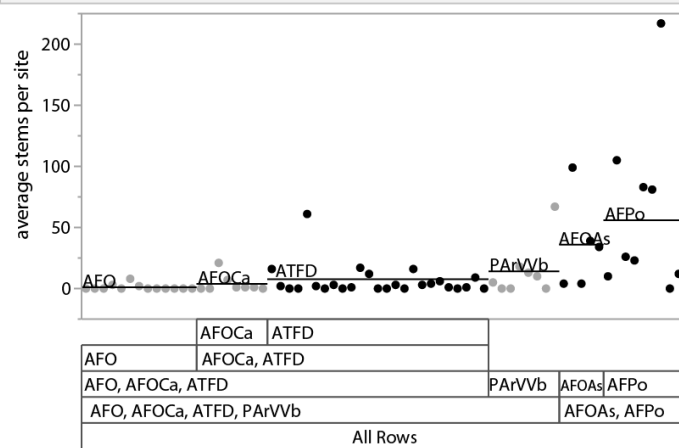
RSquare	RMSE	Number of Splits	N	AICc
0.175	15.650962	4	70	597.059

A. saccharum - seedlings



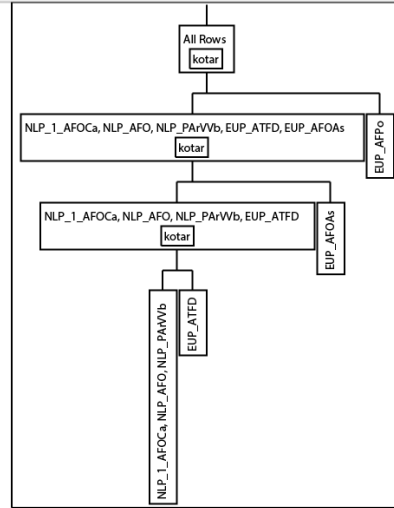
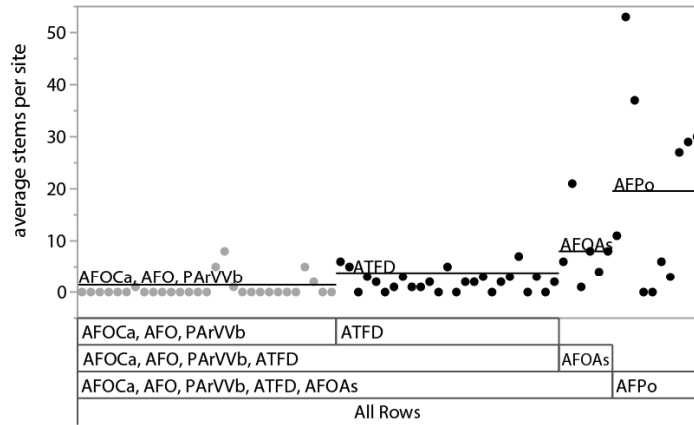
RSquare	RMSE	N	Number of Splits	AICc
0.558	80.550183	69	3	812.431

A. Saccharum - browse sensitive saplings



RSquare	RMSE	N	Number of Splits	AICc
0.305	28.385976	69	5	673.383

A. saccharum - small saplings above browse



RSquare	RMSE	N	Number of Splits	AICc
0.460	6.9778735	70	3	481.573

APPENDIX C: RESULTS OF NONPARAMETRIC WILCOXON TESTS

Results of nonparametric Wilcoxon tests comparing stem densities of the three smallest size classes of the three most dominant species across similar habitat classes between regions. High compares the two high classes between regions (NLP – AFOCa, EUP – AFOAs), Medium compares the two medium classes (NLP – AFO, EUP – AFPO), and low compares the two low classes (NLP – ParVVb, EUP – ATFD). Bolded values indicate significance after Bonferroni correction ($p \leq 0.0019$).

Species	Size Class	Habitat Class	Prob > S
<i>F. grandifolia</i>	Seedlings	High	0.2098
		Medium	0.0006
		Low	0.0017
	Browse sensitive saplings	High	0.2028
		Medium	0.0002
		Low	<.0001
	Browse free Saplings	High	0.4858
		Medium	0.0038
		Low	0.0146
<i>A. rubrum</i>	Seedling	High	0.0163
		Medium	0.0276
		Low	0.0034
	Browse sensitive saplings	High	0.6154
		Medium	0.003
		Low	<.0001
	Browse free saplings	High	1.0000
		Medium	0.0005
		Low	<.0001
<i>A. saccharum</i>	Seedling	High	0.0031
		Medium	0.1753
		Low	0.0007
	Browse sensitive saplings	High	0.0085
		Medium	<.0001
		Low	0.1831
	Browse free saplings	High	0.001
		Medium	0.0005
		Low	0.028

APPENDIX D: QUALIFICATION OF DESIRABLE AND UNDESIRABLE SPECIES

Category	Species	Qualifications
desirable	<i>Acer rubrum</i>	canopy species, commercially valuable
	<i>Acer Saccharum</i>	canopy species, commercially valuable
	<i>Betula alleghaniensis</i>	canopy species, commercially valuable
	<i>Betula papyrifera</i>	canopy species, important successional species
	<i>Picea glauca</i>	canopy species
	<i>Pinus resinosa</i>	canopy species, commercially valuable
	<i>Pinus strobus</i>	canopy species, commercially valuable
	<i>Populus grandidentata</i>	canopy species
	<i>Populus tremuloides</i>	canopy species, important successional species
	<i>Prunus serotina</i>	canopy species, commercially valuable
	<i>Quercus rubra</i>	canopy species, commercially valuable
	<i>Thuja occidentalis</i>	canopy species
	<i>Tilia americana</i>	canopy species
	<i>Tsuga canadensis</i>	canopy species, commercially valuable
	<i>Ulmus americana</i>	canopy species
undesirable	<i>Abies balsamea</i>	commercially low value species,
	<i>Acer pensylvanicum</i>	understory species, can occur at high enough densities to suppress desirable stems
	<i>Amelanchier interior</i>	understory species
	<i>Crataegus coccinea</i>	understory species,
	<i>Dirca palustris</i>	understory species
	<i>Fagus grandifolia</i>	currently impacted by BBD
	<i>Fraxinus americana</i>	currently impacted by emerald ash borer
	<i>Ostrya virginiana</i>	understory species, occurs at high enough densities to suppress desirable stems
	<i>Prunus pensylvanica</i>	understory species, can occur at high enough densities to suppress desirable stems
	<i>Sorbus americana</i>	understory species

