Productivity, Recovery, Diversity, and Function of Aspen-dominated Forests Vary in Response to Biomass Harvest Severity

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INTRODUCTION

Understanding the consequences of management on forest productivity, structure, diversity, composition, and function is increasingly important considering projected increases in both natural and anthropogenic disturbance severity and frequency with global environmental change (Dale et al. 2001). Increasing widespread adoption of practices aimed at emulating natural disturbance processes and resulting structures in order to maintain structural complexity, sustain diversity, and increase resilience in forests is coinciding with a worldwide rise in demand for forest-derived bioenergy feedstocks (Franklin et al. 1997, Fischer et al. 2006, Janowiak and Webster 2010, Lindenmayer et al. 2012). In the temperate and boreal forests of North America, harvest residues constitute a significant source of such feedstocks. Utilizing harvest residues for bioenergy production may help reduce greenhouse gas emissions and mitigate climate change impacts (Millar et al. 2007), but removing these post-harvest legacies could reduce forest complexity (Berger et al. 2013, Littlefield and Keeton 2013), productivity (Walmsley et al. 2009, Helmisaari et al. 2011, Wall 2012), and diversity (Riffel et al. 2010, Bouget et al. 2012).

The research presented in this dissertation examined both short- and medium-term impacts of removing harvest residues on several components of aspen-dominated forests in the upper Lake States region, USA. Chapter 1 examines the medium-term response of standing biomass and forest structure to the combined effects of organic matter removal and soil compaction 15 years after harvest. Chapter 2 evaluates changes in composition, species diversity, functional diversity, and trait expression in response to organic matter removal and soil compaction over a 15-year period. Additionally, this chapter bridges the largely theoretical fields of functional and community ecology with silviculture by comparing a variety of diversity-related indices in an applied setting. Lastly, with states like Minnesota developing guidelines to address the concerns about residue removal listed above, the effects of integrating aggregated overstory retention with bioenergy harvests were investigated in Chapter 3. Both the effectiveness of aggregates in achieving ecological objectives and potential trade-offs with traditional forest management goals were assessed.

Data from the Long-Term Soil Productivity Study (LTSP) provided the opportunity to explore 15 year impacts from organic matter removal combined with different levels of soil disturbance on regeneration across a range of soil textures. Results presented in Chapter 1 demonstrate that regeneration, above-ground biomass production, and structural development at different sites vary in response to different disturbance severities. At the Huron National Forest (sandy soils), the removal of harvest residues reduced above-ground biomass production, but no negative effect was observed following whole-tree harvest (WTH) compared to stem-only harvest (SOH) at Ottawa or Chippewa National Forests (clayey and silty loam soils, respectively). Maximum diameter and the density of stems greater than 5 cm diameter (at breast height, 1.4 m) exhibited negative responses to increased disturbance severity at two sites, indicating potential for slowed structural development.

Chapter 2 examines the response of community composition, species diversity, and functional diversity to disturbance severity at the LTSP sites. As with standing biomass results presented in Chapter 1, diversity and composition responses to disturbance varied by site. On silty loam soils, removing the forest floor (FFR) increased species richness over WTH alone whereas FFR resulted in the lowest species richness on clayey soils and no differences occurred on sandy soils. Although several metrics were used to assess community response to disturbance, only indicator species analysis detected a shift in composition and structure that occurred following the most severe harvest treatment combination at the silty loam site. Building off Chapter 1, these results show that a combination of approaches to quantifying community and diversity dynamics is necessary to capture shifts in function and structure that were evident in analyses of standing biomass.

Given the medium-term impacts of harvest residue removal observed with the LTSP study, Chapter 3 focuses more narrowly on the short-term effects of this management practice on the structure and composition of tree regeneration and the herbaceous community when combined with aggregated overstory retention, a method designed to mitigate potentially detrimental impacts of clearcut harvesting on biodiversity. Species richness, evenness, diversity (H'), and aspen sucker density did not differ between SOH and WTH, but ordination with non-metric multidimensional scaling (NMS) and indicator species analysis revealed compositional differences between the resulting communities. Aspen emerged as a significant indicator species for SOH when abundance (based on cover) was relativized by treatment. This trend may have occurred because WTH favored abundance of species that can compete with aspen, also suggested by indicator species analysis.

Examination of aggregated overstory retention was two-pronged. First, the effectiveness of small aggregates (0.1 ha) at providing refugia for interior forest species was assessed by comparing species diversity measures and understory community composition between aggregates and intact forest controls. Composition of the aggregate understory community was intermediate between intact forest and harvested areas as expected. Some interior forest species such as *Trientalis borealis* showed preference for the conditions present in aggregates based on indicator species analysis. Aggregates also affected surrounding harvested areas. Aspen densities were significantly different between aggregate interiors and harvested areas, but contrary to expectations, differences did not exist between plots located near aggregate edges and plots 20 m out from aggregates. At least in the short-term, ecological objectives aimed at providing refugia and complexity were achieved with no apparent trade-off in regeneration densities.

Overall, results indicate that responses to the level of disturbance occurring as a result of harvest residue removal differ among sites, even when dominated by the same overstory species, but there is potential for severe harvest disturbance to reduce standing biomass and favor shrub species over trees. Also, when evaluating disturbance impacts, it is important to avoid relying on a single measure of diversity or composition because potential impacts could be obscured. Lastly, retaining small aggregates of overstory reserves may provide refugia for some interior plant species without compromising regeneration objectives, at least in the short term.

CHAPTER 1

Harvest residue removal and soil compaction impact forest productivity and recovery: potential implications for bioenergy harvests

Introduction

Forests have been suggested as a supply of alternative sources of energy feedstocks for offsetting fossil fuel consumption (Millar et al. 2007, Becker et al. 2009, Aguilar and Saunders 2010, Buford and Neary 2010); however, increases in demand for forest-derived bioenergy feedstocks could translate to an increase in harvest-related disturbance severity and frequency with associated ecological impacts (Berger et al. 2013). At the same time natural disturbance events (windthrow, fire, etc.) and stressors (e.g. drought) may also increase in frequency and severity as climate change progresses (Dale et al. 2001, Turner et al. 2010). Uncertainty regarding how ecosystems will respond to changes in disturbance, both natural and anthropogenic, poses a serious challenge to the development of long-term sustainable forest management and conservation strategies (Dale et al. 2001, Joyce et al. 2009).

Given the uncertainty surrounding ecosystem responses to potential increases in disturbance, sustainable forest management requires a better understanding of how disturbance severity affects forest productivity and successional development. Generally, forest development occurs more quickly on more fertile sites (Franklin et al. 2002, Larson et al. 2008, Ryan et al. 2008, Hardiman et al. 2011), but disturbance itself can degrade site quality through depletion of nutrients and changes in the understory environment (Stoeckeler 1948, Thiffault et al. 2011). Also, increased disturbance severity or compound disturbance events may push ecosystems outside the range of natural variation (Paine et al. 1998, Lindenmayer et al. 2004). These changes in disturbance severity may favor the establishment and growth of dense understory layers (Royo and Carson 2006) as has been observed in white spruce forests (Eis 1981) and, to some extent, with trembling aspen (*Populus tremuloides* Michx.; Landhausser and Lieffers 1998) in boreal regions. Such an understory can interfere with the establishment of tree species historically adapted to a site, thus slowing or changing forest developmental trajectories (Royo and Carson 2006).

Results from studies examining the effects of harvest residue removal to date have varied depending on site quality, time since disturbance, and forest type. In nutrient-poor forests, removal of harvest residues (i.e., slash) can reduce nutrient availability and tree growth (Walmsley et al. 2009, Helmisaari et al. 2011, Morris et al. 2014); however, negative effects may not be detected in some cases until 10-20 years following harvest (Egnell and Valinger 2003, Helmisaari et al. 2011, Mason et al. 2012, Vanguelova et al. 2010). Findings from Long Term Soil Productivity (LTSP) study sites in boreal aspen and black spruce forests suggest that while tree densities may not respond negatively to the removal of harvest residues, tree height can be detrimentally impacted (Kabzems 2012, Morris et al. 2014). Even where site productivity appears to recover, the reduction in above-ground biomass caused by initial post-harvest declines in site productivity can persist for over 30 years (Egnell 2011). On richer sites the effects are more difficult to discern (Smolander et al. 2008, Smolander et al. 2010, Roxby and Howard 2013). Fully assessing ecosystem response to disturbance requires quantifying severity in terms of not only the death or removal of biomass, but also impacts to soil given the pervasive influence harvest-related soil disturbance may have on forest community development (Halpern 1988, Roberts 2007). The design of the LTSP study network allows assessing these different effects in a way applicable to bioenergy harvests.

Studies that consider impacts to soil, herbaceous biomass, shrub biomass, and other ecological response variables, will increase understanding of the potential long-term impacts that increased levels of feedstock harvests may have on ecosystem structure and function. For example, quantifying productivity in non-tree plant species concurrently with tree species can elucidate competitive interactions among different guilds and the processes behind community disturbance responses (Grewal 1995, Royo and Carson 2006). Additionally, the rate of post-disturbance structural development gives an indication of engineering resilience (hereafter ‘resilience’; Larson et al. 2008), which represents the length of time required for a system to return to its pre-disturbance state (Holling 1996). If disturbance severity influences species composition (e.g. Halpern 1988), structural development, and resilience, then anticipated impacts on future functions will vary similarly, as will the degree to which forest stands accommodate different management objectives (Schwenk et al. 2012).

We examined how aspen-dominated forests growing on three different soil textures across the northern Lake States region respond to a gradient of disturbance severity created through different combinations of biomass removal and soil compaction. We show how above-ground productivity and structure respond to experimentally-controlled variations of stand-replacing disturbance and that responses vary across a range of sites. The responses to differing disturbance severities are used to demonstrate how forests may respond to bioenergy feedstock procurement of differing severity and whether some sites may be more resilient to such practices. Because of potential nutrient losses and greater departure from natural disturbance, we hypothesized that above-ground productivity would decrease with increasing disturbance severity across all sites. We also expected that structural development following the most severe disturbance would lag behind less severely impacted stands because of lowered site quality, which is known to be directly tied to the rate of structural development (Franklin et al. 2002, Ryan et al. 2008). These hypotheses were tested using experimental sites associated with the LTSP network, established in the early 1990s. Three LTSP installations in the Lake States located within the Chippewa, Ottawa, and Huron-Manistee National Forests, provide the opportunity to assess how forests dominated by the same species but distributed across a landscape respond to different levels of disturbance severity over 15 years.

Methods

Study Sites

The study includes three sites within the Laurentian Mixed Forest Province extending from northern Minnesota, USA to Lower Michigan, USA. Each site was dominated by aspen (*P. tremuloides* Michx.) prior to harvest. The Chippewa National Forest (Chippewa) installation (47° 18’ N, 94° 31’ W) occurs on silty loam Frigid Haplic Glossudalfs, receives approximately 64 cm precipitation each year, and is the most productive of the three sites (site index 23 m height at age 50 (SI_{50}) for aspen; Voldseth et al. 2011). Important species prior to harvest included aspen (Curtis Importance Value=58%), sugar maple (*Acer saccharum* Marshall, 11%) and basswood (*Tilia americana* L., 9%). In terms of relative biomass, aspen maintained a similar dominance 15 years after harvest (52.0%). The Huron-Manistee site (Huron ; 44° 38’ N, 83° 31’ W) has a SI_{50} of 19 m for aspen (Stone 2001). Soils are sandy, classified as Frigid Entic Haplorthods and Frigid Typic Udipsamments and annual precipitation is approximately 75 cm (Voldseth et al. 2011). Before harvest important species in addition to aspen (57%)

included big-toothed aspen (*P. grandidentata* Michx. 31%) and white pine (*Pinus strobus* L., 4%). Site-wide species composition was similar 15 years post-harvest with aspen (41.8%) and big-toothed aspen (34.1%) dominating, followed by red oak (11%). The Ottawa National Forest installation (Ottawa ; 46° 37' N, 89° 12' W) occurs on clayey Frigid Vertic Glossudalfs. This site receives approximately 77 cm precipitation annually and has a SI_{50} of 17-18 m for aspen (Voldseth et al. 2011, Stone 2001). Following aspen (50%), balsam fir (*Abies balsamea* [L.] Mill., 33%) and white spruce (*Picea glauca* [Moench] Voss, 14%) dominated prior to harvest. Aspen abundance was comparatively greater 15 years post-harvest (87.5%) with balsam fir (4.7%) and white spruce (0.01%) making up smaller components than pre-harvest levels.

Experimental Design

The severity of disturbance has been quantified in terms of organic matter removal and soil compaction, two factors likely affected during the procurement of biofuel feedstocks from forests. These two factors, each with three levels, were crossed using a factorial design resulting in nine unique treatments examined over time (Fig. 1.1).

The three organic matter removal levels are named according to the traditional harvest method they most closely resemble. These levels included: 1) stem-only harvest (SOH), in which shrubs and merchantable tree boles were removed leaving behind harvest residues (branches and non-merchantable tops); 2) whole-tree harvest (WTH) in which all aboveground portions of trees and shrubs were removed; and 3) whole-tree harvest plus forest floor removal (FFR) in which the forest floor was removed in addition to all above-ground woody biomass. Shrubs such as hazel (*Corylus cornuta* Marshall and *C. americana* Walter) often grow densely in this region and can inhibit tree regeneration, so they were removed from all treated plots at the time of harvest. WTH is a best approximation of the harvest practices associated with biomass feedstock procurement, given the focus of these harvests on removing materials, such as tree tops, and tree limbs which normally would be left on site after traditional harvests. Some states and countries have developed guidelines that recommend removal of only a portion of harvest residues for use in bioenergy production (i.e. MFRC 2007); this study, as it was originally designed in the 1990s, only allows assessment of extremes within the range of residue levels that might be removed as bioenergy feedstocks.

The compaction levels included no additional compaction above normal levels associated with conventional harvesting (C0), moderate compaction (C1), and heavy compaction (C2). Moderate compaction and heavy compaction were intended to increase soil bulk density by 15% and 30%, respectively, over levels normally associated with harvesting (Stone 2001). Actual results varied slightly by soil texture and depth (Voldseth et al. 2011). Plots at the Ottawa, Chippewa, and Huron National Forests were harvested during winter in 1991, 1992, and 1993, respectively. Stands regenerated naturally, mostly through root suckers and stump sprouts. At the Chippewa installation, late season snow delayed the compaction application for 10 plots, so aspen seedlings were planted to compensate for any suckers damaged during treatment. The majority of these seedlings died due to the high level of compaction. Harvest operations are described in detail by Stone (2001).

Treatments were applied to 0.16 ha plots (40 m x 40 m) as well as to 5 m buffers surrounding these plots (0.25 ha total area) and generally replicated three times at each location. Treatment implementation at the Ottawa differed slightly from the other sites with five replicates of the WTH/C0 treatment, two replicates of SOH/C1, and only one replicate with SOH/C2. Woody vegetation was sampled in four 1.26 m radius (5 m^2) circular subplots per plot at Chippewa and Ottawa 5 years following harvest. During the 10 and 15 year sampling periods at these sites and all three sampling periods at the Huron NF, nine 1.78 m radius (10 m^2) circular subplots per plot were sampled. For each individual stem at least 15 cm tall, species and diameter at 15 cm were recorded. In each measurement year, a random azimuth and distance (range of 1 to 3 m) from a permanent sample point center was used to determine the location of five 1 m^2 clip-plots per treated plot for sampling above-ground herbaceous vegetation. Clip-plot locations in subsequent years were constrained to be at least 1 m from the previous sample location. Herbaceous vegetation was clipped at the peak of the growing season (late July or early August), oven-dried at 60° C for 48 hours, and weighed to determine biomass.

Analysis

Above-ground biomass of woody species was calculated 5, 10, and 15 years post-harvest with species-specific allometric equations developed using material from several locations across the Lake States, including the Chippewa and Ottawa National Forests (Perala and Alban 1994). Woody species that can occupy dominant canopy positions in closed canopy conditions at some stage of development in these forests were classified as ‘trees’. The ‘shrubs’ category comprised all remaining woody species except for the genus *Rubus* which was included with herbaceous plants during sampling. Live standing biomass at each measurement period was used as a surrogate for net aboveground productivity in our analyses.

Three structural attributes were used to assess forest structural development in response to organic matter removal and compaction over time. These included density of stems and quadratic mean diameter, two conventional measures of forest structure. Additionally, we analyzed the maximum basal diameter (maxBD) as a response variable. Larger diameter trees and greater variability in tree diameter are both commonly used to describe structural development, particularly when comparing the structure of managed forests to that of old-growth (i.e. Larson et al. 2008. Silver et al. 2013). The forests sampled for the present study are young, so “large” trees are absent, but the diameter of the largest trees present in each stand provides some indication of structural development at this early stage.

Diameter was measured at a height of 15 cm (basal diameter, BD) in the field with diameter at breast height (DBH, 1.4 m) measured for only a subset of stems. To enable comparison with other studies DBH was estimated using the following equation:

$$\text{DBH} = 0.88 * \text{BD} – 0.254 \; (r^2 = 0.9476, p<0.0001)$$

where DBH is diameter at breast height (cm) and BD is basal diameter (cm).

The influence of organic matter removal and compaction on productivity and structure was assessed with mixed-model repeated measures ANOVA using the SAS MIXED procedure (SAS Institute, Inc. 2010). The statistical model used was as follows:

$$Y_{ijkl} = \text{OMR} + \text{CPT} + \text{TIME} + (\text{OMR} * \text{CPT}) + (\text{OMR} * \text{TIME}) + (\text{CPT} * \text{TIME}) + (\text{OMR} * \text{CPT} * \text{TIME}) + e_{ijkl}$$

where OMR is organic matter removal, CPT is compaction, TIME is the number of years since harvest, and Y_{ijkl} is above-ground biomass, stem density, or diameter at the *i*th level of OMR, the *j*th level of CPT, the *k*th level of time, and the *l*th level of plot. Plots were included as random effects while OMR, CPT, and TIME were treated as fixed effects. Type III sums of squares were used for all analyses to account for the unbalanced design at the Ottawa NF. Each site was analyzed separately because soil texture, the main characteristic distinguishing them, was not replicated. Some response variables required power transformations to meet ANOVA assumptions for equal variances among groups and normally distributed residuals. Tukey-adjusted multiple comparisons were used to distinguish among effects of factor levels where warranted.

