SILVICULTURAL STRATEGIES FOR PROMOTING RESILIENT TREE REGENERATION IN MANAGED NORTHERN HARDWOOD FORESTS, MICHIGAN, USA

By

Evan James Farinosi

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

Forestry – Doctor of Philosophy

2025

ABSTRACT

Northern hardwood forests (NHF) of the upper Great Lakes region have undergone a century of structural simplification and compositional homogenization due to exploitative logging of old-growth stands and the ubiquitous application of selection silviculture in second-growth stands. Contemporary partial harvests often fail to regenerate well-stocked, species-diverse regeneration layers, a pattern attributed to low light availability and deer browsing, among many other limiting factors. This dissertation investigates silvicultural strategies for promoting well-stocked, diverse tree regeneration in managed NHF of northern Michigan, USA, as these conditions are likely to strengthen NHF resilience to future disturbances.

Chapter 2 examines six-year diversity and stocking outcomes following a harvest intensity gradient representing four silvicultural systems: single-tree/small group selection, shelterwood, large group selection, and seed tree. Across 72 stands, species diversity and stocking of a species group desirable for biomass productivity objectives increased with harvest intensity, mainly through the addition of shade-intolerant species. However, a group of largely shade-tolerant and midtolerant species desired for NHF wood economics objectives was less responsive to harvest intensity. Stocking of these groups also exhibited marked regional variation, suggesting that harvest intensity alone does not fully determine early regeneration outcomes.

In Chapter 3, individual species analyses revealed stocking of shade-intolerant species was associated with increased harvest intensity, whereas shade-tolerant and midtolerant species were best predicted by advance regeneration and pre-harvest canopy tree density, suggesting pre-harvest stand structure is critical for many important NHF species. As browsing pressure increased, some browsing-preferred species exhibited slightly reduced stocking, while stocking

of prominent browsing-resilient or avoided species increased modestly; deer browsing likely exerts its greatest influence on regeneration outcomes by shaping the structure and composition of advance regeneration in the decades preceding harvest, rather than in the years that follow.

Given the importance of advance regeneration for many NHF species, Chapter 4 examines regeneration dynamics by relating sugar maple (*Acer saccharum*) seedling density to the diameter and density of local seed sources. Seedling counts were most strongly predicted by the density of sugar maple stems > 40 cm dbh within 35 – 40 m. Applying this relationship to a state resource-wide dataset of 126 managed NHF stands revealed that many stands lack sufficient densities of these large-diameter seed sources, which could constrain the establishment of dense advance regeneration layers, suggesting a need to revise residual stand targets.

Chapter 5 investigates direct seeding as a method to augment regeneration diversity. Ten native or assisted migration candidate species were sown across a gradient of harvest intensity in plots that were either accessible or inaccessible to seed predators. Establishment was highest for large-seeded species that were buried, and was not influenced by harvest intensity. In contrast, small-seeded, broadcast-sown species exhibited lower and more variable establishment, especially following high-intensity harvests. Although seed predation reduced establishment across all treatments, it was not severe in most stands, suggesting that direct seeding may be a viable strategy for increasing diversity in NHF regeneration layers.

Together, these findings suggest that silvicultural practices such as increased harvest intensity, large-diameter seed source retention, and artificial regeneration practices such as direct seeding are likely to foster more diverse and resilient regeneration layers in managed northern hardwood forests of the upper Great Lakes region.

To my parents, Gretchen & James,
and my wife, Kathryn,
who have given me everything.

ACKNOWLEDGEMENTS

To my parents: I could not have asked for better. I could never thank you enough for the sacrifices you have made for me, or the unconditional love you have shown me. I won the lottery at birth.

-

To Kathryn: Thank you for all the sacrifices, both large and small, that you have made to allow me to pursue my passion. You stuck with me through stressful years, and you didn't have to. I won the lottery a second time the day you married me. Our daughters could not have a better woman to guide them, and I cannot wait to witness the process. I love you, Katie.

-

To Vera, Tessa, and our third little girl: I tear up when I consider how fortunate I am to spend my days with you. You and your mother mean everything to me. Three more lottery wins.

-

To Mike: It was an honor to work for you – and then alongside you. I loved our long car rides, I loved our conversations, and I would not change a thing about the last 15 (okay, 14) years… not even the spilled coffee. You are the reason I am sitting at a desk in Constitution Hall, working in a job that I love and feel competent to perform. For this, and more, I am forever indebted to you.

-

To John: Our field chats came at a pivotal time for me, and I am forever indebted to you as well.

-

To Jason H., Mike D., Tim, and the rest: Now that the government is signing my paychecks, I can more fully appreciate what a massive lift it was to get this project off the ground. Thank you.

To Lucas, Catherine, and Melissa: Few others can understand the scope and scale of this project – or the Sisyphean task it could sometimes feel like. Thank you for being there when I needed you.

-

To the members of our field crews: The number of you it has taken to keep "The Big Northern Hardwoods Project" running is staggering. Over the last decade, more than 50 of you – a conservative estimate – put in long field days to establish and monitor this study that stretches from Cadillac to Copper Harbor. We endured some tough days together – but also shared unforgettable experiences. We dealt with frozen paint guns while marking timber; we spooked fawns during spring pellet counts; we got stung by ground bees and cursed our way to "plot center"; we also saw the best of what northern Michigan has to offer. I could write an acknowledgement section the length of this dissertation filled with our stories, if only I had a better memory. All that to say: thank you for spending time with me in the woods. And for not quitting when you got stung by those bees.

-

And finally, to Kevin: You rock, Ace.

TABLE OF CONTENTS

CHAPTER 1:

INTRODUCTION

Northern hardwood forests (NHF) occupy over 20 million hectares of the eastern United States and Canada, from the upper Great Lakes region to the Canadian Maritimes (Rogers et al., 2022). These forests support complex ecological systems and contribute significantly to rural communities through tourism and the forest products industry (Dickmann and Leefers, 2003). Prior to European settlement, NHF were structurally complex, compositionally diverse, and predominantly uneven-aged due to frequent, small-scale natural disturbances such as windthrow (Frelich and Lorimer, 1991; Crow et al., 2002). However, intensive logging of this cover type in the region around the turn of the 20th century largely eliminated these stand characteristics (Whitney, 1987; Schulte et al., 2007).

The resulting second-growth forests that regenerated following this period – now between 90 and 120 years old (Henry and Walters, 2023a) – have been managed primarily for shade-tolerant, economically valuable species such as sugar maple (*Acer saccharum* Marsh.). Early management focused on tending young stands, and later transitioned to single-tree selection (STS) as stands matured (Eyre and Zillgitt, 1953; Arbogast, 1957; Kern et al., 2014). As a result of both the early exploitative logging and the long-term application of low-intensity partial cutting practices such as STS, contemporary NHF are characterized by reduced structural, species, and functional diversity relative to their pre-European settlement counterparts (Schulte et al., 2007). More recently, additional canopy diversity losses have resulted from successional trends (Hlina et al., 2020), preferential removal of high-value species (Nyland, 1992), and the spread of invasive pests and pathogens (Liebhold et al., 2013). While past management largely prioritized timber production, enhancing the long-term resilience of these forests to future disturbance has become a central challenge for contemporary forest managers.

Increasing species diversity is a key management strategy for enhancing forest resilience (Yachi and Loreau, 1999; Thompson et al., 2009). However, studies examining the effects of single-tree selection on species diversity in NHF suggest this widely used silvicultural system often produces poor regeneration outcomes (Crow et al., 2002; Neuendorff et al., 2007; Henry and Walters, 2023b) – even for sugar maple (Henry et al., 2021). This pattern likely reflects multiple limiting factors, including low densities or absence of local seed sources (Willis et al., 2016; Henry and Walters, 2023b) or conducive germination substrates (Marquis, 1964; Marx and Walters, 2008; Willis et al., 2015), low-light environments that limit the survival or growth of diverse seedling and sapling layers (Marquis, 1969; Neuendorff et al., 2007; Henry and Walters, 2023b), competition with non-target vegetation (Walters et al., 2016; Elenitsky et al., 2020), and intense, selective browsing by white-tailed deer (*Odocoileus virginianus*) (Curtis and Rushmore, 1958; Côté et al., 2004; Bradshaw and Waller, 2016; Walters et al., 2020a). As a result, many STS-managed stands exhibit regeneration layers that are understocked or stocked with species undesirable for management (Matonis et al., 2011; Walters et al., 2022). Alternative silvicultural treatments that retain canopy diversity, increase light availability to regeneration strata, and otherwise create conditions for species-diverse seedling establishment and sapling recruitment – even in the presence of persistent browsing pressure and competing vegetation (Walters et al., 2020a) – may therefore be necessary when relying on natural regeneration. However, such approaches have not been widely tested in contemporary NHF stands of the upper Great Lakes region (Walters et al., 2020b).

The primary goal of this dissertation is to investigate silvicultural practices that may foster robust, species-diverse regeneration layers in NHF. In the first two experimental chapters, I examine early stocking outcomes following alternative silvicultural system harvests, using data collected from a subset of sites within a landscape-scale manipulative experiment conceived and implemented in collaboration with the Michigan Department of Natural Resources and with in-kind support from private industry (Walters et al., 2020b). Four distinct harvest treatments representative of different silvicultural systems were tested in 72 treatment blocks located within managed NHF stands across northern Michigan. The harvest treatments included (Nyland, 2016):

1) **Single-tree/small group selection (ST-SG):** an uneven-aged system harvest in which dispersed individual trees were harvested to achieve a residual basal area of 75 ft^2 ac^{-1}, combined with systematic establishment of 0.15 ac small group selection gaps. This treatment was intended to broadly replicate contemporary silvicultural prescriptions within managed NHF.
2) **Shelterwood (SH):** an even-aged system harvest in which approximately 50% canopy cover was retained in order to provide seed and to moderate understory microclimate conditions.
3) **Large group selection (LG):** an uneven-aged system harvest in which five replicates of four gap sizes (0.3, 0.5, 0.7 and 1 ac) were systematically established.
4) **Seed tree (ST):** an even-aged system harvest in which 6 – 8 dominant canopy trees per acre were retained as seed sources, but provided negligible understory microclimate moderation.

Relative to ST-SG, the more intensive harvest treatments increase post-harvest light availability and could potentially alter how deer browsing influences recruitment outcomes. If these treatments promote greater species diversity and enhanced seedling-to-sapling recruitment, they would provide compelling evidence in support of management alternatives to ST-SG in the region.

In Chapter 2 (*Species diversity and stocking responses to a harvest intensity gradient in managed northern hardwood forests, Michigan, USA*), I evaluate how harvest intensity influences stocking outcomes across the four previously described harvest treatments. Using six-year post-harvest data from 72 stands (30 ac (12.1 ha) treatment blocks), I examine species diversity and stocking responses among different shade tolerance classes and species groups that are relevant to management. I test the following hypotheses:

1) Species diversity will be positively associated with harvest intensity (i.e., ST > LG > SH > ST-SG) and with increasing light availability (i.e., gap size) within the ST-SG and LG treatments. This relationship will largely be driven by increased representation of shade-intolerant species.
2) Stocking will also be positively associated with harvest intensity and with increasing light availability within the ST-SG and LG treatments.
3) Stocking variation among stands will be substantial despite significant treatment-level effects, with spatial patterns in stocking outcomes reflecting regional trends observed by forest managers and recent research (i.e., poor stocking outcomes in the south-central Upper Peninsula and northern Lower Peninsula).

In Chapter 3 (*Drivers of regional variation in tree regeneration following harvest in managed northern hardwood forests, Michigan, USA),* I explore species-specific drivers of the stocking patterns observed in Chapter 2. Using the same set of stands, I assess how post-harvest stocking of individual species is shaped not only by harvest intensity, but also by pre-harvest stand structure and spatially varying factors such as site quality and deer activity. I test the following hypotheses:

1) Target species stocking will vary regionally, and will broadly align with spatial patterns of site quality, with relationships reflecting species silvics.
2) Species-level stocking will be jointly influenced by harvest intensity, deer browsing pressure and species-specific stem densities, with the strongest predictors reflecting species silvics. Specifically:
    a) Pre-harvest stand structure (i.e., densities of advance regeneration and/or canopy trees) will most strongly predict post-harvest stocking of shade-tolerant and midtolerant species.
    b) Harvest intensity (i.e., ST > LG > SH > ST-SG) will most strongly predict stocking of shade-intolerant, early-successional species.
    c) Deer browsing pressure will reduce the stocking of species that are selectively browsed, but will not affect species that are typically avoided or resilient to browsing.

In Chapter 4, (*Large-diameter sugar maple density drives seedling production: implications for northern hardwood forest management*), I examine how the size and density of canopy sugar maple trees influences seed production and first-year seedling density in 60 managed and unmanaged NHF stands in the central Upper Peninsula of Michigan. As advance regeneration layers are important for many shade-tolerant and midtolerant tree species – and since seed production is known to scale with tree diameter – understanding the relationship between canopy tree size and density, seed availability, and seedling establishment is critical for evaluating stand-level regeneration potential. I then apply the resulting seedling prediction model to 126 NHF stands historically managed with partial-harvesting across northern Michigan to assess seed and seedling production potential as inferred from large-diameter sugar maple density. I test the following hypotheses:

1) Seed and seedling density will be positively related, though substantial inter-stand variation will be observed due to unquantified factors (e.g., seed predation, microenvironment, weather/climate). However, variation in seed density, seedling density and the residuals of the seed-seedling relationship will not exhibit strong spatial patterning across the relatively small 1.7-million-hectare study region.
2) Seedling density will be positively related to the density of canopy sugar maple trees (i.e., > 25 cm dbh), with relationships strengthening when restricted to progressively larger trees (e.g., > 30 cm, > 35 cm, etc.). Furthermore, these relationships will be stronger for tree density parameters that are restricted to (or weighted more heavily in favor of) trees closer to seedling plots (e.g., < 35 m, < 30 m, etc.). Assuming broadly similar management practices across the study area, no spatial patterning of canopy tree size/density is expected.
3) When interpreted in the context of modeled seed-seedling relationships, canopy tree size/density data from 126 managed stands (*126Data*) from across northern Michigan will indicate some stands are characterized by low and potentially seedling-limiting

densities of large-diameter sugar maple. As with earlier predictions, spatial patterning is not expected, given broad consistency in management over the last six decades.

In Chapter 5 (*Augmenting tree seedling diversity via direct seeding: the influence of harvest intensity, granivory, seed traits, and sowing method on first-year establishment*), I use a subset of research sites from the alternative silvicultural systems study (Chapters 2 & 3) in the northern Lower Peninsula of Michigan to test whether species diversity can be increased through direct seeding. Ten tree species were seeded using operationally relevant sowing methods, and I examine how seed size, sowing method and environmental conditions – including variation in harvest intensity and seed predation – influence first-year establishment outcomes. I test the following hypotheses:

1) When considering all species:
    a) Seedling establishment will be lower under more exposed understory conditions created by more intensive harvests (i.e., ST < SH < SG).
    b) Seed predators will reduce seedling establishment (i.e., lower establishment proportion in uncaged subplots), with stronger effects expected under lower harvest intensities (i.e., SG > SH > ST).
2) When considering seed size/sowing method groupings:
    a) Among small-seeded/broadcast-sown species, establishment in caged subplots will be positively associated with seed mass, especially under harsh microenvironments (i.e., ST). However, species with greater seed mass will also experience greater losses to seed predation.

b) Among large-seeded/buried species, seed mass will not be associated with establishment proportion or seed predation.

In Chapter 6 (*Conclusion*), I review the findings from the preceding chapters and discuss how modifications to contemporary silvicultural practices could potentially promote well-stocked, species-diverse regeneration in managed northern hardwood forests of the upper Great Lakes region.

CHAPTER 2:

SPECIES DIVERSITY AND STOCKING RESPONSES TO A HARVEST INTENSITY GRADIENT IN MANAGED NORTHERN HARDWOOD FORESTS, MICHIGAN, USA

2.1 Abstract

Northern hardwood forests (NHF) are a major forest type of eastern North America. Over several decades, low-intensity single-tree/small group selection (ST-SG) silviculture, combined with deer browsing pressure and other factors, has resulted in poor tree regeneration – particularly sapling recruitment – in some areas of the upper Great Lakes region. Alternative silvicultural systems characterized by more intensive harvesting than ST-SG may improve regeneration outcomes but remain largely untested in the region. Using a landscape-scale silvicultural experiment in northern Michigan, USA, I evaluated six-year species diversity and stocking outcomes across 72 managed NHF stands, each subjected to one of four 12.1 ha (30 ac) harvest treatments: ST-SG, shelterwood (SH), large group selection (LG), or seed tree (ST). I tested the hypotheses that increased harvest intensity and within-treatment light availability would 1) increase species diversity, 2) increase stocking of desirable species, and that 3) stocking outcomes would exhibit regional variation.

Species diversity within *Trees+Shrubs* and *Trees* stocking categories increased with harvest intensity. Stocking (% of milacre plots occupied) was high across treatments (*Trees+Shrubs*, mean > 90% in all treatments; *Trees*, 72% (LG) to 84% (ST)). Stocking of species designated desirable for biomass productivity objectives (*FTG-Biomass*) was lower overall but increased with harvest intensity, ranging from 30% in ST-SG to 58% in ST relative to *Trees*; shade-intolerant species largely drove stocking increases. Stocking of *FTG-Wood* (a subset of *FTG-Biomass* species valued

for traditional NHF wood economics) was lower and less responsive to harvest intensity, and substantial within-treatment variation was observed for both *FTG* categories. Gap size within LG and ST-SG treatments had no significant effect on either species diversity or stocking. The proportion of stands exceeding 40% *FTG-Biomass* stocking (a common threshold criterion for sufficient stocking, equivalent to 400 well-spaced stems per acre) was greater for ST than other treatments (ST = 18/19; SH = 10/18; LG = 9/18; ST-SG = 7/17), though *FTG-Wood* stocking only exceeded 40% in 10/19 ST stands. Regional patterns of *FTG-Biomass* and *FTG-Wood* stocking were pronounced, with reduced stocking in the south-central Upper Peninsula and northern Lower Peninsula.

These results suggest more intensive harvests than currently used in NHF of the upper Great Lakes region can increase species diversity and improve early stocking outcomes of desirable tree species, particularly for biomass productivity objectives. However, strong regional and stand-level variability in outcomes underscores the need to consider additional factors – such as site quality, pre-harvest stand structure, and browsing pressure – when designing silvicultural prescriptions.

2.2 Introduction

Northern hardwood forests (NHF) span over 20 million hectares across the eastern United States and Canada, from the upper Great Lakes region to the Canadian Maritimes. These forests – primarily dominated by sugar maple (*Acer saccharum* Marsh.) in the Lake States – provide myriad ecological, economic, and social benefits to the region (Rogers et al., 2022). Since the mid-20th century, NHF have been managed to maintain or create uneven-aged structure using single-tree selection (STS) (Eyre and Zillgitt, 1953; Arbogast, 1957). This silvicultural system was designed to emulate the low intensity disturbance regimes that characterized NHF prior to European settlement (i.e., wind and ice damage, age-related canopy tree senescence; Frelich and Lorimer, 1991), primarily through periodic partial harvests aimed at removing dispersed large-diameter canopy trees and tending across smaller size classes (Arbogast, 1957; Kern et al., 2014). After each round of partial cutting, new cohorts of largely shade-tolerant trees are expected to recruit into successively larger size classes, thereby creating or maintaining uneven-aged structure over time.

More recently, a growing awareness of poor regeneration outcomes and limited structural heterogeneity in STS-managed NHF (Angers et al., 2005) has led researchers to explore the use of group selection gaps (Kern et al., 2013; Poznanovic et al., 2013, Walters et al., 2016), and some forest managers have begun incorporating these gaps into STS management practices (J. Hartman, Michigan DNR, personal communication). However, regionally variable tree regeneration outcomes persist following the use – or attempted application (Pond et al., 2014) – of selection silviculture in NHF of northern Michigan, with low sapling densities in many areas after multiple rounds of partial cutting, particularly for species desired for wood economics (e.g., south-central Upper Peninsula and northern Lower Peninsula, Matonis et al., 2011; Walters et al., 2020b; Walters et al., 2022), which threatens the paradigm of sustainable NHF management (Walters et al., 2020b; Henry and Walters, 2023b). Poor regeneration diversity is particularly concerning, given species diversity should broadly increase forest resilience to future disturbances (Yachi and Loreau, 1999; Thompson et al., 2009), including climate change (Rogers et al., 2017) and invasive pest/pathogen outbreaks (Chapman et al., 2017; Liebhold et al., 2013).

Many interacting factors may limit species-diverse tree regeneration in NHF, including landscape-scale changes in forest composition since European settlement (Schulte et al., 2007), local seed sources limitations (Willis et al., 2016; Henry and Walters, 2023b), and insufficient coarse woody debris (Hura and Crow, 2004; Marx and Walters, 2008) or mineral soil substrate (Willis et al., 2015) that is necessary for the germination and establishment of small-seeded species. Additionally, low-light environments created by small individual canopy gaps or beneath STS-managed canopies can limit the number of species able to compete (Webster and Lorimer, 2005; Kern et al., 2014; Henry et al., 2023b). Intense and selective browsing pressure from white-tailed deer (*Odocoileus virginianus*) is also a well-documented concern (Côté et al., 2004; Bradshaw and Waller, 2016; Walters et al., 2020a). As a result of these factors, sapling layers are often understocked and/or dominated by a few shade-tolerant, large-seeded, browsing-resilient or avoided species, such as ironwood (*Ostrya virginiana* (Mill) K. Koch) or American beech (*Fagus grandifolia* Ehrh.) (Nolet et al., 2008; Matonis et al., 2011; Henry et al., 2023b). Sapling layers composed of these commercially undesirable species can further limit light to developing seedling strata (Elenitsky et al., 2020). In light of these challenges, forest managers are increasingly interested in modifying NHF silvicultural practices to improve tree regeneration outcomes.

While many of these limitations are difficult to directly overcome, increasing light availability to regenerating trees via increased harvest intensity is a straightforward silvicultural tool. Various silvicultural systems employ harvest treatments that are designed to create higher post-harvest light environments than STS (Nyland, 2016), and research has shown shelterwood (Godman and Tubbs, 1973; Kelty and Nyland, 1981; Godman, 1992), group selection (Arsenault et al., 2011; Poznanovic et al., 2013, Knapp et al., 2019; Sabo et al. 2019), and clearcut systems

(Wang and Nyland, 1993), occasionally in conjunction with other stand treatments (e.g., controlling deer density, reduction of undesirable sapling layers via herbicide, Kelty and Nyland, 1981; Sage et al., 2003), can increase species diversity through the addition of midtolerant and shade-intolerant species. Furthermore, increased harvest intensity has been shown to create greater densities of regenerating trees (Leak and Solomon 1975; Poznanovic et al., 2013), which may in turn increase the number of successfully recruited stems despite increased stand utilization by deer following heavier harvests (Ripley and Campell, 1960; Harlow and Downing, 1969). As such, more intense harvests may create dense, species-diverse regeneration with a greater probability of recruiting through deer browsing bottlenecks. However, silvicultural practices and research in the upper Great Lakes region have largely focused on gap-based partial cutting systems (Kern et al., 2013, 2014; Knapp et al., 2019, 2021), with studies of even-aged systems few and of limited spatial extent (see Walters et al. 2020b for a review). As such, more information regarding the regional efficacy of alternative silvicultural systems would benefit forest management in this region.

While more intense harvests may benefit tree regeneration, shrubs may also respond favorably (primarily *Rubus* spp.), and can compete strongly with tree seedlings (Shields and Webster, 2007; Kern et al., 2013; Walters et al., 2016). *Rubus* has been shown to inhibit tree regeneration for more than a decade in some instances, particularly when the density of advance regeneration is low immediately following disturbance (Widen et al., 2018). Alternatively, shrub layers may benefit tree regeneration by concealing and/or protecting seedlings from deer browsing, especially for tree regeneration that can avoid being outcompeted by shrubs (e.g., advance regeneration and fast-growing species that establish soon after harvest; Walters et al., 2016). Nevertheless, persistent shrub layers with potential to stymie seedling-to-sapling recruitment are an undesirable management outcome.

Relatedly, not all tree species are acceptable for biomass productivity, wood economics, or other objectives of forest management (Walters et al., 2022). At an extreme, some of the least desirable tree species for management may have some combination of low wood value (e.g., American beech, ironwood, striped maple (*Acer pensylvanicum* L.), mountain maple (*A. spicatum* L.)), an incapability of attaining maturity/maximum biomass in the near term due to pests/pathogens (e.g., American beech, white ash (*Fraxinus americana* L.)), and/or may be superabundant competitors of more desirable species (e.g., American beech, ironwood). Silvicultural treatments that result in prolonged post-harvest dominance of these species would be at odds with sustainable NHF management.

Assessing regeneration outcomes relative to management objectives following harvest is often accomplished through stocking surveys. Importantly, stocking plots account for both stem density and spatial distribution of stems, with a full stocking designation indicating adequately dense and well-distributed stems of desirable species (Burkhart et al., 2019). Survey designs vary, but one method proposed for NHF involves assessing a number of relatively small fixed-area plots for the presence of a single dominant stem, which is classified as either desirable or undesirable for management (Leak, 2007). Since deer browsing and shrub competition disproportionately affect trees < 137 cm tall (Walters et al., 2020a), focusing stocking surveys on saplings above this height is likely to provide a more accurate assessment of near- to mid-term canopy composition than surveys considering smaller size classes (Harris et al., 2022). These surveys can address multiple questions relevant to forest managers: Is the stand rapidly returning to tree cover? What are the relative contributions of important functional groups (e.g., shrubs, commercially valuable trees) occupying the regeneration layer? Is regeneration composed of a diverse mix of desirable species? While not as detailed as comprehensive regeneration surveys, stocking surveys are an efficient means of quantifying important regeneration trends in the years following harvest.

In this chapter, I focus on the relationship between harvest intensity and species diversity/stocking outcomes for species groups relevant to management; Chapter 3 examines additional potential drivers that may affect stocking outcomes for individual species. Data are sourced from six-year stocking surveys conducted across 72 managed NHF stands that were each subjected to one of four harvest treatments in northern Michigan, USA (Walters et al., 2020b). The four treatments included a harvest consistent with the currently dominant ST-SG system and three harvests consistent with alternative systems: shelterwood (SH), large group selection (LG) and seed tree (ST) (see methods). Collectively, these treatments represent a gradient of harvest intensity and understory light availability: ST-SG < SH < LG < ST. I evaluate stocking survey results to address the following hypotheses:

1) Species diversity will be positively associated with harvest intensity (i.e., ST > LG > SH > ST-SG) and with increasing light availability (i.e., gap size) within the ST-SG and LG treatments. This relationship will largely be driven by increased representation of shade-intolerant species.
2) Stocking will also be positively associated with harvest intensity and with increasing light availability within the ST-SG and LG treatments.

3) Stocking variation among stands will be substantial despite significant treatment-level effects, with spatial patterns in stocking outcomes reflecting regional trends observed by forest managers and recent research (i.e., poor stocking outcomes in the south-central Upper Peninsula and northern Lower Peninsula).

2.3 Methods

2.3.1 Data collection

Stocking surveys were performed in stands that are part of a larger landscape-scale silvicultural study employing a factorial design to test the effects of four harvest treatments and two understory treatments on the development of dense, species-diverse tree regeneration; the treatments are described in greater detail by Walters et al. (2020b) and briefly summarized here. Project stands are largely owned and managed by the State of Michigan (n = 118), with the rest owned and managed by private industry (n = 22). Four harvest treatments were tested (Figure 2.1; Nyland, 2016):

1) **Single-tree/small group selection (ST-SG):** an uneven-aged system harvest in which dispersed individual trees were harvested to achieve a residual basal area of 75 ft^2 ac^{-1}, combined with systematic establishment of 0.15 ac small group selection gaps. This treatment was intended to broadly replicate contemporary silvicultural prescriptions within managed NHF.
2) **Shelterwood (SH):** an even-aged system harvest in which approximately 50% canopy cover was retained in order to provide seed and to moderate understory microclimate conditions.

3) **Large group selection (LG):** an uneven-aged system harvest in which five replicates of four gap sizes (0.3, 0.5, 0.7 and 1 ac) were systematically established.
4) **Seed tree (ST):** an even-aged system harvest in which 6 – 8 dominant canopy trees per acre were retained as seed sources, but provided negligible understory microclimate moderation.

When marking outside designated geo-referenced gap locations (or in treatments without systematic gap installation), species diversity and vigorous, large-diameter trees were considered priorities for retention (Chapter 4).

Due to the landscape-scale scope of this study, obtaining stand-scale light availability estimates was impractical. However, increased canopy openness has been shown to increase light transmission (Grayson et al., 2012; Keasberry et al., 2016; Walters et al., 2016), such that harvest intensity is a reasonable proxy for understory light availability (i.e., ST-SG < SH < LG < ST). Each 30 ac (12.1 ha) research block was assigned a single harvest treatment, and all blocks were harvested in winter 2017/2018. In approximately half of these stands (n = 72), research specifications called for retaining felled tree crowns following harvest to provide barriers to deer browsing on tree regeneration; stocking survey data presented here was collected on these sites. Understory herbicide and scarification treatments were conducted in 2020 on the remaining 68 sites; six-year stocking surveys (as well as comprehensive regeneration surveys) are planned for summer 2026.

Prior to stocking surveys, tree and shrub species were categorized as desirable or undesirable for forest management (Tables 2.1, 2.2). These classifications were chosen in consultation with forest managers, and were based on rewarding species that would contribute to biomass productivity and/or wood economics (desirable) and penalizing low value, hyper-abundant competitors of desirable species (undesirable); it should be acknowledged that classification schemes can vary with management goals (Walters et al., 2022). Specific species classified as undesirable are either unable to attain maturity/maximum biomass due to pests and pathogens (e.g., American beech, ash spp.) or are small-statured shrubs and trees that compete with more desirable canopy species for growing space, and often occupy outsized proportions of growing space in the under/midstory (e.g., American beech, ironwood, *Acer* shrubs, *Rubus* spp., *Sambucus racemosa* L.). Notably, pin cherry (*Prunus pensylvanica* L.f.) was designated as desirable. While small-statured and of no economic value, pin cherry establishes and grows quickly following harvest, and may diminish the dominance of shrub competition. Furthermore, it may foster longer-term recruitment of shade-tolerant species (e.g., sugar maple), which are likely to survive beneath the relatively shallow canopies of pin cherry (Longwood, 1951; Marquis, 1967; Leak, 1988; but see Ristau and Horsley, 2006).

During summer 2023 (sixth growing season post-harvest), 405 systematically located milacre plots (Figure 2.1) were surveyed for a single dominant stem (Leak, 2007). Each plot was classified as one of four stocking categories:

1) **Free to Grow (FTG):** stem of a species designated desirable for biomass productivity or wood economics objectives that is ≥ 137 cm tall, up to 10 cm dbh, and is not overtopped by any competing vegetation < 10 cm dbh.
2) **Desirable:** stem of a species designated desirable for biomass productivity or wood economics objectives that is ≥ 50 cm tall, < 137 cm tall, and is not overtopped by any competing vegetation < 10 cm dbh.

3) **Undesirable:** stem of a species designated undesirable for management objectives that is ≥ 50 cm tall and up to 10 cm dbh (see Table 2.1).

4) **Empty:** no woody stem ≥ 50 cm tall and up to 10 cm dbh is present.

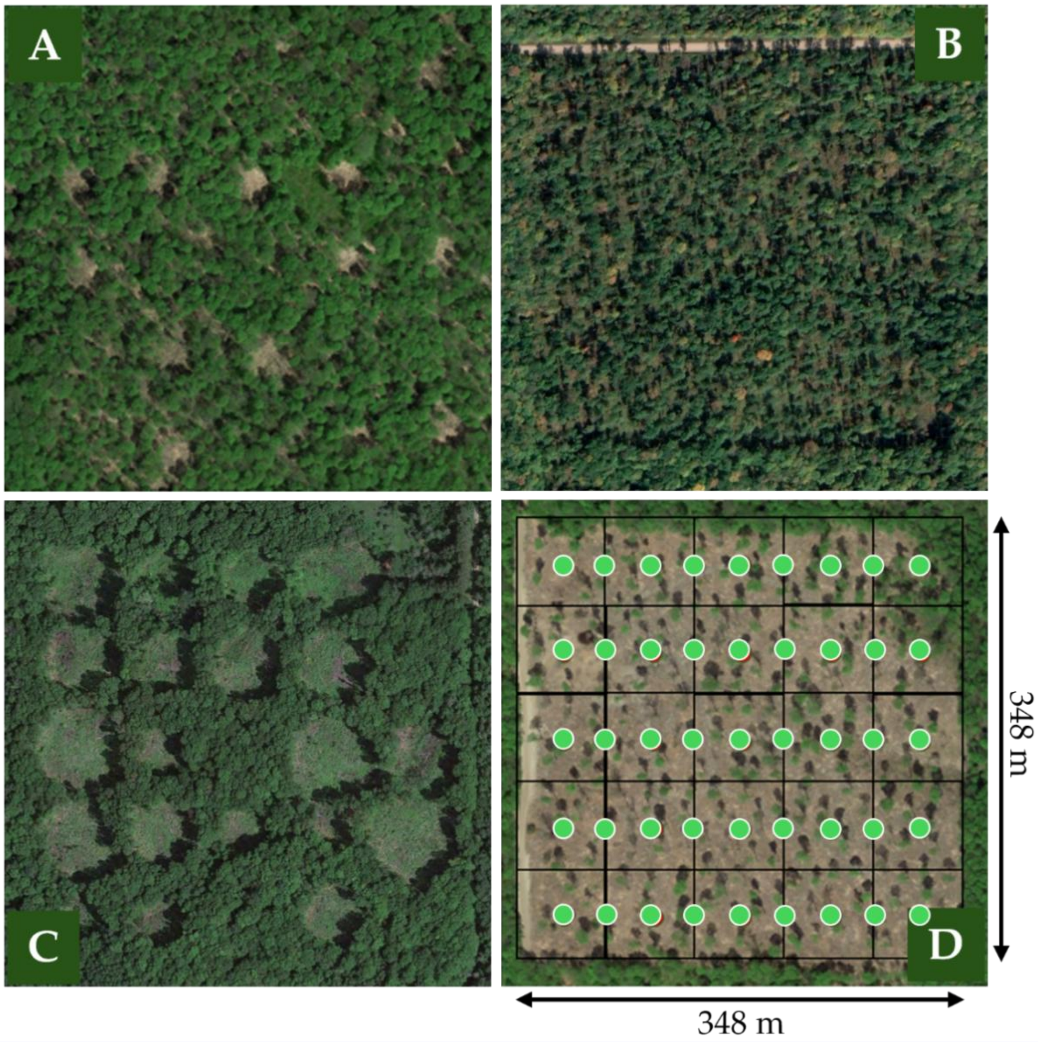

Figure 2.1. Aerial imagery of four 30 ac (12.1 ha) experimental harvest treatments: A, single-tree/small group selection (ST-SG); B, shelterwood (SH); C, large group selection (LG); D, seed tree (ST). Green circles on the ST panel signify stocking survey clusters and are located at both the center points of a 5 x 5 grid overlaying each treatment unit (~70 m spacing) and at additional east/west midpoints (~ 35 m from center points), for a total of 45 clusters. In each cluster, nine milacre stocking plots were established in a 3 x 3 grid at a spacing of 6 m. As such, a total of 405 milacre plots were surveyed in each stand.

Table 2.1. Stocking survey categories.

Stocking Category	**Stocking plot dominated by stem of:**
Trees+Shrubs	a tree or woody shrub species.
Trees	a tree species.
FTG-Biomass	a tree species designated desirable for biomass productivity objectives.
FTG-Wood	a tree species designated desirable for wood economics objectives.

Table 2.2. Tree and woody shrub species or species groups identified as dominant stems in stocking survey plots during the sixth growing season post-harvest. Proportion (%) = study-wide proportion of stocking plots dominated by the species; Sites (n) = number of sites on which the species was the dominant stem in at least one survey plot (total n = 72); Biomass/Wood = management desirability of species for biomass productivity/wood economics objectives; Tolerance Class = shade tolerance class designation (tolerant, midtolerant, intolerant). Tolerance class designation was synthesized from multiple authoritative sources (Burns and Honkala, 1990; Niinemets and Valladares, 2006; Humbert et al., 2007) and institutional experience.

Tree Species	**Latin binomial**	**Proportion (%)**	**Sites (n)**	**Biomass / Wood**	**Tolerance Class**
Alternate-leaved dogwood	*Cornus alternifolia* L.f.	< 1	12	Y / N	Mid
American beech	*Fagus grandifolia* Ehrh.	10.3	47	N / N	Tol
Bigtooth aspen	*Populus grandidentata* Michx.	1.1	21	Y / N	Int
Black ash	*Fraxinus nigra* Marsh.	< 1	4	N / N	Mid
Black cherry	*Prunus serotina* Ehrh.	7	58	Y / Y	Int
Balsam fir	*Abies balsamea* [L.] Mill.	< 1	29	Y / N	Tol
Balsam poplar	*Populus balsamifera* L.	< 1	13	Y / N	Int
Basswood	*Tilia americana* L.	1.1	30	Y / Y	Mid
Chokecherry	*Prunus virginiana* L.	< 1	16	Y / N	Mid
Eastern hemlock	*Tsuga canadensis* (L.) Carr.	< 1	10	Y / Y	Tol
Eastern white pine	*Pinus strobus* L.	< 1	14	Y / Y	Mid
Elm	*Ulmus* spp.	< 1	25	Y / Y	Mid
Green ash	*Fraxinus pennsylvanica* Marsh.	< 1	6	N / N	Mid
Ironwood	*Ostrya virginiana* (Mill) K. Koch	12.1	56	N / N	Tol
Mountain ash	*Sorbus americana* Marsh.	< 1	5	Y / N	Mid
Mountain maple	*Acer spicatum* Lam.	< 1	5	N / N	Tol
Northern red oak	*Quercus rubra* L.	1	18	Y / Y	Mid
Northern white cedar	*Thuja occidentalis* L.	< 1	1	Y / N	Tol
Paper birch	*Betula papyrifera* Marsh.	< 1	21	Y / N	Int

Table 2.2. (cont'd)

Pin cherry	*Prunus pensylvanica* L.f.	4.1	38	Y / N	Int
Quaking aspen	*Populus tremuloides* Michx.	1.7	35	Y / N	Int
Red maple	*Acer rubrum* L.	10.3	49	Y / Y	Mid
Red pine	*Pinus resinosa* Ait.	< 1	1	Y / N	Int
Serviceberry	*Amelanchier* spp.	< 1	41	Y / N	Tol
Silver maple	*Acer saccharinum* L.	< 1	1	Y / N	Mid
Sugar maple	*Acer saccharum* Marsh.	21.6	71	Y / Y	Tol
Striped maple	*Acer pensylvanicum* L.	< 1	15	N / N	Tol
Tamarack	*Larix laricina* (Du Roi) K. Koch	< 1	1	Y / N	Int
White ash	*Fraxinus americana* L.	5	36	N / N	Int
White spruce	*Picea glauca* (Moench) Voss	< 1	14	Y / N	Tol
Willow	*Salix* spp.	< 1	5	Y / N	Int
Yellow birch	*Betula alleghaniensis* Britton	1.8	30	Y / Y	Mid
<u>Shrub Species</u>					
Beaked hazelnut	*Corylus cornuta* Marsh.	< 1	19	N / N	na
Common buckthorn	*Rhamnus cathartica* L.	< 1	1	N / N	na
Canada yew	*Taxus canadensis* Marsh.	< 1	1	N / N	na
Honeysuckle	*Lonicera* spp.	< 1	4	N / N	na
Leatherwood	*Dirca palustris* L.	< 1	8	N / N	na
Maple-leaf viburnum	*Viburnum acerifolium* L.	< 1	4	N / N	na
Olive	*Elaeagnus* spp.	< 1	3	N / N	na
Red elderberry	*Sambucus racemosa* L.	2.5	33	N / N	na
Raspberry/Blackberry	*Rubus* spp.	10.8	68	N / N	na
Sumac	*Rhus* spp.	< 1	4	N / N	na
Tag alder	*Alnus incana* (L.) Moench	< 1	1	N / N	na
Thimbleberry	*Rubus parviflorus* Nutt.	< 1	1	N / N	na
Witch-hazel	*Hamamelis virginiana* L.	< 1	2	N / N	na

2.3.2 *Analysis: Species diversity as a function of harvest treatment*

For diversity and stocking analyses I considered four species categories (Table 2.1). To examine the relationship between species diversity and harvest treatment (or gap size within ST-SG and LG treatments), stocking data were used to calculate Hill numbers. These estimates are derivations of commonly used diversity indices (i.e., species richness, Shannon, and Simpson) but allow for the intuitive comparison of these indices for a given stand or treatment (Chao et al., 2014). Ease of comparison stems from Hill numbers plainly reporting the number of species for each index, as opposed to nonlinear diversity values that are unique to each index. Sample coverage estimates were high (e.g., > 0.85) for all sites and indices; asymptotic species diversity estimates were calculated for each diversity index and site, and modeled by treatment for *Trees+Shrubs*, *Trees*, *FTG-Biomass* and *FTG-Wood* categories (Table 2.1). Nonparametric Steel-Dwass all pairs comparisons were conducted for each index-by-category combination. Diversity analyses were conducted in R (R Core Team, 2024) using the iNEXT package (Hsieh et al., 2016) and comparison tests were conducted in JMP 17 Pro (JMP, 2023).

2.3.3 *Analysis: Shade tolerance class and stocking category proportions as a function of harvest*

To examine the relationship between shade tolerance class proportion and harvest treatment, I assigned shade tolerance scores for each tree species, pooled species into three tolerance classes (i.e., tolerant, midtolerant, intolerant), and calculated stand level stocking proportion data for each class; data used for these calculations were restricted to stocking plots dominated by a tree. Tolerance scores and subsequent class designations were derived from Burns and Honkala (1990), Niinemets and Valladares (2006), Humbert et al. (2007), and institutional experience (Table 2.2). To examine relationships between stocking category and harvest treatment (or between gap sizes within the LG treatment and single-tree matrix vs. small group selection gaps within the ST-SG treatment), I calculated stand-level stocking proportion data for *Trees+Shrubs*, *Trees*, *FTG-Biomass*, and *FTG-Wood* categories. All proportional data analyses used generalized regression models with a beta distribution and were performed in JMP 17 Pro (JMP, 2023).

Survey data used for both shade tolerance and stocking category analyses were limited to locations within each treatment where forest managers would expect sapling recruitment to occur. Thus, stand-scale shade tolerance class and stocking category proportion analyses utilized all plots surveyed in ST, SH and the ST-SG treatments, but plots surveyed in the unharvested matrix within the LG treatment (~50%) were excluded. Additionally, fewer than 405 plots were sampled on some sites for various reasons (e.g., open water, roadways). As such, analyses based on proportions rather than absolute values (e.g., number of stocked plots) allowed accurate comparisons among sites.

2.3.4 *Analysis: Spatial patterning of FTG stocking*

Stand-level stocking (i.e., the proportion of plots within each stand classified as adequately stocked) for all four stocking categories was mapped with JMP Graph Builder. These mapped stands were then labeled to indicate whether stands were < 40% or ≥ 40% stocked, a criterion commonly used in even-aged stocking guides to distinguish between sufficient and insufficient stocking – roughly equivalent to 400 well-spaced stems per acre (Leak et al., 1987).

To assess spatial patterning in stocking data, I conducted a series of spatial autocorrelation (SA) analyses in ArcGIS Pro (ESRI, 2023). I began with Global Moran's I test (Ord and Getis, 1995) to evaluate whether SA existed for each stocking category. When SA was detected, I used the Hot Spot Analysis (Getis-Ord Gi*; Getis and Ord, 1992) tool to identify spatial clusters of high or low stocking proportions that differed significantly from random spatial distributions; harvest treatments were pooled for this analysis. Within the Hot Spot Analysis, I selected the "Zone of Indifference" conceptualization method, which weighted response values within a user defined distance band most heavily, with steep reductions in weighting beyond a certain distance threshold. After utilizing the Incremental Spatial Autocorrelation tool, maximal SA was detected at 105,000 m (65.2 miles). However, the geography of the study area and the general clustering of stand locations (i.e., four relatively distinct regional clusters largely divided by Great Lakes and/or distances > 40 miles) suggested a distance band of 40 miles (64,373 m) would more accurately represent patterns of landscape scale variation (i.e., hot spot cluster algorithms wouldn't use values from sites across large bodies of water or markedly different environmental conditions, such as winter snow depth in the central-western Upper Peninsula); Global Moran's I remained highly significant at this distance.

2.4 Results

2.4.1 General stocking survey characteristics

Stocking surveys tallied 32 tree and 13 shrub species or species groups (e.g., *Rubus* spp.) ≥ 50 cm tall and up to 10 cm dbh occupying dominant growing positions in plots (Table 2.2). Among these, a small subset of species had a study-wide proportion greater than five percent: sugar maple (21.6%) was the most abundant species, followed by ironwood (12.1%), red maple (10.3%), American beech (10.3%), black cherry (7.0%) and white ash (5.0%). *Rubus* spp. were the most abundant shrubs (10.8%), with red elderberry (2.5%) the only other shrub occupying > 1% of plots (Table 2.2). Approximately 80% of total surveyed plots had a dominant stem of one of these eight species.

Constancy of species representation among sites (n = 72) varied (Table 2.2). Sugar maple and *Rubus* spp. were nearly ubiquitous (71 and 68 sites with at least one dominant stem among the 405 plots, respectively), followed by black cherry (58), ironwood (56), red maple (49), American beech (47), serviceberry (41), pin cherry (38) and white ash (36) (Table 2.2).