APPENDIX E: DECISION SUPPORT TOOL, COMPONENTS AND RATIONALE

Introduction

The Michigan Department of Natural Resources (MDNR) started pre-emptive salvage harvests in forests with high beech components in an effort to capture timber value before mortality. The regeneration strata within these stands are largely dominated by beech, however density of beech saplings and associate species differ markedly between regions. The regeneration period (4-6 years after harvest) is the most critical time of a stand's lifecycle. Growth dynamics during this time determine future composition and density, and directly impact future wildlife value, timber value, resiliency, and forest sustainability. Forest management and monitoring during the regeneration period is essential to ensure that forests can be managed sustainably in perpetuity. Information gained from regeneration monitoring can determine actions needed to obtain adequate regeneration, and potential timeframes for those actions. Objective (3) of this study was to assess the regeneration potential and likely management outcomes of my study stands. I created a decision support tool informed by data collected from objective (1) and (2) designed to provide guidance to managers when assessing whether a stand can be maintained, restored, or best managed by conversion to an alternate coertype or more novel silviculture. Stands that qualify to be maintained meet minimum stocking requirements and are likely to regenerate naturally without further intervention. Stands that may need to be restored show potential for regeneration, but may require additional treatments to ensure adequate regeneration. Lastly, stands where conversion is recommended are characterized by chronic regeneration failure and face additional regeneration bottlenecks (e.g., lack of seed supply, deer herbivory, competing understory vegetation, or inadequate substrate), requiring more intensive silviculture treatments or conversion to an alternate coertype.

MDNR timber specialists noticed that several hardwood species (i.e., sugar maple, red maple, red oak) regenerate well underneath alternate covertypes including red pine plantations and aspen stands. Marginal hardwood stands could be converted to these alternate covertypes that act as a nurse crop for hardwood regeneration, with the intent to reconvert back into a hardwood covertype once regeneration standards are met. This conversion-reconversion process would result in a shifting mosaic landscape of alternating covertypes over large temporal scales. If planned at the regional level, proportions of converted and reconverted covertypes could be held constant, keeping overall proportion of covertypes equal. As a result, overall proportion of northern hardwood and red pine/aspen stands would remain constant at the landscape level.

Our objective was to create a dichotomous key based upon stocking of desirable and undesirable trees in different height strata for use by decision makers during future management of northern hardwood stands, particularly those with high beech components impacted by BBD. Decision support tools such as SILVAH have already been created and adopted in northeastern forests, resulting in localized research-management frameworks that inform best management practices (Stout and Brose, 2014). After developing our tool I will take inventory data from our 69 BBD impacted, salvage stands through the system to assess their future potential for continued management via selection silviculture, continued selection management but with additional treatments to foster successful regeneration, or stands with low potential for natural regeneration that would be ideal candidates for conversion to other cover types.

Methods

To characterize the regeneration strata in a manner useful for management decisions I assessed (1) total density and (2) total stocking of desirable and undesirable stems. Regeneration density measures are useful when assessing landscape level patterns (region and habitat class),

however collecting data on stem density is resource intensive and when summed to produce a stems per hectare measurement fails to account for the evenness of species. I use measures of stocking to account for evenness at the stand level and to analyze data in way that is applicable to forest managers. Data needed to assess stocking within a stand should be obtained through regeneration surveys which can be used to quickly assess evenness and regeneration adequacy by assessing pre-determined minimum stocking requirements, in contrast to counting individual stems. Stocking surveys are often perceived as complex and resource intensive, which may lead to the decision to disregard regeneration monitoring altogether. Therefore, it is equally important that the stocking survey methodology be carried out in a resource-efficient manner as it is important that the survey provide a dataset that can adequately represent regeneration potential in a stand.

Analysis of desirable and undesirable categories

Stem counts from my 69 study sites were pooled into *desirable* or *undesirable* categories by classification of pest/pathogen impacts (beech, white ash), economic value (understory or overstory species) and relative representation (common or rare species) (Appendix D). *Desirable* species were classified as commercial stems capable of reaching canopy position (e.g., sugar maple, red maple, yellow birch, hemlock, etc.), and *undesirable* species were predominately understory species or species currently being impacted by invasive pests or pathogens (e.g., beech, ironwood, white ash etc.). Classification of species can be subjective in the decision tool, and many species that I classified as undesirable have ecological and wildlife value. However, for the scope of this analysis I focused on commercial species capable of reaching a canopy position.

Statistical Analysis

To standardize measurements across *desirable* and *undesirable* categories and reduce variation, all nine subplots were summed to produce a single stem count per site value. These measurements were then binned into six size classes designed to portray important stages within the regeneration strata that take the size dependency of browsing pressure into consideration (see Table 1). Stem count data was often overdispersed and zero-inflated, resulting in the decision to model stem counts using generalized regression with a negative binomial distribution and logarithmic link function (fit model platform, JMP Pro 13). I used the elastic net estimation method, a regularized methodology that avoids overfitting and collinearity among parameters via selection and shrinkage of variables (Crotty and Barker, 2014), to obtain mean \pm 95% confidence interval estimates for both desirable and undesirable categories. The three smallest size classes (i.e., seedlings, browse sensitive saplings, and browse free saplings) were modelled as a function of habitat class, deer density, and BA. Every iteration of these parameters and their interactions was run, and model selection was finalized using a backwards elimination process with AICc validation. Models that fell within two AICc units of the lowest AICc score were also considered (Burnham and Anderson, 2002), but were only chosen if they resulted in a R^2 value $>10\%$.