Results

Biomass Production

Both main factors and their interaction (OMR * CPT) resulted in significant differences in total above-ground biomass at all three sites (Table 1.1). Removing harvest residues did not negatively affect total standing biomass at the Chippewa or Ottawa sites (Fig. 1.2). In fact, with the addition of light compaction (C1) both WTH (23.894 ± 4.367 Mg/ha) and FFR (24.329 ± 5.498 Mg/ha) yielded higher total above-ground biomass at Chippewa compared with SOH (11.426 ±2.360 Mg/ha; Fig. 1.2). Similarly at Ottawa, WTH resulted in higher biomass when combined with C1 (23.183 ±6.525 Mg/ha) or C2 (14.867 ± 3.801) compared to FFR (9.402 ± 3,235 and 10.554 ± 3.520 Mg/ha, respectively) with SOH intermediate (Fig. 1.2). In contrast, removing residues did result in decreased total above-ground biomass at the Huron site (sandy soils) except when compaction was most severe (C2) in which case the biomass among OMR severity levels did not differ (Fig. 1.2, Appendix A).

With respect to compaction, no trends in total standing biomass were consistent among the sites. Total biomass declined with increasing CPT at Chippewa (Fig. 1.2). At Ottawa, the intermediate compaction level (C1) appears to increase total biomass, but only when combined with SOH or WTH (Fig. 1). At Huron, there were no significant differences among CPT levels when OMR was held constant even though CPT was a significant factor by itself (Table 1.1, Appendix A) and biomass appears to increase with an increase in compaction above C0 (Fig. 1.2).

When total biomass is divided into its component guilds, responses to disturbance again varied by site. Trees consistently dominated the biomass pools. Accordingly, trends in tree biomass followed those reported above for total above-ground biomass (Fig. 1.2). Shrub biomass increased with increasing disturbance at Chippewa. Shrub biomass at this site was greatest following FFR (FFR > SOH, WTH; p=0.0397, 0.0004). Increasing compaction also resulted in greater shrub biomass (Fig. 1.2), but the CPT factor was not significant by itself. Because of the TIME*CPT interaction, we analyzed shrub biomass independently for the 15 year sampling period, and compaction did have a significant effect (F=5.54, p=0.0133) with shrub biomass greater following C2 than C0 (p=0.0126). In contrast, shrubs exhibited a negative response to greater disturbance at Ottawa. Where heavy compaction occurred shrub biomass decreased with increasing organic matter removal (SOH >WTH, FFR; p=0.0404, 0.0533). When combined with WTH, increasing compaction also decreased shrub biomass (C0 > C1, p=0.0301). At Huron, WTH may have favored shrub biomass (Fig. 1.2), but the effects were not significant. Likewise, herbaceous biomass showed no relationship to the disturbance severity associated with either factor. However, at both the Chippewa and Ottawa locations, increasing compaction increased the proportion of biomass allocated to herbaceous plants (C1, C2 > C0 at both sites; Fig. 1.2, Appendix A).At Ottawa, FFR increased herbaceous biomass over WTH when in combination with increased compaction (C1 or C2, Appendix A).

Most biomass measures varied significantly with time (Table 1.1, Appendix B). The only exception was shrub biomass at the Huron site which constituted a very small proportion of total aboveground biomass (Fig.1.1). Tree biomass increased over time at all three sites. At the Chippewa site, in particular, shrub biomass was greater where severe compaction decreased tree biomass at the 15 year sampling period (Fig.1.1). Herbaceous biomass decreased over time at Chippewa NF, but continued to increase up to 15 years after harvest at Ottawa NF.

Structure

Both main factors and their interaction significantly influenced diameter at the Chippewa and Ottawa sites (fine-textured soils) whereas at Huron (sandy soils) only OMR and the OMR*CPT interaction were significant effects (Table 1.2). Holding OMR constant at SOH, increasing compaction (C1 or C2) reduced the mean for the largest diameter trees (maxBD) at Chippewa (Fig.1.3). Increased compaction also reduced max diameter when combined with FFR (Fig.1.3, Appendix A). Maximum diameter increased at Chippewa following WTH compared to SOH, but only in combination with intermediate compaction (C1; Fig.1.3, Appendix A). Similarly, at Huron maxBD was greater following SOH compared with WTH and FFR when combined with C1 ($p=0.0396$, $p<0.0001$; Appendix A). At the Ottawa site, pairwise comparisons yielded no significant differences in diameter attributable to OMR severity levels even though the main effect was significant in the model (Table 1.2).

At Chippewa NF, both the CPT factor and CPT * TIME interaction significantly affected stem density. Holding TIME constant, density decreased with increasing compaction (C0>C1>C2, $p<0.05$) during each time period. At the Ottawa site, both OMR and the OMR * CPT interaction showed a significant effect on tree stem density over time (Table 1.2), but no pairwise comparisons between OMR levels emerged as significant. An assessment of trees > 5 cm DBH in the last sampling period alone (15 years post-harvest) confirms the significant effect of OMR on density ($F=6.12$, $p=0.0106$). The greatest stem densities occurred following WTH, but significant differences only emerge when that treatment is combined with intermediate compaction (C1: WTH > FFR, $p=0.0077$; Fig. 1.3). At the Huron NF, neither main factor affected tree stem densities over time when all diameters are considered (Table 1.2). However, if analysis is limited to stems ≥ 5.0 cm DBH 15 years post-harvest, OMR does have an effect ($F=5.30$, $p=0.0163$) with densities significantly greater when harvest residues are retained (SOH > WTH, FFR; $p=0.0380$, 0.0245).

As would be expected, tree diameter and stem density changed significantly over time at all three sites. At Chippewa stem density did not differ significantly between years 5 and 10, but did decrease substantially by year 15 (Y5, Y10 > Y15; $p= 0.0068$, 0.0325). At Ottawa NF, OMR * TIME was significant, so changes over time were assessed while holding OMR constant. Only with WTH did densities differ among years (5 > 15, $p=0.0089$). At Huron NF, stem density decreased between 5 and 10 years post-harvest, but year 15 did not differ from year 10 (5 > 10, 15; $p<0.0001$). Both measures of diameter (QMD and maxBD) increased over time at all sites (Y15 > Y10 > Y5, $p<0.0001$).

Discussion

Across sites, standing biomass was generally greatest where both diameter (QMD and maxBD) and density were also greatest (Fig. 1.4). Treatment effects varied among sites, but within sites these three aspects of structure responded to disturbance severity in concert. At Chippewa and Ottawa, the removal of harvest residues did not detrimentally impact total above-ground standing biomass or diameter growth. At the Huron installation, however, standing biomass, diameter growth, and tree density all declined with increasing organic matter removal.

The short period of time (15 years) since stand-replacing disturbance somewhat limits assessment of structural development, but even at this early stage, severe compaction at Chippewa and Ottawa and severe organic matter removal (FFR) at all three sites appeared to delay the accumulation of larger trees (Appendix B). At the Ottawa NF, the temporal trend in stem density gives some indication of structural development. In contrast to the other two sites, stem density declined little over time at this site except where WTH occurred (Appendix B). As a stand develops, there is generally a predictable decline in stem densities due to self-thinning processes, so a delay in decreasing densities may indicate slower structural development in general compared to the other sites. While removing harvest residues (WTH) may improve growing conditions for species (like aspen) that regenerate through root suckers and hasten development compared with SOH, the additional loss of nutrients associated with removing the forest floor (FFR) may have had a negative effect.

One advantage of looking at the effects of soil compaction and harvest removal over time rather than exclusively at an ‘endpoint’ is a greater ability to discern the processes affecting changes in the main variables of interest, such as above-ground biomass. At the Chippewa, those stands most severely impacted in terms of soil compaction showed an increase in shrub biomass 15 years post-harvest that coincided with decreased tree biomass relative to other treatments. Because the shrub response to compaction did not emerge until 15 years had passed (Fig. 1.2), we can infer that the original disturbance negatively impacted tree regeneration in a direct way, possibly through damage to aspen root systems because of rutting (Bates et al. 1993). Shrubs have likely increased over time in response to that original impact on trees rather than directly outcompeting trees because of some advantage conferred immediately following the disturbance (Royo and Carson 2006). It should cause concern that the most severe disturbance treatment (FFR/C2) results in a community dominated by shrubs 15 years after harvest with no indication of return to the pre-disturbance composition or structure (Fig. 1.2).

While the lack of replication prevents statistical comparisons among soil textures in our analysis, other studies have observed different responses depending on soil texture (Powers et al. 2005, Morris et al. 2014) or general site quality (Page-Dumroese et al. 2000, Thiffault et al. 2011) and this may contribute to the differences we observed. With the addition of compaction (C1 or C2), removing harvest residues resulted in higher aboveground biomass at the Chippewa and Ottawa sites despite evidence that K decreased with increasing organic matter removal at Chippewa (Voldseth et al. 2011). The soils at Chippewa and Ottawa are considered more nutrient-rich than at Huron, so it may be that where nutrients are not already limiting, the effect of retained harvest residues on the microenvironment can hinder tree establishment and growth. In other regions where forest regeneration depends more on sexual reproduction or planting than the aspen-dominated forests discussed here, harvest residues and litter tend to benefit seedling germination and growth by decreasing soil moisture loss and mitigating extreme conditions in the microenvironment (Gray and Spies 1997, Roberts et al. 2005, Walmsley et al. 2009, Thiffault et al. 2011) or by reducing competing vegetation (Stevens and Hornung 1990, Roberts et al. 2005). Additionally, harvest residues eventually provide valuable substrate for species that require decaying woody debris for seedling germination (Shields et al. 2007, Marx and Roberts 2008, Cornett et al. 2001). When the dominant species can regenerate vegetatively through root suckering and is managed using a coppice system, as with aspen in this study, these effects may not prove beneficial for total aboveground biomass production. Instead, the decrease in soil surface temperatures that results from shading by woody debris or dense understory cover (Zabowski et al. 2000) can potentially shorten the growing season and decrease annual growth rates in aspen (Zasada and Schier 1973, Grewal 1995, Landhausser and Lieffers 1998, Fraser et al. 2002).

Forest regrowth and productivity at Huron was negatively impacted by increasing severity of residue removal even though only the two extremes (SOH and FFR) differed significantly once the interaction of main effects was considered. Because sandy soils tend to be of poorer nutrient quality, the detrimental impact of residue removal might be explained by an associated loss of nutrients (Federer et al. 1989, Thiffault et al. 2011). While mineral soil C and N pools have not exhibited a response to OMR over 15 years at this site (Kurth et al. 2014) an analysis of soil cations 10 years after harvest indicated a significantly lower concentration of Ca associated with FFR when compared to SOH 10-20 cm below the surface (Voldseth et al. 2011). This supports concerns expressed in other studies about the potential for Ca losses with residue removal following harvest of aspen and other species that store large amounts of Ca in their tissue (Alban 1982, Silkworth and Grigal 1982, Federer et al. 1989). Additionally, the higher levels of fine and coarse woody debris following SOH may alter the microenvironment by reducing exposure and increasing soil moisture (Gray et al. 2002, Roberts et al. 2005, Walmsley et al. 2009), thus increasing biomass production compared to FFR. Leaving residues on site (SOH) increased total above-ground biomass over other OMR treatments except when the most severe compaction treatment (C2) was held constant (Fig. 1.2, Appendix A). The increase in compaction resulting from C2 would be expected to decrease soil pore space and increase water-holding capacity (Greacen and Sands 1980, Powers et al. 1999, Stone et al. 2001), which may have equalized the moisture-retaining effects of SOH relative to WTH and FFR. The positive (but insignificant) relationship between greater biomass production and increasing compaction (Fig. 1.2) indicates that water may be limiting as has been observed in other LTSP studies on sandy soils (Powers et al. 1999, Powers et al. 2005), providing some support for this hypothesis.

An analysis of bulk density 10 years after harvest at each site indicates that the soils at Huron and Chippewa had started to recover from the compaction treatments (Voldseth et al. 2011). However, no significant differences in bulk density at the Ottawa site (clay soils) were observed between sampling periods immediately following harvest and 10 years post-harvest (Voldseth et al. 2011). Based on these trends, we suspect that the responses to compaction observed in biomass production and structure at the Chippewa site, even 15 years post-harvest, were largely realized immediately after treatment. Wet conditions were present when compaction was applied, so damage to aspen root systems may have occurred, which combined with effects of compaction on conditions for seedlings and sprouts during their first growing season, may have generated differences that are still evident 15 years later. At the Ottawa site, however, it is not possible to distinguish between these effects and how continued compaction might affect hydrology, gas exchange, or other processes that influence forest growth.

Some studies have concluded that richer sites should not experience nutrient deficiencies that limit regeneration following WTH (Boyle et al. 1973, Silkworth and Grigal 1982) with any nutrients lost via harvesting having little noticeable effect on productivity. Recent research indicates that soil disturbance has greater potential to negatively impact net primary productivity than stand mortality or dead wood removal (Peters et al. 2013). Our results at the Chippewa and Ottawa sites align with these findings at present, but as has occurred in other studies, negative effects on productivity may manifest later in stand development (Egnell and Valinger 2003, Mason et al. 2012).

Conclusions

The LTSP network provides a unique opportunity to study the medium-term ecological effects of removing harvest residues. This is particularly important as interest in using those residues for bioenergy production increases and organizations develop management guidelines in anticipation of potential impacts. Our results demonstrate that increased disturbance severity resulting from the removal of harvest residues for bioenergy feedstocks may have a negative effect on structural development and, at least on some sites, above-ground biomass production. While no intermediate levels of harvest residue removal were tested, this study does affirm the need for management guidelines that include provisions for retaining living and dead tree biomass following harvest and for minimizing soil disturbance. Further research should investigate the effects of retaining a portion of residues across a range of sites.

Additionally, our results highlight the importance of accounting for site differences when developing guidelines intended to mitigate impacts from bioenergy feedstock procurement. Such considerations have been integrated by some regional site-level guidelines (Herrick et al. 2009); however, most recommendations generically apply to all site types (e.g., MFRC 2007). While removing residues may improve the growing environment on fine-textured soils for species that regenerate vegetatively as occurred at the Chippewa and Ottawa sites, care should be taken to minimize soil disturbance as reductions in tree biomass may occur and, if the disturbance is severe enough, shrubs may increase in dominance. On poorer, sandy soils such as those at the Huron NF, the removal of harvest residues may not be appropriate both because of potential for nutrient losses as well as reductions in moisture availability, particularly in light of projections for more severe and more frequent drought conditions in the future.

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Table 1.1 Summary of type III tests of fixed effects for aboveground biomass in different pools over 15 years following biomass harvest. Abbreviations for the factors are as follows: organic matter removal, OMR; compaction, CPT. Results are reported for LTSP installations at the Chippewa National Forest, Minnesota (CH), the Huron-Manistee National Forest, Michigan (HM), and the Ottawa National Forest, Michigan (OT). Effects with $p \leq 0.05$ are shown in bold.

			Above-ground biomass		Tree biomass		Shrub biomass		Herbaceous biomass	
	Source	df	F	P-value	F	p-value	F	P-value	F	P-value
CH (loamy)	OMR	2	**3.86**	**0.0272**	**8.73**	**0.0005**	**8.95**	**0.0004**	0.61	0.5496
	CPT	2	**45.92**	**<0.0001**	**131.92**	**<0.0001**	0.83	0.4404	**89.81**	**<0.0001**
	TIME	2	**154.97**	**<0.0001**	**148.56**	**<0.0001**	**58.73**	**<0.0001**	**72.94**	**<0.0001**
	OMR*CPT	4	2.49	0.0543	**4.15**	**0.0053**	2.41	0.0605	**3.17**	**0.0209**
	OMR*TIME	4	1.17	0.3338	0.19	0.9418	0.19	0.9423	0.17	0.9516
	CPT*TIME	4	1.81	0.1409	2.01	0.1063	**5.62**	**0.0008**	2.04	0.1019
	CPT*OMR*TIME	8	0.47	0.8728	0.28	0.971	0.33	0.9514	0.33	0.9514
HM (sandy)	OMR	2	**7.59**	**0.0013**	**6.94**	**0.0021**	**11.58**	**<0.0001**	2.45	0.0961
	CPT	2	**3.51**	**0.037**	**3.22**	**0.0478**	1.34	0.2701	2.58	0.0856
	TIME	2	**83.94**	**<0.0001**	**67.17**	**<0.0001**	1.24	0.2976	**23.14**	**<0.0001**
	OMR*CPT	4	**2.71**	**0.0395**	2.3	0.0707	1.2	0.3199	1.64	0.1767
	OMR*TIME	4	0.09	0.9857	0.05	0.9946	0.1	0.9805	0.33	0.8551
	CPT*TIME	4	0.03	0.9985	0.05	0.9945	0.1	0.9819	0.2	0.9377
	CPT*OMR*TIME	8	0.07	0.9997	0.04	1	0.17	0.9938	0.12	0.9983
OT (clay)	OMR	2	**12.12**	**<0.0001**	**10.06**	**0.0002**	**5.16**	**0.0091**	**11.14**	**<0.0001**
	CPT	2	**5.51**	**0.0069**	**3.56**	**0.0358**	**4.27**	**0.0195**	**8.23**	**0.0008**
	TIME	2	**144.53**	**<0.0001**	**79.41**	**<0.0001**	**10.71**	**0.0001**	**9.16**	**0.0004**
	OMR*CPT	4	**5.18**	**0.0014**	**6.06**	**0.0005**	**3.16**	**0.0215**	**7.73**	**<0.0001**
	OMR*TIME	4	0.77	0.5519	0.65	0.6281	0.78	0.542	1.47	0.2243
	CPT*TIME	4	0.17	0.9518	0.03	0.9987	0.42	0.7938	0.08	0.9885
	CPT*OMR*TIME	8	1.26	0.2839	0.94	0.4956	2.03	0.0617	1.87	0.0863

Table 1.2 Summary of type III tests of fixed effects for forest structural attributes following biomass harvest. Abbreviations are as follows: organic matter removal, OMR; compaction, CPT; maximum basal diameter (99th percentile), BDmax; quadratic mean diameter, QMD. Results are reported for LTSP installations at the Chippewa National Forest, Minnesota (CH), the Huron-Manistee National Forest, Michigan (HM), and the Ottawa National Forest, Michigan (OT). Effects with $p \leq 0.05$ are shown in bold.