2.4.2 *Species diversity as a function of harvest treatment*

Stand-level species richness generally increased with harvest intensity, yet variation among stands within treatment was substantial (Figure 2.2). ST (all four stocking categories) and SH (*FTG-Biomass*, *FTG-Wood*) had higher absolute species richness than ST-SG, whereas LG values were intermediate (Figure 2.2). A similar pattern was generally observed for common and dominant species diversity indices among harvest treatments, but absolute differences in diversity among harvest treatments diminished as the number of eligible species declined in category subsets (i.e., number of eligible species: *Trees+Shrubs* > *Trees* > *FTG-Biomass* > *FTG-Wood*) (Figure 2.2). Diversity increases from ST-SG to ST ranged from 48% (*Trees*, dominant species) to 95% (*FTG-Biomass*, dominant species). Species diversity among different gap sizes within ST-SG and LG did not significantly differ for any stocking category or diversity index (Appendix A, Figure A.1).

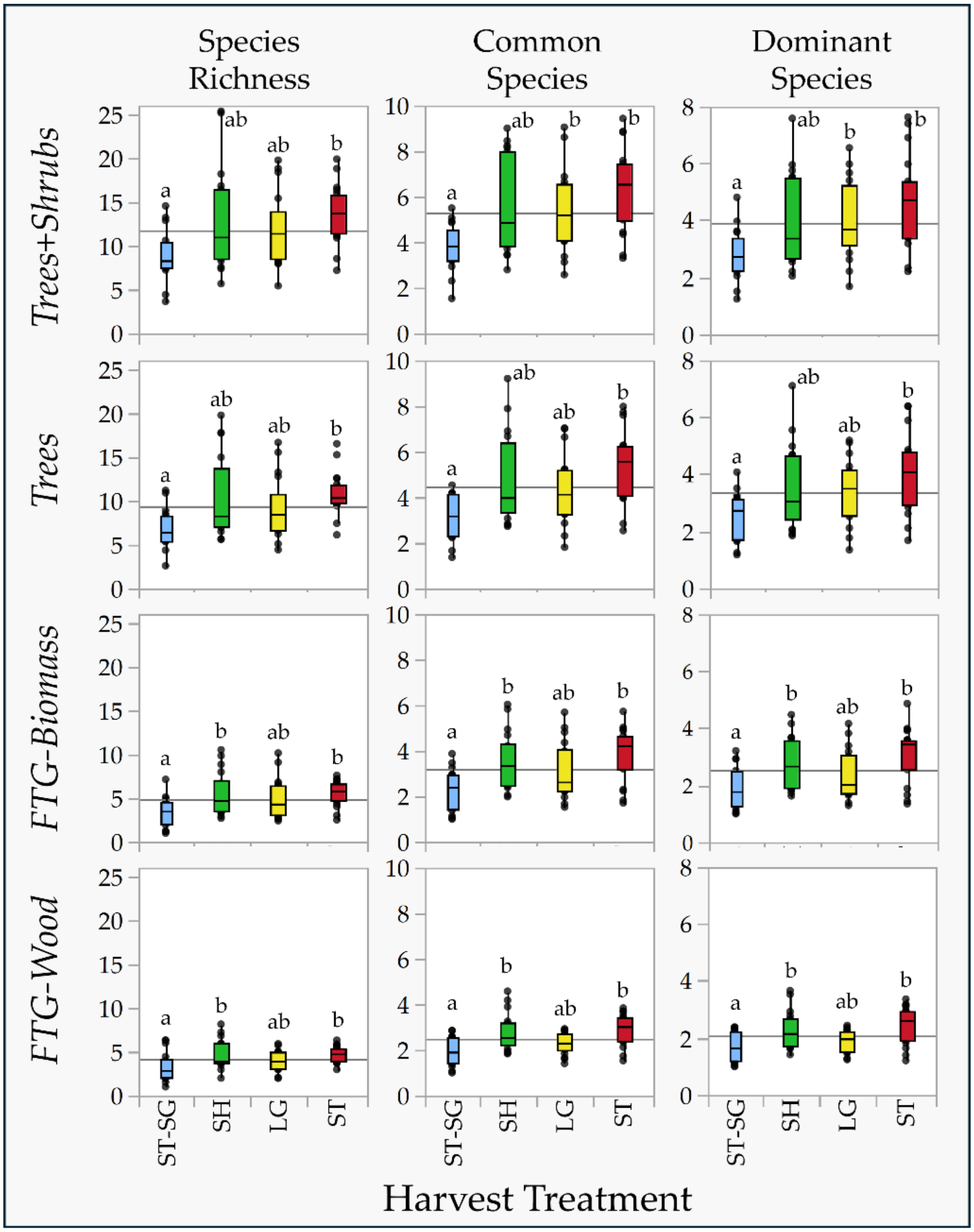

Figure 2.2. Hill number estimates of absolute species richness, Hill-Shannon diversity (common species), and Hill-Simpson diversity (dominant species) as a function of harvest treatment. Estimates are shown for four stocking categories: all woody stemmed species (*Trees+Shrubs*), only trees (*Trees*), and free-to-grow stems of species designated desirable for biomass productivity objectives (*FTG-Biomass*) or wood economics objectives (*FTG-Wood*). Box plot hinges correspond to the 25th percentile, median, and 75th percentile; whiskers extend to 1.5 times the interquartile range. Steel-Dwass all pairs comparison tests were conducted within each panel; box plots sharing the same letter are not significantly different at level $\alpha = .05$. Note change in y-axis values among diversity indices.

2.4.3 Shade tolerance class proportions as a function of harvest treatment

Stocking for species shade tolerance classes responded differently to harvest treatment intensity (Figure 2.3). Shade-tolerant species proportion declined with harvest intensity, constituting 74% of all tree stems in ST-SG vs. 54% in ST. Conversely, the stocking of shade-intolerant tree species increased with harvest intensity, and was 33% of stems in ST vs. 18% in ST-SG. Midtolerant stocking peaked in SH, where it was significantly higher than in ST-SG (24 vs. 11%, respectively, p = 0.0392). The aggregate proportion of midtolerant and intolerant stems increased with harvest intensity (Figure 2.3). All three tolerance classes were dominated by stems from a small number of tree species (Table 2.3).

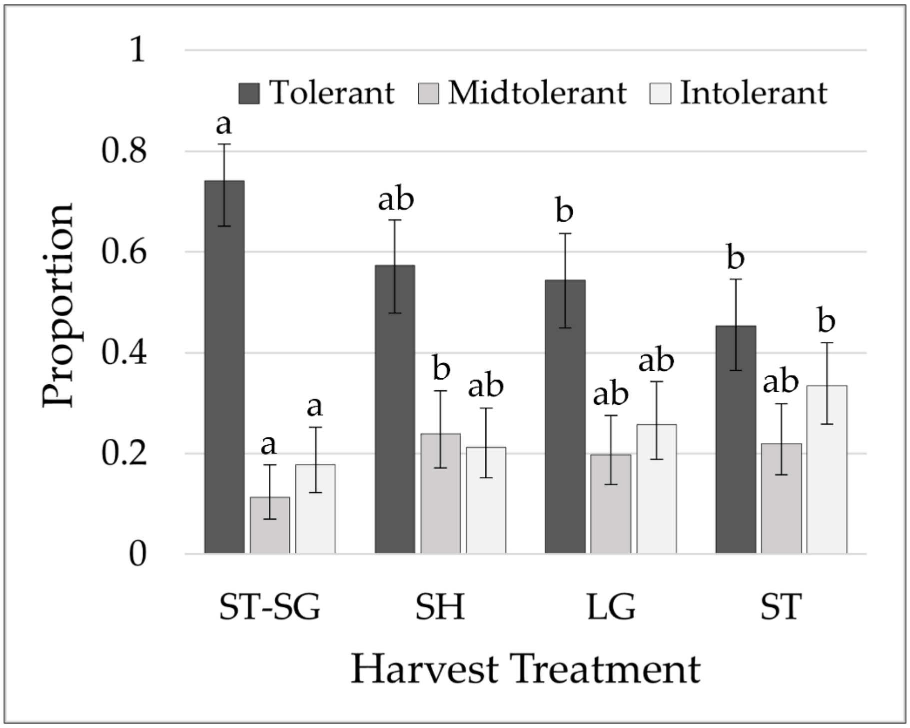

Figure 2.3. Predicted proportion of plots dominated by a tree species stem ≥ 50 cm tall, modeled using beta regression as a function of shade tolerance class and harvest treatment. Tukey-Kramer Honest Significant Difference (HSD) tests were used for pairwise comparisons among harvest treatments within shade tolerance classes; treatments sharing a letter are not significantly different at $\alpha = 0.05$.

Table 2.3. Proportion of survey plots (%) dominated by the four most abundant tree species within each shade tolerance class, and the aggregate proportion of plots these species dominate within each class.

Tolerance Class	**Species**	**Species Proportion (%)**	**Aggregate Proportion (%)**
Tolerant	Sugar maple	0.47	0.96
	Ironwood	0.26	
	American beech	0.22	
	Serviceberry	0.01	
Midtolerant	Red maple	0.62	0.86
	Yellow birch	0.11	
	Basswood	0.07	
	Northern red oak	0.06	
Intolerant	Black cherry	0.35	0.94
	White ash	0.25	
	Pin cherry	0.20	
	Aspen spp.	0.14	

2.4.4 Stocking as a function of harvest treatment

Trees+Shrubs stocking was ≥ 90% (i.e., > 90% of plots contained a woody shrub or tree stem ≥ 50 cm tall) for all treatments (Figure 2.4). *Trees* stocking (i.e., woody shrubs excluded) was > 70% across all harvest treatments, with stocking in LG significantly lower than in ST (71 vs. 85%, p = 0.0217); woody shrub stocking was often higher in LG vs. ST, though differences were not significant due to high stand-level variation (Appendix A, Figure A.2). *FTG-Biomass* stocking generally increased with harvest intensity (e.g., 30% in ST-SG vs. 58% in ST), but stand-level variation within all treatments was high, ranging from 2 – 76% (ST-SG), 8 – 96% (SH), 7 – 96% (LG), and 4 – 93% (ST) (not shown). *FTG-Wood* stocking trended higher in the alternative harvest treatments than in ST-SG but differences were not statistically significant (Figure 2.4). Within both LG and ST-SG, *Trees+Shrubs* stocking was > 90% regardless of light environment, though stocking was slightly lower in the unharvested matrix relative to harvest gaps of any size. Stocking variation within gap size was considerable for *Trees*, *FTG-Biomass* and *FTG-Wood* stocking categories (Figure 2.5) and no statistical differences in stocking among gap sizes were observed.

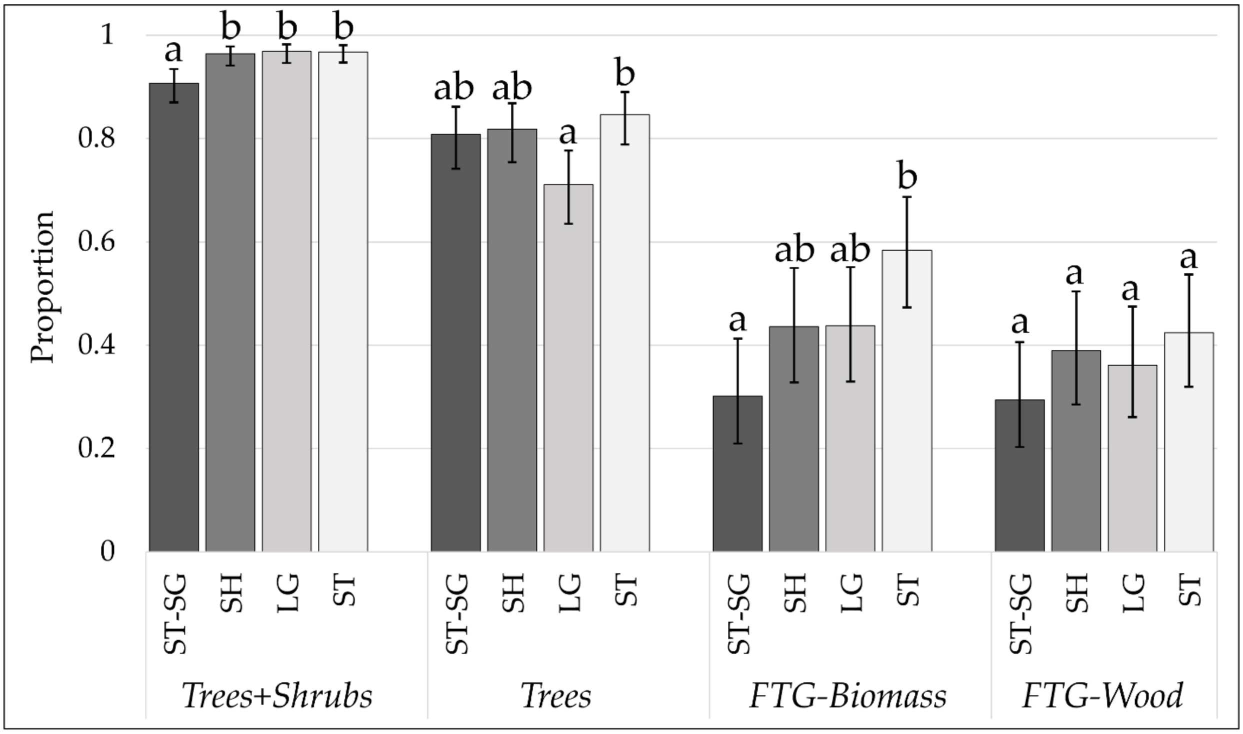

Figure 2.4. Predicted stocking proportions modeled using beta regression as a function of harvest treatment for four stem categories: all woody stems (*Trees+Shrubs*), tree stems only (*Trees*), or free-to-grow stems of species designated desirable for biomass productivity objectives (*FTG-Biomass*) or wood economics objectives (*FTG-Wood*). Tukey-Kramer Honest Significant Difference (HSD) tests were used for pairwise comparisons within each stocking category; treatments sharing a letter are not significantly different at $\alpha = 0.05$.

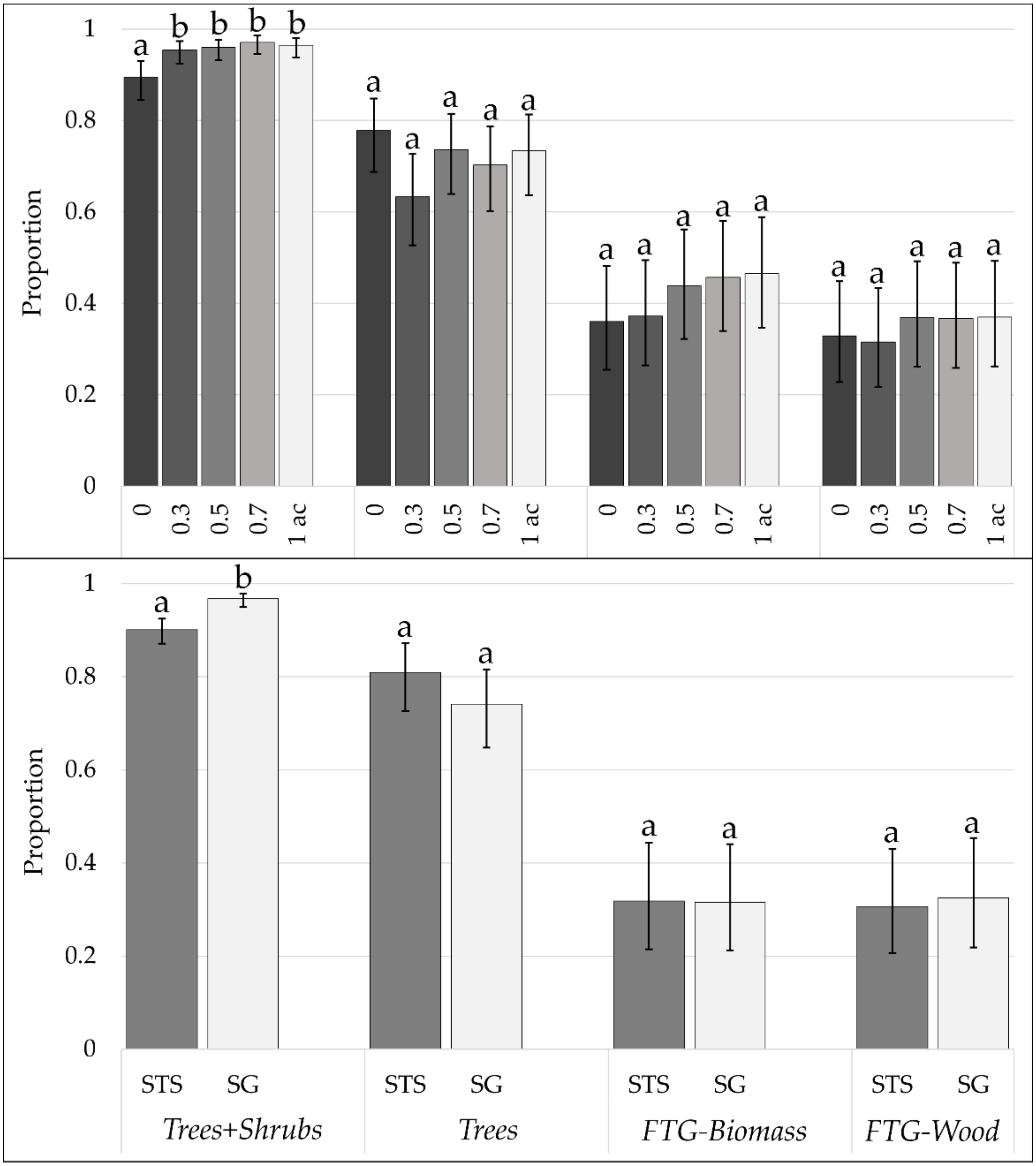

Figure 2.5. Predicted stocking proportions modeled using beta regression as a function of gap size for four stem categories: all woody stems (*Trees+Shrubs*), tree stems only (*Trees*), or free-to-grow stems of species designated desirable for biomass productivity objectives (*FTG-Biomass*) or wood economics objectives (*FTG-Wood*). The top panel compares the unharvested matrix and four gap sizes within the LG treatment; the bottom panel compares single-tree selection (STS) and 0.15 ac small group selection (SG) gaps. Tukey-Kramer Honest Significant Difference (HSD) tests were used for pairwise comparisons within each stocking category; treatments sharing a letter are not significantly different at $\alpha = 0.05$.

2.4.5 Spatial patterning of stocking

Mapped values of *FTG-Biomass* and *FTG-Wood* stocking for ST-SG, SH, and LG treatments revealed strong regional variation (Figures 2.6, 2.7). Considering the *FTG-Biomass* category, ST almost universally met the 40% stocking (i.e., minimal sufficient stocking) threshold (18/19 stands). However, when considering the more restrictive *FTG-Wood* category, fewer ST stands reached this threshold (10/19), and ST stocking exhibited regional patterning similar to less intense harvest treatments (Figure 2.6). High percent stocking clusters were observed in the northwestern Upper Peninsula and portions of the eastern Upper Peninsula, whereas low % stocking clusters were observed in the south-central Upper Peninsula and most of the northern Lower Peninsula (NLP) (Figure 2.7). No strong regional variation was detected for *Trees+Shrubs*, and a much smaller stocking depression cluster confined to a portion of the south-central Upper Peninsula was observed for the *Trees* category (not shown).

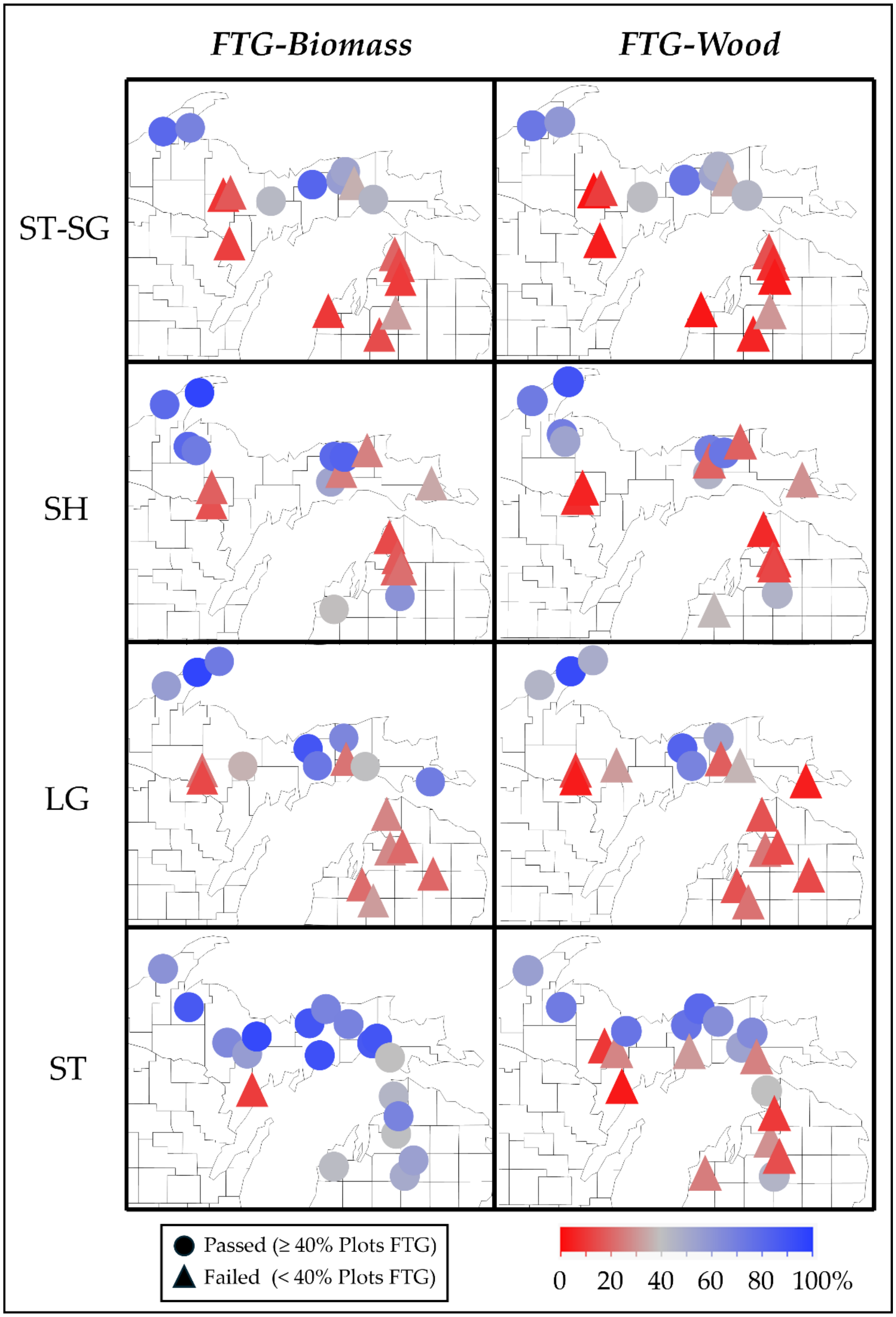

Figure 2.6. Stand-level *FTG-Biomass* and *FTG-Wood* stocking (%) by harvest treatment. Color gradients represent stocking levels from 0% (bright red) to 100% (dark blue), with 40% (gray) denoting the threshold for minimum adequate stocking (equivalent to 400 stems ac^{-1}; Leak, 1987). Circles indicate ≥ 40% stocking; triangles indicate < 40% stocking.

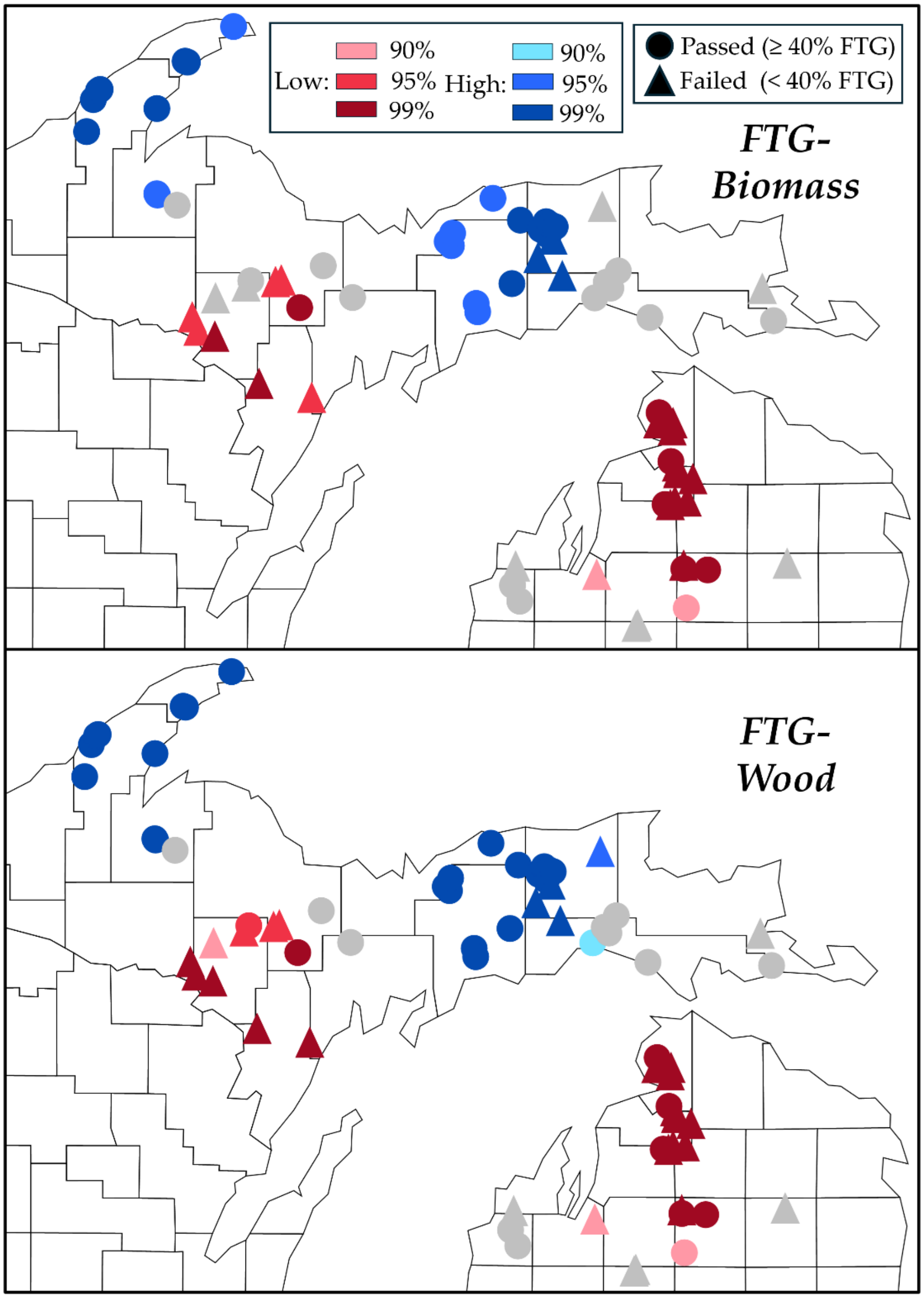

Figure 2.7. Results of Hot Spot Analysis (Getis-Ord Gi*) identifying statistically significant spatial clusters of stands with higher (blue) or lower (red) *FTG-Biomass* and *FTG-Wood* stocking proportions than expected under a random spatial distribution. High-value clusters are shown in light blue (90% confidence), medium blue (95%), dark blue (99%); low-value clusters are shown in light red (90% confidence), medium red (95%), dark red (99%). Stand shape denotes whether the stand met the threshold for minimum adequate stocking (≥40%, equivalent to 400 stems ac^{-1}; Leak, 1987). Circles indicate ≥ 40% stocking; triangles indicate < 40% stocking.

2.5 Discussion

In managed northern hardwood forests of northern Michigan, increased harvest intensity generally resulted in higher species diversity and greater stocking, whether considering all tree and shrub species, only trees, or subsets of tree species important for biomass productivity or wood economics objectives. Despite this overall trend, stand-level variation in stocking was substantial and exhibited strong spatial patterning. These findings suggest the efficacy or optimality of different harvest treatments should be evaluated at both regional and local scales.

2.5.1 Species diversity increases with harvest intensity, but is generally low and highly variable

Many studies examining species compositional changes following silvicultural treatments in NHF report patterns consistent with these findings, i.e., species diversity tends to increase with harvest intensity (Eyre and Zillgitt, 1953; Marquis, 1967; Leak and Solomon, 1975; Leak and Filip, 1977; Wang and Nyland, 1993; Poznanovic et al., 2013; Knapp et al., 2019; Sabo et al., 2019; Rogers et al., 2021; but see Metzger and Tubbs, 1971). Collectively, these studies suggest increased diversity following more intensive harvesting is largely driven by the addition of midtolerant and shade-intolerant species to the regeneration layer; these species are often excluded from the understories of forests managed with low-intensity partial cutting practices (e.g., single-tree selection).

Contrary to the positive diversity trends observed with increased harvest intensity, no significant relationships between increasing gap size and species diversity within LG or ST-SG treatments (range = 0.3 to 1 ac in LG; single-tree gap vs. 0.15 ac in ST-SG) (Appendix A, Figure A.1) were observed. There was a trend in the LG treatment toward increased diversity from intact canopy understories (gap size = 0) to 0.5 ac gaps, but within-treatment variability was substantial.

Weak effects of gap size on woody species diversity are at odds with Knapp et al. (2019) and Sabo et al. (2019), and several studies from the northeastern United States and Canada, which generally report increased diversity with gap size (Roberge, 1987; McClure and Lee, 1993; Leak, 2005). However, these results are consistent with work from the upper Great Lakes region by Bolton and D'Amato (2011), who also found no relationship between increases in gap size and tree diversity, though their largest gap size was only 0.1 ac. In contrast, Kern et al. (2013) and Knapp et al. (2021), examining a wider range of gap sizes (max 0.4 ac) in northern Wisconsin, observed a decrease in diversity with increasing gap size. While the maximum gap sizes in these studies were smaller than in this study, the collective findings suggest that increasing gap size alone may have limited influence on tree diversity in NHF, particularly in the upper Great Lakes region. This is likely due to other interrelated stand-level factors that drive regeneration dynamics, including local seed source and conducive germination substrate availability (Marquis, 1967; Tubbs and Metzger 1969; Shields et al., 2007; Willis et al., 2016), density and composition of advance regeneration (Wilson and Jensen, 1954; Metzger, 1980; Wang and Nyland, 1993; Webster and Lorimer, 2005; Danyagri et al., 2017; Widen et al., 2018), negative effects of competing vegetation (Walters et al., 2016; Widen et al., 2018), as well as browsing pressure (Côté et al., 2004; Walters et al., 2016, 2020a) and browsing selectivity (Cook, 1946; Curtis and Rushmore, 1958), among other factors. The influence of several of these factors on post-harvest regeneration outcomes is explored further in Chapter 3.

Regardless of harvest treatment or stocking category, median species diversity was low given the relatively high number of species naturally occurring in NHF. For example, median stand richness in the *FTG-Biomass* category was five species, despite 25 species being classified as eligible for this category. Moreover, among stands meeting the 40% FTG stocking threshold (n = 43), the two most prevalent *FTG-Biomass* species comprised > 50% of the total stocking proportion in 98% of stands, and more than 75% of total stocking proportion in 63% of stands (not shown). These results indicate that average stand-scale diversity is low, even in stands considered sufficiently stocked.

2.5.2 Harvest intensity influences stocking categories in unique ways

Stocking of both *Trees+Shrubs* and *Trees* was high across all treatments, including in unharvested forest understories (gap size = 0), and increased modestly with harvest intensity for *Trees+Shrubs*, but not for *Trees*. Increases in stocking and/or stem density of woody vegetation with increasing harvest intensity are expected outcomes (Leak and Solomon, 1975; Poznanovic et al., 2013). However, the modest increases observed in this study likely reflect the nature of the stocking metric used, and the effect size would likely have been greater if stocking surveys had also considered absolute stem densities of milacre plots. Furthermore, high stocking proportions observed even in unharvested understories (i.e., non-gap areas within the LG treatment) likely reflect the widespread presence of advance regeneration – particularly stems of sugar maple, ironwood and American beech – that are common in NHF understories of the region (pre-harvest regeneration survey data, Walters et al., 2022).

Contrary to the general pattern of increasing stocking with harvest intensity, stocking of *Trees* was lowest – and shrub stocking highest – in the LG treatment. The prevalence of woody shrubs (primarily *Rubus* spp.) in NHF harvest gaps has been noted in other studies (Walters et al., 2016; Widen et al., 2018; Knapp et al., 2021), but has not been compared across a wide range of harvest treatments as in this study. Elevated woody shrub cover in gaps may be influenced by patterns of deer movement and browsing pressure: the matrix of gaps and unharvested forest creates abundant forest-edge habitat that is preferred by deer, which may concentrate browsing pressure on vegetation within gaps (VanderMolen and Webster, 2021). Importantly, implicating deer use/browsing as a causal agent of low tree and high shrub stocking patterns assumes deer browsing disproportionately suppresses tree regeneration over *Rubus* growth (Ripley and Campbell, 1960; see further discussion on regional variation).

While stocking of *Trees* was generally high across treatments, stocking of tree species desired for biomass productivity objectives (*FTG-Biomass*) was much lower, ranging from 38% (ST-SG) to 70% (ST) of *Trees* stocking; *FTG-Wood* stocking lagged *Trees* stocking by an even wider margin. Stocking of both FTG categories also exhibited greater variability among sites than stocking for *Trees*; variable success in promoting desirable hardwoods has been observed among other studies of even-aged systems. In the upper Great Lakes region, shelterwood treatments successfully established sugar maple regeneration (Godman and Tubbs, 1973) while clearcutting failed to do so (Metzger and Tubbs, 1971). Group selection treatments have yielded mixed results: some promoted sugar maple across multiple gap sizes (Knapp et al., 2019, maximum gap size 0.4 ac) or produced high and/or increasing sugar and red maple regeneration densities with increasing gap size (Poznanovic et al., 2013, maximum gap size class 0.3 ac), while others reported low and declining sugar maple regeneration densities, particularly in relatively large gaps (Kern et al., 2013; Knapp et al., 2021, maximum gap size class 0.4 ac).

2.5.3 Strong regional variation in stocking outcomes

High regional variation in desirable tree stocking was apparent, with particularly low values in the south-central UP and the NLP. NHF in these regions are known to face regeneration challenges, in part due to decades of low-intensity partial harvesting in regions with high deer populations (Miller, 2004; Donovan, 2005; Shi et al., 2006; Matonis et al., 2011; Henry et al., 2023b). In these regions, only 10 of 35 stands met the minimum *FTG-Biomass* stocking threshold of 40% (i.e., ≥ 400 well-spaced, free-to-grow stems of desirable species per acre). Eight of these stands received the ST treatment, and their stocking levels were both lower than those of ST stands in other regions and relied more heavily on early-successional species rather than shade-tolerant and midtolerant species traditionally promoted through NHF management (i.e., *FTG-Wood* species). Such strong regional variation in stocking outcomes suggests that spatially varying factors independent of harvest treatment are influencing regeneration dynamics. Likely contributors include pre-harvest stand composition (Webster and Lorimer, 2005; Danyagri et al., 2017), site quality (Burger and Kotar, 2003) and browsing pressure (Curtis and Rushmore, 1958; Richards and Farnsworth, 1971); the influence of these factors on stocking is explored further in Chapter 3.

2.5.4 Implications for Management

This analysis demonstrates that increasing harvest intensity generally enhanced both species diversity and the stocking of desirable tree species. Six years post-harvest, alternative silvicultural treatments often outperformed the currently dominant ST-SG system. Given the spatial patterning in stocking success, these findings suggest even-aged systems – particularly ST harvests – may be more effective in regions with chronically poor regeneration outcomes, such as the south-central Upper Peninsula and northern Lower Peninsula. However, these results also reveal important nuances with implications for future management, including the relationship between harvest intensity and species composition, how this relationship interacts with stocking survey timing to affect the interpretation of survey outcomes, and how regional factors shape stocking independently of harvest treatment.

Notably, harvest intensity was positively related to stocking of *FTG-Biomass* but not *FTG-Wood*. The latter category consists primarily of shade-tolerant and midtolerant species that have historically been managed via ST-SG, and stocking of these species is likely less responsive to harvest intensity within the six-year timeframe of this study. In contrast, *FTG-Biomass* includes several shade-intolerant, early-successional species such as aspen, pin cherry and paper birch. Although not traditionally managed through ST-SG, some of these species (e.g., aspen, paper birch) provide valuable wood products and could be viable management targets under a broadened NHF silvicultural paradigm—one that includes early-successional species as interim canopy occupants. This management change would inevitably extend the timeline for achieving desired stocking of valuable mid- to late-successional hardwoods, as these species may initially be suppressed beneath intolerant species canopies. However, in the absence of desirable advance regeneration, few other low-input silvicultural options relying on natural regeneration remain. Moreover, the fundamental concept of forest succession would suggest overtopping canopies of intolerant species may facilitate longer-term recruitment of desired tolerant and midtolerant species by moderating understory light conditions and suppressing undesirable shrub layers (Leak, 2005). Managing for successional transition could also maintain greater long-term canopy diversity through the deliberate retention of longer-lived intolerant species.

The influence of harvest intensity on species composition also has implications for both the timing and interpretation of stocking surveys. Higher-intensity harvests result in high-light environments, promoting faster height growth in all species and favoring those species with the greatest growth rate potential (i.e., shade-intolerant species, Walters et al., 2016). Thus, FTG (particularly *FTG-Biomass*) stocking likely develops more rapidly following more intense harvests. Given stocking was assessed six years post-harvest, it is possible that *FTG-Wood* stocking in lower-intensity treatments (e.g., ST-SG) is underestimated relative to more intense treatments. Supporting this notion, Henry and Walters (2023a) found that canopy sugar maples on these largely even-aged sites often varied in age by more than two decades, suggesting a prolonged establishment phase for trees ultimately comprising the canopy. However, additional presence/absence data collected during stocking surveys shows high inter-stand variability in the proportion of milacre plots occupied by at least one stem ≥ 50 cm tall of a species designated desirable for wood economics objectives (Appendix A, Figure A.3), indicating the potential for additional *FTG-Wood* recruitment from the current regeneration layer may be limited; regions with low *FTG-Wood* stocking tended to also exhibit limited stocking in smaller size classes, particularly the south-central Upper Peninsula (not shown).

Alternatively, while longer-term stocking in less intensive harvests may be underestimated at six-years, it is also possible that stocking of high quality *FTG-Wood* stems is currently overestimated, particularly in ST-SG. Due to minimal overstory disturbance during harvesting, ST-SG stands likely contain a higher proportion of long-suppressed stems (Henry and Walters, 2023a) relative to other treatments. These stems may have limited potential for producing high-quality wood products and/or responding with adequate diameter growth following release (Baral et al., 2016). The low-light post-harvest conditions in this treatment also reduce the rate of seedling-to-sapling recruitment. As such, more intense harvest treatments may yield better long-term stocking outcomes for a broader range of desirable species, including shade-tolerant sugar maple (Leak, 2005). However, potential tradeoffs associated with heavy canopy removal – such as increased stem defect due to excessive stump sprouting or epicormic branching – should also be considered when evaluating future prescriptions.

Notably, the regional clustering of poorly stocked stands – particularly the limited response of *FTG-Wood* species to increased harvest intensity – underscores the influence of spatially variable factors that are independent of harvest treatment on stocking outcomes. These likely include site quality (Burger and Kotar, 2003), deer impacts (Matonis et al., 2011), and pre-harvest stand structure (Webster and Lorimer, 2005; Danyagri et al., 2017), among others. Moreover, pronounced regional variation in stocking outcomes highlights a key challenge for managers relying on natural regeneration: while optimizing silvicultural prescriptions can increase the probability of success, it does not guarantee it. In the following chapter, I examine additional potential drivers of stocking outcomes in detail, with the aim of identifying both constraints and opportunities for improving natural regeneration outcomes across managed NHF in the upper Great Lakes region.

CHAPTER 3:

DRIVERS OF REGIONAL VARIATION IN TREE REGENERATION FOLLOWING HARVEST IN MANAGED NORTHERN HARDWOOD FORESTS, MICHIGAN, USA

3.1 Abstract

Regeneration challenges are common in northern hardwood forests (NHF) managed using partial cutting systems in the upper Great Lakes region. Prior results from a landscape-scale silvicultural systems study showed that greater harvest intensity increased tree regeneration diversity and stocking six-years post-harvest, but regional variation in stocking was substantial. Using additional data collected on these sites, I posited that interactions between harvest intensity, pre-harvest stand structure (i.e., advance regeneration and/or canopy stem densities) and spatially varying factors affecting structure/composition (e.g., deer use, site quality) would help explain these regional patterns, with silvics explaining interspecific differences.

Nonmetric multidimensional scaling (NMS) ordination revealed that stocking composition was associated with landscape-scale gradients in site quality and browsing pressure. Browsing-resilient and avoided species were prominent in the south-central Upper Peninsula and the northern Lower Peninsula, regions characterized by high site quality and high browsing pressure; browsing-preferred species were more abundant in the eastern UP and northwestern UP, regions of poor to moderate site quality and lower browsing pressure.

Species-specific stocking models indicated that stocking was influenced by a combination of harvest intensity, pre-harvest stand structure and browsing pressure, with impacts varying among species. Intolerant species such as pin cherry, aspen and black cherry responded strongly to harvest intensity (i.e., ST-SG < SH < LG < ST), while shade-tolerant and midtolerant species

were generally more influenced by the density of larger pre-harvest regeneration layers and/or the canopy class in the case of prolific stump sprouting species such as basswood, black cherry, and red maple. Pre-harvest densities of stems ≥ 50 cm tall were generally more predictive of stocking outcomes than stems < 50 cm tall, despite the latter having up to an order of magnitude greater density than all larger size classes combined. Browsing pressure was modestly negatively associated with stocking of browsing-preferred yellow birch and northern red oak, while it was positively associated with stocking of species generally considered less palatable, including American beech, ironwood and *Rubus* spp.

These results suggest that early post-harvest stocking outcomes are primarily shaped by pre-harvest stand structure, harvest intensity, and local browsing pressure – all of which can be influenced by forest managers. Promoting species-diverse canopies, increasing the abundance of well-established advance regeneration, and tailoring harvest intensity to species silvics and local site conditions will likely improve regeneration outcomes. Additionally, efforts to mitigate deer impacts – such as increasing the spatial scale of harvest operations – may reduce browsing pressure on advance regeneration, which could ultimately promote a broader range of desirable NHF species.

3.2 Introduction

Poor tree regeneration outcomes have been widely documented following decades of uneven-aged management practices in northern hardwood forests (NHF) of the upper Great Lakes region (Miller, 2004; Donovan, 2005; Matonis et al., 2011; Henry et al., 2021, Henry and Walters, 2023b). In response to concerns about long-term sustainability and growing interest in enhancing NHF resilience to a range of ecological stressors (Thompson et al., 2009), forest managers are interested in identifying alternative silvicultural practices that may increase the density and diversity of NHF regeneration layers (Kern et al., 2013; Sabo et al., 2019; Walters et al., 2020b; Bartlick et al., 2023). Results from six-year stocking surveys in a landscape-scale silvicultural experiment in northern Michigan (Walters et al., 2020b) demonstrated that greater harvest intensity tended to increase the abundance of shade-intolerant and midtolerant species and generally led to higher sapling stocking of desirable species (Farinosi, Chapter 2). However, stocking outcomes varied widely among stands that received the same harvest prescription, and showed substantial regional and sub-regional variability regardless of harvest intensity. Additionally, regeneration layers were often dominated by a limited number of species. Since promoting desirable NHF species – and tree species diversity more broadly – is a key management objective, identifying additional environmental drivers of post-harvest stocking outcomes at the species level could help refine silvicultural prescriptions and improve regeneration outcomes.

Pre-harvest stand structure – both in the canopy and regeneration layers – is likely a primary driver of post-harvest regeneration and stocking outcomes. The size, presence and/or density of mature individuals of key NHF species can strongly influence seed availability (Farinosi, Chapter 4), seedling/sapling abundance (Peterson and Carson, 1996; Willis et al., 2016; Farinosi, Chapter 4) and regeneration via sprouting (Arthur et al., 1997; Nieves et al., 2022), and may be dictated by range limits, changes in stand composition due to land use change and forest succession, or pest and pathogen impacts, among other factors (Schulte et al., 2007; Nyland, 1992; Hlina et al., 2020; Liebhold et al., 2013). Irrespective of cause, regeneration harvests – regardless of intensity – are unlikely to succeed in recruiting desirable NHF species if local propagule sources aren't present.

Even in stands with relatively diverse canopies, contemporary management practices have largely favored shade-tolerant species. For the past 60 years, single-tree selection silviculture has been the dominant management system in NHF across the upper Great Lakes region (Arbogast, 1957; Kern et al., 2014), and was designed primarily to promote the regeneration of high-value, shade-tolerant sugar maple (*Acer saccharum* Marsh.). Residual light environments following these low-intensity partial harvests are not conducive to regeneration of other desirable but less shade-tolerant species, such as yellow birch (Webster and Lorimer, 2005). Over time, the use of this system has contributed to declines in regeneration layer diversity (Neuendorff et al., 2007).

Contemporary stand structure is also influenced by regional-scale environmental variation, particularly site quality. NHF are found over a broad gradient of soil fertility in Michigan (Host et al., 1987; Burger and Kotar, 2003). On high quality sites – characterized by greater soil water-holding capacity and nutrient availability (Baribault et al., 2010) – sugar maple and basswood (*Tilia americana* L.) often dominate. In contrast, lower quality sites tend to support red maple (*Acer rubrum* L.) (Burger and Kotar, 2003). Importantly, site quality is not randomly distributed across the northern Michigan landscape (Henry et al., 2021); rather, it is shaped by underlying geomorphological and edaphic variation (Zak et al., 1989). As such, forest stand composition varies both regionally and sub-regionally across northern Michigan with resource availability.