Decision support tool: components and rationale

To create our decision support tool, I devised a dichotomous key with decision points that evaluate (1) minimum stocking densities of *desirable* and *undesirable* species in different regeneration height strata to assess potential for successful regeneration (i.e. free to grow) and (2) potential and likely bottlenecks to regeneration. Each decision point is complete with an assessment protocol that guides users through the key until a final treatment point is reached. Stocking surveys are required to gather data after a minimum time period which allows new

stems to exceed the browse threshold following the last harvest entry (i.e., > 5 years). These surveys can vary in size and intensity, but I recommend using 1.82 m radius plots (6 ft) dispersed evenly throughout a stand at a density of at least one plot per acre in stands ≤ 20 acres, with one additional plot per additional five acres in larger stands (Marquis, 1987). 1.82 m (6 ft.) radius lots are large enough to adequately characterize the understory of a stand, but small enough to be completed in a timely and resource-efficient manner (1-2 minutes per plot).

Setting minimum stocking thresholds for desirable species is a primary component of our key. Minimum stocking thresholds represent the absolute minimum density of desirable species found in the regeneration strata that can guarantee adequate recruitment of desirable species into the canopy strata in future harvest cycles. Forest managers have traditionally used stocking guides (Arbogast Jr, 1957; Leak et al., 1987) to assess minimum stocking densities, often referred to as the B-line. However, most stocking guides fail to provide information on trees < 10 cm DBH (Gingrich, 1967), and these stems are often the most crucial stems to assess regeneration potential in a stand. Additionally, most stocking guides are designed for forests with uneven age structures and many northern hardwoods stands in Michigan would fail to meet the assumptions of uneven aged management.

I set minimum stocking thresholds in two size classes, browse sensitive saplings (25-137 cm tall) and browse free saplings (< 5 cm DBH, and >137 tall). Browse free saplings represent the first sapling size class that is free from deer herbivory and competing herbaceous vegetation; two of the primary barriers to regeneration of managed northern hardwoods. I propose a density of 950 “free to grow” stems per hectare as a minimum stocking threshold for browse free saplings. One 1.82 m radius plot (6 ft) represents the growing space needed by one tree when a stand reaches a merchantable size (large pole timber-small saw timber, average DBH = 25-28

cm) (Stein, 1992), thus having one free to grow desirable stem in the same plot would expand to roughly 950 stems per hectare. Stocking charts for even aged Allegheny hardwoods and northern hardwoods estimate from 741-1,235 stems per hectare when a stand reaches merchantable size (Leak, 1969; Stout and Nyland, 1986). Browse sensitive saplings (25-137 cm tall) that do not exceed the browse threshold have the potential to face pressure from deer herbivory and/or competing vegetation. I propose a density of 2,850 stems per hectare (3 stems per plot) as a minimum stocking threshold for this size class, to account for these potential barriers to regeneration.

In addition to minimum stocking standards within plots, it is also important to set a minimum proportion of stocked plots within a stand. 100% stocking is rare within a stand, because the distribution of desirable canopy trees is often heterogenous. Because 100% stocking is an unreasonable goal, a smaller proportion of stocked plots will produce an adequate mature stand. A minimum threshold of 70% stocked plots has been recommended for numerous forest types (Grisez, T.J., 1973; Marquis and Bjorkbom, 1982).

I also assessed likely barriers to regeneration including competing vegetation, deer herbivory, and seed supply. Competing vegetation is measured as an ocular estimation of total ground cover, and if > 70% of plots have > 30% ground cover of herbaceous vegetation they will likely not regenerate (Marquis, 1987). Deer herbivory is measured as the proportion of palatable and unpalatable stems that are present in the browse sensitive size class. I do not propose directly quantifying deer density within a stand (pellet counts), but instead suggest using information already being collected (stocking of palatable and unpalatable species) to infer deer herbivory pressure. Adequacy of seed supply and residual overstory quality are measured using the basal area angle count sampling technique (BA sweep) with an angle gauge or prism wedge. Users will

conduct a BA sweep (> 14 cm DBH) at each regeneration point, and if >70% of plots have a proportion > 60% of desirable species the plot passes requirements.

While the number of plots required to assess a stand is high, data recorded and time spent at each individual plot can be minimal. Data recorded does not need to be a full inventory, but instead can be a quick assessment of stocking standards. At each point the user will check if the plot is stocked with desirable species and adequate total density in the browse free strata, check if the plot is stocked in the browse sensitive strata, take an ocular estimation of seedling and competing vegetation % cover, and conduct a BA sweep. Each point should only take 1-2 minutes, resulting in a quick efficient method of assessing regeneration potential.

Assumptions

Our decision support tool was designed to assess bottlenecks to regeneration and stocking levels within the regeneration strata of candidate stands. Proper use of the tool requires that five underlying assumptions are met:

- 1. The system is designed to assess regeneration in even aged stands, or areas within uneven stands where regeneration is expected (i.e. regeneration gaps)*

This assumption ensures that regeneration potential is only assessed where regeneration is expected. Northern hardwoods in Michigan are most commonly managed under the single-tree selection system, with a residual BA ranging from 17-20 m²/ha. The majority of these stands are thinned for crop tree release and maintain a relatively high canopy closure, so assessing regeneration throughout the entire stand would not only be resource intensive, but also misleading. Therefore, I suggest that stands managed with uneven aged selection systems only be assessed within regeneration gaps (BA < 16 m²/ha).

2. *Free-to-grow status is defined as desirable, healthy and well-spaced stems that exceed the browse threshold (137 cm tall).*

Regeneration success requires that candidate stems meet free-to-grow standards. These standards include assessing vigor, height, and degree of competition among candidate stems. The growing space of a candidate stem is assessed in a one-meter radius circular plot. Stems must exceed 137 cm (browse threshold), must be healthy vigorous stems (ocular assessment), and must be at least 150% taller than any undesirable stems or vegetation that fall within the one meter plot (*Silviculture Surveys Procedures Manual*, 2018).