			BDmax		QMD		Stem density	
	Source	df	F	P-value	F	P-value	F	P-value
CH (loamy)	OMR	2	**5.04**	**0.01**	**11.4**	**<0.0001**	**3.67**	**0.032**
	CPT	2	**23.76**	**<0.0001**	**9.99**	**0.0002**	**53.55**	**<0.0001**
	TIME	2	**205.1**	**<0.0001**	**150**	**<0.0001**	**21.22**	**<0.0001**
	OMR*CPT	4	**3.18**	**0.0204**	2.34	0.067	0.17	0.9521
	OMR*TIME	4	0.71	0.5878	2.44	0.0585	0.22	0.9267
	CPT*TIME	4	0.83	0.5117	**0.92**	**0.4612**	0.46	0.766
	OMR*CPT*TIME	8	0.23	0.9834	0.33	0.9509	0.23	0.9828
HM (sandy)	OMR	2	**8.86**	**0.0005**	**3.43**	**0.0398**	0.95	0.3934
	CPT	2	0.1	0.2571	1.73	0.1871	0.61	0.549
	TIME	2	**216.2**	**<0.0001**	**53.4**	**<0.0001**	**10.57**	**0.0001**
	OMR*CPT	4	**3.77**	**0.0091**	0.86	0.4953	2.6	0.0858
	OMR*TIME	4	0.64	0.6372	0.02	0.9994	0.08	0.9874
	CPT*TIME	4	0.09	0.9842	0.14	0.9685	0.15	0.9628
	OMR*CPT*TIME	8	0.08	0.9997	0.06	0.9999	0.09	0.9994
OT (clay)	OMR	2	**6.51**	**0.0031**	**12.7**	**<0.0001**	**3.56**	**0.036**
	CPT	2	**9.03**	**0.0004**	2.83	0.0685	0.79	0.4579
	TIME	2	**259.8**	**<0.0001**	**231**	**<0.0001**	**71.92**	**<0.0001**
	OMR*CPT	4	**3.88**	**0.0081**	**4.56**	**0.0032**	**2.59**	**0.0481**
	OMR*TIME	4	0.37	0.8281	0.96	0.4368	0.67	0.6165
	CPT*TIME	4	0.31	0.8686	1	0.419	**3.44**	**0.0147**
	OMR*CPT*TIME	8	0.78	0.6223	1.08	0.3983	1.83	0.0941

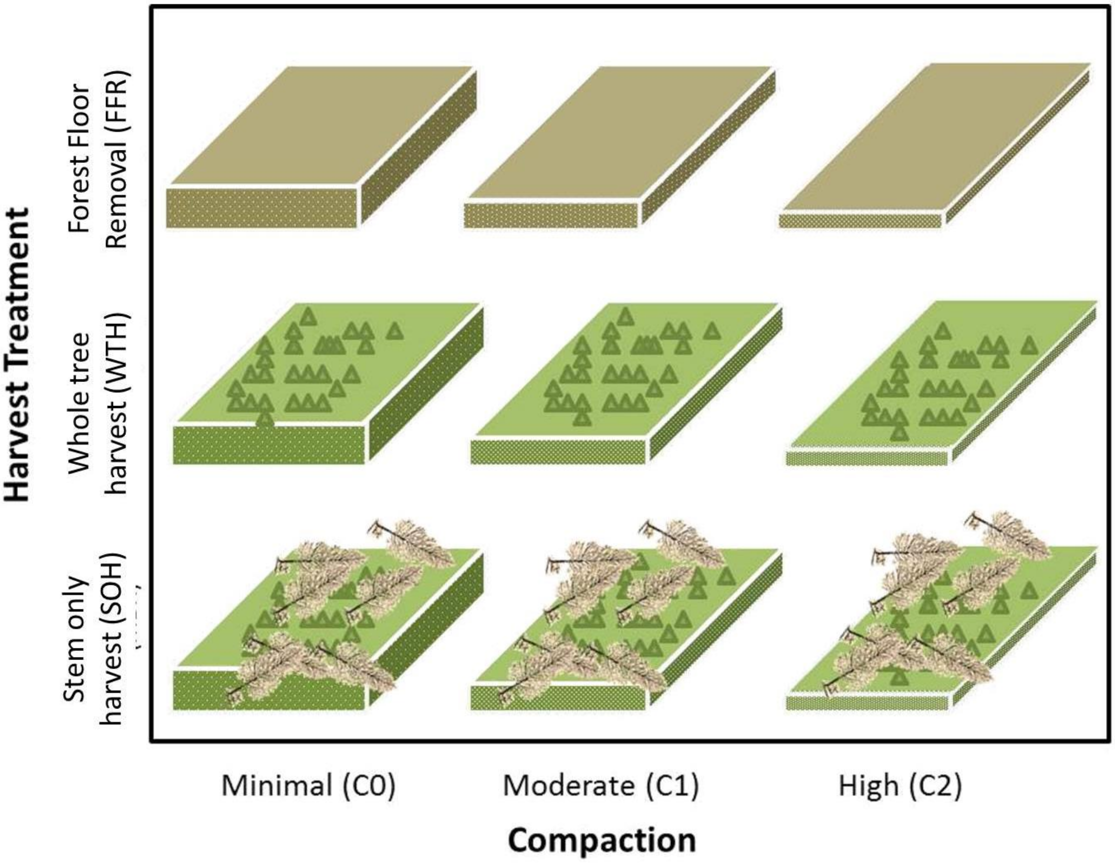

Figure 1.1 Experimental design for the Long-Term Soil Productivity Study.

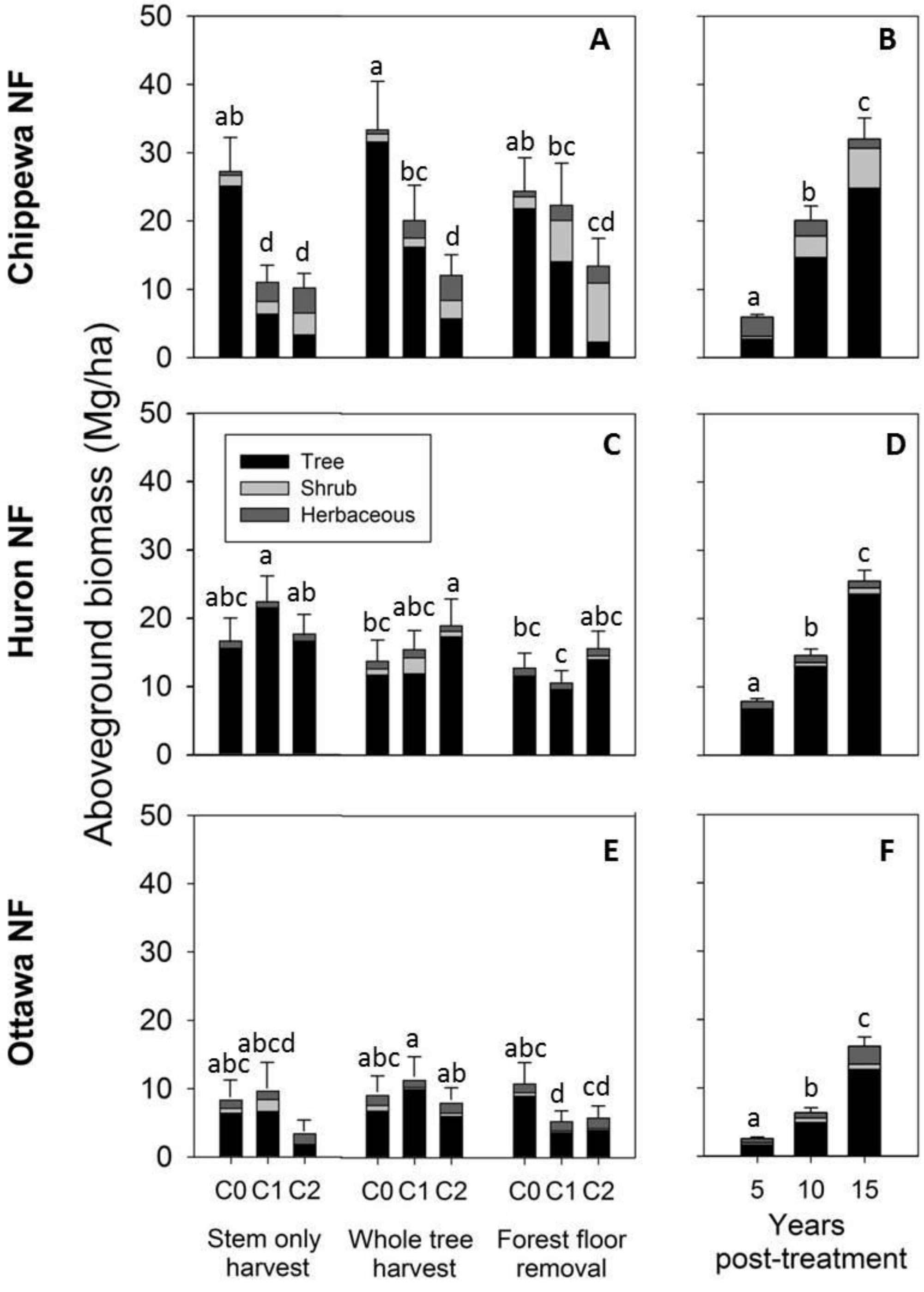

Figure 1.2 Total above-ground biomass including trees, shrubs, and herbaceous plants at Chippewa (panel A), Huron (panel C), and Ottawa (panel E). Panels on the right (B,D,F) show corresponding trends in above-ground biomass across treatments over time. Treatments are abbreviated as follows: C0, no compaction; C1, minimal compaction; C2, moderate compaction. Bars indicate standard error. No standard error or significance is shown for the SOH/C2 treatment at Ottawa because this treatment was not replicated.

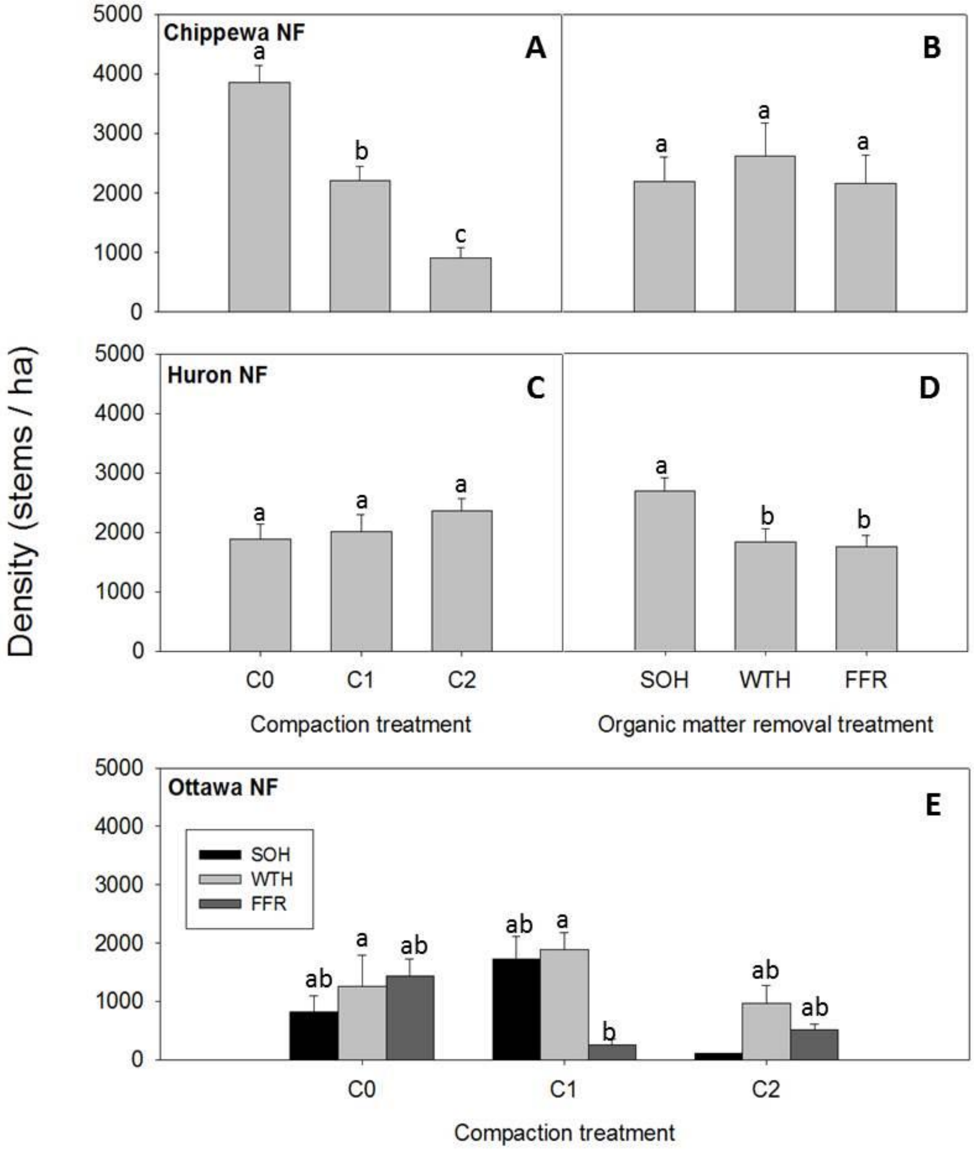

Figure 1.3 Density of trees greater than 5 cm DBH 15 years following harvest. For the Chippewa and Huron National Forests, there was no significant effect of OMR * CPT, so means are presented for each factor individually. Panels A and B shows mean density according to levels of compaction and organic matter removal, respectively, at Chippewa NF. Panels C and D show mean density by levels of compaction and organic matter removal, respectively, at Huron NF. A significant OMR * CPT interaction was observed at Ottawa NF, so means are presented for each individual factorial combination for this site in panel E. Bars indicate standard error and letters indicate where significant differences among treatments occur. No standard error or significance is shown for the SOH/C2 treatment in Panel E because there was no replication for this treatment.

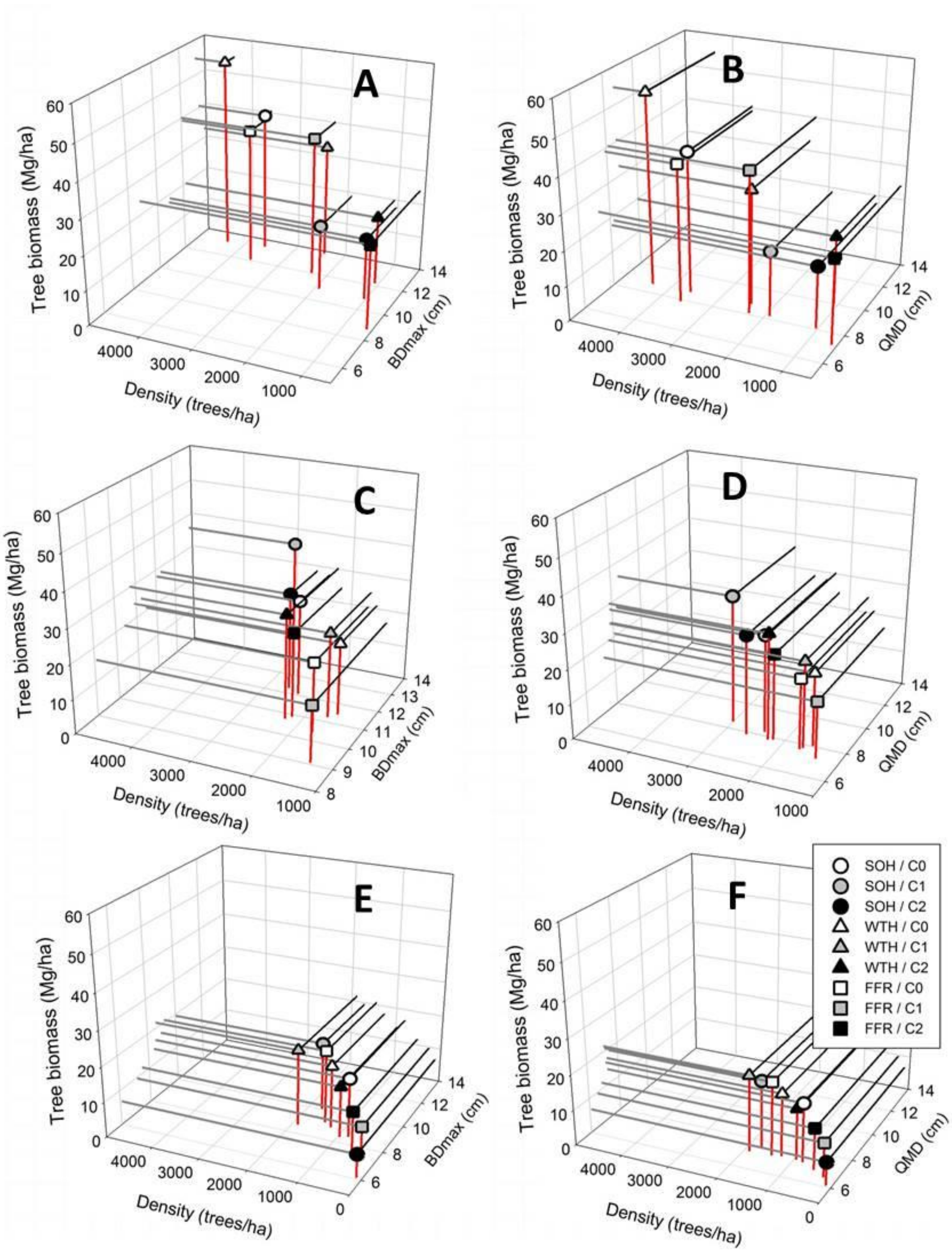

Figure 1.4 The relationships among tree biomass, tree stem density, and diameter 15 years following harvest at Chippewa (panels A and B), Huron (panels C and D), and Ottawa (panels E and F) study sites. A tree was defined as having diameter at breast height > 5.0 cm. Symbol shape (circle, square, triangle) corresponds to the OMR factor (SOH, stem-only harvest, WTH, whole-tree harvest, FFR, forest floor removal). Symbol color (white, grey, black) indicates the CPT factor level (C0, no compaction; C1, minimal compaction; C2, moderate compaction).

