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PLANT COMMUNITY RESPONSE TO NOVEL SILVICULTURAL TREATMENTS
IN GREAT LAKES NORTHERN HARDWOODS

By
Stefan F. Hupperts

A DISSERTATION

Submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

In Forest Science

MICHIGAN TECHNOLOGICAL UNIVERSITY

2019

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This dissertation has been approved in partial fulfillment of the requirements for the Degree of DOCTOR OF PHILOSOPHY in Forest Science.

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Preface

Chapter 2 of this dissertation includes work from a multi-authored, peer-reviewed journal article. Subsequent chapters include work in various stages of preparation. Copyright (Chapter 2), authorship, and status for each chapter are provided below. The Chapter 2 publication is acknowledged in a footnote on the first page of the chapter. Request for permission to reprint published material from the Institute of Chartered Foresters via Oxford University Press is included in Appendix A.

Chapter 2, Promoting structural and species diversity in Great Lakes northern hardwoods: A conceptual model and its application: © by the Institute of Chartered Foresters. Permission to use copyright material is included in Appendix A. Stefan F. Hupperts and Yvette L. Dickinson conceived the review, with input from Christopher R. Webster and Christel C. Kern. S.F. Hupperts wrote the original manuscript. All authors contributed to manuscript edits.

Chapter 3, Initial regeneration response following novel silvicultural treatments in Great Lakes northern hardwoods: in preparation for submission to the peer-review journal *Forest Ecology and Management*. Yvette L. Dickinson and Stefan F. Hupperts conceived the study. Study design by Y.L. Dickinson, Christopher R. Webster, and Robert E. Froese. Field work, data analysis, and original manuscript preparation performed by S.F. Hupperts. Input provided by all authors.

Chapter 4, Increasing plant taxonomic diversity masks a decline in phylogenetic diversity following experimental management disturbances in a northern hardwood forest: in preparation for submission to the peer-reviewed *Journal of Ecology*. Yvette L. Dickinson and Stefan F. Hupperts conceived the study. Y.L. Dickinson, Christopher R. Webster, and Robert E. Froese designed the study. S.F. Hupperts conducted all field work, data analysis, and manuscript preparation. All authors provided input and contributed to manuscript edits.

Chapter 5, Clearcut strips, deer exclosures, and herbicide show early promise for sugar maple recruitment in areas experiencing regeneration failure: in preparation for the peer-review journal *Canadian Journal of Forest Research*. American Forest Management, Inc. conceived and designed the study, in addition to conducting all field work. Stefan F. Hupperts performed data analysis and wrote the original manuscript. Yvette L. Dickinson and Christopher R. Webster provided input and manuscript edits.

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Abstract

The objective of this dissertation is to assess plant community response across a range of silvicultural disturbances and test ecological hypotheses to better inform ecologists and forest managers. To provide context for the utility of revising silvicultural systems, I review natural disturbance regimes and historical practices that have shaped contemporary Great Lakes northern hardwood forests (Chapter 2). Further, I identify important ways to expand the silvicultural toolbox and better emulate natural disturbance regimes. Building on this theoretical underpinning, I investigate the initial regeneration and plant community response to two novel silvicultural experiments: the Northern Hardwood Experiment for Enhancing Diversity (NHSEED) near Alberta, Michigan, and a strip clearcut experiment near Mountain Iron, Michigan. Three themes emerged from the findings in this dissertation. First, seedlings and saplings receive few benefits from reduced canopy cover if they cannot overcome additional limitations. For example, yellow birch (*Betula alleghaniensis* Britt.) seedling density was better predicted by conspecific overstory basal area and litter depth variation than silvicultural treatments (Chapter 3), and sugar maple recruitment into the sapling size class in clearcut strips may be limited by deer browse (Chapter 5). Second, silvicultural disturbances tend to favor low-mass fruit, long-lived fruit, or vegetative reproduction, except for sugar maple which relies on robust advance regeneration to benefit from overstory disturbances (Chapters 3, 4 and 5). Third, the relationship between disturbance severity and diversity is not conclusive. Initial responses to silvicultural disturbances did not follow the intermediate disturbance hypothesis, which proposes

that diversity is maximized at intermediate levels of disturbance intensity or frequency (Chapter 4). Moreover, taxonomic and phylogenetic diversity do not always respond similarly to disturbances (Chapter 4), suggesting that both indices should be incorporated into informed management decisions. Integrating these findings into management planning may allow better predictions to silvicultural disturbances now and in the future.

1. Introduction

Disturbances are among the most important determinants of ecosystem structure and function, and understanding how they shape successional pathways is a fundamental objective of forest ecology. Plant community responses to disturbance are often monitored to assess the resistance (i.e. ability to remain relatively unchanged) or resilience (i.e. ability to recover within a defined time period) of an ecosystem to a given disturbance and responses are often regulated by dispersal, environmental, or competitive filtering effects (Kraft et al. 2015, Cadotte and Tucker 2017, Kohler et al 2017, Timpane-Padgham et al 2017). Low-severity disturbances, for example, often create environmental conditions which might favor species from the regional pool that have higher shade tolerance and heavier fruits, along with adaptations to low nutrient availability (McIntyre et al. 1995). In contrast, high-severity disturbances often favor species from the regional pool that have low shade tolerance, high growth rates, and low-mass or long-lived fruits. Because the regional species pool is continually changing due to migration and non-native species introductions, understanding the traits associated with plant community assembly could provide more comprehensive information to ecologists and forest managers planning for future conditions (Fukami et al. 2005, Messier et al. 2010). Further, emulating natural disturbance regimes is a primary goal of contemporary silviculture (Long 2009).

Taxonomic diversity is a common index for monitoring ecosystem characteristics over temporal and spatial scales. Ecosystems with high relative diversity are commonly assumed to be more resilient to disturbances owing to higher response

diversity, or the variety of different reactions among species, when compared to ecosystems with low relative diversity (Elmqvist et al. 2003). Taxonomic diversity is undoubtedly the most frequently reported index, but phylogenetic and trait diversity can provide further insight into the underlying factors that govern community assembly and species interactions (Mason et al. 2005, Cavender-Bares et al. 2009, Mouillot et al. 2013). Comparing taxonomic, phylogenetic, and trait diversity indices may consequently provide a more comprehensive understanding of disturbance effects on plant communities.

The relationship between disturbance severity, disturbance frequency, and diversity has often been assumed to follow the Intermediate Disturbance Hypothesis (IDH). This hypothesis proposes that high-severity or frequency disturbances promote disturbance-adapted species at the expense of disturbance-intolerant species, while low-severity or frequency disturbances tend to promote a contrasting assemblage of species. Intermediate severity or frequency disturbances, however, fail to exclude disturbance-adapted and disturbance-intolerant species and consequently promote communities of greater taxonomic diversity (Grime 1973, Connell and Slatyer 1977, Connell 1978). Criticisms remain (Fox 2013), as many studies have found little evidence of the IDH in field experiments. Testing the IDH in the context of silvicultural disturbances could reveal important insights into community assembly following management-based disturbances.

Contemporary silviculture aims to emulate natural disturbance regimes and incorporate them into management practices. In the Great Lakes northern hardwood

ecosystem of North America, pre-European settlement forests were structured by disturbances and indigenous practices within the range of natural variability (Frelich and Lorimer 1991, Whitney 1994, Zhang et al. 1999). Northern hardwood forests are characterized by a wide spectrum of disturbance severity, ranging from low-severity windthrow to catastrophic blowdown, with substantial variation in frequency. Catastrophic disturbances (>1.0 ha) are somewhat rare in Great Lakes northern hardwoods, with 722 – 1210 yr rotation periods (Canham and Loucks 1984, Zhang et al. 1999), yet are fundamental in structuring the ecosystem by creating environmental conditions favorable for disturbance-adapted species. In contrast, lower-severity windthrow events topple large, senescent trees, creating gaps favorable for species adapted to intermediate-severity disturbances (Tubbs 1977, Frelich and Lorimer 1991). Further, indigenous people used fire to manage forests in the Great Lakes region, though this practice was primarily limited to fire-prone forests, grasslands, and savannas (Whitney 1994, Zhang et al. 1999). This range in windthrow severity is credited with maintaining structural and species diversity in Great Lakes northern hardwood forests (Frelich and Lorimer 1991), but shifting disturbance regimes or declines in forest structural diversity could influence successional pathways. During the late nineteenth century, European settlers clearcut vast stands of white pine- (*Pinus strobus* L.) and red pine- (*Pinus resinosa* Sol. Ex Aiton) dominated forests throughout the Great Lakes region during a period known as the ‘cutover’ (Whitney 1994, Gough 1997). This severe disturbance was exacerbated by repeated burning of residual slash. Further attempts at conversion to agricultural land contributed to a substantial loss of

ecological legacies, or the species interactions, adaptations, and biological components remaining following a disturbance (Webster et al. 2018).

Abandoned agricultural fields ultimately succeeded to hardwood-dominated second-growth forests, and initial periods of high-grading progressed to the widespread application of single-tree selection as planned forest management became more prevalent (Jacobs 1987, Kern et al. 2014a, Pond et al. 2014). Under single-tree selection, individual trees are harvested across a range of diameter sizes to attain a pre-determined residual basal area, and repeated every 10 – 20 yrs. This harvesting system uses less severe disturbances than other common systems and is typically conducted during winter to limit soil disturbance from harvesting machinery. Low-severity harvesting combined with limited soil disturbance favors shade tolerant species such as sugar maple (*Acer saccharum* Marsh.) at the expense of intolerant or midtolerant species (Angers et al. 2005, Neuendorff et al. 2007). Along with exploitative harvesting and single species management, the widespread (Pond et al. 2014) and decades-long application of single-tree selection has contributed to a decline in structural and species diversity (Schulte et al. 2007) which could reduce the adaptive capacity of Great Lakes northern hardwoods (Duveneck et al. 2014). In other regions of the Great Lakes, however, biological challenges have interacted with traditional management to instead cause regeneration failure, including that of sugar maple. Long-term application of single-tree selection and the loss of old, mature trees could be reducing seed input and causing declines in advance regeneration. Overwhelming browse pressure from increasing white-tailed deer (*Odocoileus virginianus* Zimmerman) populations

combined with heightened competition from shrubs and graminoids are further compounding efforts to regenerate sugar maple, and healthy stand development appears grim without shifts in silvicultural systems.

Alternative silvicultural systems historically not applied in northern hardwoods have recently been explored as tools to restore structural, species, and trait diversity (Kern et al. 2017, Raymond and Bédard 2017, Webster et al. 2018). Shelterwoods, for example, are intermediate-severity disturbances when compared to single-tree selection and clearcut and may create environmental conditions suitable for regeneration of shade midtolerant species (Raymond et al. 2009). Combined with soil disturbance techniques to create heterogenous germination site conditions, herbicide application to reduce competition from shrubs and graminoids, and eliminating browse pressure from white-tailed deer, such methods may be viable alternatives to traditional single-tree selection harvesting in unhealthy stands. Moreover, using experimental manipulations to explore alternative silvicultural systems could provide a unique opportunity to test ecological hypotheses among different management practices.

1.1 Objectives of this dissertation research

This dissertation research aims to reconcile theory and practice by using novel silvicultural experiments to test well-known ecological hypotheses, and alternative regeneration techniques. My primary objective is to assess ground-layer plant community responses and regeneration dynamics across a range of novel silvicultural treatments. First, I review the disturbance and management history of Great Lakes

northern hardwoods and propose a conceptual model to inform management systems. Second, I assess regeneration dynamics to identify initial species responses among treatments in a novel silvicultural experiment - the Northern Hardwood Silvicultural Experiment for Enhancing Diversity (NHSEED) - at the Michigan Tech University Ford Forest in Alberta, Michigan. Third, I test the Intermediate Disturbance Hypothesis by assessing the response of plant community composition, taxonomic diversity, trait diversity, and phylogenetic diversity in the context of the NHSEED experiment. I then investigate the use of alternate clearcut and selection harvesting strips to regenerate sugar maple in localized areas of regeneration failure. In the final chapter I provide a brief synthesis and provide general conclusions.

2. Promoting structural and species diversity in Great Lakes northern hardwoods: a conceptual model and its application¹

2.1 Abstract

Forest ecosystems are shaped by their historical disturbance regime. Structural and species diversity are driven by disturbance frequency, patch size, and microsite disturbance severity in forests across the globe. Forest management in Lake State northern hardwoods, however, has primarily used high-frequency, low- to moderate-severity canopy disturbance, and low severity microsite disturbance harvesting techniques such as single-tree selection. Catastrophic disturbances during European settlement followed by the widespread and long-term use of uniform approaches to forest management have homogenized managed forests and created a need to emulate a fuller range of historically prevalent natural disturbances. We present a conceptual model based on complex adaptive forest management that proposes five primary factors including mean patch size, proportion disturbed, frequency, degree of exposed mineral soil, and coarse woody debris input. This model demonstrates the need for a greater range of silvicultural systems to more closely emulate the range of variability associated with natural disturbance regimes. In Great Lakes northern hardwoods, using a greater variety of silvicultural systems including those with larger patch cuts and greater soil disturbance, may restore and promote structural and tree species diversity in these

¹This chapter © by the Institute of Chartered Foresters 2018. *Citation:* Hupperts, S.F., Y.L. Dickinson, C.R. Webster, C.C. Kern. Promoting structural and species diversity in Great Lakes northern hardwoods: a conceptual model and its application. *Forestry: An International Journal of Forest Research* 92(1): 16-25.

forests by creating greater microsite heterogeneity. Applying this conceptual model to forests more broadly, while still considering regionally-specific factors, may help restore species and structural diversity and ultimately, ecosystem resilience.

2.2 Introduction

Long-term use of systematic forest management has tended to simplify the structure of forests worldwide (Hall *et al.*, 2003; Angers *et al.*, 2005; Montes *et al.*, 2005; Neuendorff *et al.*, 2007; Yoshida *et al.*, 2017). A shift in natural disturbance severity such as reduced gap sizes due to fewer large trees, and subsequent declines in species diversity owing to fewer suitable germination sites (Woods, 2000; Zhang *et al.*, 2000; Schulte *et al.*, 2007), could make forests less resilient to future disturbances and consequently less economically reliable (Niese and Strong, 1992; Dymond *et al.*, 2014, 2015). Long-term implementation of uniform management may reduce structural diversity (Angers *et al.*, 2005; Neuendorff *et al.*, 2007) and species functional trait diversity (Neuendorff *et al.*, 2007; Curzon *et al.*, 2017), which are integral components of ecosystem resilience and resistance (Yachi and Loreau, 1999; Elmqvist *et al.*, 2003; Tilman *et al.*, 2006; Downing *et al.*, 2012). Higher functional trait diversity can contribute to greater complementarity or functional redundancy, which consequently strengthen resilience or resistance, respectively (Downing *et al.*, 2012). Ecosystem resilience is an especially critical attribute in the face of global change if novel disturbance regimes become predominant (Holling, 1973; Elmqvist *et al.*, 2003; Drever *et al.*, 2006; Messier *et al.*, 2013; Deroose and Long, 2014).

In this paper, we review the importance of natural disturbances to forest composition, structure, and function, and discuss the impact of European settlement and forest management practices on forests using northern hardwoods in the Great Lakes region as a case study. Furthermore, we propose a conceptual model to demonstrate the mismatch between historical natural disturbance regimes and settlement and forest management disturbances on a stand scale. Finally, we posit that forest managers need to implement a greater range of silvicultural systems to adequately emulate natural disturbance regimes and maintain forest ecosystem resilience. We discuss an example specific to Great Lakes northern hardwoods, though our conceptual model can be applied to forests across the globe using five identifiable components of disturbance.

2.3 Historical natural disturbance regimes

2.3.1 Disturbance effects on landscape-level patterns

Natural disturbances are fundamental processes in forest ecosystems across the globe. Pickett and White (1985) define a disturbance as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment.” Niches created by natural disturbances, for example, are largely credited with maintaining ecosystem biodiversity (Ricklefs, 1976; Denslow, 1980). Moreover, stand structure, plant community composition, and biogeochemical cycles are often highly correlated with the regional disturbance regime (Pickett and White 1985; Oliver and Larson, 1996; Halpin

and Lorimer, 2016). As such, ecosystems are strongly influenced by their disturbance history.

Forest ecosystems across North America are no exception. A defining feature of eastern hemlock (*Tsuga canadensis* (L.) Carrière) - white pine (*Pinus strobus* L.) - northern hardwood forests in the Great Lakes region, for example, is the range of severity of windthrow disturbances under which these species evolved (Whitney, 1987, 1994; Frelich and Lorimer, 1991; Hanson and Lorimer, 2013). Though some species such as eastern hemlock and American beech (*Fagus grandifolia* Ehrh.) have more limited distribution, Great Lakes northern hardwoods generally had similar natural disturbance regimes across their range. Large windthrow events typically had high severity but long-return intervals, while small windthrow events had relatively low severity but short-return intervals. For example, Zhang *et al.* (1999) estimated a presettlement rotation period of 722 yr for catastrophic windthrow (>1.0 ha) in northern hardwoods in the Luce District of Upper Michigan, and Canham and Loucks (1984) estimated a return time of 1210 yr for windthrow greater than 1.0 ha when pooling all forest types across northern Wisconsin. Though catastrophic blowdowns were rare, an extensive gradient of blowdown severity existed ranging from treefall to stand-leveling. A rotation period of 94 yr and 236 yr was estimated for moderate (≥ 140 km/hr) and severe (≥ 180 km/hr) windthrow, respectively, in northern hardwoods across the Great Lakes region from Minnesota to New York (Frelich and Lorimer, 1991). Moreover, frequent low severity windthrow (51-69 years for >10% canopy removal) maintained hemlock - hardwood dominance in western Upper Michigan (Frelich and Lorimer,

1991; Frelich, 2002). The small gaps created by treefall allowed shade-tolerant species to persist, while larger gaps promoted the recruitment of less tolerant species such as yellow birch (*Betula alleghaniensis* Britt.). To contrast, severe fire typically had much longer return intervals. Catastrophic fire reached a rotation period upwards of 2600 yr in Upper Michigan (Zhang *et al.*, 1999; Frelich and Lorimer, 1991). Despite their infrequency, catastrophic disturbances were critical for maintaining diversity in these forests (Woods, 1984, 2000; Frelich, 2002). Species such as white pine, red oak (*Quercus rubra* L.), and paper birch (*Betula papyrifera* Marshall) were recruited following fires that exposed mineral soil and decreased competition from sugar maple (*Acer saccharum* Marshall; Frelich, 2002). Lastly, evidence suggests that Indigenous peoples used fire as a management tool, though the extent of intentional fire use varied among regions and forest types (Whitney, 1994; Zhang *et al.*, 1999).

2.3.2 Disturbance effects on microsites

While disturbances of stand-level or greater patch size affect whole forest ecosystems, species-specific responses are driven by changes in microsite conditions such as light availability, surface soil moisture, temperature, and available nutrients. Such factors are important for plant germination and survival, and are frequently driven by patch size and abundance of both exposed mineral soil and coarse woody debris (Roberts and Gilliam, 1995; Roberts, 2004; Bailey *et al.*, 2012). Light availability, for example, often structures understory plant communities and, consequently, tree seedling communities (Scheller and Mladenoff, 2002; Burton *et al.*, 2014; Sabatini *et al.*, 2014).

Moreover, gaps created by windthrow or treefall have been shown to promote both plant species diversity and functional diversity in ecosystems across the globe due to differences in light requirements and shade tolerance among species (Ricklefs, 1976; Denslow, 1980; Kern *et al.*, 2014a). Small canopy disturbances such as treefall favor shade tolerant species, while large canopy disturbances such as severe windthrow typically favor shade intolerant species. Shade tolerant understory herbs often respond negatively to the wide fluctuations in temperature and moisture typically resulting from disturbances that simultaneously increase light availability (Small and McCarthy, 2002). Moreover, the highest densities of shade mid-tolerant yellow birch and tolerant hemlock have been found in the southern edges of large gaps after two (Raymond *et al.*, 2006) and ten (Poznanovic *et al.*, 2014) growing seasons, owing to the creation of adequate germination substrate but relatively little tolerance for wide fluctuations in temperature or rooting zone moisture.

Surface soil moisture is highly heterogenous among microsites throughout forest stands due to differences in aspect, vegetation cover, underlying soil substrate, organic matter content, and topographic location. Natural disturbances such as windthrow and wildfire can further increase heterogeneity of soil moisture among microsites (Peterson *et al.*, 1990; Ritter *et al.*, 2005; Poznanovic *et al.*, 2014b). Small-scale disturbances generally maintain greater consistency in soil moisture, while large-scale disturbances generally create greater variability in soil moisture (Guo *et al.*, 2002). For example, previous work has demonstrated that soil moisture increases with gap size immediately following harvest, likely a result of less canopy interception and fewer trees transpiring

(Burton *et al.*, 2014). On the other hand, rapidly invading shrubs may instead decrease soil moisture (Royo and Carson, 2006). Furthermore, soil moisture and light availability are often correlated and consequently affect the composition of tree recruits in gaps (Poznanovic *et al.*, 2014b).

Natural disturbances also greatly affect available nutrient dynamics. As with soil moisture, small disturbances generally maintain greater consistency in available nutrient levels while large disturbances typically create a pulse of available nutrients. Though often dependent on remaining vegetation, rates of nitrogen mineralization and nitrification generally increase after disturbances due to the large input of organic matter, subsequent increase in microbial activity, and less uptake by trees (Likens *et al.*, 1970; Attiwill and Adams, 1993). Moreover, the composition of canopy trees has a large effect on soil nutrient dynamics. Sugar maple-dominated stands have high rates of nitrogen mineralization and nitrification, while hemlock-dominated stands have lower rates of nitrogen mineralization and nitrification, largely due to differences in leaf chemistry between species (Lovett and Mitchell, 2004; Lovett *et al.*, 2004). On the other hand, Mladenoff (1987) observed the opposite trend under recently created treefall gaps.

Surface soil moisture and available nutrients are also often correlated with the abundance of coarse woody debris, which has a higher and more stable moisture content when compared to mineral soil and leaf litter (Jurgensen *et al.*, 1997; Laiho and Prescott, 2004; Bailey *et al.*, 2012). For example, coarse woody debris adsorbs up to 220% of its dry mass in water, compared to 20-40% for mineral soil (Fraver *et al.*,

2002). The ability of decaying woody debris to retain soil moisture and unique fungal communities appears to favor yellow birch and hemlock regeneration, which often have greater germination and survival on decaying woody debris (Marx and Walters, 2008; Poznanovic *et al.*, 2014a). Decaying logs further provide substrate for fungi important in nutrient cycling and symbiotic relationships (Heilmann-Clausen and Christensen, 2003; Poznanovic *et al.*, 2014a; Dove and Keeton, 2015).

The interacting effects of natural disturbances and competing vegetation can further influence regeneration dynamics. For example, the longevity of raspberry (*Rubus* spp.) seeds and prolific growth of raspberry following a disturbance makes it an important competitor in some northern hardwood forests following disturbance (Donoso and Nyland, 2006; Kern *et al.*, 2017). Moreover, Kern *et al.* (2013a) found that the abundance of competing shrubs increased with gap size. Another strong competitor, sedge (*Carex* spp.) reproduces vegetatively, a trait that allows it to spread rapidly without relying on seed germination (Hale *et al.*, 2006; Powers and Nagel, 2009). The abundance of raspberry and sedge in recently disturbed (natural and anthropogenic) northern hardwoods is a prime example of the systematic rise of recalcitrant understory layers worldwide due to interacting effects of management and elevated levels of herbivory (Royo and Carson, 2006).

2.4 Recent disturbance regimes

2.4.1 European settlement-related disturbances

The Great Lakes forests fueled rapid industrial growth and settlement during the late nineteenth century. Extensive areas of pine forest were logged within several decades during this period, referred to as the “cutover” (Gough, 1997; Wales, 1939; Whitney, 1994). Following the cutover, largely unintentional slash fires of residual debris nearly eliminated remaining biological legacies such as seed banks, coarse woody debris, symbiotic organisms, organic nutrients, and advance regeneration that would otherwise promote ecosystem resilience (Whitney, 1987; Johnstone *et al.*, 2016). As a result, these two major successive disturbances dramatically altered forest cover by favoring sprouting species such as maple, oak, paper birch, and aspen (*Populus tremuloides* Michx. and *P. grandidentata* Michx.). Rapidly growing white-tailed deer (*Odocoileus virginianus*) densities from 1920-1940s (Leopold *et al.*, 1947) further favored a transition from conifers to hardwoods (Ross *et al.*, 1970; Rooney and Waller, 2003; Zenner and Peck, 2009). Following the peak of logging in the Great Lakes around 1892, almost all merchantable pine and hemlock were logged by 1920 (Whitney, 1987; Williams, 1989). When pine was almost depleted in Michigan by the 1890s, a new focus on hardwoods emerged. Consequently, the primary lumber species shifted by 1912 from pine to sugar maple (Whitney, 1987).

2.4.2 Forest management practices

Major advances in silviculture for the northern hardwoods were developed between 1930-1950s. Though many approaches were developed, single-tree selection became widespread in the western Great Lakes, with approximately 85% of non-

industrial managed land using uneven-aged management comprised primarily of single-tree selection (Jacobs, 1985; Kern *et al.*, 2014b). Under single-tree selection, trees are extracted singly and dispersed across a range of diameter sizes until a residual basal area goal is reached, then repeated every 10 - 20 yr (e.g., Wisconsin DNR *Silviculture Handbook*, 2003). This silvicultural system primarily favors shade tolerant species such as sugar maple by creating openings of approximately 0.004 - 0.03 ha on a decadal basis (Crow *et al.*, 2002; Wisconsin Forest Management Guidelines, 2011; Kern, *et al.*, 2014b). In addition to its low-severity canopy removal, winter harvesting with low-impact machinery further minimizes soil microsite disturbance, limiting opportunities for trees that require bare mineral soil to regenerate. Frequent harvest entries, upper diameter limits proposed by the widely used Arbogast Guide (Arbogast, 1957), and mill preferences also limited development of old-senescent trees and large coarse woody debris, further homogenizing stand structure by decreasing microsite variability created when large trees are toppled by windstorms, and ultimately reducing the abundance of several economically valuable species such as yellow birch (Webster and Lorimer, 2005; Neuendorff *et al.*, 2007; Shields *et al.*, 2007; Salk *et al.*, 2011).