3. *The overstory (>14 cm DBH) will be managed optimally until final harvest.*

Overstory conditions are largely absent from the key to simplify the structure and complexity of the key, but also to allow for considerations or management goals that fall outside the stand level. The quality of the residual overstory is necessary information when making decisions that consider stand conversion, however these decisions may also be influenced by goals that fall outside information collected at the stand level (i.e. trying to maintain proportions of cover types within an eco-region). Therefore, decisions to convert a stand may occur within a short or long time frame depending on management goals, and should be assessed outside of this key.

4. *Reducing BA through more intensive silviculture will reduce browsing pressure within a stand.*

Walters et al. (2016) conducted a manipulative, stand-scale harvest gap size experiment assessing how varying gap sizes effects the interaction of light availability, shrub-herb competition, and deer herbivory on regeneration dynamics in northern hardwood stands of Michigan. Results of this experiment suggested areas with a low BA (large patch cuts)

experience decreased pressure from deer browse, even within a matrix characterized by high deer densities. Levels of shrub-herb competition often increase following large patch cuts, effectively overwhelming local deer herbivory, acting as a physical deterrent, and/or making seedlings more difficult to find (Walters et al., 2016).

5. *Desirable and undesirable categories are user defined.*

Our study uses commercial value and pressure from pests/pathogens to place species into *desirable* or *undesirable* categories, however these definitions do not include other considerations (i.e. wildlife value) that may be important to management decisions. Therefore, *desirable* and *undesirable* categories can be defined at the user's discretion to fit their management goals.

Study Stands

To meet the requirements of assumption one (only assessing regeneration in areas where the canopy is sufficiently disturbed that recruitment of regeneration is needed and expected), I only analyzed plots with a BA ≤ 16 m²/ha, and to ensure that a significant proportion of the candidate stand could be assessed, I focused on stands where at least 1/3 of the regeneration plots had a BA ≤ 16 m²/ha. 57 (NLP = 23, EUP = 34) of the total 69 stands met these requirements, and the remainder were dropped from further analysis.

Results

Decision Support Tool

The most important size class to assess regeneration adequacy is the browse free sapling class (0-5 cm DBH and >137 cm tall). Stems in this class are free of pressure from deer herbivory and competing vegetation, while also representing young vigorous stems with the

potential to reach canopy status. The key for this system starts by assessing regeneration within this class and proceeds from there:

Is the stand adequately stocked with desirable species in the browse free strata (0-2 in. DBH >137 cm tall)?

*- Yes, >70% of regeneration plots (6ft. radius) have at least 1 desirable stem (*fully stocked plots = 950 stems per hectare.) Proceed to Chart A*

*- No, <70% of regeneration plots (6ft. radius) have at least 1 desirable stem. (*fully stocked plots = 950 stems per hectare.) Proceed to Chart B*