Deer browsing pressure is a well-documented constraint on hardwood regeneration (Côté et al., 2004; Donovan, 2005; Matonis et al., 2011; Walters et al., 2020a.). Through selective browsing practices (Bradshaw and Waller, 2016; Patton et al., 2021), deer can shift the composition of regenerating tree communities (Curtis and Rushmore, 1958; Horsely et al., 2003; Bradshaw and Waller, 2016). As with site quality, deer abundance varies considerably across northern Michigan (Shi et al., 2006). For example, contrasting regeneration patterns – such as sugar maple regeneration in areas with deep winter snowpacks in the north-central Upper Peninsula (UP) of Michigan versus American beech (*Fagus grandifolia* Ehrh.) and ironwood (*Ostrya virginiana* (Mill) K. Koch) regeneration in the south-central UP and northern Lower Peninsula (NLP) (Walters et al. 2020b) – are associated with contrasting legacies of long-term deer use across these regions (Shi et al., 2006; Matonis et al., 2011; VanderMolen and Webster, 2021). However, deer density/use estimates in previous studies have often shown weak or inconsistent relationships with sapling density and composition, possibly because short-term studies may fail to capture the cumulative impacts of long-term deer browsing pressure on tree regeneration (Matonis et al., 2011; Henry et al., 2021). Importantly, site quality may also indirectly affect and/or be confounded with deer use/browsing patterns, as both tend to covary across the upper Great Lakes region (Henry et al., 2021).

Given concerns regarding poor regeneration outcomes – and the likelihood that these patterns are shaped by multiple interacting factors – it is critical to understand how the stocking of individual species relates to multiple environmental/biological drivers. In this chapter, I first investigate regional variation in species composition across northern Michigan, focusing on how these patterns relate to site quality and indices of deer use. I then develop species-specific models of tree regeneration (based on six-year stocking outcomes) as a function of harvest intensity, pre-harvest stand structure (i.e., seedling/sapling advance regeneration and canopy composition), and deer use/browsing pressure. These analyses should expand our understanding of why different silvicultural harvests succeed or fail, and should assist in selecting site conditions and/or fostering site conditions that improve regeneration outcomes. Specifically, I predict the following:

1) Target species stocking will vary regionally, and will broadly align with spatial patterns of site quality, with relationships reflecting species silvics.
2) Target species stocking will be jointly influenced by harvest intensity, deer browsing pressure and pre-harvest target species stem densities, with the strongest predictors reflecting species silvics. Specifically:
    a) Pre-harvest stand structure (i.e., densities of advance regeneration and/or canopy trees) will most strongly predict post-harvest stocking of shade-tolerant and midtolerant species.
    b) Harvest intensity (i.e., ST > LG > SH > ST-SG) will most strongly predict stocking of shade-intolerant, early-successional species.
    c) Deer browsing pressure will reduce the stocking of species that are selectively browsed, but will not affect species that are typically avoided or resilient to browsing.

3.3 Methods

3.3.1 *Data collection*

This study utilized a subset of research sites from a landscape-scale silvicultural experiment aimed at identifying silvicultural systems that could promote well-stocked and species-diverse regeneration layers (Walters et al., 2020b). The experiment includes 140 – 30 ac (12.1 ha) research blocks (118 state-ownership, 22 industry) distributed across the northern Lower Peninsula (NLP), eastern Upper Peninsula (EUP) and western Upper Peninsula (WUP). In the winter of 2017-2018, each block received one of four harvest treatments (Nyland, 2016):

1) **Single-tree/small group selection (ST-SG):** an uneven-aged system harvest in which dispersed individual trees were harvested to achieve a residual basal area of 75 ft^2 ac^{-1}, combined with systematic establishment of 0.15 ac small group selection gaps. This treatment was intended to broadly replicate contemporary silvicultural prescriptions within managed NHF.
2) **Shelterwood (SH):** an even-aged system harvest in which approximately 50% canopy cover was retained in order to provide seed and to moderate understory microclimate conditions.
3) **Large group selection (LG):** an uneven-aged system harvest in which five replicates of four gap sizes (0.3, 0.5, 0.7 and 1 ac) were systematically established.
4) **Seed tree (ST):** an even-aged system harvest in which 6 – 8 dominant canopy trees ac^{-1} were retained as seed sources, but provided negligible understory microclimate moderation.

Aside from systematic gap installation, timber marking prioritized retention of vigorous, large-diameter stems and a diverse mix of canopy species. Furthermore, the experiment was designed to span a wide gradient of post-harvest understory light environments. Although light availability was not measured directly, canopy removal intensity is known to correlate with light transmission (Grayson et al., 2012; Keasberry et al., 2016; Walters et al., 2016). As such, light availability within the experiment could reasonably be ranked ST-SG < SH < LG < ST.

In addition to the four harvest treatments, each site received one of two understory treatments. Sixty-eight research blocks received both herbicide application and forest floor scarification to examine the influence of competing vegetation removal and mineral soil substrate creation on regeneration outcomes. In the remaining 72 blocks, felled tree crowns were left scattered across each stand following harvest, with the intent to examine their influence on deer browsing patterns; this chapter focuses on stocking survey data collected on these felled-tree crown sites (see further).

3.3.2 Vegetation sampling

Pre-harvest stand structure was assessed on each site in summer 2017 (Henry et al., 2021). Surveys were conducted using nested circular plots placed systematically on a 25-point sampling grid across each harvest block. At each survey point, stems < 50 cm were tallied in two 1 m^2 plots (50 m^2 per stand), stems 50 – 136 cm tall and 137 cm to < 5 cm dbh were tallied (and measured at dbh) in a 2 m radius plot (314 m^2 per stand), and all stems ≥ 5 cm dbh were tallied (and their dbh recorded) in a 6 m radius plot (2827 m^2 per stand).

Site quality for each stand was evaluated using the Burger and Kotar (2003) habitat classification system, which infers soil moisture and nutrient availability from assemblages of herbaceous understory species. These results were then binned into four nutrient/moisture classes for analysis: poor to poor-medium/dry to dry mesic; medium/dry mesic; medium-rich/dry mesic-mesic; and rich-very rich/mesic (Henry et al., 2021).

In the summer of 2018 (the first growing season post-harvest) similar regeneration surveys were conducted with slightly increased sampling intensity for two classes: stems < 50 cm tall were sampled in 2 m radius plots (314 m^2 per stand), and stems 50 – 136 cm tall were sampled in 4 m radius plots (1256 m^2 per stand). These pre-harvest and early post-harvest size class data were used as predictors in species abundance models (see further).

3.3.3 Deer sampling

Deer use was estimated at each site using fecal pellet count surveys, which reflect deer activity from autumn leaf fall (2018) to the time of the survey (spring 2019) (Forsyth et al., 2007). Surveys were conducted from mid-April through late May, and leaf-off was assumed to be November 1 for all sites (Henry et al., 2021); stand-level results were adjusted to account for different time periods between assumed leaf off and actual survey dates. Belt transects (2,512 m^2; 628 m total length, 4 m wide) were subdivided into 103 – 6 m segments and surveyed for pellets. The proportion of segments occupied by at least one pellet pile served as the index of deer use.

Browsing pressure was assessed in the summer of 2020 at the nine interior regeneration sampling locations within each stand, using 4 m radius circular plots (452 m^2 per stand). Browsing damage on both terminal and lateral buds was collected on seedlings that were between 50 and 136 cm tall at the end of the previous growing season. While browsing damage was collected for all species, sugar maple was used to generate a per-stem browsing pressure index applicable to all species, as it is broadly palatable to deer (thus should be sensitive to browsing pressure) and seedlings in the target size class were present in more stands (61/72 stands) than any other species. As such, the final browsing pressure index was calculated as the proportion of sugar maple buds browsed after bud set in late summer 2019 and prior to budbreak in 2020. The browsing pressure index was not necessarily expected to scale with the deer use index, as browsing pressure is a function of both deer use and browse availability/composition, and due to the fact that the time periods captured by each of these indices did not entirely overlap.

3.3.4 Six-year stocking surveys

In the sixth growing season post-harvest (2023), stocking of the regeneration layer was assessed in each stand using milacre (4 m^2) plots surveyed at 405 systematically distributed locations. In each plot, the identity of the dominant woody stem was recorded (Leak, 2007; Harris et al., 2022), and was further classified into one of four categories (Farinosi, Chapter 2):

1) **Free to Grow (FTG):** stem of a species designated desirable for biomass productivity or wood economics objectives that is ≥ 137 cm tall, up to 10 cm dbh, and is not overtopped by any competing vegetation < 10 cm dbh.
2) **Desirable:** stem of a species designated desirable for biomass productivity or wood economics objectives that is ≥ 50 cm tall, < 137 cm tall, and is not overtopped by any competing vegetation < 10 cm dbh.
3) **Undesirable:** stem of a species designated undesirable for management objectives that is ≥ 50 cm tall and up to 10 cm dbh (see Table 2.1, Chapter 2).
4) **Empty:** no woody stem ≥ 50 cm tall and up to 10 cm dbh is present.

For both NMS visualization and individual species modeling (see sections 3.3.5 and 3.3.6), FTG and Desirable category data were combined for species considered desirable for management.

3.3.5 Analysis: NMS ordination

To examine patterns in species composition and their relationships with environmental variables, I conducted nonmetric multidimensional scaling (NMS) (Kruskal, 1964; Mather, 1976) using the autopilot feature in PC-ORD 7 (McCune and Mefford, 2016). NMS is an ordination method that visually represents three-dimensional species-environment relationships in a series of two-dimensional plots. In this analysis, similarities in stand-level species composition are inferred from the spatial proximity of stands within the ordination space, which is calculated based solely on collected species proportion data (see Table 3.1 for included species); environmental variables are overlaid post-hoc to aid interpretation of species composition patterns.

The environmental variables examined included harvest treatment, indices of deer use (pellet counts) and browsing pressure (sugar maple browsing damage), site quality (described previously), and stand location within the study area (region); for brevity, NMS results of the harvest treatment environmental variable are located in Appendix B (Figures B.1.5, B.1.6). The region variable consisted of five categories: the northern Lower Peninsula (NLP); the eastern Upper Peninsula north and south (EUP-N, EUP-S); and the western Upper Peninsula north and south (WUP-N, WUP-S). The initial east-west division of the UP was part of the experimental design to ensure an even distribution of harvest treatments across a large land base, and to capture the variation in NHF compositions and regeneration dynamics that occur across the UP (Walters et al., 2020b). The north-south regional divisions of the EUP and WUP were based on well-documented differences in lake-effect snow patterns, which are likely to influence seasonal deer use (Shi et al., 2006). I used the 150 cm winter precipitation isoline described by Scott and Huff (1996) for these divisions. While somewhat arbitrary, I believe these divisions are likely to capture meaningful ecological variation across the study area.

3.3.6 *Analysis: Species abundance models*

To investigate how harvest intensity, deer browsing pressure, and pre-harvest stand structure (i.e., pre-harvest advance regeneration and canopy classes) influence stocking outcomes, I developed species-specific predictive models of stocking abundance. Stocking data used for this analysis were collected in locations within each treatment where sapling recruitment would be expected to occur. This included all plot data from ST, SH and ST-SG treatments and harvested areas within the LG treatment (~50% of plots). Fewer than 405 plots were sampled on some sites, primarily due to the omission of plots with no capacity to become forested (e.g., bodies of water or logging roads). Sites were standardized via fixed proportion expansion to 405 plots per site prior to analysis. Given a strong and confounded regional and site quality component to stocking composition observed in NMS, similar regional/site quality patterns for overstory trees (Henry and Walters, 2023b), and well-established macro-scale range limitations for some species (e.g., American beech), I restricted these models to sites where the target species occurred in at least one survey, and excluded region and site quality from these analyses. Similarly, the deer use index was excluded due to covariation with harvest treatment (not shown).

Pre-harvest and one-year post-harvest stand structure survey data was divided into four size classes considered meaningful to tree species' life histories and forest dynamics (Henry et al., 2023). Stems < 50 cm tall represent local seed and sprout sources and are more likely to experience mortality from competition due to their stature. Stems 50 – 136 cm tall reflect either 1) well-established advance regeneration that may have been recruitment-limited prior to harvest due to deer browsing or competing vegetation (from shrub to canopy), or 2) fast-growing, shade-intolerant species that established after harvest. Stems 137 cm tall to 10 cm dbh were largely comprised of shade-tolerant advance regeneration saplings which had largely transcended deer browsing and shrub competition, and thus have a higher likelihood of reaching maturity (Walters et al. 2020a). Stems > 10 cm dbh represent mature canopy or subcanopy trees, which in some species can sprout prolifically after harvest (e.g., red maple, Nieves et al., 2022).

Most models were restricted to sites where the target species was observed in at least one survey year (see earlier rationale). However, all sites were included in models for pin cherry and *Rubus* spp., as these species often establish from long-lived seed banks and are typically absent in closed-canopy pre-harvests forests (pin cherry, Marks, 1974; M. Walters unpublished data; *Rubus*, Graber and Thompson, 1978).

Browsing pressure estimates were unavailable for 11 sites where no sugar maple stems in the 50 – 136 cm height class were present. Three of these sites – all located in the EUP – were dominated by red maple. To estimate browsing pressure on these sites, I fit a generalized regression model (beta distribution) predicting sugar maple browsing from red maple browsing on sites with ≥ 10 stems of each species in the 50 – 136 cm class ($R^2 = 0.406$, $p < .0001$, $n = 60$). These modeled values were used to impute sugar maple browsing pressure for the three red maple-dominated sites. The remaining eight sites had canopies dominated by sugar maple and were located in areas known for high deer densities (five in the south-central UP, three in the southern NLP), and regeneration layers largely consisted of beech (2), ironwood (1), or black cherry (5). I explored similar scaling relationships between sugar maple and these other species, but they were weaker (sugar maple vs. ironwood: $R^2 = 0.200$, $p < .0001$, $n = 69$; sugar maple vs. black cherry: $R^2 = 0.155$, $p = 0.0004$, $n = 69$; sugar maple vs. American beech: no discernable relationship). Due to their lower predictive power, these relationships were not used for imputation.

Nevertheless, these eight sites showed clear signs of legacy browsing impacts (e.g., extremely low stem counts for all species except beech or ironwood, with signs of repeated browsing damage). As such, I wanted to find a way to incorporate them into the multi-predictor models. However, I also recognize that browsing indices for these sites would be, at best, imprecise assignations based on assumptions. As such, I examined three model variants for each species:

1) **NoBR:** Excludes browsing pressure as a predictor, enabling inclusion of all sites where the target species occurred. Any species model in which browsing is tested and found to be statistically insignificant is, by definition, reduced to this model variant.
2) **BR3:** Includes measured sugar maple browsing data plus the three red maple-imputed sites.
3) **BR11:** Includes an additional eight sites exhibiting signs of heavy browsing damage, which were assigned the maximum browsing pressure value observed in the dataset (1.0). As such, this model variant includes all 11 sites for which sugar maple browsing data were not available to collect.

Stocking data, expressed as the proportion of plots per site in which the target species was the dominant stem, were modeled using generalized regression with a beta distribution and logit link function in JMP 17 Pro (JMP, 2023). Predictor variables included harvest treatment, size class densities (pre- or post-harvest), and the browsing pressure index. Bi-directional stepwise model selection was performed using the Akaike information criterion (AIC; Akaike, 1974). Preliminary analysis showed that non-transformed stem density variables often produced poor fits. As such, density predictor variables were square-root transformed (+1), and the use of 3-knot splines was evaluated. Transformations and splines were retained if they improved AIC scores and visual model fit. Model selection was conducted separately for pre- or post-harvest size class predictor sets (see Appendix B, Table B.2 for post-harvest models). Final models were evaluated for extreme outliers (studentized residuals) and high leverage points (Cook's D); while some statistical outliers and leverage points were identified, all were considered biologically valid and were retained. AIC scores were compared within, but not among, model variants (e.g., within NoBR), as sample size differed among variants.

3.4 Results

3.4.1 NMS Ordination

NMS ordination analysis included 26 tree and two shrub species or species complexes (Table 3.1). The final NMS ordination resulted in a three-dimensional solution with a stress value of 12.4 – well within the commonly accepted range of 10 – 20 for ecological community data (McCune and Grace, 2002). Axes 1, 2 and 3 accounted for 44.9, 25.2 and 15.8% (respectively) of the variance in species stocking survey composition, and totaled 86%. Balsam fir (*Abies balsamea* [L.] Mill.), black cherry, red maple and serviceberry (*Amelanchier* spp.) were prominent in the EUP (both N and S) (Figure 3.1, Panels 1, 2) on sites classified as poor – poor medium/dry-dry mesic and experiencing relatively low browsing pressure (Figure 3.1, Panels 3, 4). In contrast, eastern hemlock (*Tsuga canadensis* (L.) Carr.), northern red oak (*Quercus rubra* L.), sugar maple, yellow birch and mountain maple (*Acer spicatum* Lam.) were more common in the northwestern Upper Peninsula (WUP-N) where site quality was variable but generally lower, and browsing pressure was low. Basswood, ironwood and *Rubus* spp. were tightly clustered in ordination space and most abundant on richer sites (Figure 3.1, Panels 3, 4) in more heavily browsed regions – the NLP and WUP-S (Figure 3.1, Panels 1, 2). The abundance of a few species was more closely related to harvest treatment. American beech and striped maple (*Acer pensylvanicum* L.) were associated with ST-SG and SH harvest sites (Appendix B, Figures B.1.5, B.1.6) in the NLP (Figure 3.1, Panels 1, 2), while aspen (*Populus grandidentata* Michx., *P. tremuloides* Michx.) and pin cherry stocking was associated with increased harvest intensity rather than with site quality or browsing pressure (Appendix B, Figures B.1.5, B.1.6).

Spatial patterns of deer use and browsing pressure indices appeared largely orthogonal. Increased deer use was positively associated with harvest intensity (Appendix B, Figures B.1.5, B.1.6), whereas browsing pressure was higher in the NLP and WUP-S (Figure 3.1, Panels 1, 2). Site quality was also generally higher in these heavily browsed regions (Figure 3.1, Panels 1 vs. 3 and 2 vs. 4).

Table 3.1. Species that were the dominant stem in at least one stocking plot on a minimum of five study sites and were included in the nonmetric multidimensional scaling (NMS) analysis. Species with sufficient data for individual species modeling (Tables 3.2, 3.3) are marked with an asterisk (*) and labeled in Figure 3.1; full species labeling for all NMS ordinations are provided in Appendix B (Figures B.1.1 – B.1.6).

Common Name	Latin Binomial	Abbreviation
American beech*	*Fagus grandifolia* Ehrh.	AB
Bigtooth aspen*	*Populus grandidentata* Michx.	ASP
Black cherry*	*Prunus serotina* Ehrh.	BC
Balsam fir*	*Abies balsamea* [L.] Mill.	BF
Balsam poplar	*Populus balsamifera* L.	BP
Basswood*	*Tilia americana* L.	BW
Chokecherry	*Prunus virginiana* L.	CC
Dogwood	*Cornus* spp.	DW
Eastern hemlock	*Tsuga canadensis* (L.) Carr.	HEM
Eastern white pine	*Pinus strobus* L.	WP
Elm	*Ulmus* spp.	ELM
Ironwood*	*Ostrya virginiana* (Mill) K. Koch	IW
Mountain maple	*Acer spicatum* Lam.	MM
Northern red oak*	*Quercus rubra* L.	RO
Paper birch	*Betula papyrifera* Marsh.	PB
Pin cherry*	*Prunus pensylvanica* L.f.	PC
Quaking aspen*	*Populus tremuloides* Michx.	ASP
Red elderberry	*Sambucus racemosa* L.	ELD
Red maple*	*Acer rubrum* L.	RM
Raspberry/Blackberry*	*Rubus* spp.	RUB
Serviceberry*	*Amelanchier* spp.	SB
Sugar maple*	*Acer saccharum* Marsh.	SM
Striped maple	*Acer pensylvanicum* L.	STM
White ash*	*Fraxinus americana* L.	WA
White spruce	*Picea glauca* (Moench) Voss	WS
Yellow birch*	*Betula alleghaniensis* Britton	YB

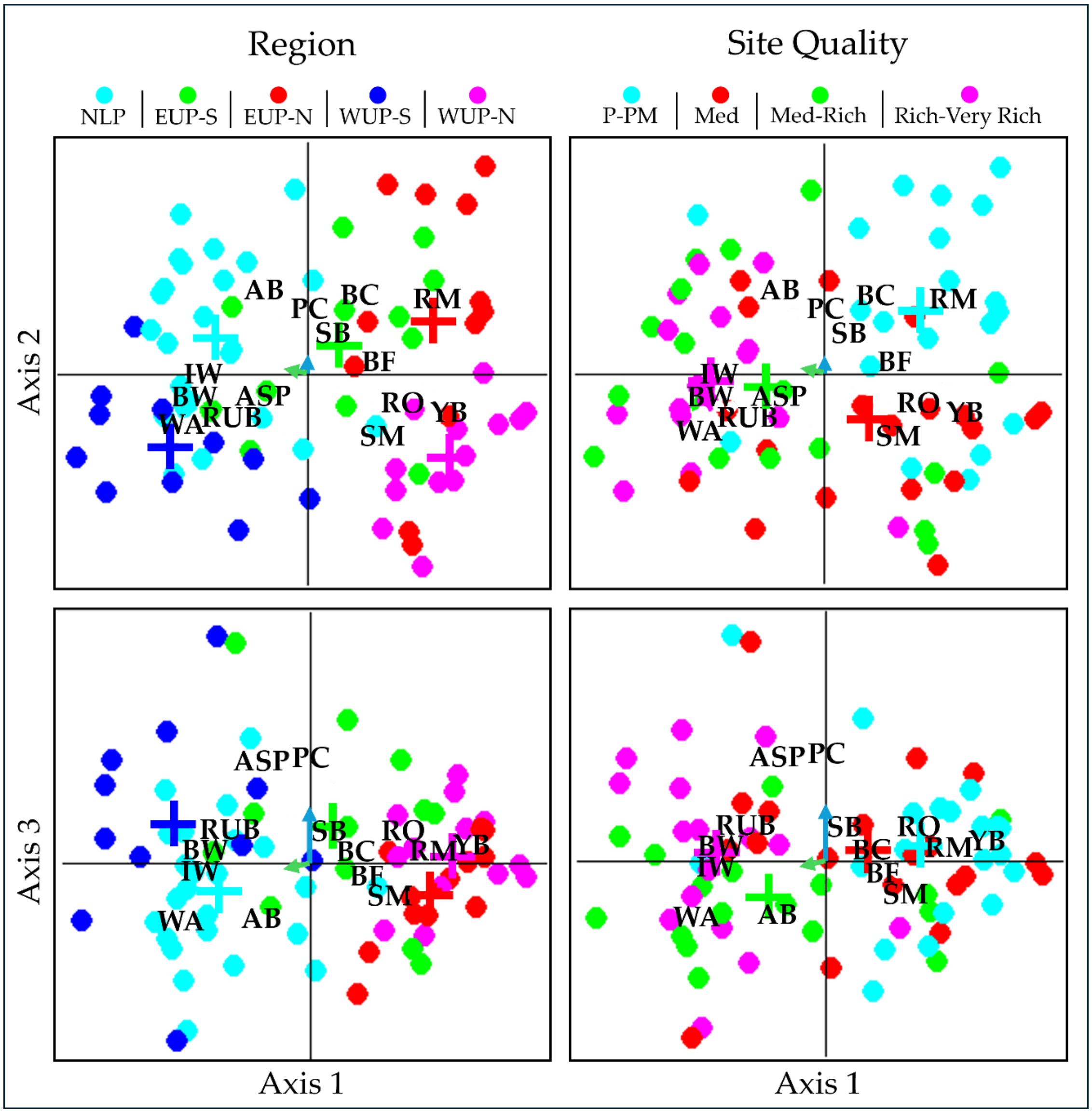

Figure 3.1. Nonmetric multidimensional scaling (NMS) ordination of stand-level stocking composition. Distance between stands (colored circles) reflects similarity (adjacent) or dissimilarity (distant) in species composition. Panels 1 and 3 (left column) display two distinct views of the same three-dimensional ordination, with stands shaded by region. Panels 2 and 4 (right column) show the same ordination views as Panels 1 and 3, respectively, but with stands shaded by site quality. Group centroids for region (left column) and site quality class (right column) are shown as large plus signs (+). Comparing Panels 1 vs. 2 and Panels 3 vs. 4 allows visual assessment of how region and site quality relate withing the ordination space. The third NMS axis view (Axis 2 vs. 3) is not shown, as it did not provide additional spatial separation. Environmental vectors representing indices of deer use (blue arrow) and browsing pressure (green arrow) are shown as arrows projecting from the origin of each plot. Panels showing full species labeling for all NMS ordinations (plus panels for the harvest intensity environmental variable) are provided in Appendix B (Figures B.1.1 – B.1.6).

3.4.2 *Species models: the influence of pre-harvest size class density*

Models incorporating pre-harvest target species structure, harvest treatment, and browsing pressure were significant across all evaluated species. Explanatory power and predictor importance generally aligned with species' silvics, with full species models explaining up to 87% of variation in stocking (e.g., ironwood; Table 3.2). For most species, pre-harvest stem densities – particularly in larger regeneration and canopy size classes – were the strongest predictors of stocking six-years post-harvest.

Species varied in which size classes were most influential, with patterns largely corresponding to shade tolerance (Table 3.2). Stocking of shade-tolerant and midtolerant species – such as sugar maple, American beech, balsam fir, and yellow birch – were best predicted by densities in the 137 cm – 10 cm dbh class. Basswood, red maple, and black cherry were best predicted by pre-harvest densities of stems > 10 cm dbh, along with smaller classes; these species exhibited strong post-harvest stump sprouting from mature stumps (E. Farinosi, personal observation). Notably, regeneration size classes ≥ 50 cm tall were more consistently associated with stocking outcomes than shorter stems, despite the latter often being far more abundant (Appendix B, Table B.1). White ash, a species known to be shade-tolerant as a seedling but less tolerant at larger sizes, was unique in this regard, as stocking was best predicted by densities of stems < 50 cm tall. Shade-intolerant pin cherry and aspen were not significantly associated with any pre-harvest size class densities, consistent with their tendency to establish following disturbance (Table 3.2).

Across all species, the effect size (i.e., slope) of pre-harvest stem density predictors included in the final species model generally increased with size class, peaking in either the 137 cm – 10 cm dbh or > 10 cm dbh classes (Table 3.3). This suggests that, on a per-capita basis, larger advance regeneration and canopy trees were more likely to contribute to post-harvest stocking than smaller individuals. Models incorporating first-year post-harvest size class densities showed broadly similar patterns, but overall fit was generally poorer; these models are not discussed further (see Appendix B, Table B.2).

Table 3.2. Whole-model and partial-factor significance values (Wald chi-square values) from generalized regression models (beta distribution) predicting six-year post-harvest stocking. The model variant (NoBR, BR3, BR11) with the lowest AIC score is presented for each species. Predictors included pre-harvest stem density by size class (stems ha^{-1}), harvest treatment (four levels) and deer browsing pressure (BP; proportion of sugar maple buds 50 – 136 cm tall browsed in the second growing season post-harvest). All retained predictors had positive effects, except browsing pressure (+/-) and nominal variables. Species are ordered by descending shade tolerance (Niinemets and Valladares, 2006; *Rubus alleghaniensis* score applied to the *Rubus* spp. group), except for pin cherry (Burns and Honkala, 1990; Walters et al., 2014). N reflects stands where a species occurred in any size class in any survey year, except for pin cherry and *Rubus*, for which all sites were included. Species present on fewer than 20 sites were excluded from analysis. *Rubus* models did not incorporate size class predictors due to lack of pre-harvest data.

Spp.	**Tolerance**	**Model**	**n**	**R^2**	**< 50 cm**	**50 - 136 cm**	**137 cm - 10 cm dbh**	**> 10 cm dbh**	**Harvest**	**Harvest x Size Class**	**BP**
BF	Tol	NoBR	45	0.565	24.3	ns	40.6	ns	ns	ns	--
SM	Tol	NoBR	72	0.765	ns	22.8	65.6	ns	ns	ns	--
AB	Tol	BR11	54	0.785	ns	ns	14.4	ns	27.1	12.9	5.5 (+)
IW	Tol	BR11	64	0.871	ns	19.1	54.9	29.9	27.8	ns	15.7 (+)
SB	Tol	NoBR	64	0.231	ns	24	ns	ns	ns	ns	--
BW	Tol	NoBR	47	0.481	16.9	ns	8.0	9.3	ns	ns	--
RM	Mid	NoBR	62	0.817	ns	11.6	22.6	33.1	ns	ns	--
YB	Mid	BR11	52	0.511	7.7	18.2	37.4	ns	13.4	ns	5.9 (-)
RO	Mid	NoBR	25	0.677	16.5	17.2	ns	ns	ns	ns	--
RUB	Int	BR11	72	0.273	--	--	--	--	14.4	--	12.8 (+)
WA	Int	NoBR	49	0.729	73.1	ns	23.4	ns	ns	ns	--
BC	Int	NoBR	66	0.753	ns	37.5	5.8	57.6	15.1	ns	--
PC	Int	NoBR	72	0.112	ns	ns	ns	ns	9.0	ns	--
ASP	Int	NoBR	47	0.165	ns	ns	ns	ns	9.7	ns	--

Table 3.3. Mean pre-harvest stem densities, minimum mean densities (derived from the proportion of stocking plots dominated by the species), and effect sizes (i.e., slopes) for significant predictors in beta regression models, including harvest treatment, size classes, and browsing pressure (BP). Estimates are drawn from the species-specific model with the lowest AIC score in Table 3.2; see Table 3.2 and Methods for additional model details.

Spp.		**Model intercept**	**Harvest ST-SG**	**Harvest SH**	**Harvest LG**	**Harvest ST**	**< 50 cm**	**50 - 136 cm**	**137 cm - 10 cm dbh**	**> 10 cm dbh**	**BP**
BF	stems ha^{-1}		17	17	17	17	324	ns	80	ns	ns
	slope	-4.98	ns	ns	ns	ns	0.343	ns	0.523	ns	ns
SM	stems ha^{-1}		410	410	410	410	ns	1126	1139	ns	ns
	slope	-1.61	ns	ns	ns	ns	ns	0.434	0.763	ns	ns
AB	stems ha^{-1}		637	382	200	151	ns	ns	1005	ns	0.485
	slope	-2.79	1.115	0.725	0.146	0	ns	ns	0.864	ns	0.222
IW	stems ha^{-1}		231	306	188	149	ns	233	543	14	0.444
	slope	-2.50	0.475	0.864	0.355	0	ns	0.071	1.39	0.444	0.245
SB	stems ha^{-1}		21	21	21	21	ns	38	ns	ns	ns
	slope	-4.78	ns	ns	ns	ns	ns	0.407	ns	ns	ns
BW	stems ha^{-1}		32	32	32	32	338	ns	17	17	ns
	slope	-4.35	ns	ns	ns	ns	0.473	ns	0.238	0.310	ns
RM	stems ha^{-1}		185	185	185	185	ns	296	199	59	ns
	slope	-2.45	ns	ns	ns	ns	ns	0.361	1.175	0.564	ns
YB	stems ha^{-1}		17	36	33	61	292	46	26	ns	0.373
	slope	-3.67	-1.215	-0.529	-0.605	0	0.273	0.426	0.596	ns	-0.282
RO	stems ha^{-1}		47	47	47	47	578	46	ns	ns	ns
	slope	-4.00	ns	ns	ns	ns	0.581	0.541	ns	ns	ns
RUB	stems ha^{-1}		157	242	413	290	na	na	na	na	0.434
	slope	-1.99	-0.742	-0.221	0.387	0	na	na	na	na	0.343
WA	stems ha^{-1}		102	102	102	102	2973	ns	71	ns	ns
	slope	-3.15	ns	ns	ns	ns	0.840	ns	0.475	ns	ns
BC	stems ha^{-1}		91	110	112	183	ns	49	48	12	ns
	slope	-2.53	-0.735	-0.546	-0.529	0	ns	0.419	0.254	0.512	ns
PC	stems ha^{-1}		74	94	122	184	ns	ns	ns	ns	ns
	slope	-2.52	-0.962	-0.714	-0.439	0	ns	ns	ns	ns	ns
ASP	stems ha^{-1}		59	84	77	170	ns	ns	ns	ns	ns
	slope	-2.61	-1.1	-0.747	-0.833	0	ns	ns	ns	ns	ns

3.4.3 *Species models: the influence of harvest intensity and deer browsing pressure*

Harvest treatment significantly influenced the stocking of multiple species (Table 3.2). Comparing mean minimum stem densities derived from proportional stocking data, stocking of many shade-intolerant and midtolerant species increased significantly with harvest intensity.

From the least intense (ST-SG) to most intense treatment (ST), black cherry increased by a factor of 2, pin cherry by 2.5, aspen by 2.8 and yellow birch by 3.6 (Table 3.3). *Rubus* stocking peaked in the LG treatment, where it was 2.6 times greater than in ST-SG.

The two most common species considered undesirable for management responded differently to harvest treatment – and from other species. Ironwood stocking was greatest in the SH treatment and generally remained high across all treatments, whereas American beech declined as harvest intensity increased, with LG and ST treatments showing 3.2 and 4.2 times lower stocking, respectively, than ST-SG (Table 3.3; Figure 3.2). For beech, a significant interaction between harvest treatment and pre-harvest sapling density (137 cm – 10 cm dbh) indicated the ST treatment disproportionately reduced beech stocking on sites where initial sapling densities were higher (not shown). Stocking of several important tolerant/midtolerant species including balsam fir, sugar maple, basswood, red maple, and northern red oak showed no significant response to harvest treatment (Table 3.2).

Stocking of yellow birch and northern red oak was negatively associated with browsing pressure (Table 3.2; Appendix B, Table B.3), though this relationship was retained only in the BR11 model variant. For yellow birch, the effect size of browsing pressure was modest compared to the influence of pre-harvest stem densities. For red oak, the model excluding browsing pressure (NoBR) provided a better fit (i.e., lower AIC) than the model with 11 imputed browsing estimates (BR11) (Table 3.2; Appendix B, Table B.3). Conversely, stocking of species generally considered browsing-resilient or avoided – American beech, ironwood, and *Rubus* – increased with browsing pressure (Table 3.2). Notably, this inverse relationship was weaker in the BR3 model (and not statistically significant for beech), and in all cases, the effect size of browsing pressure remained modest after accounting for other predictors such as harvest treatment and pre-harvest stem densities (Table 3.3).

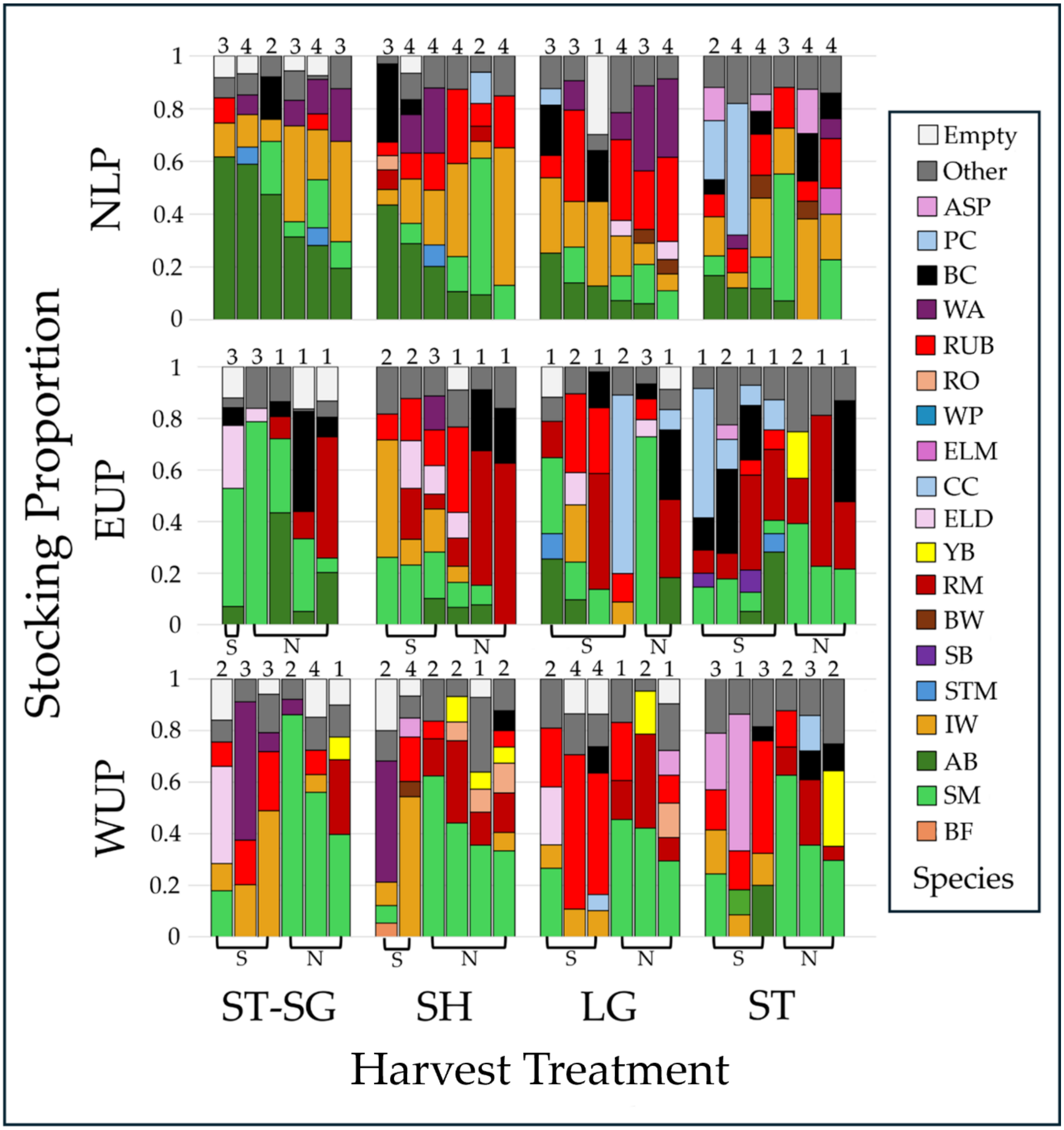

Figure 3.2. Stand-level species stocking proportions based on dominant stems in milacre plots. Sites are grouped by harvest treatment, with northern and southern Upper Peninsula locations indicated by "N" and "S", respectively. Site quality is shown above each site and coded as follows: 1 = poor to poor-medium; 2 = medium; 3 = medium-rich; 4 = rich to very rich (Burger and Kotar, 2003).

3.5 Discussion

3.5.1 Site quality, browsing pressure, and variation in species composition among regions

Six years after harvest, patterns of stand composition and species abundance varied considerably across regions and with site quality. Further, substantial stocking variation within these strata were observed, which these results suggest were largely driven by interactions between pre-harvest stand structure (i.e., advance regeneration and sprout-producing canopy trees), harvest intensity, and local deer browsing pressure. These findings highlight the potential for managers to use data on contemporary stand structure and browsing pressure to design and predict the outcomes of harvest treatments, and to promote pre-harvest stand structure that results in desirable post-harvest regeneration outcomes.

High site quality and high browsing pressure in the WUP-S and NLP corresponded with increased stocking of ironwood, *Rubus,* basswood, white ash, and (moreso in the NLP) American beech; many of these species are generally considered low-preference browse (e.g., ironwood, Metzger, 1990; white ash, Michael, 1988; beech, Cowan et al., 1970) and are typically associated with rich mesic sites (e.g., basswood and white ash, Burns and Honkala, 1990; ironwood, Voss, 2012). Conversely, regions with lower site quality and lower browsing pressure were characterized by associations comprised of browsing-susceptible species such as yellow birch, eastern hemlock, northern red oak and sugar maple (WUP-N), or red maple and black cherry (EUP). It's important to note that these results do not necessarily imply a causal link between site quality and browsing pressure. Instead, the covariation observed likely reflects broader ecological patterns. Lower-quality sites, particularly in the northern UP, experience deeper winter snowpacks and reduced deer activity from late fall through spring; high-quality sites, typically located in the NLP and southern UP, receive less snow and support higher winter deer densities (Shi et al., 2006). As such, multiple environmental gradients may act as a competitive filter for browsing-sensitive species. Stocking results from the northern vs. southern WUP support this interpretation: while mature sugar maple dominated nearly every stand (indicating stand capacity to adequately grow the species), sugar maple stocking (Figure 3.2) and pre-harvest regeneration density (not shown) was extremely low in the WUP-S, and highest in the WUP-N.

3.5.2 Pre-harvest stand structure

Pre-harvest densities of regeneration size classes and canopy stems (i.e., > 10 cm dbh) were generally strong predictors of six-year stocking outcomes. This relationship was most consistent for shade-tolerant and midtolerant species, which have traditionally been the focus of uneven-aged management in NHF. Notably, regeneration size classes ≥ 50 cm tall were particularly important for many of these species. However, pre-harvest regeneration survey data indicate that average densities of these larger regeneration classes are generally low across much of the northern Michigan NHF resource (Henry et al., 2021, 2023; Walters et al., 2022; Appendix B, Table B.1).

These findings, along with those of previous studies, suggest that current understory composition is shaped by multiple interacting factors. These include the absence of local seed sources (Willis et al., 2016; Henry et al., 2023), inadequate germination substrates (Marx and Walters, 2008; Willis et al., 2015), and insufficient light availability following low-intensity partial harvesting (Crow et al., 2002; Webster and Lorimer, 2005; Henry et al., 2021; Henry and Walters, 2023b). Furthermore, regional variation in chronic deer browsing pressure (Donovan, 2005; Matonis et al., 2011) and site quality (this study) likely influences propagule availability, seedling establishment and relative competitive status. Regardless of the specific limitations present on a site, overcoming regeneration bottlenecks to foster well-established advance regeneration – particularly stems ≥ 50 cm tall – will likely be key to successfully regenerating shade-tolerant and midtolerant species within practical post-harvest timeframes (Wang and Nyland, 1993; Webster and Lorimer, 2005; Danyagri et al., 2017).

3.5.3 Harvest intensity

Harvest intensity was a significant driver of stocking for shade-intolerant species, with one exception: white ash. Unlike other intolerant species, white ash stocking was unrelated to harvest intensity and was instead positively associated with < 50 cm tall seedlings and, to a lesser extent, stems in the 137 cm – 10 cm dbh class. This pattern is consistent with the species' silvics: white ash is shade-tolerant as a seedling (Burns and Honkala, 1990) but exhibits much lower tolerance as a sapling (Niinemets and Valladares, 2006).

Due to the tendency of aspen species to regenerate via root suckering, I was surprised not to find a positive relationship between post-harvest aspen stocking and pre-harvest densities of mature stems. This may partially reflect limitations in sampling intensity: aspen stems were observed in some stands but not captured in pre-harvest surveys (E. Farinosi, personal observation). Alternatively, some of these stems may have been past the point of vigorous vegetative sprouting, given most of these stems likely initiated following stand clearing disturbance (i.e., exploitative harvesting) over a century ago (Henry and Walters, 2023a).

Notably, stocking of American beech was negatively associated with harvest intensity. Beech appeared to be affected more than other species by the sudden environmental change accompanying intense harvesting (leaf loss, stem dieback, E. Farinosi, personal observation).

Alternatively, decreases in American beech recruitment relative to sugar maple following harvest has been documented in other regions (Angers et al., 2005; Nolet et al., 2008; Danyagri et al. 2019); compared to these studies, the more intense overstory harvests conducted in this study could have further exacerbated interspecific competition at the expense of beech.

3.5.4 Deer browsing

Deer browsing pressure had a modestly negative effect on yellow birch stocking six-years post-harvest; similar patterns were observed for sugar maple, red maple, and northern red oak, but more variance was ultimately explained by pre-harvest stem densities than by the index of browsing pressure, and the term was not retained in final models. Conversely, browsing pressure was positively associated with American beech, ironwood, and *Rubus* stocking (Tables 3.1, 3.2). These divergent responses to browsing damage are consistent with known ungulate browsing patterns: species such as maples, red oak and yellow birch are selectively browsed, whereas ironwood is less palatable, and beech is largely avoided (Stoeckeler et al., 1957; Sanders et al., 2023).

Importantly, the fact that browsing was only a modestly negative predictor for early post-harvest stocking of palatable species does not necessarily imply browsing is unimportant in shaping forest regeneration outcomes. Rather, it may hint at a legacy effect: the cumulative impact of chronic browsing over time may have already altered pre-harvest regeneration layers, such that its effects are embedded in the structural conditions that strongly predict early stocking outcomes. This could also explain why beech, ironwood and *Rubus* stocking was positively associated with browsing pressure – not because browsing directly promoted their recruitment, but because browsing suppressed more palatable species, leading to increased recruitment rates of less palatable species (Richards and Farnsworth, 1971; Bradshaw and Waller, 2016; Sanders et al., 2023). Notably, stocking of additional species may have also been influenced by browsing pressure (or other variables), but low abundance or inconsistent occurrence across sites may have limited the ability to detect clear relationships.

3.5.5 Management Implications

These results clearly demonstrate that early post-harvest stocking outcomes can be predicted with relatively high confidence based on three factors: pre-harvest stand structure, harvest intensity, and local deer browsing pressure. Importantly, all three are variables that forest managers can influence through silvicultural planning.

For many key shade-tolerant and midtolerant NHF species, the state of the advance regeneration layer is the primary determinant of early stocking outcomes, regardless of harvest intensity or post-harvest deer browsing pressure. In managed NHF lacking sufficient advance regeneration, new management approaches will likely be required to promote desirable advance regeneration layers. First, prescriptions should prioritize retention of canopy species diversity while simultaneously bolstering residual tree vigor (e.g., through crown competitor removal) to enhance seed production. Second, increasing the intensity of partial cutting is likely to promote vigorous, large-statured regeneration via increased light availability over extended time periods post-harvest – conditions that are likely to improve resilience to browsing damage. Third, managers might also consider expanding the spatial scale of partial harvesting practices, applying treatments across large blocks simultaneously to dilute browsing impacts and reduce repeated damage to seedlings in the browsing zone (Royo et al., 2017; Walters et al., 2020b).