Several recent studies have demonstrated the declining structural and species diversity of northern hardwoods due to management practices. Neuendorff *et al.* (2007) reported an increase in the relative density of sugar maple and concurrent decrease in relative density of yellow birch after 40 years of single-tree selection in an Upper Michigan northern hardwood forest. Seedling and sapling layers were dominated by sugar maple in both managed stands and stands unmanaged since European settlement,

but unmanaged stands had greater species richness. Moreover, in sugar maple-dominated forests of southwest Quebec, the continuous application of selection cutting created dense foliage layers throughout the stand understory due to the large post-harvest recruitment of advance regeneration (Angers *et al.*, 2005). The authors suggest that the long-term application of selection systems in sugar maple-dominated forests may yield homogenized stand structure and composition, along with limited biodiversity at the stand and landscape scale. Also in southwest Quebec, Doyon *et al.* (2005) observed that low horizontal heterogeneity within single-tree selection stands was significantly correlated to avian assemblages, and ultimately recommended the application of more diverse silvicultural systems. On a landscape scale, Schulte *et al.*, (2007) summarized anthropogenic disturbances and found an increase in dominance of both sugar and red maple from pre- to post-settlement in the Great Lakes states of Minnesota, Wisconsin, and Michigan due to the initial widespread harvesting of pine followed by repeated slash fires and finally, the widespread and long-term application of single-tree selection.

2.4.3 Emerging disturbances

Though historically-prevalent natural disturbances continue to shape forest ecosystems, several additional influences have arisen since settlement due to regional and global change. The effect of increasing white-tailed deer populations on regeneration in Great Lakes northern hardwood forests has been well-documented in the last two decades (Alverson *et al.*, 1988; Rooney and Waller, 2003; Powers and Nagel,

2009; Kern *et al.*, 2012), particularly because deer populations in northeastern Wisconsin and southern Upper Michigan are relatively high (WDNR, 1998; Rooney and Waller, 2003; Powers and Nagel, 2009; Sabo *et al.*, 2017). The survival of preferentially browsed seedlings, including sugar maple, is compromised in regions with high deer populations due to intense herbivory, leaving behind unpalatable and economically undesirable species such as ironwood (*Ostrya virginia*; Matonis *et al.*, 2011). High deer herbivory further promotes the rapid spread of Pennsylvania sedge (*Carex pensylvanica*) by decreasing the cover of preferentially browsed herbs, seedlings and saplings, therefore reducing competition for resources (Powers and Nagel, 2009).

European earthworms represent another major influence on regeneration dynamics in northern hardwood forests. European earthworm invasion likely exacerbates the negative impacts of deer herbivory by dramatically altering soil conditions and consuming the forest floor, which sugar maple seeds rely on as a germination substrate (Hale *et al.*, 2006, Corio *et al.*, 2009). For example, Corio *et al.* (2009) found lower seedling stem counts of sugar maple in heavily earthworm invaded stands when compared to less invaded stands. Moreover, earthworm invasion is often highly correlated with the spread of Pennsylvania sedge, further complicating tree regeneration dynamics in impacted forests (Bohlen *et al.*, 2004; Hale *et al.*, 2006).

While the effects of earthworm invasion on tree regeneration are largely indirect, other nonnative pests have caused devastating declines in native tree species through direct impacts. Beech bark disease complex (*Cryptococcus fagisuga* Lindinger and *Nectria coccinea* var. *faginata* (Pers.) Fr.), emerald ash borer (*Agrilus planipennis*

Fairmaire), European gypsy moth (*Lymantria dispar* L.), and oak wilt (*Bretziella fagacearum* (T. W. Bretz) J. Hunt) are several examples of nonnative invasive pests which have greatly impacted Great Lakes forests (Gandhi and Herms, 2010; Pugh *et al.*, 2011; Lovett *et al.*, 2016). The death of important tree species such as American beech, ash (*Fraxinus* spp.), and oak (*Quercus* spp.) can have large indirect effects on plant community ecology and biogeochemical cycles, not to mention the large economic impacts (Aukema *et al.*, 2011; Lovett *et al.*, 2016).

Yet another threat, climate change will likely impact Great Lakes forests as deviations from historical temperature and precipitation trends are likely to cause shifts in plant species composition. Higher winter temperatures may favor species currently at their northern range, while negatively influencing species currently at their southern range. Combined with less frequent but more intense precipitation events, drought-tolerant species (e.g., oaks and aspen) may fare better than less drought-tolerant species such as sugar maple, yellow birch, and eastern hemlock (Handler *et al.*, 2014). Though restoration efforts are typically guided by historic species composition, this reliance may prove irrelevant in the face of climate change (Harris *et al.*, 2006).

2.5 Disturbance-based forest management

The emergence of ecological forestry and complexity science has offered insights into how forests can be managed as disturbance-based, complex adaptive systems (Drever *et al.*, 2006; Messier *et al.*, 2013). Disturbance-based silviculture uses regionally-specific natural disturbance regimes as blueprints for management practices

to maintain adaptive and resilient forest ecosystems (Drever *et al.*, 2006; Messier *et al.*, 2013).

Rather than focusing management on a single objective such as timber production or wildlife habitat, managing forests for ecosystem resilience requires the holistic consideration of ecosystem components, temporal and spatial scales, and their interactions, which also helps maintain ecosystem services (Messier *et al.*, 2013).

Ecosystem services are benefits provided by the provisional, regulating, cultural, and supporting components of an ecosystem (*Millenium Ecosystem Assessment*, 2005).

Without the ability of a forest ecosystem to quickly recover from a perturbation, people cannot reliably depend on the forest for the services it provides. Managing forests as complex adaptive systems therefore fits well within the framework of ecosystem services. For example, a resilient forest ecosystem can provide clean water, timber, and fiber. It mitigates unexpected flooding disasters because it has evolved under its current (albeit, pre-climate change) disturbance regime (Seymour and Hunter, 1999). A resilient forest ecosystem can naturally purify water by filtering contaminants, absorbing nutrients, and preventing soil erosion, though this depends on the successional state of the forest. It provides aesthetics and recreational opportunities, and further provides spiritual benefits by maintaining species diversity, and consequently species that may be historically important to Indigenous and local communities (Gadgil *et al.*, 1993, Emery *et al.*, 2014). Functional trait diversity, which often links above and belowground processes (Bardgett *et al.*, 2014; Alberti *et al.*, 2017), is another key component of ecosystem resilience (Elmqvist *et al.*, 2003; Downing *et al.*, 2012; Whitfield *et al.*,

2014). The functional trait diversity of a resilient ecosystem may help maintain a balanced nutrient budget and regulate species populations, consequently limiting the opportunity for invasion (Davis *et al.*, 2000; Downing *et al.*, 2012).

The increasing threats of climate change and species invasion require adaptability in management techniques. Though the severity of future natural disturbances is unpredictable, applying a variety of silvicultural systems using historically-prevalent natural disturbances as a management blueprint, within the natural range of variability, gives the ecosystem greater potential to maintain productivity, stability, and resilience (Drever *et al.*, 2006; Messier *et al.*, 2013, Nolet *et al.*, 2018).

2.6 Conceptual models to identify gaps in management and find solutions

2.6.1 Identifying management gaps

Historically, there has been a mismatch between silvicultural practices and regionally specific disturbance regimes on a stand scale. As Figure 2.1 illustrates, treefall is characterized by a relatively small mean patch size, small proportion of stand disturbed, low degree of exposed mineral soil, low coarse woody debris input, but relatively high frequency. Consequently, microsites with a thick leaf litter layer overlaying pit-mound topography, and little understory light availability, are common across stands which historically experienced treefall as the dominant disturbance regime and are particularly favorable for sugar maple and American beech regeneration (Tubbs, 1977; Frelich, 2002; Kern *et al.* 2013b; Gauthier *et al.*, 2016). On the other hand, windthrow events that have lower disturbance frequencies combined with greater mean

patch size, more exposed mineral soil, and more coarse woody debris input tended to favor additional species such as hemlock, yellow birch, aspen, and white pine (Frelich, 2002; Webster and Lorimer, 2002; Prévost and Raymond, 2012). Furthermore, high-severity fires were at the opposite end of the spectrum from treefall by having relatively low frequency combined with high mean patch size, high degree of exposed mineral soil, and high input of coarse woody debris (albeit charred) consequently favoring a greater abundance of pioneer species such as paper birch and aspen (Frelich, 2002). Overall, the large range of these disturbances tended to maintain greater structural and species diversity than seen today.

Historical management practices, on the other hand, have focused on the extremes of these disturbances. The cutover, including subsequent slash fires, most closely emulated high-severity fires (high on all axes of Figure 2.2). Single-tree selection has since been the dominant silvicultural system in forests with planned management, yet represents only a narrow range of each axis (Figure 2.2). Single-tree selection is typically characterized by a moderately small mean patch size, intermediate proportion of stand disturbed, moderately high frequency, and moderately low coarse woody debris input (Després *et al.*, 2016). Additionally, the degree of exposed mineral soil is largely dependent on soil conditions during harvest and the type of machinery (Napp *et al.*, 2009). For example, deep snow cover during winter harvesting often minimizes soil disturbance while in contrast, little or no snow cover during harvesting will increase the degree of soil disturbance, particularly if the soil is not frozen (Berger *et al.* 2004; Kern *et al.*, 2006). Though several studies have recommended a variety of

harvesting systems to maintain structural and species diversity (Doyon *et al.*, 2005; Nolet *et al.*, 2018), silvicultural systems which emulate the full range of disturbances between these two extremes have, until recently, received little attention. In 1957, Arbogast explicitly stated that yellow birch requires the occasional patch cut of ~0.04 ha near a seed tree, in addition to exposed mineral soil, to emulate the favorable conditions for germination and survival provided by higher-severity disturbances (Arbogast Jr., 1957). More recent guidelines have recommended larger gaps (Wisconsin Department of Natural Resources, 2011) or greater use of regular and irregular shelterwoods (Raymond *et al.*, 2009; Lussier and Meek, 2014; Raymond and Bédard, 2017); however, these have yet to be intentionally implemented on a large scale and monitored long-term.

A further mismatch has unfolded between historic disturbances regimes and emerging threats such as deer herbivory, European earthworm invasion, invasive pests, and climate change. For example, the disturbance impacts of European earthworm invasions did not exist when historic disturbance regimes predominated. The mean patch size, proportion of stand disturbed, degree of exposed mineral soil, coarse woody debris input, and disturbance frequency from these relatively recent disturbances do not overlap historical disturbance regimes and consequently create new disturbance regimes in which current species did not evolve. Promoting forest resilience by increasing stand-scale structural and species diversity could help mitigate the negative impacts of these emerging threats (Nagel *et al.*, 2017).

Though single-tree selection retains canopy cover, aesthetic value, and suitable germination sites for shade-tolerant species, its widespread application without the necessary modifications has led to landscape-scale homogenization of Great Lakes forests with planned management (Schulte *et al.*, 2007). This homogenization has resulted in fewer large trees, subsequently reduced gap sizes following windthrow, and consequently a decline in suitable germination sites for shade intolerant and midtolerant species. The abundance of simplified forests resulting from past land use and management history have now created a need to increase structural and functional trait diversity.

2.7.2 Finding solutions

To capture the range of silvicultural systems which best emulate natural disturbances in northern hardwoods, Figure 2.2 replaces the historically prevalent disturbance regimes shown in Figure 2.1 with the silvicultural systems which most closely emulate those disturbances based on mean patch size, proportion of stand disturbed, frequency, degree of exposed mineral soil, and coarse woody debris input. For example, sugar maple regeneration is best promoted by emulating a regime with small mean patch size, small to moderate proportion of stand disturbed, high frequency, low degree of exposed mineral soil, and low coarse woody debris input (Figure 2.1). The corresponding silvicultural system includes single-tree selection combined with winter harvesting (i.e. snow on) to minimize soil disturbance (Figure 2.2). However, because single-tree selection traditionally removes up to 40% of the canopy, Nolet *et al*

(2014) proposed a frequent, low-intensity harvesting system which could more closely emulate low-severity disturbances in northern hardwoods. In contrast, yellow birch regeneration requires greater disturbance and is best promoted by a regime with intermediate mean patch size, intermediate proportion of stand disturbed, intermediate frequency, intermediate degree of exposed mineral soil, and intermediate coarse woody debris input (Figure 2.1). Consequently, silvicultural systems for increasing the abundance of yellow birch in northern hardwoods should supplement single-tree selection with larger disturbances such as irregular shelterwoods combined with mechanical scarification and tip-up mounds to increase the degree of exposed mineral soil and coarse woody debris input (Figure 2.2; Godman and Krefting, 1960; Lorenzetti *et al.*, 2008, Gauthier *et al.*, 2016). An irregular shelterwood begins with an establishment cut similar to a regular shelterwood. Additional cuts are optional, but the two remaining cohorts are always maintained. Regenerating seedlings are protected, can establish, and grow for several decades (Raymond *et al.*, 2009). Irregular shelterwood systems and ‘structural complexity enhancements’ have been recently explored in Québec and New England, respectively, as methods for increasing structural and species diversity in northern hardwoods (Keeton, 2006; Raymond and Bédard, 2017).

In addition to the five main components of disturbances discussed here, regionally-specific influences and future interactions must still be considered. Competing vegetation, deer and insect herbivory dynamics, and invasive species continually shape forest development and disturbance-based management alone may not sufficiently restore species diversity. The effects of climate change further confound

efforts to restore species diversity (Harris *et al.*, 2006; Peters *et al.*, 2013) because a shift in native species abundances and interspecific interactions due to warming temperatures, drought, or other effects may make the ecosystem vulnerable to invasive species. The potential for novel interactions consequently makes it difficult to predict regeneration dynamics, but increasing ecosystem resilience with greater structural and species diversity could help prevent ecosystem degradation (Downing *et al.*, 2012; Lindenmayer *et al.*, 2016).

Disturbance spectrum models are not foreign to management literature; indeed, numerous conceptual models have been proposed (Seymour *et al.*, 2002; Kimmins, 2004; Roberts, 2004; Roberts, 2007; Drever *et al.*, 2006; Raymond *et al.*, 2013). Seymour *et al.* (2002) compared management systems to natural disturbances using the ‘natural disturbance comparability index’, which expresses the deviation of management systems from the upper limit of natural disturbance parameters. This model is useful for quantifying the degree of emulation when limited to patch size and disturbance frequency; however, disturbances are more nuanced than simply patch size and frequency. We expand upon this model by incorporating other important aspects of disturbances that strongly influence regeneration dynamics including coarse woody debris input and degree of exposed soil. Future studies which quantify these additional components along a gradient of natural and management disturbances would further strengthen our conceptual model. Building upon conceptual models, Kimmins (2004) provides a comprehensive qualitative model to demonstrate which seral stages are favored by various silvicultural systems. Additionally, Raymond *et al.* (2013) compared

silvicultural systems to natural disturbances in temperate mixedwood forests based on disturbance severity, size, and frequency. The range of comparisons are useful, but these models are limited by the absence of microsite components. A three-axis model proposed by Roberts (2004, 2007) examines characteristics of natural and silvicultural disturbances based on percent canopy removed, percent understory removed, and percent forest floor or soil removed or disrupted. Most silvicultural systems were found to only represent a narrow range of these components. These models provide an important foundation for future work, and we have built upon them by incorporating an important temporal gradient. Lastly, Drever *et al.* (2006) thoroughly presented a strong theoretical reasoning behind natural disturbance based management that laid further groundwork for future management objectives. We build upon the above models by explicitly incorporating relevant microsite components and offering specific management systems to emulate the desired natural disturbance.

In conclusion, structural and species diversity are strongly influenced by patch size, proportion of stand disturbed, frequency, degree of exposed mineral soil, and coarse woody debris input. By comparing historically prevalent disturbance regimes to regional silvicultural systems, our conceptual model illustrates the need to emulate a fuller range of natural disturbances to restore and promote species diversity in northern hardwoods in the upper Great Lakes based on these five components. For example, single-tree selection should be supplemented with larger disturbances to promote the regeneration of declining species such as yellow birch. Though our conceptual model is focused on northern hardwood forest ecosystems, it can easily be applied to other forest

types using the five identifiable components of disturbance, which are important components of any disturbance type across the globe. Using our conceptual model with other forest types more broadly would further provide a unique qualitative approach for emulating natural disturbances and consequently, promoting forest ecosystem resilience. In all cases, however, regionally-specific influences should still be considered.

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Figure 2.1. Conceptual model showing historically prevalent disturbance regimes in Great Lakes northern hardwoods, and the tree species best promoted by the resulting microsite conditions. Historical disturbances were variable, promoting a large diversity of tree species across the landscape. Italicized species have shown evidence of decline in Great Lakes northern hardwoods.

¹(Tubbs, 1977; Kern *et al.*, 2013a; Beaudet *et al.*, 2014)

²(Frelich and Lorimer, 1991; Scharenbroch and Bockheim, 2007; Marx and Walters, 2008)

³(Gastaldello *et al.*, 2007; Lorenzetti *et al.* 2008; Gauthier *et al.*, 2016; Lambert *et al.*, 2016)

⁴(Peltzer *et al.*, 2000; Schulte *et al.*, 2007; Rich *et al.*, 2007; Vodde *et al.*, 2015)

⁵(Frelich and Lorimer, 1991; Reich *et al.*, 2001; Rich *et al.*, 2007; Vodde *et al.*, 2015)

⁶(Frelich and Reich, 1995; Friedman and Reich, 2005)

Figure 2.2. Conceptual model illustrating techniques for restoring tree regeneration diversity based on historic disturbance regime and the species promoted by each disturbance type. Current management of northern hardwoods in the Great Lakes region is typically focused on single-tree selection and small gap cutting. Larger gaps, shelterwood, irregular shelterwood and clearcutting are rarely implemented.

¹(Raymond *et al.* 2009)

3. Initial regeneration response following novel silvicultural treatments in Great Lakes northern hardwoods

3.1 Introduction

The loss of structural and species diversity is a critical issue facing forest managers in eastern North America (Webster et al. 2018). Following extensive land-use change during the nineteenth century, twentieth century management systems have tended to promote shade-tolerant species over others (Angers et al. 2005, Neuendorff et al. 2007), reducing compositional diversity and resilience to future disturbances (Puettmann 2011, Neill and Puettmann 2013). Vulnerability to irreversible change is further compounded by rising global temperatures, shifting weather patterns, species range shifts, exotic species invasion, and intensifying pest outbreaks (Hulme 2005, Lindner et al. 2010, Grimm et al. 2013). Increasing forest resilience by promoting structural heterogeneity and species diversity has consequently become an important objective among silviculturalists and forest managers (Puettmann et al. 2009, Messier et al. 2013).

Structural heterogeneity created by natural disturbances is widely credited with contributing towards plant species diversity in forests worldwide (Ricklefs 1976, Denslow 1980, Frelich and Lorimer 1991, Swanson et al. 2011, Hanson and Lorimer 2013). Windthrow is the predominant historical disturbance in Great Lakes northern hardwoods, but substantial variation exists in severity and frequency. Low and moderate-severity windthrow occurred over intervals of decades to centuries, respectively, while catastrophic (>1.0 ha) windthrow events ranged from ~722 yr

rotation period in regions of Upper Michigan (Zhang et al. 1999) to ~1210 yr return time when pooling all forest types in northern Wisconsin (Canham and Loucks 1984). Large gaps created by the toppling of mature, senescent trees increased light availability and exposed mineral soil, processes which were thought to maintain pre-settlement populations of mid-tolerant species such as yellow birch (*Betula alleghaniensis* Britt.) and eastern hemlock (*Tsuga canadensis* (L.) Carrière) (Tubbs 1977, Frelich and Lorimer 1991).

The role of other disturbances in structuring northern hardwoods is less prominent. Catastrophic fire was much less frequent than windthrow, with a rotation period upwards of 2600 years in northern hardwood forests of Upper Michigan (Frelich and Lorimer 1991, Zhang et al. 1999). Red pine (*Pinus resinosa* Sol. ex Aiton), northern red oak (*Quercus rubra* L.), and paper birch (*Betula papyrifera* Marshall) respond positively to fire but the cool, moist understories of northern hardwood forests reduce the likelihood of such disturbances and consequently, the importance of these species in northern hardwood forests (Zauert et al. 2004, Abrams 2008).

Though natural disturbance regimes and indigenous peoples structured pre-settlement forests within the range of natural variability (Frelich and Lorimer 1991, Whitney 1994, Zhang et al. 1999), European colonizers initiated substantial change on the landscape. Great Lakes forests were fundamentally altered during the ‘cutover’, when vast expanses of white (*Pinus strobus* L.) and red pine – dominated forests were clearcut and residual slash burned (Whitney 1994, Gough 1997). Subsequent shifts to agriculture further contributed to a loss of ecological legacies, or the species

interactions, adaptations, and biological components remaining following a disturbance (Webster et al. 2018). When abandoned agricultural fields succeeded to hardwood-dominated second-growth forests, initial high-grading was replaced by widespread application of single-tree selection (Jacobs 1987, Kern et al. 2014a, Pond et al. 2014). Under this system, single trees are extracted across a range of diameter sizes to reach a residual basal area goal, and repeated every 10 – 20 yrs. Along with low-severity canopy removal, the common practice of winter harvesting further minimizes soil disturbance and reduces opportunities for regeneration by mid-tolerant species and those which require soil disturbance (Berger et al. 2004, Kern et al. 2006). Consequently, the widespread and decades-long application of single-tree selection has tended to decrease the abundance of mid-tolerant species (Webster and Lorimer 2005, Neuendorff et al. 2007), increase the abundance of tolerant species (Angers et al. 2005, Neuendorff et al. 2007), and ultimately decrease species diversity across the Great Lakes region (Schulte et al. 2007).

To restore and maintain species diversity, attention has turned toward silvicultural systems historically not applied in northern hardwoods. Regular and irregular shelterwood systems, for example, have recently been explored in Quebec and elsewhere as alternatives to single-tree selection (Raymond et al. 2009, Raymond and Bédard 2017). Regular shelterwood systems begin with an establishment harvest leaving 30-70% residual canopy cover (Nyland et al. 2016). The environmental conditions created by the residual canopy (e.g. shade, wind protection) buffer seedlings from large fluctuations in temperature and evapotranspiration rates (Nyland et al. 2016).

After ~5 yrs, the residual canopy is harvested to increase the growing space of established seedlings. In contrast, irregular shelterwood systems delay the final harvest or eliminate it altogether (Raymond et al. 2009). Intermediate light availability created by shelterwood and irregular shelterwood systems may subsequently promote regeneration of mid-tolerant species. Coupling these alternative harvesting systems with site preparation methods may further alleviate the decline in species diversity. For example, scarification removes the organic layer to expose mineral soil and promote the germination of small-seeded species that cannot penetrate a thick litter layer (Lorenzetti et al. 2008, Gauthier et al. 2016). Creating pit-mound topography to emulate treefall is another option for restoring diversity, as previous work has demonstrated the unique niches created by residual tip-up mounds and pits (Peterson et al. 1990, Kern et al. 2019) which can favor regeneration of yellow birch and eastern hemlock (Tubbs 1977). Though several silvicultural harvesting trials were established decades ago in Great Lakes northern hardwoods (Eyre and Zillgitt 1953, Erickson et al. 1990, Kern et al. 2014a), they are nonreplicated and with additional design flaws must be interpreted with caution.

Using a silvicultural experiment in Upper Michigan, the objectives of this study are 1) quantify the effects of silvicultural treatments on short-term regeneration in a northern hardwood forest, and 2) identify underlying conditions which may drive treatment differences. We hypothesized that 1) intermediate disturbances such as shelterwoods would promote mid-tolerant species regeneration, while pit-mound topography and scarification would promote regeneration of small-seeded species such

as yellow birch, and 2) treatment differences would be driven by changes in canopy openness, leaf litter depth, and soil moisture. To test our hypotheses, we applied harvesting treatments ranging from single-tree selection to shelterwood and clearcut, along with site preparation treatments including the creation of pit-mound topography and scarification. Measurements were conducted one growing season prior to and two growing seasons following main treatment application.

3.2 Materials and Methods

3.2.1 Study Area

The study plots are located within the Northern Hardwood Silvicultural Experiment to Enhance Diversity (NHSEED) near Alberta, Michigan at the Ford Center Research Forest (46°37', 88°29'W) within the northern hardwood forest type. Average daily temperatures (1981-2010) in Alberta range from -10.8°C in January to 18.1°C in July for a yearly average of 4.7°C (NOAA 2016). Precipitation averages 88.9 cm with 390.1 cm of snowfall (2007-2016, MRCC 2016). Soils are moderately well drained, primarily consisting of cobbly silt loam overlaying Precambrian bedrock with several isolated low-lying areas (Albert 1995).

A pine-hardwood forest type dominated the site prior to extensive harvesting from ca. 1900 to 1938 (Erickson et al. 1990). Single-tree selection management has subsequently been applied since the 1960s, resulting in uneven-sized stands heavily dominated by a canopy of sugar maple (*Acer saccharum* Marsh.), which occupies 80% of total basal area. Less dominant canopy species include red maple (*Acer rubrum* L) with 8% of total basal area, and yellow birch (*Betula alleghaniensis* Britton), with 5% of total basal area. Other species include eastern hemlock (*Tsuga canadensis* L.), balsam fir (*Abies balsamea* (L.) Mill.), green ash (*Fraxinus pennsylvanica* Marsh.), black cherry (*Prunus serotina* Ehrh), American elm (*Ulmus americana* L.), black ash (*Fraxinus nigra* Marsh.), eastern white pine (*Pinus strobus* L.), ironwood (*Ostrya virginia* (P. Mill.) K. Kock), northern white cedar (*Thuja occidentalis* L.), trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), northern

red oak (*Quercus rubra* L.), black spruce (*Picea mariana* (Mill.) B.S.P.), and white spruce (*Picea glauca* (Moench) Voss).