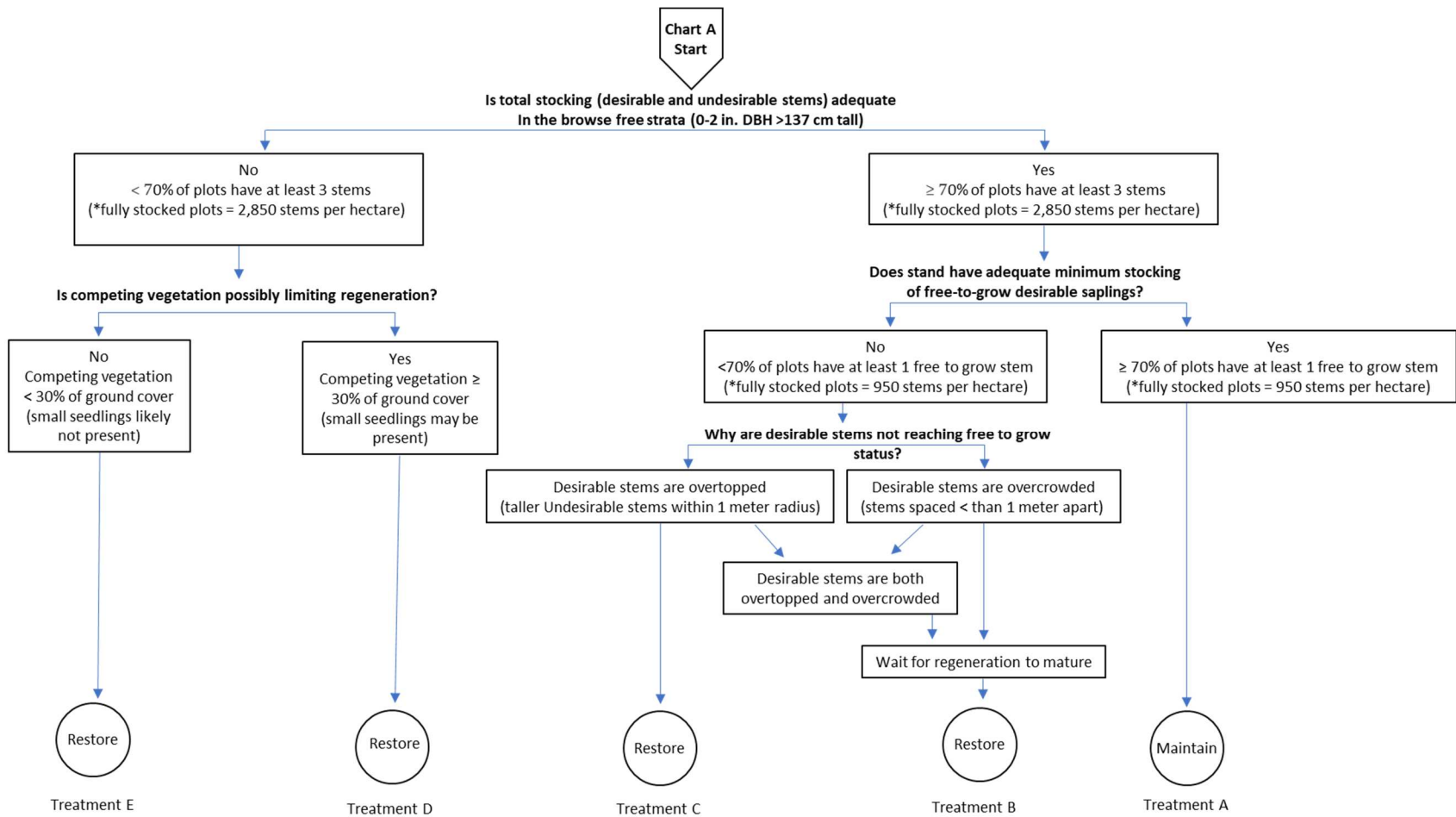
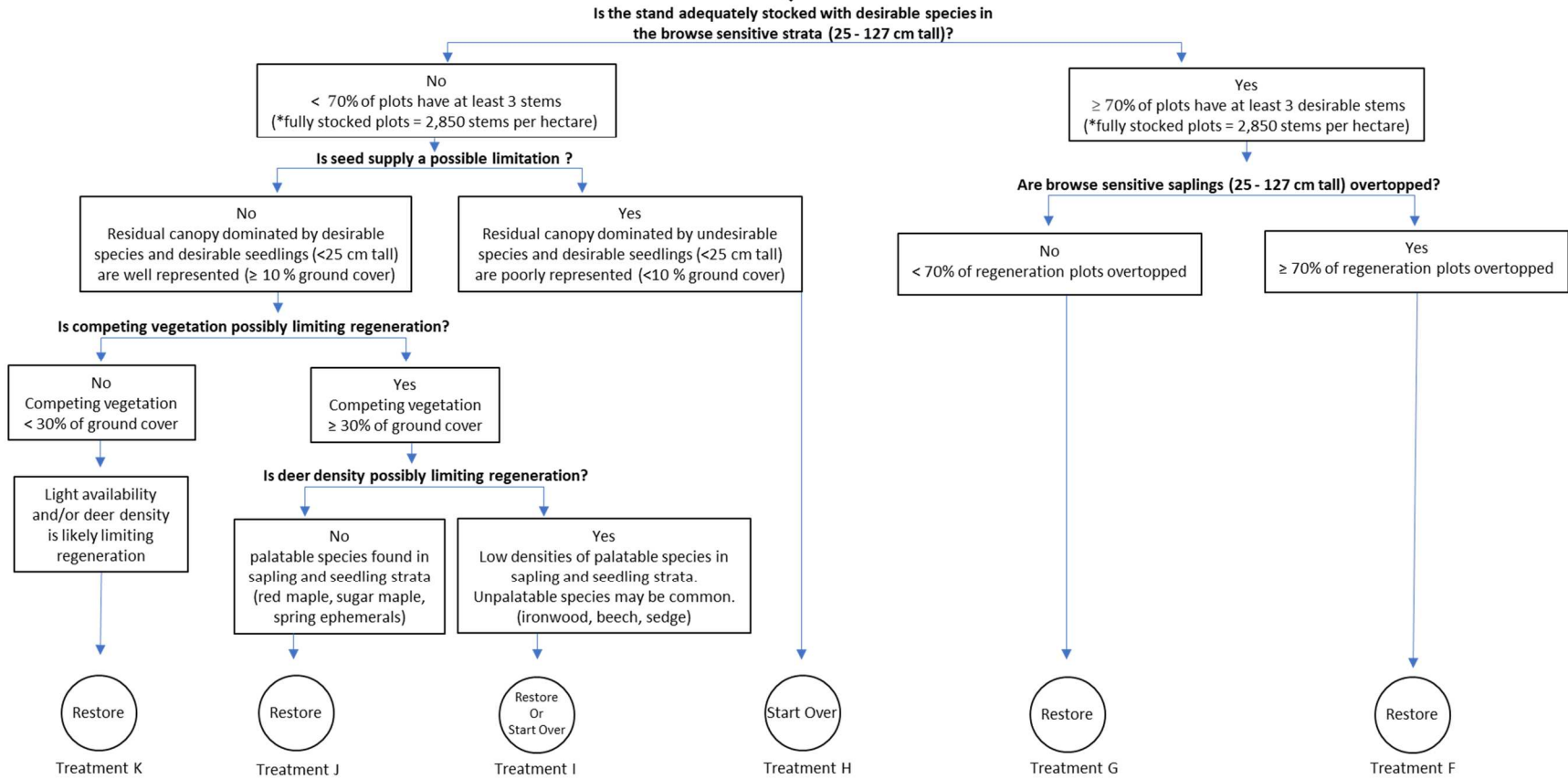


Chart B
Start



Instructions

Users will gather necessary information through regeneration surveys and collect the following data at each 1.82 m (6 ft) regeneration plot.

1. Total stocking in the browse free sapling class (minimum = 3 total stems)
2. Stocking of free to grow desirable stems in the browse free sapling class (minimum = 1 stem)
 - a. If desirable stems do not meet free to grow requirements, record why (i.e. are desirable stems overtopped or overcrowded?).
3. Stocking of desirable stems in the browse sensitive sapling class (minimum = 3 stems)
4. Ocular estimation of desirable and undesirable seedling (% ground cover)
5. Ocular estimation of competing vegetation (% ground cover)
6. BA sweep (BAF 10) with proportion of *desirable* and *undesirable* stems

Upon completion of data collection users will start at the beginning of the key and summarize regeneration plot data based off criteria of each decision point, until a treatment recommendation is reached (See Appendix F for full description of treatments).

Results of Decision Support Tool

Using the data collected from chapter one, I took the 57 stands that met the underlying assumptions of our tool ($BA < 16\text{m}^2/\text{ha}$) through the decision points to identify trends in both evenness of regeneration within stands, as well as proportions of stands that would regenerate naturally, require additional treatments for adequate regeneration, or be candidates for conversion.