Building on earlier findings that greater harvest intensity promotes shade-intolerant species (Chapter 2), these results demonstrate that in the absence of advance regeneration, early post-harvest increases in diversity may not include appreciable stocking gains for desirable shade-tolerant and midtolerant species. However, growing environments created by early-successional species may facilitate gradual ingress of shade-tolerant and midtolerant species given adequate seed sources are present (Leak, 2005).

Nonetheless, combined legacies of low-intensity partial harvesting and persistent deer browsing damage in some stands/regions may have created stand conditions that are difficult to overcome (Côté et al., 2004; Matonis et al., 2011; Henry et al., 2023). In stands where canopy diversity is low, advance regeneration layers are depauperate or dominated by undesirable species, and recent prescriptions focused on improving seed sources and increasing partial harvest intensity have largely failed to produce desirable regeneration outcomes, artificial regeneration should be considered. As planting and protecting trees from browsing damage at management scales is cost prohibitive, targeted low-density plantings of species that play outsized ecological roles such as oaks (e.g., hard mast production) and conifers (e.g., mast and heterogeneous stand structure) may be more feasible. Other options could include direct seeding (Farinosi, Chapter 5), or, in extreme cases, partial stand conversion to conifer plantation (e.g., red pine) for the next rotation in order to create more favorable establishment conditions for NHF species beneath those canopies (Vander Yacht et al., 2023).

CHAPTER 4:

LARGE-DIAMETER SUGAR MAPLE DENSITY DRIVES SEEDLING PRODUCTION: IMPLICATIONS FOR NORTHERN HARDWOOD FOREST MANAGEMENT

4.1 Abstract

Seed production generally scales with tree diameter, thus retaining larger trees following harvests may improve natural regeneration outcomes. Here I examine relationships between canopy tree diameter/density, seed production and first-year seedling density following a mast year for sugar maple (*Acer saccharum* Marsh.), the dominant species and management focus in northern hardwood forests (NHF). In 60 NHF stands distributed across the central Upper Peninsula, Michigan, USA, I surveyed seed production (1 m^2) and first-year seedling density (21.07 m^2) at the center of a 40 m radius plot, in which the distance and diameter of all canopy sugar maples > 25 cm dbh was measured. I then examined spatial patterning and relationships between seed, seedling and canopy tree parameters, and related seedling density to both canopy sugar maple density (e.g., ∑counts, ∑BA) and diameter:distance indices (e.g., $\sum \text{diameter}^2/\text{distance}$) for different diameter classes. Finally, I interpreted the results of the seedling count versus stem diameter/density analysis in the context of canopy sugar maple diameter distributions for a separate data set consisting of 126 managed NHF stands across northern Michigan.

Viable seed and first-year seedling densities exhibited a strong linear relationship ($R^2 = 0.71$, $p < .0001$), predicting 7% of viable seed became seedlings, though inter-stand variation was substantial. Landscape patterns in seed and seedling density were apparent, and deviations in seedling density from the predicted viable seed versus seedling density relationship revealed

increased seedling establishment from southern to northern latitudes. Among tested expressions of canopy sugar maple density, simple counts of stems > 40 cm dbh related most strongly to seedling counts, and this relationship was strongest for the 40 m radius ($R^2 = 0.145$, $p = 0.0025$) plot size compared to smaller radii. Landscape-scale spatial patterning of > 40 cm dbh sugar maple densities was weak and didn’t match patterns of seed or seedling density, indicating the size and density of large trees and unquantified spatially varying factors interact to affect seed and seedling density. Among the 60 study sites, densities of trees > 40 cm dbh ranged from 0 to 88 ha^{-1}, with corresponding predicted seedling counts ranging from 38,355 to 354,364 ha^{-1} respectively. In comparison, the median density of stems > 40 cm dbh for the additional 126 managed NHF stands was 28 ha^{-1}, suggesting low densities of large diameter sugar maple could constrain advance regeneration establishment in many managed NHF stands. Management changes such as retaining higher densities of > 40 cm dbh trees may increase seedling establishment. However, many factors affect seedling establishment and seedling-to-sapling transitions (e.g., deer browsing pressure, low light environments), which ultimately shape regeneration outcomes.

4.2 Introduction

Tree species often exhibit minimum size thresholds for seed production (Thomas, 1996; Wright et al., 2005; Bronson, 2020), above which seed output positively associates with increasing size (Greene and Johnson, 1994; Nygren et al., 2017; Minor and Kobe, 2019). Sugar maple (*Acer saccharum* Marsh.), the dominant species in northern hardwood forests (NHF), follows this pattern (Minor and Kobe, 2019). NHF cover approximately 20 million hectares from Minnesota to the Canadian Maritimes (Rogers et al., 2022), and are predominately managed using selection silvicultural systems, which are designed to promote the regeneration of economically valuable sugar maple and other shade-tolerant species (Kern et al., 2014; Nyland, 2016).

Selection systems typically involve partial harvests every 10 – 20 years, with individual dispersed trees removed across all size classes, including all or nearly all trees above a designated maximum diameter. These systems rely on natural regeneration, with new cohorts assumed to recruit from seedling banks (Marks and Gardescu, 1998) into the sapling layer and ultimately into mature canopy classes over successive entries. Early management guidance for selection management developed by Arbogast (1957) suggested all trees > 61 cm (24 in) dbh should be harvested, with trees 41 – 61 cm (16 – 24 in) dbh considered optimal size for sawtimber. However, shifting markets and mill specifications now allow for sawlogs as small as 25 cm (10 in) dbh (Dan Heckman, Michigan Department of Natural Resources, personal communication). This shift may be exerting downward pressure on the residual density of large-diameter sugar maple trees in managed stands, potentially reducing seed inputs and thereby limiting seedling establishment.

A small number of studies have examined the relationship between sugar maple diameter and seed production. Minor and Kobe (2017) found the probability of seed production reaches 0.5 at approximately 24 cm dbh (estimated from graph by E. Farinosi), which aligns with the findings of Clark et al. (2004). These studies also report increased seed production with further increases in diameter, though the relationship is modest – possibly due to the underrepresentation of large-diameter (e.g., > 40 cm dbh) trees in these studies. If a positive relationship between large-diameter tree density and seed production or seedling establishment exists, then retaining more large-diameter trees could increase the rate of seedling establishment (Nygren et al., 2017).

However, numerous factors aside from tree size are known to influence seed production and seedling establishment, potentially obscuring the direct effects of proximate seed sources. Seed production varies among individual trees irrespective of diameter (e.g., super-producers; Minor and Kobe, 2017), interannually due to masting cycles (Garrett and Graber, 1995; Graignic et al., 2014; Cleavitt and Fahey, 2017), with soil resource availability (Cleavitt et al., 2011; Halman et al., 2013) and with weather patterns and climate regimes (Scott and Huff, 1996); interactions between these biotic and abiotic factors further complicate seed production processes. Furthermore, seed-to-seedling transitions may be influenced by pathogens or predation (e.g., seed predation by small mammals, Hsia and Francl, 2009; seedling mortality caused by fungi, caterpillars or small mammals, Cleavitt et al., 2014), competition or allelopathy from understory vegetation (e.g., *Carex pensylvanica,* Powers and Nagel, 2009; Randal and Walters, 2019), soil texture (MSU Extension, 1981), and microclimatic stresses such as early-spring freeze-thaw cycles (Guiden et al., 2019) and late-spring drought – both of which may be exacerbated by a reduced winter snowpack (Wilson et al., 2020).

Notably, the effects of these factors may vary spatio-temporally at local to regional scales. For instance, the density, distance and diameter of individual seed-bearing trees (Ribbens et al., 1994; Nathan and Muller-Landau, 2000) can strongly influence seed rain and thus seedling densities at local scales (i.e., 0 – 100 m). In contrast, mast events occur irregularly and can vary at both coarse (100+ km, Graignic et al., 2014) and fine (4 – 10 km, Masaki et al., 2020) spatial scales. Patterns of winter precipitation – critical for spring soil moisture recharge – also show regional variability (Scott and Huff, 1996).

In this study, I evaluated local (plot-scale) relationships between canopy sugar maple size and density, seed production and first-year seedling establishment, as well as regional-scale spatial patterning in these parameters and their relationships. Notably, the autumn preceding the first-year seedling census was a strong mast year for sugar maple across the central Upper Peninsula of Michigan, USA, confirmed by survey data (stand mean = five million seeds ha^{-1}) and documented by other researchers across the greater region (southeastern Ontario, MacMillan and Aarssen, 2017). While my primary focus is on local tree size and density effects, I also examined regional trends in seed and seedling production and considered potential mechanisms underlying observed spatial variation. Using data on seed/seedling density and canopy tree size/density (i.e., stems > 25 cm dbh within 40 m of seedling survey plots) from 60 managed and unmanaged NHF stands (*60Data*), I tested the following predictions:

1) Seed and seedling density will be positively related, though substantial inter-stand variation will be observed due to unquantified factors (e.g., seed predation, microenvironment, weather/climate). However, variation in seed density, seedling density, and the residuals of the seed-seedling relationship will not exhibit strong spatial patterning across the relatively small 1.7-million-hectare study region.
2) Seedling density will be positively related to the density of canopy sugar maple trees (i.e., > 25 cm dbh), with relationships strengthening when restricted to progressively larger trees (e.g., > 30 cm, > 35 cm, etc.). Furthermore, these relationships will be stronger for tree density parameters that are restricted to (or weighted more heavily in favor of) trees closer to seedling plots (e.g., < 35 m, < 30 m, etc.). Assuming broadly

similar management practices across the study area, no spatial patterning of canopy tree size/density is expected.

3) When interpreted in the context of modeled seed-seedling relationships, canopy sugar maple size/density data from 126 managed stands (*126Data*) from across northern Michigan will indicate some stands are characterized by low and potentially seedling-limiting densities of large-diameter sugar maple. As with earlier predictions, spatial patterning is not expected, given broad consistency in management over the last six decades.

4.3 Methods

4.3.1 Design and data collection

In November 2013 I identified 68 NHF stands in the central Upper Peninsula of Michigan with the aid of inventory data and personnel from the Michigan Department of Natural Resources and Plum Creek Timber Company. All stands were either managed for sawtimber with partial cutting systems or were not actively managed, and were selected to represent a broad range of mature tree diameters and densities. This dataset is hereafter referred to as the *60Data*, reflecting the number of sites at which both seedling density and 40 m radius canopy tree data were successfully collected.

At each site, I established two adjacent 1.83 m (6 ft) radius circular plots for tallying first-year sugar maple seedlings, totaling 21.04 m^2 per site. I established two census plots, as I originally designed the study to incorporate examining seedling mortality and associated factors, with one of the two plots supplemented with seed to assure I had sufficient seedling establishment on all sites. However, the supplemental seed was nonviable, and there was no statistical difference in seedling numbers between supplemented and natural plots (ANOVA, F ratio 0.0007, p > F = 0.9791). As such, data from both plots were pooled for all analyses in this chapter.

To estimate seed production, I established a 0.57 m radius (1 m^2) circular plot immediately adjacent to the seedling census plots. All contents of the leaf litter layer (leaves, fine branches, seeds) in the plots were collected in early Winter (December 2013) and transported to Michigan State University; sugar maple seeds were then separated from other materials. Each seed was dissected to determine the proportion of filled versus unfilled seeds. From this I developed two seed production estimates: total seed and viable seed.

To estimate canopy tree size and density I measured the diameter and distance from plot center of all living sugar maple trees > 25 cm dbh within a 40 m radius of the three-plot centroid. While there were other species in every stand, only sugar maple stems were quantified. Based on stand inventory data and field observations, sugar maple accounted for > 50% of stems in all stands, and > 75% in most.

In 2014, first-year seedling densities were assessed at three time points: early June, mid-July and September. Seedling counts were highest in June and lowest in September (data not shown); June values are used for all analyses in this report aside from an examination of late season seedling mortality. Mature tree data could not be collected for seven stands due to harvesting operations or inaccessibility, and seed/seedling density data were missing from one additional site. As a result, sample size (n) ranged from 60 to 67 stands depending on the specific analysis.

4.3.2 Analysis

Relationships between seed production and seedling density in the *60Data* were evaluated with several candidate models. Exploratory analyses revealed a linear bivariate relationship, but exhibited heteroscedasticity and a right-skewed distribution. Data transformations (e.g., $\text{Log}_{10}+1$) were explored but created novel distribution issues. Both standard least squares and generalized linear regression models with negative binomial and Poisson distributions were assessed using JMP 17 Pro (JMP, 2023). Standard least squares models using untransformed data were ultimately selected, as they provided the best overall fit and residual behavior relative to alternatives. Stand-level residuals of the seed vs. seedling relationship (i.e., stands with more or fewer seedlings than predicted for a given level of seed input) were also evaluated. Due to heteroscedasticity, deviations were expressed as a percentage of the predicted value (e.g., site *x* produced 30% more seedlings than predicted by the model fit to all sites).

I examined relationships between sugar maple canopy tree density and seedling counts using generalized regression models with a negative binomial distribution. Multiple candidate expressions of canopy tree density were tested by comparing their relationships with seedling counts using both the full canopy tree data set and for both tree diameter- and distance (plot radius)-restricted data sets (see further). Canopy tree density expressions included summed stem counts and summed basal area within the 40 m radius plot. I also evaluated indices that incorporated both diameter and distance of trees from the three-plot seedling survey centroid; these indices gave greater weight to larger and closer trees. These indices included $\sum$count/d, $\sum$count/$d^{1/2}$, $\sum$diameter (or BA)/d, and $\sum$diameter(or BA)/$d^{1/2}$.

To assess the influence of canopy tree diameter on tree-seedling relationships, I constructed diameter-restricted subsets by progressively excluding smaller trees in 5 cm dbh increments (e.g., trees > 30 cm, > 35 cm, etc.). Although I did not expect large trees to be poor seed/seedling producers, I also tested the reverse scenario by excluding the largest trees (e.g., all trees < 60 cm, < 55 cm, etc.), and also evaluated combinations of large diameter and small diameter exclusion.

To examine spatial patterning in seed and seedling density, stand-level deviations from predicted seedling values, and canopy tree size and density, spatial autocorrelation analyses were conducted in ArcGIS Pro 3.3 (ESRI 2023). Global Moran's I tests (Ord and Getis, 1995) were used to determine if spatial autocorrelation was present within the study area; results indicated highly significant spatial autocorrelation was present across a wide range of fixed distance bands (i.e., the radius of the local neighborhood response values used to detect spatial relationships) for all variables of interest. The Incremental Spatial Autocorrelation tool was then used to determine the distance band that maximized spatial autocorrelation results (e.g., z-scores, p-values) for each parameter (see further). Hot Spot Analysis was then conducted, which identifies clusters of sites that have significantly higher or lower response values than expected under a random spatial distribution. This analysis generates a Getis-Ord Gi* statistic (Getis and Ord, 1992) for each site that includes a z-score, a p-value and a confidence level bin (i.e., 90%, 95% or 99%) that are used to classify each site as part of a high-value cluster, low-value cluster, or not significant. Hot Spot Analysis requires the user to select a "Conceptualization of Spatial Relationships" method; I selected "Zone of Indifference", which combines fixed and inverse distance weighting methods (ESRI, 2023). This method was selected because I had no reason to expect *a priori* that a fixed or inverse distance reflected any environmental or biological mechanism; rather, results from the Incremental Spatial Autocorrelation tool informed distance band selection. A mean distance band of 37,800 m was used for the *60Data* parameters, while 61,000 m was selected for the *126Data* (see further). I report both statistically significant results from the Hot Spot Analysis and spatial trends that were visually evident but not statistically significant. Maps depicting various stand-level response values and results of spatial analyses were made using the Graph Builder function in JMP 17 Pro (JMP, 2023).

4.3.3 Additional data set

An additional dataset was used to evaluate landscape-scale stand densities of canopy trees in the size classes identified in the *60Data* as important for seed and seedling production. This dataset included 126 managed NHF stands with a history of partial harvesting over the last 60 years. These stands were drawn from a larger set of 140 stands comprising another study (Walters et al., 2020b; Henry et al., 2021; Henry and Walters, 2023b); I excluded stands where red maple – rather than sugar maple – was likely the dominant successional climax species (Burger and Kotar, 2003). All stands were considered ready for partial harvest by standard single-tree selection criteria (i.e., > 23 m^2 ha^{-1} BA and well stocked in sawtimber classes; Arbogast, 1957). Stands were owned and managed by either the State of Michigan (n = 112) or private forest industry (n = 14). Within each 30 ac (12.1 ha) treatment block, I established a systematic 25-point sampling grid (Chapter 2, Figure 2.1). At each point, I surveyed all sugar maple trees > 25 cm dbh within a 6 m radius circular plot (113 m^2), resulting in 2825 m^2 of sampled area per stand.

4.4 Results

4.4.1 *Density and spatial patterning of seed production and first-year seedlings*

In managed and unmanaged NHF stands in the central Upper Peninsula (*60Data*), total and viable seed densities, viable seed proportion, and first-year seedling densities were generally high, but exhibited substantial inter-stand variation (Figure 4.1). The densities of seeds and seedlings were highly right-skewed; relatively few stands had very high values. Conversely, viable seed proportion was approximately normally distributed, with a median value of 0.345 (Figure 4.1). At one site, litter samples contained no viable seeds (0 of 2 total seeds in collected leaf litter), and at eight sites I sampled no seedlings (21.04 m^2 sampled) despite sampling viable seed (1 m^2 sampled) on seven of those sites (range: 6 – 76 viable seeds).

Landscape-scale spatial patterns in seed and seedling density were evident (Figure 4.2). Hot Spot Analysis (Figure 4.2, bottom row) identified a significant cluster of lower total seed density, viable seed density, and viable seed proportion in the northern tier of the study area; viable seed proportion was also significantly lower in the southern tier. A cluster of significantly lower first-year seedling densities overlapped with a lower viable seed proportion cluster in the southern tier (Figure 4.2, bottom row). In contrast, several sites in the middle latitudes of the study area showed significant clustering of higher values for total seed, viable seed, and first-year seedling densities; viable seed proportion and first-year seedling densities were also significantly higher for a cluster of sites located in the extreme east of the study region (Figure 4.2, bottom row). Despite regional trends and significant spatial patterning for seed and seedling parameters, there was strong variation among individual sites in close proximity, particularly at mid- to low-latitude for seeds, and mid-to high-latitudes for seedlings (Figure 4.2, top row).

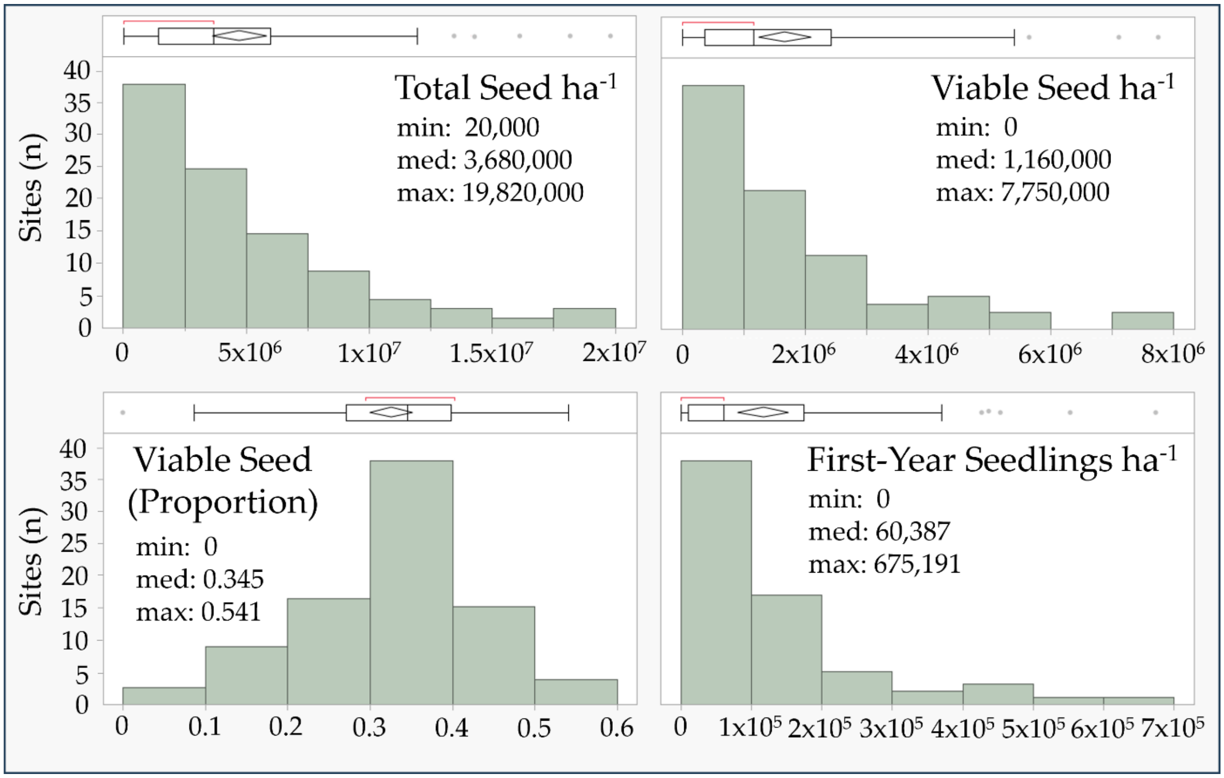

Figure 4.1. Distributions of total seed ha^{-1}, viable seed ha^{-1}, viable seed proportion and first-year seedlings ha^{-1} from managed and unmanaged northern hardwood forest (NHF) stands in the central Upper Peninsula of Michigan (*60Data*). Box plot hinges represent the 25th percentile, median, and 75th percentile; whiskers extend to 1.5 times the interquartile range.

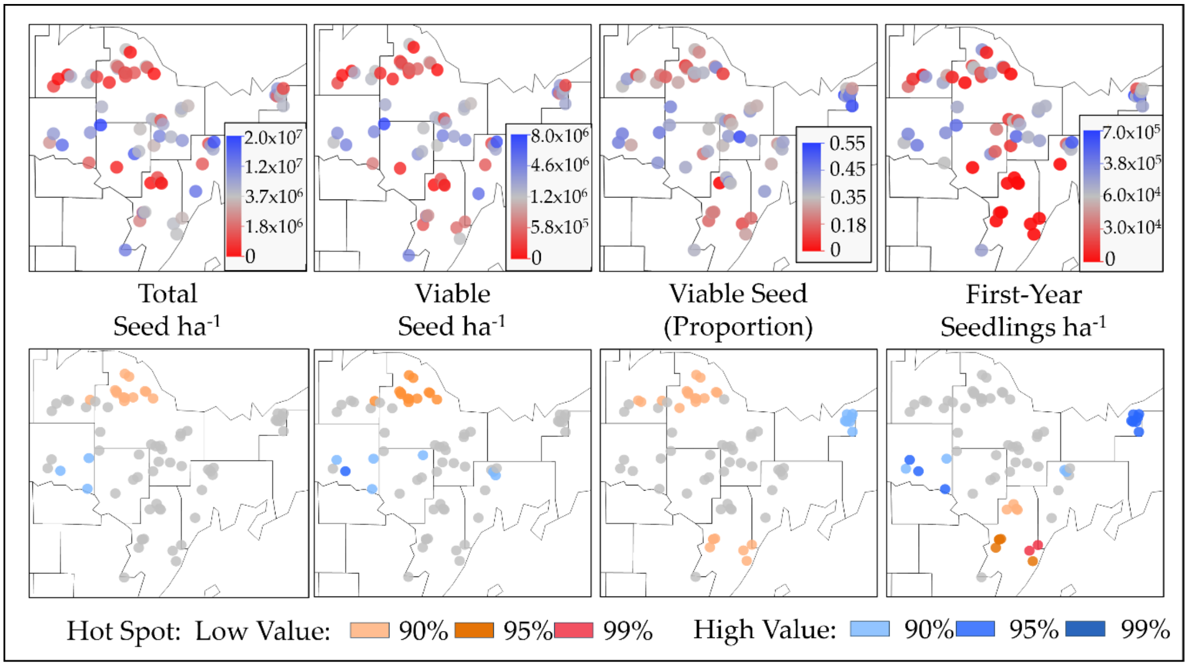

Figure 4.2. Stand-level estimates (top row) and Hot Spot Analysis results (bottom row) for total seed ha^{-1}, viable seed ha^{-1}, viable seed proportion and first-year seedlings ha^{-1} (columns 1-4, respectively) from managed and unmanaged northern hardwood forest (NHF) stands in the central Upper Peninsula of Michigan (*60Data*). The Hot Spot Analysis used a zone of indifference distance band of 37,800 m, corresponding to the mean distance at which Global Moran's I *z*-scores were maximized for *60Data*. High-value clusters are shaded light blue (90% confidence), medium blue (95%), and dark blue (99%); low-value clusters are shaded light orange (90%), dark orange (95%), and red (99%).

4.4.2 Seed production versus first-year seedling density

Viable seed density (sampled in December 2013) was linearly related to first-year seedling density in 2014; however, substantial stand-to-stand variation was evident in this relationship (Figure 4.3). Spatial patterning emerged when comparing observed seedling establishment to the values predicted by the seedling-viable seed relationship (Figure 4.4, left panel). Strong positive deviations (i.e., more seedlings than predicted) occurred primarily in the north, while a distinct region of negative deviations (i.e., fewer seedlings than predicted) was identified in the south (Figure 4.4, left panel). These patterns were detected during Hot Spot Analysis, as was a high-value cluster in the extreme eastern portion of the study area (Figure 4.4, right panel). Nevertheless, inter-stand variation among nearby sites was apparent, particularly at middle to high latitudes (Figure 4.4, left panel).

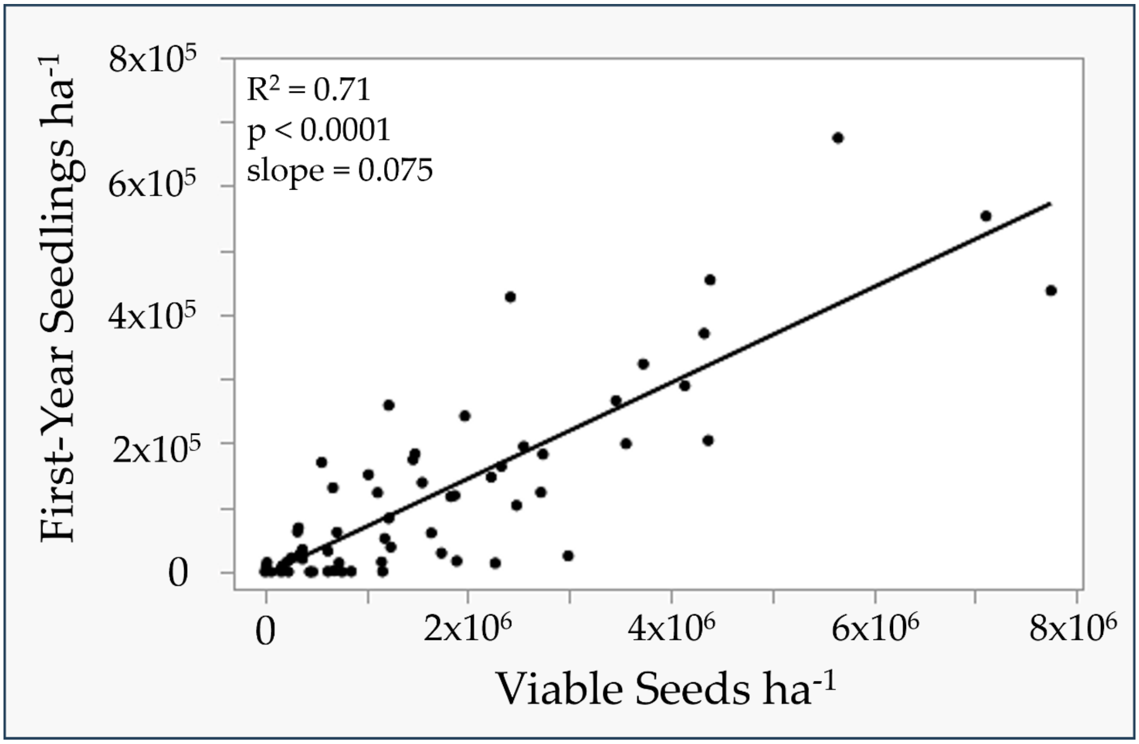

Figure 4.3. The relationship between first-year seedling density and viable seed rain collected the previous fall from managed and unmanaged northern hardwood forest (NHF) stands in the central Upper Peninsula of Michigan (*60Data*). Regression results are based on a least-squares model.

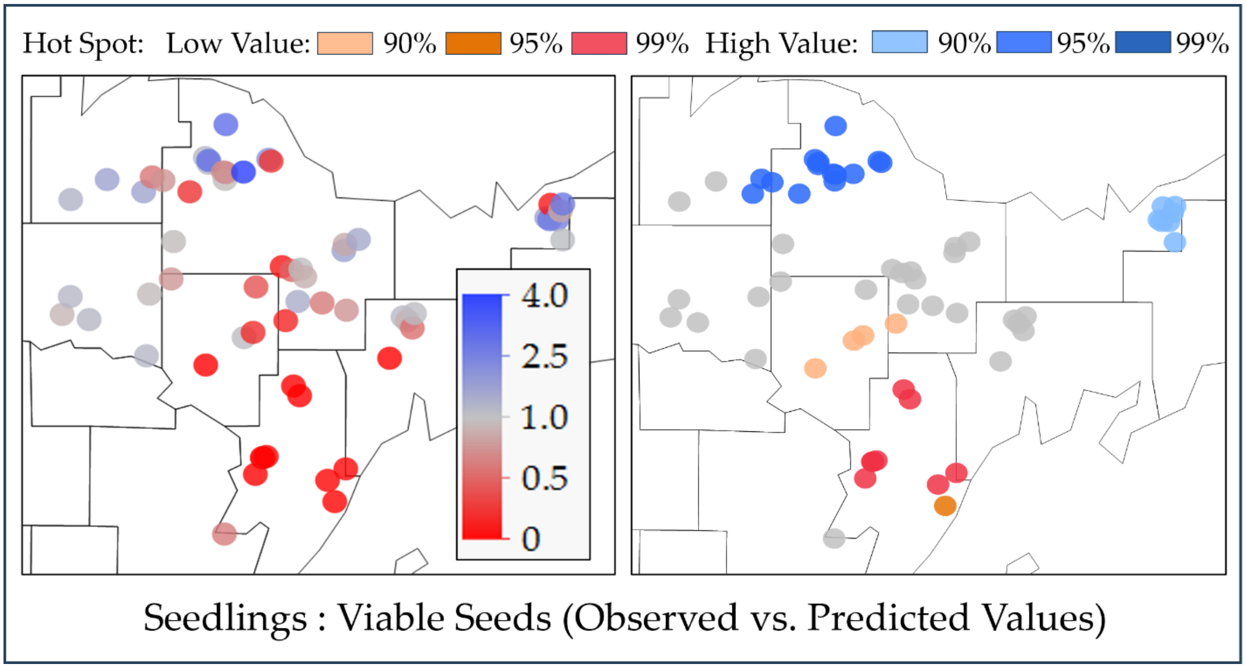

Figure 4.4. Spatial patterning in observed versus predicted seedling establishment based on the relationship between seedling density and viable seed rain (Figure 4.3) from managed and unmanaged northern hardwood forest (NHF) stands in the central Upper Peninsula of Michigan (*60Data*). The left panel shows stand-level ratios of observed to predicted values; the right panel presents results of Hot Spot Analysis. Stands with fewer than 10 viable seeds were excluded. See Figure 4.2 legend for additional Hot Spot Analysis details.

4.4.3 Canopy tree size and density versus seedling density

Despite the strong and functionally direct relationship between tree size/density and seed production, my primary focus is on the relationship between tree size/density and seedling density. This emphasis reflects the much greater sampling intensity for seedlings (21 m^2) compared to seeds (1 m^2) and because seedlings are the focus of management criteria for tree regeneration. Parallel analyses of tree size and density versus seed production yielded similar results (Appendix C, Table C.1).

Maximum explained variance in first-year sugar maple seedling density occurred when canopy tree data were restricted to stems > 40 cm dbh ($R^2 = 0.145$, Figure 4.5); more inclusive data subsets including all trees > 35 cm, > 30 cm, or > 25 cm dbh reduced explanatory power, as did subsets excluding all trees > 40 cm (i.e., classes only including trees > 45 and > 50 cm dbh) (Figure 4.5). Furthermore, iteratively removing largest diameter trees first (e.g., restricted to trees < 60 cm, < 55 cm dbh, etc.) consistently diminished explained variance across all data subsets (e.g., all trees > 25 cm dbh included, trees < 40 cm dbh excluded, etc.) (not shown). As such, the density of sugar maple trees > 40 cm dbh was the strongest predictor of seedling counts in this study. Analyses of total seed and viable seed production relationships with tree size and density were very similar to those for seedlings, with relationships strongest for simple tree counts and peaking at 40 cm dbh ($R^2 = 0.15$ for total seeds, $R^2 = 0.13$ for viable seed; Appendix C, Table C.1).

Compared to simple tree counts, relationships for corresponding size class subsets were weaker for summed basal area of trees (data not shown), suggesting larger trees (e.g., 60 cm vs. 40 cm dbh) do not contribute more to seedling production, at least not proportional to their basal area. Diameter-distance indices (e.g., $\sum \text{diameter}^2/\text{distance}$) were also consistently weaker predictors of first-year seedling density than simple counts of large trees (data not shown). Relatedly, compared to full plot (40 m radius) relationships between > 40 cm dbh tree density and first-year seedling density, relationships for smaller radii subsets weakened with decreasing distance/plot radius for tree density (Figure 4.6), though tree density from 35 m and 40 m radius plots had nearly identical explanatory power ($R^2 = 0.144$ vs. 0.145, respectively).

The relationship between seedling density and the density of sugar maple trees > 40 cm dbh in the *60Data* revealed a clear positive trend across a broad range of tree densities (0 – 88 ha^{-1}), although variation in seedling density was substantial (Figure 4.7, top panel). The fitted function predicted 38,355 first-year seedlings ha^{-1} at 0 trees > 40 cm dbh ha^{-1} and 354,364 seedlings ha^{-1} at 88 trees ha^{-1}. Hot Spot Analysis of > 40 cm dbh sugar maple canopy tree densities showed no statistically significant spatial patterning (Figure 4.8, right panel), though two clusters of three high-density sites were visually evident: one on the western edge of the study area and another in the north-central region (Figure 4.8, left panel). These localized patterns did not align spatially with the broader regional trends in seed or seedling density discussed previously (Figures 4.2, 4.4).

Across 126 managed NHF stands distributed throughout northern Michigan (*126Data*), the median stand density of sugar maple stems > 40 cm dbh was 28 trees ha^{-1}. Only 25% of stands had more than 40 ha^{-1}, while another 25% had fewer than 17 ha^{-1} (Figure 4.7, bottom panel). Hot Spot Analysis identified low-value clusters in the northern Lower Peninsula (all State-owned stands) and the south-central Upper Peninsula (four industry-owned, two State-owned). A high-value cluster was also detected in the central portion of the eastern Upper Peninsula (all State-owned stands) (Figure 4.9).

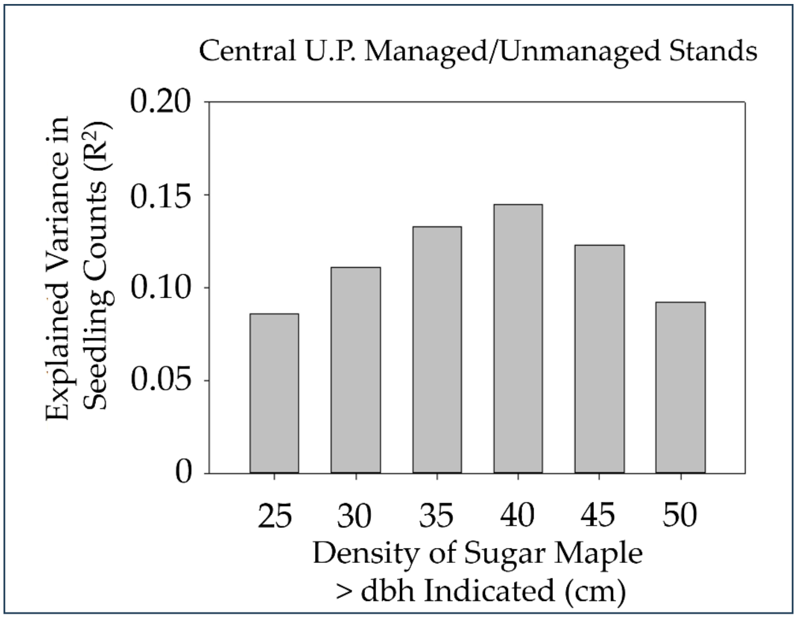

Figure 4.5. R^2 values from generalized regression models relating first-year seedling counts to the density of sugar maple trees > 25 cm dbh in managed and unmanaged northern hardwood forest (NHF) stands in the central Upper Peninsula of Michigan (*60Data*). The corresponding relationship using trees > 40 cm dbh is shown in Figure 4.6.

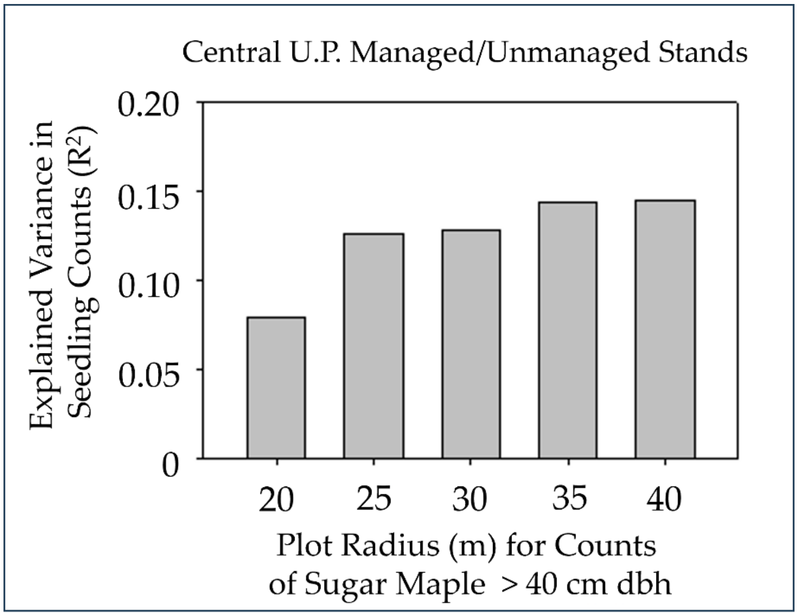

Figure 4.6. R^2 values from generalized regression models (negative binomial distribution) relating first-year seedling counts to the density of sugar maple trees > 40 cm dbh, evaluated for the full plot radius (40 m) and for nested radius subsets < 40 m in managed and unmanaged northern hardwood forest (NHF) stands in the central Upper Peninsula of Michigan (*60Data*).

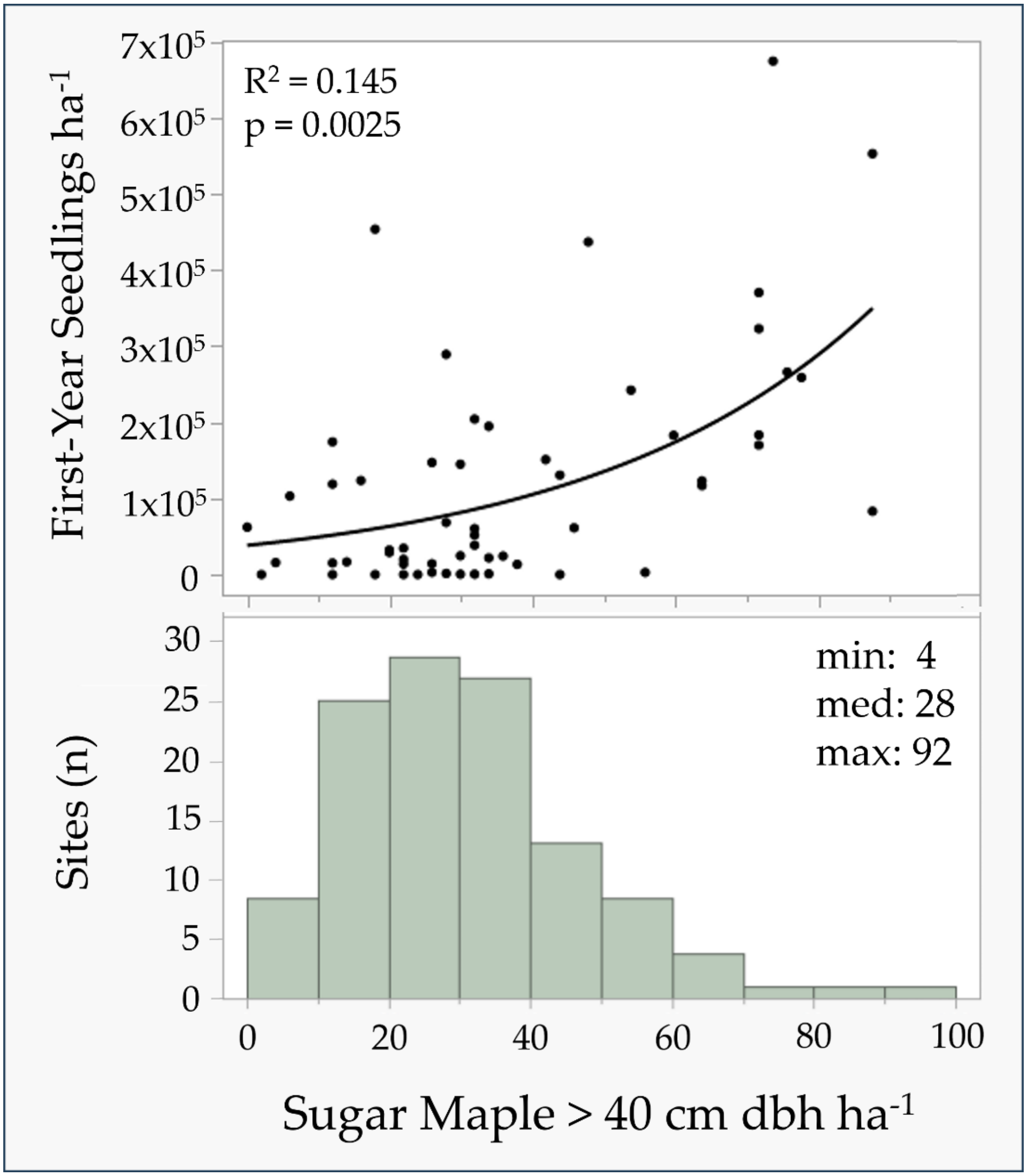

Figure 4.7. Top panel: sugar maple seedling density as a function of > 40 cm dbh sugar maple density in managed and unmanaged northern hardwood forest (NHF) stands in the central Upper Peninsula of Michigan (*60Data*). The model predicts seedlings counts but is presented on a ha^{-1} basis. Bottom panel: density of sugar maples > 40 cm dbh across 126 state- and industry-managed stands (*126Data*).

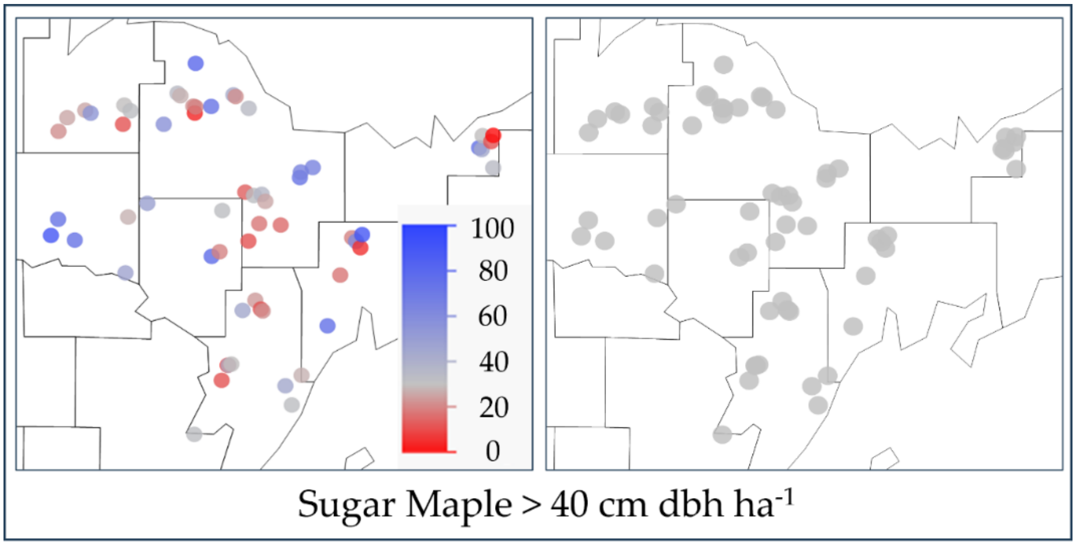

Figure 4.8. Spatial patterning in the density of sugar maple trees > 40 cm dbh in managed and unmanaged northern hardwood forest (NHF) stands in the central Upper Peninsula of Michigan (*60Data*). Left panel shows stems ha^{-1} estimates; right panel shows results of Hot Spot Analysis. No statistically significant spatial clusters were detected. See Figure 4.2 legend for additional Hot Spot Analysis details.