3.2.2 Experimental design

Four harvest treatments were applied across three blocks of eighteen treatment units in a randomized block design. Harvest treatments include single-tree selection (STS, $n = 3$ treatment units), irregular shelterwood with high (60%) canopy retention (ISH, $n = 6$ treatment units), irregular shelterwood with low (30%) canopy retention (ISL, $n = 6$ treatment units), and patch clearcut (CC, $n = 3$ treatment units). Each treatment unit is split-plot with three ~ 2.4 ha split units for site preparation treatments ($n = 54$ split units, Figure 3.1). Two 15 m^2 circular sapling (> 30 cm tall, < 5 cm dbh) plots were placed in each split unit and randomly located greater than 20 m from the edge of the unit ($n = 108$). Circular 3 m^2 seedling (< 30 cm tall) plots were centered within each sapling plot. Half the ISH and ISL treatments will undergo a final harvest once seedlings have established (~ 5 yr). Owing to its historical and continuing wide-spread application throughout Great Lakes hardwood forests (Jacobs 1987, Kern et al. 2014a), we use STS as our experimental control to represent the ‘business as usual’ model. Site preparation treatments, each applied to 18 split units, include untreated reference, artificial pit-mound topography, and mechanical scarification. Sites were harvested in February and March 2017 when snow cover and cold soil minimized forest floor disturbances from the harvest treatment. Small diameter trees (< 5 cm dbh) were cut by brush saw and left on-site in August 2017. To emulate windthrow damage, artificial pit-

mound topography was created during initial harvest by removing the tree and attached root ball from the soil and placing within ~5 m of the residual pit (Figure 3.1). Average mound density ± 1 SE was 11.9 mounds ha⁻¹ (± 2.2), but mound density varied substantially among canopy disturbance treatments (Table 3.1). Mechanical scarification was implemented in October 2017 using a salmon blade to mix the O and A horizons.

Owing to the nature of operational scale experiments, several caveats emerged that may influence our findings. First, creating artificial pit-mound topography is not an intended use of harvesting machinery. Due to operational constraints, fewer mounds were created and residual mounds were substantially smaller in volume than originally planned, an outcome which likely limited the effect size of this treatment when compared to pit-mound topography created by natural windthrow. Second, logging operations in northern hardwoods typically ignore saplings less than 5 cm dbh. As a result, remaining saplings taller than breast height were cut and left in place in ISH, ISL, and CC treatments in August 2017, five to six months following the main harvest. Third, scarification is applied during snow-free seasons whereas harvesting in northern hardwoods is conducted during winter to minimize soil disturbance. As a result, the scarification treatment was applied in October 2017, seven to eight months following the main harvest.

3.3.3 Measurements

Seedling and sapling counts for all species were tallied in each respective plot during the 2016 (pre-treatment) and 2018 (post-treatment) growing seasons. Saplings identified as stump sprouts or suckers were noted as such. Canopy openness was measured at the center of each seedling plot with hemispherical photographs during the 2015 and 2018 field seasons. Though other pre-treatment measurements were taken one year following pre-treatment photographs, canopy conditions were relatively unchanged. Using a Sigma 4.5 mm F2.8 EX HSM fisheye lens attached to a Nikon D3200 digital camera at 1 m height pointed directly vertical, photographs were taken once during the growing season when canopy leaves were fully expanded, overcast conditions prevailed, exposure was uniform, and solar disc not visible. Litter (Oi layer) depth was measured with a ruler at ten randomly chosen locations within each sapling plot. Soil water content (SWC) was recorded once per month during the growing season (June, July August) from 2016 – 2018 with a Theta Probe Soil Moisture Sensor (Delta-T Devices Ltd., Cambridge UK) in each sapling plot, calibrated for mineral soil. Measurements were taken in two consecutive days and at least 36 hrs following a precipitation event. Seventeen measurements were taken in each plot: one measurement at plot center and four in each cardinal direction at intervals of 50 cm.

3.4.4 Data Analysis

We tested the effect of silvicultural system and microsite conditions on post-treatment seedling and sapling density of each species using generalized linear models with negative binomial regression. To address the three caveats described above, we

included previous year densities as a covariate. The effects of silvicultural system on the proportion of saplings identified as stump sprouts were tested using generalized linear models. Sugar maple was the only species with enough sprouts or suckers to test. The effects of silvicultural system on microsite conditions were assessed using generalized linear mixed effect models, with treatment unit nested within block included as a random factor. Seasonal variation in SWC was assessed by pooling the monthly measurements within each plot and calculating the coefficient of variation (CV, calculated as $[\text{standard deviation} * 100] / \text{mean}$ and expressed as a percentage). Within-plot litter depth variation was assessed by calculating the CV of litter depth within each plot. Pairwise multiple comparisons were conducted with the ‘emmeans’ package (Lenth 2018) using Tukey’s HSD correction. Differences among silvicultural treatments pre- or post-treatment are indicated by interactions between disturbance treatments and year, while the lack of a year interaction suggests that pre-disturbance differences may have persisted post-treatment. However, a significant year effect indicates that changing microsite conditions may have been associated with the overall disturbance (Table 3.2).

To test our second objective, the effects of microsite conditions on seedling and sapling species composition from 2016 to 2018 were assessed with permutational multivariate analysis of variance (PERMANOVA, *adonis* function in ‘vegan’ package of R 3.5.0, Oksanen et al. 2018) using Bray-Curtis distance matrices constrained within blocks. Species that occurred in fewer than 2% of plots were excluded and four plots with incomplete microsite data were removed ($n = 212$). The effects of silvicultural treatment on seedling composition were also assessed with PERMANOVA using Bray-

Curtis distance matrices constrained within blocks. Density was averaged by split unit ($n = 54$), and predictor variables included harvest treatment, site preparation treatment, and year. Pairwise multiple comparisons were conducted with the *pairwise.perm.manova* function in the ‘RVAideMemoire’ package (Hervé 2019) using Holm’s multiple comparison adjustment. Changes in composition across years were visualized with nonmetric multidimensional scaling (NMDS) ordination using Bray-Curtis distances. Ordinations were constructed with the *metaMDS* function in the ‘vegan’ package of R 3.5.0, with 999 iterations. Species that occurred in fewer than 2% of plots were removed from the matrix, and environmental variables were relativized by maximum value of each variable along with all species. Average point scores from the first two axes of each disturbance treatment were graphed, and environmental variables and species or traits fitted as vectors onto the community ordination using the *envfit* function.

Table 3.1. Average (± 1 SE) pit-mound density and area among canopy disturbance treatments in ~2.4 ha split units within a northern hardwood forest of Upper Michigan, USA. CC, clearcut; ISL, irregular shelterwood – low residual; ISH, irregular shelterwood – high residual; STS, single-tree selection.

Canopy disturbance treatment	Pit-mound density (ha⁻¹)	Pit-mound area (m² ha⁻¹)
CC	15.0 (6.7)	37.5 (12.2)
ISL	14.2 (3.9)	74.1 (11.5)
ISH	9.8 (4.2)	26.5 (9.5)
STS	8.7 (0.9)	47.3 (6.9)
<i>All</i>	11.9 (2.2)	45.0 (9.6)

Figure 3.1. Layout of the Northern Hardwood Silvicultural Experiment for Enhanced Diversity near Alberta, Michigan, USA, overlaid on hillshaded digital elevation model. Colors denote harvest treatment and patterns denote site preparation treatment.

3.3 Results

3.3.1 Microsite conditions

Harvest treatments were differentially associated with canopy openness (harvest $\times$ year interaction, $p < 0.001$, Table 3.2), and had a marginal effect on intraseasonal soil water content (SWC) variation (harvest $\times$ year interaction, $p = 0.052$, Table 3.2) and within-plot litter depth variation (harvest $\times$ year interaction, $p = 0.07$, Table 3.2). In 2018, canopy openness was highest in clearcut (CC) treatments and decreased with harvest severity (Figure 3.2). Within-plot variation in litter depth generally increased each year, and in 2018 was higher in irregular shelterwood – low residual (ISL) plots (Figure 3.2). Litter depth declined from pre- to post-treatment but pre-treatment differences remained post treatment, i.e. greater litter depth in single-tree selection (STS) stands and declining with increasing harvest severity (Figure 3.2). Harvest treatments had no effect on SWC.

Site preparation treatments were only correlated with litter depth variation (site preparation $\times$ year interaction, $p = 0.002$, Table 3.2), which generally increased post-treatment and was highest in scarification treatments. Main effects of site preparation treatments on litter depth ($p = 0.006$, Table 3.2) and intraseasonal SWC variation ($p = 0.023$, Table 3.2) were present prior to treatment application.

3.3.2 Regeneration

Overall, harvest treatments tended to have a greater effect than site preparation treatments on seedling density (Tables 3.3 and 3.4, Figure 3.3). Non-significant harvest

× covariate interactions suggest that treatments were correlated with seedling density regardless of pre-treatment density. Red maple (*Acer rubrum* L.) was nearly twice as abundant ($p(>\chi^2) < 0.001$, Table 3.3) in ISH and ISL harvest treatments when compared to STS and CC treatments, regardless of pre-treatment seedling density. Sugar maple (*A. saccharum* Marsh.) was more abundant in ISH, ISL, and STS when compared to CC harvest treatments ($p(>\chi^2) < 0.001$, Table 3.3, Figure 3.3), but black cherry (*Prunus serotina* Ehrh.) was not correlated with harvest treatments. There was no effect of silvicultural treatment on yellow birch (*Betula alleghaniensis* Britt.) density ($p(>\chi^2) = 0.586$, Table 3.3). Sugar maple was marginally correlated with site preparation treatments ($p(>\chi^2) = 0.038$, Table 3.3), however a marginal site preparation × covariate interaction suggests any effect was generally dependent on pre-treatment density. Lastly, there was a marginal harvest × site preparation treatment effect on red maple seedling density, ($p(>\chi^2) = 0.062$, Table 3.3), but the nature of the interaction is unclear due to non-significant differences using pairwise comparisons (Figure 3.3).

Seedling density was correlated with few stand or microsite conditions. Canopy openness was negatively correlated with red maple ($p < 0.015$, Table 3.5, Figure 3.4) and sugar maple ($p < 0.001$, Table 3.5, Figure 3.4) seedling density. Yellow birch seedling density was positively correlated with litter depth variation ($p = 0.029$, Table 3.5, Figure 3.4), and conspecific overstory basal area had a marginal positive effect on yellow birch seedling density ($p = 0.053$, Table 3.5, Figure 3.4). Average litter depth, SWC, and intraseasonal variation in SWC had no effect on seedling densities.

Harvest was associated with sapling density of red maple ($p(>\chi^2) = 0.013$, Tables 3.6 and 3.7, Figure 3.5), though a harvest $\times$ covariate interaction suggests it depended on pre-treatment sugar maple density. Harvest was also associated with sugar maple ($p(>\chi^2) = 0.005$, Table 3.6) and black cherry ($p(>\chi^2) < 0.001$, Table 3.6), but like red maple was generally dependent on pre-treatment density. Sugar maple sapling density response was mixed, but black cherry sapling density increased nearly two-fold in ISH and ISL harvest treatments (Figure 3.5). Ironwood increased in most harvest treatments ($p(>\chi^2) = 0.023$, Table 3.6), particularly CC treatments, regardless of pre-treatment density. Site preparation was associated with ironwood ($p(>\chi^2) < 0.001$, Table 3.6), which was generally higher in reference and pit-mound treatments, but response strength varied depending on pre-treatment ironwood sapling density ($p(>\chi^2) < 0.046$, Table 3.6). Black cherry increased most in stands without site preparation ($p(>\chi^2) < 0.046$, Table 3.6), regardless of pre-treatment sapling density, and red maple was marginally higher in reference and pit-mound treatments ($p(>\chi^2) < 0.046$, Table 3.6) regardless of pre-treatment sapling density. Red maple was the only species correlated with a harvest $\times$ site preparation interaction ($p < 0.001$, Table 3.6). Though not significant, there was a lower proportion of sugar maple saplings identified as stump sprouts in STS when compared to other harvest treatments (Table 3.8, Figure 3.6).

3.3.3 Composition

Seedling species composition was correlated with all measured microsite conditions (Table 3.9a), particularly canopy openness (PERMANOVA, $R^2 = 0.019$, p

= 0.001, Table 3.9a). Unexplained variance, however, remained high ($R^2 = 0.938$, Table 3.9a). Microsite conditions may have translated to silvicultural treatment effects, but without a treatment $\times$ year interaction our results must be interpreted with caution. However, seedling composition was associated with the interaction of harvest $\times$ site preparation ($R^2 = 0.078$, $p = 0.014$, Table 3.9b), and was marginally associated with harvest ($R^2 = 0.037$, $p = 0.069$, Table 3.9b). Composition was most correlated with year ($R^2 = 0.087$, $p = 0.001$, Table 3.9b), likely indicating a response to the overall disturbance. Nonmetric multidimensional scaling (NMDS) ordinations illustrate shifts in composition from pre- to post-treatment along an opposing canopy openness – litter depth gradient (Figure 3.7). Harvest treatments show greater divergence in seedling composition when compared to site preparation treatments, though substantial overlap remains among treatments.

Sapling composition was correlated with canopy openness (PERMANOVA, $R^2 = 0.065$, $p = 0.014$, Table 3.10a) and intraseasonal variation in SWC ($R^2 = 0.017$, $p = 0.031$, Table 3.10a). Like seedling composition, unexplained variance remained high ($R^2 = 0.958$, Table 3.10a). Translating to overall silvicultural treatment effects, sapling composition was correlated with harvest treatments ($R^2 = 0.065$, $p = 0.002$, Table 3.10b), site preparation treatments ($R^2 = 0.040$, $p = 0.024$, Table 3.10b), and the interaction of harvest $\times$ site preparation ($R^2 = 0.073$, $p = 0.033$, Table 3.10b). There was no significant shift in composition from pre- to post-treatment, and without a significant treatment $\times$ year interaction these findings should be interpreted with caution. Like seedling composition, however, NMDS ordinations illustrate diverging composition

among harvest treatments in 2018 along an opposing canopy openness – litter depth gradient, along with plot-level litter depth variation (Figure 3.8). Ironwood and black cherry saplings were a stronger proportion of post-treatment composition when compared to pre-treatment composition, while balsam fir was more associated with pre-treatment composition (Figure 3.8).

Table 3.2. Mixed model effects of harvest treatment, site preparation treatment, and year on microsite conditions in a managed northern hardwood forest of Upper Michigan, USA. Treatment unit nested within block was included as a random factor. Models first included all treatment interactions and were then simplified if no interaction effect was detected. Lower order interactions were retained if higher order interactions were statistically significant. Asterisks indicate statistical significance ($p < 0.05$), italicized values indicate marginal significance ($0.05 < p < 0.10$).

Predictor	Canopy openness (n = 213)				Litter depth (n = 215)				SWC (n = 216)			
	RMSE		AIC		RMSE		AIC		RMSE		AIC	
	0.070		-503.075		0.508		339.586		0.069		-508.830	
	Df _{num}	Df _{den}	F-value	p-value	Df _{num}	Df _{den}	F-value	p-value	Df _{num}	Df _{den}	F-value	p-value
Intercept	1	201	100004.75	<0.001*	1	206	98.875	<0.001*	1	201	46766.19	<0.001*
Harvest	3	201	41.34	<0.001*	3	206	9.851	<0.001*	3	201	1.74	0.160
Site Preparation	2	201	0.24	0.788	2	206	5.224	0.006*	2	201	2.50	0.084
Year	1	201	646.80	<0.001*	1	206	184.771	<0.001*	1	201	6.42	0.012*
Harvest t × Site Preparation	-	-	-	-	-	-	-	-	-	-	-	-
Harvest × Year	3	201	35.37	<0.001*	-	-	-	-	6	201	2.97	0.009*
Df _{num} , numerator degrees of freedom; Df _{den} , denominator degrees of freedom												

Predictor	SWC Intraseasonal CV (n = 216)				within-plot litter depth CV (n = 215)			
	RMSE		AIC		RMSE		AIC	
	1.240		749.707		0.110		-308.477	
	Df _{num}	Df _{den}	F-value	p-value	Df _{num}	Df _{den}	F-value	p-value
Intercept	1	198	160.520	<0.001*	1	201	81647.55	<0.001*
Harvest	3	198	1.181	0.318	3	201	4.69	0.003*
Site Preparation	2	198	3.862	0.023*	2	201	5.56	0.005*
Year	1	198	75.144	<0.001*	1	201	84.68	<0.001*
Harvest × Site Preparation	6	198	2.152	0.049*	-	-	-	-
Harvest × Year	3	198	2.627	0.052	3	201	2.39	0.070
Site Preparation × Year	-	-	-	-	2	201	6.62	0.002*
CV, coefficient of variation; Df _{num} , numerator degrees of freedom; Df _{den} , denominator degrees of freedom;								

Table 3.3. Generalized linear model effects with negative binomial distribution of harvest and site preparation treatments on seedling (< 30 cm tall) density in a managed northern hardwood forest in Upper Michigan, USA. Pre-treatment (2016) density was included as a covariate to account for pre-treatment differences. Consequently, a significant covariate interaction suggests that the strength of a treatment effect depends on pre-treatment density. Models were constructed using backwards elimination. Lower order interactions were retained if higher order interactions were statistically significant. Asterisks indicate statistical significance ($p < 0.05$), italicized values indicate marginal significance ($0.05 < p < 0.10$). Species that occurred in fewer than 5% of plots were excluded.

Predictor	Red maple (n = 108)				Sugar maple (n = 106)			
	RMSE		AIC		RMSE		AIC	
	Df _{num}	Dev.	Df _{den}	Res. Dev.	Df _{num}	Dev.	Df _{den}	Res. Dev.
Null			107	259.090			105	229.53
Harvest	3	53.034	104	206.056	3	33.133	102	196.39
Site Preparation	2	1.025	101	115.876	2	4.848	99	135.10
Covariate	1	59.155	103	116.901	1	56.442	101	139.95
Harvest × Site Prep	6	12.005	90	89.597	6	11.931	88	114.28
Harvest × Covariate	3	1.469	98	114.406	3	3.691	96	131.41
Site Prep × Covariate	2	12.805	96	101.602	2	5.205	94	126.21
Df _{num} , numerator degrees of freedom; Dev., deviance; Df _{den} , denominator degrees of freedom; Res. Dev., residual deviance.								

Predictor	Black cherry (n = 108)					Yellow birch (n = 107)				
	RMSE			AIC		RMSE			AIC	
	0.87			257.43		0.933			474.49	
	Df _{num}	Dev.	Df _{den}	Res. Dev.	p > χ^2	Df _{num}	Dev.	Df _{den}	Res. Dev.	p > χ^2
Null			107	143,548				106	99,534	
Harvest	3	3.527	104	140.021	0.317	3	1.937	103	97.598	0.586
Site Preparation	2	0.80	101	95.846	0.961	2	3.934	101	93.664	0.140
Covariate	1	44.096	103	95.926	<0.001*	1	0.424	100	93.240	0.515
Harvest × Covariate	3	1.873	98	93.972	0.599	-	-	-	-	-
Site Prep × Covariate	2	6.899	96	87.074	0.032*	-	-	-	-	-
Df _{num} , numerator degrees of freedom; Dev., deviance; Df _{den} , denominator degrees of freedom; Res. Dev., residual deviance.										

Table 3.4. Average seedling (< 30 cm tall) density (stems ha⁻¹ ± standard error) across harvest treatments, site preparation treatments, and years in a managed northern hardwood forest of Upper Michigan, USA. Species that occurred in fewer than 5% of plots were excluded. STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut.

	2016				2018				
	STS	ISH	ISL	CC	STS	ISH	ISL	CC	
Red maple	Reference	2777.5 (2002.9)	6666.0 (6666.0)	14998.5 (10902.5)	1111.0 (1111.0)	3333.0 (962.2)	5277.3 (4311.8)	45273.3 (43619.5)	1666.5 (962.2)
	Pit-mound	3333.0 (3333.0)	15276.3 (14619.8)	8332.5 (5804.9)	6666.0 (3848.6)	1666.5 (1666.5)	21109.0 (14462.2)	4721.8 (3144.8)	3888.5 (2222.0)
	Scarification	555.5 (555.5)	4444.0 (2343.7)	33607.8 (33607.8)	0.0 (0.0)	2222.0 (1469.7)	16109.5 (7906.9)	49439.5 (45871.0)	555.5 (555.5)
Sugar maple	Reference	22775.5 (21947.5)	13054.3 (5224.4)	26931.8 (10437.6)	7777.0 (3379.0)	14998.5 (13332.0)	8332.5 (1924.3)	20275.8 (5617.1)	4999.5 (2545.6)
	Pit-mound	5555.0 (555.5)	17200.5 (7777)	48606.5 (18469.4)	7221.5 (2222)	6666.0 (4409.1)	10554.5 (6960.4)	17776.0 (8591.4)	1666.5 (0.0)
	Scarification	11665.5 (10842.9)	33052.3 (13832.4)	22220.0 (11883.0)	13332.0 (10928.0)	27219.5 (21392.2)	13887.5 (3617.2)	21109.0 (15819.6)	0.0 (0.0)
Yellow birch	Reference	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	8888.0 (7285.3)	15554.0 (6853.2)	1944.3 (512.1)	6110.5 (5299.1)
	Pit-mound	0.0 (0.0)	555.5 (351.3)	0.0 (0.0)	0.0 (0.0)	11665.5 (11665.5)	13332.0 (9830.9)	15831.8 (7067.1)	30552.5 (22734.8)
	Scarification	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	12776.5 (7221.5)	36385.3 (17670.2)	16665.0 (5977.8)	6666.0 (6666.0)
Black cherry	Reference	3333.0 (3333.0)	1666.5 (1666.5)	3333.0 (1551.4)	3888.5 (2421.4)	555.5 (555.5)	3610.75 (2994.037)	1994.3 (904.3)	2777.5 (2777.5)
	Pit-mound	1111.0 (1111.0)	3333.0 (1875.6)	3333.0 (2108.0)	2777.5 (1469.7)	2222 (1469.7)	3055.3 (1171.8)	2222.0 (1405.3)	1666.5 (1666.5)
	Scarification	555.5 (555.5)	6110.5 (2907.8)	9721.3 (9060.8)	5555.0 (5555.0)	2777.5 (1111)	4444.0 (1647.9)	4444.0 (3816.4)	8888.0 (8888.0)

Table 3.5. Generalized linear models with negative binomial distribution of microsite environment on 2018 seedling (< 30 cm tall) density in a managed northern hardwood forest of Upper Michigan, USA. Asterisks indicate statistical significance ($p < 0.05$), italicized values indicate marginal significance ($0.05 < p < 0.10$).

Predictor	Red maple (n = 104)				Sugar maple (n = 107)				Yellow birch (n = 106)			
	RMSE		AIC		RMSE		AIC		RMSE		AIC	
	Est.	St. Error	z-value	p-value	Est.	St. Error	z-value	p-value	Est.	St. Error	z-value	p-value
Intercept	1.541	0.439	3.512	<0.001*	1.877	0.260	7.209	<0.001*	0.079	0.544	0.146	0.884
Canopy openness	-0.023	0.009	-2.487	0.015*	-0.018	0.006	-3.352	<0.001*	-	-	-	-
Litter depth within-plot variation	-	-	-	-	-	-	-	-	0.012	0.006	2.244	0.025*
Conspecific overstory basal area	-	-	-	-	-	-	-	-	0.256	0.132	1.940	0.052
Est., estimate; St. Error, standard error.												

Table 3.6. Generalized linear model effects of harvest and site preparation treatments on sapling (> 30 cm tall, < 5 cm dbh) density in a managed northern hardwood forest in Upper Michigan, USA. Previous year data was included as a covariate. Consequently, a significant covariate interaction suggests that the strength of a treatment effect depends on pre-treatment density. Models first included all treatment interactions and were then simplified if no interaction effect was detected. Lower order interactions were retained if higher order interactions were statistically significant. Asterisks indicate statistical significance ($p < 0.05$), italicized values indicate marginal significance ($0.05 < p < 0.10$). Species that occurred in fewer than 5% of plots were excluded.

Predictor	Red maple (n = 108)					Sugar maple (n = 108)				
	RMSE			AIC		RMSE			AIC	
	0.70			158.29		1.09			760.15	
	Df _{num}	Dev.	Df _{den}	Res. Dev.	p > χ^2	Df _{num}	Dev.	Df _{den}	Res. Dev.	p > χ^2
Null			107	173.709				107	196.22	
Harvest	3	10.714	104	162.665	0.013*	3	12.798	104	183.43	0.005*
Site Preparation	2	4.923	101	107.256	0.085	2	1.674	101	138.60	0.433
Covariate	1	50.816	103	112.180	<0.001*	1	43.149	103	140.28	<0.001*
Harvest $\times$ Site Prep	6	45.356	93	52.182	<0.001*	-	-	-	-	-
Harvest $\times$ Covariate	3	9.718	99	97.538	0.008*	3	8.710	98	129.89	0.033*
Site Prep $\times$ Covariate	-	-	-	-	-	2	2.096	96	127.80	0.351

Predictor	Ironwood (n = 108)					Black cherry (n = 108)				
	RMSE		AIC			RMSE		AIC		
	0.54		148.72			0.947		465.68		
	Df _{num}	Dev.	Df _{den}	Res. Dev.	p > χ^2	Df _{num}	Dev.	Df _{den}	Res. Dev.	p > χ^2
Null			107	118.198				107	241.080	
Harvest	3	9.487	104	108.711	0.023*	3	20.126	104	220.953	<0.001*
Site Preparation	2	17.607	101	52.062	<0.001*	2	6.990	101	134.611	0.030*
Covariate	1	39.043	103	69.668	<0.001*	1	79.353	103	141.600	<0.001*
Harvest × Site Prep	6	12.148	91	31.843	0.059	6	26.975	90	96.872	<0.001*
Harvest × Covariate	2	1.933	99	50.129	0.380	3	6.623	98	127.987	0.085
Site Prep × Covariate	2	6.138	97	43.991	0.046*	2	4.140	96	123.847	0.126

Table 3.7. Average sapling (> 30 cm tall, < 5 cm dbh) densities (stems ha⁻¹ ± standard error) across harvest treatments, site preparation treatments, and years in a managed northern hardwood forest of Upper Michigan, USA. Species that occurred in fewer than 5% of plots were excluded. STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut.