CHAPTER 2

Functional diversity measures respond to increasing disturbance severity, but fail to capture a compositional and structural shift in managed forests

Introduction

Species diversity has long been associated with the provision of ecosystem services and with ecosystem resilience (Tilman et al. 1996, Loreau et al. 2001, Elmqvist et al. 2003, Folke et al. 2004, Lavorel et al. 2013), although the strength of those relationships varies with scale, interactions with other species, and species-specific qualities (Tilman et al. 1997, Hooper and Vitousek 1997, Loreau et al. 2001). Increasingly, functional diversity is emphasized as a valuable and potentially more useful tool for assessing ecosystem health and restoration success relative to traditional species identity-based approaches (Tilman et al. 1997, Folke et al. 2004, Suding et al. 2008, Mayfield et al. 2010, Laughlin 2014). Functional diversity indices enable a more direct assessment of potential disturbance impacts on ecosystem processes without making assumptions about the consequences of diminished species diversity (Mason et al. 2005, Petchey and Gaston 2008, Mouillot et al. 2013).

Community assembly rules describe how the environment filters species, determining composition and ultimately function, through its effect on plant traits (Keddy 1992). The degree to which the resulting functional diversity affects ecosystem services may also depend on the environment and associated stresses (Loreau et al. 2001, Paquette and Messier 2011, Lienin and Kleyer 2012, Laliberte and Tylianakis 2013). At both broad, biome scales and finer, ecosystem scales the availability of resources can influence the direction and magnitude of functional diversity effects on productivity (Paquette and Messier 2011, Laliberte and Tylianakis 2013). In anticipation of projected changes in disturbance severity and frequency with global environmental change, it may be valuable to increase the research focus on ‘response rules’ and the implications they have for functional diversity (Keddy 1992). This entails investigating how disturbance (rather than ambient environmental conditions) influences community composition by filtering species according to their ability to persist or recolonize (i.e. Chillo et al. 2011, Maeshiro et al. 2013, Niell and Puettmann 2013). The resulting species composition then determines function through the representation of "effect traits" that influence ecosystem processes like productivity and nutrient cycling (Diaz and Cabido 2001, Suding et al. 2008). Such an investigation requires not only some quantification of function and structure (e.g. Mouillot et al. 2013), but also a framework for quantifying disturbance severity (Roberts 2007).

Many studies have examined species diversity-ecosystem function relationships along disturbance severity or stress gradients, but those gradients are usually linear and often based on a single variable (i.e. Wilson and Tilman 2002, Chillo et al. 2011) whereas the effects of disturbance may be more complex (Townsend et al. 1997, Roberts 2007). Disturbance severity in forests, specifically, is often quantified in terms of overstory tree mortality (i.e. Oliver and Larson 1990, Frelich and Reich 1998); however, these events may also impact understory vegetation and soil conditions. Accounting for the multidimensional nature of disturbance impacts enables comparisons across both natural and anthropogenic disturbance types and increases the likelihood that more subtle changes to composition and diversity will be observed (Roberts 2007). For example, comparisons among plant functional group responses to thinning treatments versus various levels of comparable canopy cover in unharvested forest demonstrated that ancillary disturbance caused by harvest operations might drive functional change (Niell and Puettman 2013). Nevertheless, the utility of quantifying functional diversity to assess disturbance impacts that accompany forest management treatments related to resource procurement, restoration, or the achievement of other objectives remains largely untested at operational scales.

Removal of harvest residues for bioenergy production has been proposed around the globe as a potential mitigation strategy for reducing greenhouse gas emissions (Millar et al. 2007, Aguilar and Saunders 2010, Buford and Neary 2010), but it increases management-related disturbance severity and has potential to alter functional diversity in forests. This change in land-use practice affects above-ground biomass production, forest structure, and nutrient cycling to varying degrees depending on site characteristics, land-use history, and time since harvest (Helmisaari et al. 2011, Mason et al. 2012, Berger et al. 2013, Curzon et al. 2014). While many reviews stress the importance of potential changes to species richness that may result (e.g. Riffel et al. 2011, Berger et al. 2013, Janowiak and Webster 2010) far less is known about impacts to function. The increase in anthropogenic disturbance frequency and severity that may occur in response to higher demand for forest-derived bioenergy feedstocks will shape the composition, structure, and function of resulting forest communities (Turner et al. 1998, Bernhardt-Romermann et al. 2011), as well as their ability to respond to future disturbances (Costa et al. 2012). Accordingly, understanding those effects and how they vary with disturbance severity and abiotic site conditions is imperative for informing future forest policy and management decisions that maintain critical forest functions in the face of change.

In this study we tested the applicability of a suite of established methods for quantifying diversity and functional responses to disturbances associated with removing harvest residues for bioenergy, an emerging issue in sustainable forest management. We addressed the following questions: (1) Do measures of functional diversity and measures of species diversity exhibit the same response to disturbance severity? (2) Does the increase in disturbance associated with harvest residue removal reduce functional diversity in forest systems dominated by vegetative reproduction? (3) What particular traits differ among the communities that reassemble following disturbances with different severities? (4) Do these responses indicate whether the resilience of forests managed for bioenergy feedstocks and other products might be impaired in light of projected changes to natural disturbance regimes? We examined community composition, species diversity, functional diversity, and individual plant traits in response to harvest-related disturbance severity using data from three Long Term Soil Productivity (LTSP) study installations distributed across the Laurentian Mixed Forest Province in the northern U.S. This long-term dataset provided a novel and valuable opportunity to address the above questions across a range of conditions over time.

Methods

Study Sites

This study utilizes data from the Lake States installations of the Long-Term Soil Productivity (LTSP) Study established by the USDA Forest Service in the early 1990s (Table 2.1; Powers et al. 2005). Together, the three sites represent a range of habitat conditions for aspen (*Populus tremuloides,* Michx.) across the upper Lake States region in the northern U.S. Aspen dominated all forest stands prior to treatment (Curtis Importance Value ≥ 50%), but the sites differ in terms of soil texture. Site locations and descriptions are provided in Table 2.1.

Experimental Design

We quantified disturbance severity in terms of organic matter removal and soil compaction, two factors related to removing residues following conventional harvest for use as biofuel feedstocks. Three levels for each factor were crossed using a factorial design resulting in nine treatment combinations (Fig. 1.1). The three organic matter removal levels included stem only harvest (SOH), in which shrubs and merchantable tree stems were removed leaving behind harvest residues, whole tree harvest (WTH) in which all aboveground portions of trees and shrubs were removed, and whole tree harvest plus forest floor removal (FFR) in which the forest floor was removed in addition to all above-ground woody biomass. The compaction levels included no additional compaction above normal levels associated with conventional harvesting (C0), moderate compaction (C1), and heavy compaction (C2). Moderate and heavy compaction were intended to increase soil bulk density by 15% and 30%, respectively, over C0 (Stone 2001), but results varied by soil texture and depth (Voldseth et al. 2011). Stands regenerated naturally and mostly vegetatively through root suckers or stump sprouts. Harvest operations occurred in winter and are described in detail by Stone (2001).

Treatments were applied to 40 m x 40 m (0.16 ha) plots as well as to 5 m buffers surrounding these plots (0.25 ha total area) and generally replicated three times at each location. Due to operational difficulties, treatment implementation at Ottawa differed with five replicates of the WTH/C0 treatment, two replicates of SOH/C1, and only one replicate with SOH/C2.

Field Sampling

Prior to harvest, all trees > 10 cm diameter at breast height (DBH, 1.4 m) in each 0.16 ha plot were identified and measured. Additionally, woody species < 10 cm DBH and at least 15 cm tall were measured in four 1.13 m radius (4 m^2) subplots per plot. Biomass was estimated per unit area for both trees and the woody understory using allometric equations (Jenkins et al. 2003) and summed on each plot.

During the first post-harvest sampling period (5 years), tree and shrub regeneration was measured in four systematically located 1.26 m radius (5 m^2) circular subplots per plot at Chippewa and Ottawa. For the first post-harvest sampling period at Huron and in all remaining periods at all sites, nine systematically located 1.78 m radius (10 m^2) subplots were sampled. Diameter at 15 cm and species were recorded for each woody stem at least 15 cm tall. Species abundance is quantified with above-ground biomass estimated using allometric equations for each post-harvest sampling year (Perala and Alban 1994). These equations were developed using material from several locations across the Lake States, including the Chippewa and Ottawa National Forests where two of our sites occur (Perala and Alban 1994).

Data Summary and Analysis

This experiment is based on an ANOVA design with two three-leveled factors fully crossed and replicated (in most cases); however, we also used empirical data from these treatments that quantified disturbance severity to examine responses over a continuum of management disturbance. Specifically, for assessment using fourth corner analysis (described in detail below), compaction was quantified continuously as the difference between pre- and immediately post-treatment bulk density. For this same analysis, we used estimates of the amount of live biomass in the form of merchantable stems or whole trees removed from each plot based on the harvest factor (SOH or WTH). We assumed that all material was effectively removed from the site and that no additional material (from breakage or poorly formed stems) was left behind on those plots treated with SOH.

Community composition

Patterns in the composition of the tree and shrub community 15 years post-harvest were examined using non-metric multidimensional scaling (NMS; Kruskal 1964, Mather 1976, McCune and Grace 2002). Species abundance, based on above-ground biomass estimates, was relativized across plots such that analysis revealed which conditions most affected individual species (McCune and Grace 2002). Species occurring in fewer than three of the plots at each site were removed to reduce noise (McCune and Grace 2002). However, these species were not excluded from analyses described below that focused on diversity rather than community structure. Dissimilarity matrices were calculated using Sorensen distances.

Differences in community composition between treatment factors and their interactions were also assessed using perMANOVA (Anderson 2001). Where perMANOVA indicated significant differences between factors ($p < 0.05$), Indicator Species Analysis was used to identify species strongly associated with individual treatments based on the frequency of their occurrence, abundance, and exclusiveness to each treatment (Dufendre and Legendre 1997). Designation as an indicator species required an indicator value > 25 ($p < 0.05$). NMS and indicator species analysis were all conducted using PC-Ord 6.0 (McCune and Mefford 2011). Analyses of treatment effects on community composition were conducted using the vegan package (Oksanen et al. 2013) in R (R Core Team 2013, v 3.0.2).

Species traits

We focused on continuously measured (rather than qualitative) plant traits relating most closely to function in terms of response to disturbance and effects on ecosystem processes (Cornelisson et al. 2003, Lavorel. et al. 2007, Suding et al. 2008). Values for these traits were collected from the literature with preference given to studies in the Lake States region with replication to better capture the range of potential values for each trait (Appendix A). Prior to analysis, values for each trait were standardized to the standard deviate (z-score) across all species observed within the study (Villeger et al. 2008, Dray and Legendre 2008). This may prevent comparison of raw functional diversity indices reported here to other studies, but it does allow comparison among treatments and sites while equalizing the weight given to each trait and meeting statistical assumptions (Villeger et al. 2008).

Functional diversity indices

To date, there is no single, all-encompassing index for effectively quantifying the complexity of functional diversity (Mason et al. 2005, Mouillot et al. 2013). Instead, similarly to species diversity, multiple indices that describe different aspects of function complement one another when analyzed and interpreted together (Mouillot et al. 2013). We selected functional evenness (FEve), functional richness (FRic), functional divergence (FDiv), and functional dispersion (FDis) to collectively assess the effect of biomass harvest disturbance on functional diversity. These indices are all fairly well established in the literature and, while not sufficient individually, offer insight into community change when interpreted in sum (Mouillot et al. 2013). Briefly, FEve parallels species evenness in that greater evenness corresponds to greater equity in the distribution and abundance of species in multi-dimensional functional trait space (Mason et al. 2005, Villeger et al. 2008). Functional richness describes the relative volume of functional trait space that is occupied, given the species composition and abundance of a particular community (Mason et al. 2005, Villeger et al. 2008). Functional divergence quantifies the representation of extreme versus moderate trait values in a community (Mason et al. 2005, Villeger et al. 2009). Higher functional divergence indicates that a greater abundance of species express extreme (high or low) rather than moderate values for traits. Lastly, functional dispersion (FDis) describes both the volume of trait space occupied by a community and the spread of species within that space (Laliberte and Legendre 2010, Mouillot et al. 2013). Unlike the other indices, FDis is independent of species richness. It is comparable to Rao's Q (Botta-Dukat 2005), and the two are often strongly correlated (Laliberte and Legendre 2010). Each functional diversity index was calculated for the tree and shrub component of forest communities in each plot prior to treatment as well as 5, 10, and 15 years post-harvest. The change that occurred in each index value between pre-treatment sampling and each post-harvest sampling year was calculated and used as our unit for analysis. Indices were estimated with the FD package (Laliberte and Shipley 2011) in R (R Core Team 2013, v 3.0.2).

Statistical analysis

The response to treatments of species richness (change since pre-treatment in the number of tree and shrub species present, ΔSR), species evenness (change in the relative abundance of those species), diversity (change in the Shannon Diversity Index, H'), community composition (NMS axis scores), ΔFEve, ΔFRic, ΔFDiv, and ΔFDis was assessed with mixed-model repeated measures ANOVA using the SAS MIXED procedure (SAS Institute, Inc. 2012). The statistical model was as follows:

$$Yijkl = \text{OMR} + \text{CPT} + \text{TIME} + (\text{OMR X CPT}) + (\text{OMR X TIME}) + (\text{CPT X TIME}) + (\text{OMR X CPT X TIME}) + eijkl$$

where OMR is organic matter removal, CPT is compaction, TIME is the number of years since harvest, and Y_{ijkl} is one of the response variables listed above at the *i*th level of OMR, the *j*th level of CPT, the *k*th level of time, and the *l*th level of plot. Plots were included as random effects while OMR, CPT, and TIME were treated as fixed effects. Type III sums of squares were used for all analyses to account for the unbalanced design at Ottawa. Tukey-adjusted post-hoc pairwise comparisons were used to distinguish factor levels where warranted.

Fourth corner analysis

A direct relationship between disturbance severity and the expression of functional traits across each site was established using the fourth corner method (Legendre et al. 1997, Dray et al. 2014). This analysis relates a matrix of environmental variables to a matrix of species traits via a matrix of species abundance in sampled, treated plots (Legendre and Legendre 2012). In this study, the environmental variables consisted of three measures for disturbance severity associated with the removal of harvest residues: bulk density increase, pre-treatment coarse woody debris retention, and live biomass removed at harvest. Because data were not available for estimating the amount of biomass removed with FFR, we excluded plots receiving this treatment from this portion of the analysis. Species abundance was quantified in terms of above-ground biomass, relativized by plot. We examined only continuously measured variables, so a Pearson's correlation coefficient (r) was calculated for each pair of environmental (disturbance severity) variables and traits. The significance of those relationships was then determined by comparing the statistics to those generated using 49000 random permutations (Dray et al. 2014). Additionally, the False Discovery Rate (FDR)-adjustment was used to protect against potential inflation of Type I error with multiple tests (Benjamini and Hochberg 1995, Dray et al. 2014).

The methods by which rows and columns are randomized for permutations determine exactly which hypotheses are being tested (Dray and Legendre 2008). For this study, we used a simultaneous combination of models 2 and 4 such that both entire rows (plots) and entire columns (species) were permuted (Legendre and Legendre 2012, ter Braak et al. 2012, Dray et al. 2014). Fourth corner analysis was conducted using the ade4 package (Dray and Dufour 2007, v. 1.6-2) in R (R Core Team 2013, v 3.0.2).

Results

Community composition

Harvest impacts significantly affected community composition at two (CH, OT) of the three sites. In both cases, soil compaction appears to have had a stronger influence than the level of organic matter removal (Table 2.2). On sandy soils (HM), perMANOVA did not indicate a significant response of community composition to either disturbance factor (Table 2.2).

On silty loam soils (Chippewa), compaction significantly affected community composition as represented by NMS axes 1 and 2, but not axis 3 (Table 2.2). Based on species correlations with these axes (Table 2.3) *Betula papyrifera* Marsh., *Salix sp., Quercus macrocarpa,* Michx., *Amelanchier sp.,* and *Corylus sp.* were associated with more heavily compacted soils while *Populus tremuloides* Michx. was associated with less compaction (Fig. 2.1). Analysis with perMANOVA confirmed the compositional differences among communities treated with different levels of compaction (p <0.05). Indicator species analysis identified *Acer spicatum* Lam., *Cornus sericea* L., *Dirca palustris* L, *Ostrya virginiana* Mill., and *P. tremuloides* as indicative of the least severe compaction treatment (C0). *Salix sp.* and *Rosa sp.* both indicated severe compaction (C2).

On clayey soils (Ottawa), compaction significantly affected patterns in community composition, particularly along NMS Axis 1, where *Prunus serotina* Ehrh. and *Amelanchier spp.* were associated with plots receiving less compaction (Fig. 2.1, Table 3). Although OMR*CPT was a significant effect for Axis 2, neither main factor was significant (Table 2.2). Again, perMANOVA confirmed the influence of compaction indicated by the response of Axis 1 to treatments (p<0.05). Only two species emerged as significant indicators, *Abies balsamea* and *Prunus serotina*, both associated with the least severe compaction treatment (C0).

Tree and shrub species diversity

Species richness and composition varied across the study with only 23.5% of all 34 tree and shrub species observed occurring at all sites. Both soil compaction and organic matter removal had significant effects on species richness, species evenness, and diversity (H'), but those effects were often complicated by interactions, and few consistent trends emerged across sites (Table 2.4).

On silty loam soils FFR resulted in greater species richness than WTH (Table 2.4). On clayey soils the opposite trend emerged with SOH and WTH both resulting in greater species richness than FFR (Table 2.4). The severity of organic matter removal did not significantly influence change in species richness on sandy soils. On the finer-textured, silty loam and clayey soils severe compaction increased species richness over

C0. CPT*TIME was not significant (p=0.0604), but closer examination of means suggests that the relationship between CPT and species richness may diminish over time (Table 2.4). Species richness also varied with time on both clayey and silty loam soils with means greater 10 and 15 years post-harvest when compared to the 5-year sampling period. Mean richness at both sites was greater in year 15 than in year 10, but not significantly, potentially suggesting an asymptote in this response. Species evenness consistently increased over time at all three sites although responses to disturbance severity varied (Table 2.4). SOH resulted in greater species evenness on both sandy and clayey soils, but only in combination with intermediate compaction (C1) at the latter site. Organic matter removal did not directly influence species evenness on silty loam soils, but increased compaction (C1 and C2) did result in greater species evenness than C0, depending on the organic matter removal treatment (Table 4).