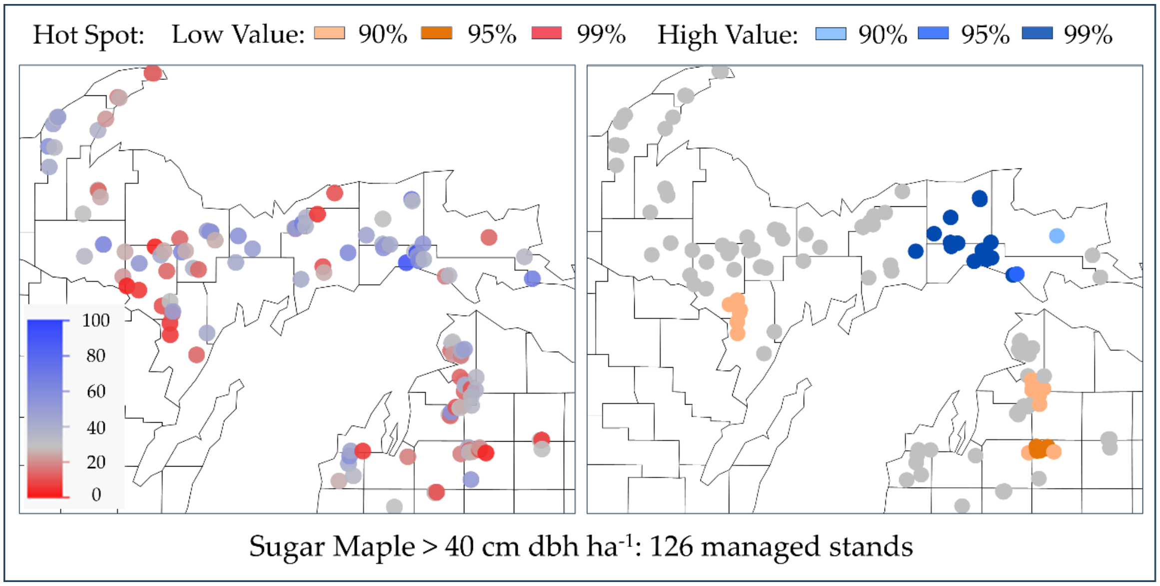

Figure 4.9. Spatial patterning of the density of sugar maple stems > 40 cm dbh across 126 managed northern hardwood forest (NHF) stands spanning northern Michigan (*126Data*). The left panel shows stand-level density estimates (stems ha^{-1}); the right panel presents results of Hot Spot Analysis. The analysis used a zone of indifference distance band of 61,000 m, selected based on the value that maximized the Global Moran's I z-score for *126Data* while accounting for geographical constraints (see Methods). See Figure 4.2 legend for additional Hot Spot Analysis details.

4.5 Discussion

As hypothesized, viable seed density was strongly related to first-year seedling density in mature managed and unmanaged NHF stands of the central Upper Peninsula. This relationship was highly linear with an intercept near zero, indicating the relationship is not seed density-dependent (e.g., no evidence of negative density dependence; Janzen, 1970). Importantly, only a small proportion of sugar maple seeds – seven percent, on average – ultimately became seedlings. Nevertheless, even at this low rate, the exceptionally high seed production observed during the mast year preceding the seedling census (maximum 7.75 million viable seeds ha^{-1}) translated into high seedling densities (maximum 0.675 million ha^{-1}). These results suggest that mast years can contribute substantially to the replenishment of understory seedling banks (MacMillan and Aarssen, 2017).

I hypothesized that seed and seedling variation would not show spatial patterning across the study area; however, strong spatial patterning was observed. While I lack direct evidence for underlying mechanisms, it is likely that multiple, regionally varying factors may be driving these spatial patterns. Although this study was relatively limited in extent (1.7 million ha), masting is known to vary spatially at both coarse (> 100 km) and fine (4 – 10 km) scales (Graignic et al., 2014; Masaki et al., 2020). Another potential driver is snowpack depth, which was greatest in the northern portion of the study area. Deep snowpacks enhance spring soil water recharge and have been associated with increased soil moisture into the early growing season (Wilson et al., 2020), which may improve late spring germination and early seedling establishment. This could help explain why northern stands exhibited disproportionately high seedling establishment rates relative to seed availability.

However, these same northern sites may also be more drought-prone during summer. Shallow, lower water holding capacity soils in the north, relative to the southern Upper Peninsula (MSU/USDA 1981), combined with lake-effect weather patterns that reduce growing season precipitation (Scott and Huff, 1996) may contribute to increased late-season seedling mortality at higher latitudes. These environmental factors could help explain the elevated first-year seedling mortality observed in this portion of the study area (Figure 4.10). Nevertheless, drought conditions do not occur every summer, and the generally more favorable germination and establishment conditions at high latitudes may increase first-year survival and thus better support long-term maintenance of sugar maple seedling banks.

Multiple factors may help explain why southern sites in the study area exhibited the lowest viable seed density, viable seed proportion, first-year seedling density, and seedling establishment relative to model predictions. In terms of seed production, these southern stands frequently lacked appreciable hardwood litter layers and were often dominated by *Carex pensylvanica* – a condition not observed in northern sites (E. Farinosi, personal observation). This vegetation may have made for greater foraging cover for predators such as mice and chipmunks in the weeks prior to leaf litter collection, relative to northern stands where hardwood leaf litter predominated (Ostfeld et al., 1997). Lower-than-expected seedling densities in these southern stands may also reflect a continuation of elevated seed predation after seed sampling, limited snowpacks that increased both the frequency of freeze-thaw events and early spring water stress (Wilson et al., 2020), and belowground competition for water with *C. pensylvanica* (Powers and Nagel, 2009; Randal and Walters, 2019) and other graminoids.

Sugar maple seed production and first-year seedling densities were related to the size and density of canopy sugar maple trees, which was hypothesized. Specifically, the density of trees > 40 cm dbh (15.7 in) within 35 – 40 m of seedling plots best explained variation in seed and seedling abundance. This stand-level approach differs from individual-tree models examining the relationship between diameter and the onset and/or volume of seed production (Clark et al., 2004), yet findings were broadly consistent. For example, my interpretation of Figure 1 in Minor and Kobe (2017) suggests that approximately 50% of sugar maple trees produce seed at 23 cm dbh, and 99% at 32 cm dbh, with seed output increasing with diameter. Thus, it seems reasonable to infer that trees < 25 cm dbh – and even those < 40 cm dbh – may contribute little to overall seed production, particularly on a per-tree basis. Moreover, while a stand with high densities of small trees (e.g., < 40 cm dbh) would produce seed, a similar stand that also contained trees > 40 cm dbh would likely produce substantially more, with practical implications for management.

Summed basal area indices performed poorly relative to simple tree counts, which was counter to expectations. This finding suggests very large trees (e.g., 60 cm vs. 40 cm dbh) may not contribute disproportionally to seedling production, at least in the densities at which they were found in this study. For size-distance relationships developed from canopy tree densities within 40 m, I found no evidence of fine-scale spatial effects on seedling density. Simple tree counts within the 40 m survey radius were the strongest predictors of seedling abundance. However, 35 m and 40 m radius counts yielded nearly identical explanatory power ($R^2 = 0.144$ vs. 0.145, respectively), suggesting trees > 35 m from seedling plots likely had little influence.

Collectively, these results suggest sugar maple canopy densities within 35 – 40 m of seedling plots have the greatest influence on seed availability and seedling density. This was somewhat unexpected, as quantified seed distribution kernels for individual sugar maple trees show the vast majority of seed falls within 20 m of the parent tree (Caspersen and Saprunoff, 2005). One possible explanation is the large variation in seed production among trees of similar size (Minor and Kobe, 2017). Seed from just a few "super-producer" trees within the 40 m radius plots may have disproportionately contributed to both seed rain and seedling establishment. In such cases, simple counts of trees above a minimum diameter threshold may better capture effective seed input than distance-weighted indices. For example, in a diameter:distance index, a large tree close to plot center receives high weighting, but may actually contribute little if it produces few seeds—whereas a super-producer farther away could have a much greater impact despite being down-weighted by distance.

Spatial patterning in the density of large canopy sugar maple trees was not statistically significant, which was expected. This result was expected, given the widespread use of partial-harvesting practices in northern Michigan for many decades. Two small clusters of stands with relatively high densities of large-diameter sugar maple were visible. These stands were either State parks (n = 2) or state-managed stands with no recent harvest history (n = 5); other dispersed stands with high large tree counts also fit this pattern. Importantly, this weak spatial patterning bore little resemblance to the regional-scale spatial trends observed for viable seeds or seedlings. Together, these findings indicate first-year seedling establishment is driven by a combination of tree size and density, along with unquantified factors that vary across the landscape. Given myriad biotic and abiotic factors influencing seed and seedling production, the 14% of variation in first-year seedling density explained by the density of sugar maples > 40 cm dbh – serving as a proxy for potential long-term seed input – is strong evidence for seed/seedling limitation in some stands.

As expected, the majority of state- and industry-managed stands in the *126Data* had densities of > 40 cm dbh sugar maple that fell within a range likely understocked for seed and seedling production objectives. However, I did unexpectedly observe spatial patterning in large-diameter sugar maple density using Hot Spot Analysis. These patterns suggest that managers in the northern Lower and southern central Upper Peninsula may have developed or retained fewer large-diameter sugar maples than those in the central portion of the eastern Upper Peninsula. Stand age is unlikely to explain these differences, as most stands were initiated following high-intensity, exploitative logging in the early 20th century (Henry and Walters, 2023a).

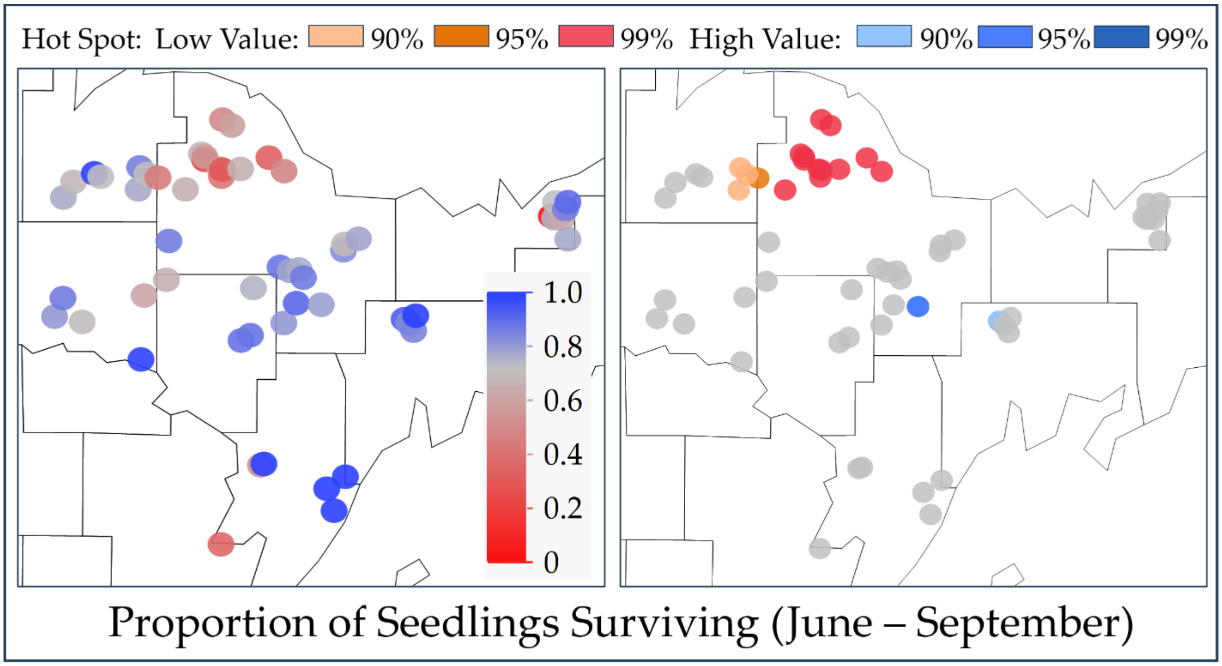

Figure 4.10. Proportion of first-year seedlings recorded in the June census that remained alive in late September across managed and unmanaged northern hardwood forest (NHF) stands in the central Upper Peninsula of Michigan (*60Data*). The left panel shows stand-level proportions; the right panel presents results of Hot Spot Analysis. Refer to Figure 4.2 legend for additional Hot Spot Analysis details.

4.5.1 Forest management implications

These findings carry clear implications for northern hardwood forest management. When relying on natural regeneration, maintaining or cultivating relatively high densities of larger sugar maple trees, particularly those > 40 cm dbh, appears important for maximizing seed production and the subsequent establishment of advance regeneration. Given financial optima for sugar maple logs largely increase with diameter up to approximately 40 – 50 cm dbh (Cockwell and Casperson, 2014; Dey et al., 2017), modifying silvicultural approaches to retain more large-diameter stems than is currently typical should enhance regeneration outcomes without sacrificing economic value.

Emerging evidence suggests high stand basal area following selection silviculture prescriptions can negatively impact sugar maple seedling-to-sapling transitions (Harmala, 2021; Henry et al., 2021). When considered alongside potential seed/seedling limitations, this suggests maintaining lower residual stand densities over successive partial harvests (e.g., harvest to 60 ft^2ac^{-1} residual basal area rather than 80 ft^2ac^{-1}) and retaining higher densities of stems > 40 cm dbh – or those likely to reach this size over multiple cutting cycles – may increase the probability of seedling establishment and sapling recruitment.

Further, transitioning from uneven-aged to even-aged systems in areas where uneven-aged systems have been largely ineffective (Henry et al., 2021, 2023; Farinosi, Chapters 2, 3) could help foster higher densities of large-diameter sugar maple trees. For example, the shelterwood system is designed to retain and enhance the vigor of larger trees in a stand, allowing them to serve as seed sources while also moderating understory microclimate (Nyland, 2016). A shelterwood seed cut ranging from 16 – 24 $m^2\ ha^{-1}$ (40 – 60 $ft^2\ ac^{-1}$) with a minimum residual tree diameter of 40 cm (15.7 in) should provide both sufficient density of large-diameter trees for seed and seedling production (i.e., 74 - 111 trees ha^{-1}) and an understory environment favorable for seedling establishment.

CHAPTER 5:

AUGMENTING TREE SEEDLING DIVERSITY VIA DIRECT SEEDING: THE INFLUENCE OF HARVEST INTENSITY, GRANIVORY, SEED TRAITS, AND SOWING METHOD ON FIRST-YEAR ESTABLISHMENT

5.1 Abstract

Stand-level tree regeneration diversity is often limited by the availability of seed. Direct seeding offers a potential method to enhance tree species diversity and forest resilience to climate change and other disturbances, though its success depends on multiple factors. In this study I assessed seedling establishment following direct seeding of ten tree species in northern Michigan, USA, focusing on the effects of harvest intensity, seed predation, seed size, and sowing method.

Five paired plots (seed predator exclosure vs. uncaged) were established in 18 stands that had been subjected to one of three harvest treatments that differed in disturbance intensity (seed tree > shelterwood > small group selection), and thus in the openness/severity of forest floor environments. A known number of stratified seeds of four native and six assisted migration candidate species were sown in late April and the proportion of seed becoming seedlings was assessed at the end of the first growing season.

Seedling establishment was generally highest in the least intense harvests (small group selection), but results varied by seed size and sowing method. Large-seeded species (e.g., *Carya, Castanea, Juglans, Quercus*), sown 2.5 cm deep, exhibited high establishment that was unaffected by harvest treatment or seed size. Conversely, small-seeded species (e.g., *Betula, Liriodendron, Pinus*), which were broadcast-sown and mixed into the upper 1 cm of soil, had lower and more variable establishment proportions that were sharply reduced in more intense harvests, with

increasing effect size as seed mass decreased. Seed predation significantly reduced establishment in uncaged subplots for all species (range = 35.3% (*Quercus rubra*) to 76.2% (*Pinus strobus*)), but harvest treatment had no practical influence on seed predation rate.

Matching seed traits (e.g., mass) to microsite conditions is critical for species with small energy reserves. Despite predation, establishment in uncaged subplots was relatively high under optimal conditions (6% for *Betula papyrifera* to 67% for *Q. rubra*). These findings suggest direct seeding could be a viable approach to overcoming species diversity challenges caused by local seed limitations in managed NHF.

5.2 Introduction

Promoting tree species diversity is crucial for several forest management goals, including maintaining forest biomass productivity (e.g., carbon sequestration, wood products), providing food and habitat for wildlife, and ecological resilience to landscape-scale disturbance agents (e.g., climate change, Isbell et al., 2015; pest-pathogen outbreaks/introductions, Marini et al., 2022; ungulate browsing, Walters et al., 2020a). Across the maple (*Acer saccharum* Marsh. and *Acer rubrum* L.)-dominated northern hardwood forests (NHF) of the upper Great Lakes region of North America (Rogers et al., 2022), tree species diversity has declined since European settlement (Schulte et al., 2007), and current regeneration layers suggest this trend is likely to continue (Vickers et al., 2019; Henry et al., 2023). These forests are essential habitat for a wide range of species and are a source of high-value forest products that support rural economies, making the declining state of stand-level diversity a significant concern for forest managers.

Multiple factors have contributed to the decline in tree species diversity in NHF. Early indiscriminate logging practices by Europeans removed seed sources from many stands, homogenizing stand composition (Schulte et al., 2007), while several pest and pathogen epidemics have further reduced the number of viable canopy species (USFS Eastern Region Forest Health Conditions Report, 2020). Furthermore, disturbance regimes have largely been shaped by periodic low-intensity partial harvests via single-tree selection silviculture for the past 60 years (Kern et al., 2014). These harvests have been shown to simplify forest structure and decrease tree species diversity (Crow et al., 2002). Meanwhile, regeneration layers are frequently subjected to intense ungulate browsing pressure, often selectively targeting certain species (Walters et al., 2020a). These conditions result in regeneration layers that are often understocked and/or dominated by a limited number of shade-tolerant species that are either resilient to browsing or are rarely browsed (Nyland et al., 2006; Neuendorff et al., 2007), which will eventually degrade canopy species diversity further (Reed et al., 2022). Stressors such as climate change and novel pests and pathogens (Parmesan and Yohe, 2003; Paradis et al., 2008, Rosenberger et al., 2017) threaten to further reduce NHF diversity. Given the critical role that diversity plays in forest resilience, and the likelihood that current management practices will continue to degrade it, reversing the decline in native tree species diversity in managed NHF has become a primary objective for many forest managers.

Increases in NHF tree species diversity could occur via natural regeneration following changes to current disturbance regimes, such as the implementation of silvicultural systems that include greater harvest intensities than single-tree selection. Promising alternatives include large group selection, shelterwood, and seed tree systems, which are currently being evaluated (Walters et al. 2020b; VanderMolen and Webster, 2021; Hupperts et al., 2022; Bartlick et al., 2023; Jones et al., 2023). However, relying solely on natural regeneration to enhance diversity is likely to fail in many instances due to the absence of local seed sources (Willis et al., 2016; Bartlick et al. 2023; Henry and Walters, 2023b), as many species that were historic components of NHF are often locally absent from the canopy stratum, either due to successional trends (e.g., paper birch (*Betula papyrifera*) Marsh., Hlina et al., 2020) or past selective removal (e.g., eastern white pine (*Pinus strobus* L.), yellow birch *(Betula alleghaniensis* Britt.), eastern hemlock (*Tsuga canadensis* (L.) Carr.) (Nyland, 1992; Schulte et al., 2007)). Given the current compositions of many NHF, local reintroduction of native species will likely be necessary in many stands.

In addition to silvicultural practices focused on natural regeneration and the localized reintroduction of native species, forest managers are considering the practice of assisted migration (Iverson et al., 2019; Pike et al., 2020) to foster resilience to climate change. Assisted migration practices in NHF should prioritize species from the adjacent central hardwood biome that fulfill both climate adaptation goals and current or anticipated compromised NHF ecological functions, such as mast provision or conifer structure (Walters et al., 2022).

Incorporating a mix of both native and ecologically supportive non-native tree species into managed NHF following regeneration harvests could help promote functional redundancy (i.e., the presence of multiple species performing similar ecological roles, and should increase forest resilience to future disturbances (Rosenfeld, 2002; Hisano et al., 2018)). Importantly, supplemental tree diversity projects do not need to be implemented at high densities: even the addition of a few successfully recruited stems per acre could help fill underperforming or missing ecosystem functions, while also serving as local seed sources for future regeneration cohorts.

Tree species introduction could occur via planting seedlings and/or saplings or sowing seeds. Planting sapling stock that is large enough to have bypassed critical recruitment bottlenecks such as shrub competition and deer browsing pressure (Walters et al., 2016, 2020a) may have a high per-unit success rate, but high stock and planting costs limit its use (~30 U.S. dollars to grow/outplant a northern red oak (*Quercus rubra* L.) sapling (Jason Hartman, MI DNR, personal communication)). Using smaller seedling stock is less expensive than planting larger stock types, but still includes moderate planting costs. In addition, seedling selection from nurseries may be limited for many species and/or genotypes, as commercial nurseries tend to focus on species that are easy to transplant and commercially popular (Clark et al., 2023) and are unlikely to stock multiple genotypes (e.g., seedlings from multiple hardiness zones or ecoregions, Pike et al., 2020), limiting seedling availability. In contrast, if seeds are available or collectable, direct seeding can be accomplished more cheaply than planting seedlings/saplings for a broad range of species and genotypes.

While direct seeding has potential benefits regarding cost and species/genotype selection, it introduces greater uncertainties in developing established seedlings and ultimately sapling recruits compared to planting. This is primarily because seeds are likely more susceptible to harsh germination and establishment environments, as well as granivory. Many direct seeding attempts have suffered heavy losses to seed predators, particularly small mammals (Bramble and Sharp, 1949; Roe, 1963; Sluder, 1965; Mignery, 1975; Manson et al., 1998; Raymond et al., 2003; Barton et al., 2015). However, some studies have shown that manipulations of overstory and/or understory vegetation densities can lower seed removal rates (Manson et al., 1998; Buckley and Sharik, 2002; George and Bazzaz, 1999; St-Denis et al., 2013; Hall et al., 2019). As such, it is possible that direct seeding coupled with silvicultural treatments (e.g., intense harvesting, removing understory vegetation) could increase the likelihood of acceptable seedling establishment proportions via changing seed predators' perceived foraging risk (Lima and Dill, 1990). However, increasing overstory harvest intensity can produce harsh microclimates that may negatively affect germination and early seedling survival (Gray and Spies, 1996; Prevost et al., 2010; Willis et al., 2015), especially for species that must be broadcast-sown on or near the soil surface.

Further, direct seeding success may vary among species due to differences in key seed traits. Seed mass has been shown to be important via its positive relationships with both seedling establishment (Westoby et al., 1997; Moles and Westoby, 2004) and early seedling survival (Walters et al., 2023) in harsh microclimates. However, while producing larger seeds may confer resilience to abiotic seedling establishment bottlenecks, larger seeds are often heavily consumed by seed predators, particularly small mammals (Ivan and Swihart, 2000; Clotfelter et al., 2007; Falls et al., 2007).

Relatedly, seed traits (i.e., mass) inform operationally-relevant direct seeding methods: Larger seeds are often buried with seed drills or other tools (e.g., nuts and acorns in this study), while small-seeded species are generally broadcast-sown onto recently scarified soil to increase mineral soil contact and soil-seed mixing (e.g., birches, pines, and yellow poplar in this study) (Nyland, 2016). These distinct sowing methods most closely emulate the conditions necessary for optimal establishment outcomes for the respective species.

In this study, I examine how seedling establishment proportions, following operationally relevant direct seeding methods for ten tree species (four native to NHF and six from the central hardwood region, Table 5.1), are affected by harvest treatment, seed predation, species seed size/sowing method and their interaction. I propose the following hypotheses:

1) When considering all species:
    a) Seedling establishment will be lower under more exposed understory conditions created by more intensive harvests (i.e., ST < SH < SG).
    b) Seed predators will reduce seedling establishment (i.e., lower establishment proportion in uncaged subplots), with stronger effects expected under lower harvest intensities (i.e., SG > SH > ST).
2) When considering seed size/sowing method groupings:
    a) Among small-seeded/broadcast-sown species, establishment in caged subplots will be positively associated with seed mass, especially under harsh microenvironments (i.e., ST). However, species with greater seed mass will also experience greater losses to seed predation.
    b) Among large-seeded/buried species, seed mass will not be associated with establishment proportion or seed predation.

Table 5.1. Key characteristics of focal species. Maximum latitude refers to the species' northernmost range in the upper Midwest and into Canada. The latitudinal extent of this study ranged from 44.380 (southernmost site) to 44.476 (northernmost site). Climate adaptation projection scores for northern Michigan are simplified from the USFS Climate Change Tree Atlas (v4.0).

Common Name	Latin Binomial	Maximum Latitude	Seed Mass (g)	Sowing Method	Wildlife Value	Economic Value	Climate Adaptation Projection
Black walnut	*Juglans nigra* L.	44.752	5.5	buried	mast	high	good
Northern red oak	*Quercus rubra* L.	48.621	3.5	buried	mast	high	good
American chestnut	*Castanea dentata* (Marsh.) Borkh.	42.007	3.2	buried	mast	high	na
Pignut hickory	*Carya glabra* (P. Mill) Sweet.	43.669	2.5	buried	mast	moderate	good

Table 5.1 (cont'd)

Bitternut hickory	*Carya cordiformis* (Wangenh.) K. Koch	47.327	2.3	buried	mast	moderate	good
Eastern white pine	*Pinus strobus* L.	50.764	1.9x10^{-2}	broadcast	mast, structure	moderate	fair
Shortleaf pine	*Pinus echinata* Mill.	39.692	1.1x10^{-2}	broadcast	mast, structure	high	fair
Yellow poplar	*Liriodendron tulipifera* L.	43.524	5x10^{-3}	broadcast	mast	moderate	good
Yellow birch	*Betula alleghaniensis* Britt.	48.626	4x10^{-4}	broadcast	mast	high	fair
Paper birch	*Betula papyrifera* Marsh.	54.346	3x10^{-4}	broadcast	mast	moderate	fair/poor

5.3 Methods

5.3.1 Study sites

This study was conducted on 18 NHF sites in the northern Lower Peninsula of Michigan (Figure 5.1); all sites are owned by the State of Michigan and managed by the Michigan Department of Natural Resources. Site quality, an indirect measure of site productivity, was assessed using a habitat classification system that utilizes assemblages of understory herbaceous species as a proxy for soil moisture and nutrient regimes (Burger and Kotar, 2003). All study sites fell into the *Acer saccharum-Fagus grandifolia/Osmorhiza claytonii* or *Acer saccharum-Fagus grandifolia/Osmorhiza claytonii-Caulophyllum thalictroides* categories, the two most productive upland types in the region.

Experimental 12.1 ha (30 ac) harvests were conducted across these stands in Winter 2017/2018 as part of a larger project comparing outcomes of multiple silvicultural systems (Walters et al., 2020b). Six randomly assigned replicates of three distinct harvest treatments (Figure 5.1) were used for this study: the seed tree system (where 6 – 8 canopy trees per acre were retained), the shelterwood system (where 50% canopy cover in evenly spaced trees was retained) and the single-tree/small group selection system (where single dispersed trees and circular groups (0.15 ac, 28 m diameter) of trees were removed (hereafter called small group selection, as only these gaps were utilized here)). In summer 2020, herbicide and scarification treatments were applied to these sites, which killed understory vegetation and exposed bare mineral soil, creating favorable regeneration conditions and a realistic management scenario to examine the efficacy of direct seeding.

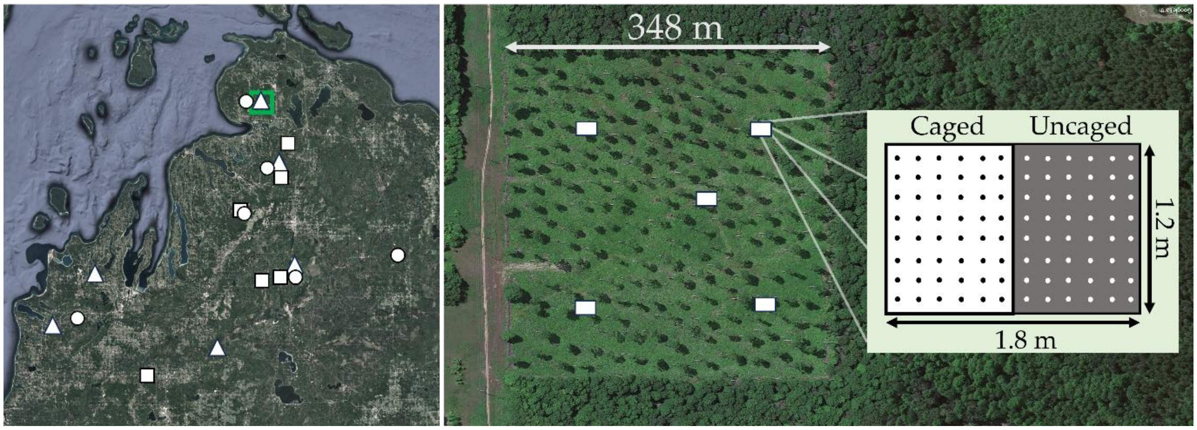

Figure 5.1. Map of study sites and approximate plot locations, with inset illustrating plot design. Each site received a single 12.1 ha (30 ac) overstory harvest treatment (seed tree treatment shown in Google Earth imagery). Circles denote small group selection sites, squares indicate shelterwood harvests, and triangles represent seed tree harvests. Seeds of black walnut, northern red oak, American chestnut and the hickory species were buried to a depth of 2.5 cm at randomly assigned grid-points (see inset); other species were broadcast sown and mixed into upper 1 cm of soil.

5.3.2 *Species selection*

Species studied were deemed good candidates for diversity enhancement and climate adaptation goals as they bolster important ecosystem values in decline in NHF (Table 5.1, Walters et al., 2022). These included five large-seed hard mast producing species with high timber value: northern red oak, black walnut (*Juglans nigra* L.), bitternut hickory (*Carya cordiformis* (Wangenh.)

K. Koch), pignut hickory (*Carya glabra* (P. Mill) Sweet.) and American chestnut (*Castanea dentata* (Marsh.) Borkh.). Apart from northern red oak, which is currently a minor component in NHF, these species are native to southern Michigan and/or the central hardwood biome. Two species that could provide conifer structure and smaller-seeded hard mast were tested: eastern white pine and shortleaf pine (*Pinus echinata* Mill.). Eastern white pine has historically been a minor yet important component of NHF, whereas shortleaf pine is native to the southern central hardwood region and has a northern range limit of southern Ohio. I also included yellow poplar (*Liriodendron tulipifera* L.), a fast-growing early-successional species with a northern range limit of southern Michigan, and yellow birch and paper birch, both of which have declined in the upper Great Lakes region over the last century due to harvest practices (yellow birch, Neuendorff et al., 2007) or successional trends (paper birch, Hlina et al., 2020).

Tree seed for northern red oak, bitternut hickory, pignut hickory, black walnut and yellow poplar was collected from naturally occurring trees in the Lansing, MI area (USDA plant hardiness zone 5); American chestnut seed was provided by The American Chestnut Foundation (zone 6); eastern white pine was provided by the MI DNR (zones 4/5); shortleaf pine (zone 7), paper birch (zone 5) and yellow birch (zone 5) were purchased from Sheffield's seed company (Locke, NY). In fall 2020 seeds were stratified following USFS Woody Plant Seed Manual (2008) guidelines and institutional experience.

5.3.3 Study Design and Implementation

Seeds were sown in field plots in late April 2021. Five plots were established at approximately the same locations on all seed tree and shelterwood sites (Figure 5.1). Due to harvest design, small group selection gaps were not present at analogous locations within the single-tree/small group selection treatment; five gaps were randomly selected from the inner 4.3 ha (10.7 ac) of these sites to match the plot locations in the other two treatments as closely as possible. Importantly, plots were consistently established in the southern portion of each gap just north of the canopy drip line; this was done to minimize gap-position-driven variation in microclimate and resources among gaps and to establish a lower exposure/lower light treatment clearly distinguishable from shelterwood and seed tree treatments. Southern gap locations receive the least amount of growing season solar radiation and likely retain the highest soil water availability among gap positions (Raymond et al., 2006; Prevost and Raymond, 2012).

Prior to sowing seed, each plot was raked to create a uniform and level mineral soil surface. Each 1.2 x 1.8 m (4 x 6 ft) plot was then split into 0.9 x 1.2 m (3 x 4 ft) subplots. In each subplot, ten seeds of each large-seeded species (hickories, oak, walnut, chestnut) were sown approximately 2.5 cm (1 in) below the surface in a grid at approximately 15 cm (6 in) spacing. For small-seeded species, each subplot received 100 seeds of eastern white pine, 50 seeds of shortleaf pine, and approximately 350 yellow poplar, 1500 yellow birch and 1500 paper birch seeds (estimated based on seed weight vs. number relationships), which were broadcast-sown and lightly worked into the upper 1 cm (0.4 in) of the soil with a rake following the sowing of large-seeded species. The assignment of species to the buried or broadcast-sown groups was based on their optimal establishment conditions, which vary due to differences in seed size (USFS Woody Plant Seed Manual, 2008). Following sowing of seeds, one subplot was covered with a 0.6 cm (0.25 in) mesh hardware cloth cage to protect seeds from predators, while the other half remained uncaged (Figure 5.1). Immediately following field sowing, a greenhouse germination trial was conducted for each species to estimate seed viability and germination proportions under favorable conditions (i.e., adequately watered potting soil in moderate light environment).

An initial seedling survey occurred in late June 2021, and a second survey was performed in late September 2021. In addition, plots were visited to check for fencing/seedling damage on two additional dates in July and August. More seedlings of all species in all plots were tallied in September than June. It was clear that many seeds (particularly of small-seeded species) had not yet germinated by the late June survey, thus the September survey was used for all analyses. In September, hemispherical canopy photos were derived from spherical panoramic images taken at a height of 1.5 m (5 ft) with a smartphone (Arietta, 2022) and cover of lower vegetation < 1.5 m (5 ft) tall (including seedlings, herbs and shrubs) was ocularly estimated for each subplot. Total transmission (light) values calculated from hemispherical canopy photos were used as a proxy for germination microenvironment harshness, as increased solar radiation results in higher soil temperatures and lower moisture availability at the soil surface, which has been shown to negatively affect germination and young seedling survival (Caldeira et al., 2013). Percent cover of vegetation < 1.5 m (5 ft) tall was used to estimate the degree to which this vegetation affects light availability for young seedlings, with likely competitive effects in plots with low to moderate solar radiation and potentially facilitative in plots with higher levels of solar radiation (Walters et al., 2016; Walters et al., 2023).

5.3.4 Statistical Analyses

A split-plot design was used for analysis, with the whole plot factor being harvest treatment (fixed, categorical; six replications (sites) per treatment) and the subplot factor being caging status (fixed, categorical; five plots per site), with species (fixed, categorical; ten species) also being considered. The response variable was the proportion of seedlings that successfully established by the end of the first growing season out of the total seed sown in each subplot for each species, and therefore was assumed to follow a binomial distribution. Greenhouse viability estimates could not be used in these analyses due to subplot level establishment occasionally being higher than the greenhouse estimate for many species. Site and plot were treated as random effects in the full model to account for both inter- and intra-site conditions that could affect seedling establishment. Given the non-normal distribution of the proportion data and the incorporation of random effects, generalized linear mixed models were used. A full model was constructed with treatment, caging status, species and their interactions as fixed effects, and site and plot as random effects. Additionally, individual models were fit for each species, which included treatment, caging status, with/without their interaction as fixed effects, and site and plot as random effects. A single model for each species was then selected based on AIC scores, determining whether to include or omit the harvest x caging interaction. Model estimates of establishment as a function of harvest type (limited to caged subplots to isolate harvest treatment effects) and as a function of caging status (to examine seed predation effects) were then compared using Tukey-Kramer post-hoc comparison tests.

Spearman's rank correlations were performed to examine how species' seed kernel mass related to multiple metrics, including caged seedling establishment (i.e., Does seed size affect establishment rates?), environmental reduction (1 - small group selection establishment % / seed tree harvest establishment; i.e., Does seed size affect establishment as harvest intensity increases?) and seed predation intensity (i.e., Does seed size affect seed predation intensity?). Greenhouse germination proportion was used as the denominator for these analyses, as rank correlations relied on model estimates rather than subplot level data. Because sowing method likely confounded these relationships, these analyses were conducted separately within sowing method groups (i.e., buried 2.5 cm vs. broadcast-sown and mixed into upper 1 cm of soil). Finally, generalized regression models with a beta distribution were used to examine the relationship between plot-level light availability and seedling establishment proportions for each species. Statistical modeling was conducted using the betareg package (Cribari-Neto and Zeileis 2010) in R v4.2.2 (R Core Team, 2024) and nonparametric analyses were performed in JMP 17 Pro (JMP, 2023). Analysis of hemispherical canopy photographs for total light transmission was conducted in Gap Light Analyzer (GLA) v2.1 (Frazer et al., 1999).

5.4 Results

Among harvest treatments, I expected understory light levels – and therefore microclimate severity – to be broadly ordered as small group selection < shelterwood < seed tree. I confirmed this ranking with plot level light availability measurements from hemispherical canopy photos: harvest treatment total transmission means were 22.3% (small group selection), 36.4% (shelterwood) and 75.3% (seed tree) (not shown). subplots, suggesting small mammals were the primary seed predators. One uncaged subplot showed uprooting of three established seedlings by an unknown animal, and three caged subplots were destroyed by bears/humans, but no others were disrupted. Descriptive statistics of seedling establishment for all species and treatment combinations are provided in Appendix D (Table D.1).

During site visits, deer and turkey tracks were noted in a small number of subplots, though none of these subplots showed signs of seed excavation or seedling uprooting by these species (e.g., no widespread soil disturbance). However, chewed nut hulls from buried project seed and localized signs of seed excavation were present on every site and in many uncaged

Full model results (Table 5.2) indicated all main effects (harvest, caging status and species) significantly influenced the proportion of seedlings established from seeds, as did the two-way interactions between species and harvest type/caging status ($p < .0001$ for both). Addition of the harvest x caging interaction term improved model fit ($p < .0001$), though Wald Chi^2 values indicated the effect size was extremely small relative to other terms. Interpretation of model coefficients indicated that seed predation intensity was greatest in the shelterwood treatment and least in the small group selection treatment; however, this hypothesis test was insignificant ($p = 0.18$), and no clear rank order could be established from the data. The three-way interaction term was insignificant ($p = .0699$), indicating that differences in the effect of caging status across harvest types did not significantly vary across individual species. Given my interest in individual species responses and the significant two-way interaction of species with harvest and/or seed predation effects, I decomposed the data into species-specific models (Table 5.3). Given weak species-harvest-caging three-way interactions and weak harvest x caging interactions for individual species models (Table 5.3), I focus on species models of harvest and caging effects, but not their combination.

Species models (Table 5.3) indicated that all species sown to 2.5 cm depth, (i.e., black walnut, northern red oak, American chestnut, hickories) had similar establishment proportions across harvest treatments in caged subplots (Figure 5.2). In contrast, the establishment of small-seeded, broadcast-sown species (i.e., yellow poplar, birch, pine) in caged subplots differed among harvest treatments ($p < .0001$, Table 5.3), and were inversely related to harvest intensity as estimated by harvest treatment mean light levels (Figure 5.2). All species models indicated significant differences in establishment proportion between caged and uncaged subplots ($p < .0001$, Table 5.3); establishment in uncaged subplots was invariably lower, with relative establishment reductions (harvest treatments pooled) ranging from 35.3% for northern red oak to 76.2% for eastern white pine (Figure 5.3).

For the broadcast-sown species group, there was a positive relationship between seed kernel mass and establishment proportion in caged subplots (harvest treatment values pooled) for all species, (Spearman's rank correlation: $\varrho = 0.9$, $p = .0374$, Figure 5.4, top panel). Further, when comparing the differences in establishment between environmental extremes (i.e., 1 – (caged seed tree establishment / caged small group selection establishment)) for the broadcast-sown group, larger reductions in establishment were associated with smaller seed kernel mass ($\varrho = - 0.9$, $p = 0.0374$, Figure 5.4, middle panel). These trends were similar in uncaged subplots (Appendix D, Figure D.2). In contrast, there was a positive relationship between seed kernel mass seed predation extent for broadcast-sown species ($\varrho = 0.7$, $p = .1041$, Figure 5.4, bottom panel). For the buried seed group, establishment in caged plots, environmental reduction and seed predation were not associated with seed kernel mass (not shown).

Considerable plot-to-plot variation of light availability within each harvest treatment was apparent (note x-axis treatment ranges in Figure 5.5). When caged establishment proportions for harvest-sensitive species (i.e., small-seeded, broadcast-sown; Table 5.3) were regressed on plot-level light availability (harvest treatments pooled), an inverse relationship was found (Figure 5.5). This relationship reveals that harvest treatments have high spatial heterogeneity in understory light availability and associated microenvironments, with consequences for seedling establishment. In addition, given the continuity of these relationships within and across harvest treatments, these relationships reinforce the notion that differences in treatment mean light environments and associated microenvironments are likely driving differences in seedling establishment across treatments. Adding percent cover estimates for vegetation < 1.5 m tall as an additional factor to these regression models (i.e., establishment proportion as a function of light and % cover) did not explain additional variation (not shown).

Table 5.2. Full results from a generalized linear mixed model testing the effects of species, harvest treatment (three levels), caging status (caged vs. uncaged), and their interactions on the proportion of seedlings established at the end of the first growing season. Species, harvest type, and caging status were included as fixed effects; site and plot were modeled as random effects. Bold p-values indicate statistical significance at level $\alpha = 0.05$.

Factor	df	Wald Chi-Square	Prob > Chi-Square
Species	9	32814.6	**< 0.0001**
Harvest	2	45.7	**< 0.0001**
Caging Status	1	2270.9	**< 0.0001**
Species x Harvest	18	1050.9	**< 0.0001**
Species x Caging Status	9	354.6	**< 0.0001**
Harvest x Caging Status	2	18.1	**< 0.0001**
Species x Harvest x Caging Status	18	27.5	0.0699

Table 5.3. Results of generalized linear mixed models (beta distribution) testing the effects of harvest treatment (three levels), caging status (caged vs. uncaged), and their interaction on the proportion of seedlings established for ten species at the end of the first growing season. Species are ordered from largest to smallest average seed kernel mass. Model selection was based on AIC scores, with only models retaining all main effects considered. Bold p-values indicate statistical significance at level $\alpha = 0.05$.

Species	**Harvest**			**Caging**			**Harvest x Caging**		
	χ^2	**df**	**$p > \chi^2$**	χ^2	**df**	**$p > \chi^2$**	χ^2	**df**	**$p > \chi^2$**
Black walnut	4.65	2	0.0980	60.05	1	**< 0.0001**	-	-	-
Northern red oak	1.75	2	0.4173	228.16	1	**< 0.0001**	-	-	-
American chestnut	0.60	2	0.7394	282.34	1	**< 0.0001**	-	-	-
Pignut hickory	1.60	2	0.4486	134.17	1	**< 0.0001**	-	-	-
Bitternut hickory	2.57	2	0.2763	88.68	1	**< 0.0001**	-	-	-
Eastern white pine	40.87	2	**< 0.0001**	819.66	1	**< 0.0001**	9.21	2	**0.0100**
Shortleaf pine	28.20	2	**< 0.0001**	281.16	1	**< 0.0001**	6.83	2	**0.0329**
Yellow poplar	29.64	2	**< 0.0001**	38.51	1	**< 0.0001**	-	-	-
Yellow birch	91.46	2	**< 0.0001**	205.49	1	**< 0.0001**	-	-	-
Paper birch	84.16	2	**< 0.0001**	509.81	1	**< 0.0001**	11.44	2	**0.0033**

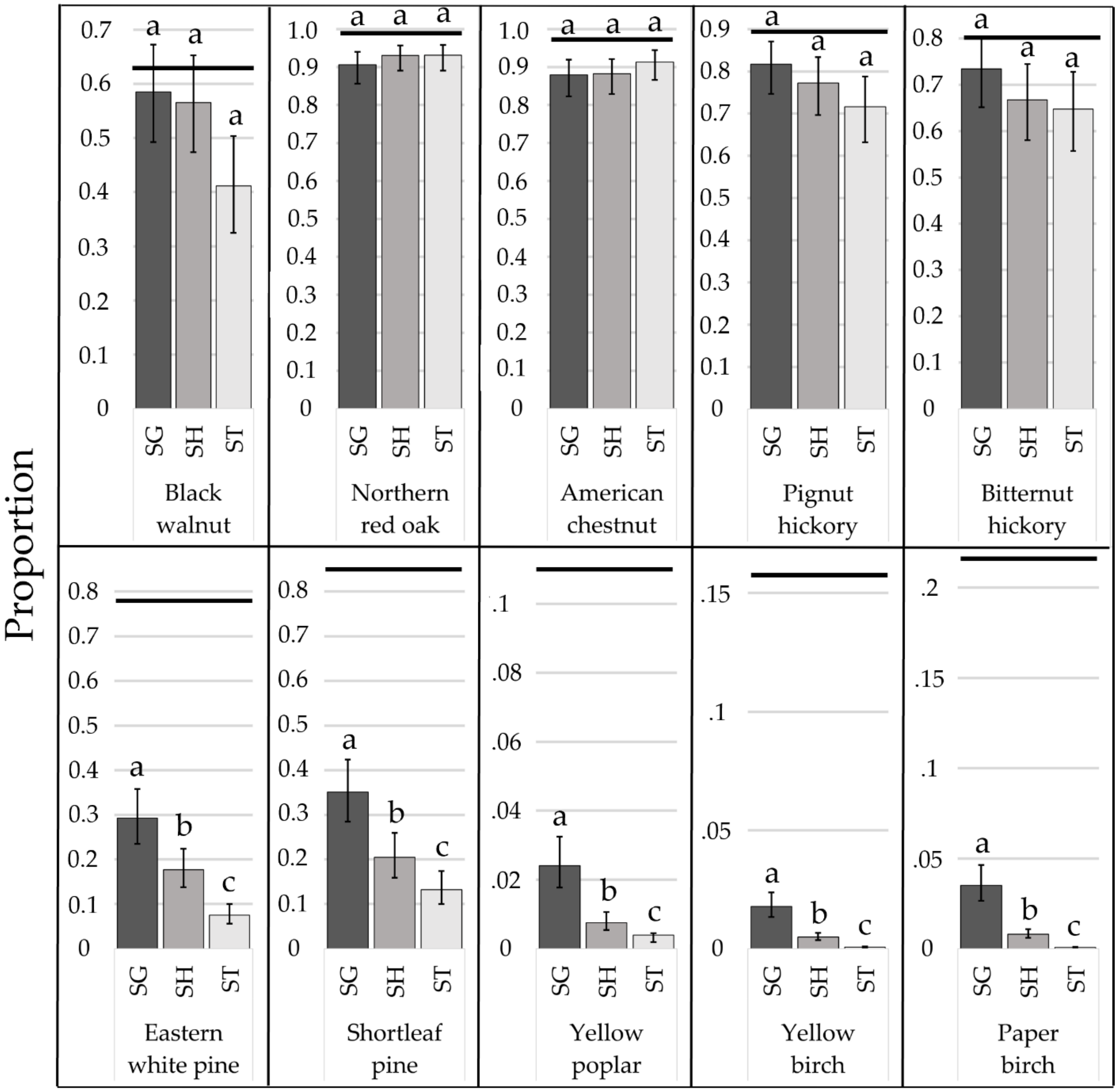

Figure 5.2. Results of generalized regression models (beta distribution) testing the effects of harvest treatment on seedling establishment in caged subplots at the end of the first growing season, with 95% confidence intervals. Harvest treatments include small group selection (SG), shelterwood (SH) and seed tree (ST). The y-axis represents the proportion of seedlings established relative to the total number of seeds sown; the horizontal black bars indicate greenhouse-derived seed viability estimates for each species. Tukey-Kramer Honest Significant Difference (HSD) tests were used for pairwise comparisons within each species panel; treatments sharing a letter are not significantly different at $\alpha = 0.05$. Species are ordered from largest to smallest seed kernel mass. Note species-specific y-axes.