2016					2018				
	STS	ISH	ISL	CC		STS	ISH	ISL	CC
Red maple	Reference	0.0 (0.0)	555.6 (555.6)	111.1 (111.1)	0.0 (0.0)	0.0 (0.0)	666.7 (666.7)	388.9 (388.9)	555.6 (555.6)
	Pit-mound	0.0 (0.0)	388.9 (277.8)	111.1 (70.3)	111.1 (111.1)	111.1 (111.1)	388.9 (277.8)	555.6 (281.1)	1111.1 (949.3)
	Scarification	0.0 (0.0)	222.2 (111.1)	777.8 (777.8)	0.0 (0.0)	111.1 (111.1)	500.0 (319.1)	277.8 (277.8)	0.0 (0.0)
Sugar maple	Reference	10555.6 (7674.8)	7611.1 (1882.5)	14777.9 (4379.0)	6777.8 (3560.8)	9222.3 (6296.2)	5833.4 (1688.2)	15277.9 (3946.3)	9111.2 (4138.1)
	Pit-mound	12444.5 (7113.8)	6111.1 (2373.7)	12389.0 (2657.5)	5222.2 (2119.9)	8444.5 (2452.0)	6000.0 (1605.6)	15889.0 (4575.0)	5777.8 (2230.6)
	Scarification	10888.9 (4522.9)	18055.7 (9643.9)	7055.6 (2108.9)	4555.6 (618.6)	5888.9 (1281.4)	10944.5 (3835.0)	7000.0 (3104.4)	2444.5 (444.4)
Ironwood	Reference	0.0 (0.0)	388.9 (388.9)	0.0 (0.0)	333.3 (333.3)	0.0 (0.0)	222.2 (222.2)	277.8 (277.8)	1000.0 (1000.0)
	Pit-mound	0.0 (0.0)	222.2 (164.8)	222.2 (164.8)	222.2 (222.2)	777.8 (777.8)	555.6 (351.4)	666.7 (602.5)	1777.8 (1175.9)
	Scarification	0.0 (0.0)	55.6 (55.6)	0.0 (0.0)	333.3 (333.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	333.3 (333.3)
Black cherry	Reference	111.1 (111.1)	3555.6 (2359.7)	2277.8 (1518.8)	333.4 (509.2)	111.1 (111.1)	6444.5 (3510.5)	6833.4 (2976.2)	9888.9 (3379.3)
	Pit-mound	444.4 (222.2)	1555.6 (805.8)	1222.2 (850.6)	666.7 (384.9)	666.7 (384.9)	3111.1 (2139.0)	2944.5 (2155.8)	2444.5 (728.6)
	Scarification	2222.2 (2222.2)	1000.0 (501.9)	2055.6 (1474.3)	4444.5 (4444.5)	1444.5 (1281.4)	2055.6 (920.6)	6111.1 (5108.2)	2111.1 (2111.1)

Table 3.8. Generalized linear model effects of silvicultural treatments on proportion of 2018 sugar maple saplings (> 30 cm tall) identified as stump sprouts in a managed northern hardwood forest in Upper Michigan, USA.

Predictor	Sugar maple (n = 97)					
	Df _{num}	Dev	Df _{den}	Res. Dev	F-value	p-value
Null			96	21.92		
Harvest	3	0.379	93	21.54	0.540	0.656
Site preparation	2	0.213	91	21.33	0.455	0.636

Df_{num}, numerator degrees of freedom; Dev, deviation; Df_{den}, denominator degrees of freedom; Res Dev, residual deviation.

Table 3.9. Effects of (a) microsite conditions, and (b) silvicultural treatments on seedling species composition in 3 m² plots in a managed northern hardwood forest of Upper Michigan, USA. Permutations were constrained within blocks. Models first included all treatment interactions and were then simplified if no interaction effect was detected. Lower order interactions were retained if higher order interactions were statistically significant. Asterisks indicate statistical significance ($p < 0.05$), italicized values indicate marginal significance ($0.05 < p < 0.10$). Despite significant main treatment effects, the lack of a treatment $\times$ year interaction effect suggests little difference among treatments but rather an overall disturbance effect on seedling composition.

(a)

	df	Sum. Sq	Mean Sq	F-value	R ²	p-value
Canopy openness	1	1.375	1.375	4.075	0.019	0.001*
Litter depth	1	0.811	0.811	2.404	0.011	0.021*
Soil Water Content (SWC)	1	0.764	0.764	2.263	0.010	0.026*
SWC intraseasonal variation (SWC CV)	1	0.905	0.905	2.683	0.012	0.024*
Litter within-plot variation (Litter CV)	1	0.721	0.721	2.136	0.010	0.041*
Residuals	206	69.519	0.337		0.938	
Total	211	74.096			1.000	

(b)

	df	Sum. Sq	Mean Sq	F-value	R ²	p-value
Harvest	3	1.131	0.377	1.495	0.037	<i>0.069</i>
Site preparation	2	0.706	0.353	1.399	0.023	0.135
Year	1	2.703	2.703	10.713	0.087	0.001*
Harvest $\times$ Site preparation	6	2.424	0.404	1.601	0.078	0.014*
Residuals	95	23.967	0.252		0.775	
Total	107	30.932			1.000	

Table 3.10. Effects of (a) microsite conditions, and (b) silvicultural treatments on sapling species composition in 15 m² plots in a managed northern hardwood forest of Upper Michigan, USA. Permutations were constrained within blocks. Models first included all treatment interactions and were then simplified if no interaction effect was detected. Lower order interactions were retained if higher order interactions were statistically significant. Asterisks indicate statistical significance ($p < 0.05$), italicized values indicate marginal significance ($0.05 < p < 0.10$). Despite significant main treatment effects, the lack of a treatment $\times$ year interaction effect suggests little difference among treatments.

(a)

	df	Sum. Sq	Mean Sq	F-value	R ²	p-value
Canopy openness	1	0.673	0.676	2.793	0.013	0.014*
Litter depth	1	0.202	0.202	0.834	0.004	0.511
Soil Water Content (SWC)	1	0.241	0.241	0.998	0.005	0.445
SWC seasonal variation (SWC CV)	1	0.888	0.888	3.673	0.017	0.031*
Litter depth within-plot variation (Litter CV)	1	0.202	0.202	0.835	0.004	0.548
Residuals	206	49.828	0.242		0.958	
Total	211	52.037			1.000	

(b)

	df	Sum. Sq	Mean Sq	F-value	R ²	p-value
Harvest	3	1.316	0.439	2.547	0.065	0.002*
Site preparation	2	0.799	0.399	2.320	0.040	0.008*
Year	1	0.219	0.219	1.273	0.011	0.250
Harvest $\times$ Site preparation	6	1.480	0.247	1.433	0.073	0.033*
Residuals	95	16.362	0.172		0.811	
Total	107	20.176			1.000

Figure 3.2. Average microsite conditions among years and disturbance treatments in 15 m² plots of a managed northern hardwood forest of Upper Michigan, USA (n = 54). Letters indicate significant differences among harvest treatments across both years using Tukey's correction ($\alpha = 0.05$). Note that litter depth, soil water content (SWC), SWC intraseasonal variation, and within-plot litter depth variation were also correlated with site preparation treatments (Table 4.2). STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut.

Figure 3.3. Average seedling (< 30 cm tall) density (stems ha⁻¹ ± standard error) across harvest treatments, site preparation treatments, and years in a managed northern hardwood forest in Upper Michigan, USA. Species that occurred in fewer than 5% of plots were excluded. Note species-specific y-axis ranges. Despite statistically significant effects of harvest on red maple seedling density, post-hoc tests using Tukey's correction failed to detect treatment differences. STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut; Scar, scarification.

Figure 3.4. Seedling density (stems ha^{-1}) as a function of microsite environment in a managed northern hardwood forest of Upper Michigan, USA. Only 2018 measurements were analyzed. Seedling density was measured in 3 m^2 circular plots nested within basal area measurement plots of 0.03 ha. STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut.

Figure 3.5. Average sapling (> 30 cm tall, < 5 cm dbh) density (stems ha⁻¹ ± standard error) across harvest treatments, site preparation treatments, and years in a managed northern hardwood forest of Upper Michigan, USA. Species that occurred in fewer than 5% of plots were excluded. Note species-specific y-axis ranges. Lowercase letters denote significant differences in sapling density among harvest treatments. Despite statistically significant effects of harvest on other sapling species, post-hoc tests using Tukey's correction failed to detect differences among harvest or site preparation treatments. STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut; Scar, scarification.

Figure 3.6. Average proportion (± 1 standard error) of sugar maple saplings (> 30 cm tall, < 5 cm dbh) identified as stump sprouts or suckers in 15 m^2 plots in a managed northern hardwood forest of Upper Michigan, USA. Only 2018 values are shown. There was no difference among treatments. STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut.

Figure 3.7. Nonmetric multidimensional scaling (NMDS) ordination comparing pre-treatment (2016) and post-treatment (2018) plot-level seedling composition ($n = 212$). Each point represents the average ($\pm$ standard deviation) seedling community composition of a) harvest treatment, and b) site preparation treatment using the first two ordination axes. Distance between plots represents the similarity of their composition. Vectors represent microsite variables. The direction and length of each vector indicate the relative treatment influence on the response variables. Vectors were scaled to fit the ordination. Lowercase letters denote significant differences in compositional between years with Holm's adjustment ($\alpha = 0.05$). Despite a statistically significant harvest $\times$ treatment interaction, post-hoc tests using Holm's adjustment failed to detect treatment differences. SWC, soil water content; SWC CV, intraseasonal SWC coefficient of variation; Litter CV, within-plot litter depth coefficient of variation.

Figure 3.8. Nonmetric multidimensional scaling (NMDS) ordination comparing pre-treatment (2016) and post-treatment (2018) plot-level ground-layer sapling composition ($n = 212$). Each point represents the average ($\pm$ standard deviation) seedling community composition of a) harvest treatment, and b) site preparation treatment using the first two ordination axes. Distance between plots represents the similarity of their composition. Vectors represent microsite variables. The direction and length of each vector indicate the relative treatment influence on the response variables. Vectors were scaled to fit the ordination. Lowercase letters denote significant differences in composition between among harvest treatments with Holm's multiple comparison adjustment ($\alpha = 0.05$). Composition in CC stands was marginally different from composition in STS stands. SWC, soil water content; SWC CV, intraseasonal SWC coefficient of variation; Litter CV, within-plot litter depth coefficient of variation.

3.4 Discussion

We predicted that intermediate harvesting and site preparation methods would promote the regeneration of mid-tolerant species such as yellow birch (*Betula alleghaniensis* Britt.). Though silvicultural treatments favored other species, we found that yellow birch seedling density was better predicted by residual conspecific basal area and within-plot litter depth variation. Moreover, seedling and sapling composition was structured along a canopy openness and litter depth gradient, and harvesting caused more divergent composition when compared to site preparation treatments.

3.4.1 Regeneration

Overall, we found harvest treatment to affect seedling densities of red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and black cherry (*Prunus serotina* Ehr.), regardless of pre-treatment seedling densities. In contrast, site preparation treatment was only marginally correlated with sugar maple, though the strength of the response varied with pre-treatment density. In contrast to our first hypothesis however, yellow birch was not correlated with harvest or site preparation treatment, likely owing to large variation among plots. For example, 2018 yellow birch seedling density ranged from 1944.3 ($\pm$ 512.1) seedlings ha⁻¹ in irregular shelterwood – low residual (ISL) harvest with no site preparation, to 36385.3 ($\pm$ 17670.2) seedlings ha⁻¹ in irregular shelterwood – high residual (ISH) harvest with scarification. We had also expected average litter depth to influence yellow birch seedling density but found no evidence to support this relationship. Instead, yellow birch regeneration in 2018 was

better predicted by the residual basal area of nearby conspecific trees and within-plot litter depth variation, suggesting that propagule availability and microsite heterogeneity are important determinants of germination, or because fewer plots than anticipated were in completely scarified areas. Previous work from a non-replicated trial in Upper Michigan partially supports our findings by recommending canopy gaps along with nearby seed tree retention and mineral soil exposure to regenerate yellow birch (Eyre and Zillgitt 1953). Though propagule availability and stochasticity often drive immediate responses to disturbance (Kreyling et al. 2011, Måren et al. 2018), continued survival and recruitment into the sapling size class will likely depend on microsite conditions created by silvicultural treatments. For example, yellow birch is not considered drought tolerant (Erdmann 1990, Poznanovic et al. 2013), and Metzger (1980) found marginally more yellow birch on somewhat poorly drained sites when compared to mesic sites in strip clearcuts in Upper Michigan. High-severity silvicultural treatments such as ISL and clearcut (CC) harvesting tended to have lower, but not significant, SWC compared to ISH and STS treatments. Coupled with more exposure, evapotranspiration is likely greater when compared to low-severity treatments and could inhibit yellow birch survival in ISL and CC treatments. Scarification may also exacerbate potential drought effects if soils have relatively low SWC prior to treatment application (Prévost et al. 2010), but we recorded relatively similar SWC in scarified plots from pre-treatment to post-treatment. Continuing to monitor yellow birch seedling recruitment into the sapling class will consequently be essential to understanding its long-term response to these silvicultural treatments.

Sugar maple seedling density tended to be lowest in CC treatments, while black cherry tended to be lowest in STS treatments, potentially reflecting contrasting life history traits. Low sugar maple density in CC treatments is likely attributable to either low advance regeneration or competition from shade intolerant species. Though sugar maple may have higher drought tolerance (Roberts and Dong 1993) and higher growth rates under increased light availability (Lorenzetti et al. 2008) when compared to yellow birch, we found no difference in response two growing seasons following the main harvest. In contrast to sugar maple, black cherry is shade intolerant and has been found to respond positively to increased light availability (Jagodziński et al. 2019, Shabaga et al. 2019). Moreover, black cherry may delay germination for up to three years, allowing for this species to quickly germinate following an increase in growing space from disturbances such as harvesting (Marquis 1990, Falk et al. 2010). On the other hand, Shields et al (2007) found no difference in black cherry seedling density among harvest-created gaps and reference sites after two growing seasons in a similar forest. Seven and twelve years later, Poznanovic et al (2013) and Knapp et al (2019), respectively, also found negligible differences in black cherry seedling density among the same gaps and reference sites. In our study, black cherry was not associated with site preparation treatment, suggesting it either may not require extensive soil disturbance to germinate, or has a substantial proportion of seeds that have yet to germinate. The lower density of black cherry seedlings in STS stand may be attributable to either lower disturbance severity and consequently fewer seedlings germinating, or instead lower propagule availability.

Silvicultural treatments had a greater effect on saplings than seedlings, though treatment effects were largely dependent on the density of advance regeneration. Red maple, ironwood, and black cherry sapling densities tended to be highest in 2018, likely owing to greater recruitment from stump sprouts emerging under high light conditions the previous year. For example, black cherry sapling density increased in 2018 in nearly all treatments except STS. Shields et al (2007) found no difference in black cherry sapling densities two growing seasons following group harvesting in a similar forest, and Poznanovic et al (2013) observed negligible differences in black cherry density nine years following harvesting in the same study. Six year later, however, Knapp et al (2019), found higher black cherry sapling densities in medium group openings (740 – 1210 m²) when compared to single-tree selection reference sites. Though we found treatment effects on black cherry sapling density, a marginal harvest × covariate interaction suggests that response strength may be dependent on pre-treatment sapling density. The largest increases, however, were in the severe harvest treatments (i.e. ISL and CC), while density in STS plots remained low each year.

Sugar maple sapling density generally increased in all treatments, perhaps owing to sapling recruitment. For instance, the higher proportion of sugar maple sapling stump sprouts we observed in ISH, ISL, and CC treatments, though not statistically different from STS, could reflect more rapid recruitment of seedling stump sprouts into the sapling height class after emerging under higher light availability.

3.4.2 Composition

Silvicultural treatments were correlated with both seedling and sapling composition, with several microsite conditions mediating treatment differences. Confirming our second hypothesis, seedling composition was most strongly divergent along a canopy openness and litter depth gradient, with SWC, intraseasonal SWC variation, and within-plot litter depth variation less important. Plots with higher densities of sugar maple were more strongly correlated with increasing litter depth and tended to comprise a greater proportion of composition prior to treatment application. Ordinations also illustrate no difference in composition among site preparation treatments. Seedling abundance immediately following a disturbance is typically driven more by propagule and substrate availability rather than inter- or intraspecific competition (Foster and Dickson 2004, Foster et al. 2011, Marteinsdóttir 2014). In subsequent years, however, increasing competition within and among species as growing space declines may strongly influence composition among treatments (Kraft et al. 2015, Cadotte and Tucker 2017). Seedling survival into the sapling height class is therefore imperative for future forest structure and function.

Sapling composition was similarly correlated with silvicultural treatments, but fewer measured microsite conditions were driving observed differences. Similar to seedling composition, canopy openness was the strongest driver of sapling composition, followed by intraseasonal variation in SWC. Higher growth rates due to increasing light availability in high-severity treatments is likely driving observed shifts, but without a harvest $\times$ year interaction effect our results must be interpreted with caution. Compositional change in saplings, particularly following the first growing season after

the main harvest treatment, may be strongly driven by seedlings from previous years that are recruited into the sapling age class. In contrast to seedling composition, site preparation treatments had a significant effect on sapling composition likely owing to pre-treatment differences, as ordination groupings remain largely overlapping. Overall, harvest treatments created a wide range in canopy openness which strongly influenced composition, while site preparation treatments likely failed to create a similar spread in SWC, litter depth, and variation in such conditions. As with seedlings, increasing competition in subsequent years may yield more divergent sapling communities.

3.4.3 Conclusion

Using a silvicultural experiment in a northern hardwood forest of Upper Michigan, we found that silvicultural treatments modified microsite conditions to influence seedling and sapling regeneration and composition. We hypothesized a positive response by mid-tolerant yellow birch to intermediate canopy disturbances and site preparation treatments but found that regeneration was better predicted by conspecific basal area and within-plot litter depth variation. Further, we found that in general, seedlings emerging under high light conditions are likely recruited into the sapling size class sooner than seedlings under low light conditions. Confirming our second hypothesis, several microsite conditions were strongly correlated with seedling and sapling composition. Canopy openness was the strongest factor to influence seedling and sapling composition and consequently mediated potential silvicultural

treatment effects. Site preparation treatments also influenced composition, but pre-treatment differences were likely driving any treatment effects.

We failed to see a positive response of yellow birch to silvicultural treatments, likely because large variation within stands was masking potential treatment effects. Yellow birch seedling density was instead better predicted by residual conspecific basal area and within-plot litter depth variation. Consequently, high residual irregular shelterwood harvesting coupled with scarification may be a viable option for yellow birch regeneration only when mature yellow birch individuals are retained in close proximity. Continued monitoring, however, is necessary for testing this hypothesis beyond the short-term responses reported in this study.

The statistical methods used in this chapter may present an important caveat. Linear mixed effects models included treatment unit nested within block as a random effect. This may not accurately account for the restricted randomization of split units being nested within treatment units, and may overestimate the significance of the detected statistical relationships. Future analyses should account for this discrepancy by identifying the random effect as split unit nested within treatment unit, further nested within block.

4. Increasing plant taxonomic diversity masks a decline in phylogenetic diversity following experimental management disturbances in a northern hardwood forest

4.1 Introduction

Disentangling the effects of canopy and forest floor disturbances on the taxonomic, trait, and phylogenetic diversity of plant communities has received little attention in northern hardwood forests but may be important for determining the mechanisms by which disturbances influence plant communities. Disturbances play an important role in ecosystem processes by creating environmental conditions which filter certain traits over others (Denslow 1980, Loehle 2000, Nathan and Muller-Landau 2000, Díaz et al. 2007, Mouillot et al. 2013, Marks et al. 2016). Early successional species are typically characterized by traits that compete best in environments with high light and nutrient availability, while many mid- and late-successional species have traits better suited for competing in low light and nutrient environments (McIntyre et al. 1995). According to the Intermediate Disturbance Hypothesis (IDH), the enormous resource release following high-severity disturbances tends to favor colonization by few, dominating species (Grime 1973, Connell and Slatyer 1977, Connell 1978). In contrast, competition for limited resources in mature, undisturbed forests typically reduces the opportunity for outside species to colonize the site, resulting in relatively species-poor plant communities (Connell 1978). Intermediate levels of disturbance severity, however, promote colonization by disturbance-adapted species but are not severe enough to eliminate disturbance-intolerant species and consequently tend to yield communities with higher taxonomic diversity. Disturbances are therefore important

determinants of taxonomic diversity, but is plant taxonomic diversity correlated more with canopy disturbances or forest floor disturbances, which often co-occur? Further, do taxonomic, trait, and phylogenetic diversity respond similarly to disturbances?

Trait and phylogenetic indices could provide a more comprehensive understanding of disturbance effects (Mason et al. 2005, Cavender-Bares et al. 2009, Mouillot et al. 2013). Such indices have become increasingly useful for understanding the underlying processes that govern community assembly and interspecific competition, but few studies have assessed changes in plant trait and phylogenetic diversity following disturbances in northern hardwood forests. Low trait diversity is typically assumed to imply trait redundancy and more environmental filtering processes, while high trait diversity usually implies more competitive filtering processes (Gerhold et al. 2015, Kuebbing et al. 2017). Despite its recent popularity in community ecology, trait diversity indices depend on the quantity and type of measured traits and may consequently be inconsistent among different studies (Pakeman 2014, Cadotte et al. 2017). Phylogenetic diversity, however, may better capture the entire suite of traits derived from a species evolutionary history (Faith 1992). Though criticisms remain regarding the assumptions of substituting phylogenetic diversity for trait diversity (Cadotte et al. 2017, Mazel et al. 2018), phylogenetic indices could provide a better understanding of community responses to disturbance than taxonomic or trait diversity alone (Mouillot et al. 2013, Le Bagousse-Pinguet et al. 2019). For example, greater taxonomic diversity following a disturbance may simply be driven by the addition of

closely related species, owing to more environmental filtering processes over competitive filtering processes (Villéger et al. 2010, Pakeman 2011).

In Great Lakes northern hardwood forests, natural disturbances are primarily comprised of windthrow and can range from single treefall to catastrophic blowdown, creating a gradient of environmental heterogeneity (Frelich and Lorimer 1991, Zhang et al. 1999, Hanson and Lorimer 2013). In accordance with the IDH, this variation in disturbances is likely responsible for maintaining landscape-level taxonomic diversity across in these forests (Lorimer and Frelich 1994, Zhang et al. 1999). However a long-term decline in tree taxonomic diversity may be due to historical management practices (Angers et al. 2005, Doyon et al. 2005, Neuendorff et al. 2007, Schulte et al. 2007). Consequently, contemporary management in Great Lakes hardwood forests has focused on disturbance-based silvicultural systems to better emulate historical natural disturbance regimes and restore species diversity. Along with variations in harvesting intensity to emulate windthrow severity (Raymond et al. 2009, Kern et al. 2017, Webster et al. 2018), mechanical duff layer removal to expose mineral soil has been used to emulate windthrow by favoring traits of desired species that are typically less competitive in sites with thick duff layers, such as rapid growth and low-mass fruit production (Gross 1984, Seiwa and Kikuzawa 1996, Gastaldello et al. 2007, Willis et al. 2015).

Harvesting and site preparation methods are tools to manipulate canopy and forest floor disturbance severity, respectively, and each disturbance type may have unique impacts on plant community composition. Disentangling the effects of canopy

and forest floor disturbances on plant community composition, and comparing the responses of taxonomic, trait, and phylogenetic diversity to these disturbances, could provide valuable insight into the processes structuring plant community development. A plant community that remains unchanged for several years following a disturbance can be assumed to be resistant to that disturbance (Holling 1973), while a substantial shift in species or trait composition may imply little resistance to that disturbance. Comparing the magnitude of change of plant communities to contemporary management disturbances may consequently help quantify plant community resistance.

In this study we attempt to disentangle the effects of canopy and forest floor disturbances on plant community composition. Further, we assess the short-term responses of plant taxonomic, trait, and phylogenetic diversity to management-based disturbances of varying severity. We hypothesized 1) plant communities would be more resistant to (i.e., less correlated with) canopy disturbances than forest floor disturbances, and 2) that taxonomic, trait, and phylogenetic diversity would follow the Intermediate Disturbance Hypothesis. To test our hypotheses we implemented a range of silvicultural disturbances, including harvesting and site preparation treatments, in a northern hardwood forest. Plant community composition was assessed before and one or two consecutive growing seasons after treatment application and compared to environmental conditions such as canopy openness, leaf litter depth, and soil water content.

4.2 Materials and Methods

4.2.1 Study Area

Study plots are part of the Northern Hardwood Silvicultural Experiment to Enhance Diversity (NHSEED) near Alberta, Michigan (46°37', 88°29'W) within the northern hardwood forest type. Average daily temperatures (1981-2010) in Alberta range from -10.8°C in January to 18.1°C in July for a yearly average of 4.7°C (NOAA 2016). Precipitation averages 88.9 cm annually with 390.1 cm of snowfall (2007-2016, MRCC 2016). Soils are moderately well drained, primarily consisting of cobbly silt loam overlaying Precambrian bedrock with isolated low-lying areas (Albert 1995). A pine-hardwood forest type dominated the site prior to extensive harvesting ca. 1900 to 1938 (Erickson et al. 1990). Single-tree selection management has subsequently been applied since the 1960s, resulting in uneven stands heavily dominated by a canopy of sugar maple (*Acer saccharum* Marsh.), which occupies 80% of total basal area. Other canopy species include red maple (*Acer rubrum* L), with 8% of total basal area, and yellow birch (*Betula alleghaniensis* Britton), with 5% of total basal area.