Species diversity (H') only responded to disturbance severity on silty loam and clayey soils. On silty loam, greater H' occurred following C1 compared with C0, but only in combination with SOH. On clayey soils, the opposite response to compaction occurred. When combined with WTH, C0 increased H' compared to C1. Also on clayey soils, both SOH and WTH resulted in greater diversity than FFR in the absence of compaction (Table 2.4).

Functional diversity measures

Change in functional dispersion (ΔFDis) following disturbance varied widely among sites. On silty loam soils, ΔFDis positively increased with C1 when in combination with SOH and FFR. When combined with WTH, however, C1 decreased ΔFDis and resulted in lower FDis than occurred pre-treatment (Fig. 2.2). On sandy soils, there was no effect of disturbance severity on ΔFDis . On clayey soils, ΔFDis was negative across all treatments. Increased compaction (C1 and C2) on clayey soils resulted in a greater reduction in FDis than C0 when combined with SOH or WTH but no effect when applied in combination with FFR.

Change in functional evenness (ΔFEve) from pre-harvest values was positive across all sites. Additionally, ΔFEve showed no response to compaction at any site. On sandy soils WTH resulted in greater positive ΔFEve than FFR. On clayey soils, SOH led to a greater increase in ΔFEve than either WTH or FFR (Fig. 2.2).

The change in functional richness from pre-harvest conditions (ΔFRic) was significantly affected by the organic matter removal treatment on both silty loam and sandy soils. On silty loam, both SOH and FFR resulted in a greater increase in FRic than WTH (Fig. 2.2). On sandy soils, ΔFRic was greater following FFR than WTH. Also on these soils, any additional compaction (C1 or C2) diminished the increase in FRic compared to C0 (Fig. 2.2). While there was a significant OMR*CPT on ΔFRic on clayey soils, neither main factor was significant by itself (Table 5).

Mean functional divergence (FDiv) declined following harvest at all three sites; however it showed little sensitivity to disturbance severity. On silty loam soils, the removal of harvest residues lessened the reduction in FDiv compared with SOH (Fig. 2.2. 2). No other significant effects were observed for this response.

Direct effect of harvest impacts on functional traits

Fourth corner analysis yielded weak associations between harvest impacts and functional traits. Following an adjustment for multiple testing, only one relationship remained significant at $p < 0.1$; at Huron there was a positive correlation (r=0.24, p=0.08) between the amount of biomass removed at harvest and the specific gravity of woody species that were present 15 years following harvest (Fig. 2.2).

Without correcting for multiple testing, a few additional relationships emerge (Fig. 2.3). Coincident with specific gravity, shade tolerance was positively correlated with the amount of biomass removed at Huron. At Ottawa, a negative correlation existed between leaf P concentration (P mass) and the amount of pre-harvest coarse woody debris retained. There was also a negative correlation between compaction in the upper 10 cm of mineral soil and drought tolerance at this site. At Chippewa no significant associations between harvest disturbance and plant traits were observed.

Discussion

Multiple studies examining functional diversity and species diversity relationships have concluded that land-use change may have greater impacts on function (as quantified through changes in functional traits) than might be inferred from species richness alone (Flynn et al. 2009, Chillo et al. 2011, Ziter et al. 2013). However, in other cases species richness has better predicted productivity than measures of functional richness (Vila et al. 2007). Our study demonstrates variable diversity responses to disturbance severity across a range of soil textures that cannot be adequately described or quantified with any single index or metric. Rather, each measure of functional diversity, species diversity, and community composition offers complementary information about ecosystem response, and might best be interpreted in combination to more fully understand forest response to disturbance.

According to the intermediate disturbance hypothesis (IDH), species richness should assume a unimodal distribution along disturbance frequency and severity gradients (Connel 1978), although empirical studies have produced mixed results relative to this prediction (Floder and Sommer 1999, Mackey and Currie 2001, Shea et al. 2004). Patterns in species richness response to disturbance severity varied among our sites as well. No interactions between organic matter removal and soil compaction occurred, so species richness was essentially evaluated along two gradients of disturbance severity relating to organic matter removal and compaction. On silty loam soils the two extreme harvest treatments, SOH (ΔSR =0.703) and FFR (ΔSR =1.07), increased mean species richness over pretreatment means whereas WTH reduced species richness (ΔSR=-0.85), a completely opposite trend from what might be expected based on the IDH. Means for ΔSR increased (but not significantly) with disturbance severity on sandy soils and decreased with increasing severity on clayey soils (SOH (ΔSR = 0.61), WTH (ΔSR = 0.24) > FFR (ΔSR=-1.37; Table 2.4). Overall, species richness response differed greatly among sites and did not peak at intermediate levels of the disturbance effects tested in this study.

In contrast with predictions for species richness, FRic is expected to monotonically decrease as disturbance severity increases and resulting conditions filter species by their traits (Cornwell et al. 2006, Flynn et al. 2009, Mouillot et al. 2013). With respect to compaction, we did see a decrease in FRic with increasing disturbance severity on sandy soils. Otherwise, our results do not support this expectation. Instead, FRic showed no response to compaction on silty loam soils or to any level of disturbance severity on clayey soils. On sandy soils, the additional removal of the forest floor actually resulted in an increase in FRic over WTH. On silty loam soils, FFR also led to higher FRic than WTH, as did SOH. These patterns are all directly opposite of that observed for above-ground standing tree biomass (Curzon et al. 2014). We suspect that FRic responded to changes in competition from *P. tremuloides*, the dominant overstory tree species, rather than directly to the filtering effect of greater disturbance severity.

Based on our results, the effect of removing harvest residues for bioenergy production on functional diversity likely varies depending on site conditions. In the case of FDiv, all harvest treatments appear to have a negative effect across sites. On silty loam soils, the retention of residues with SOH decreased FDiv the most, meaning that the mean representation of extreme trait values was less across those plots. Neither compaction nor the level of organic matter removal significantly affected FDiv at the other sites. FDis, the most holistic of the functional diversity measures we tested (Laliberte and Legendre 2008), increased with the removal of harvest residues on silty loam soils but only in combination with compaction. As discussed above, this result may speak more to the response of *P. tremuloides* to treatments than to any direct response of FDis to harvest residue removal. This suggests that measures of functional diversity, even FDis which is independent of species richness, may also be regulated by productivity and its indirect effect on resource availability (Reich et al. 2012).

Our results do not indicate a consistent response of functional diversity to harvest-related disturbance severity, but, as mentioned above, we did observe what may be a trade-off between maximizing above-ground productivity and maintaining species and functional diversity. Several measures of both species and functional diversity occur at their lowest mean value where standing tree biomass was observed at its maximum (Curzon et al. 2014). Examples for organic matter removal include species richness, species evenness, H’, FRic, and FDs on silty loam soils and species richness and H’ on sandy soils. With respect to compaction, FRic, FEve, FDis, species evenness, and H’ on silty loam, and FDis, species richness, species evennness, and H’ on sandy soils were at their minimum where tree biomass was maximized. (On clayey soils most measures of both functional and species diversity paralleled those observed for tree biomass.) The ability of *P. tremuloides* to reproduce vigorously from root suckers makes it highly competitive following disturbance (Frey et al. 2003), and the increase in a dominant species is known to potentially decrease species diversity through competitive exclusion (Grime 1973, Reich et al. 2012). So, those conditions (i.e. severe compaction on silty loam or clayey soils) that impair or slow the regeneration of *P. tremuloides* (i.e. Bates et al. 1993) may indirectly increase different aspects of diversity by reducing competition and site occupancy by this species. Our results support those reported by other studies that show negative relationships between biomass production or C storage and species richness in boreal forest (Reich et al. 2012), FDis in boreal forest (Ziter et al. 2013), FDiv in grasslands (Grigulis et al. 2013) and FDiv in semi-arid forest (Conti and Diaz 2013).

The distribution of response traits in a community prior to disturbance, particularly those related to regeneration strategies and dispersal, will influence ecosystem processes after disturbance due to their influence on expression of effect traits (e.g., characteristics relating to nutrient cycling and storage) through post-disturbance filtering (Diaz and Cabido 2001, Suding et al. 2008). Of the 11 traits evaluated in our study, only 4 responded directly to the continuously measured proxies for our disturbance severity treatments. Shade tolerance and specific gravity (wood density) both correlated positively with the amount of biomass removed during harvest at our poorest site, on sandy soils. It is intuitive that these two traits exhibited the same response as they tend to correlate positively to one another, but whereas shade tolerance might be considered a response trait, specific gravity has more direct implications for nutrient and carbon cycling as it influences decay rates and above-ground carbon storage (Cornelissen et al. 2003). The negative association between the amount of pre-treatment coarse woody debris retained and leaf P concentration observed on clayey soils may also have implications for nutrient cycling, although P does not tend to be a limiting nutrient in the forests we examined (but see Naples and Fisk 2010). Perhaps most interesting, results from the clayey site indicated that increasing mineral soil bulk density may decrease mean drought tolerance at the plot scale (0.16 ha). This is a rough measure of stress response, and the statistical significance of the test was weak, but this association may merit further investigation. The resilience of forest ecosystems to drought is of particular concern given projections for potential increases in future drought frequency and severity in this region (Bachelet et al. 2001).

Of the two disturbance factors examined, only compaction had a significant effect on community composition. This result is important to highlight because it indicates a shift in community structure that was not captured by any of the other response variables quantifying diversity or function reported here. On silty loam soils (CH) two shrubs, *Salix sp*. and *Rosa sp*., were identified as indicator species for the most severe compaction treatment. This is in contrast to *P. tremuloides*, the dominant overstory tree, which was indicative of minimal compaction (C0). At this site, increased compaction had a significant negative effect on total above-ground biomass, specifically on tree biomass, especially when combined with FFR (Curzon et al. 2014). In fact, over the course of 15 years after harvest those plots receiving the most severe disturbance treatment (FFR/C2) were increasingly dominated by shrub species (Curzon et al. 2014). While not captured by any of the functional diversity indices or the trait analysis, this change in community composition and structure will undoubtedly affect the provision of ecosystem services, particularly if current conditions persist. This suggests that in some cases even a combination of functional and species diversity measures may fail to detect changes in important ecosystem processes such as above-ground biomass production. Thus, we argue for the use of a suite of indicators to assess the impacts of a given management practice on ecosystem structure and function versus focusing on single metrics that, although designed to describe common relationships, may not fully capture potential impacts.

Conclusions

Rather than following predictions based on the IDH, the response of species and functional diversity along the disturbance severity gradient tested in this study appears to be more consistently influenced by the abundance of (and competition from) *P. tremuloides,* the dominant species in these ecosystems, as it is affected by disturbance. Conditions that favored *P. tremuloides* regeneration and growth led to greater mean standing biomass, at least up to 15 years following harvest, but this maximization of biomass coincided in most cases with a reduction in species richness, FDis, and FRic except where disturbance severity was greatest (as with FFR) in which case both productivity and diversity tended to decline. Thus, short-term maximization of standing biomass may mean a sacrifice in species and functional diversity in a system dominated by species regenerating vegetatively (i.e., coppice systems).

Despite exhibiting sensitivity to disturbance severity across sites, measures of species and functional diversity did not capture the shift in dominance from tree to shrub species that occurred following the most severe disturbance treatment on silty loam soils. This finding highlights the need for further work in refining methods for quantifying function. It also reinforces previous suggestions that no single index or measure fully captures the complexity of ecosystem functional change, but that multiple approaches used in combination may be worthwhile and most effective.

While consistent trends did not emerge among the three sites in this study, our results do show that the removal of harvest residues for use as bioenergy feedstocks and the potential for associated soil disturbance may affect functional diversity, species diversity, community composition, and specific plant traits. Thus, guidelines aimed at mitigating impacts from management related to the procurement of bioenergy feedstocks from forests should take site differences into account and strive to minimize soil disturbance during harvest entries.

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Table 2.1 Site locations and descriptions.

Study Site	Harvest Year	Location	Aspen (% pre-harvest biomass)	Site index[a] (m)	Precipitation (cm/year)	Soils	Soil texture
Chippewa (CH)	1991	47° 18’ N, 94° 31’ W	58	23	64	Frigid Haplic Glossudalfs	silty loam
Huron (HM)	1992	44° 38’ N, 83° 31’ W	57	19	75	Frigid Entic Haplorthods, Frigid Typic Udipsammentss	sandy
Ottawa (OT)	1993	46° 37’ N, 89° 12’ W	50	17-28	77	Frigid Vertic Glossudalfs	clayey

[a] Aspen, age 50

Table 2.2 Treatment effects on woody species composition 15 years after harvest based on analysis using perMANOVA. Abbreviations are as follows: CH, Chippewa; HM, Huron; OT, Ottawa; OMR, organic matter removal; CPT, compaction.

Site	Source	df	F	p-value
CH (silty loam)	OMR	2	1,36	0.0776
	CPT	2	**2.26**	**0.0004**
	OMR*CPT	4	0.85	0.7954
HM (sandy)	OMR	2	1.33	0.1292
	CPT	2	0.98	0.4834
	OMR*CPT	4	0.71	0.9404
OT (clay)	OMR	2	1.44	0.0686
	CPT	2	**1.65**	**0.0196**
	OMR*CPT	4	1.15	0.2170

Table 2.3 Kendall's τ correlations between the relative abundance (above-ground biomass) of shrub and tree species and NMS axes. Species in bold correlate with at least one NMS axis ($p < 0.05$). If a species was a significant indicator (indicator value > 25, $p < 0.05$), the max group (treatment) is listed in the Indicator Species Analysis (ISA) column. Treatment abbreviations are as follows: A1, NMS axis 1; A2, NMS Axis 2; C0, light compaction; C2, heavy compaction.

	Chippewa NF			Huron-Manistee NF			Ottawa NF		
Species	A1	A2	ISA	A1	A1	ISA	A1	A2	ISA
Abies balsamea	n/a	n/a		-0.15	-0.13		0.35	0.07	C0
Acer rubrum	-0.13	0.28		-0.29	**-0.49**		0.02	**0.50**	
A. saccharum	0.16	-0.32		n/a	n/a		n/a	n/a	
A. spicatum	-0.35	-0.16	C0	n/a	n/a		n/a	n/a	
Alnus sp.	n/a	n/a		n/a	n/a		0.09	-0.41	
Amelanchier sp.	-0.11	**0.55**		-0.30	0.21		**0.53**	0.17	
Betula papyrifera	**0.55**	-0.04		n/a	n/a		n/a	n/a	
Carpinus caroliniana	n/a	n/a		0.15	-0.03		n/a	n/a	
Corylus sp.	-0.37	**0.44**		**-0.44**	-0.12		0.18	0.37	
Cornus drummondii	-0.42	-0.02		n/a	n/a		n/a	n/a	
C. sericea	-0.24	0.04	C0	n/a	n/a		0.17	-0.06	
Crataegus sp.	-0.22	0.25		n/a	n/a		n/a	n/a	
Diervilla lonicera	0.24	0.42		0.14	-0.19		0.15	0.32	
Dirca palustris	-0.11	-0.43	C0	n/a	n/a		n/a	n/a	
Fraxinus americana	n/a	n/a		0.35	-0.23		n/a	n/a	
F. nigra	-0.09	-0.24		n/a	n/a		n/a	n/a	
Lonicera canadensis	0.23	0.35		n/a	n/a		0.12	-0.39	
Ostrya virginiana	-0.28	-0.21	C0	n/a	n/a		n/a	n/a	
Picea glauca	n/a	n/a		n/a	n/a		-0.08	-0.06	
Pinus strobus	n/a	n/a		**0.55**	-0.03		n/a	n/a	
Populus balsmifera	0.48	-0.05		n/a	n/a		n/a	n/a	
P. grandidentata	-0.35	-0.23		0.23	-0.30		n/a	n/a	
P. tremuloides	**-0.46**	-0.24	C0	-0.37	0.16		0.16	-0.41	
Prunus serotina	-0.20	0.26		-0.36	-0.34		**0.47**	**0.37**	C0
P. virginiana	-0.33	-0.03		0.21	-0.28		0.26	**0.35**	
Quercus alba	n/a	n/a		**-0.52**	-0.08		n/a	n/a	
Q. macrocarpa	-0.10	**0.55**		n/a	n/a		n/a	n/a	
Q. rubra	0.09	0.12		-0.30	-0.12		n/a	n/a	
Ribes sp.	0.15	0.08		n/a	n/a		0.40	0.15	
Rosa sp.	-0.08	0.42	C2	n/a	n/a		-0.16	-0.08	
Salix sp.	**0.71**	0.07	C2	n/a	n/a		-0.24	0.21	
Tilia americana	-0.07	-0.34		n/a	n/a		n/a	n/a	
Ulmus sp.	-0.29	-0.33		n/a	n/a		n/a	n/a	
Viburnum sp.	n/a	n/a		0.29	**-0.44**		-0.36	0.10	

Table 2.4 Repeated measures results for measures of species diversity. Abbreviated as follows: OMR, organic matter removal; CPT, compaction; C0, no compaction; C1, minimal compaction; C2, moderate compaction; SOH, stem-only harvest; WTH, whole-tree harvest; FFR, forest floor removal; CH, Chippewa; HM, Huron; OT, Ottawa.