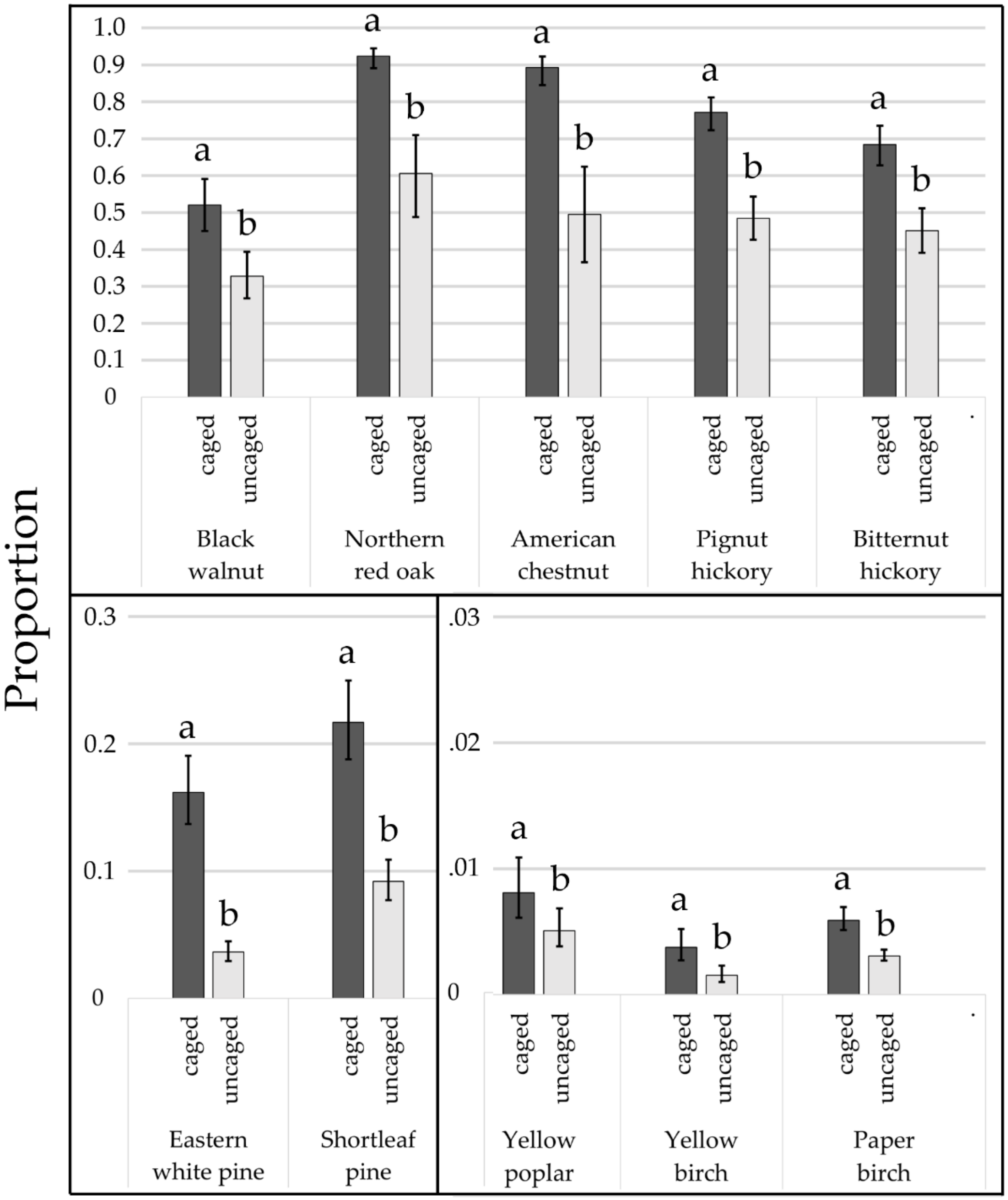

Figure 5.3. Results of generalized regression models (beta distribution) testing the effects of seed protection (caged vs. uncaged) on seedling establishment proportion at the end of the first growing season, with 95% confidence intervals. Harvest treatments were pooled due to weak or non-significant harvest x caging interactions. Tukey-Kramer Honest Significant Difference (HSD) tests were used for pairwise comparisons of caging for each species; treatments sharing a letter are not significantly different at $\alpha < 0.05$. Species are ordered from largest to smallest seed kernel mass. Note three distinct y-axes.

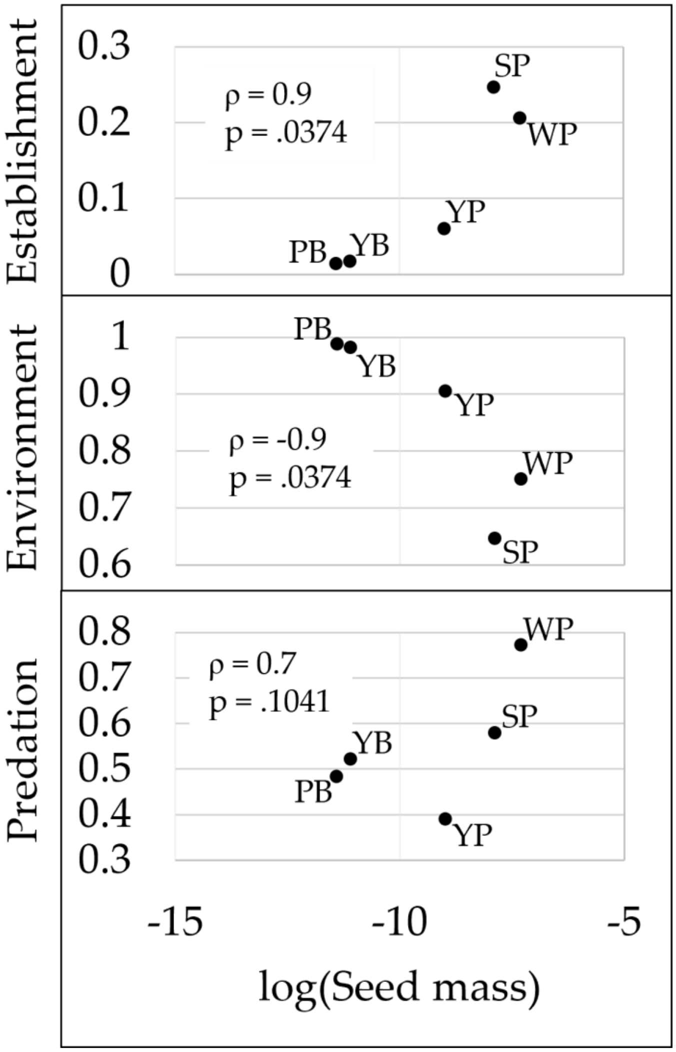

Figure 5.4. Spearman's rank correlations between seed kernel mass of broadcast-sown species and three establishment metrics. Top panel: seedling establishment proportion in caged subplots (harvest treatments pooled). Middle Panel: proportional reduction in establishment between environmental extremes in caged subplots, calculated as 1 – (seed tree establishment proportion / small group selection establishment proportion). Bottom panel: proportional reduction in establishment between caged and uncaged subplots.

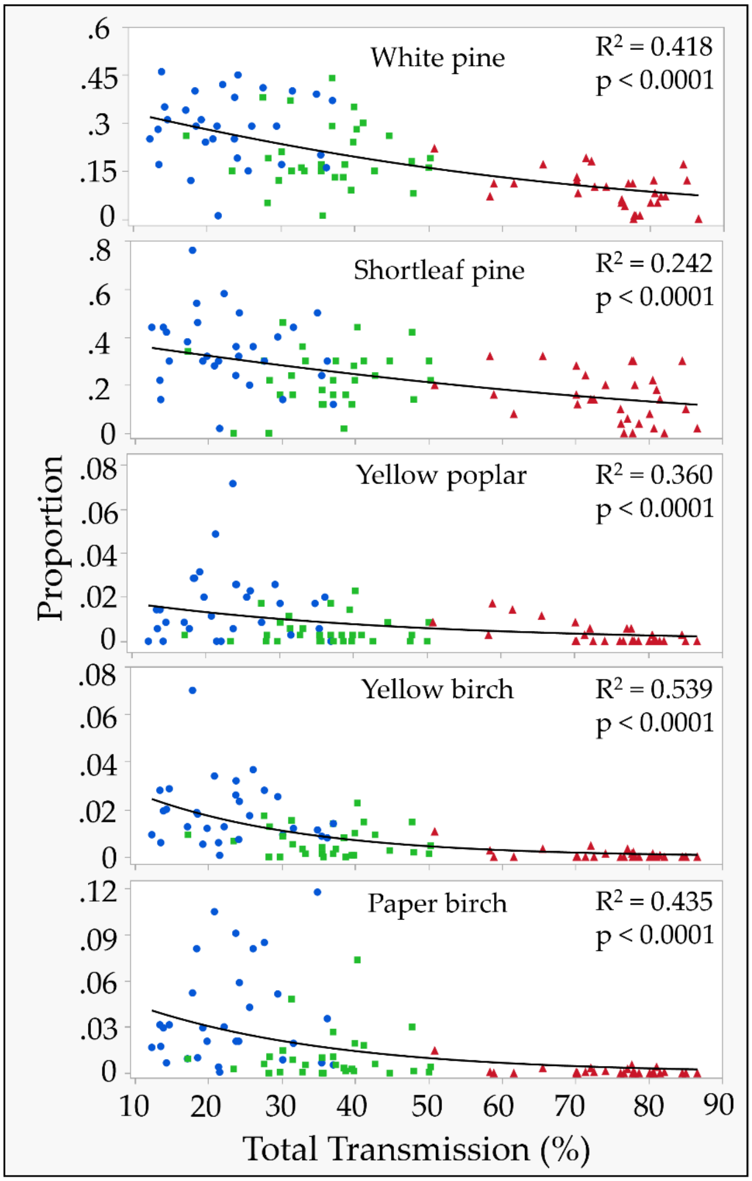

Figure 5.5. Relationship between plot-level light availability (total transmission percentage) and seedling establishment proportion in caged subplots for species exhibiting differential establishment across harvest treatments (Table 5.3). Colors and shapes indicate harvest treatment: blue circles denote small group selection, green squares indicate shelterwood, and red triangles represent seed tree. Note variable y-axes across species panels. Corresponding results for uncaged seed were also significant and are presented in Appendix D (Figure D.3). Mean light availability by treatment: small group selection = 23.0%, shelterwood = 36.4%, seed tree = 74.5%.

5.5 Discussion

5.5.1 Harvest intensity and seed predation impact establishment success

As hypothesized, seedling establishment declined with increasing harvest intensity, although the magnitude of this effect varied by species. Prior studies have shown greater harvest intensities can increase solar radiation, elevating soil temperatures and reducing water availability in surface layers (Marquis, 1964; Caldeira et al., 2013). While soil temperature and water availability were not measured, field observations supported the presence of harsher microclimates in more heavily harvested treatments.

Seed predation significantly reduced establishment, consistent with past findings (Bramble and Sharp, 1949; Roe, 1963; Sluder, 1965; Mignery, 1975; Raymond et al., 2003; Barton et al., 2015). Chewed hulls in most field plots suggested that seeds were most likely consumed as opposed to cached. This was unsurprising, given the spring sowing window and evidence of reduced caching behavior in spring (Rusch et al., 2014). However, I did not find strong evidence to suggest seed predation was reduced following more intense harvesting. Although including the interaction between harvest treatment and caging status significantly improved model fit (Table 5.2), the effect size was extremely small relative to other model terms, and the marginal effects in the full model were determined to be insignificant. Therefore, no statistically significant ordering of relative establishment reductions by harvest treatment could be established; it is possible that with increased sample size, a clearer picture could have formed. Relationships between harvest intensity and the likelihood of seed predation are mixed in the literature. Some studies report negligible differences in seed removal between various degrees of overstory harvest and uncut forest (Plucinski and Hunter, 2001; Bellocq et al., 2005; Kellner et al., 2014).

However, Buckley and Sharik (2002) found that small mammals removed significantly fewer buried northern red oak acorns following relatively small (0.4 ha) clearcuts compared to uncut controls (12% vs. 59%, respectively) in previously-unthinned red pine plantations in northern Michigan.

Understory vegetation dynamics are likely a key factor in seed predation intensity. Studies have demonstrated that small mammal foraging activity is higher in locations covered with woody shrubs, herbaceous vegetation and/or coarse woody debris (Brown et al., 1988; Kikuzawa, 1988; Ostfeld et al., 1997; Greenler et al., 2019), including after harvest (Kellner and Swihart, 2014; Kellner et al., 2016). While logging slash was largely removed from study sites, woody shrub cover (e.g., *Rubus*) and herbaceous coverage was relatively high and expanding in all harvests during the first growing season following herbicide and scarification treatments. As such, well-developed understory vegetation may have provided similar degrees of protection for foraging small mammals across treatments.

5.5.2 *Species traits and sowing method interact with harvest intensity and seed predation*

The hypothesis that species with larger seed kernel mass within the broadcast-sown group would be less impacted by harsh microclimates following more intense overstory harvesting was supported. Larger seed kernel mass likely confers resilience to harsh germination conditions in various ways, such as by promoting accelerated root and shoot growth and/or the ability to survive longer periods of low resource availability (Grime and Jeffrey 1965; Westoby et al., 1997). Nevertheless, establishment of broadcast-sown species was greatly reduced across the microclimatic gradient created by the harvest treatments, with these gradients likely driven largely by differences in solar radiation. This is consistent with other studies that found interspecific differences in establishment success are often related to seed size (St-Denis et al., 2013; Willis et al., 2015). In contrast, and as hypothesized, establishment of buried species was unaffected by harvest treatment, likely due to their orders-of-magnitude larger seed kernels and the moderated conditions created by sowing at 2.5 cm depth.

Sowing methods, based on operational norms and species silvics, necessarily exposed small-seeded species to harsher surface conditions. While fine-tuning soil coverage may have improved outcomes, I focused on realistic methods, making the microclimatic constraints I observed directly relevant to the practice of broadcast sowing. Relatedly, strategic plot placement likely also contributed to results: plots in the small group selection treatment were established in the southern portion of gaps – a location known for lower solar radiation and cooler, moister soils (Raymond et al., 2006; Prevost and Raymond, 2012). This experimental design choice may help explain why some broadcast-sown species sometimes performed better in small group selection gaps than in shelterwood harvests, even when total light transmission was similar (e.g., yellow poplar and birch species, Figure 5.5). As such, it's important to note that broadcast sowing in more exposed gap positions would likely yield poorer results.

The hypothesis that sowing method would create different predation patterns was only partially supported: no significant association between seed kernel mass and predation losses was detected for either broadcast-sown species (i.e., unexpected) or buried species (i.e., expected). These results are largely consistent with a meta-analysis examining this relationship (Moles et al., 2003). However, predator size and foraging strategy may also mediate selectivity. In a cafeteria-style feeding trial, Ivan and Swihart (2000) found large seeds with high caloric/lipid values were preferentially selected by squirrels (*Sciurus carolinensis*, *Sciurus niger* and *Tamiasciurus hudsonicus*) in west-central Indiana; however, in the same study, *Peromyscus leucopus* was found to be less selective than squirrels. Furthermore, St-Denis et al. (2013) observed increased seed predation on small-seeded paper birch relative to large-seeded northern red oak, however oak seed was buried deeper than birch seed. This study design, which necessitated separation of large-seeded/buried and small-seeded/broadcast-sown groups for analysis, limited my ability to detect cross-group trends (Garcia and Houle, 2002; Heinrich, 2014).

5.5.3 Management implications

This study provides evidence that direct seeding can be viable in managed northern hardwood forests, provided sowing method, species traits (e.g., seed kernel mass in this study), timing and stand/microsite conditions are carefully considered. Large-seeded species sown at 2.5 cm depth in late spring achieved high establishment rates regardless of harvest intensity. Furthermore, maximum establishment in uncaged subplots ranged from 55 to 67% for large-seeded species (Table 5.4), and was above 40% in aggregate across 13 of 18 stands (Figure 5.6, top panel). However, establishment was low enough on the five remaining sites to reasonably consider direct seeding a failure. Notably, this study followed two consecutive years of abundant northern red oak seed production in the northern Lower Peninsula (E. Farinosi, personal observation), and the three sites with the highest predation losses for oak and other large-seeded species were those with oak in the canopy and abundant acorns on the forest floor. Prioritizing direct seeding on sites less likely to experience mast-driven fluctuations in small mammal populations – or timing spring sowing to follow a mast failure – might increase the success rate of direct seeding (Greenberg and Zarnoch, 2018), regardless of factors such as seed size or sowing method.

For small-seeded species, successful establishment was influenced by both seed predation and harvest intensity (Figure 5.2; Figure 5.6, bottom panel). Broadcast seeding onto mineral soil/humus seedbeds (Raymond et al., 2003; Willis et al., 2015) was most successful in small group selection gaps, where maximum establishment proportions ranged from 6 – 19% (Table 5.4). Given the microclimate and predation challenges broadcast-sown seeds face, these figures are encouraging. However, environments that maximize seedling establishment may not always align with those that support long-term growth and recruitment. Willis et al. (2015) found that although establishment rates were highest in small group selection gaps (< 23 m diameter), subsequent growth and survival were maximized in higher-light, large group selection gaps (24 – 50 m diameter). As such, identifying the optimal combination of germination-establishment environment and post-establishment growth environment for small-seeded species is critical. Notably, two shelterwood sites exhibited establishment rates for small-seeded species equivalent to or greater than those in small group selection gaps (Figure 5.6, bottom panel); both exhibited signs of relatively high soil water holding capacity (higher organic material/clay content, E. Farinosi, personal observation). When evaluating candidate sites for broadcast seeding, forest managers might consider assessing soil texture or other indicators of increased water holding capacity, particularly when working in more heavily harvested stands.

Assuming successful seedling establishment, competing vegetation (Royo and Carson, 2006) and browsing damage (Côté et al., 2004) remain primary challenges to long-term success (Walters et al., 2016, 2020a). Measures such as competition control and short-term protection of individual trees or small groups of trees with exclosures could help facilitate seedling-to-sapling recruitment. Additionally, careful selection of seeding locations – such as choosing appropriately sized breaks in the canopy into which trees can eventually recruit – will ultimately enhance the long-term success of direct seeding projects.

Table 5.4. Maximum uncaged seedling establishment proportion for each species and the harvest treatment in which this proportion was found. Establishment is expressed relative to seed germination under ideal greenhouse conditions. SG = small group selection gaps; SH = shelterwood.

Species	Sowing Method	Maximum Uncaged Establishment Proportion	Harvest Treatment
Black walnut	Buried (2.5 cm)	.635	no difference
Northern red oak	Buried (2.5 cm)	.667	no difference
American chestnut	Buried (2.5 cm)	.557	no difference
Pignut hickory	Buried (2.5 cm)	.562	no difference
Bitternut hickory	Buried (2.5 cm)	.638	no difference
Eastern white pine	Broadcast (0 – 1 cm)	.092	SG = SH
Shortleaf pine	Broadcast (0 – 1 cm)	.191	SG = SH
Yellow poplar	Broadcast (0 – 1 cm)	.153	SG
Yellow birch	Broadcast (0 – 1 cm)	.068	SG
Paper birch	Broadcast (0 – 1 cm)	.062	SG

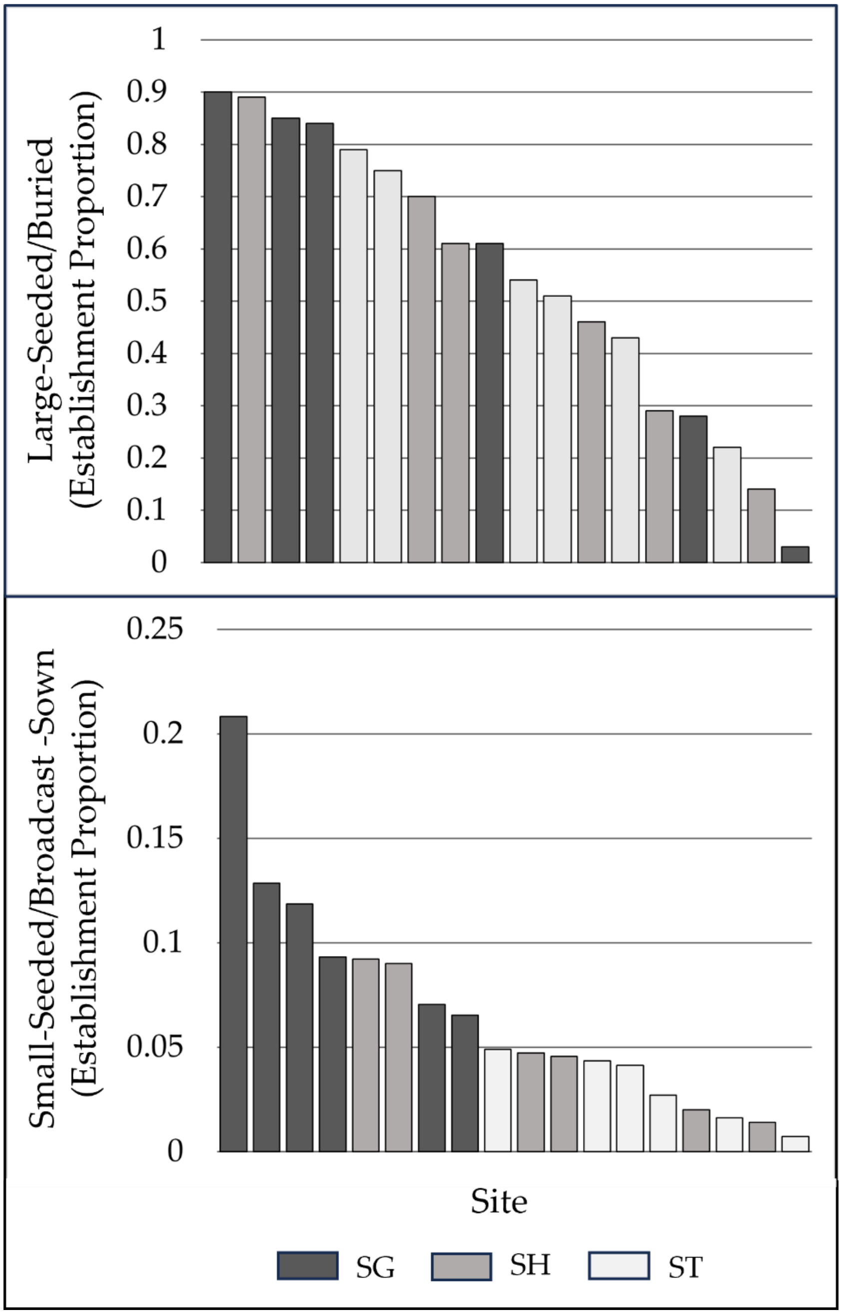

Figure 5.6. Site-level seedling establishment proportion for large-seeded/buried and small-seeded/broadcast-sown species in uncaged subplots. SG = small group selection gaps; SH = shelterwood; ST = seed tree.

CHAPTER 6:

CONCLUSION

This dissertation explored multiple silvicultural strategies for promoting resilient regeneration layers in managed northern hardwood forests (NHF) of northern Michigan: increasing harvest intensity, retaining large-diameter canopy trees to support robust advance regeneration layers, and using direct seeding to proactively supplement stand diversity. Across four experimental chapters, results consistently indicated that strategic shifts in current management practices could support the development of more diverse, resilient NHF systems.

Analysis of stocking surveys conducted six years after the implementation of a landscape-scale silvicultural systems experiment (Chapter 2) revealed that species diversity was positively associated with harvest intensity. While overall stocking was high across all treatments – exceeding 90% when considering woody shrubs and tree species, and over 70% for tree species alone – the stocking of tree species designated desirable for biomass productivity objectives increased with harvest intensity, largely due to greater representation of shade-intolerant species. Notably, the aggregate stocking of economically valuable NHF shade-tolerant and midtolerant species was not strongly influenced by harvest intensity, and instead exhibited distinct regional patterning. These results suggest environmental factors beyond harvest intensity played a key role in shaping stocking outcomes.

To explain the regional variation in stocking outcomes observed in Chapter 2, I evaluated how factors beyond harvest intensity – specifically pre-harvest stand structure and spatially varying factors such as site quality and deer use – related to species-level stocking patterns (Chapter 3). Nonmetric multidimensional scaling ordination revealed that stand composition was broadly associated with regional patterns of deer browsing pressure and site quality, which generally covaried across the study area. Species typically considered browsing-resilient or avoided were more abundant in regions with higher browsing pressure and higher site quality (e.g., the south-central Upper Peninsula and northern Lower Peninsula), while browsing-preferred species were more common in regions with lower indices of browsing pressure and site quality (e.g., the eastern Upper Peninsula and northwestern Upper Peninsula). Stocking of aspen and pin cherry increased with harvest intensity, while American beech declined; however, as previewed in Chapter 2, most shade-tolerant and midtolerant species did not exhibit strong responses to harvest intensity. Instead, their stocking was best predicted by pre-harvest stem densities in multiple size classes ≥ 50 cm tall, indicating that advance regeneration and/or mature canopy density were key drivers of early stocking outcomes. Deer browsing pressure was inversely related to stocking of yellow birch and northern red oak and positively related to stocking of American beech, ironwood and *Rubus*, though effect sizes were modest; it is likely that the primary influence of deer on early stocking outcomes occurs through long-term, cumulative browsing impacts on the structure and composition of advance regeneration layers, rather than post-harvest browsing pressure.

Given that early recruitment patterns for many species were strongly driven by the presence of advance regeneration, these results underscore the importance of management practices that promote its development. Since the formation of advance regeneration begins with seed production and seedling establishment, Chapter 4 focused on how the size and density of mature sugar maple – the premier NHF tree species – related to seed production and first-year seedling density across 60 stands in the central Upper Peninsula. I found a strong relationship between viable seed rain and first-year seedling counts, with a notable north-to-south gradient in reduced seedling establishment relative to predicted values based on seed availability. This pattern suggests that environmental conditions varying along this gradient likely influenced seedling establishment rates. Furthermore, the density of sugar maple trees > 40 cm dbh within 35 – 40 m of the sampling location was the strongest predictor of seedling counts. When this diameter threshold was applied to a dataset of 126 managed NHF spanning northern Michigan, many managed stands exhibited relatively low densities of large-diameter sugar maples. These findings suggest that modifying management practices to retain higher densities of large-diameter stems could increase seed production and improve the long-term potential for establishing robust sugar maple advance regeneration layers in these forests.

Finally, given that many NHF stands have species-poor canopies due to a range of historical and ecological factors, artificial regeneration practices are likely to play an increasingly important role in efforts to enhance species diversity. To evaluate the potential of direct seeding as a tool for diversifying regeneration layers, I experimentally seeded ten tree species – selected for their potential to bolster ecological functions such as mast production and stand structure – across a gradient of harvest intensity: small group selection gaps, shelterwood harvests and seed tree harvests. Large-seeded species (e.g., black walnut, northern red oak, American chestnut, pignut hickory and bitternut hickory) sown 2.5 cm below the soil surface established at high proportions and were largely unaffected by harvest intensity. In contrast, establishment of small-seeded, broadcast sown species (e.g., white pine, shortleaf pine, yellow poplar, yellow birch and paper birch) was strongly and inversely related to harvest intensity, reflecting their sensitivity to harsher microclimatic conditions following more intense canopy removal. While seed predation reduced establishment across all species, losses were not necessarily prohibitive, and may be acceptable in a management context. These results suggest that direct seeding could serve as a practical, cost-effective strategy for increasing regeneration diversity in managed NHF stands following various harvest treatments.

Together, these findings highlight the potential of novel silvicultural approaches to foster more diverse regeneration layers in northern hardwood forests of the upper Great Lakes region. While the long-term outcomes of the alternative silvicultural systems study (Chapters 2 & 3) will depend on successional trajectories unfolding over decades – along with the outsized influence of natural disturbance events such as the major ice storm that struck the northern Lower Peninsula in late winter 2025 – early results suggest that a combination of some level of increased harvest intensity, retention of larger-diameter seed sources, and the strategic use of artificial regeneration to restore degraded ecosystem functions represents a proactive path toward strengthening the resilience of this invaluable resource to future disturbance.

WORKS CITED

Akaike, J., 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19(6), 716-723.

Angers, V.A., Messier, C., Beaudet, M., Leduc, A., 2005. Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. *Forest Ecology and Management* 217(2-3), 275-293.

Arbogast, C., Jr., 1957. Marking guides for northern hardwoods under the selection system. *USDA Forest Service Station Paper No. 56*. Lake State Forest Experiment Station, St. Paul, MN.

Arietta, A.Z., 2022. Estimation of forest canopy structure and understory light using spherical panorama images from smartphone photography. *Forestry* 95, 38-48.

Arsenault, J.E., Saunders, M.R., Seymour, R.S., Wagner, R.G., 2011. First decadal response to treatment in a disturbance-based silviculture experiment in Maine. *Forest Ecology and Management* 262, 404-412.

Arthur, M.A., Muller, R.N., Costello, S., 1997. Species composition in a central hardwood forest in Kentucky 11 years after clear cutting. *American Midland Naturalist* 137, 274-281.

Baral, S.K., Danyagri, G., Girouard, M., Hebert, F., Pelletier, G., 2016. Effect of suppression history on growth response and stem quality of extant northern hardwoods following partial harvests. *Forest Ecology and Management* 372, 236-246.

Baribault, T.W., Kobe, R.K., Rothstein, D.E., 2010. Soil Calcium, Nitrogen, and Water Are Correlated with Aboveground Net Primary Production in Northern Hardwood Forests. *Forest Ecology and Management* 260, 723-733.

Bartlick, C.I., Burton, J.I., Webster, C.R., Froese, R.E., Dickinson, Y.L., 2023. An experimental approach to identify drivers of tree regeneration diversity, composition, and heterogeneity in northern hardwood forests. *Forest Ecology and Management* 546, 121320.

Barton, C., Miller, J., Sena, K., Angel, P., French, M., 2015. Evaluating the Use of Tree Shelters for Direct Seeding of *Castanea* on a Surface Mine in Appalachia. *Forests* 6, 3514-3527.

Bellocq, M.I., Jones, C., Dey, D.C., Turgeon, J.J., 2005. Does the shelterwood method to regenerate oak forests affect acorn production and predation? *Forest Ecology and Management* 205, 311-323.

Bolton, N.W., D'Amato, A.W., 2011. Regeneration responses to gap size and coarse woody debris within natural disturbance-based silvicultural systems in northeastern Minnesota, USA. *Forest Ecology and Management* 262, 1215-1222.

Bradshaw L., Waller D.M., 2016. Impacts of white-tailed deer on regional patterns of forest tree recruitment. *Forest Ecology and Management* 375, 1-11.

Bramble, W.C., Sharp, W.M., 1949. Rodents as a factor in direct seeding on spoil banks in Central Pennsylvania. *Journal of Forestry* 47(6), 477-478.

Bronson, M.T., 2020. Age and size effects on first cone production among white spruce trees. *Canadian Journal of Forest Management* 50, 519-522.

Brown, J.S., Kotler, B.P., Smith, R.J., Wirtz II, W.O., 1988. The effects of owl predation on the foraging behavior of hetermyid rodents. *Oecologia* 76, 408-415.

Buckley, D.S., Sharik, T.L., 2002. Effect of Overstory and Understory Vegetation Treatments on Removal of Planted Northern Red Oak Acorns by Rodents. *Northern Journal of Applied Forestry* 19(2): 88-92.

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

Burkhart, H.E., Avery, T.E., Bullock, B.P., 2019. *Forest Measurements* (6th ed.). Waveland Press, Long Grove, IL.

Burns, R.M., Honkala, B.H., 1990. *Silvics of North America: 2. Hardwoods*. Agriculture Handbook 654. United States Department of Agriculture - Forest Service, Washington, D.C.

Caldeira, M.C., Ibanez, I., Nogueira, C., Bugalho, M.N., Lecomte, X., Moreira, A., Pereira, J.S., 2013. Direct and indirect effects of tree canopy facilitation in the recruitment of Mediterranean oak. *Journal of Applied Ecology* 51, 349-358.

Caspersen, J.P., Saprunoff, M., 2005. Seedling recruitment in a northern temperate forest: the relative importance of supply and establishment limitation. *Canadian Journal of Forest Research* 35, 978-989.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and Extrapolation with Hill Numbers: A Framework for Sampling and Estimation in Species Diversity Studies. *Ecological Monographs* 84(1), 45-67.

Chapman, D., Purse, B.V., Roy, H.E., Bullock, J.M., 2017. Global Trade Networks Determine the Distribution of Invasive Non-Native Species. *Global Ecology and Biogeography* 26(8), 907-917.

Clark, J.S., LaDeau, S., Ibanez, I., 2004. Fecundity of trees and the colonization-competition hypothesis. *Ecological Monographs* 74, 415-442.

Clark, P.W., D'Amato, A.W., Palik, J.P., Woodall, C.W., Dubuque, P.A., Edge, G.J., Hartman, J.P., Fitts, L.A., Janowiak, M.K., Harris, L.B., Montgomery, R.A., Reinikainen, M.R., Zimmerman, C.L., 2023. A lack of ecological diversity in forest nurseries limits the achievement of tree-planting objectives in response to global change. *BioScience* 73(8), 575-586.

Cleavitt, N.L., Fahey, T.J., Battles, J.J., 2011. Regeneration ecology of sugar maple (*Acer saccharum*): seedling survival in relation to nutrition, site factors, and damage by insects and pathogens. *Canadian Journal of Forest Research* 41, 235-244.

Cleavitt, N.L., Battles, J.J., Fahey, T.J., Blum, J.D., 2014. Determinants of survival over 7 years for a natural cohort of sugar maple seedlings in a northern hardwood forest. *Canadian Journal of Forest Research* 44, 1112-1121.

Cleavitt, N.L., Fahey, T.J., 2017. Seed production of sugar maple and American beech in northern hardwood forests, New Hampshire, USA. *Canadian Journal of Forest Research* 47, 985-990.

Clotfelter, E.D., Pederson, A.B., Cranford, J.A., Ram, N., Sajdr, E.A., Nolan, V., Ketterson, E.D., 2007. Acorn mast drives long-term dynamics of rodent and songbird populations. *Oecologia* 154, 493-503.

Cockwell, M., Caspersen, J., 2014. Sources of variation in the net value of sugar maple trees: implications for tree selection and operations management. *Forest Products Journal* 64(7-8), 250-258.

Cook, D.B., 1946. Summer Browsing by Deer on Cut-over Hardwood Lands. The Journal of Wildlife Management 10(1), 60-63.

Côté, S.D., Rooney, T.P., Tremblay, J., Dussault, C., Waller, D.M., 2004. Ecological Impacts of Deer Overabundance. *Annual Review of Ecology, Evolution, and Systematics* 35, 113-147.

Cowan, R. L.; Jordan, J. S.; Grimes, J. L.; Gill, J. D. 1970. Comparative nutritive values of forage species. In: Range and wildlife habitat evaluation – a research symposium: Proceedings; 1968 May; Flagstaff; Tempe, AZ. Misc. Publ. 1147. Washington, DC: U.S. Department of Agriculture, Forest Service: 48-56.

Crow, T.R., Buckley, D.S., Nauertz, E.A., Zasada, J.C., 2002. Effects of management on the composition and structure of northern hardwood forests in Upper Michigan. *Forest Science* 48, 129-145.

Curtis, R., Rushmore, F., 1958. Some Effects of Stand Density and Deer Browsing on Reproduction in an Adirondack Hardwood Stand. *Journal of Forestry* 56(2), 116-121.

Danyagri, G., Baral, S.K., Girouard, M., Adegbidi, H.G., Pelletier, G., 2017. The role of advanced regeneration at time of partial harvest on tolerant hardwood stands development. *Canadian Journal of Forest Research* 47, 1410-1417.

Danyagri, G., Baral, S.K., Pelletier, G., 2019. Effects of Disturbance and Site Factors on Sapling Dynamics and Species Diversity in Northern Hardwood Stands. *Forest Ecology and Management* 444, 225-234.

Dey, D.C., Dwyer, J., Wiedenbeck, J., 2017. Relationship between tree value, diameter, and age in high-quality sugar maple (*Acer saccharum*) on the Menominee Reservation, Wisconsin. *Journal of Forestry* 115(5), 397-405.

Dickmann, D.I., Leefers, L.A., 2003. *The Forests of Michigan*. University of Michigan Press, Ann Arbor, MI.

Donovan, G., 2005. Chronic regeneration failure in northern hardwood stands: A liability to certified forest landowners. In: Cook, B. ed. Proceedings, Forest and Wildlife – Striving for Balance, Michigan Society of American Foresters.

Elenitsky, L.M., Walters, M.B., Farinosi, E.J., 2020. Tree Regeneration Structure Following Beech Bark Disease-Motivated Harvests: Factors Associated with Patterns and Management Implications. *Forests* 11(2), 180.

Eyre, F.H., Zillgitt, W.M., 1953. Partial cuttings in northern hardwoods of the Lake States: twenty-year experimental results. Technical Bulletin LS-1076, 124.

Falls, J.B., Falls, E.A, Fryxell, J.M., 2007. Fluctuations of deer mice in Ontario in relation to seed crops. *Ecological Monographs* 77, 19-32.

Forsyth, D.M., Barker, R.J., Moriss, G., Scroggie, M.P., 2007. Modeling the relationship between fecal pellet indices and deer density. *Journal of Wildlife Management* 71, 964-970.

Frazer, G.W., Canham, C.D., Lertzman, K.P., 1999. Gap light analyzer (GLA): imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, user's manual and program documentation (version 2.0). Simon Fraser University/Institute of Ecosystem Studies, Burnaby, British Columbia/Millbrook, New York, USA

Frelich, L.E., Lorimer, C.G., 1991. Natural disturbance regimes in hemlock-hardwood forests of the Upper Great Lakes region. *Ecological monographs* 61(2), 145-164.

Garcia, D., Banuelos, M.J., Houle, G., 2002. Differential effects of acorn burial and litter cover on Quercus rubra recruitment at the limit of its range in eastern North America. *Canadian Journal of Botany* 80, 1115-1120.

Garrett, P., Graber, R., 1995. Sugar maple seed production in northern New Hampshire. USDA Forest Service Northeastern Forest Experiment Station 697, 1-6.

George, L.O., Bazzaz, F.A., 1999. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. *Ecology* 80(3), 833-845.

Getis, A., Ord, J.K., 1992. The analysis of spatial association by use of distance statistics. *Geographic Analysis* 24, 189-206.

Godman, R.M., Tubbs, C.H., 1973. Establishing even-age northern hardwood regeneration by the shelterwood method – a preliminary guide. Research Paper NC-99. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station.

Godman, R.M. 1992. Applying the shelterwood system. In: Hutchinson, J.G., ed. Northern hardwood notes. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station.

Graignic, N., Tremblay, F., Bergeron, Y., 2014. Geographical variation in reproductive capacity of sugar maple (*Acer saccharum* Marshall) northern peripheral populations. *Journal of Biogeography* 41, 145-157.

Graber, R.E., Thompson, D.F., 1978. Seeds in the organic layers and soil of four beech-birch-maple stands. Research Paper NE-401. Broomall, PA: United States Department of Agriculture, Forest Service, Northeastern Forest Experiment Station.

Gray, A.N., Spies, T.A., 1996. Gap Size, Within-Gap Position and Canopy Structure Effects on Conifer Seedling Establishment. *Journal of Ecology* 84(5), 635-645.

Grayson, S.F., Buckley, D.S., Henning, J.G., Schweitzer, C.J., Gottschalk, K.W., Loftis, D.L., 2012. Understory light regimes following silvicultural treatments in central hardwood forests in Kentucky, USA. *Forest Ecology and Management* 279, 66-76.

Greene, D.F., Johnson, E.A., 1994. Estimating the mean annual seed production of trees. *Ecology* 75, 642-647.

Greenler, S.M., Estrada, L.A., Kellner, K.F., Saunders, M.R., Swihart, R.K., 2019. Prescribed fire and partial overstory removal alter an acorn-rodent conditional mutualism. *Ecological Applications* 29(7), e01958.

Greenberg, C.H., Zarnoch, S.J., 2018. A test of predator satiation hypothesis, acorn predator size, and acorn preference. *Canadian Journal of Forest Research* 48, 237-245.

Grime, J.P., Jeffrey, D.W., 1965. Seedling establishment in vertical gradients of sunlight. *Journal of Ecology* 53(3), 621-642.

Guiden, P.W., Connolly, B.M., Orrock, J.L., 2019. Seedling responses to decreased snow depend on canopy composition and small-mammal herbivore presence. *Ecography* 42, 780-790.

Hall, S.L., Barton, C.D., Sena, K.L., Angel, P., 2019. Reforesting Appalachian Surface Mines from Seed: A Five-Year Black Walnut Pilot Study. *Forests* 10, 573.

Halman, J.M, Schaberg, P.G., Hawley, G.J., Pardo, L.H., Fahey, T.J., 2013. Calcium and aluminum impacts on sugar maple physiology in a northern hardwood forest. *Tree Physiology* 33, 1242-1251.

Harlow, R.F., Downing, R.L., 1969. The effects of size and intensity of cut on production and utilization of some deer foods in the Southern Appalachians. *Transactions of the Northeast Fisheries and Wildlife Conference* 26**,** 45-55.

Harmala, H., 2021. Understory dynamics across 62-years of a northern hardwood management gradient study. Open Access Master's Thesis. Michigan Technological University.

Harris, L.B., C.W. Woodall, D'Amato A.W., 2022. Increasing the Utility of Tree Regeneration Inventories: Linking Seedling Abundance to Sapling Recruitment. *Ecological Indicators* 145, 109654.

Heinrich, B., 2014. American Chestnut Seed Dispersal and Regeneration. *Northeastern Naturalist* 21(4), 619-629.

Henry, C.R., Walters, M.B., Finley, A.O., Roloff, G.J., Farinosi, E.J., 2021. Complex drivers of sugar maple (*Acer saccharum*) regeneration reveal challenges to long-term sustainability of managed northern hardwood forests. *Forest Ecology and Management* 479, 118541.

Henry, C.R., Walters, M.B., 2023a. Sugar maple (*Acer saccharum*) age structure reveals limited establishment and development of age cohorts in response to selection management in northern hardwood forests. *Forest Ecology and Management* 546, 121356.

Henry, C.R., Walters, M.B., 2023b. Tree species size class patterns portend compositional shifts and low resilience in managed northern hardwood forests. *Ecosphere* 14, e4621.

Hisano, M., Searle, E.B., Chen, H.Y.H., 2018. Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. *Biological Reviews* 93, 439-456.

Hlina, P.S., Anderson, D.S., Schwarting, R.J., 2020. Analyzing vegetative cover of the Bois Brule River watershed re-visited in northwestern Wisconsin, Part 1: Forest stand changes (1968 to 2016). *The Great Lakes Botanist* 59, 1-23.

Horsely, S.B., Stout, S.L., DeCalesta, D.S., 2003. White-Tailed Deer Impact on the Vegetation Dynamics of a Northern Hardwood Forest. *Ecological Applications* 13(1), 98-118.

Host, G.E., Pregitzer, K.S., Ramm C.W., Hart J.B., Cleland D.T., 1987. Landform-mediated differences in successional pathways among upland forest ecosystems in Northwestern Lower Michigan. *Forest Science* 33, 445-457.

Hsia, J.F., Francl, K.E., 2009. Postdispersal sugar maple (*Acer saccharum*) seed predation by small mammals in a northern hardwood forest. *The American Midland Naturalist* 162(2), 213-223.

Hsieh, T. C., Ma, K.H., Chao, A., 2016. INEXT: An R Package for Rarefaction and Extrapolation of Species Diversity (Hill Numbers). *Methods in Ecology and Evolution* 7(12), 1451-1456.