4.2.2 Experimental design

Four harvest treatments were applied across three blocks of eighteen treatment units in a randomized block design. Harvest treatments include single-tree selection (STS, n = 3 treatment units), irregular shelterwood with high (60%) canopy retention (ISH, n = 6 treatment units), irregular shelterwood with low (30%) canopy retention (ISL, n = 6 treatment units), and patch clearcut (CC, n = 3 treatment units). Each treatment unit is split-plot with three ~2.4 ha split units for site preparation treatments (n = 54 split units, Figure 4 .1). Two 15 m² circular plots were placed in each split unit and

randomly located greater than 20 m from the edge of the unit ($n = 108$). Half the ISH and ISL treatments will undergo a final harvest once seedlings have established (~5 years). Owing to its historical and continuing wide-spread application throughout Great Lakes hardwood forests (Jacobs 1987, Kern et al. 2014a, Pond et al. 2014), we use STS as our experimental control to represent the ‘business as usual’ model. Forest floor disturbance treatments, each applied to 18 split units, include untreated reference, artificial pit-mound topography, and mechanical scarification. Sites were harvested in February and March 2017 when snow cover and cold soil minimized forest floor disturbances from the canopy disturbance treatment. Small diameter trees (<5 cm dbh) were cut by brush saw and left on-site in August 2017 following field measurements. To emulate windthrow damage, artificial pit-mound topography was created during initial harvest by removing the tree and attached root ball from the soil and placing within ~5 m of the residual pit (Figure 4.1). Owing to challenges of operational scale experiments, average mound density (± 1 SE) was inconsistent among treatments, ranging from 8.7 (± 0.9) in STS treatments to 15.0 (± 6.7) in CC treatments. Mechanical scarification was implemented in October 2017 using a salmon blade to mix the A and O horizon, including the duff layer.

4.2.3 Environmental conditions

Canopy openness was measured at each plot with hemispherical photography during the 2015 and 2018 field seasons. Though other pre-treatment measurements were taken one year following pre-treatment photographs, canopy conditions were relatively

unchanged. Using a Sigma 4.5 mm F2.8 EX HSM fisheye lens attached to a Nikon D3200 digital camera at 1 m height pointed directly vertical, photographs were taken once during the growing season when canopy leaves were fully expanded, overcast conditions prevailed, exposure was uniform, and solar disc not visible. Litter (Oi layer) depth was measured with a ruler at ten randomly chosen locations within each 15 m² plot. Soil water content (SWC) was recorded once per month during the second week of each growing season month (June, July, August) in 2016 and 2018 with a Theta Probe Soil Moisture Sensor (Delta-T Devices Ltd., Cambridge UK) in each plot, calibrated for mineral soil. Measurements were taken in two consecutive days and at least 36 hrs following a precipitation event. Seventeen measurements were taken in each plot: one measurement at plot center and four in each cardinal direction at intervals of 50 cm.

4.2.4 Plant Community

To assess plant community dynamics, all vascular plant species less than 1.37 m in height were assessed during the 2016 and 2018 growing seasons in each 15 m² plot using eight cover classes: 1%; 2-5%; 6-10%; 11-25%; 26-50%; 51-75%; 76-95%; and 96-100%. Most plants were identified to species level, but those in genera *Amelanchier*, *Carex*, *Hieracium*, *Trillium*, and *Viola* along with families Poaceae and Juncaceae were identified to genus- or family-level, respectively, owing to challenges identifying to species level given their phenology and timing of sampling. Cover classes were then converted to midpoints of respective cover ranges prior to all analyses.

4.2.5 Diversity indices

For a comprehensive assessment of diversity responses, we calculated taxonomic, phylogenetic, and trait alpha diversity. Taxonomic alpha diversity was calculated using Shannon's diversity index. We also assessed several life history traits post-hoc to capture a range of above and belowground traits including fruit type, growth form, mycorrhizae type, and coefficient of conservatism. Growth forms were compiled using the USDA PLANTS Database and the Kew Seed Information Database. Fruit types were compiled using the USDA PLANTS Database, Gleason & Cronquist (1991), and several online sources. Mycorrhizae type was compiled using Brundrett & Tedersoo (2018) and coefficient of conservatism, a regionally-specific measure of species affinity for disturbance, was compiled using Chadde (2014). On a 0-10 scale, a coefficient of zero corresponds to a high affinity for disturbance, while a coefficient of 10 corresponds to a low affinity for disturbance. Introduced species were given a coefficient of zero. For taxa not identified to species level, the coefficient was averaged among all possible regionally-identified species within the genus which could naturally occur in the given conditions.

Trait alpha diversity was quantified using an index of trait dispersion, which measures the distribution of traits in niche space based on the relative abundance of each trait; a high abundance of similar traits will decrease dispersion, while a moderate abundance of unique or similar traits will increase dispersion (Mason et al. 2005, Kuebbing et al. 2017). Analyses were conducted using the *dbFD* function in the 'FD'

package of R 3.5.0 software (Laliberté & Legendre 2010; Laliberté et al 2014; R Core Development Team 2018).

Phylogenetic alpha diversity was quantified by first constructing a phylogenetic tree of all recorded taxa using the *phylo.maker* function in the ‘V.Phylomaker’ package of R 3.5.0 software (Qian and Jin 2019, R Core Development Team 2018). The total branch length of each taxon was measured to produce an index of phylogenetic diversity, which is positively correlated with species richness and therefore cannot be accurately compared among samples of varying richness (Kembel et al 2010). To account for this, our reported value of phylogenetic diversity is a standardized effect size, calculated by comparing observed phylogenetic diversity to a null model of random taxa from the total pool. A negative value corresponds to more clustered phylogenies when compared to the null model of phylogenetic diversity, while a positive value corresponds to overdispersion. The standardized effect size was calculated using the *ses.pd* function in the ‘picante’ package of R 3.5.0 software, with “taxa.labels” specified as the null model at 999 runs and 1000 iterations (Kembel et al 2010, R Core Development Team 2018).

To assess the heterogeneity of plant communities across spatial scales, we calculated beta-dispersion as a measure of beta-diversity. Taxonomic beta-dispersion was calculated with the *betadisper* function in the ‘vegan’ package of R 3.5.0 software, using the Bray-Curtis dissimilarity measure. Phylogenetic beta-dispersion was calculated by first using the *phylosor* function in the ‘picante’ package of R 3.5.0 software to create a distance matrix of the fraction of branch-length shared between the

constructed phylogenetic tree and a pruned phylogenetic tree. We then calculated beta-dispersion using the *betadisper* function in the ‘vegan’ package.

4.2.6 Data analysis

To test our first hypothesis, the relationships among environmental conditions and plant community composition were assessed with permutational multivariate analysis of variance (PERMANOVA, *adonis* function in ‘vegan’ package of R 3.5.0, Oksanen et al., 2018) using Bray-Curtis distance matrices constrained within blocks. Rare species were retained in the analysis, but four plots with incomplete environmental data were removed. The effects of disturbance treatment on plant community composition and composition of life history traits were also assessed with PERMANOVA using Bray-Curtis distance matrices constrained within blocks. To account for repeated measures, we used the average change in cover (2018 minus 2016, $n = 54$) as the response variable, with canopy and forest floor disturbance as predictor variables. Models first included all treatment interactions and were then simplified if no interaction effect was detected. Pairwise multiple comparisons were conducted with the *pairwise.perm.manova* function in the ‘RVAideMemoire’ package (Hervé 2019) using Holm’s multiple comparison adjustment. Changes in composition were visualized with nonmetric multidimensional scaling (NMDS) ordination using Bray-Curtis distances. Ordinations were constructed with the *metaMDS* function in the ‘vegan’ package of R 3.5.0, with 999 iterations. Rare species were included in the matrix, and environmental variables were relativized by maximum value of each variable along with all species.

Average point scores from the first two axes of each disturbance treatment were graphed, and environmental variables and species or traits fitted as vectors onto the community ordination using the *envfit* function. Indicator species and traits were identified using the *multipatt* function in the ‘indicspecies’ package of R 3.5.0 with 999 permutations (De Cáceres and Legendre 2009). To identify indicators of disturbance treatments, we only included post-treatment measurements.

To test our second hypothesis, we used linear mixed effects models with treatment unit nested within block included as a random factor to examine the effect of disturbance treatment on plot-level environmental conditions and diversity indices. Seasonal variation in SWC was included by calculating the coefficient of variation (CV, calculated as $[\text{standard deviation}/\text{mean}] * 100$ and expressed as a percentage) of the three-month plot-level average of SWC. Within-plot litter depth CV was calculated using the ten measurements per plot. We included genera *Amelanchier*, *Hieracium*, *Trillium*, *Viola*, families Cyperaceae and Poaceae, and species in taxonomic diversity indices to avoid underestimating the influence of abundant taxa. As such, our reported values do not represent true species diversity but rather relative taxonomic diversity. Response variables were then Box-Cox transformed as necessary to meet assumptions. Tests were conducted using the *lme* function in the ‘nlme’ package in R 3.5.0 software (Pinheiro et al. 2018) and fitted by the Satterthwaite test. Pairwise multiple comparisons were conducted with the ‘emmeans’ package (Lenth 2018) using Tukey’s HSD correction. Within-treatment pairwise comparisons of pre-treatment and post-treatment beta-dispersion, along with among treatment beta-dispersion comparing 2016 to 2018

site-level beta-dispersion, were assessed with Tukey's Honestly Significant Difference. Lower beta-dispersion corresponds to less compositional heterogeneity within or among treatments and similarly suggests that plot level composition is retained at the treatment level.

Figure 4.1. a) Layout of the Northern Hardwood Silvicultural Experiment for Enhanced Diversity near Alberta, Michigan, USA. Canopy and forest floor disturbance treatments were applied in a randomized block design across 54 ~2.4 ha split units. Colors denote canopy disturbance treatment and patterns denote forest floor disturbance treatment. b) Illustration depicting site preparation treatments. Pit-mound topography was created by removing the tree with attached root ball from the soil and placing nearby. Scarification was implemented using a salmon blade to mix the A and O horizons, including the duff layer.

4.3 Results

4.3.1 Microsite conditions

Disturbance treatments were correlated with all microsite conditions, and several interactions between disturbance treatments and year indicate that differences among disturbance treatments were only found pre- or post-disturbance while the lack of a year interaction suggests that pre-disturbance differences persisted. Canopy disturbance treatments created a gradient of canopy openness, as expected ($F_{\text{canopy disturbance} \times \text{year}} = 37.34, p < 0.001$, Table 4.1, Figure 4.2). Mean litter depth in 2018 was nearly half that of 2016 ($F_{\text{year}} = 184.77, p < 0.001$, Table 4.1, Figure 4.2), but observed declines with increasing canopy and forest floor disturbance severity were present prior to disturbances. Though average litter depth decreased, within-plot variation in litter depth increased in all treatments and scarified treatments had the greatest variation ($F_{\text{forest floor disturbance} \times \text{year}} = 6.62, p = 0.002$, Table 4.1, Figure 4.2). Moreover, the ISL canopy disturbance tended to yield greater within-plot litter depth variation than other canopy disturbance treatments ($F_{\text{canopy disturbance} \times \text{year}} = 2.39, p = 0.07$, Table 4.1, Figure 4.2).

Average June-August volumetric soil water content (SWC) was not correlated with canopy disturbance. Though marginally lower in scarified treatments, such differences were present prior to disturbance (Table 4.1, Figure 4.2). Lastly, intraseasonal variation in SWC increased in ISH and ISL canopy disturbances from 2016 to 2018 and were higher than STS and CC disturbances in 2018 ($F_{\text{canopy disturbance} \times \text{year}} = 2.85, p = 0.039$, Table 4.1, Figure 4.2).

4.3.2 Species and trait composition

Environmental conditions were strong predictors of species and trait composition, and these relationships translated to overall disturbance treatment effects (Table 4.2). Species composition was correlated with all measured environmental conditions, but most correlated with canopy openness ($R^2 = 0.072$, $p = 0.001$, Table 4.2). Translating to treatment effects, the change in species composition was most correlated with canopy disturbance ($R^2 = 0.098$, $p = 0.001$, Table 4.2) followed by forest floor disturbance ($R^2 = 0.055$, $p = 0.015$, Table 4.2), but we failed to detect an interaction among treatments. The greatest gains in cover were from Cyperaceae species, *Galeopsis tetrahit*, *Veronica officinalis*, and *Rubus idaeus*, while the greatest losses in cover were from *Dryopteris carthusiana*, *Lonicera canadense*, and *Maianthemum canadense* (Table 4.3).

Like species composition, the composition of fruit types was most correlated with canopy openness ($R^2 = 0.109$, $p = 0.001$, Table 4.4), but was also correlated with litter depth ($R^2 = 0.022$, $p = 0.001$, Table 4.4) and SWC ($R^2 = 0.024$, $p = 0.001$, Table 4.4). There were marginal effects of intraseasonal SWC variation ($R^2 = 0.011$, $p = 0.055$, Table 4.4) and within-plot litter depth variation ($R^2 = 0.007$, $p = 0.066$, Table 4.4) on fruit type composition. In terms of treatments, canopy disturbance had the greatest effect on the change in fruit type composition ($R^2 = 0.109$, $p = 0.003$, Table 4.4), followed by forest floor disturbance ($R^2 = 0.062$, $p = 0.019$, Table 4.4). Like species composition, we failed to detect an interaction among treatments.

Nonmetric multidimensional scaling ordination further illustrates overall effects of disturbance treatments in driving species dissimilarity of plots across years and mediated by changes in environmental conditions (Figure 4.3). The ordination illustrates an overall shift in plot-level composition along an opposing canopy openness - litter depth gradient. Grouping plots by canopy disturbance demonstrates the increasing dissimilarity among treatments over time, though considerable overlap remains. Grouping plots by forest floor disturbance also illustrates marginally increasing dissimilarity among treatments, though considerable overlap similarly remains despite statistically significant differences in the change in species composition among forest floor disturbance treatments.

Like species composition, the composition of fruit types was correlated with canopy disturbance and driven by a gradient of canopy openness, litter depth, and SWC (Figure 4.4). Along an opposing canopy openness – litter depth gradient, composition was strongly structured by low-mass fruit types such as capsules, achenes, schizocarps, and nutlets, though drupelets were also strongly favored by greater canopy openness. In contrast, composition under lower canopy openness was more strongly structured by high-mass fruit types such as berries, pomes, and cones, in addition to spores from ferns and fern allies. Like species composition, canopy disturbance groupings reflect diverging fruit type composition, while grouping by forest floor disturbance illustrates little divergence over time despite a statistically significant effect on the change in composition.

4.3.3 Indicators

Several species were indicators of year or canopy and forest floor disturbance. There were ten species and two mycorrhizal types indicating 2018, likely from an overall disturbance effect. Further, there were three growth form indicators, four fruit type indicators (Table 4.5). Moreover, there were nine species indicators of canopy disturbance treatment, along with two fruit type indicators and no growth form or mycorrhizal type indicators of canopy disturbance treatment (Table 4.5). Only three species were indicators of forest floor disturbance treatment, and there were no growth form, fruit type, or mycorrhizal type indicators of forest floor disturbance (Table 4.5).

4.3.4 Taxonomic, phylogenetic, and trait diversity

Taxonomic diversity (TD), phylogenetic diversity (PD), and trait diversity (TrD) were most associated with year (Table 4.6), suggesting an overall disturbance effect. TD was also associated with a canopy disturbance $\times$ year interaction ($F = 2.65$, $p = 0.050$, Table 4.6, Figure 4.5), indicated by higher TD in 2018 STS and ISH canopy treatments when compared to other treatments and years. We failed to detect a disturbance $\times$ year interaction effect on PD and TrD, however, indicating that differences among treatments in 2018 were present prior to disturbance treatments. From 2016 to 2018, TD generally increased in all treatments except CC (Figure 4.5), in which average TD declined in reference forest floor disturbance treatments and remained unchanged in pit-mound and scarification treatments. In 2016, average TD ranged from $1.5 (\pm 0.1)$ to $2.0 (\pm 0.1)$, while in 2018 average TD ranged from $1.7 (\pm$

0.1) in CC treatments to 2.2 (± 0.2) in STS treatments (Table 4.7). TrD generally increased or remained unchanged in each treatment (Figure 4.5). In 2016, average TrD ranged from 0.41 (± 0.1) to 0.51 (± 0.01) and in 2018 average TrD ranged from 0.46 (± 0.02) to 0.52 (± 0.01 , Table 4.7). In contrast to TD and TrD, phylogenetic diversity (PD) remained unchanged or deviated further negative from the null model in all treatments (Figure 4.5). PD ranged from -0.76 (± 0.01) to 0.11 (± 0.32) in 2016 relative to the null model, and in 2018 ranged from -1.4 (± 0.07) to -0.31 (± 0.41) relative to the null model (Table 4.7). Gains in cover were dominated by orders Poales, Lamiales, and Rosales, while losses were driven by Polypodiales, Dipsacales, and Asparagales (Table 4.3).

Taxonomic and phylogenetic beta diversity within each treatment combination remained unchanged from 2016 to 2018 (Table 4.8). In 2016, average taxonomic beta diversity ranged from 0.387 to 0.508, and in 2018 ranged from 0.415 in ISH canopy disturbance treatments with no forest floor disturbance, to 0.515 in ISL canopy disturbance with pit-mound forest floor disturbance (Table 4.9). From 2016 to 2018, site-level (i.e. among all treatments) taxonomic beta-diversity marginally decreased from an average of 0.493 to 0.469 ($p = 0.07$, Tables 4.9 and 4.10), but site-level phylogenetic beta-diversity remained unchanged ($p = 0.54$, Table 4.10).

Table 4.1. Mixed model effects of canopy disturbance, forest floor disturbance, and year on microsite conditions in a managed northern hardwood forest in Upper Michigan, USA. Treatment unit nested within block was included as a random factor. Models first included all treatment interactions and were then simplified if no interaction effect was detected. Lower order interactions were retained if higher order interactions were statistically significant. Asterisks indicate statistical significance ($p < 0.05$), italicized values indicate marginal significance ($0.05 < p < 0.10$).

Predictor	Canopy openness (n = 213)				Litter depth (n = 215)				SWC (n = 216)			
	RMSE		AIC		RMSE		AIC		RMSE		AIC	
	Df _{num}	Df _{den}	F-value	p-value	Df _{num}	Df _{den}	F-value	p-value	Df _{num}	Df _{den}	F-value	p-value
Intercept	1	189	65100.40	<0.001*	1	194	98.869	<0.001*	1	189	46766.19	<0.001*
Canopy dist	3	12	26.85	<0.001*	3	12	9.851	<0.001*	3	12	0.56	0.649
Forest floor (FF) dist	2	189	0.24	0.790	2	194	5.224	0.006*	2	189	2.97	0.054
Year	1	189	680.35	<0.001*	1	194	184.771	<0.001*	1	189	7.63	0.006*
Canopy dist × FF dist	-	-	-	-	-	-	-	-	6	189	3.52	0.003*
Canopy dist × Year	3	189	37.34	<0.001*	-	-	-	-	-	-	-	-
Df _{num} , numerator degrees of freedom; Df _{den} , denominator degrees of freedom; dist, disturbance												

SWC Intraseasonal CV (n = 216)				within-plot litter depth CV (n = 215)				
	RMSE	AIC		RMSE	AIC			
	1.240	749.707		0.110	-308.477			
Predictor	Df _{num}	Df _{den}	F-value	p-value	Df _{num}	Df _{den}	F-value	p-value
Intercept	1	186	160.529	<0.001*	1	189	81646.49	<0.001*
Canopy dist	3	12	0.578	0.640	3	12	4.69	0.022*
Forest floor (FF) dist	2	186	4.193	0.017*	2	189	5.56	0.005*
Year	1	186	81.586	<0.001*	1	189	84.68	<0.001*
Canopy dist × FF dist	6	186	2.337	0.034*	-	-	-	-
Canopy dist × Year	3	186	2.852	0.039*	3	189	2.39	0.070
FF dist × Year	-	-	-	-	2	189	6.62	0.002*
CV, coefficient of variation; Df _{num} , numerator degrees of freedom; Df _{den} , denominator degrees of freedom; dist, disturbance								

Table 4.2. Permutational multivariate analysis of variance (PERMANOVA) effects of a) microsite conditions ($n = 212$), and b) disturbance treatments ($n = 54$) on ground-layer plant species composition in 15 m² plots in a managed northern hardwood forest of Upper Michigan, USA. Disturbance treatment effects were tested on composition gain scores (absolute value of 2018 minus 2016 cover) to account for repeated measures, and permutations constrained within blocks. No treatment interactions were detected and therefore removed from the final model. Asterisks indicate statistical significance ($p < 0.05$).

a)

	df	Sum. Sq	Mean Sq	F-value	R ²	p-value
Canopy openness	1	2.806	2.806	17.135	0.072	0.001*
Litter depth	1	0.803	0.803	4.906	0.021	0.001*
Soil Water Content (SWC)	1	0.820	0.820	5.006	0.021	0.001*
SWC intraseasonal variation (CV)	1	0.470	0.470	2.872	0.012	0.003*
Litter depth within plot variation (CV)	1	0.283	0.283	1.729	0.007	0.029*
Residuals	206	33.730	0.164		0.867	
Total	211	39.134			1.000	

df, degrees of freedom; Sum. Sq, sum of squares; Mean sq, mean squares; CV, coefficient of variation.

b)

	df	Sum. Sq	Mean Sq	F-value	R ²	p-value
Canopy disturbance	3	1.081	0.360	1.602	0.086	0.006*
Forest floor disturbance	2	0.729	0.365	1.621	0.058	0.023*
Residuals	48	10.797	0.225		0.856	
Total	53	12.607			1.000	

df, degrees of freedom; Sum. Sq, sum of squares; Mean sq, mean squares; CV, coefficient of variation.

Table 4.3b. Mean species gain scores (change in percent cover $\pm$ SE) from 2016 to 2018 among treatments in a northern hardwood forest of Upper Michigan, USA. Blue shading indicates cover gain and red shading indicates cover loss. STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut; Ref, reference; PM, pit-mound; Scar, scarification.