Site	Source	Δ Species richness					Δ Species evenness			
		df	F	p-value	pairwise comparisons	p-value (adjusted)	F	p-value	pairwise comparisons	p-value (adjusted)
CH (silty loam)	OMR	2	**3.78**	**0.0293**	**FFR > WTH**	**0.0323**	1.32	0.2752		
	CPT	2	**11.7**	**<0.0001**	**C0 > C1,C2**	**0.0101, 0.0001**	**13.12**	**<0.0001**	**SOH: C1 > C0**	**0.0026**
	TIME	2	**13.6**	**<0.0001**	**Y10, Y15 > Y5**	**0.0010, < 0.0001**	0.43	0.6506		
	OMR*CPT	4	2.41	0.0604			**2.96**	**0.028**		
	OMR*TIME	4	2	0.0604			0.37	0.8259		
	CPT*TIME	4	**2.33**	**0.0674**			0.82	0.5174		
	OMR*CPT*TIME	8	0.49	0.8584			0.32	0.9552		
HM (sandy)	OMR	2	0.28	0.7542			**4.5**	**0.0157**	**CO: WTH > FFR**	**0.0194**
	CPT	2	0.76	0.4739			**6.44**	**0.0031**	**WTH: C0 > C2**	**0.0204**
	TIME	2	1.6	0.2116			0.43	0.6512		
	OMR*CPT	4	2.49	0.0545			**3.28**	**0.0177**		
	OMR*TIME	4	0.26	0.9012			0.14	0.9645		
	CPT*TIME	4	0.37	0.8311			0.31	0.8702		
	OMR*CPT*TIME	8	0.33	0.9527			0.17	0.9939		
OT (clay)	OMR	2	**6.39**	**0.0034**	**SOH, WTH > FFR**	**0.0121, 0.0096**	**4.51**	**0.0159**	**SOH > FFR**	**0.0118**
	CPT	2	0.86	0.4278			**6.97**	**0.0021**	**C0 > C1,C2**	**0.0009, 0.0009**
	TIME	2	**28**	**<0.0001**	**Y10, Y15 > Y5**	**<0.0001**	0.79	0.4573		
	OMR*CPT	4	2.03	0.1045			2.01	0.1073		
	OMR*TIME	4	0.76	0.5595			0.46	0.7646		
	CPT*TIME	4	0.29	0.883			0.21	0.9316		
	OMR*CPT*TIME	8	1.22	0.3063			0.54	0.8207		

Table 2.4, continued

Site	Source	Species diversity (H')				
		df	F	p-value	pairwise comparisons	p-value (adjusted)
CH (silty loam)	OMR	2	2.2	0.1204		
	CPT	2	**10.05**	**0.0002**	**SOH: C1 > C0**	**0.0041**
	TIME	2	0.04	0.9654		
	OMR*CPT	4	**3**	**0.0263**		
	OMR*TIME	4	0.41	0.801		
	CPT*TIME	4	0.29	0.8852		
	OMR*CPT*TIME	8	0.36	0.9349		
HM (sandy)	OMR	2	**3.52**	**0.0367**		
	CPT	2	**6.47**	**0.0031**		
	TIME	2	0.13	0.8814		
	OMR*CPT	4	**2.96**	**0.0281**		
	OMR*TIME	4	0.09	0.986		
	CPT*TIME	4	0.16	0.9577		
	OMR*CPT*TIME	8	0.16	0.9954		
OT (clay)	OMR	2	**7.07**	**0.002**	**WTH: C0 > C1**	**0.0057**
	CPT	2	**5.07**	**0.0099**	**C0: SOH, WTH > FFR**	**0.0027, 0.0009**
	TIME	2	0.18	0.8354		
	OMR*CPT	4	2.37	0.0653		
	OMR*TIME	4	0.76	0.5562		
	CPT*TIME	4	0.25	0.9109		
	OMR*CPT*TIME	8	0.53	0.8283		

Table 2.5 Repeated Measures ANOVA results showing how different functional diversity indices responded to treatment. Abbreviations are as follows: FEve, functional evenness; FDiv, functional divergence; FDis, functional dispersion; Rao's Q, functional entropy.

Site	Source	ΔFEve			ΔFDiv		ΔFDis		ΔFRic	
		df	F	p-value	F	p-value	F	p-value	F	p-value
CH (silty loam)	OMR	2	0.25	0.7811	**9.38**	**0.0003**	2.16	0.1249	**8.3**	**0.0007**
	CPT	2	1.2	0.3094	**2.27**	**0.1133**	**12.25**	**<0.0001**	0.05	0.9541
	TIME	2	**3.92**	**0.0259**	**32.53**	**<0.0001**	0.07	0.9347	**11.12**	**<0.0001**
	OMR*CPT	4	1.44	0.2334	0.52	0.7204	**3.33**	**0.0165**	0.97	0.4335
	OMR*TIME	4	0.44	0.7774	0.24	0.9169	1.07	0.3829	2.38	0.0629
	CPT*TIME	4	0.61	0.6553	**5.55**	**0.0008**	0.75	0.5655	1.21	0.3177
	OMR*CPT*TIME	8	0.42	0.9011	0.33	0.8255	0.22	0.9862	0.33	0.9501
HM (sandy)	OMR	2	**3.3**	**0.0446**	0.08	0.9199	2.23	0.1175	**3.66**	**0.0323**
	CPT	2	0.11	0.8965	0.76	0.4729	0.79	0.4579	**8.01**	**0.0009**
	TIME	2	0.23	0.7938	**10.19**	**0.0002**	0.07	0.93	**6.82**	**0.0023**
	OMR*CPT	4	1.99	0.1094	1.6	0.1885	1.07	0.382	0.91	0.4674
	OMR*TIME	4	0.45	0.7688	0.55	0.7016	0.03	0.9985	0.14	0.9682
	CPT*TIME	4	0.38	0.8241	0.68	0.6084	0.38	0.8215	0.51	0.7251
	OMR*CPT*TIME	8	0.52	0.8347	0.27	0.972	0.13	0.9979	0.16	0.9955
OT (clay)	OMR	2	**10.3**	**0.0002**	**3.78**	**0.0295**	**3.29**	**0.0454**	1.69	0.1944
	CPT	2	0.76	0.4738	1.62	0.209	**6.43**	**0.0033**	0.96	0.3887
	TIME	2	0.09	0.9109	**4.8**	**0.0124**	0.09	0.9171	2.35	0.1054
	OMR*CPT	4	0.99	0.4226	2.24	0.0775	**2.58**	**0.0488**	**2.62**	**0.0461**
	OMR*TIME	4	1.38	0.2535	0.47	0.7567	0.49	0.7394	0.51	0.7264
	CPT*TIME	4	0.12	0.9766	1.83	0.1384	0.23	0.922	0.19	0.9413
	OMR*CPT*TIME	8	0.86	0.5547	**2.36**	**0.0307**	0.4	0.9179	0.69	0.6976

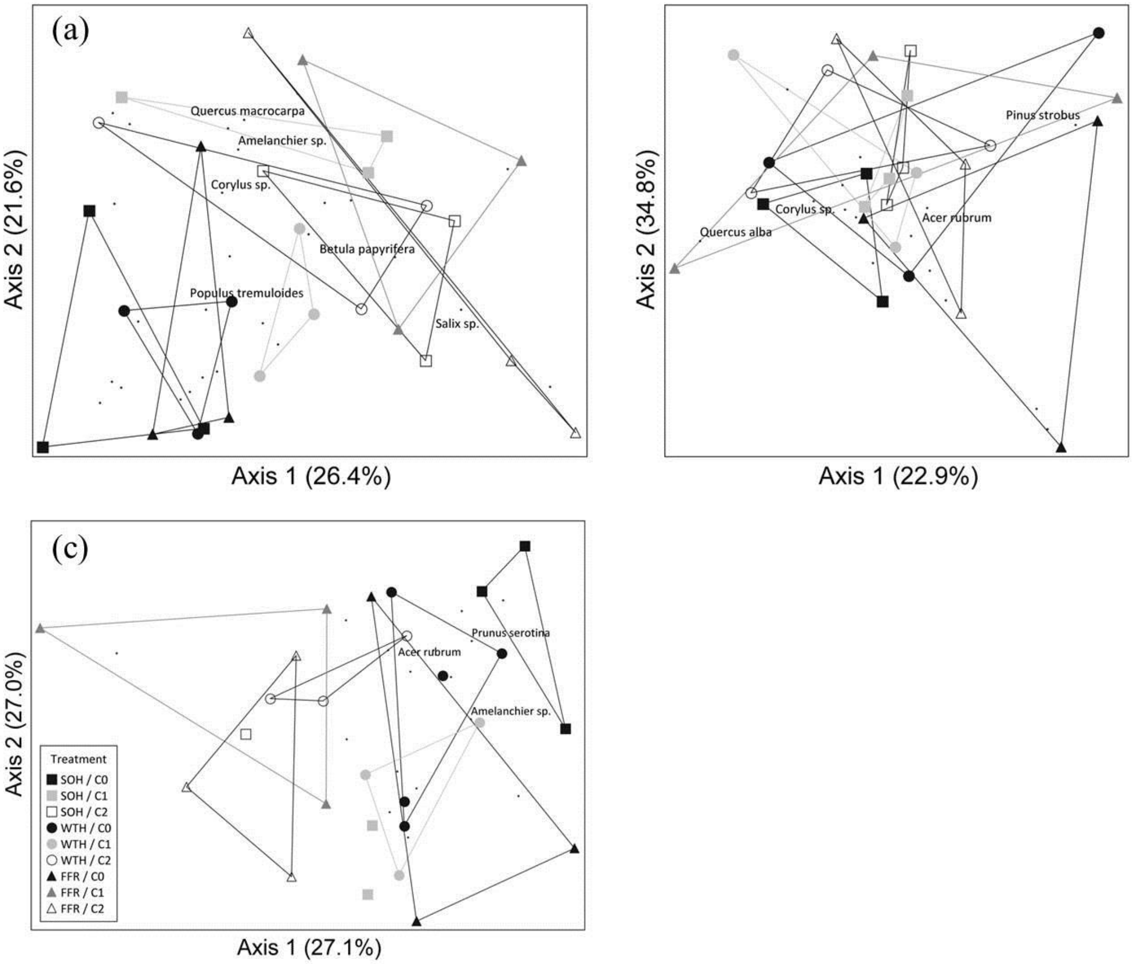

Figure 2.1 Non-metric multidimensional scaling (NMS) ordination of treated plots in woody species space. Each site is presented separately with the Chippewa National Forest in panel (a), the Huron National Forest in panel (b), and the Ottawa National Forest in panel (c). The legend in panel (c) applies to all. Treatment abbreviations are as follows: SOH, stem only harvest; WTH, whole tree harvest; FFR, forest floor removal; C0, no additional compaction; C1, moderate compaction; C2, heavy compaction. Species pictured are significantly correlated ($p<0.05$) with one of the two axes shown. All species correlations are listed in Table 2.3.

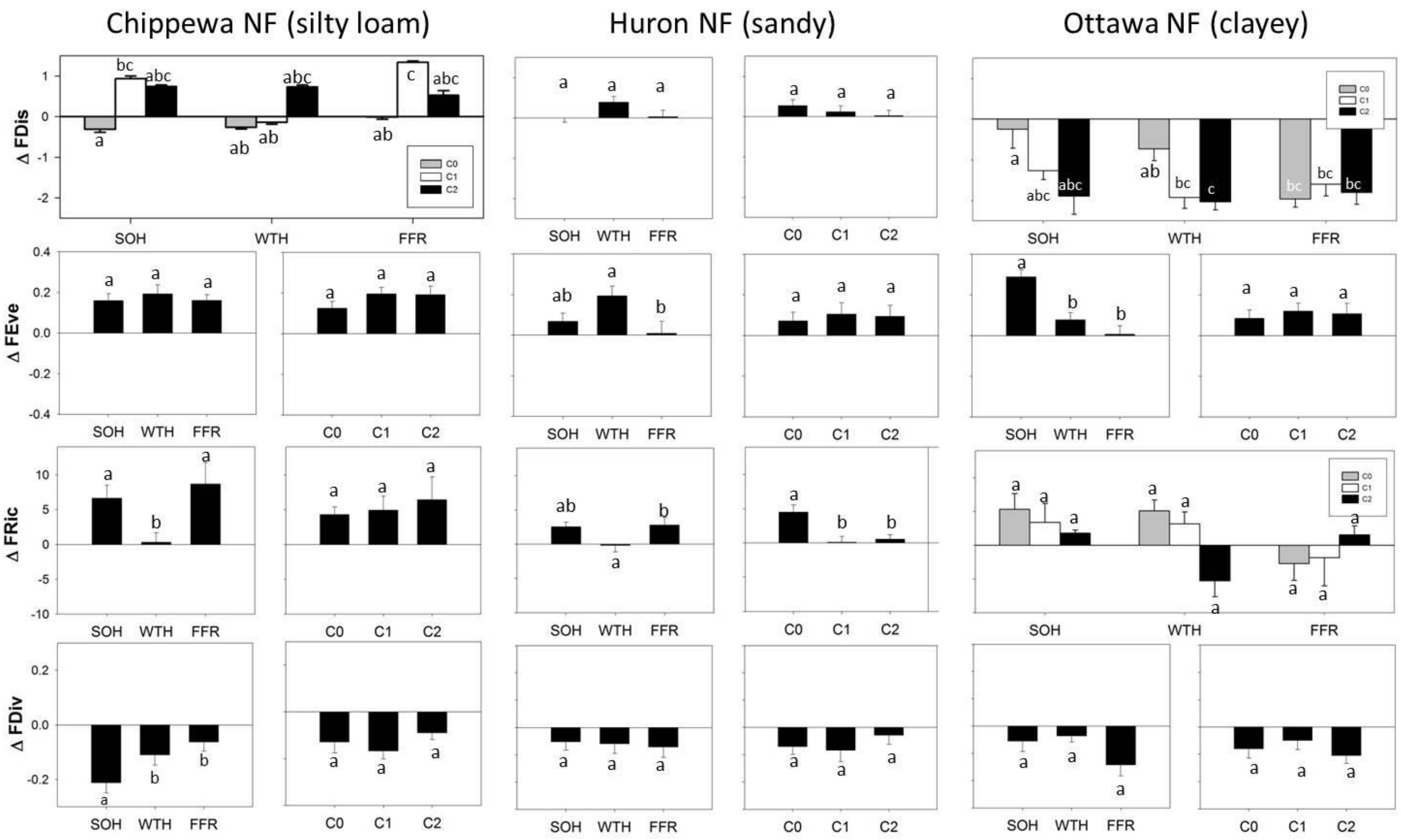

Figure 2.2 Change in functional diversity from pre-harvest to 15 years post-harvest by treatment. Lower-case letters indicate significant differences ($p<0.05$) where they occur. Four panels show means for each of the nine factorial combinations because of a significant OMR*CPT interaction. Otherwise, mean change is presented by factor. Panels are organized by site (indicated across the top) and by functional diversity index (indicated along the left). Abbreviations for the indices are as follows: FDiv, functional divergence; FRic, functional richness; FEve, functional evenness; and FDis, functional dispersion.

	BD (10 cm)	BM harvest (Mg/ha)	pre-harvest CWD retained (m3/ha)
Rooting depth			
Shade tolerance		(+) HM	
Drought tolerance	(-) OT		
Flood tolerance			
Seed mass			
Height			
Leaf longevity			
SG		(+) HM*	
LMA			
N mass			
P mass			(-) OT

Figure 2.3 Results of the fourth-corner tests. Light grey cells indicate negative correlations and dark grey cells indicate positive correlations between functional traits and treatment conditions. White cells indicate an absence of significant association. Sites are abbreviated as follows: CH, Chippewa NF (silty loam soils); HM, Huron-Manistee NF (sandy soils); OT, Ottawa NF (clayey soils). Traits with significant relationships ($p \leq 0.05$, without adjustment for multiple testing) are shown. * indicates significance with $p < 0.1$ after adjustment for multiple testing with the Benjamini and Hochberg method (Benjamini and Hochberg 1995, Dray et al. 2014).

CHAPTER 3

Early understory response to aggregated overstory retention and removal of harvest residues in aspen-dominated forests

Introduction

In recent decades, a paradigm shift in forest management has led to greater emphasis on practices that increase structural and compositional complexity both to maintain ecosystem services under current conditions as well as to best ensure ecosystem resilience given uncertainty about future disturbance regimes and climate (Franklin et al. 1997, Fischer et al. 2006, Lindenmayer et al. 2012). Retention of reserve trees following harvest is one method for maintaining structural complexity in managed forests. Aggregated reserve trees, in particular, have been promoted because of value they provide in terms of ’lifeboating‘ interior forest species in areas being managed using clearcutting-based regeneration methods (Franklin et al. 1997). As such, much research has focused on the effectiveness of aggregates on maintaining pre-harvest understory species richness and community composition with particular focus on interior edge effects (e.g. Nelson and Halpern 2005, Aubrey et al. 2009). Aggregated reserve trees have also been recognized for their influences on surrounding disturbed areas by altering the microclimate, providing habitat for both flora and fauna, supplying seed, and enriching fine and coarse woody debris pools, key components for maintaining forest structural complexity and species diversity (Bradshaw 1992, Franklin et al. 1997, Baker et al. 2013).

The retention of woody debris following harvests is also recognized as an important component of prescriptions aimed at achieving complexity-based objectives (Harmon 2001). Utilization of harvest residues as bioenergy feedstocks may reduce the levels of post-harvest woody debris on site creating a greater need to better understand the influence of these legacies on regeneration, biodiversity, and other forest ecosystem processes. Many regions of the globe are developing and implementing guidelines aimed specifically at 'biomass harvests' in response to higher demand for bioenergy feedstocks (Stupak et al. 2007, Evans et al. 2010). These guidelines have in common recommendations for some overstory retention as well as some retention of harvest residues (e.g. MFRC 2007, Herrick et al. 2007, PA DCNR 2008, MI DNRE 2010), and they have been developed based on the best scientific data available, but in many cases those data have been limited (Janowiak et al. 2010, Berger et al. 2013).

Concerns that removing harvest residues for use as bioenergy feedstocks may negatively impact future productivity and native biodiversity have prompted renewed interest in research examining whole-tree harvesting and residue removal impacts on forests. Studies in Europe (e.g., Helmisaari et al. 2011, Bouget et al. 2012, Mason et al. 2012), Canada (Haeussler and Kabzems 2005, Morris et al. 2014) and across the United States (Riffel et al. 2011), including the Southeast (Huntington et al. 2000), the Northeast (Mika and Keeton 2012, Littlefield and Keeton 2012, Roxby and Howard 2013), the West (Page-Dumrose et al. 2010), and the Lake States (Peckham and Gower 2011, Klockow et al. 2012, Curzon et al. 2014) have reported varying results depending on harvest disturbance severity, forest type, and site quality. Research exploring impacts of whole-tree harvesting on species diversity have demonstrated reductions in abundance and diversity of birds and invertebrates (Riffel et al. 2011) as well as saproxylic species (Bouget et al. 2012) and bryophytes (Dynesius et al. 2008), but surprisingly little is known about potential impacts to vascular plant species composition and diversity (but see Haeussler and Kabzems 2005).