Humbert, L., Gagnon, D., Kneeshaw, D., Messier, C., 2007. A shade tolerance index for common understory species of northeastern North America. *Ecological Indicators* 7(1), 195-207.

Hupperts, S.F., Webster, C.R., Froese, R.E., Bal, B., Dickinson, Y., 2022. Influence of Strip Clearcuts, Deer Exclusion and Herbicide on Initial Sapling Recruitment in Northern Hardwood Forests. *Forests* 13(7), 1149.

Hura, C.E., Crow, T.R., 2004. Woody debris as a component of ecological diversity in thinned and unthinned northern hardwood forests. *Natural Areas Journal* 24, 57-64.

Isbell, F., Tilman, D., Polasky, S., Loreau, M., 2015. The biodiversity-dependent ecosystem service debt. *Ecology Letters* 18(2), 119-134.

Ivan, J.S., Swihart, R.K., 2000. Selection of mast by granivorous rodents of the central hardwood forest region. *Journal of Mammalogy* 81(2), 549-562.

Iverson, L.R., Prasad, A.M., Peters, M.P., Matthews, S.N., 2019. Facilitating adaptive forest management under climate change: A spatially specific synthesis of 125 species for habitat changes and assisted migration over the Eastern United States. *Forests* 10, 989.

Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104(940), 501-528.

JMP, Version 17.0. SAS Institute Inc., Cary, NC, 2023.

Jones, P.D., Sabo, A.E., Forrester, J.A., Mladenoff, D.J., McDill, M.E., 2023. Northern hardwoods seedlings respond to a complex of environmental factors when deer herbivory is limited. *Forest Ecology and Management* 527, 120600.

Keasberry, A.M., Hart, J.L., Dey, D.C., and C.J. Schweitzer. 2016. Spatial patterns of irradiance and advanced reproduction along a canopy disturbance severity gradient in an upland hardwood stand. *Forests* 7, 73.

Kellner, K.F., Swihart, R.K., 2014. Changes in small mammal microhabitat use following silvicultural disturbance. *American Midland Naturalist* 172(2), 348-358.

Kellner, K.F., Riegel, J.K., Swihart, R.K., 2014. Effects of silvicultural disturbance on acorn infestation and removal. *New Forests* 45, 265-281.

Kellner, K.F., Lichti, N.I., Swihart, R.K., 2016. Midstory removal reduces effectiveness of oak (*Quercus*) acorn dispersal by small mammals in the Central Hardwood Forest region. *Forest Ecology and Management* 375, 182-190.

Kelty, M.J., Nyland, R.D., 1981. Regenerating Adirondack Northern Hardwoods By Shelterwood Cutting And Control of Deer Density. *Journal of Forestry*. 79, 22-26.

Kern, C.C., D'Amato, A.W., Strong, T.F., 2013. Diversifying the composition and structure of managed, late-successional forests with harvest gaps: What is the optimal gap size? *Forest Ecology and Management* 304, 110-120.

Kern, C.C., Erdmann, G.G., Kenefic, L.S., Palik, B.J., Strong, T.F., 2014. Development of the selection system in northern hardwood forests of the Lake States: An 80-year silviculture research legacy. In: Hayes, D.C., Stout, S.L., Crawford, R.H., Hoover, A.P. (Eds), *USDA Forest Service Experimental Forests and Ranges: Research for the Long Term*. Springer, New York, 201-223.

Kikuzawa, K., 1988. Dispersal of *Quercus mongolica* Acorns in a Broadleaved Deciduous Forest 1. Disappearance. *Forest Ecology and Management* 25, 1-8.

Knapp, S.P., Webster, C.R., Kern, C.C., 2019. Can group selection with legacy retention change compositional trajectories in conventionally managed hardwoods? *Forest Ecology and Management* 448, 174-186.

Knapp, S.P., Kern, C.C., Webster, C.R., 2021. Harvested opening size affects cohort development and failures in a second-growth northern hardwood forest. *Forest Ecology and Management* 482, 118804.

Kruskal, J.B., 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29(2), 115-129.

Leak, W.B., Wilson Jr., R.W., 1958. Regeneration after cutting of old-growth northern hardwoods in New Hampshire. USDA Forest Service Station Paper, Northeastern Forest Experiment Station (103), Upper Darby, PA.

Leak, W.B., Solomon, D.S., 1975. Influence of residual stand density on regeneration of northern hardwoods. United States Department of Agriculture Forest Service Research Paper NE-310. Northeastern Forest Experiment Station, Upper Darby, PA.

Leak, W.B., Filip, S.M., 1977. Thirty-eight Years of Group Selection in New England Northern Hardwoods. *Journal of Forestry* 75(10), 641-643.

Leak, W.B., Solomon, D.S., DeBald, P.S., 1987. Silvicultural guide for northern hardwood types in the northeast (revised). USDA Forest Service Station Paper, Northeastern Forest Experiment Station (603), Broomall, PA.

Leak, W.B., 1988. Effects of weed species on northern hardwood regeneration in New Hampshire. *Northern Journal of Applied Forestry* 5, 235-237.

Leak, W.B., 2005. Effects of small patch cutting on sugar maple regeneration in New Hampshire northern hardwoods. *Northern Journal of Applied Forestry* 22(1), 68-70.

Leak, W.B. 2007. Accuracy of regeneration surveys in New England northern hardwoods. *Northern Journal of Applied Forestry* 24(3), 227-229.

Liebhold, A.M., Mccullough, D.G., Blackburn, L.M., Frankel, S.J., von Holle, B., and Aukema, J.E., 2013. A Highly Aggregated Geographical Distribution of Forest Pest Invasions in the USA. *Diversity and Distributions* 19(9), 1208-16.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68, 619-640.

Longwood, F.R., 1951. Why release young maple from pin cherry? United States Department of Agriculture Forest Service, Lakes States Forest Experiment Station. Station Technical Note 360.

MacMillan, J., Aarssen, L.W., 2017. Recruitment success for mast year cohorts of sugar maple (*Acer saccharum*) over three decades of heavy deer browsing. *The American Midland Naturalist* 178(1), 36-46.

Manson, R.H., Ostfeld, R.S., Canham, C.D., 1998. The effects of tree seed and seedling density on predation rates by rodents in old fields. *Ecoscience* 5(2), 183-190.

Marini, L., Ayres, M.P., Herve, J., 2022. Impact of stand and landscape management on forest pest damage. *Annual Review of Entomology* 67, 181-199.

Marks, P.L., 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood systems. *Ecological M*onographs 44, 73-88.

Marks, P.L., Gardescu, S., 1998. A case study of sugar maple (*Acer saccharum*) as a forest seedling bank species. *The Journal of the Torrey Botanical Society* 125(4), 287-296.

Marquis, D.A., 1964. Effect of seedbed condition and light exposure on paper birch regeneration. *Journal of Forestry* 62(12), 876-881.

Marquis, D.A., 1967. Clearcutting in northern hardwoods: Results after 30 years. USDA Forest Service Research Papers, Northeastern Forest Experiment Station (NE-85), Upper Darby, PA.

Marquis, D.A., 1969. Silvical requirements for natural birch regeneration. USDA Forest Service Research Papers, Northeastern Forest Experiment Station (NE-85), Upper Darby, PA.

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

Masaki, T., Abe, S., Naoe, S., Koike, S., Nakajima, A., Nemoto, Y., 2020. Horizontal and elevational patterns of masting across multiple species in a steep montane landscape for the perspective of forest mammal management. *Journal of Forest Research* 25, 92-100.

Mather, P.M., 1976. *Computational methods of multivariate analysis in physical geography*. J. Wiley & Sons, London.

Matonis, M.S., Walters, M.B., Millington, J.D.A., 2011. Gap-, stand-, and landscape-scale factors contribute to poor sugar maple regeneration after timber harvest. *Forest Ecology and Management* 262(2), 286-298.

McClure, J.W., Lee, T.D., 1993. Small-scale disturbance in a northern hardwoods forest—effects on tree species abundance and distribution. *Canadian Journal of Forest Research* 23(7), 1347-1360.

McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, Oregon, USA.

McCune, B., Mefford, M.J., 2016. PC-ORD. Multivariate Analysis of Ecological Data. Version 7.0. MjM Software, Gleneden Beach, Oregon, USA.

Metzger, F.T., Tubbs, C.H., 1971. The influence of cutting method on regeneration of second-growth northern hardwoods. *Journal of Forestry* 69(9), 559-564.

Metzger, F.T., 1980. Strip clearcutting to regenerate northern hardwoods. Research Paper NC-186. United States Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, MN.

Metzger, F.T., 1990. *Ostrya virginiana* (Mill.) K. Koch eastern hophornbeam. In: Burns, R.M., Honkala, B.H., 1990. *Silvics of North America. Volume 2. Hardwoods*. Agriculture Handbook 654, 490-496. United States Department of Agriculture - Forest Service, Washington, D.C.

Michael, E.D., 1988. Effects of white-tailed deer on Appalachian hardwood regeneration. In: Smith, H.C, Perkey, A.W., Kidd, W.E., Jr., Guidelines for regenerating Appalachian hardwood stands: Workshop proceedings; 1988 May 24-26. SAF Publication 88-03, Morgantown, WV.

Michigan State University Extension & United States Department of Agriculture Soil Conservation Service. 1981. Soil association map of Michigan. https://www.canr.msu.edu/uploads/resources/pdfs/soil_association_map_of_michigan_(e1550).pdf

Mignery, A.L., 1975. Direct-seeding Oaks on the Cumberland Plateau in Tennessee. USDA Forest Service Research Paper, Southern Forest Experiment Station.

Miller, R., 2004. Regeneration in a Heavily Browsed Northern Hardwood Stand Twelve Years After Scarification and Fencing. Research Report, Michigan State University Upper Peninsula Tree Improvement Center, Escanaba, Michigan.

Minor, D. M., Kobe, R.K., 2017. Masting synchrony in northern hardwood forests: super-producers govern population fruit production. *Journal of Ecology* 105, 987-998.

Minor, D.M., Kobe, R.K., 2019. Fruit production is influenced by tree size and size-asymmetric crowding in a wet tropical forest. *Ecology and Evolution* 9, 1458-1472.

Moles, A.T., Warton, D.I., Westoby, M., 2003. Do small-seeded species have higher survival through seed predation than large-seeded species? *Ecology* 84(12), 3148-3161.

Moles, A.T., Westoby, M., 2004. Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology* 92, 372-383.

Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15, 278-285.

Neuendorff, J.K., Nagel, L.M., Webster, C.R., Janowiak, M.K., 2007. Stand Structure and Composition in a Northern Hardwood Forest after 40 Years of Single-Tree Selection. *Northern Journal of Applied Forestry* 24, 197-202.

Nieves, J.M., Ward, J.S., Royo, A.A., McDill, M.E., Kreye, J.K., Steiner, K.C., 2022. Stand and site characteristics affect the probability of stump sprouting in some eastern North American hardwoods. *Forest Ecology and Management* 511, 120136.

Nolet, P., Bouffard, D., Doyon, F., Delagrange, S., 2008. Relationship between canopy disturbance history and current sapling density of *Fagus grandifolia* and *Acer saccharum* in a northern hardwood landscape. *Canadian Journal of Forest Research* 38(2), 216-225.

Nygren, M., Rissanen, K., Eerikainen, K., Saksa, T., Valkonen, S., 2017. Norway spruce cone crops in uneven-aged stands in southern Finland: A case study. *Forest Ecology and Management* 390, 68-72.

Nyland, R.D., 1992. Exploitation and greed in eastern hardwood forests. *Journal of Forestry* 90, 33-37.

Nyland, R.D., Bashant, A.L., Bohn, K.K., Verostek, J.M., 2006. Interference to Hardwood Regeneration in Northeastern North America: Controlling Effects of American Beech, Striped Maple, and Hobblebush. *Northern Journal of Applied Forestry* 23(2), 122-132.

Nyland, R.D., 2016. *Silviculture: Concepts and Applications*, third ed. Waveland Press, Long Grove, IL.

Ord, J.K., Getis, A., 1995. Local spatial autocorrelation statistics: distributional issues and an application. *Geographical Analysis* 27, 286-306.

Ostfeld, R.S., Manson, R.H., Canham, C.D., 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology* 78, 1531-1542.

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

Parmesan, C.P., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37-42.

Patton SR., Russell, M.B., Windmuller-Campione M.A., Frelich, LE., 2021. White-tailed deer herbivory impacts on tree seedling and sapling abundance in the Lake States Region of the USA. *Annals of Forest Science* 78, 91.

Peterson, C.J., Carson, W.P., 1996. Generalizing forest regeneration models: the dependence of propagule availability on disturbance history and stand size. *Canadian Journal of Forest Research* 26, 45-52.

Pike, C., Potter, K.M., Berrang, P., Crane, B., Baggs, J., Leites, L., Luther, T., 2020. New seed-collection zones for the Eastern United States: The eastern seed zone forum. *Journal of Forestry* 118(4), 444-451.

Plucinski, K.E., Hunter Jr., M.L., 2001. Spatial and temporal patterns of seed predation on three tree species in an oak-pine forest. *Ecography* 24, 309-317.

Pond, N.C., Froese, R.E., Nagel, L.M., 2014. Sustainability of the Selection System in Northern Hardwood Forests. Forest Science 60(2), 374-381.

Powers, M.D., Nagel, L.M., 2009. Pennsylvania sedge cover, forest management and deer density influence tree regeneration dynamics in a northern hardwood forest. *Forestry* 82(3), 241-254.

Poznanovic, S.K., Webster, C.R., Bump J.K., 2013. Maintaining mid-tolerant tree species with uneven-aged forest management: 9-year results from a novel group-selection experiment. *Forestry* 86(5), 555-567.

Prevost, M., Raymond, P., Lussier, J.M., 2010. Regeneration dynamics after patch cutting and scarification in yellow birch – conifer stands. *Canadian Journal of Forest Research* 40, 357-369.

Prevost, M., Raymond, P., 2012. Effect of gap size, aspect and slope on available light and soil temperature after path-selection cutting in yellow birch-conifer stands, Quebec, Canada. *Forest Ecology and Management* 274, 210-221.

R Core Team (2024). _R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Randal, J.A., Walters, M.B., 2019. Competition and tolerance of low soil water favor *Carex* dominance over establishing *Acer* seedlings in managed temperate mesic forests. *Forest Ecology and Management* 449, 117481.

Raymond, P., Munson, A.D., Ruel, J.C., Philippe, N., 2003. Group and single-tree selection cutting in mixed tolerant hardwood–white pine stands: Early establishment dynamics of white pine and associated species. *The Forestry Chronicle* 79(6).

Raymond, P., Munson, A.D., Ruel, J.C., Coates, K.D., 2006. Spatial patterns of soil microclimate, light, regeneration, and growth within silvicultural gaps of mixed tolerant hardwood – white pine stands. *Canadian Journal of Forest Research* 36(3), 639-651.

Reed, S.P., Royo, A.A., Fotis, A.T., Knight, K.S., Flower, C.E., Curtis, P.S., 2022. The long-term impacts of deer herbivory in determining temperate forest stand and canopy structural complexity. *Journal of Applied Ecology* 59, 812-821.

Ribbens, E, Silander, J.A., Pacala, S.W., 1994. Seedling recruitment in forests – calibrating models to predict patterns of tree seedling dispersion. *Ecology* 75(6), 1794-1806.

Ripley, T.H., Campbell, R.A., 1960. Browsing (by deer) and stand regeneration in clear- and selectively-cut hardwoods. *Transactions of the 25th North American Wildlife Conference, Washington* 407-415.

Ristau, T.E., Horsley, S.B., 2006. When Is Pin Cherry (*Prunus pensylvanica* L.) a Problem in Allegheny Hardwoods? *Northern Journal of Applied Forestry* 23(3), 204-210.

Roberge, M.R., 1987. Management of a yellow birch-maple stand by cutting in groups: 15-year results. Information Report LAU-X-72. Natural Resources Canada, Canadian Forest Service – Laurentian Forestry Centre, Quebec, Quebec, Canada.

Roe, E.I., 1963. Direct seeding conifers in the Lake States: a review of past trials. Research Paper, Lake States Forest Experiment Station.

Rogers, B.M., Jantz, P., Goetz, S.J., Hole, W., 2017. Vulnerability of Eastern US Tree Species to Climate Change. *Global Change Biology* 23, 3302–3320.

Rogers, N.S., D'Amato, A.W., Leak, W.B., 2021. Long-term evolution of composition and structure after repeated group selection over eight decades. *Canadian Journal of Forest Research* 51, 1080-1091.

Rogers, N.S., D'Amato, A.W., Kern, C.C., Bedard S., 2022. Northern hardwood silviculture at a crossroads: Sustaining a valuable resource under future change. *Forest Ecology and Management* 512: 120139.

Rosenberger, D.W., Aukema, B.H., Venette, R.C., 2017. Cold tolerance of mountain pine beetle among novel eastern pines: A potential for trade-offs in an invaded range? *Forest Ecology and Management* 400, 28-37.

Rosenfeld, J.S., 2002. Functional redundancy in ecology and conservation. *Oikos* 98(1), 156-162.

Royo, A.A., Carson, W.P., 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research* 36, 1345-1362.

Royo, A.A., Kramer, D.W., Miller, K.V., Nibbelink, N.P., Stout, S.L., 2017. Spatio-temporal variation in foodscapes modifies deer browsing impact on vegetation. Landscape Ecology 32, 2281-2295.

Runkle, J.R., 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology 62(4), 1041-1051.

Rusch, U.D., Midgley, J.J., Anderson, B., 2014. Seasonal fluctuations in rodent seed caching and consumption behaviour in fynbos shrublands: Implications for fire management. *South African Journal of Botany* 93, 217-221.

Sabo, A.E., Forrester, J.A., Burton, J.I., Jones, P.D., Mladenoff, D.J., Kruger, E.L., 2019. Ungulate exclusion accentuates increases in woody species richness and abundance with canopy gap creation in a temperate hardwood forest. *Forest Ecology and Management* 433, 386-395.

Sage Jr., R.W., Porter, W.F., Underwood, H.B., 2003. Windows of opportunity: white-tailed deer and the dynamics of northern hardwood forests of the northeastern US. Journal for Nature Conservation 10, 213-220.

Sanders, S., Kirschbaum, J., Schafer, N.L., Gehring, J.S., 2023. Comprehensive assessment of White-Tailed Deer Browse in the Presence of Beech Bark Disease at a Great Lakes National Park. *Natural Areas Journal* 43(1), 62-71.

Schulte, L.A., Mladenoff, D.L., Crow, T.R., Merrick, L.C., Cleland, D.T., 2007. Homogenization of northern U.S. Great Lakes forests due to land use. *Landscape Ecology* 22, 1089-1103.

Scott, R.W., Huff, F.A., 1996. Impacts of the Great Lakes on Regional Climate Conditions. *Journal of Great Lakes Research* 22, 845-863.

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

Shields, J.M., Webster, C.R., 2007. Ground-layer response to group selection with legacy-tree retention in a managed northern hardwood forest. *Canadian Journal of Forest Research* 37, 1797-1807.

Sluder, E.R., 1965. Direct seeding Scarlet Oak in the North Carolina mountains. Research Notes, Southeastern Forest Experiment Station.

St-Denis, A., Messier, C., Kneeshaw, D., 2013. Seed Size, the Only Factor Positively Affecting Direct Seeding Success in an Abandoned Field in Quebec, Canada. *Forests* 4, 500-516.

Stoeckeler, J.H., Strothmann, R.O., Krefting, L.W., 1957. Effect of deer browsing on reproduction in the northern hardwood-hemlock type in northeastern Wisconsin. *Journal of Wildlife Management* 21(1), 75-80.

Thomas, S.C., 1996. Relative size at onset of maturity in rain forest trees: a comparative analysis of 37 Malaysian species. *Oikos* 76, 145-154.

Thompson, I., Mackey, B., McNulty, S., Mosseler, A., 2009. Forest Resilience, Biodiversity, and Climate Change: A Synthesis of the Biodiversity/Resilience/Stability Relationship in Forest Ecosystems. *Secretariat of the Convention on Biological Diversity, Montreal, Technical Series* 43, 1-67.

Tubbs, C.H., Metzer, F.T., 1969. Regeneration of northern hardwoods under shelterwood cutting. *The Forestry Chronicle* 45(5), 333-337.

United States Department of Agriculture. 2008. *Woody Plant Seed Manual* (Agriculture Handbook No. 727)

United States Department of Agriculture, United States Forest Service Eastern Region Forest Health Conditions Report 2020: https://www.fs.usda.gov/sites/default/files/fs_media/seducements/Major-Forest-Conditions-2022.pdf

Niinemets, U., Valladares, F., 2006. Tolerance to shade, drought and waterlogging of temperate northern hemisphere trees and shrubs. *Ecological Monographs* 76(4) 521-547.

Vander Yacht, A.L., Kobe, R.K., Walters, M.B., 2023. Hardwood regeneration in red pine plantations: Thinning and site quality effects on changes in density and species composition from edges to interiors. *Forest Ecology and Management* 526, 120576.

VanderMolen, M.S., Webster, C.R., 2021. Influence of deer herbivory on regeneration dynamics and gap capture in experimental gaps, 18 years post-harvest. *Forest Ecology and Management* 501: 119675.

Vickers, L.A., McWilliams, W.H., Knapp, B.O., D'Amato, A.W., Dey, D.C., Dickinson, Y.L., Kabrick, J.M., 2019. Are Current Seedling Demographics Poised to Regenerate Northern US Forests? *Journal of Forestry* 117(6), 592-612.

Voss, E.G., Reznicek, A.A., 2012. *Field Manual of Michigan Flora*. University of Michigan Press. Ann Arbor, MI.

Walters, M.B., Farinosi, E.J., Willis, J.L., Gottschalk, K.W., 2016. Managing for diversity: harvest gap size drives complex light, vegetation, and deer herbivory impacts on tree seedlings. *Ecosphere* 7(8), e01397.

Walters, M.B., Farinosi, E.J., Willis, J.L., 2020a. Deer Browsing and Shrub Competition Set Sapling Recruitment Height and Interact with Light to Shape Recruitment Niches for Temperate Forest Tree Species. *Forest Ecology and Management* 467, 118134.

Walters, M.B., Roloff, G.J., Henry, C.R., Hartman, J.P, Donovan, M.L., Farinosi, E.J., Starking, M.D., 2020b. Rethinking Northern Hardwood Forest Management Paradigms with Silvicultural Systems Research: Research–Management Partnerships Ensure Relevance and Application. *Journal of Forestry* 118(3), 260–274.

Walters, M. B., Henry, C.R., Farinosi, E.J., Roloff, G.J., Donovan, M.L., Hartman, J.P., 2022. Sapling Stocking Targets for Multiple Management Goals in Northern Hardwood Forests: How Do Stands Measure Up? *Journal of Forestry* 120(4), 395-419.

Walters, M.B., Kunkle, J.M., Kobe, R.K., Farinosi, E.J., 2023. Seedling drought responses governed by root traits, stie-soil moisture regimes and overstory competition-facilitation. *Forest Ecology and Management* 546, 121356.

Wang, Z.Y., Nyland, R.D., 1993. Tree species richness increased by clearcutting of northern hardwoods in Central New York. *Forest Ecology and Management* 57(1-4), 71-84.

Webster, C.R., Lorimer, C.G., 2005. Minimum opening sizes for canopy recruitment of midtolerant tree species: A retrospective approach. *Ecological Applications* 15(4), 1245-1262.

Webster, C.R., Dickinson, Y.L., Burton, J.I., Frelich, L.E., Jenkins, M.A., Kern, C.C., Raymond, P., Saunders, M.R., Walters, M.B., Willis, J.L., 2018. Promoting and maintaining diversity in contemporary hardwood forests: Confronting contemporary drivers of change and the loss of ecological memory. *Forest Ecology and Management* 421, 98-108.

Westoby, M., Leishman, M., Lord, J., 1997. Comparative ecology of seed size and dispersal. *Philosophical Transactions of the Royal Society B* 351, 1309-1318.

Whitney, G.G., 1987. An ecological history of the Great Lakes forest of Michigan. *Journal of Ecology* 75(3), 667-684.

Widen, M.J., O'Neil, M.A.P., Dickinson, Y.L., Webster, C.R., 2018. *Rubus* persistence within silvicultural openings and its impact on regeneration: The influence of opening size and advance regeneration. *Forest Ecology and Management* 427, 162-168.

Willis, J.L., Walters, M.B., Gottschalk, K.W., 2015. Scarification and gap size have interacting effects on northern temperate seedling establishment. *Forest Ecology and Management* 347, 237-246.

Willis, J.L., Walters, M.B., Farinosi, E., 2016. Local Seed Source Availability Limits Young Seedling Populations for Some Species More Than Other Factors in Northern Hardwood Forests. *Forest Science* 62, 440-448.

Wilson, R.W., Jensen, V.S., 1954. Regeneration after clear-cutting second-growth northern hardwoods. Forest Research Note NE-27. United States Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. Upper Darby, PA.

Wilson, G., Green, M., Brown, J., Campbell, J., Groffman, P., Duran, J., Morse, J., 2020. Snowpack affects soil microclimate throughout the year. *Climatic Change* 163, 705-722.

Wright, S.J., Jaramillo, M.A., Pavon, J., Condit, R., Hubbell, S.P., Foster, R.B., 2005. Reproductive size thresholds in tropical trees: variation among individuals, species and forests. *Journal of Tropical Ecology* 21, 307-315.

Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences* 96, 1463-1468.

Zak, D.R., Host, G.E., and Pregitzer, K.S., 1989. Regional variability in nitrogen mineralization, nitrification, and overstory biomass in northern lower Michigan. *Canadian Journal of Forest Research* 19(12), 1521-1526.

APPENDIX A: SUPPLEMENTAL TABLES AND FIGURES, CHAPTER 2

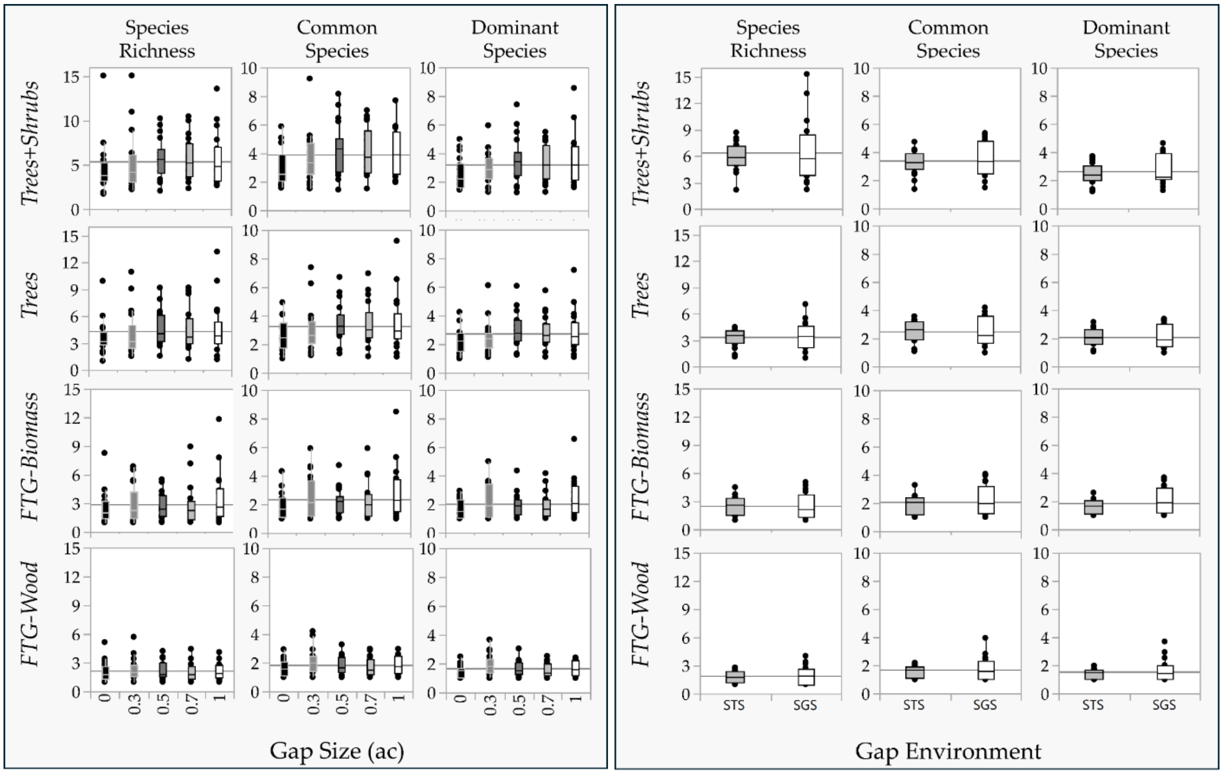

Figure A.1. Hill number estimates of absolute species richness, Hill-Shannon diversity (common species), and Hill-Simpson diversity (dominant species) as a function of gap environment with the LG treatment (no gap, 0.3, 0.5, 0.7, and 1 ac) and the ST-SG treatment (single-tree selection matrix vs. 0.15 ac small group selection gaps). Estimates are shown for four stocking categories: all woody stemmed species (*Trees+Shrubs*), only trees (*Trees*), and free-to-grow stems of species designated desirable for biomass productivity objectives (*FTG-Biomass*) or wood economics objectives (*FTG-Wood*). Box plot hinges correspond to the 25th percentile, median, and 75th percentile; whiskers extend to 1.5 times the interquartile range. Steel-Dwass all pairs comparison tests were conducted within each panel; no significant differences among gap size were detected in either harvest treatment. Note change in y-axis values among diversity indices.

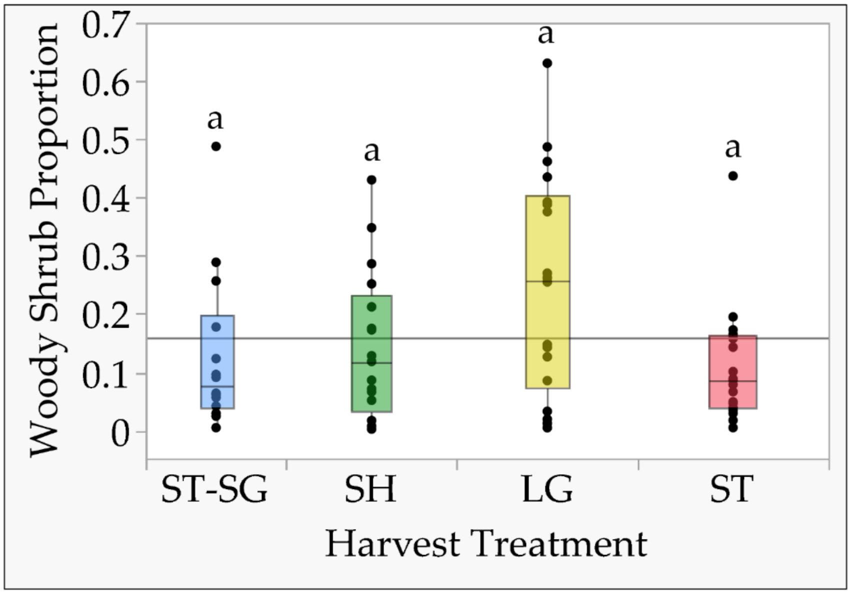

Figure A.2. Relationship between harvest treatment and stocking proportion of woody shrub species (primarily *Rubus* spp.). Box plot hinges correspond to the 25th percentile, median, and 75th percentile; whiskers extend to 1.5 times the interquartile range. Steel-Dwass all pairs comparison tests were conducted across harvest treatments; treatments sharing the same letter are not significantly different at level $\alpha = .05$.

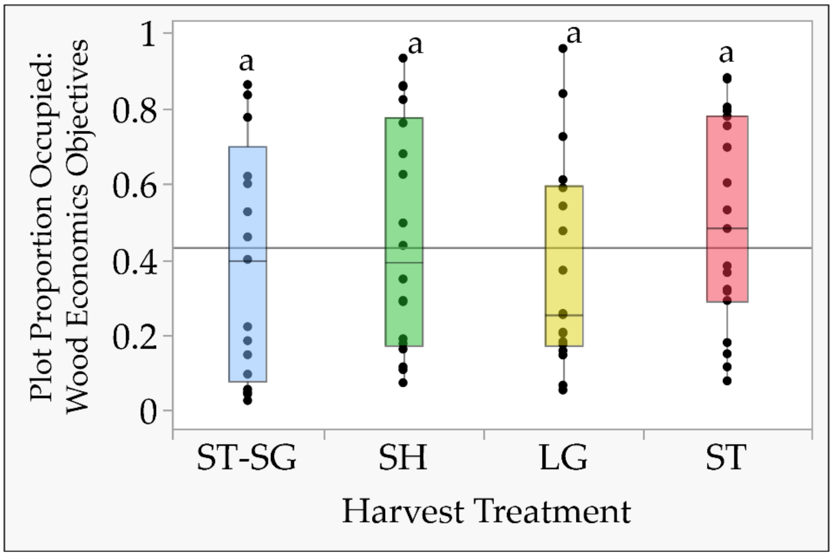

Figure A.3. Relationship between harvest intensity and proportion of plots containing at least one stem ≥ 50 cm tall of a species designated desirable for wood economics objectives. Box plot hinges correspond to the 25th percentile, median, and 75th percentile; whiskers extend to 1.5 times the interquartile range. Steel-Dwass all pairs comparison tests were conducted across harvest treatment; treatments sharing the same letter are not significantly different at level $\alpha = .05$.

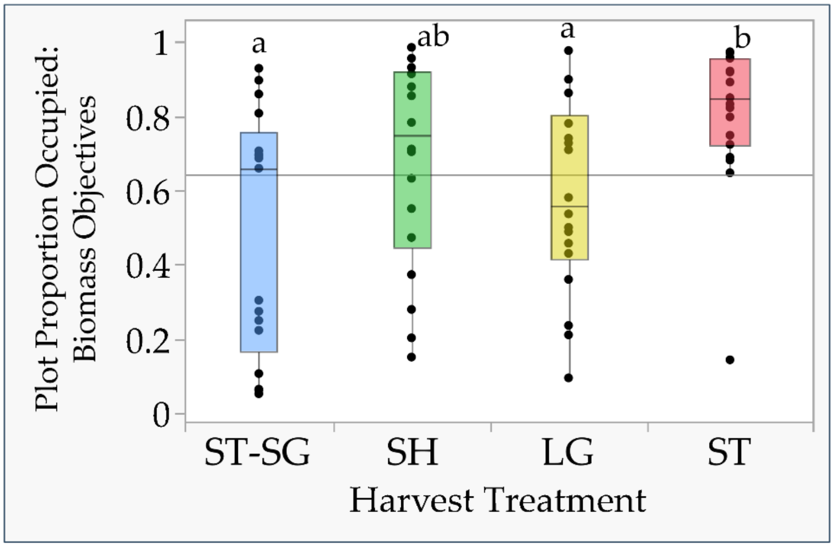

Figure A.4. Relationship between harvest intensity and proportion of plots containing at least one stem ≥ 50 cm tall of a species designated desirable for biomass productivity objectives. Box plot hinges correspond to the 25th percentile, median, and 75th percentile; whiskers extend to 1.5 times the interquartile range. Steel-Dwass all pairs comparison tests were conducted across harvest treatment; treatments sharing the same letter are not significantly different at level $\alpha = .05$.

APPENDIX B: SUPPLEMENTAL TABLES AND FIGURES, CHAPTER 3

Table B.1. Descriptive statistics of pre-harvest (2017) or early post-harvest (2018) stem densities by size class for variables used in beta regression models.

		Pre-harvest (2017) stem density				Post-harvest (2018) stem density			
Species (n sites)	**Stems ha^{-1}**	**< 50 cm**	**50 - 136 cm**	**137 cm - 10 cm dbh**	**> 10 cm dbh**	**< 50 cm**	**50 - 136 cm**	**137 cm - 10 cm dbh**	**> 10 cm dbh**
BF	Mean	324	57	116	27	91	7	12	2
(45)	Median	0	0	27	7	32	0	2	0
	Range	0 - 3800	0 - 953	0 - 895	0 - 262	0 - 1243	0 - 86	0 - 121	0 - 67
SM	Mean	60778	2011	1408	284	17055	314	423	57
(72)	Median	35600	541	870	287	9889	111	133	52
	Range	200-433135	0 - 14713	49-6950	0 - 534	0 - 274393	0 - 4020	0 - 3277	0 - 153
AB	Mean	1811	709	1339	37	1102	94	311	5
(54)	Median	400	319	919	27	702	57	148	0
	Range	0 - 21799	0 - 5189	0 - 5906	0 - 190	0 - 7070	0 - 549	0 - 1834	0 - 35
IW	Mean	1737	393	754	10	922	106	230	2
(64)	Median	600	96	371	7	319	57	116	0
	Range	0 - 13600	0 - 5604	0 - 4179	0 - 47	0 - 4522	0 - 860	0 - 1646	0 - 17
SB	Mean	677	37	7	0	1144	54	5	0
(64)	Median	99	0	0	0	301	12	0	0
	Range	0 - 7600	0 - 541	0 - 96	0 - 2	0 - 8725	0 - 541	0 - 156	0
BW	Mean	430	25	40	42	675	32	5	7
(47)	Median	200	0	0	32	462	7	0	2
	Range	0 - 1798	0 - 255	0 - 731	0 - 109	0 - 5256	0 - 151	0 - 64	0 - 35
RM	Mean	15550	603	383	67	3316	171	104	15
(62)	Median	7601	32	64	27	1147	25	15	2
	Range	0 - 69399	0 - 4458	0 - 5676	0 - 329	0 - 30063	0 - 1243	0 - 1124	0 - 124
YB	Mean	292	47	52	12	462	27	10	5
(52)	Median	0	0	2	2	32	0	0	0
	Range	0 - 3200	0 - 477	0 - 729	0 - 124	0 - 10319	0 - 311	0 - 264	0 - 47
RO	Mean	741	89	42	10	991	64	17	5
(25)	Median	400	0	0	2	343	5	0	0
	Range	0 - 3000	0 - 445	0 - 499	0 - 64	0 - 3981	0 - 558	0 - 124	0 - 32
WA	Mean	5103	502	141	10	3222	109	54	1
(49)	Median	1999	128	0	2	1018	32	7	0
	Range	0 - 47400	0 - 8056	0 - 924	0 - 42	0 - 34170	0 - 1401	0 - 583	0 - 10
BC	Mean	1848	96	74	15	667	52	42	2
(66)	Median	600	0	5	0	287	7	2	0
	Range	0 - 17599	0 - 1050	0 - 867	0 - 222	0 - 6338	0 - 684	0 - 949	0 - 32
PC	Mean	7	5	7	0	509	114	12	0
(72)	Median	0	0	0	0	0	0	0	0
	Range	0 - 255	0 - 287	0 - 408	0 - 10	0 - 16020	0 - 7307	0 - 566	0
ASP	Mean	54	10	27	0	655	116	25	1
(47)	Median	0	0	0	0	32	7	0	0
	Range	0 - 1401	0 - 383	0 - 549	0 - 10	0 - 9266	0 - 1408	0 - 524	0 - 22

Table B.2. Beta regression model results predicting stocking abundance six years post-harvest using either pre-harvest (top panel) or early post-harvest (bottom panel) stem densities by size class, harvest treatment, and browsing pressure as predictors. The model variant with the lowest AIC score is presented for each species.

Pre-harvest (2017)

Species	Model	n	R^2	< 50 cm	50 - 136 cm	137 cm - 10 cm dbh	> 10 cm dbh	Harvest	Harvest x Size class	Browsing Pressure
BF	NoBR	45	0.565	< .0001	ns	< .0001	ns	ns	ns	ns
SM	NoBR	72	0.765	ns	< .0001	< .0001	ns	ns	ns	ns
AB	BR11	54	0.785	ns	ns	0.0001	ns	< .0001	0.0048	0.0191 (+)
IW	BR11	64	0.871	ns	< .0001	< .0001	< .0001	< .0001	ns	< .0001 (+)
SB	NoBR	64	0.231	ns	< .0001	ns	ns	ns	ns	ns
BW	NoBR	47	0.481	< .0001	ns	0.0046	0.0023	ns	ns	ns
RM	NoBR	62	0.817	ns	0.0006	< .0001	< .0001	ns	ns	ns
YB	BR11	52	0.511	0.0054	< .0001	< .0001	ns	0.0039	ns	0.0151 (-)
RO	NoBR	25	0.677	< .0001	< .0001	ns	ns	ns	ns	ns
RUB	BR11	72	0.273	na	na	na	na	0.0024	na	0.0004 (+)
WA	NoBR	49	0.729	< .0001	ns	< .0001	ns	ns	ns	ns
BC	NoBR	66	0.753	ns	< .0001	0.0163	< .0001	0.0018	ns	ns
PC	NoBR	72	0.112	ns	ns	ns	ns	0.0291	ns	ns
ASP	NoBR	47	0.165	ns	ns	ns	ns	0.0217	ns	ns

Post-harvest (2018)

Species	Model	n	R^2	< 50 cm	50 - 136 cm	137 cm - 10 cm dbh	> 10 cm dbh	Harvest	Harvest x Size class	Browsing Pressure
BF	NoBR	45	0.528	0.0154	ns	< .0001	ns	ns	ns	ns
SM	NoBR	72	0.778	ns	0.0011	< .0001	ns	0.0084	ns	ns
AB	NoBR	54	0.491	ns	ns	< .0001	ns	ns	ns	ns
IW	BR11	64	0.883	ns	< .0001	< .0001	< .0001	< .0001	ns	< .0001 (+)
SB	NoBR	64	0.334	ns	< .0001	ns	ns	ns	ns	ns
BW	NoBR	47	0.384	0.0001	ns	0.0006	ns	ns	ns	ns
RM	NoBR	62	0.738	0.0008	ns	< .0001	< .0001	ns	ns	ns
YB	NoBR	52	0.490	ns	< .0001	< .0001	ns	ns	ns	ns
RO	NoBR	25	0.526	ns	< .0001	ns	ns	ns	ns	ns
RUB	BR11	72	0.273	na	na	na	na	0.0024	na	0.0004 (+)
WA	NoBR	49	0.645	< .0001	ns	0.0003	ns	ns	ns	ns
BC	NoBR	66	0.650	0.0003	ns	< .0001	ns	0.0061	ns	ns
PC	NoBR	72	0.112	ns	ns	ns	ns	0.0291	ns	ns
ASP	NoBR	47	0.583	< .0001	ns	< .0001	ns	0.0185	ns	ns

Table B.3. All unique model variants for each species. Whole-model and partial-factor significance values (Wald chi-square values) from generalized regression models (beta distribution) predicting six-year post-harvest seedling-sapling stocking. Predictors included pre-harvest stem density by size class (stems ha^{-1}), harvest treatment (four levels) and deer browsing pressure (proportion of sugar maple buds 50 – 136 cm tall browsed in the second growing season post-harvest). All retained predictors had positive effects, except browsing pressure (+/-) and nominal variables. Species are ordered by descending shade tolerance (Niinemets and Valladares, 2006; *Rubus alleghaniensis* score applied to the *Rubus* spp. group), except for pin cherry (Burns and Honkala, 1990; Walters et al., 2014). Sites (*n*) reflects stands where a species occurred in any size class in any survey year, except for pin cherry and *Rubus*, for which all sites were included. Species present on fewer than 20 sites were excluded from analysis. *Rubus* models did not incorporate size class predictors due to lack of pre-harvest data.