Starting at the first decision point of the key:

“Is the stand adequately stocked with desirable species in the browse free strata (0-5 cm DBH >137 cm tall)?”

Nine stands (All in the EUP, 26%) met minimum stocking requirements in the browse free strata and were taken through chart A (stands that can be maintained or require less intense treatments). The first decision point of chart A assesses total stocking (density of desirable and undesirable stems) to ensure that desirable stems have proper growth habits. While high densities of undesirable stems may suppress regeneration, moderate quantities can be advantageous to help train desirable stems into larger size classes. All nine stands met minimum total stocking standards ($\geq 60\%$ of plots have at least 3 stems, 100% stocked = 2,850 stems per hectare). The next decision point assesses the free-to-grow status of desirable stems. To meet free-to-grow standards, stems must not be overcrowded or overtopped by undesirable stems. I did not collect explicit spatial data of saplings within our dataset so could not assess overcrowding of stems, however I did record information on the tallest sapling (5-10 cm DBH) within each plot to assess overtopping of candidate stems. Two stands met free-to-grow standards ($\geq 70\%$ of plots have at least one free to grow stem, 100% stocked = 950 stems per hectare), while the remaining seven stands were predominately overtopped by either beech or pin cherry. Overall this left two stands (3% of total) that could be maintained and would likely regenerate naturally, and seven stands (12% of total) that would require less intensive treatments (precommercial thinning) to ensure adequate regeneration.

Going back to the original decision point to assess the remaining stands:

“Is the stand adequately stocked with desirable species in the browse free strata (0-5 cm DBH >137 cm tall)?”

The remaining 48 stands (NLP = 23, EUP = 25) failed regeneration requirements in the browse free strata and were taken through chart B (stands considered for conversion or requiring more intense treatments). The first decision point of chart B assesses adequate regeneration in the browse sensitive sapling class ($\geq 70\%$ of plots have at least 3 stems, 100% stocked = 2,850 stems per hectare). Only three stands met these requirements (NLP = 1, EUP = 2), and all three were overtopped by undesirable species. These stands have potential to meet adequate stocking standards in the browse free strata, however, are not free of pressure from deer herbivory yet. Another regeneration survey should be completed in 2 years, and if desirable stems exceed the browse threshold, they could be released with treatment (herbicides or thinning) of dominant undesirable stems. The remaining 45 stands (80% of total) failed regeneration requirements in the browse free strata as well as the browse sensitive strata, making them ideal candidates for conversion or more intensive silvicultural treatments to promote regeneration.

The next decision point for these stands assesses local seed supply by measuring composition of the residual overstory and ground cover of desirable seedlings. Canopy composition is measured through a BA sweep, and if $>70\%$ of plots have $\geq 60\%$ of the total composition made of desirable species, the plot meets requirements. Of the 45 stands, nine (16% of total) were dominated by undesirable species, representing stands that fail regeneration requirements in both the browse sensitive and browse free strata's and have a low quality residual canopy. These stands represent the worst-case scenario in our decision system, and will require intensive treatments to meet regeneration or be candidates for conversion.

The remaining 34 stands (56% of total) are characterized by regeneration failure in both sapling strata, but are dominated by desirable species in the canopy strata, providing an adequate seed supply. The remaining decision points assess the potential regeneration bottlenecks within

these stands including shrub-herb competition, deer herbivory, and substrate limitations. Shrub herb competition occurred at very low densities within our stands (average 5% cover) leaving deer herbivory as a likely component of regeneration failure. These stands would be ideal candidates for more extreme silvicultural techniques aimed at decreasing browse pressure despite high densities of deer in the surrounding landscape and will require understory treatments aimed at removing the beech dominated understory.

Table A.1: Results of Decision Support System

Region	Chart	Outcome	Treatment	# of stands	% of stands in region	% of total stands
EUP	A	Maintain	A - stand will regenerate naturally	2	6%	3%
	A	Restore - less intensive	C – release treatment	7	21%	12%
	B	Restore - more intensive	F - regeneration monitoring followed by release	2	6%	3%
	B	Restore - most intensive	J - Herbicide/Scarify understory and reduce residual BA	22	65%	39%
	B	Conversion	H - conversion or more extreme	1	2%	2%
NLP	A	Maintain	A - stand will regenerate naturally	0	0%	0%
	A	Restore - less intensive	C – release treatment	0	0%	0%
	B	Restore - more intensive	F - regeneration monitoring followed by release	1	4%	2%
	B	Restore - most intensive	J - Herbicide/Scarify understory and reduce residual BA	14	61%	25%
	B	Conversion	H - conversion or more novel silviculture	8	35%	14%

APPENDIX F: PROPOSED TREATMENTS

Chart A: Stands with potential to regenerate naturally or requiring less intensive treatments to ensure adequate regeneration

A – Maintain – Candidate stand meets minimum stocking requirements of desirable species in the browse free strata (100% stocking = 950 stems per hectare) as well as minimum stocking density (100% stocking = 2,850 stems per acre) needed to train desirable stems to larger size classes. Additionally, desirable stems meet minimum free-to-grow standards (100% stocking = 950 stems per hectare), and will regenerate naturally. No additional treatments are required.

B – Restore – Candidate stand meets minimum stocking requirements of desirable species in the browse free strata as well as minimum stocking density needed to train desirable stems to larger size classes. However, candidate stems do not meet free-to-grow standards because they are overcrowded by undesirable species. Wait for stems to mature (2-3 years), and release desirables with a precommercial thinning.

C – Restore - Candidate stand meets minimum stocking requirements of desirable species in the browse free strata as well as minimum stocking density needed to train desirable stems to larger size classes. However, candidate stems do not meet free-to-grow standards because they are overtopped by undesirable species. Use a release treatment to favor desirable stems.