In ecosystems dominated by trees relying primarily on vegetative reproduction where nutrients are not limiting, the removal of residues may provide at least initial benefit to tree regeneration by improving microsite conditions for root sucker growth (Bella 1986, Fraser et al. 2002, Curzon et al. 2014). On the other hand, many studies indicate negative effects on nutrient availability and tree growth (Walmsley et al. 2009, Helmisaari et al. 2011, Wall 2012), and any initial reductions in stocking or growth caused by post-harvest declines in nutrient availability may persist even if site productivity recovers over time (Egnell 2011).

Similarly, if removal of residues causes short-term impacts on understory species composition, diversity, and abundance it may have long-term effects on function as this community can influence forest stand development and succession (Lorimer et al. 1994, Landhauser and Lieffers 1998, Royo and Carson 2006). Existing studies provide valuable information about responses to whole-tree harvesting, a practice closely related to procuring bioenergy feedstocks from forests, but they generally were not designed to examine the continuum along which residues are likely to influence ecosystem processes. Moreover, there has been little focus on the potential impacts of these practices on understory plant community structure and function (Lamers et al. 2013, Riffel et al. 2011), despite the potential for alteration of this critical ecosystem component under increasing harvest severities

While the ecological benefits of reserve trees have been demonstrated for multiple systems (Aubrey et al. 2009, Gustafson et al. 2012, Baker et al. 2013, Fedrowitz et al. 2014, Palik et al. 2014), important tradeoffs may exist in the growth of developing regeneration due to the influence of retained trees on understory resource availability

(Bradshaw 1992, Mitchell et al. 2007, Urgenson et al. 2013, Bose et al. 2014). This may be particularly important in in coppice-systems such as those dominated by aspen (*Populus tremuloides* Michx.; Brais et al. 2004, Gradowski et al. 2010) where auxin inhibition by reserved mature trees may limit regeneration density. For example, dispersed retention of reserve trees has been shown to reduce aspen sucker densities, particularly when the retained overstory trees are themselves aspen, presumably because of hormone inhibition of sprouting (Frey et al. 2003, Gradowski et al. 2010). Additionally, many studies assessing the effectiveness of reserves at providing habitat and lifeboat services compare composition and diversity between those reserves and old-growth forests, but there is value in learning more about how community composition, structure and diversity in reserves compare to managed, but intact and mature forest.

We investigated whether aggregated overstory retention currently recommended for harvest in aspen-dominated forests effectively provides refugia for interior forest species. Additionally, we determined how those aggregates influenced species composition and abundance of regeneration in the surrounding harvested areas (c.f. Bradshaw 1992) in combination with different levels of harvest residue (slash) removal associated with the procurement of feedstocks for bioenergy production. We hypothesized the understory community composition of aggregates would be intermediate between intact forest and clearcuts, and that those intermediate conditions would result in the highest species richness and diversity. We also expected greater graminoid cover in harvested areas relative to aggregates and controls, particularly where slash was removed and woody debris levels were lower. In terms of seedling densities, we hypothesized that more shade-tolerant tree species would dominate regeneration in the aggregate understory compared to dominance by shade-intolerant, early successional species outside of the aggregates. Additionally, we expected the aggregates to exert an effect on regeneration at the edge of the harvested areas through shading, seed provision and, potentially, through regulation of auxin levels from retained aspen stems and suppression of suckering response (Frey et al. 2003). Lastly, based on other studies of aspen sucker response, we expected lower abundance of aspen regeneration in association with greater retention of woody debris (Bella 1986, Fraser et al. 2002, Curzon et al. 2014).

Methods

Study sites

Sampling occurred at the following four sites in northern Minnesota, USA: Independence (IN; 47.01 N, 92.59 W), Melrude (MR; 47.25 N, 92.32 W), Pelican Lake (PL; 48.01 N, 92.98 W), and Lost River (LR; 48.14 N, 92.97 W). Aspen dominated at all locations, having regenerated following clearcut harvests in the 1940s and 1950s. Other important species prior to harvest included black ash (*Fraxinus nigra* Marshall), red maple (*Acer rubrum* L.), balsam fir (*Abies balsamea* L.) and paper birch (*Betula papyrifera* Marshall) with minor components of white pine (*Pinus strobus* L.), white spruce (*Picea glauca* Moench.), sugar maple (*Acer saccharum* Marshall), and American basswood (*Tilia americana* L.). Each site included over 40 ha such that treatments could be implemented at an operational scale on 10 stands, each 4 ha in size. The four sites ranged in elevation between 395 to 428 m asl with slopes less than 8%. At IN soils were predominantly Inceptisols. Otherwise, soils belonged to the Alfisol order, all ranging in texture from silty loam to stony loam. Mean annual precipitation is approximately 66 cm. Harvest occurred in winter, 2010 (Klockow et al. 2013).

Experimental design

This study is part of a larger experiment designed to assess the ecological impacts of removing harvest residues for use as bioenergy feedstocks and of retaining overstory reserve trees (see Klockow et al. 2013 for more detail on study design). Within that larger experiment, we focused on the effects of aggregated overstory reserves and slash retention. In particular, the following subset of treatments was examined in the current study: 1) the interior of aggregated overstory reserves ("aggregates"), 2) stem only harvest (SOH), 3) whole tree harvest (WTH), and 4) intact forest (controls). Treatments with aggregated overstory reserves followed recommendations made by the Minnesota Forest Resources Council with 5% of canopy trees retained in aggregates (determined by area). This was accomplished by reserving overstory aggregates approximately 0.1 ha in size (18 m radius). Stem only harvests involved the removal of only the merchantable bole portion of harvested trees with all other materials retained on site, whereas whole tree harvests removed entire harvested trees from the stand. Given the operational nature of this study, actual woody debris levels varied following treatment due to breakage, so they were measured continuously across the SOH and WTH treatments.

Field sampling

Transects, oriented north-south, were centered on one randomly selected overstory retention aggregate for each of the above-mentioned slash retention treatments at each site. Identical transects were also placed in the center of intact forest control stands. Each transect was 84 meters in length such that plots located at each transect end were located approximately one tree height away from the aggregate edge. Rectangular understory plots (1 x 3 m) were placed 2 m, 7 m, 22 m, and 42 m from each aggregate center along the north-south transect such that a range of conditions relative to the aggregate interior and edge were represented. The distance from center of the 2 m plots was determined randomly and intended to capture interior aggregate conditions. Subsequent plots were placed to represent interior edge conditions (7 m from center), exterior edge conditions (22 m from center), and open conditions (42 m from center). Within each plot percent cover was estimated for all vascular species less than 1 m tall during June and July, 2012. Additionally, all woody stems < 2.5 cm diameter at breast height (1.37 m) were counted so that regeneration densities could be estimated. Each rectangular plot was bisected by a woody debris transect. Where coarse woody debris (CWD) intersected the transect, diameter at the point of intersection was recorded if ≥ 7.5 cm. CWD was also identified to species when possible, and decay was estimated using a five-class system (Sollins 1982). In a similar fashion, fine woody debris (FWD, 7.5 cm > diameter > 0.5 cm) was tallied and measured in three randomly selected 0.4 m subsections of the woody debris transect. Each piece was classified as either decayed or not decayed.

Soil moisture was measured at the corner of each plot closest to aggregate center using a TDR probe (ML2x ThetaProbe Soil Moisture Sensor; Dynamax, Houston, TX) . Three moisture readings were collected and averaged for each point. All soil moisture measurements were collected on one of two consecutive days in mid-August, 2012 so only late season moisture is represented. Leaf area index (LAI) was estimated with FV2200 (Li-COR Biosciences, Inc. 2010) using light readings collected with a Licor

LAI-2000 Plant Canopy Analyzer (LiCor, Inc., Lincoln Nebraska), also at the point where each plot intersected the transect. If understory shrubs obscured readings taken at 1.0 m above the ground, an additional reading was taken at a higher level to better capture overstory conditions and prevent overestimation of LAI. The latter readings were used for analysis. In 2012, sampling occurred at dusk, at dawn, or under cloudy skies to ensure continuous, diffuse sky conditions. Because the canopy within and near aggregates is not continuous, no view restrictor was used. In 2013, additional readings were necessary for some plots due to technical issues the previous year. These readings were either collected at dawn without a view restrictor as described above, or two readings were collected for each plot on a clear day in the morning and in the afternoon with the unit facing east or west, respectively, and using a 180° view restrictor to block the sun (Comeau et al. 2006). Calculation of LAI required "above-canopy" readings of light interceptance sampled at the same time as understory readings. These were collected every 15 s using a second unit stationed in a nearby clearing. Sampling occurred in late July and early August when foliage was at its peak.

Analysis

The structure of community composition among plots was determined using non-metric multi-dimensional scaling (NMS; Kruskal 1964, Mather 1976, McCune and Grace 2002). Abundance, based on percent cover estimates, was relativized across plots such that analysis revealed which conditions most affected individual species (McCune and Grace 2002). Species occurring in fewer than five plots (5%) across the study were removed to reduce noise (McCune and Grace 2002). These species were not excluded from estimates of species evenness, richness, and diversity (H'). Dissimilarity matrices used for NMS were calculated using Sørensen distances.

Differences in community composition among treatments were analyzed using multi-response permutation procedures (MRPP, McCune and Grace 2002). Where MRPP indicated significant differences among groups ($p < 0.05$), Indicator Species Analysis was used to identify species strongly associated with treatments based on the frequency of their occurrence, abundance, and exclusiveness to particular treatments (Dufendre and Legendre 1997). Designation as an indicator species required an indicator value > 25 ($p < 0.05$). NMS, MRPP, and indicator species analysis were all conducted using PC-Ord 6.0 (McCune and Mefford 2011).

Analysis of Variance (ANOVA) was used to determine the influence of treatments on understory species richness, species diversity, species evenness and seedling densities using the SAS MIXED procedure (SAS Institute, Inc. 2012). Site and stand were included as random effects while treatment (control, aggregate, WTH, SOH) was a fixed effect. Tukey-adjusted post-hoc pairwise comparisons were used to compare means between individual treatments. Some response variables required a log- or power-transformation to meet ANOVA assumptions for homoscedasticity. Abundance of non-native species was highly skewed, so a non-parametric rank-transformation was used prior to ANOVA for assessment of treatment effects on this species group (Sokal and Rohlf 1995, Fawcett and Salter 1984). Differences in abiotic and response variables were assessed between transects oriented north and south of the aggregates using t-tests or Wilcoxon rank-sum tests where normality assumptions could not be met. Because no differences were observed, all transects were treated equally and grouped in analysis.

Environmental characteristics related to treatments varied continuously across this operational study (Klockow et al. 2013, Fig. 3.1), so we also assessed the relationship between response variables and a suite of treatment effects (soil moisture, LAI, CWD, and FWD) using Pearson's R correlation coefficient.

Results

As expected, aggregated reserves generally exhibited understory characteristics intermediate between those observed in intact forest controls and harvested areas. Seedling densities and plant cover responded most strongly to overstory treatment, species diversity measures generally indicated disturbed versus undisturbed (control) conditions, and community composition responded to both overstory treatment and harvest residue removal.

Relationships between treatments and environmental variables

The variables measured to quantify disturbance effects from treatments (soil moisture, LAI, CWD, and FWD) varied widely across the study (Fig. 3.1). Soil moisture was greatest and LAI least in harvested areas, with aggregates containing conditions between those plots and controls. Neither CWD nor FWD volume differed between SOH and WTH (Fig. 3.1). In fact, CWD levels were statistically indistinguishable among all four treatment conditions.

Understory community composition

Ordination of relative species abundance demonstrated that both overstory reserves and slash retention influenced the composition of the understory plant community. As expected, the composition of aggregated reserves was intermediate in ordination space between control and harvested plots (Fig. 3.2). The SOH treatment showed the greatest compositional dissimilarity from intact forest controls (Fig. 3.2). Axis 1 (20.8% of variance explained) ranged from clearcut treatments in the negative portion to intact forest controls in the positive portion. Soil moisture, LAI, and FWD were significantly correlated with Axis 1 with LAI positively correlated (greater for control stands) and soil moisture and FWD negatively correlated (generally greater for harvested stands) with this axis. Species positively correlated with Axis 1 included interior species such as *Clintonia borealis, Dryopteris carthusiana, Lycopodium clavatum, L. dendroideum, Maianthemum canadense* and *Streptopus roseus* whereas aspen, *Rubus pubescens, R. idaeaus.*, and many graminoids had significant negative correlations (Table 3.1). While Axis 2 and Axis 3 do not explain compositional differences attributable to harvest (Fig. 3.2), soil moisture had a significant, negative correlation with both suggesting that moisture gradients may contribute to the variability observed within treatments along these axes.

MRPP significantly distinguished the four treatment groups (aggregate, SOH, WTH, and control; $p < 0.05$), but the test statistics provided only weak evidence of differences and suggested wide variability within each treatment group. The comparison of communities within aggregates and control plots yielded an agreement statistic (A) of 0.016, and the heterogeneity within the two slash retention treatments was only just less than expected by chance (A=0.007, p=0.0355). The greatest distinction was between control plots and SOH (A=0.0297). Differences among sites and the large number of plots (96) may have contributed to the relatively high stress in the NMS ordination (20.9%) and variability within groups (McCune and Grace 2002). Given this relatively high stress value, we treated this analysis as exploratory and used it primarily to inform interpretation of other results.

Indicator species analysis identified three sedge species, *Carex deweyanna, C. intumescens*, and *C. leptonerva*, and one grass species (*Poa pratensis*) as well as *Petasides frigidus* and *Rubus pubescens* as indicative of WTH (Table 3.1). In contrast, aspen, *B. papyrifera*, *Asarum canadense*, and a suite of other forbs showed preference for SOH (Table 3.1). The aggregates appeared to provide refugia habitat for balsam fir, the most shade-tolerant tree species forming a significant component of these communities. Additionally, *Cornus cornuta* and *Aster cilolatus* were indicative of the aggregates (Table 3.1). *Trientalis borealis* was not identified as a significant indicator species, but it did occur most prevalently in aggregates relative to other treatments. Both *Lycopodium dendroideum* and *L. clavatum* occurred almost exclusively in control plots and were indicator species for this condition. *Clintonia borealis* also strongly associated with intact forest in the controls (Table 3.1).

As expected, graminoid cover was significantly greater in harvested plots than in either aggregates or controls (Table 3.2). Even though total graminoid cover did not differ between the two slash retention treatments (Table 3.2), indicator species analysis suggested preference of some graminoid species for WTH. Cover of nonnative species was also greater in harvested areas than in aggregates and controls. Mean nonnative cover increased from control plots at the low extreme to WTH although only those two treatments differed significantly from one another due to high variability (Table 3.2). *Poa pratensis*, identified as an indicator for WTH, constituted a large portion of the nonnative cover for this condition.

Species diversity

A total of 118 species was identified across the study. Of those species that occurred in at least two stands, 2 occurred exclusively in control plots (*L. clavatum* and *L. uniflora*), 1 with SOH (*Geranium bicknellii*), and 1 with WTH (*Spirea alba*). We assessed three standard metrics for estimating species diversity: richness, evenness, and the Shannon index (H'). Species richness and H' were both lowest in the control plots which differed significantly from the other three treatments. No differences in richness or H' were observed among aggregates, WTH, and SOH. Species evenness followed a similar trend except that mean values for aggregates were intermediate between (and statistically indistinguishable from) controls and the two harvested treatments (Table 3.2). Species richness had significant positive correlations with FWD volume, soil moisture availability, and aspen density and a negative correlation with LAI (Fig. 3.3).

Seedling densities

As predicted, abundance of balsam fir (the most shade-tolerant tree common on these sites) was greatest in the aggregated reserves (Fig. 3.4). Also as predicted, aspen density (the most shade-intolerant species in the study) was greater in harvested plots than either aggregates or controls (Table 3.2, Fig. 3.4) and negatively correlated with LAI (Fig. 3.3). However, densities of aspen did not differ between harvested edge plots and those plots > 20 m from aggregate edges (Fig. 3.4). Contrary to expectations, the density of *Acer rubrum* and *Fraxinus nigra* stems did not differ with respect to location within or outside of aggregates. Instead, those densities remained relatively constant with distance from aggregate center (Fig. 3.4).

Although indicator species analysis indicated a preference of aspen for the SOH condition and aspen densities correlated positively with FWD volume, post-hoc comparisons did not distinguish means between the two slash treatments. Instead, differences were only detected between harvested (SOH and WTH) and unharvested (controls and aggregates) areas.

Discussion

This study assessed the combined effects of aggregated overstory retention for achievement of ecological objectives and the removal of harvest residues to meet rising demand for bioenergy feedstocks at an operational scale. While larger reserves may be desirable, our results show that small aggregates (0.1 ha) maintain conditions intermediate between harvested areas and intact forest that allow provision of at least short-term refugia for a limited number of interior forest plant species. These aggregated reserves will likely enhance the structural and compositional complexity of the regenerating forest over time. The effects of residue removal are less clear and reflect the wide variability of harvest effects that might be expected at this scale.

Relationships between treatments and environmental variables

Canopy cover varied widely across the study and even within treatments as indicated by LAI, however the trends observed follow what would be expected given levels of overstory retention. Some retained trees in many of the aggregates had already snapped or uprooted during severe storms occurring during the first and second growing season following harvest, contributing to lower LAI even in the interior of those reserves. Also, whereas other studies have reported comparable light environments between interior aggregates and intact forest, the radii of the aggregates studied here (approximately 18 m) are well within the range of edge effects reported elsewhere (Fraver 1994, Heithecker and Halpern 2007). Trends in our instantaneous measures of soil moisture are consistent with those collected continuously over the growing season in another study conducted in these areas with no differences observed in soil moisture between residue removal treatments (Kurth et al. 2014). Our failure to detect any ameliorating effects from retained woody debris that might be expected with SOH (Zabowski et al. 2000, Heithecker and Halpern 2006) is likely due to the comparable levels of woody debris associated with WTH (Fig. 3.1). As this was an operational study, significant breakage did occur during the winter harvest, and woody debris levels likely varied spatially across the stands, potentially leading to less distinction between residue removal treatments (Klockow et al. 2013). Late summer soil moisture varied between harvested areas and controls with aggregates intermediate. This is in contrast to soil moisture trends observed in other studies of aggregated retention where aggregates have not differed from harvested or control areas (Heithecker and Halpern 2007), but is consistent with other observations on these sites (Kurth et al. 2014).