Spp.	Tol.	Model	Sites	R^2	AIC	< 50 cm	50 - 136 cm	137 cm - 10 cm dbh	> 10 cm dbh	Harvest	H x S.C.	Browsing Pressure
BF	Tol	NoBR	45	0.565	ns	24.3	ns	40.6	ns	ns	ns	ns
SM	Tol	NoBR	72	0.765	ns	ns	22.8	65.6	ns	ns	ns	ns
AB	Tol	NoBR	54	0.763	-178.6	ns	ns	19.1	ns	28.2	10.7	na
		BR3	47/54	0.763	-178.6	ns	ns	19.1	ns	28.2	10.7	ns
		BR11	54	0.785	-180.9	ns	ns	14.4	ns	27.1	12.9	5.5 (+)
IW	Tol	NoBR	64	0.819	-231.4	4.6	16.6	55.7	6.2	18.4	ns	na
		BR3	56	0.834	ns	ns	ns	78.2	22.2	18.6	ns	10.1 (+)
		BR11	64	0.871	-247.5	ns	19.1	54.9	29.9	27.8	ns	15.7 (+)
SB	Tol	NoBR	64	0.231	ns	ns	24	ns	ns	ns	ns	ns
BW	Tol	NoBR	47	0.481	ns	16.9	ns	8.0	9.3	ns	ns	ns
RM	Mid	NoBR	62	0.817	-277.9	ns	11.6	22.6	33.1	ns	ns	ns
YB	Mid	NoBR	52	0.450	-331.3	7.2	11.3	48.0	ns	10.5	ns	na
		BR3	47/52	0.450	-331.3	7.2	11.3	48.0	ns	10.5	ns	ns
		BR11	52	0.511	-334.4	7.7	18.2	37.4	ns	13.4	ns	5.9 (-)
RO	Mid	NoBR	25	0.677	-153.1	16.5	17.2	ns	ns	ns	ns	na
		BR3	21/25	0.677	-153.1	16.5	17.2	ns	ns	ns	ns	ns
		BR11	25	0.580	-151.0	34.8	ns	ns	ns	ns	ns	11.3 (-)
RUB	Int	NoBR	72	0.147	-171.2	na	na	na	na	12.1	na	na
		BR3	64	0.250	-177.7	na	na	na	na	13.9	na	6.0 (+)
		BR11	72	0.273	-180.3	na	na	na	na	14.4	na	12.8 (+)
WA	Int	NoBR	49	0.729	ns	73.1	ns	23.4	ns	ns	ns	ns
BC	Int	NoBR	66	0.753	ns	ns	37.5	5.8	57.6	15.1	ns	ns
PC	Int	NoBR	72	0.112	ns	ns	ns	ns	ns	9.0	ns	ns
ASP	Int	NoBR	47	0.165	ns	ns	ns	ns	ns	9.7	ns	ns

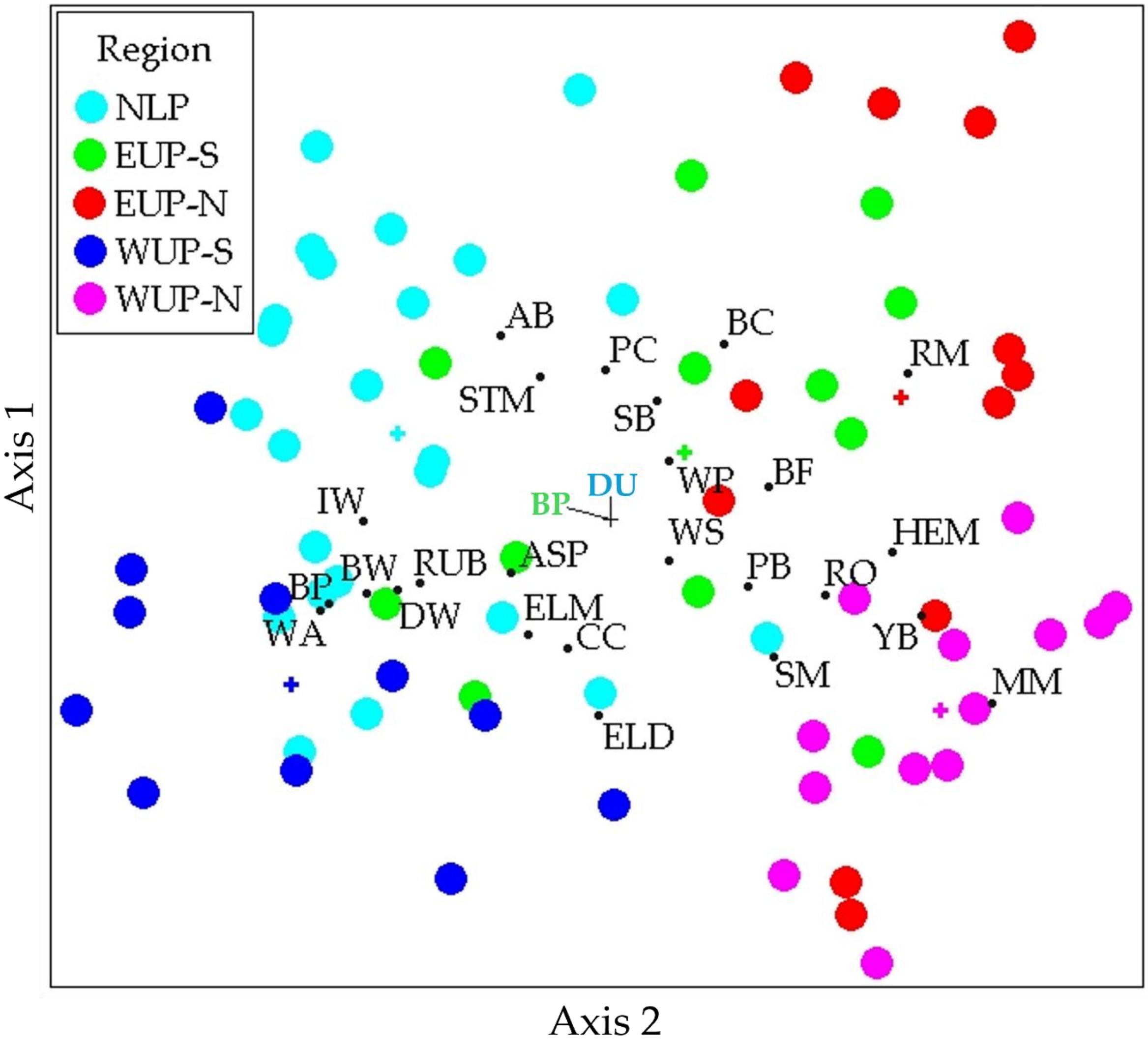

Figure B.1.1. Nonmetric multidimensional scaling (NMS) ordination of stand-level stocking composition. Distance between stands (colored circles) reflects similarity (adjacent) or dissimilarity (distant) in species composition. Figures B.1.1 and B.1.2 display two distinct views of the same three-dimensional ordination, with stands shaded by region. Group centroids for each region are shown as plus signs (+). How region, site quality, and harvest treatment relate can be compared by examining Figures B.1.1/B.1.2, Figures B.1.3/B.1.4, and Figures B.1.5/B.1.6, as these pairings display the same axis views for these three environmental variables. Indices of deer use (DU) and browsing pressure (BP) are shown as arrows moving out from the center of each plot.

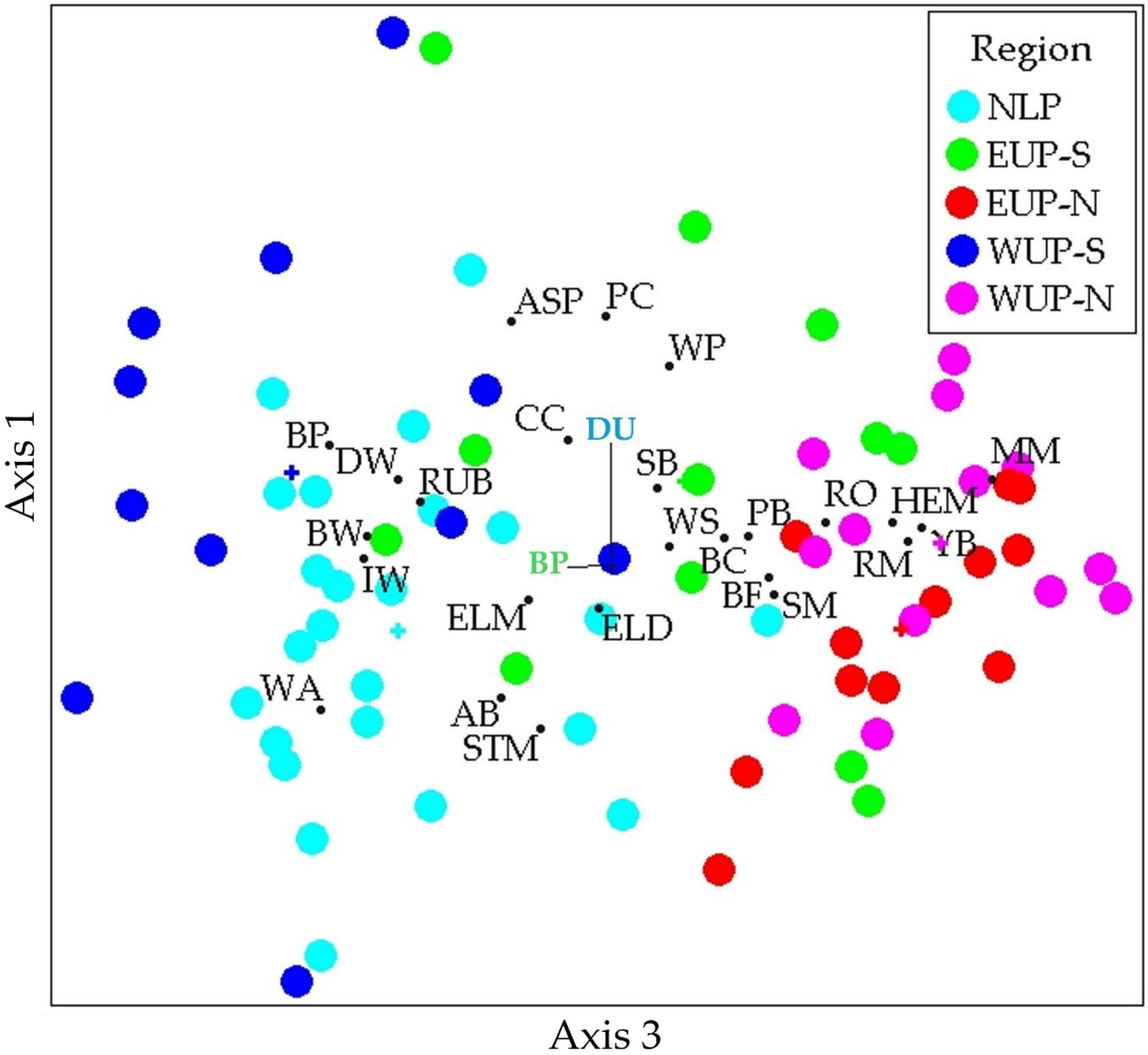

Figure B.1.2. Nonmetric multidimensional scaling (NMS) ordination of stand-level stocking composition. Distance between stands (colored circles) reflects similarity (adjacent) or dissimilarity (distant) in species composition. Figures B.1.1 and B.1.2 display two distinct views of the same three-dimensional ordination, with stands shaded by region. Group centroids for each region are shown as plus signs (+). How region, site quality, and harvest treatment relate can be compared by examining Figures B.1.1/B.1.2, Figures B.1.3/B.1.4, and Figures B.1.5/B.1.6, as these pairings display the same axis views for these three environmental variables. Indices of deer use (DU) and browsing pressure (BP) are shown as arrows moving out from the center of each plot.

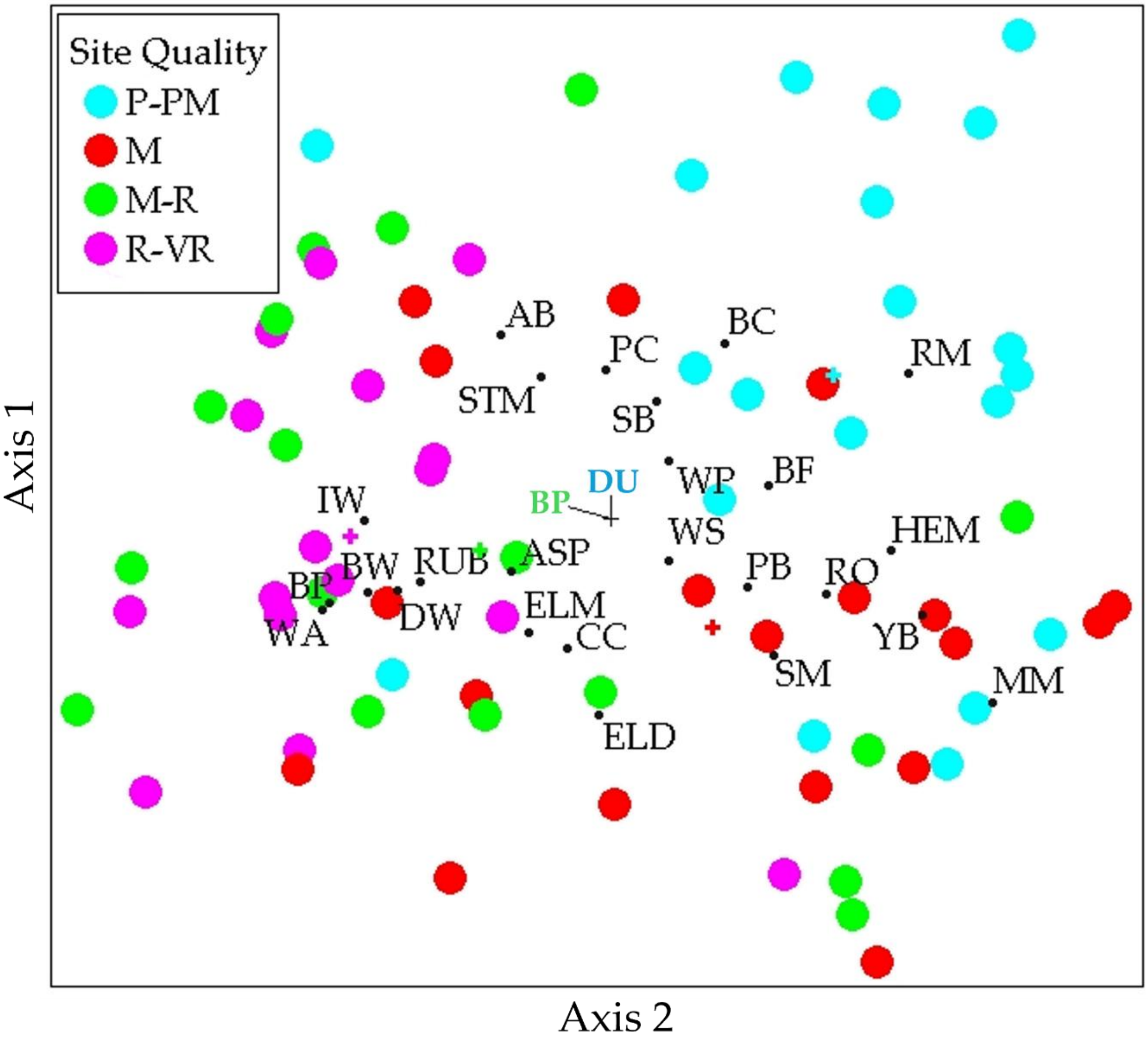

Figure B.1.3. Nonmetric multidimensional scaling (NMS) ordination of stand-level stocking composition. Distance between stands (colored circles) reflects similarity (adjacent) or dissimilarity (distant) in species composition. Figures B.1.3 and B.1.4 display two distinct views of the same three-dimensional ordination, with stands shaded by site quality. Group centroids for each region are shown as plus signs (+). How region, site quality, and harvest treatment relate can be compared by examining Figures B.1.1/B.1.2, Figures B.1.3/B.1.4, and Figures B.1.5/B.1.6, as these pairings display the same axis views for these three environmental variables. Indices of deer use (DU) and browsing pressure (BP) are shown as arrows moving out from the center of each plot.

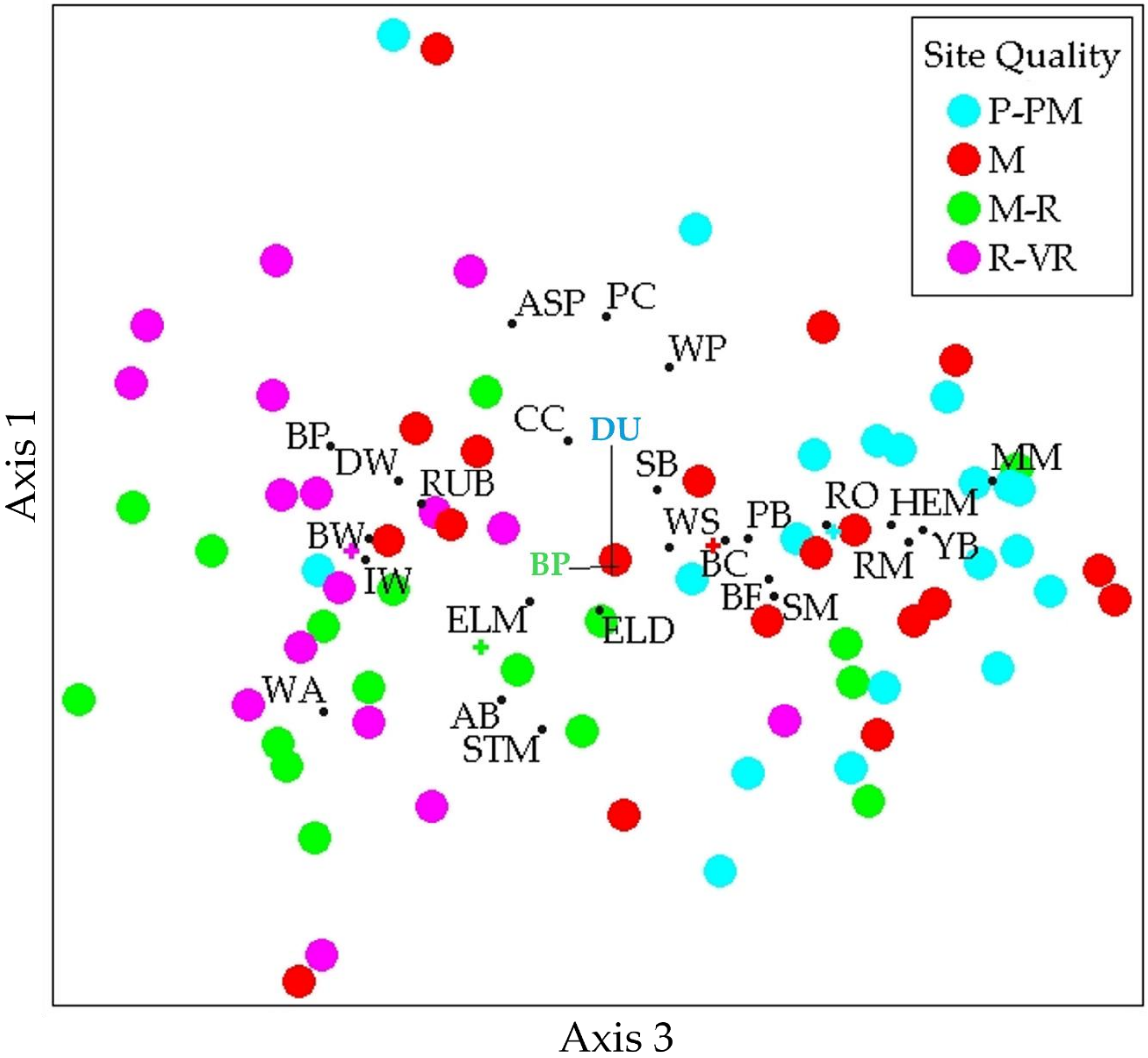

Figure B.1.4. Nonmetric multidimensional scaling (NMS) ordination of stand-level stocking composition. Distance between stands (colored circles) reflects similarity (adjacent) or dissimilarity (distant) in species composition. Figures B.1.3 and B.1.4 display two distinct views of the same three-dimensional ordination, with stands shaded by site quality. Group centroids for each region are shown as plus signs (+). How region, site quality, and harvest treatment relate can be compared by examining Figures B.1.1/B.1.2, Figures B.1.3/B.1.4, and Figures B.1.5/B.1.6, as these pairings display the same axis views for these three environmental variables. Indices of deer use (DU) and browsing pressure (BP) are shown as arrows moving out from the center of each plot.

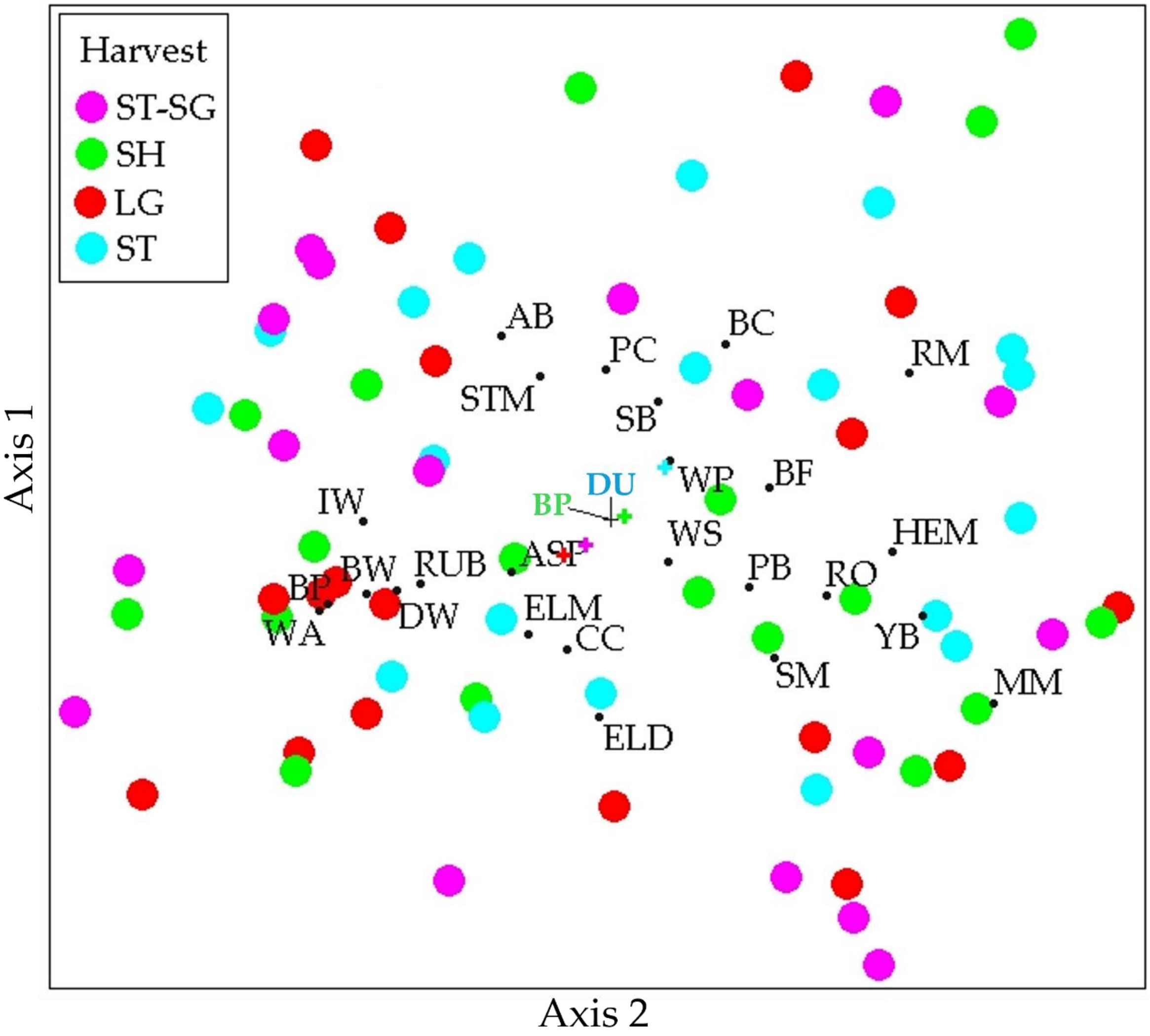

Figure B.1.5. Nonmetric multidimensional scaling (NMS) ordination of stand-level stocking composition. Distance between stands (colored circles) reflects similarity (adjacent) or dissimilarity (distant) in species composition. Figures B.1.5 and B.1.6 display two distinct views of the same three-dimensional ordination, with stands shaded by harvest treatment. Group centroids for each region are shown as plus signs (+). How region, site quality, and harvest treatment relate can be compared by examining Figures B.1.1/B.1.2, Figures B.1.3/B.1.4, and Figures B.1.5/B.1.6, as these pairings display the same axis views for these three environmental variables. Indices of deer use (DU) and browsing pressure (BP) are shown as arrows moving out from the center of each plot.

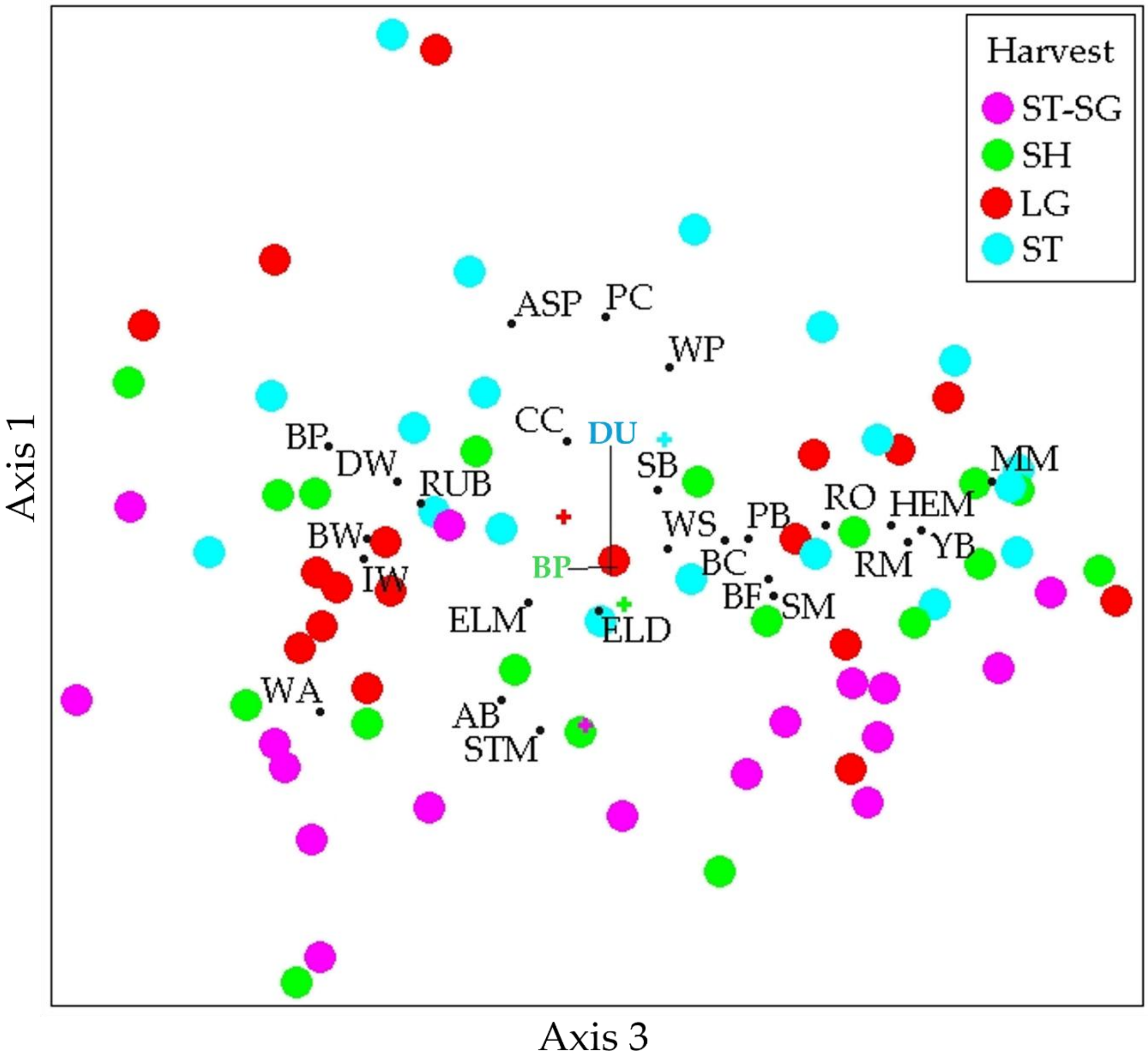

Figure B.1.6. Nonmetric multidimensional scaling (NMS) ordination of stand-level stocking composition. Distance between stands (colored circles) reflects similarity (adjacent) or dissimilarity (distant) in species composition. Figures B.1.5 and B.1.6 display two distinct views of the same three-dimensional ordination, with stands shaded by harvest treatment. Group centroids for each region are shown as plus signs (+). How region, site quality, and harvest treatment relate can be compared by examining Figures B.1.1/B.1.2, Figures B.1.3/B.1.4, and Figures B.1.5/B.1.6, as these pairings display the same axis views for these three environmental variables. Indices of deer use (DU) and browsing pressure (BP) are shown as arrows moving out from the center of each plot.

APPENDIX C: SUPPLEMENTAL TABLES AND FIGURES, CHAPTER 4

Table C.1. R^2 and p-values for generalized regressions (negative binomial distribution) relating sugar maple total seed, filled seed and seedling counts to the number of sugar maple trees within 40 m radius plots. Tree counts were progressively restricted by diameter class in 5 cm increments. Seedling model values correspond to those shown in Figure 4.5. P-values are indicated as * < 0.05, ** < 0.01.

Tree counts restricted to diameters indicated	Total seed R^2 (p-value)	Filled seed R^2 (p-value)	Seedlings R^2 (p-value)
> 25 cm	0.028	0.055	0.086*
> 30 cm	0.075*	0.096*	0.111**
> 35 cm	0.129**	0.131**	0.133**
> 40 cm	0.150**	0.133**	0.145**
> 45 cm	0.113*	0.107*	0.123**
> 50 cm	0.094*	0.088*	0.094*

APPENDIX D: SUPPLEMENTAL TABLES AND FIGURES, CHAPTER 5

Table D.1. Descriptive statistics for seedling establishment of ten species sown following three harvest treatments in either caged or uncaged subplots. Values represent treatment-level means and standard deviations.

			Establishment from total seed sown (%)			**Establishment from viable seed estimate (%)**
Species	**Harvest Type**	**Caging**	**Mean (SD)**	**Median**	**Range**	**Mean**
American chestnut	Small Group Gaps	Caged	87 (13)	90	50 - 100	89.7
		Uncaged	52 (39)	65	0 - 100	53.6
	Shelterwood	Caged	86 (14)	90	40 - 100	88.7
		Uncaged	42 (40)	35	0 - 100	43.3
	Seed Tree	Caged	90 (10)	90	90 - 100	92.7
		Uncaged	54 (35)	70	0 - 100	55.7
Northern red oak	Small Group Gaps	Caged	90 (14)	90	40 - 100	90.9
		Uncaged	60 (14)	70	0 - 100	60.6
	Shelterwood	Caged	92 (9)	90	70 - 100	92.9
		Uncaged	50 (38)	55	0 - 100	50.5
	Seed Tree	Caged	92 (11)	100	60 - 100	92.9
		Uncaged	66 (29)	80	0 - 100	66.7
Black walnut	Small Group Gaps	Caged	58 (17)	60	20 - 80	92.0
		Uncaged	40 (28)	40	0 - 90	63.5
	Shelterwood	Caged	56 (22)	60	10 - 90	88.9
		Uncaged	35 (28)	40	0 - 90	55.6
	Seed Tree	Caged	42 (22)	45	10 - 80	66.6
		Uncaged	26 (24)	25	0 - 80	41.2
Bitternut hickory	Small Group Gaps	Caged	72 (18)	80	20 - 100	90.0
		Uncaged	51 (33)	55	0 - 100	63.8
	Shelterwood	Caged	65 (21)	70	10 - 100	81.3
		Uncaged	45 (32)	40	0 - 100	56.3
	Seed Tree	Caged	64 (27)	70	0 - 100	80.0
		Uncaged	42 (23)	40	10 - 90	52.5
Pignut hickory	Small Group Gaps	Caged	80 (15)	80	40 - 100	90.0
		Uncaged	49 (34)	55	0 - 100	55.1
	Shelterwood	Caged	75 (14)	75	50 - 100	84.3
		Uncaged	50 (29)	50	10 - 100	56.2
	Seed Tree	Caged	70 (17)	70	20 - 100	78.7
		Uncaged	45 (25)	50	0 - 90	50.6
Eastern white pine	Small Group Gaps	Caged	28.6 (10.8)	29	1 - 46	36.7
		Uncaged	7.2 (7.2)	5.5	0 - 28	9.2
	Shelterwood	Caged	19.9 (10.1)	17	1 - 44	25.5
		Uncaged	5.0 (7.6)	3	0 - 37	6.4
	Seed Tree	Caged	9.0 (5.8)	9	0 - 22	11.5
		Uncaged	2.6 (3.3)	1	0 - 11	3.3

Table D.1. (cont'd)

Shortleaf pine	Small Group Gaps	Caged	34.4 (15)	32	2 - 76	40.5
		Uncaged	16.3 (13.4)	15	0 - 52	19.1
	Shelterwood	Caged	22.7 (11.9)	22	0 - 46	26.6
		Uncaged	9.5 (11.3)	7	0 - 40	11.3
	Seed Tree	Caged	14.9 (10.4)	14	0 - 32	17.3
		Uncaged	7.6 (8.1)	4	0 - 34	8.9
Yellow poplar	Small Group Gaps	Caged	3.7 (2.9)	3	0.4 - 11	24.2
		Uncaged	2.3 (2.2)	2	0 - 10	15.3
	Shelterwood	Caged	1.4 (1.3)	1.2	0 - 4.4	9.2
		Uncaged	0.7 (0.8)	0.4	0 - 3.2	4.5
	Seed Tree	Caged	0.6 (0.9)	0	0 - 3.2	3.6
		Uncaged	0.4 (0.6)	0	0 - 2.4	2.6
Yellow birch	Small Group Gaps	Caged	1.9 (1.4)	1.6	0.06 - 7	11.7
		Uncaged	0.9 (0.7)	0.9	0 - 2.5	6.2
	Shelterwood	Caged	0.7 (0.6)	0.4	0 - 2.3	4.1
		Uncaged	0.3 (0 .4)	0.06	0 - 1.4	1.8
	Seed Tree	Caged	0.1 (0.2)	0	0 - 1.1	0.7
		Uncaged	0.03 (0.06)	0	0 - 0.2	0.2
Paper birch	Small Group Gaps	Caged	3.7 (3.2)	2.9	0.06 - 1.7	16.9
		Uncaged	1.4 (1.5)	1	0 - 5.1	6.8
	Shelterwood	Caged	1.1 (1.6)	0.5	0 - 7.3	4.8
		Uncaged	0.4 (1.1)	0.06	0 - 5.5	2.0
	Seed Tree	Caged	0.1 (0.3)	0	0 - 1.5	0.6
		Uncaged	0.08 (0.16)	0	0 - 0.7	0.3

Table D.2. Generalized linear mixed model estimates of seedling establishment at the end of the first growing season. The establishment proportions listed are used in Figure 5.2.

Species	Harvest	Caging Status	n	Establishment (%)	Species	Harvest	Caging Status	n	Establishment (%)
American chestnut	SG	Caged	30	87.9 (2.5)	Eastern white pine	SG	Caged	30	29.2 (3.1)
		Uncaged	30	51.0 (4.8)			Uncaged	30	6.0 (0.9)
	SH	Caged	30	88.3 (2.3)		SH	Caged	30	17.6 (2.2)
		Uncaged	30	41.7 (4.6)			Uncaged	30	3.9 (0.6)
	ST	Caged	30	91.3 (2.0)		ST	Caged	30	7.5 (1.1)
		Uncaged	30	55.8 (4.7)			Uncaged	30	2.0 (0.3)
Northern red oak	SG	Caged	30	93.0 (3.0)	Shortleaf pine	SG	Caged	30	35.1 (3.6)
		Uncaged	30	59.8 (9.8)			Uncaged	30	14.5 (2.0)
	SH	Caged	30	91.3 (3.6)		SH	Caged	30	20.5 (2.6)
		Uncaged	30	54.2 (10.0)			Uncaged	30	7.9 (1.2)
	ST	Caged	30	95.1 (2.3)		ST	Caged	30	13.2 (1.9)
		Uncaged	30	68.5 (8.9)			Uncaged	30	6.7 (1.1)
Pignut hickory	SG	Caged	30	78.8 (3.9)	Yellow poplar	SG	Caged	30	2.4 (0.4)
		Uncaged	30	51.4 (5.7)			Uncaged	30	1.5 (0.2)
	SH	Caged	30	76.9 (4.1)		SH	Caged	30	0.8 (0.1)
		Uncaged	30	48.6 (5.7)			Uncaged	30	0.4 (0.007)
	ST	Caged	30	72.6 (4.6)		ST	Caged	30	0.3 (0.006)
		Uncaged	30	42.9 (5.6)			Uncaged	30	0.2 (0.006)
Bitternut hickory	SG	Caged	30	73.4 (3.9)	Paper birch	SG	Caged	30	3.5 (0.05)
		Uncaged	30	50.6 (4.8)			Uncaged	30	1.4 (0.02)
	SH	Caged	30	66.8 (4.2)		SH	Caged	30	0.8 (0.01)
		Uncaged	30	44.3 (4.6)			Uncaged	30	0.3 (0.005)
	ST	Caged	30	64.7 (4.4)		ST	Caged	30	0.06 (0.001)
		Uncaged	30	40.4 (4.6)			Uncaged	30	0.03 (0.01)
Black walnut	SG	Caged	30	58.5 (4.7)	Yellow birch	SG	Caged	30	1.7 (0.03)
		Uncaged	30	40.0 (4.6)			Uncaged	30	0.9 (0.01)
	SH	Caged	30	56.5 (4.6)		SH	Caged	30	0.5 (0.008)
		Uncaged	30	33.2 (4.3)			Uncaged	30	0.2 (0.004)
	ST	Caged	30	41.1 (4.6)		ST	Caged	30	0.06 (0.001)
		Uncaged	30	25.7 (3.8)			Uncaged	30	0.02 (0.0007)

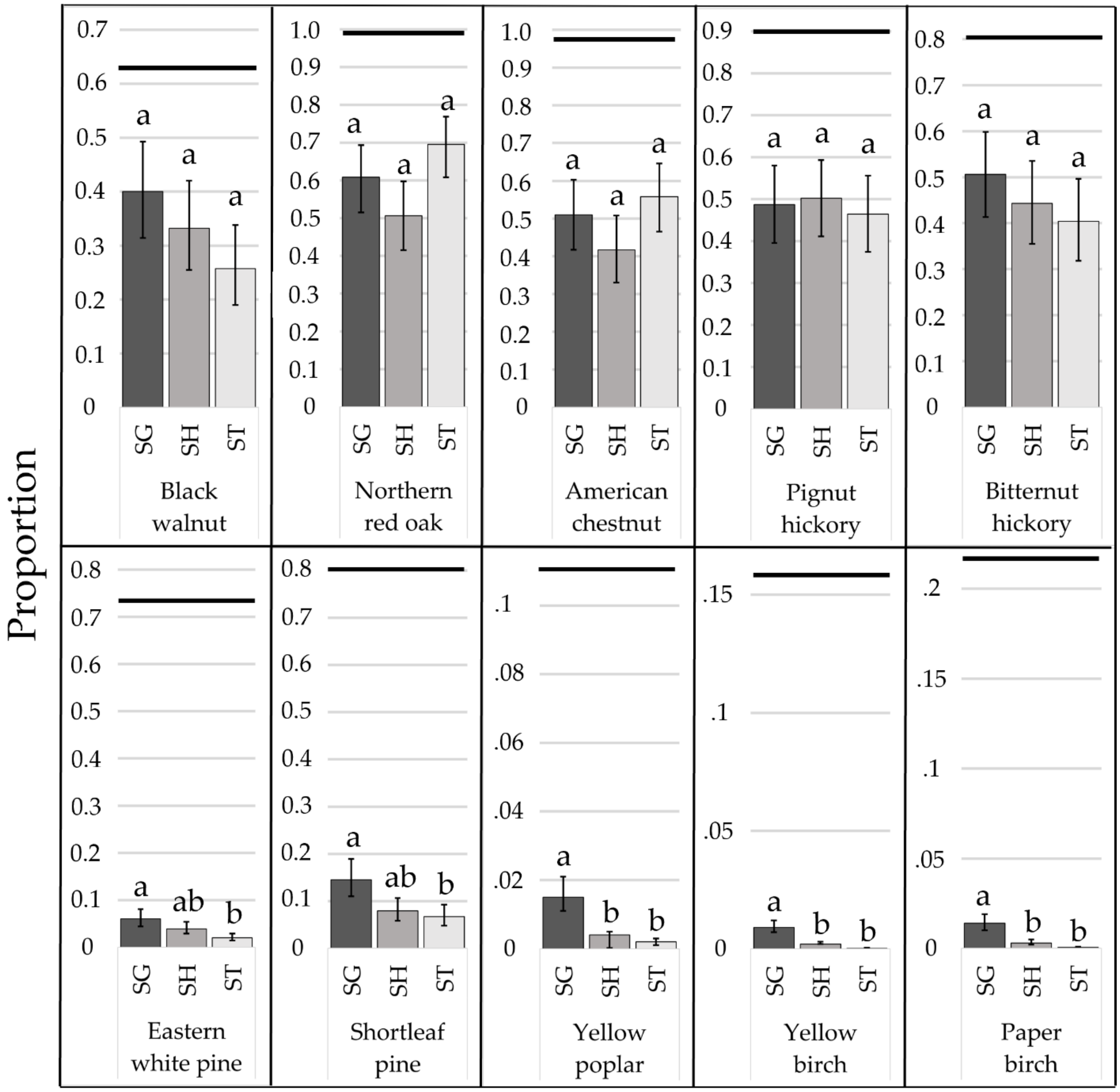

Figure D.1. Results of generalized regression models (beta distribution) testing the effects of harvest treatment on seedling establishment in uncaged subplots at the end of the first growing season, with 95% confidence intervals. Harvest treatments include small group selection (SG), shelterwood (SH) and seed tree (ST). The y-axis represents the proportion of seedlings established relative to the total number of seeds sown; the horizontal black bars indicate greenhouse-derived seed viability estimates for each species. Tukey-Kramer Honest Significant Difference (HSD) tests were used for pairwise comparisons within each species panel; treatments sharing a letter are not significantly different at $\alpha = 0.05$. Species are ordered from largest to smallest seed kernel mass. Note species-specific y-axes.

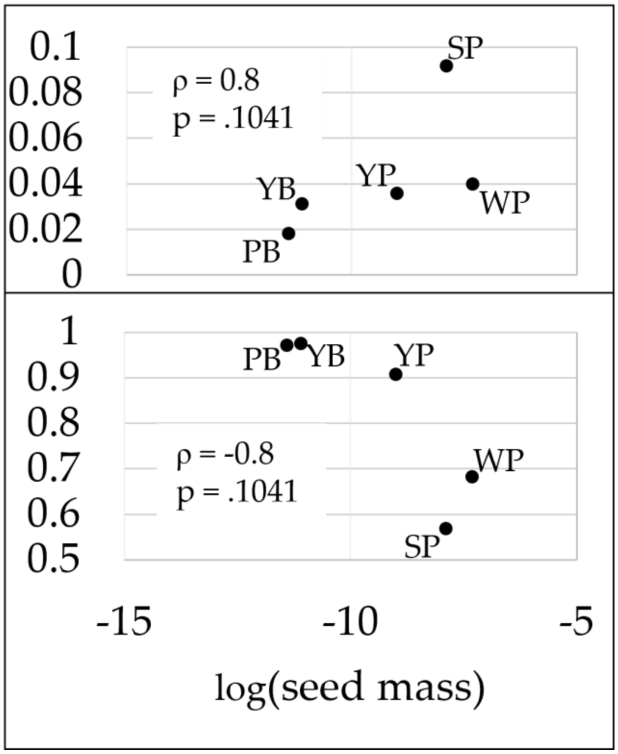

Figure D.2. Spearman's rank correlations between seed kernel mass of broadcast-sown species in uncaged subplots and two establishment metrics. Top panel: seedling establishment proportion in uncaged subplots (harvest treatments pooled). Bottom panel: proportional reduction in establishment between environmental extremes in uncaged subplots, calculated as 1 – (seed tree establishment proportion / small group selection establishment proportion).

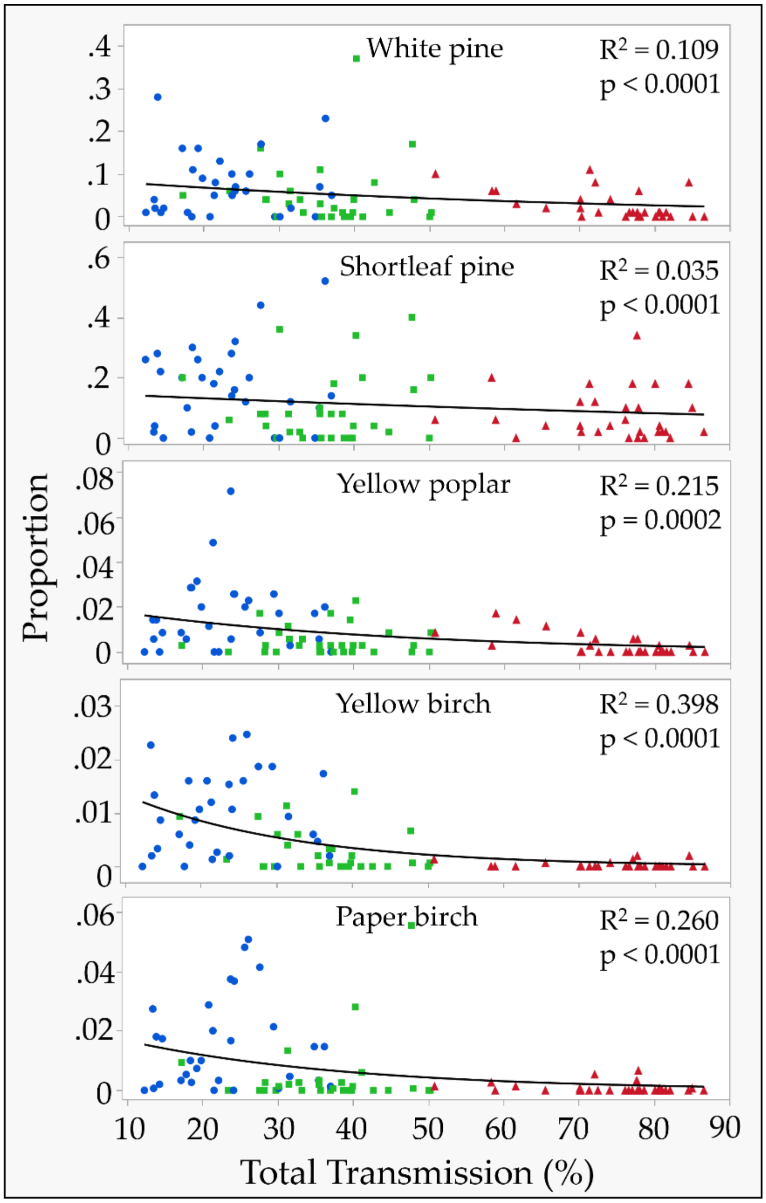

Figure D.3. Relationship between plot-level light availability (total transmission percentage) and seedling establishment proportion in uncaged subplots for species exhibiting differential establishment across harvest treatments (Table 5.3). Colors and shapes indicate harvest treatment: blue circles denote small group selection, green squares indicate shelterwood, and red triangles represent seed tree. Note variable y-axes across species panels. Corresponding results for uncaged seed were also significant and are presented in Appendix D. Mean light availability by treatment: small group selection = 23.0%, shelterwood = 36.4%, seed tree = 74.5%.