D – Restore - Candidate stand meets minimum stocking requirements of desirable species in the browse free strata, but overall stocking is low (< 2,850 stems per hectare) potentially resulting in poor growth form of candidate stems. Additionally, competing vegetation is likely limiting

regeneration (>30% ground cover). Herbicide understory to reduce competing vegetation, and potentially scarify if seedlings occur at low densities (<10% ground cover). Follow up with regeneration monitoring.

E – Restore - Candidate stand meets minimum stocking requirements of desirable species in the browse free strata, but overall stocking is low (< 2,850 stems per hectare) potentially resulting in poor growth form of form of candidate stems. Competing vegetation does not occur at high enough densities, so substrate is likely limiting. Scarify understory to overcome limitation, and follow up with regeneration monitoring.

Chart B: Stands that require more intensive treatments to ensure adequate regeneration or candidates for conversion

F – Restore – Candidate stand fails minimum stocking requirements in the browse free strata, but meets minimum stocking requirements in the browse sensitive strata, demonstrating the potential for adequate regeneration. This situation assumes deer herbivory is limiting, but not to the point of regeneration failure. Additionally, desired stems are overtopped by larger size classes. If stems are overtopped by recruits of undesirable species, release desirable species with a precommercial thinning. If stems are overtopped by a dense layer of saplings, targeted herbicide application or non-selective herbicide application of the entire understory may be required to ensure adequate regeneration.

G – Restore - Candidate stand fails minimum stocking requirements in the browse free strata, but meets minimum stocking requirements in the browse sensitive strata demonstrating the potential

for adequate regeneration. This situation assumes deer herbivory is limiting, but not to the point of failure. Desirable stems are not overtopped by undesirable recruits or a dense sapling layer. Reduce the residual BA by creating large regeneration gaps or converting to an even aged structure (shelterwood). Consider leaving the tops of harvested trees (experimental treatment) within the stand to further reduce browsing pressure.

H – Start Over – Stand fails minimum stocking requirements in both the browse free and browse sensitive strata and the residual canopy is dominated by undesirable species, resulting in an inadequate seed supply. These stands are the worst-case scenario in this system and are ideal candidates for conversion. Conversion can either happen after a clear-cut or through successive thinnings over multiple harvest cycles, depending on the quality of the residual overstory as well as overarching management goals. If conversion is not ideal, then intensive restoration treatments are required, including planting of desirable species that exceed the browse threshold or scarification of the understory followed by broadcast seedling of desirable species.

I – Restore or Start Over – Stand fails minimum stocking requirements in both the browse free and browse sensitive strata, but the residual canopy is dominated by desirable species representing an adequate seed supply. Competing shrub-herb competition and unpalatable species within the seedling and sapling are also found at high densities, indicating shrub-herb competition, substrate limitation, deer herbivory, or any combination of these stressors are likely contributors to inadequate regeneration. These stands face significant pressure to regeneration, requiring more intensive treatments including herbicide/scarification of the understory to reduce undesirable sapling layer and shrub-herb competition. Additionally, the residual BA should be

reduced to promote a higher diversity of regeneration and reduce browsing pressure within the stand, followed by regeneration monitoring.

Stands that fall within this category could also be ideal stands for conversion, considering the amount of stressors that are needed to overcome regeneration limitations. Candidate stands that fall within this category and are also on low quality habitat types (ParVVb, ATFD) would be ideal candidates for conversion while stands on higher habitat qualities would be best managed through restoration.

J – Restore - Stand fails minimum stocking requirements in both the browse free and browse sensitive strata, but the residual canopy is dominated by desirable species representing an adequate seed supply. Competing shrub-herb competition is found at low levels indicating that deer density and/or substrate limitation are likely contributors to inadequate regeneration. The understory should be herbicided/scarified to diminish the undesirable sapling layer, and the residual BA should be reduced to reduce pressure from deer herbivory.

APPENDIX G: FINAL MODEL SELECTION, REGENERATION STRATA

Species	Region	Size class	Model Terms	AICc	R²	Prob > ChiSquare	Parameters	
<i>A. Saccharum</i>	EUP	Seedlings	H + D	396.38	0.63	H = <.0001 D = 0.0004	5	
		Browse Sensitive Saplings	H + D + BA + (H*D) + (H*BA) + (D*BA)	278.48	0.48	H = <.0001 (D*BA) = <.0001	5	
		Browse Free Saplings	H + D + BA + (H*D) + (H*BA)	223.74	0.5	H = <.0001	5	
		Recruits	H + D + BA + (H*D) + (H*BA) + (D*BA) + (H*D*BA)	210.16	0.27	(H*BA) = 0.0021 H = 0.0037 (H*D) = 0.0039 (H*D*BA) = 0.0045	6	
	NLP	Seedlings	H + D + BA + (H*D) + (H*BA) + (D*BA) + (H*D*BA)	317.56	0		4	
		Browse Sensitive Saplings	H + BA	128.11	0.15	H = 0.0121	3	
		Browse Free Saplings	H + D + BA + (H*D) + (H*BA)	64.665	0.21	H*BA = .0020	6	
		Recruits	H + D + BA	159.82	0.24	D = .0001	5	
	<i>A. rubrum</i>	EUP	Seedlings	H + BA	432.13	0.72	H = <.0001	5
			Browse Sensitive Saplings	H	308.83	0.53	H = <.0001	4
Browse Free Saplings			H + D + BA + H*D) + (H*BA) + (D*BA) + (H*D*BA)	245.56	0.57	H = <.0001 BA = <.0001	5	
Recruits			H + D + BA + (H*D) + (H*BA)	154.09	0.37	H = .0001 (H*BA) = .0068	5	
NLP		Seedlings	H + D + BA	307.67	0.28	H = <.0001	4	
		Browse Sensitive Saplings	H	68.72	0.08		3	
		Browse Free Saplings	H + D + BA + (H*D) + (H*BA) + (D*BA) + (H*D*BA)	28.54	0.08	H = .0004	5	
		Recruits	H	26.36	0.09	H = <.0001	3	
<i>F. grandifolia</i>	EUP	Seedlings	H + D + BA + (H*D)	221.3	0.32	H = <.0001 BA = .0003	5	
		Browse Sensitive Saplings	H + BA	332.82	0.25	H = .0002 BA = 0.0287	5	