Order	Family	Genus	Species	Form	Fruit	Myc	CoC	Gain Score
Poales	Cyperaceae	-	-	Sedge	Achene	NM/AM	4.6	10.3 (1.4)
Lamiales	Lamiaceae	<i>Galeopsis</i>	<i>tetrahit</i>	Herb - annual	Schizocarp	AM	0.0	5.7 (0.9)
Lamiales	Plantaginaceae	<i>Veronica</i>	<i>officinalis</i>	Herb - perennial	Capsule	AM	0.0	4.5 (1.0)
Rosales	Rosaceae	<i>Rubus</i>	<i>idaeus</i>	Shrub	Drupelet	AM	3.0	1.8 (0.3)
Poales	Poaceae	-	-	Grass	Caryopsis	AM	3.9	1.5 (0.6)
Rosales	Rosaceae	<i>Prunus</i>	<i>serotina</i>	Tree	Drupe	AM	3.0	1.1 (0.5)
Sapindales	Sapindaceae	<i>Acer</i>	<i>saccharum</i>	Tree	Samara	AM	5.0	0.8 (0.7)
Fagales	Betulaceae	<i>Betula</i>	<i>alleghaniensis</i>	Tree	Nutlet	ECM	7.0	0.7 (0.0)
Fagales	Betulaceae	<i>Ostrya</i>	<i>virginiana</i>	Tree	Nutlet	ECM	5.0	0.7 (0.1)
Malpighiales	Violaceae	<i>Viola</i>	spp.	Herb - perennial	Capsule	AM	4.9	0.4 (0.1)
Lycopodiales	Lycopodiaceae	<i>Huperzia</i>	<i>lucidula</i>	Clubmoss	Spore	AM	7.0	0.3 (0.3)
Polypodiales	Athyriaceae	<i>Athyrium</i>	<i>filix-femina</i>	Fern	Spore	AM	5.0	0.3 (0.2)
Rosales	Rosaceae	<i>Prunus</i>	<i>virginiana</i>	Shrub	Drupe	AM	3.0	0.3 (0.1)
Asterales	Asteraceae	<i>Solidago</i>	<i>flexicaulis</i>	Herb - perennial	Cypselae	AM	6.0	0.2 (0.1)
Pinales	Pinaceae	<i>Abies</i>	<i>balsamea</i>	Tree	Cone	ECM	5.0	0.2 (0.1)
Asterales	Asteraceae	<i>Lapsana</i>	<i>communis</i>	Herb - annual/perennial	Cypselae	AM	0.0	0.2 (0.1)
Sapindales	Sapindaceae	<i>Acer</i>	<i>rubrum</i>	Tree	Samara	AM	3.0	0.2 (0.1)
Polypodiales	Dryopteridaceae	<i>Onoclea</i>	<i>sensibilis</i>	Fern	Spore	AM	5.0	0.2 (0.1)
Asterales	Asteraceae	<i>Symphyotrichum</i>	spp.	Herb - perennial	Cypselae	AM	3.7	0.2 (0.2)
Caryophyllales	Polygonaceae	<i>Rumex</i>	<i>obtusifolius</i>	Herb - perennial	Achene	NM	0.0	0.1 (0.1)
Myrtales	Onagraceae	<i>Epilobium</i>	<i>ciliatum</i>	Herb - perennial	Capsule	AM	3.0	0.1 (0.1)
Asterales	Asteraceae	<i>Cirsium</i>	<i>palustre</i>	Herb - biennial	Cypselae	AM	0.0	0.1 (0.0)
Osmundales	Osmundaceae	<i>Osmunda</i>	<i>claytoniana</i>	Fern	Spore	AM	6.0	0.1 (0.0)
Rosales	Rosaceae	<i>Rubus</i>	<i>canadensis</i>	Shrub	Drupelet	AM	2.0	0.1 (0.0)
Lamiales	Lamiaceae	<i>Scutellaria</i>	<i>lateriflora</i>	Herb - perennial	Schizocarp	AM	5.0	0.1 (0.1)
Rosales	Rosaceae	<i>Rubus</i>	<i>alleghaniensis</i>	Shrub	Drupelet	AM	2.0	0.1 (0.0)
Dipsacales	Caprifoliaceae	<i>Sambucus</i>	<i>racemosa</i>	Shrub	Drupe	AM	5.0	0.1 (0.0)
Cornales	Cornaceae	<i>Cornus</i>	<i>alternifolia</i>	Shrub	Drupe	AM	7.0	0.1 (0.0)

Order	Family	Genus	Species	Form	Fruit	Myco	CoC	Gain Score
Gentianales	Rubiaceae	<i>Mitchella</i>	<i>repens</i>	Herb - perennial	Berry	AM	6.0	0.1 (0.0)
Rosales	Rosaceae	<i>Fragaria</i>	<i>virginiana</i>	Herb - perennial	Achene	AM	1.0	0.1 (0.0)
Equisetales	Equisetaceae	<i>Equisetum</i>	<i>sylvaticum</i>	Herb - perennial	Spore	AM	7.0	0.1 (0.0)
Pinales	Pinaceae	<i>Pinus</i>	<i>strobus</i>	Tree	Cone	ECM	5.0	0.1 (0.0)
Ranunculales	Ranunculaceae	<i>Ranunculus</i>	spp.	Herb - perennial	Achene	AM	2.4	0.1 (0.0)
Myrtales	Onagraceae	<i>Epilobium</i>	<i>leptophyllum</i>	Herb - perennial	Capsule	AM	8.0	0.0 (0.0)
Gentianales	Apocynaceae	<i>Apocynum</i>	<i>androsaemifolium</i>	Herb - perennial	Follicle	AM	2.0	0.0 (0.0)
Lamiales	Oleaceae	<i>Fraxinus</i>	<i>pennsylvanica</i>	Tree	Samara	AM	2.0	0.0 (0.0)
Asterales	Asteraceae	<i>Lactuca</i>	<i>canadensis</i>	Herb - biennial	Cypselae	AM	2.0	0.0 (0.0)
Boraginales	Boraginaceae	<i>Myosotis</i>	spp.	Herb - annual	Schizocarp	AM	0.0	0.0 (0.0)
Lamiales	Plantaginaceae	<i>Plantago</i>	<i>major</i>	Herb - perennial	Pyxis	AM	0.0	0.0 (0.0)
Ranunculales	Ranunculaceae	<i>Coptis</i>	<i>trifolia</i>	Herb - perennial	Follicle	AM	8.0	0.0 (0.0)
Pinales	Pinaceae	<i>Tsuga</i>	<i>canadensis</i>	Tree	Cone	ECM	8.0	0.0 (0.0)
Caryophyllales	Polygonaceae	<i>Fallopia</i>	<i>clinodis</i>	Herb - perennial	Achene	NM	1.0	0.0 (0.1)
Asparagales	Asparagaceae	<i>Maianthemum</i>	<i>racemosum</i>	Herb - perennial	Berry	AM	5.0	0.0 (0.1)
Ericales	Balsaminaceae	<i>Impatiens</i>	<i>capensis</i>	Herb - annual	Capsule	AM	2.0	0.0 (0.0)
Rosales	Rosaceae	<i>Geum</i>	<i>macrophyllum</i>	Herb - perennial	Achene	AM	6.0	0.0 (0.0)
Brassicales	Brassicaceae	<i>Barbarea</i>	<i>vulgaris</i>	Herb - biennial	Siliqua	NM	0.0	0.0 (0.0)
Apiales	Araliaceae	<i>Panax</i>	<i>trifolius</i>	Herb - perennial	Drupe	AM	8.0	0.0 (0.0)
Rosales	Rosaceae	<i>Potentilla</i>	<i>norvegica</i>	Herb - annual	Achene	AM	0.0	0.0 (0.0)
Ranunculales	Ranunculaceae	<i>Ranunculus</i>	<i>recurvatus</i>	Herb - perennial	Achene	AM	5.0	0.0 (0.0)
Asterales	Asteraceae	<i>Anaphalis</i>	<i>margaritacea</i>	Herb - perennial	Achene	AM	3.0	0.0 (0.0)
Lycopodiales	Lycopodiaceae	<i>Diplazium</i>	<i>complanatum</i>	Clubmoss	Spore	AM	7.0	0.0 (0.0)
Gentianales	Rubiaceae	<i>Galium</i>	<i>triflorum</i>	Herb - perennial	Schizocarp	AM	5.0	0.0 (0.0)
Malpighiales	Clusiaceae	<i>Hypericum</i>	<i>punctatum</i>	Herb - perennial	Capsule	AM	4.0	0.0 (0.0)
Asparagales	Iridaceae	<i>Iris</i>	<i>versicolor</i>	Herb - perennial	Capsule	AM	5.0	0.0 (0.0)
Asterales	Asteraceae	<i>Lactuca</i>	<i>biennis</i>	Herb - annual/biennial	Cypselae	AM	3.0	0.0 (0.0)
Oxalidales	Oxalidaceae	<i>Oxalis</i>	<i>acetosella</i>	Herb - perennial	Capsule	AM	9.0	0.0 (0.0)

Order	Family	Genus	Species	Form	Fruit	Myco	CoC	Gain Score
Asterales	Asteraceae	<i>Prenanthes</i>	<i>alba</i>	Herb - biennial	Cypselae	AM	5.0	0.0 (0.0)
Ericales	Ericaceae	<i>Pyrola</i>	<i>elliptica</i>	Herb - perennial	Capsule	EEM	6.0	0.0 (0.0)
Fagales	Fagaceae	<i>Quercus</i>	<i>rubra</i>	Tree	Nut	ECM	5.0	0.0 (0.0)
Ranunculales	Ranunculaceae	<i>Ranunculus</i>	<i>hispidus</i>	Herb - perennial	Achene	AM	6.0	0.0 (0.0)
Solanales	Solanaceae	<i>Solanum</i>	<i>dulcamara</i>	Herb - perennial	Berry	AM	0.0	0.0 (0.0)
Asterales	Asteraceae	<i>Solidago</i>	spp.	Herb - perennial	Cypselae	AM	3.4	0.0 (0.0)
Pinales	Cupressaceae	<i>Thuja</i>	<i>occidentalis</i>	Tree	Cone	AM	9.0	0.0 (0.0)
Pinales	Pinaceae	<i>Picea</i>	<i>glauca</i>	Tree	Cone	ECM	7.0	0.0 (0.0)
Liliales	Melanthiaceae	<i>Trillium</i>	spp.	Herb - perennial	Berry	AM	5.0	0.0 (0.0)
Asterales	Asteraceae	<i>Taraxacum</i>	<i>officinale</i>	Herb - perennial	Cypselae	AM	0.0	0.0 (0.0)
Ranunculales	Ranunculaceae	<i>Anemone</i>	<i>quinquefolia</i>	Herb - perennial	Achene	AM	6.0	0.0 (0.0)
Myrtales	Onagraceae	<i>Circaea</i>	<i>alpina</i>	Herb - perennial	Capsule	AM	7.0	0.0 (0.0)
Dipsacales	Caprifoliaceae	<i>Diervilla</i>	<i>lonicera</i>	Shrub	Capsule	AM	6.0	0.0 (0.0)
Lycopodiales	Lycopodiaceae	<i>Lycopodium</i>	<i>dendroideum</i>	Clubmoss	Spore	AM	7.0	0.0 (0.0)
Ericales	Ericaceae	<i>Pyrola</i>	<i>asarifolia</i>	Herb - perennial	Capsule	ERM	8.0	0.0 (0.0)
Ranunculales	Ranunculaceae	<i>Ranunculus</i>	<i>pensylvanicus</i>	Herb - perennial	Achene	AM	5.0	0.0 (0.0)
Malvales	Malvaceae	<i>Tilia</i>	<i>americana</i>	Tree	Nutlet	ECM	5.0	0.0 (0.0)
Asterales	Asteraceae	<i>Cirsium</i>	spp.	Herb - biennial/perennial	Cypselae	AM	0.0	0.0 (0.0)
Liliales	Liliaceae	<i>Clintonia</i>	<i>borealis</i>	Herb - perennial	Berry	AM	7.0	0.0 (0.0)
Equisetales	Equisetaceae	<i>Equisetum</i>	<i>pratense</i>	Herb - perennial	Spore	AM	9.0	0.0 (0.0)
Asterales	Asteraceae	<i>Eurybia</i>	<i>macrophylla</i>	Herb - perennial	Cypselae	AM	4.0	0.0 (0.0)
Asterales	Asteraceae	<i>Oxycoccus</i>	<i>memoralis</i>	Herb - perennial	Cypselae	AM	9.0	0.0 (0.0)
Malpighiales	Salicaceae	<i>Populus</i>	<i>grandidentata</i>	Tree	Capsule	AM/EM	3.0	0.0 (0.0)
Ericales	Ericaceae	<i>Pyrola</i>	<i>minor</i>	Herb - perennial	Capsule	EEM	10.0	0.0 (0.0)
Rosales	Rosaceae	<i>Rubus</i>	<i>flagellaris</i>	Shrub	Drupelet	AM	1.0	0.0 (0.0)
Dipsacales	Caprifoliaceae	<i>Sambucus</i>	<i>canadensis</i>	Shrub	Drupe	AM	3.0	0.0 (0.0)
Polypodiales	Thelypteridaceae	<i>Phegopteris</i>	<i>connectilis</i>	Fern	Spore	AM	7.0	0.0 (0.0)
Liliales	Melanthiaceae	<i>Trillium</i>	<i>cernuum</i>	Herb - perennial	Berry	AM	8.0	0.0 (0.0)

Order	Family	Genus	Species	Form	Fruit	Myco	CoC	Gain Score
Ericales	Ericaceae	<i>Monotropa</i>	<i>uniflora</i>	Herb - perennial	Capsule	ECM	5.0	0.0 (0.0)
Rosales	Rosaceae	<i>Prunus</i>	<i>pensylvanica</i>	Tree	Drupe	AM	4.0	0.0 (0.0)
Ranunculales	Ranunculaceae	<i>Ranunculus</i>	<i>acris</i>	Herb - perennial	Achene	AM	0.0	0.0 (0.0)
Lamiales	Oleaceae	<i>Fraxinus</i>	<i>nigra</i>	Tree	Samara	AM	5.0	0.0 (0.0)
Asterales	Asteraceae	<i>Prenanthes</i>	spp.	Herb - perennial	Cypselae	AM	5.0	0.0 (0.0)
Rosales	Ulmaceae	<i>Ulmus</i>	<i>americana</i>	Tree	Samara	AM	3.0	0.0 (0.0)
Rosales	Rosaceae	<i>Amelanchier</i>	spp.	Shrub	Pome	AM	6.0	0.0 (0.0)
Ranunculales	Ranunculaceae	<i>Anemone</i>	spp.	Herb - perennial	Achene	AM	4.0	0.0 (0.0)
Lycopodiales	Lycopodiaceae	<i>Lycopodium</i>	<i>annottinum</i>	Clubmoss	Spore	AM	7.0	0.0 (0.0)
Rosales	Rosaceae	<i>Prunus</i>	spp.	Tree	Drupe	AM	2.0	0.0 (0.0)
Saxifragales	Grossulariaceae	<i>Ribes</i>	<i>triste</i>	Shrub	Berry	AM	8.0	0.0 (0.0)
Liliales	Melanthiaceae	<i>Trillium</i>	<i>grandiflorum</i>	Herb - perennial	Berry	AM	6.0	0.0 (0.0)
Ericales	Primulaceae	<i>Trientalis</i>	<i>borealis</i>	Herb - perennial	Capsule	AM	7.0	0.0 (0.1)
Liliales	Liliaceae	<i>Streptopus</i>	<i>lanceolatus</i>	Herb - perennial	Berry	AM	7.0	-0.1 (0.0)
Apiales	Araliaceae	<i>Aralia</i>	<i>nudicaulis</i>	Herb - perennial	Drupe	AM	6.0	-0.1 (0.1)
Lamiales	Lamiaceae	<i>Clinopodium</i>	<i>vulgare</i>	Herb - perennial	Schizocarp	AM	3.0	-0.1 (0.0)
Asparagales	Asparagaceae	<i>Polygonatum</i>	<i>pubescens</i>	Herb - perennial	Berry	AM	6.0	-0.1 (0.1)
Lycopodiales	Lycopodiaceae	<i>Lycopodium</i>	spp.	Clubmoss	Spore	AM	5.0	-0.1 (0.1)
Polypodiales	Athyriaceae	<i>Deparia</i>	<i>acrostichoides</i>	Fern	Spore	AM	10.0	-0.1 (0.0)
Alismatales	Araceae	<i>Arisaema</i>	<i>triphylllum</i>	Herb - perennial	Berry	AM	5.0	-0.1 (0.0)
Polypodiales	Dryopteridaceae	<i>Gymnocarpium</i>	<i>dryopteris</i>	Fern	Spore	AM	7.0	-0.1 (0.1)
Polypodiales	Dennstaedtiaceae	<i>Pteridium</i>	<i>aquilinum</i>	Fern	Spore	AM	2.0	-0.2 (0.1)
Osmundales	Osmundaceae	<i>Osmunda</i>	<i>cinnamomea</i>	Fern	Spore	AM	7.0	-0.2 (0.1)
Asterales	Asteraceae	<i>Hieracium</i>	spp.	Herb - perennial	Cypselae	AM	0.0	-0.4 (0.3)
Asparagales	Asparagaceae	<i>Maianthemum</i>	<i>canadense</i>	Herb - perennial	Berry	AM	5.0	-0.4 (0.2)
Dipsacales	Caprifoliaceae	<i>Lonicera</i>	<i>canadensis</i>	Shrub	Berry	AM	8.0	-0.7 (0.3)
Polypodiales	Dryopteridaceae	<i>Dryopteris</i>	<i>carthusiana</i>	Fern	Spore	AM	7.0	-4.0 (0.8)

Table 4.4. Permutational multivariate analysis of variance (PERMANOVA) effects of a) microsite conditions (n = 212), and b) disturbance treatments (n = 54) on the composition of fruit types in 15 m² plots in a managed northern hardwood forest of Upper Michigan, USA. Disturbance treatment effects were tested on composition gain scores (absolute value of 2018 minus 2016 cover) to account for repeated measures, and permutations constrained within blocks. No treatment interactions were detected and therefore removed from the final model. Asterisks denote statistical significance ($p < 0.05$). Italicized values denote marginal significance ($0.05 < p < 0.10$).

a)

	df	Sum. Sq	Mean Sq	F-value	R ²	P-value
Canopy openness	1	2.468	2.468	27.178	0.109	0.001*
Litter depth	1	0.496	0.496	5.466	0.022	0.001*
Soil Water Content (SWC)	1	0.535	0.535	5.890	0.024	0.001*
SWC intraseasonal variation (CV)	1	0.242	0.242	2.668	0.011	<i>0.055</i>
Litter depth within plot variation (CV)	1	0.154	0.154	1.690	0.007	<i>0.066</i>
Residuals	206	18.708	0.091		0.828	
Total	211	22.603			1.000	

df, degrees of freedom; Sum. Sq, sum of squares; Mean sq, mean squares

b)

	df	Sum. Sq	Mean Sq	F-value	R ²	P-value
Canopy disturbance	3	1.082	0.361	2.097	0.109	0.003*
Forest floor disturbance	2	0.617	0.308	1.792	0.062	0.019*
Residuals	48	8.259	0.172		0.829	
Total	53	9.958			1.000	

df, degrees of freedom; Sum. Sq, sum of squares; Mean sq, mean squares

Table 4.5. Indicator species and traits in 15 m² plots in a managed northern hardwood forest of Upper Michigan, USA. Only significant indicators ($p < 0.05$) are shown, and only post-disturbance (2018) canopy and forest floor treatment indicators are shown. CC, clearcut; ISL, irregular shelterwood – low residual; ISH, irregular shelterwood – high residual; STS, single-tree selection.

	Year	Canopy disturbance	Forest floor disturbance
Species			
<i>Betula alleghanensis</i>	2018	-	-
<i>Cirsium palustre</i>	2018	-	-
<i>Epilobium leptophyllum</i>	-	STS, CC	-
<i>Epilobium ciliatum</i>	-	-	Scarification
<i>Equisetum sylvaticum</i>	-	STS	-
<i>Fallopia cilioides</i>	-	-	Scarification
<i>Fragaria virginiana</i>	2018	-	-
<i>Galeopsis tetrahit</i>	2018	-	-
<i>Hieracium</i> spp.	-	STS, CC	-
<i>Lapsana communis</i>	2018	-	-
<i>Lonicera canadensis</i>	-	-	Reference, Pit-mound
<i>Onoclea sensibilis</i>	-	CC	Scarification
<i>Ostrya virginiana</i>	2018	-	-
<i>Polygonatum pubescens</i>	-	ISH, ISL	-
<i>Prunus virginiana</i>	2018	-	-
<i>Rubus idaeus</i>	2018	ISL, ISH, CC	-
<i>Sambucus racemosa</i>	-	STS	-
<i>Solidago flexicaulis</i>	2018	STS	-
<i>Symphotrichum</i> spp.	-	STS, ISH	-
<i>Viola</i> spp.	2018	-	-
Growth form			
Annual herb	2018	-	-
Annual or perennial herb	2018	-	-
Biennial herb	2018	-	-
Fruit type			
Cone	2018	-	-
Drupelet	2018	ISL, ISH, CC	-
Nutlet	2018	-	-
Pyxis	-	CC	-
Schizocarp	2018	-	-
Mycorrhizal type			
ECM	2018	-	-
Nonmycorrhizal	2018	-	-

Table 4.6. Mixed model effects of canopy disturbance, forest floor disturbance, and year on taxonomic, phylogenetic, and trait alpha-diversity in a managed northern hardwood forest of Upper Michigan, USA. Models first included all treatment interactions and were then simplified if no interaction effect was detected. Asterisks denote statistical significance ($p < 0.05$). Italicized values denote marginal significance ($0.05 < p < 0.10$).

Predictor	Taxonomic diversity (n = 205)				Phylogenetic diversity (n = 211)				Trait diversity (n = 208)			
	RMSE		AIC		RMSE		AIC		RMSE		AIC	
	Df _{num}	Df _{den}	F-value	p-value	Df _{num}	Df _{den}	F-value	p-value	Df _{num}	Df _{den}	F-value	p-value
Intercept	1	192	1999.852	<0.001*	1	195	30.031	<0.001*	1	195	85573.58	<0.001*
Canopy dist	3	12	1.027	0.415	3	12	1.457	0.275	3	12	0.25	0.863
Forest floor (FF) dist	2	192	1.864	0.158	2	195	1.946	0.146	2	195	0.60	0.548
Year	1	192	15.803	<0.001*	1	195	26.769	<0.001*	1	195	11.95	<0.001*
Canopy dist × Year	3	192	2.646	<i>0.050</i>	-	-	-	-	-	-	-	-

df, degrees of freedom; Sum. Sq, sum of squares; Mean sq, mean squares; dist, disturbance.

Table 4.7. Average ($\pm$ SE) taxonomic, trait, and phylogenetic alpha-diversity across canopy and forest floor disturbances in 15 m² plots of a managed northern hardwood forest in Upper Michigan, USA (n = 108). STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut.

	2016				2018				
	STS	ISH	ISL	CC	STS	ISH	ISL	CC	
Taxonomic α -diversity	Reference	1.74 (0.17)	1.68 (0.17)	1.86 (0.08)	2.01 (0.11)	1.95 (0.20)	1.94 (0.18)	1.86 (0.10)	1.70 (0.13)
	Pit-mound	1.44 (0.2)	1.93 (0.10)	1.88 (0.11)	1.89 (0.17)	2.04 (0.06)	2.18 (0.07)	2.03 (0.13)	2.02 (0.27)
	Scarification	1.68 (0.20)	1.97 (0.07)	1.52 (0.11)	1.81 (0.05)	2.21 (0.21)	2.01 (0.09)	1.92 (0.11)	1.92 (0.08)
Trait α -diversity	Reference	0.43 (0.03)	0.47 (0.03)	0.46 (0.03)	0.51 (0.01)	0.49 (0.03)	0.46 (0.02)	0.48 (0.03)	0.47 (0.04)
	Pit-mound	0.45 (0.02)	0.47 (0.01)	0.47 (0.03)	0.47 (0.02)	0.50 (0.02)	0.52 (0.01)	0.49 (0.02)	0.50 (0.04)
	Scarification	0.46 (0.05)	0.49 (0.01)	0.42 (0.03)	0.46 (0.03)	0.52 (0.02)	0.47 (0.03)	0.50 (0.03)	0.51 (0.02)
Phylogenetic α -diversity	Reference	-0.50 (0.37)	-0.36 (0.47)	-0.41 (0.28)	-0.54 (0.1)	-0.31 (0.41)	-0.81 (0.25)	-0.72 (0.18)	-0.98 (0.20)
	Pit-mound	0.11 (0.32)	-0.62 (0.20)	-0.58 (0.17)	-0.76 (0.01)	-0.54 (0.26)	-1.17 (0.30)	-1.01 (0.09)	-1.38 (0.07)
	Scarification	0.06 (0.21)	-0.61 (0.19)	-0.26 (0.11)	-0.52 (0.20)	-1.23 (0.25)	-0.70 (0.19)	-0.86 (0.30)	-0.99 (0.14)

Table 4.8a. Pairwise comparisons of taxonomic beta-diversity within each treatment combination between 2016 and 2018 using Tukey’s Honest Significant Difference. We found no change in beta-diversity within any treatment. Italicized values denote marginal significance ($0.05 < p < 0.10$). SES, standardized effect size; STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut.

Canopy disturbance	Forest floor disturbance	Statistic	SES	Mean	p-value
STS	Reference	1.522	1.385	-0.022	0.153
	Pit-mound	0.763	0.735	-0.061	0.433
	Scarification	0.534	0.520	-0.044	0.583
ISH	Reference	0.246	0.263	-0.026	0.777
	Pit-mound	0.561	0.531	0.002	0.581
	Scarification	0.323	0.329	-0.019	0.715
ISL	Reference	0.429	0.410	-0.007	0.679
	Pit-mound	0.813	0.757	-0.003	0.421
	Scarification	1.672	1.606	-0.005	<i>0.095</i>
CC	Reference	0.278	0.286	-0.034	0.749
	Pit-mound	-0.345	-0.274	-0.049	0.781
	Scarification	0.501	0.472	-0.003	0.645

Table 4.8b. Pairwise comparisons of phylogenetic beta-diversity within each treatment combination between 2016 and 2018 using Tukey’s Honestly Significant Difference. We found no difference in beta-diversity within any treatment. SES, standardized effect size; STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut.

Canopy disturbance	Forest floor disturbance	Statistic	SES	Mean	p-value
STS	Reference	1.045	0.875	0.086	0.365
	Pit-mound	0.038	0.055	-0.021	0.979
	Scarification	0.210	0.263	-0.069	0.811
ISH	Reference	-0.726	-0.773	0.070	0.437
	Pit-mound	0.245	0.198	0.028	0.815
	Scarification	-0.571	-0.533	-0.014	0.601
ISL	Reference	-0.199	-0.197	0.010	0.873
	Pit-mound	-0.704	-0.608	-0.080	0.541
	Scarification	-0.825	-0.781	0.025	0.407
CC	Reference	0.718	0.649	0.020	0.489
	Pit-mound	-0.059	-0.028	-0.030	0.943
	Scarification	0.935	0.830	0.057	0.379

Table 4.9. Taxonomic and phylogenetic beta-diversity among year, canopy disturbance, and forest floor disturbance treatments in a managed northern hardwood forest of Upper Michigan, USA (n = 108). STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut.

	2016				2018			
	STS	ISH	ISL	CC	STS	ISH	ISL	CC
Taxonomic β-diversity	Reference	0.508	0.481	0.466	0.408	0.442	0.468	0.438
	Pit-mound	0.458	0.427	0.457	0.387	0.414	0.409	0.420
	Scarification	0.451	0.434	0.511	0.471	0.416	0.420	0.446
Phylogenetic β-diversity	Reference	0.458	0.415	0.463	0.500	0.409	0.452	0.475
	Pit-mound	0.457	0.502	0.465	0.484	0.454	0.495	0.514
	Scarification	0.469	0.490	0.450	0.487	0.459	0.510	0.484

Table 4.10. Analysis of variance of site-level (i.e. among treatments) a) taxonomic and b) phylogenetic beta-diversity in 2016 and 2018 in a managed northern hardwood forest of Upper Michigan, USA (n = 216). Italicized values denote marginal significance.

a)

	Df	Sum Sq	Mean Sq	F-value	p-value
Year	1	0.032	0.032	3.452	<i>0.065</i>
Residuals	214	1.962	0.009		

b)

	Df	Sum Sq	Mean Sq	F-value	p-value
Year	1	0.005	0.005	0.388	0.534
Residuals	214	2.544	0.012

Figure 4.2. Average microsite conditions among disturbance treatments and years in 15 m² plots in a managed northern hardwood forest of Upper Michigan, USA (n = 54). Letters indicate significant differences among canopy disturbances across both years using Tukey's correction ($\alpha = 0.05$). Note that litter depth, soil water content (SWC), SWC intraseasonal variation, and within-plot litter depth variation were also associated with forest floor disturbance (Table 2.1). STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut.

Figure 4.3. Nonmetric multidimensional scaling (NMDS) ordination comparing pre-treatment (2016) and post-treatment (2018) plot-level ground-layer plant species composition ($n = 212$) among a) canopy disturbances, and b) forest floor disturbances. Each point represents average plant community composition ($\pm$ standard deviation) of a) canopy disturbance, or b) forest floor disturbance treatment using the first two ordination axes. Distance between points represents the similarity of average treatment composition. Vectors represent microsite variables. The direction and length of each vector indicate the relative treatment influence on the response variables. Vectors were scaled to fit the ordination. We detected a canopy and forest floor disturbance effect on species composition, mediated by all measured microsite conditions. There was a marginal effect of intraseasonal SWC variation and within-plot litter depth variation. Lowercase letters denote significant differences in compositional change from 2016 to 2018 among canopy disturbances or forest floor disturbances with Holm's multiple comparison adjustment ($\alpha = 0.05$). STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut. SWC, soil water content; SWC CV, intraseasonal SWC variation; Litter CV, within plot litter depth variation.

Figure 4.4. Nonmetric multidimensional scaling (NMDS) ordination comparing pre-treatment (2016) and post-treatment (2018) plot-level ground-layer fruit type composition ($n = 212$). Each point represents average plant community composition ($\pm$ standard deviation) of a) canopy disturbance, or b) forest floor disturbance treatment using the first two ordination axes. Vectors represent microsite variables. The direction and length of each vector indicate the relative treatment influence on the response variables. Vectors were scaled to fit the ordination. We detected a canopy and forest floor disturbance effect on fruit type composition mediated by canopy openness, litter depth, and soil water content (SWC). There was a marginal effect of intraseasonal SWC variation and within-plot litter depth variation. Lowercase letters denote significant differences in compositional change from 2016 to 2018 among canopy disturbances with Holm's multiple comparison adjustment ($\alpha = 0.05$). There was a marginal but non-significant difference between scarification and reference forest floor disturbance treatments. STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut. SWC, soil water content; SWC CV, intraseasonal SWC variation; Litter CV, within plot litter depth variation.

Figure 4.5. Taxonomic, phylogenetic, and trait diversity responses (2018 minus 2016) to canopy and forest floor disturbances in 15 m² plots of a northern hardwood forest in Upper Michigan, USA. A significant year effect on all diversity indices suggests an overall disturbance effect, but there was no difference among disturbance treatments except for a marginal difference in taxonomic diversity among canopy disturbance treatments. Values reported for phylogenetic diversity are standardized effect sizes. Note different y-axis range for trait diversity response. STS, single-tree selection; ISH, irregular shelterwood – high residual; ISL, irregular shelterwood – low residual; CC, clearcut.

4.4 Discussion

Taxonomic diversity is often assumed to follow the Intermediate Disturbance Hypothesis (IDH), whereby intermediate levels of disturbance severity yield greater taxonomic diversity (Grime 1973, Connell 1978). By disentangling canopy and forest floor disturbance effects on plant communities, we found 1) little evidence to support the IDH within two years following disturbance, 2) shifting species and trait composition was driven by canopy disturbance more than forest floor disturbance, and 3) contrasting responses of taxonomic, trait, and phylogenetic diversity. These findings have important implications for plant community conservation in managed forests. Discrepancies among diversity indices could reveal false assumptions regarding the value of only using taxonomic diversity to inform management decisions.

4.4.1 Species and trait composition

We hypothesized that plant community composition would be more resistant to (i.e. less correlated with) canopy disturbance than forest floor disturbance, particularly scarification. Disturbances altered environmental conditions and were ultimately associated with species and trait composition, but we found stronger evidence for a dominant effect of canopy disturbance on plant communities which was driven by an opposing gradient of canopy openness and litter depth. These results suggest, in contrast to our hypothesis, that the plant community is slightly more resistant to forest floor disturbance than canopy disturbance. Ordinations illustrate that increasing canopy openness and concurrent decreases in litter depth were associated with, and likely

driving plot dissimilarity over time by favoring species with suitable life history traits. Fruit type reflects dispersal strategy and is also associated with disturbance adaptations (Lavorel and Garnier 2002, Bernhardt-Römermann et al. 2011). Low mass fruit types are typically wind-dispersed and more easily colonize a recently disturbed site when compared to high mass fruit types, which tend to rely on animals for dispersal (Howe and Smallwood 1982, Westoby et al. 1992). Moreover, species with low mass fruits may have consistently low population abundances in undisturbed forests but can quickly colonize recently disturbed sites via high propagule pressure of wind dispersed seeds, and ultimately dominate the site (Williamson 1996, Cassey et al. 2005). In our study *Epilobium leptophyllum*, *Hieracium* spp., *Onoclea sensibilis*, and *Rubus idaeus* were indicators of the highest severity canopy disturbance, while increasing canopy openness also favored Cyperaceae, *Viola* spp., *Solidago* spp., and the introduced herb *Galeopsis tetrahit*. Excluding *R. idaeus*, these species are characterized by small fruit types like capsules, cypselae, and schizocarps, which allow them to disperse and quickly colonize recently disturbed sites (Donoso and Nyland 2006, Kern et al. 2012, 2013b, Widen et al. 2018). Though drupelets produced by *Rubus idaeus* are larger and fleshy, they contain seeds which can remain viable for up to 60 years when buried and are commonly dispersed by birds and mammals (Donoso and Nyland 2006), traits which allows them to rapidly colonize recently disturbed sites (Kern et al. 2012, 2017).

The effect of forest floor disturbance is less clear. Despite a statistically significant effect on species composition and a marginal effect on fruit type composition, ordinations illustrate substantial overlap among forest floor disturbance

treatments, particularly with fruit type composition. The forb *Epilobium ciliatum* and fern *Onoclea sensibilis* were the only indicators of scarification, while *Lonicera canadensis* was an indicator for reference and pit-mound treatments. Our stands are heavily dominated by *Acer* species which are known to have strong positive neighborhood effects (Frelich and Reich 1999), defined as species which tend to create environmental conditions favorable for conspecific regeneration. These effects may consequently bolster plant community resistance to forest floor disturbances, as Frelich and Reich (1999) suggest that stands with strong positive neighborhood effects require more severe disturbances to shift species composition. Alternatively, non-native earthworms have already substantially modified seedbed conditions and soil properties in the region (Bal et al. 2017) and further disturbances could be muted when compared to uninvaded forests (Holdsworth et al. 2007).

4.4.2 Taxonomic, trait, and phylogenetic diversity

In contrast to our second hypothesis, diversity indices did not follow the IDH. We found higher taxonomic diversity following STS canopy disturbance, but otherwise found little difference among treatments. Though the IDH has been widely accepted for decades, previous work has found that fewer than 20% of studies support the classic unimodal response (Bongers et al. 2009, Svensson et al. 2009, Fox 2013, Mouillot et al. 2013). We similarly failed to find evidence of the IDH in our plant communities, but our study focused on immediate responses to disturbance treatments which may not reflect a longer trajectory. For example, Kern et al (2014) found higher trait diversity

(TrD) in harvest-created gaps 14 years after gap creation when compared to reference plots. On the other hand, Flynn et al (2009) found no difference in plant taxonomic diversity (TD) or TrD among natural (including forests, prairies, and marshes), semi-natural, and agricultural lands ranging from Costa Rica to the northern USA. In our study, TD and TrD generally increased from pre- to post-treatment, owing to incoming species and traits that were indicators of post-treatment communities. Without further investigation, we could conclude that management disturbances cause a short-term increase in diversity and consequently might be considered a positive effect on plant communities. The response of phylogenetic diversity (PD) in our study, however, suggests the opposite: post-treatment communities are comprised of more similar evolutionary histories when compared to pre-treatment communities. Lower PD could increase vulnerability to invasion by non-native species (Gerhold et al. 2011, 2015). In our study, a decline in PD was driven by an increase in orders Poales, Lamiales, and Rosales, including both native and non-native species such as Cyperaceae species, *Galeopsis tetrahit*, *Veronica officinalis*, and *Rubus idaeus*, suggesting that non-native species can be both passengers and drivers of declines in PD. This has important implications for ecosystem management as PD is often positively correlated with ecosystem properties such as productivity, nutrient cycling, and resilience, and a decline in PD may jeopardize community resilience to future disturbances (Cadotte et al. 2009, Tucker et al. 2019). Similarly, TrD is often positively correlated with ecosystem properties, but we likely failed to examine a broad enough range of traits to detect treatment differences. PD, however, captures species evolutionary histories and could

therefore be a more accurate measurement of adaptive capacity when compared to TD or TrD, but uncertainties remain (Tucker et al. 2019). Many assumptions surround the relationships between PD, TrD, and community resilience (Gerhold et al. 2015, Cadotte et al. 2017, Tucker et al. 2019). Moreover, maximizing PD does not always generate maximum TrD (Mazel et al. 2018), though the same study found a global average increase in TrD of 18% when PD was maximized.

Despite changes in alpha-diversity, taxonomic and phylogenetic beta-diversity remained unaltered from pre- to post-disturbance within treatment combinations, though site-level (i.e. among treatment) taxonomic beta-diversity declined. These findings suggest that plot-level composition was retained at larger spatial scales and disturbance treatments had no effect on compositional turnover within a treatment combination, but the overall disturbance decreased site-level taxonomic heterogeneity. Previous work in other forest types have found that within-disturbance beta-diversity is often lower than among-disturbance beta-diversity (Grass et al. 2015, Gómez-Díaz et al. 2017). Lower site-level taxonomic beta-diversity following disturbances in our study may be driven by the increase in disturbance-adapted species, reflecting short-term community homogenization at the species level. Continued measurement will be necessary to determine if environmental and competitive filtering increase site-level beta-diversity.

In conclusion, we found that canopy disturbance overrides forest floor disturbance effects on plant community composition, suggesting the community is more resistant to forest floor disturbance as implemented in this study. Species with low-mass or long-lived and animal-dispersed fruit types such as capsules, achenes, nutlets,

schizocarps, and drupelets were strongly favored by high-severity canopy disturbances, while traits favored by forest floor disturbances remain unclear. Further, we found little evidence to support the Intermediate Disturbance Hypothesis within the short timeframe of this study. In contrast, we found that an overall increase in taxonomic diversity was mirrored by a concurrent decrease in phylogenetic diversity, pointing toward greater similarity of evolutionary histories within post-treatment plant communities which could jeopardize community resilience to future disturbances. Monitoring the duration of lower phylogenetic diversity following a disturbance could provide critical information for managers interested in maintaining plant community resilience following a disturbance.

The statistical methods used in this chapter may present an important caveat. Linear mixed effects models included treatment unit nested within block as a random effect. This may not accurately account for the restricted randomization of split units being nested within treatment units, and may overestimate the significance of the detected statistical relationships. Future analyses should account for this discrepancy by identifying the random effect as split unit nested within treatment unit, further nested within block.

5. Clearcut strips, deer exclosures, and herbicide show early promise for sugar maple recruitment in areas experiencing regeneration failure

5.1 Introduction

Though conventional management has tended to promote sugar maple (*Acer saccharum* Marsh.) regeneration in Great Lakes northern hardwood forests (Neuendorff et al. 2007, Schulte et al. 2007, Webster and Jensen 2007), deer browse and competition from other plant species may interact with management effects and instead cause regeneration failure. In localized areas of Upper Michigan, for example, managers have observed declining sugar maple regeneration in regions with high white-tailed deer (*Odocoileus virginianus* Zimmerman) populations (Vickers et al. 2019). Increasing competition from shrubs and Pennsylvania sedge (*Carex pensylvanica* Lam.) cover may be further confounding efforts to regenerate sugar maple (Powers and Nagel 2008, Corio et al. 2009, Webster et al. 2018). Applying alternative silviculture techniques to alleviate contemporary threats may consequently prevent regeneration failure of economically desirable species, including sugar maple.

Traditional management systems in Great Lakes northern hardwoods since the early twentieth century have been largely based on the widespread use of single-tree selection (Kern et al. 2014a, Pond et al. 2014). In this system, individual trees across a range of diameter sizes are harvested singly throughout a stand to reach a residual basal area goal, and the stand is then harvested similarly every 10 – 20 years. This system tends to promote shade-tolerant sugar maple regeneration (Neuendorff et al. 2007). If

applied incorrectly, however, continued harvesting of mature trees could reduce seed input, cause declines in advance regeneration, and have long-term consequences on stand health and development.

If seed source is compromised, deer browse and competition from other plant species could exacerbate negative effects on regeneration. Intense herbivory from elevated white-tailed deer populations compromises the survival of palatable species (e.g. sugar maple) leaving behind unpalatable and economically undesirable species such as ironwood (*Ostrya virginiana* (Mill.) K. Koch, Matonis et al., 2011). Competition from shrubs (e.g. *Rubus* spp.) and graminoids (e.g. *Carex* spp.) may further suppress regeneration and alter plant communities (Kern et al. 2012, 2013b). Canopy and soil disturbances often promote the colonization of *Rubus* spp., owing to long-lived (~60 yrs), animal-dispersed seeds (Donoso and Nyland, 2006). In northern hardwood forests, graminoids such as Pennsylvania sedge reproduce vegetatively, a trait which allows this functional group to spread rapidly without depending on seed germination (Bernard 1989). Moreover, many Great Lakes northern hardwood forests have been invaded by European earthworms, which may benefit Pennsylvania sedge at the expense of other ground-layer plant species (Hale et al. 2006). Reduced competition from browsed seedlings and saplings further promotes the spread of Pennsylvania sedge. Consequently, regeneration failure in localized regions of Great Lakes northern hardwoods may be driven by the interacting effects of heightened browse pressure, increased competition from shrubs or graminoids, and earthworm invasion on consistently limited abundances of advance regeneration.

Clearcut strips may be a viable method to increase sugar maple regeneration in northern hardwood forests undergoing contemporary biological threats following decades of traditional management, yet research on the effects of clearcut strips in the Great Lakes region is limited. Strips created near ample seed source could promote regeneration of economically desirable species (Greene 2000), while also overcoming competitive effects from graminoids by increasing light availability and allowing seedlings to rapidly grow above the sedge layer. Though shrubs including *Rubus* spp. may proliferate following canopy and soil disturbances, concurrent herbicide treatment may limit shrub and graminoid competition to further promote sugar maple regeneration and survival. In a Great Lakes northern hardwoods case study, tree growth six and seven years following strip harvesting and herbicide application was driven by advance regeneration and species composition was similar to the original overstory (Metzger 1980). Yellow birch (*Betula alleghaniensis* Britt.) and red maple (*Acer rubrum* L.), however, were more abundant in cut-herbicide strips when compared to cut-only strips. Previous work in New England northern hardwood forests found an initial dominance of pin cherry (*Prunus pensylvanica* L.f.) and early successional shrubs, succeeding to a canopy with similar composition to the original overstory (Martin and Hornbeck 1989, Allison et al. 2003). On the other hand, the outcomes of these trials may not reflect the impact of clearcut strips under current conditions with high deer abundances. Consequently, there is a need to quantify the interacting effects of traditional management and present-day biological challenges on regeneration in Great Lakes northern hardwoods.

In this study we assessed the use of clearcut strips, herbicide, and deer exclosures to promote the regeneration of economically desirable species in localized Great Lakes northern hardwood stands exhibiting regeneration failure. We hypothesize 1) clearcut strips and exclosures will promote rapid seedling growth into the sapling height class, 2) herbicide application will decrease graminoid and *Rubus* spp. competition, and 3) composition of broad functional groups will be most associated with harvest treatment when compared to herbicide and exclosure treatments. To test our hypotheses, we evaluated data collected from an operational-scale experiment testing the use of clearcut strips, herbicide, and deer exclosures on regeneration in Upper Michigan, USA. Seedlings, saplings, and functional group cover was surveyed before and two seasons following treatment application.

5.2 Materials and Methods

5.2.1 Site Description

Three study sites were established in Dickinson and Menominee counties of Upper Michigan, USA (Figure 5.1). Sites are within the Northern Lake Michigan Till Plain (Albert 1995) where soils are rocky, sandy loam, with limestone bedrock approximately 9.1 to 15.2 m below the surface. The growing season typically lasts about 100 days, with average annual precipitation 71.1 to 81.3 cm (Albert 1995). Prior to treatment application, average basal area per hectare across the three study sites was $19.7 (\pm 1.2) \text{ m}^2 \text{ ha}^{-1}$, with sugar maple (*Acer saccharum* Marsh.) comprising an average of 83.7 percent of total basal area. Quadratic mean diameter, a metric used to limit skewness caused by small-diameter trees, averaged $30.4 (\pm 1.0)$ cm and average graminoid cover was $18.0 (\pm 2.1)$ percent prior to treatment application (Table 5.1).

5.2.2 Experimental design

Four treatments of alternating ~20-30 m wide strips were applied in each study site in east-west orientation with two replicates of each treatment: selection; selection and herbicide; clearcut; clearcut and herbicide. The sites were harvested during fall 2014 or summer and fall of 2015, following pre-treatment measurements, using a wheeled-processor and double-bunk forwarder. Selection harvesting removed ~21.3 percent of stand basal area, 92.2 percent of which was sugar maple (Table 5.1). Quadratic mean diameter, however, remained unchanged in the selection harvested stands (29.9 ± 1.0 cm, Table 5.1). Eleven or twelve study plots were permanently marked in clearcut strips, while six plots were established in selection strips for a total

of 71 and 36 plots, respectively (Table 5.2). Plot locations were randomly assigned with ArcGIS (Esri, Redlands, CA, USA) and permanently marked with rebar. If the edge of a plot landed within multiple treatments, it was relocated north or south 5.1 m until completely within the correct treatment. Herbicide was applied in fall 2016 initially by hand spraying before switching to a wheeled-buncher with mounted sprayer. Circular $100\text{ m}^2 \times 1.83\text{ m}$ tall deer exclosures were constructed at two of three sites in fall 2015 (shortly after harvest) and at the third site spring 2016 (several months after harvest). Two exclosures each containing one plot were constructed in clearcut strips, while one exclosure was constructed in selection strips for a total of three selection $\times$ exclosure plots and nine clearcut $\times$ exclosure plots (Table 5.2).

5.2.3 Measurements

Pre-treatment data were collected during the 2014 field season and post-treatment data collected during the 2017 field season. In each plot, sapling ($> 45.72\text{ cm}$ tall, $< 15.24\text{ cm}$ dbh) abundance was measured in one 80.94 m^2 fixed area subplot and tree seedling ($< 45.72\text{ cm}$ tall) abundance was measured in three 1 m^2 fixed area subplots nested within sapling plots. In each seedling subplot, leaf litter depth was measured using a ruler, along with cover of broad functional groups including graminoids, ferns, forbs, *Rubus* spp., small coarse woody debris ($< 15.24\text{ cm}$ diameter), large coarse woody debris ($> 15.24\text{ cm}$ diameter), exposed rock, and exposed soil. Cover was visually estimated using four cover classes: 0-25%, 26-50%, 51-75%, and 76-100%.

5.2.4 Data analysis

To test our first and second hypotheses, the effects of harvest, herbicide, and exclosure treatments on the absolute change in seedling and sapling densities were tested using linear mixed effects models ($n = 107$). Treatments were included as fixed effects, with site included as a random effect. Seedling and sapling densities were square root transformed to meet assumptions of normal distribution and equal variance. The relationship between sugar maple and ironwood seedling and sapling density, and seedling plot variables (e.g. litter depth and functional group cover) were then assessed using simple linear models pooling all plots, with seedling and sapling densities square root transformed and outliers removed. Tests were conducted using the *lme* function in the ‘nlme’ package of R 3.5.0 software (Pinheiro et al. 2018) and fitted by the Satterthwaite test. Pairwise multiple comparisons were conducted with the ‘emmeans’ package (Lenth 2018) using Tukey’s HSD correction.

To test our third hypothesis, the effects of harvest, herbicide, exclosure, and year on the change in seedling plot (1 m^2) composition (2017 cover minus 2014 cover) were assessed with permutational multivariate analysis of variance (PERMANOVA, *adonis* function in ‘vegan’ package of R 3.5.0, Oksanen et al., 2018) using Bray-Curtis distance matrices constrained within sites ($n = 214$). All variables were relativized by maximum value. Pairwise multiple comparisons were conducted with the *pairwise.perm.manova* function in the ‘RVAideMemoire’ package (Hervé 2019) using Holm’s multiple comparison adjustment. Changes in composition from 2014 to 2017 were visualized

with nonmetric multidimensional scaling (NMDS) ordination using Bray-Curtis distances. Three-axis ordinations were constructed with the *metaMDS* function in the ‘vegan’ package of R 3.5.0, with 999 iterations (Oksanen et al. 2018). Variables were then fitted as vectors onto the ordination using the *envfit* function, and treatment groupings overlaid as ellipses using the standard deviation of point scores.

Table 5.1. Average ($\pm$ SE) stand characteristics pre- and post-harvest in a managed northern hardwood forest of Upper

Michigan, USA ($n = 3$). Small WD; woody debris < 15.24 cm diameter; Large WD, woody debris > 15.24 cm diameter; BA, basal area ($\text{m}^2 \text{ ha}^{-1}$); QMD, quadratic mean diameter (cm); SM BA, sugar maple basal area ($\text{m}^2 \text{ ha}^{-1}$).

Year	Harvest	Exposed soil	Ferns	Forbs	<i>Rubus</i> spp.	Rock	Graminoids	Small WD	Large WD	BA	QMD	SM BA
2014	Clearcut	13.5 (0.6)	14.6 (1.2)	13.6 (1.1)	13.2 (0.4)	15.7 (3.2)	18.3 (4.0)	14.1 (0.6)	13.4 (0.4)	19.7 (1.3)	30.4 (1.6)	16.2 (0.7)
2014	Selection	14.4 (1.9)	14.1 (1.3)	13.3 (0.5)	12.7 (0.2)	12.5 (0.0)	17.6 (2.1)	12.8 (0.3)	12.7 (0.2)	19.2 (0.8)	30.3 (1.6)	16.8 (1.5)
2017	Clearcut	13.1 (0.1)	12.9 (0.2)	16.2 (1.5)	21.6 (4.5)	12.5 (0.0)	36.6 (7.4)	20.5 (0.4)	12.9 (0.2)	1.4 (0.5)	13.7 (5.3)	1.1 (0.5)
2017	Selection	12.7 (0.2)	16.5 (2.7)	18.1 (1.2)	14.1 (1.3)	12.5 (0.0)	33.3 (8.3)	15.7 (0.9)	12.7 (0.2)	15.1 (0.4)	29.9 (1.0)	13.5 (0.7)

Year	Harvest	Seedlings ha^{-1}	Saplings ha^{-1}	SM seedlings ha^{-1}	IW seedlings ha^{-1}	SM saplings ha^{-1}	IW saplings ha^{-1}
2014	Clearcut	23989.6 (9494.2)	1246.4 (572.9)	18820.1 (7561.6)	1922.6 (391.0)	97.8 (54.5)	405.9 (132.4)
2014	Selection	17723.2 (4626.1)	1501.0 (402.9)	14292.0 (5352.4)	937.3 (212.9)	218.6 (181.4)	323.5 (66.2)
2017	Clearcut	5857.8 (2237.5)	1034.0 (291.9)	3148.1 (1787.7)	746.3 (143.2)	192.5 (113.7)	261.5 (51.0)
2017	Selection	11252.0 (2482.3)	1291.7 (245.0)	7693.3 (3397.6)	665.9 (456.1)	156.8 (125.2)	353.9 (59.6)

Table 5.2. Plot distribution among harvest, herbicide, and exclosure treatments in a northern hardwood forest of Upper Michigan, USA.

Treatment	Plot count
Selection	24
Selection × herbicide	4
Selection × exclosure	2
Selection × herbicide × exclosure	2
Clearcut	44
Clearcut × herbicide	19
Clearcut × exclosure	6
Clearcut × herbicide × exclosure	2

Figure 5.1. Approximate locations of study sites in Dickinson and Menominee counties of Upper Michigan, USA. Sites are managed by American Forest Management, Inc. Inset image retrieved from Google Earth (2018).

5.3 Results

5.3.1 Seedlings and saplings

Overall seedling density declined substantially more in clearcut strips when compared to selection strips ($\chi^2 = 4.181$, $p(>\chi^2) = 0.041$, Table 5.3), but there were no main treatment effects on the density response of sugar maple or ironwood seedlings. The change in ironwood seedling density, however, was marginally correlated with a harvest $\times$ herbicide interaction ($\chi^2 = 5.68$, $p(>\chi^2) = 0.050$, Table 5.3). Specifically, ironwood seedling density responded positively to selection harvested strips with herbicide application (Figure 5.2). In contrast, ironwood seedling density declined following selection strips without herbicide, along with a similar decline in clearcut harvested strips (Figure 5.2).

There was no difference in the response of sugar maple saplings among harvest or herbicide treatments, but there was a positive response of sugar maple sapling density in exclosures ($F_{1,93} = 5.081$, $p = 0.027$, Table 5.4, Figure 5.2). Moreover, a neutral or negative response of sugar maple saplings in selection strips with herbicide was accompanied by a generally neutral or positive response in selection strips without herbicide ($F_{1,93} = 5.894$, $p = 0.017$, Table 5.4). Ironwood saplings had a neutral or negative response to clearcut strip harvesting, mirrored by a neutral or positive response to selection harvesting ($F_{1,103} = 13.393$, $p < 0.001$, Table 5.4). Moreover, ironwood saplings had a neutral or negative response to herbicide in both harvest treatments ($F_{1,103} = 23.832$, $p < 0.017$, Table 5.4). Ironwood saplings tended to decline more in

clearcut strips coupled with herbicide, but large variation masked a significant effect (Figure 5.2).

Sugar maple seedling density was positively correlated with the cover of exposed rock ($F_{1,212} = 18.84$, $r^2 = 0.07$, $p < 0.001$, Table 5.5, Figure 5.3) and leaf litter depth ($F_{1,212} = 18.39$, $r^2 = 0.08$, $p < 0.001$, Table 5.5, Figure 5.3), but was negatively correlated with the cover of graminoids ($F_{1,212} = 18.63$, $r^2 = 0.08$, $p < 0.001$, Table 5.5, Figure 5.3) and small (< 15.24 cm dia.) coarse woody debris ($F_{1,212} = 7.07$, $r^2 = 0.03$, $p = 0.008$, Table 5.5, Figure 5.3). Ironwood seedling density was negatively correlated by forb cover ($F_{1,212} = 4.85$, $r^2 = 0.02$, $p = 0.028$, Table 5.5, Figure 5.3) and *Rubus* spp. cover ($F_{1,212} = 4.86$, $r^2 = 0.02$, $p = 0.029$, Table 5.5, Figure 5.3).