		Browse Free Saplings	H + BA	394.31	0.25	BA = <.0001 H = .0326	5
		Recruits	H + D + BA + (H*D) + (H*BA) + (D*BA)	273.3	0.55	H = <.0001 (H*D) = <.0001 (H*BA) = .0089	7
	NLP	Seedlings	H + D + BA + (H*D) + (H*BA) + (D*BA) + (H*D*BA)	249.23	0.1		5
		Browse Sensitive Saplings	H + D + BA + H*D) + (H*BA) + (D*BA)	306.78	0.11		4
		Browse Free Saplings	H	283.31	0.28	H = .0002	4
		Recruits	H + D + BA + (H*D) + (H*BA) + (D*BA)	156.2	0.43	(D*BA) = .0019 (H*D) = .0150	6
<i>O. virginiana</i>	EUP	Seedlings	H + D	71.58	0.09	D = .0004	5
		Browse Sensitive Saplings	H + D + BA + (H*D) + (H*BA) + (D*BA)	79.48	0.3	H = <.0001 (H*BA) = <.0001	4
		Browse Free Saplings	H	104.68	0.25	H = .0011	4
		Recruits	H + D + BA + (H*D)	28.95	0.24	H = <.0001 (H*D) = .0002	4
	NLP	Seedlings	H + D + BA + (H*D)	154.61	0.33	D = (0.0026 (H*D) = .0234	5
		Browse Sensitive Saplings	H + D + BA + (H*D) + (H*BA) + (D*BA) + (H*D*BA)	230.01	0.05		4
		Browse Free Saplings	H + D + BA + (H*D) + (H*BA) + (D*BA) + (H*D*BA)	221.58	0.02		4
		Recruits	H + D + BA	79	0.12	D = .0212	5
<i>F. pennsylvanica</i>	NLP	Seedlings	H	147.98	0.26	H = .0003	4
		Browse Sensitive Saplings	H	156.25	0.32	H = .0008	4
		Browse Free Saplings	H + D + BA + (H*D) + (H*BA)	64.74	0.68	H = <.0001 (H*D) = <.0001 (H*BA) = <.0001	7
		Recruits	H + D + BA + (H*D) + (H*BA) + (D*BA)	0	0		6
<i>P. serotina</i>	NLP	Seedlings	H + D + BA + (H*D) + (H*BA) + (D*BA) + (H*D*BA)	75.28	0.08	H = .0144	4

		Browse Sensitive Saplings	$H + D + BA + (H*D) + (H*BA) + (D*BA) + (H*D*BA)$	113.26	0.02		4
		Browse Free Saplings	$H + D + BA + (H*D) + (H*BA) + (D*BA) + (H*D*BA)$	63.66	0.18	D = .0136	
		Recruits	$H + D + BA + (H*D) + (H*BA) + (D*BA) + (H*D*BA)$	887.88	0		13
<i>P. pensylvanica</i>	EUP	Seedlings	$H + D + BA + (H*D) + (H*BA) + (D*BA) + (H*D*BA)$	20.69	0.02	H = <.0001	4
		Browse Sensitive Saplings	$H + D + BA + (H*D) + (H*BA) + (D*BA) + (H*D*BA)$	16.9981	0.09	H = <.0001	5
		Browse Free Saplings	$H + D + BA + (H*D) + (H*BA) + (D*BA)$	110.09	0.41	H = <.0001 D*BA = <.0001 D = <.0001 BA = <.0001 H*BA = .0002	8
		Recruits	$H + D + BA + (H*D) + (H*BA) + (D*BA)$	103.85	0.26	H = <.0001 D*BA = .0022 D = .0072	6
<i>B. alleghaniensis</i>	EUP	Seedlings	H + D	163.32	0.15	H = .0002	3
		Browse Sensitive Saplings	$H + D + BA + (H*D)$	101.14	0.27	H = <.0001 H*D = .0034 BA = .0374	6
		Browse Free Saplings	H + D + BA	55.88	0.22	H = <.0001 D = .0013 BA = .0091	5
		Recruits	$H + D + BA + (H*D) + (H*BA) + (D*BA) + (H*D*BA)$	74.11	0.2	H = .0009 D*BA = .0233	4
<i>T. canadensis</i>	EUP	Seedlings	H + BA	57.87	0.24	H = <.0001 BA = .0104	5
		Browse Sensitive Saplings	$H + D + BA + (H*D) + (H*BA) + (H*BA) + (H*D*BA)$	36.33	0.07	H = <.0001	4
		Browse Free Saplings	$H + D + BA + (H*D) + (H*BA)$	56.37	0.2	H = <.0001 BA = .0357	5
		Recruits	$H + D + BA + (H*D) + (H*BA) + (D*BA) + (H*D*BA)$	51.7103	0.09	H = <.0001	2

<i>A. balsamea</i>	EUP	Seedlings	H + D + BA	53.33	0.08	BA = .0173	5
		Browse Sensitive Saplings	H + D + BA + (H*D)	79.49	0.33	H = <.0001 H*D = .0006 BA = .0085	7
		Browse Free Saplings	H + D + BA + (H*D)	101.31	0.31	H = <.0001 H*D = .0034	6
		Recruits	H	147.07	0.19	H = <.0001	4
<i>A. pensylvanicum</i>	EUP	Seedlings	H + D + BA	80.58	0.28	H = <.0001 D = <.0001	5
		Browse Sensitive Saplings	H + D	111.17	0.22	D = <.0001	5
		Browse Free Saplings	H + D + BA + (H*D) + (H*BA) + (D*BA) + (H*D*BA)	177.63	0		4
		Recruits	H + D + BA + (H*D) + (H*BA) + (D*BA) + (H*D*BA)	102.68	0		4

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