5.3.2 *Rubus* spp. and graminoid cover

Rubus spp. cover responded positively to both harvest treatments, but the positive response was greater in clearcut strips when compared to selection strips ($\chi^2 = 6.049$, ($p > \chi^2$) = 0.014, Table 5.6, Figure 5.4). The positive response was dampened, however, by herbicide application in both harvest treatments ($\chi^2 = 5.097$, ($p > \chi^2$) = 0.024, Table 5.6, Figure 5.4). For example, there was a near two-fold increase in *Rubus* spp. cover in clearcut strips without herbicide application when compared to clearcut strips with herbicide application (Figure 5.4).

Similar to *Rubus* spp., the overall positive response of graminoid cover to harvest treatments was dampened by herbicide application ($F_{1,98} = 23.191$, $p < 0.001$, Table 5.6, Figure 5.4), but this effect was driven by the neutral graminoid response in

clearcut strips coupled with herbicide (Figure 5.4), as indicated by a harvest $\times$ herbicide interaction ($F_{1,98} = 11.507$, $p = 0.001$, Table 5.6).

5.3.3 Composition

The change in plot ground cover composition, including sugar maple and ironwood seedlings, was greater in clearcut strips when compared to selection strips ($F_{1,101} = 3.392$, $R^2 = 0.03$, $p = 0.001$, Table 5.7, Figure 5.5a). Moreover, composition in strips receiving herbicide changed less than in strips without herbicide application ($F_{1,101} = 3.794$, $R^2 = 0.03$, $p = 0.006$, Table 5.7). A harvest $\times$ herbicide interaction ($F_{1,101} = 2.658$, $R^2 = 0.02$, $p = 0.009$, Table 5.7) demonstrated greater compositional change in clearcut strips without herbicide application (Figure 5.5b). Composition in selection strips with exclosures tended to be dominated by graminoids, while composition in selection strips without exclosures was more dominated by *Rubus* spp. ($F_{1,101} = 2.010$, $R^2 = 0.02$, $p = 0.042$, Table 5.7, Figure 5.5b). Overall, compositional change favored graminoids and *Rubus* spp. at the expense of litter depth, seedlings, and exposed rock (Figure 5.5).

Table 5.3. Mixed model effects of harvest, herbicide, exclosure, and year on sugar maple, ironwood, and overall seedling (< 45.72 cm tall) density response (2017 minus 2014) of a management northern hardwood forests in Upper Michigan, USA. Density response among three 1 m² subplots was averaged prior to analysis. Site was included as a random factor. Models first included all treatment interactions and were then simplified if no interaction effect was detected. Lower order interactions were retained if higher order interactions were statistically significant. Asterisks indicate statistical significance ($p < 0.05$), italicized values indicate marginal significance ($0.05 < p < 0.10$).

Predictor	Sugar maple (n = 99)				Ironwood (n = 104)				All seedlings (n = 103)			
	RMSE	χ^2	AIC	p > χ^2	RMSE	χ^2	AIC	p > χ^2	RMSE	χ^2	Df _{num}	p > χ^2
	25421.68		2305.668		4540.234		2046.973		40516.47			
	Df _{num}	χ^2		p > χ^2	Df _{num}	χ^2		p > χ^2	Df _{num}	χ^2		p > χ^2
Intercept	-	-	-	-	-	-	-	-	-	-	-	-
Harvest	1	0.055	0.815		1	2.403	0.121		1	4.181	1	0.041*
Herbicide	1	0.185	0.667		1	2.112	0.146		1	0.664	1	0.415
Exclosure	1	1.901	0.168		1	2.916	0.088		1	0.153	1	0.696
Harvest × Herbicide	-	-	-	-	1	3.849	0.050		-	-	-	-
Harvest × Exclosure	-	-	-	-	1	0.012	0.911		-	-	-	-
Herbicide × Exclosure	-	-	-	-	1	0.164	0.686		-	-	-	-
Harvest × Herbicide × Exclosure	-	-	-	-	1	3.178	0.075		-	-	-	-

Table 5.4. Mixed model effects of harvest, herbicide, and exclosure on sugar maple, ironwood, and overall sapling (> 45.72 cm tall, < 15.24 cm dbh) density response (2017 minus 2014) in 80.94 m² plots of a managed northern hardwood forests in Upper Michigan, USA. Site was included as a random factor. Models first included all treatment interactions and were then simplified if no interaction effect was detected. Lower order interactions were retained if higher order interactions were statistically significant. Asterisks indicate statistical significance ($p < 0.05$), italicized values indicate marginal significance ($0.05 < p < 0.10$).

Predictor	Sugar maple (n = 99)				Ironwood (n = 103)				All saplings (n = 106)			
	RMSE		AIC		RMSE		AIC		RMSE		AIC	
	353.678		1471.465		573.958		1615.185		1859.687		1914.635	
	Df _{num}	Df _{den}	F-value	p-value	Df _{num}	Df _{den}	F-value	p-value	Df _{num}	Df _{den}	F-value	p-value
Intercept	1	93	0.464	0.498	1	97	4.940	0.029*	1	100	1.526	0.220
Harvest	1	93	2.261	0.136	1	97	13.393	<0.001*	1	100	0.176	0.675
Herbicide	1	93	0.738	0.393	1	97	23.832	<0.001*	1	100	15.959	<0.001*
Exclosure	1	93	5.081	0.027*	1	97	0.767	0.383	1	100	9.013	0.003*
Harvest × Herbicide	1	93	5.894	0.017*	-	-	-	-	-	-	-	-

Table 5.5. Simple linear regression of plot-level predictors on sugar maple and ironwood seedling (< 45.72 cm tall) density in a managed northern hardwood forest in Upper Michigan, USA. Density among three 1 m² subplots was averaged prior to analysis. Asterisks indicate statistical significance ($p < 0.05$), italicized values indicate marginal significance ($0.05 < p < 0.10$). ‘+’ denotes a positive correlation, ‘-’ denotes a negative correlation.

Predictor	Sugar maple seedlings (n = 214)					Ironwood seedlings (n = 214)				
	D _{faum}	D _{den}	F-stat	R ²	P-value	D _{faum}	D _{den}	F-stat	R ²	P-value
Exposed rock	1	212	18.84	0.07 (+)	<0.001*	-	-	-	-	-
Graminoids	1	212	18.63	0.08 (-)	<0.001*	-	-	-	-	-
Small CWD	1	212	7.07	0.03 (-)	0.008*	-	-	-	-	-
Litter depth	1	212	18.39	0.08 (+)	<0.001*	-	-	-	-	-
Forbs	-	-	-	-	-	1	212	4.847	0.02 (-)	0.028*
<i>Rubus</i> spp.	-	-	-	-	-	1	212	4.858	0.02 (-)	0.029*

Table 5.6. Mixed model effects of harvest, herbicide, and exclosure on response of *Rubus* spp. and graminoid cover in a management northern hardwood forest of Upper Michigan, USA. Cover response among three 1 m² subplots was averaged prior to analysis. Site was included as a random factor. Models first included all treatment interactions and were then simplified if no interaction effect was detected. Lower order interactions were retained if higher order interactions were statistically significant. Asterisks indicate statistical significance ($p < 0.05$), italicized values indicate marginal significance ($0.05 < p < 0.10$).

Predictor	<i>Rubus</i> spp. cover (n = 105)			Graminoid cover (n = 105)			
	RMSE		AIC	RMSE		AIC	
	10.575		809.220	901.141		919.718	
	Df _{num}	χ^2	p > χ^2	Df _{num}	Df _{den}	F-value	p-value
Intercept	-	-	-	1	98	26.786	<0.001*
Harvest	1	6.049	0.014*	1	98	0.075	0.784
Herbicide	1	5.097	0.024*	1	98	23.191	<0.001*
Exclosure	1	1.230	0.267	1	98	1.862	0.176
Harvest × Herbicide	-	-	-	1	98	11.507	0.001*

Table 5.7. Permutational multivariate analysis of variance (PERMANOVA) effects of silvicultural treatment on the change in composition (absolute value of 2017 minus 2014) of ground-layer vegetation (excluding saplings) and measured microsite factors in a managed northern hardwood forest of Upper Michigan, USA (n = 107). Response variables among three 1 m² subplots were averaged prior to analysis. Asterisks indicate statistical significance ($p < 0.05$), italicized values indicate marginal significance ($0.05 < p < 0.10$).

	df	Sum. Sq	Mean Sq	F-value	R ²	P-value
Harvest	1	0.571	0.571	3.392	0.030	0.001*
Herbicide	1	0.638	0.638	3.794	0.033	0.006*
Exclosure	1	0.242	0.242	1.436	0.013	0.115
Harvest × Herbicide	1	0.447	0.447	2.658	0.023	0.009*
Harvest × Exclosure	1	0.338	0.338	2.010	0.018	0.042*
Residuals	101	16.991	0.168		0.884	
Total	106	19.227			1.000

Figure 5.2. Average (± 1 SE) sugar maple and ironwood seedling (< 45.72 cm tall) and sapling (> 45.72 cm tall, < 15.24 cm dbh) density response (2017 minus 2014) among harvest, herbicide, and exclosure treatments in a managed northern hardwood forest of Upper Michigan, USA. Note different y-axis ranges. Letters indicate significant differences among all treatment combinations using Tukey's correction ($\alpha = 0.05$). SM, sugar maple; IW, ironwood; Sel, selection strips; CC, clearcut strips.

Figure 5.3. Relationships among sugar maple and ironwood seedling (< 45.72 cm tall) density and plot-level predictors in a managed northern hardwood forest in Upper Michigan, USA. Density among three 1 m^2 subplots was averaged prior to analysis. Sel, selection strips; CC, clearcut strips.

Figure 5.4. Average (± 1 SE) *Rubus* spp. and graminoid cover response (2017 minus 2014) among harvest, herbicide, and exclosure treatments in 1 m² plots of a managed northern hardwood forest in Upper Michigan, USA. Letters indicate significant differences among all treatment combinations using Tukey's correction ($\alpha = 0.05$)

Figure 5.5a. Nonmetric multidimensional scaling ordinations illustrating the relationships among cover type, seedling (< 45.72 cm tall) density, and treatment in 1 m² plots depicting two axes of a three-axis ordination. Points represent individual plots, and distances between points represent the similarity among plots (i.e. points closer together are more similar in composition). Vectors represent understory variables. The direction and length of each vector indicate the relative treatment influence on the response variables. One ordination model was constructed, and plot composition highlighted separately each year. Ellipses indicate harvest, herbicide, or site preparation treatments based on the standard deviation of point scores for each plot. Lowercase letters denote significant differences in composition within treatments using Holm's multiple comparison adjustment ($\alpha = 0.05$). Small CWD, woody debris < 15.24 cm diameter; large CWD, woody debris > 15.24 cm diameter.

Figure 5.5b. Nonmetric multidimensional scaling ordinations illustrating the relationships among cover type, seedling (< 45.72 cm tall) abundance, and treatment in 1 m² plots depicting two axes of a three-axis ordination. Points represent individual plots, and distances between points represent the similarity among plots (i.e. points closer together are more similar in composition). Vectors represent understory variables. The direction and length of each vector indicate the treatment influence on the response variables. One ordination model was constructed, and plot composition highlighted separately each year. Ellipses indicate harvest and herbicide or exclosure interaction treatment groupings based on the standard deviation of point scores for each plot. Lowercase letters denote significant differences in composition within treatment combinations using Holm's multiple comparison adjustment ($\alpha = 0.05$). Small CWD, woody debris < 15.24 cm diameter; large CWD, woody debris > 15.24 cm diameter.

5.4 Discussion

In this study, we predicted that clearcut strips along with herbicide and deer exclosures would provide a viable alternative to traditional management systems in regions experiencing regeneration failure due to herbivory and competition. Though sugar maple seedling and sapling abundances were not correlated with harvest treatment alone, the addition of deer exclosures had a positive effect on sapling abundance while herbicide limited *Rubus* spp. and graminoid competition. These results suggest that deer browse negates any positive effect of increased light availability on seedling recruitment into the sapling size class, and herbicide may alleviate competition for resources and promote future growth.

5.4.1 Seedling and sapling regeneration

Our first hypothesis was partially supported. We had anticipated that clearcut strips and exclosures would promote seedling recruitment into the sapling size class, but sapling abundance was positively correlated with exclosure treatments, while harvest and herbicide treatments tended to decrease or have little correlation with seedling and sapling abundance. Exclosures in clearcut strip treatments, however, had the greatest positive effect on sapling abundance, highlighting the combined effect of greater light availability and less browse pressure on recruitment. Our findings suggest that the negative effect of deer browse negates any positive effect of increased light availability on sapling recruitment.

Previous work in hardwood forests has documented similar responses to harvest and exclosure treatments. For example, Trumball et al. (1989) documented significantly reduced seedling height in plots outside 1-acre deer exclosures when compared to plots inside exclosures. Moreover, in a Wisconsin northern hardwood forest, Kern et al. (2012) found that deer herbivory suppressed the growth of planted seedlings, even in harvest-created gaps with high light availability. Similarly, Matonis et al. (2011) concluded that deer herbivory overrides the benefits of increased light availability on northern hardwood seedling and sapling regeneration in harvested gaps. Our present study corroborates these findings and strengthens the evidence suggesting that deer herbivory can strongly suppress seedling growth in northern hardwood forests, even in high light environments.

Alternatively, the limited positive response of sapling recruitment in clearcut strips may be concurrently driven by inadequate advance regeneration in our stands prior to harvest. Though most plots in our study were adequately stocked with sugar maple seedlings prior to treatment application, seedlings were spatially heterogeneous with approximately 32.7 % of plots completely devoid of sugar maple seedlings. In contrast to species which maintain robust seedbanks for capturing resources following disturbances, sugar maple typically maintains abundant seedling banks (i.e. advance regeneration), and previous work has demonstrated that adequate advance regeneration can out-compete mid-tolerant and intolerant species following a severe canopy disturbance. For example, Metzger (1980) found that regeneration six and seven years following strip harvesting and herbicide application in Great Lakes northern hardwoods

was driven by advance regeneration, and several group harvesting studies have found that sugar maple continues to dominate seedling and sapling layers in silvicultural systems designed to promote mid-tolerant species (Bolton and D'Amato 2011, Knapp et al. 2019). Though sugar maple maintained dominance following harvesting in our study, deer herbivory may have prevented recruitment into the sapling size class as inadequate advance regeneration and seed source deficiencies continued to limit seedling recruitment.

5.4.2 *Rubus* spp. and graminoid cover

We hypothesized that herbicide application would suppress *Rubus* spp. and graminoid cover and positively affect seedling growth, while exclosures would have limited effects on *Rubus* spp. and graminoid cover due to low palatability. Our hypothesis was partially supported by neutral or negative responses but the responses differed by taxa and harvest treatment. Our results suggest that the increased light availability following clearcut strip treatments increases competition from *Rubus* spp., but herbicide could dampen the positive response or eliminate it altogether. Further, graminoid cover had a stronger positive response than *Rubus* spp. to increased light availability but herbicide application similarly negated any positive effects, consequently limiting graminoid competition in clearcut strips while having no effect on competition in selection strips. Shields and Webster (2007) similarly found that *Rubus* spp. competition increased with increasing light availability in harvest-created gaps, and Kern et al (2012) found that *Rubus* spp. persisted for 12 years following gap

creation. We found no effect of exclosures on *Rubus* spp. or graminoid competition in the two-year time frame of this study, but previous work has shown differing results. For example, Trumbull et al (1989) found that deer browse caused a decline in *Rubus* spp. and concurrent increase in graminoid competition 13 years following the creation of 1-acre (~0.41 ha) exclosures. Moreover, Powers and Nagel (2009) found that Pennsylvania sedge cover (a major component of our ‘graminoid’ functional group) was generally related to higher deer densities in northern hardwood forests, though it varied with management history.

Competition from *Rubus* spp. or graminoids can negatively affect seedling germination and growth, and we anticipated similar interactions in our study. We found that sugar maple seedling density was negatively related to increasing graminoid cover and similarly, increasing ironwood seedling density was negatively related to increasing *Rubus* spp. cover. Previous work has documented similar findings following management disturbances. For example, Kern et al (2013b, 2012) found that competition from *Rubus* spp. limited the growth and survival of both planted and naturally-regenerated seedlings 12 years following gap creation. Long-lived and animal-dispersed seeds of *Rubus* spp. may contribute to its ability to quickly colonize a recently disturbed site (Donoso and Nyland 2006), and the rhizomatous growth strategy of Pennsylvania sedge similarly promotes rapid colonization (Bernard 1989). Along with our findings, this adds to growing evidence that dominant understory layers following a canopy disturbance can have detrimental effects on regeneration in forests worldwide (Royo and Carson 2006). Though we found limited support for positive effects of

herbicide on sugar maple seedling and sapling density, the decline in competition from *Rubus* spp. and graminoids suggest that sugar maple seedlings may benefit from alleviated competition in future growing seasons. On the other hand, continued monitoring will be necessary to determine if one-time herbicide application has long-term effects.

5.4.3 Composition

We anticipated that the change in composition of broad functional groups would be most correlated with harvest treatment when compared to herbicide or exclosure treatments and found strong support for this hypothesis. Light is among the most limiting resources in mature northern hardwood forests (Canham et al. 1994), and sudden increases in light availability can consequently have substantial effects on ground-layer composition (Canham et al. 1994, Kern et al. 2014). In our study, diverging plot composition from 2014 to 2017 was primarily driven by harvest treatment, and clearcut strip harvesting yielded the greatest change in composition followed by herbicide treatment. Composition may have been further correlated with differences in coarse woody debris input between harvest treatments, which was higher in clearcut strips. Kraft et al (2004) similarly found that plant species cover was more correlated with harvest than deer exclosures, likely owing to changing light environments. Interestingly, ordinations suggest that a harvest $\times$ herbicide interaction effect on composition was driven by clearcut strips without herbicide applied, which

yielded the largest change in composition. These results further point to increasing competition from *Rubus* spp. and graminoids in clearcut strips.

While an herbicide effect may have been greatest in clearcut strips, ordinations suggest that the effect of exclosures on composition was greatest in selection strips. This finding may be driven by increasing sapling abundance in exclosures along with differing responses of *Rubus* spp. and graminoids. For example, *Rubus* spp. cover remained relatively unchanged in selection strips within and outside exclosures, while graminoid cover was greater in selection plots within exclosures when compared to selection plots outside exclosures. There was no overall effect of exclosures on composition, however, highlighting the limited impact of deer herbivory on the composition of broad functional groups in this study when compared to harvest and herbicide.

5.4.4 Conclusion

In this study we tested the use of clearcut strips, herbicide, and deer exclosures to quantify the effects of light environment, competition, and browse pressure, respectively, on regeneration and composition in a sugar maple-dominated northern hardwood forest with a depauperate understory. Clearcut strips increased recruitment of sugar maple seedlings into the sapling size class, but deer browse may negate this positive effect. Further, herbicide failed to increase seedling or sapling density but alleviated competition from *Rubus* spp. and graminoids, suggesting greater growth potential in treated strips. Though our findings show promise for addressing

regeneration failure due to herbivory and shrub competition in northern hardwood forests, continued observation will be necessary for a more comprehensive assessment of regeneration dynamics in this novel silvicultural experiment. We emphasize, however, that regeneration failure described in this study is localized to areas of southern Upper Michigan and northern Wisconsin, and caution against the use of strip clearcuts and herbicide in areas with adequate advance regeneration. Further, the statistical methods used in this chapter may present an important caveat. Linear mixed effects models included site as a random effect. To account for restricted randomization and potentially overestimating the significance of the detected statistical relationships, however, future analyses should include plot nested within strip, nested within site as the random effect.

6. General Conclusion

Like forests worldwide, northern hardwood forests are structured by disturbance regimes and competitive interactions among species. Consequently, understanding plant community response processes to management-based disturbances is crucial for predicting future forest dynamics and making sound management decisions. This dissertation aims to reconcile theory and practice by using novel silvicultural experiments to test ecological hypotheses and apply this knowledge to alternative regeneration techniques.

Three themes emerged from this dissertation that can inform ecologists, conservationists, and forest managers alike. First, removing an important growth limitation (i.e. closed canopy) has little benefit to seedlings and saplings if they cannot overcome additional limitations. In Chapter 3, I had predicted that yellow birch regeneration would benefit from reduced canopy cover coupled with scarification, but instead found that it was better predicted by residual conspecific basal area and spatial variation of litter depth, and not correlated with harvest or site preparation treatments. These findings suggest that yellow birch regeneration in these stands is most limited by inadequate seed source and microsite conditions, not necessarily by canopy cover. Scarification may ultimately prove useful for yellow birch regeneration but spatially heterogeneous application appears to mask a potentially positive effect in this study. Though yellow birch seedling regeneration was nearly uniform among treatments in 2018, increasing interspecific competition as resource availability declines may reveal treatments effects on seedlings that I failed to detect during the time period of this

study. Current and future work in the Northern Hardwood Silvicultural Experiment for Enhanced Diversity (NHSEED) aims to test potential seed source and seedbed limitations on regeneration and consequently, continued measurements of this experiment may provide further insight.

While my first three chapters describe a range of silvicultural tools used to better emulate natural disturbance regimes, Chapter 5 presents a unique approach to promote regeneration in localized areas experiencing severe regeneration failure, owing to interacting effects of management history and growth limitations caused by elevated herbivory and heightened competition from shrubs and graminoids. Assessing clearcut and selection strips combined with deer exclosures and herbicide, I found that the benefits of greater light availability in clearcut strips are negated if browse pressure remains high. Further, herbicide reduced the cover *Rubus* spp. and graminoids, removing a strong limitation on seedling growth by decreasing competition from other species. These findings suggest that removing an important growth limitation (i.e. light limitation) has little benefit to seedlings and saplings if they cannot escape browse or interspecific competition. There are few studies examining clearcut strips in northern hardwoods (Metzger 1980, Martin and Hornbeck 1989, Allison et al. 2003), so continued measurement will prove essential for disentangling the hierarchy of limitations that influence growth and recruitment in these stands.

A second theme in this dissertation addresses the relationships among traits and disturbance regimes. In Chapter 4, I compared the effects of canopy and forest floor disturbances on ground-layer plant communities and further, tested a well-known

hypothesis – the Intermediate Disturbance Hypothesis (IDH) – within the context of NHSEED. I found that ground-layer plant communities are more correlated with canopy disturbances as applied in this study than forest floor disturbances. Shifts in the community were driven by a substantial increase in orders Poales, Lamiales, and Rosales and concurrent declines in many species within order Polypodiales. Several traits associated with the species favored by disturbance include low-mass or long-lived fruits, rhizomatous stems, and shade intolerance or mid-tolerance, likely in addition to many unmeasured traits. In contrast, the species that declined following silvicultural disturbances are dominated by ferns and fern allies. Though ferns and fern allies are characterized by spore dispersal and rhizomes, the majority are adapted to moist environments. Inefficient xylem transport coupled with early stomatal closure likely makes these species ill-suited for higher rates of evapotranspiration found in recently disturbed environments (Brodribb and Holbrook 2004, Brodersen et al. 2012).

Intermediate and severe canopy disturbances tended to favor traits associated with the disturbance-adapted species described above, yet sugar maple continued to perform well in most treatments. This apparent contradiction may be explained by its vigorous advance regeneration. Accordingly, species typically not considered to be disturbance-adapted may benefit from overstory disturbances if they maintain robust seedling banks (as opposed to seedbanks). Forest floor disturbances like scarification, however, remain detrimental to these species and may instead favor species with adequate seedbanks by removing a strong seedbed limitation (Lorenzetti et al. 2008, Gauthier et al. 2016).

The third theme addresses the relationship between disturbance and diversity. Despite a shift in species and trait composition following disturbance treatments described in Chapter 2, I found little evidence to support the Intermediate Disturbance Hypothesis (IDH) within the short time frame of this study. The IDH proposes that species diversity is highest at intermediate spatial and temporal scales of disturbance. Rather, I found that taxonomic diversity generally increased but was not different among treatments while trait diversity remained relatively unchanged. The IDH has generally been an accepted hypothesis for decades, but has recently been disputed owing to little empirical evidence (Fox 2013). It should be noted, however, that this study was conducted only at intermediate spatial scales of disturbance; evidence of the IDH at intermediate temporal scales may still be uncovered in future studies.

The statistical methods used in this dissertation research present an important caveat. Linear mixed effect models used in chapters three and four included treatment unit nested within block as a random effect. This may not completely account for the restricted randomization of split units being nested within treatment units, and may overestimate the significance of the detected statistical relationships. Future analyses should account for this discrepancy by including split plot nested within treatment unit, further nested within block. Further, linear mixed effect models used in chapter five included site as a random effect. To accurately account for restricted randomization and similarly prevent overestimation of the significance of detected statistical relationships,

future analyses should include plot nested within strip, nested within site as the random effect.

Previous work often demonstrates that greater taxonomic diversity translates to greater trait or response diversity (i.e. the variety of different reactions among species) and consequently, greater resilience (Elmqvist et al. 2003, Downing et al. 2012). Evidence from this dissertation, however, suggests this relationship is not conclusive. Taxonomic diversity increased following most disturbance treatments, but phylogenetic diversity generally declined from pre- to post-treatment, a notable outcome with important conservation implications. Declining phylogenetic diversity suggests that post-disturbance communities have more similar evolutionary histories and potentially more similar traits when compared to pre-disturbance communities, a finding supported by the overall increase in disturbance-adapted species and concurrent decline in species which prefer moist, shaded environments. Lower phylogenetic diversity could make communities vulnerable to herbivory or further invasion by non-native species (Cadotte et al. 2009, Gerhold et al. 2011, Tucker et al. 2019), and lower response diversity may compromise resilience to future disturbances (Elmqvist et al. 2003). Phylogenetic diversity could therefore represent a more comprehensive metric for assessing plant community dynamics and for ultimately making informed management decisions.

7. References

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