Understory community composition

Our results support other findings that indicate a generally positive relationship between decreased overstory cover and an increase in both species richness and graminoid cover (Astrom et al. 2005, Craig and MacDonald 2009). Graminoids, in general, indicated harvest treatments in this study versus the reserves or intact forest conditions. While total cover did not differ between slash treatments, *Carex sp., P. pratensis,* and other graminoid species were indicators for WTH, the most severe treatment. Also, *S. alba* occurred exclusively in plots treated with WTH. While not a competitive species, *S. alba* commonly occurs in grass- and sedge- dominated communities and is considered opportunistic when disturbance disrupting dominance by other woody species occurs (Smith 2008). These shifts in understory community structure in response to residue removals may have important consequences in relation to regeneration densities on these sites given the documented impacts of graminoid competition on regeneration and growth of tree species such as aspen in these systems (Lieffers and Statdt 1994, Landhausser and Lieffers 1998). Similarly, *Pteridium aquilinum*, another species capable of inhibiting seedling growth both through direct competition for resources and allelopathy (Haeussler et al. 1990), also indicated WTH. The success of these and other competitive species in WTH sites may explain why aspen associated most strongly with SOH, contrary to expectations and observations in other studies (i.e. Bella 1986, Haeussler and Kabzems 2005, Curzon et al. 2014).

Research on the ecological impacts of green tree retention in various levels and spatial configurations has concluded that retention levels should equal or exceed 15% in order to effectively lifeboat species and enable recolonization of surrounding disturbed areas (Aubrey et al. 2009). Our study used Minnesota Forest Resources Council (MFRC 2007) guidelines as a basis for retention levels in order to test their effectiveness at achieving biodiversity and structural complexity objectives. While differences certainly exist between intact forest and aggregates in this study and the majority of habitat within the aggregates is likely edge (Fraver 1994, Heithecker and Halpern 2007), they did confer some benefit in terms of providing refugia for a limited number of understory species. At least in the short-term (two growing seasons after harvest) 5% retention in the form of aggregates (0.1 ha) provided habitat for some species typically identified as interior forest obligates (e.g. *T. borealis*, Lieffers 1995). Aggregates may have also contributed to greater *A. balsamea* regeneration near the edge compared to open conditions (42 m from aggregate center). This is in contrast to findings related to much smaller aggregated reserves with an average radius of only 5 m (0.007 ha) which exhibited little difference in diversity or composition when compared to surrounding clearcuts (Lachance et al. 2013). Long-term monitoring of the aggregates examined in this study will be critical to determine if benefits to certain interior species are transient or if in fact smaller aggregates can sustain these populations over the long term.

Species diversity

Aspen-dominated ecosystems are the most floristically rich upland forests in this region, with greater richness occurring in younger stands (Reich et al. 2001). As expected, disturbance related to harvest operations increased all measures of species diversity over that observed in the intact forest controls. This is due in part to an increase in the number of graminoid and ruderal, nonnative species (Table 3.2). However, while community composition differed between aggregates and the two harvest treatments (WTH, SOH), species richness, H’, and species evenness did not. Instead, the number and abundance of interior forest species that occurred in aggregates appears to have been balanced by the increase in graminoid and ruderal species associated with WTH and SOH.

Regeneration

Although other research in the region and elsewhere within the range of aspen has demonstrated potential for reduced sucker growth in association with more abundant woody debris (Bella 1986, Curzon et al. 2014), such a trend was not observed here. This may be in part due to the variability in woody debris levels across the study that did not correspond with slash retention treatment as closely as expected (Table 3.1, Klockow et al. 2013). We also suspect that FWD levels may influence the presence and abundance of competitive species, including *P. pratensis* and *P.aquilinum*, and thus provide a potential release effect for aspen regeneration in SOH-treated stands.

Concerns have been expressed about the potential for overstory retention to diminish productivity in surrounding regenerating stands (Gradowski et al. 2010, Bose et al. 2014, Palik et al. 2014), despite the other potential ecological benefits discussed here and elsewhere (Gustafson et al. 2012, Palik et al. 2014). Our findings indicate that aggregated retention at least in the short-term does not appear to have reduced aspen sucker densities in the immediately adjacent harvested areas, contrary to expectations. Moreover, the combined density of seedlings and suckers did not differ significantly between aggregates and harvested areas although species composition and associated shade tolerances for plant cover varied as expected. This supports the notion that, while providing some level of interior forest conditions for maintenance of understory forbs, the aggregates primarily provide edge habitat (Palik and Murphy 1990), but will likely enrich the diversity of the overstory over time by maintaining more shade-tolerant, less competitive species.

Conclusions

With this study, we examined the impacts of aggregated overstory retention, a method promoted to maintain diversity and structural complexity, combined with harvest residue removal, a practice expected to increase as demand for forest-derived bioenergy feedstocks rises. Our results suggest that aggregated reserves benefit biodiversity through provision of short-term habitat for a small number of interior forest species while also contributing greater compositional diversity at the stand scale. These ecological objectives were achieved without any apparent trade-off in initial regeneration densities in adjacent harvested areas. While the removal of harvest residues may result in highly variable levels of woody debris, operationally, this practice has potential to influence community composition. Whole tree harvest may indirectly decrease relative aspen cover and the regeneration of other tree species by creating favorable conditions for competing species such as *Carex sp., P. pratensis,* and *P. aquilinum.* Overall, the retention of biological legacies both in the overstory (live trees) and on the forest floor (dead wood) provided ecological benefits without reducing regeneration and should be incorporated into guidelines developed for biomass harvests.

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Table 3.1 Species correlations with NMS axes from Fig.1. Species shown correlate with at least one axis ($p < 0.05$). The “ISA” column indicates species emerged as indicators of specified treatments with an Indicator Value > 25 ($p < 0.05$). Abbreviations: aggregate, aggregated overstory reserves; SOH, stem only harvest; WTH, whole tree harvest.

Species	A1	A2	A3	ISA	Species	A1	A2	A3	ISA
Abies balsamea	-	-	-0.38	aggregate	*Lathyrus ochroleucus*	-	-0.40	-	
Acer spicatum	-	0.37	-		*Lonicera canadensis*	-	-	-0.33	
Actea rubra	-	-	-	SOH	*Lycopodium clavatum*	0.33	-	-	control
Arisaema triphyllum	-	0.29	-		*L. dendroideum*	0.32	-	-	control
Asarum canadensis	-	-	-	SOH	*Lycopus uniflorus*	-	-	-0.34	
Aster macrophyllus	-	-0.43	-		*Maianthemum canadense*	0.26	-	-	
A. ciliolatus	-	-	-	aggregate	*Millium effusum*	-0.30	-	-	
Athyrium filix-femina	-	-	0.26		*Mitella nuda*	-	0.33	-0.36	
Betula papyrifera	-	-		SOH	*Petasides frigidus*	-0.36	-	-	WTH
Brachyelytrum aristosum	-	-	-	SOH	*Poa pratensis*	-	-	-	WTH
Carex deweyana	-0.31	-	-	WTH	*Populus tremuloides*	-0.43	-	-	SOH
C. gracilima	-0.34	0.21	-		*Pteridium aquilinum*	-	-	-	WTH
C. intumescens	-0.51	0.27	-	WTH	*Pyrola elliptica*	-	-0.34	-	
C. leptonerva	-	-	-	WTH	*Rosa sp.*	-	-0.35	-	
Carex sp. (Ovales group)	-0.29	-	-		*Rubus idaeus*	-0.30	-	0.28	
Clintonia borealis	0.37	-	-	control	*R. pubescens*	-0.32	0.27	-	WTH
Corylus cornuta	-0.30	-	-	aggregate	*Sanicula marilandica*	-0.31	-0.29	-	
Diervilla lonicera	-0.47	-	-		*Solidago sp.*	-	-	0.32	
Dryopteris carthusiana	0.37	-	-		*Streptopus roseus*	0.28	-	-	
Equisetum sp.	-0.40	-	-		*Trillium cernuum*	-	-	-	SOH
Fraxinus nigra	-	-	-0.33		*Ulmus sp.*	-	0.36	-	
Fragaria virginiana	-0.40	-	-		Other graminoids	-0.40	-	-	
Geranium bicknellii	-	-	-	SOH	*Viburnum rafinesquianum*	-	-0.43	-	
Hepatica americana	-	-	0.42	SOH	*Viola sp.*	-	0.30	-	

Lactuca canadensis	-0.37	-	-	SOH	*Vicia sp.*	-0.35	-0.31	-	SOH
Impatiens capensis	-0.45	-	-	SOH					

Table 3.2 Vascular plant cover, seedling density, and species diversity metrics by treatment. Values are based on mean cover and frequency of all vascular species sampled in understory plots ($3m^2$) across all four sites with the standard error given in parentheses. The treatments are as follows: “controls”, intact forest; “aggregate”, aggregated overstory reserves; “SOH”, harvested plots with all slash retained; “WTH”, harvested plots with no intentionally slash retained. Lower-case letters indicate significant differences ($p < 0.05$, Tukey-adjusted pairwise comparisons).

Variable	Control (n=32)	Aggregate (n=32)	SOH (n=16)	WTH (n=16)
Total cover (%/m^2)	119.33 (7.65)a	127.65 (6.82)a	198.49 (11.75)b	204.45 (12.2)b
Graminoid cover (%/m^2)	7.16 (1.25)a	9.97 (1.10)a	37.36 (9.80)b	39.55 (8.34)b
Nonnative cover (%)	0.08 (0.05)a	0.25 (0.09)ab	2.64 (1.33)bc	5.87 (3.27)c
Species richness	24.59 (0.80)a	29.06(0.64)b	31.56 (1.16)b	31.19 (1.34)b
Species evenness	0.62 (0.01)a	0.66 (0.01)ab	0.69 (0.01)b	0.70 (0.01)b
Species diversity (H')	1.99 (0.05)a	2.24 (0.04)b	2.37 (0.07)b	2.40 (0.05)b
Seedling density (all)	7.13 (0.75)a	11.82 (1.24)b	11.92 (1.60)b	13.94 (1.70)b
Sucker density (aspen)	0.57 (0.16)a	1.28 (0.31)a	4.79 (0.91)b	4.88 (0.56)b

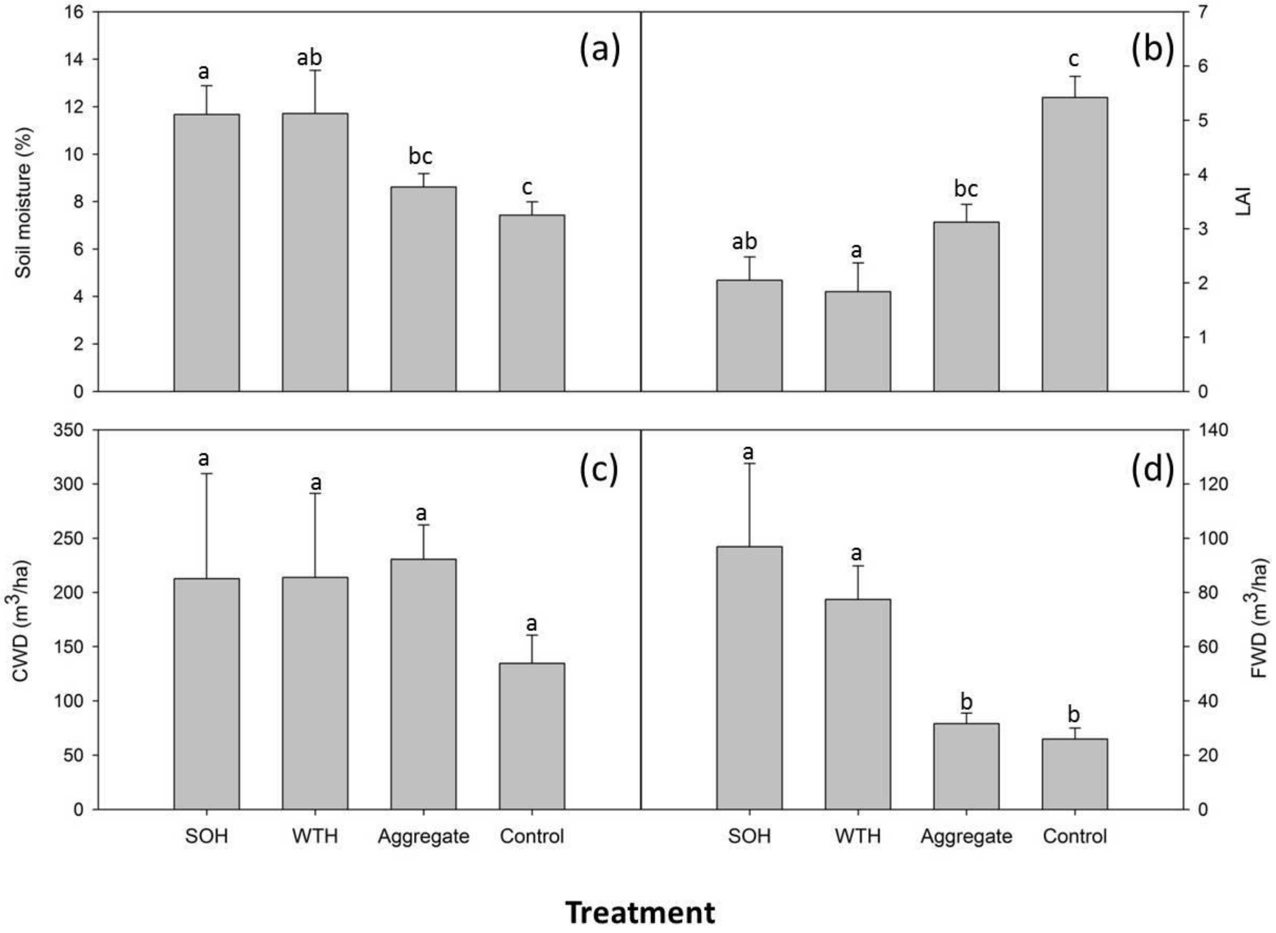

Figure 3.1 Means for coarse woody debris volume (CWD), fine woody debris volume (FWD), leaf area index (LAI) and soil moisture for each treatment across the study. Bars indicate standard error. Lower-case letters indicate significant differences where they occur as determined with post-hoc Tukey-adjusted pairwise comparisons ($p<0.05$).

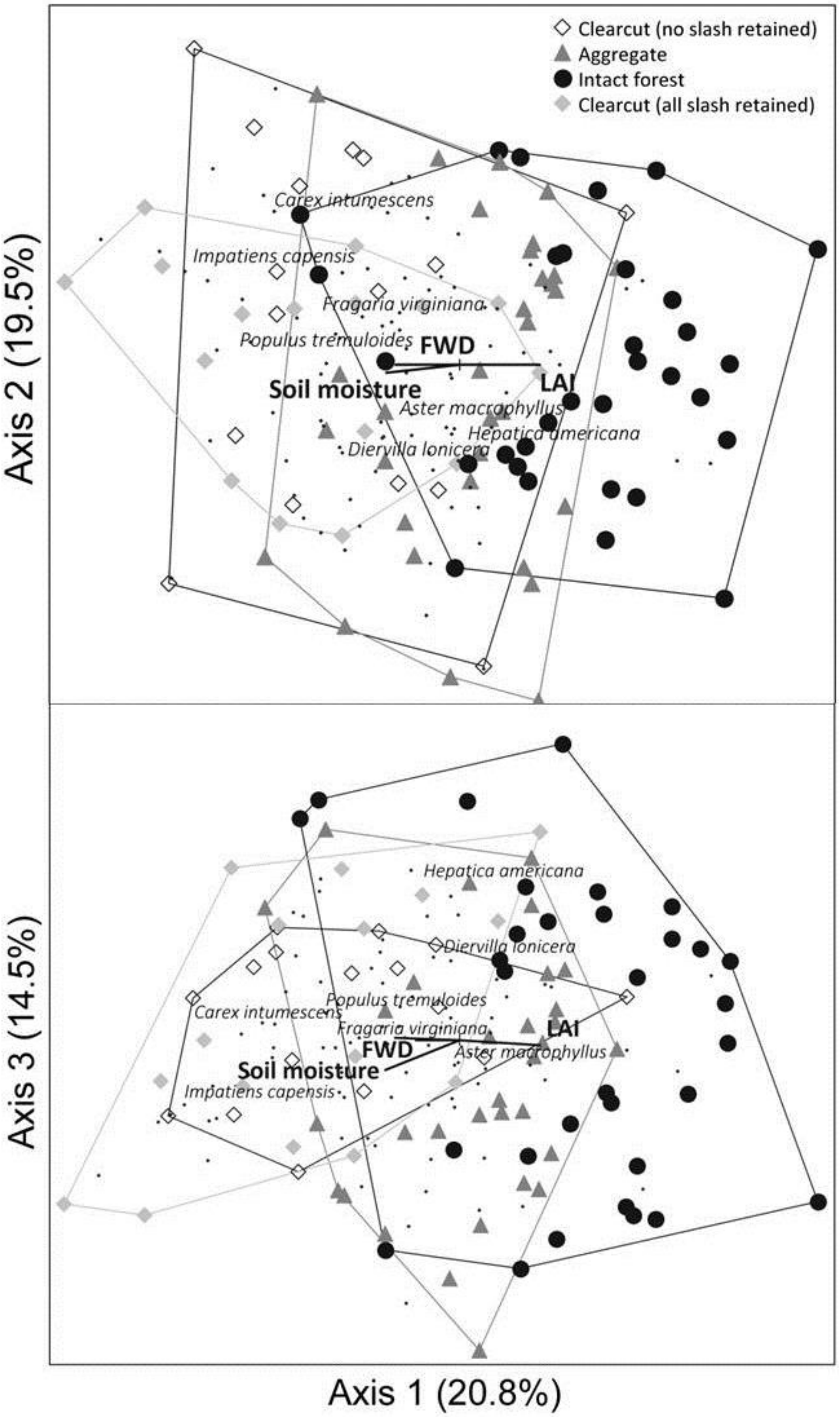

Figure 3.2 Ordination results from non-metric multidimensional scaling (NMS). Axis 1 is rotated to be parallel with leaf area index (LAI), the environmental variable that showed the strongest correlation (Kendall's $\tau = 0.32$) with community composition. Species shown arecorrelated significantly with one of the three axes (Table 3.1, $p < 0.05$.)

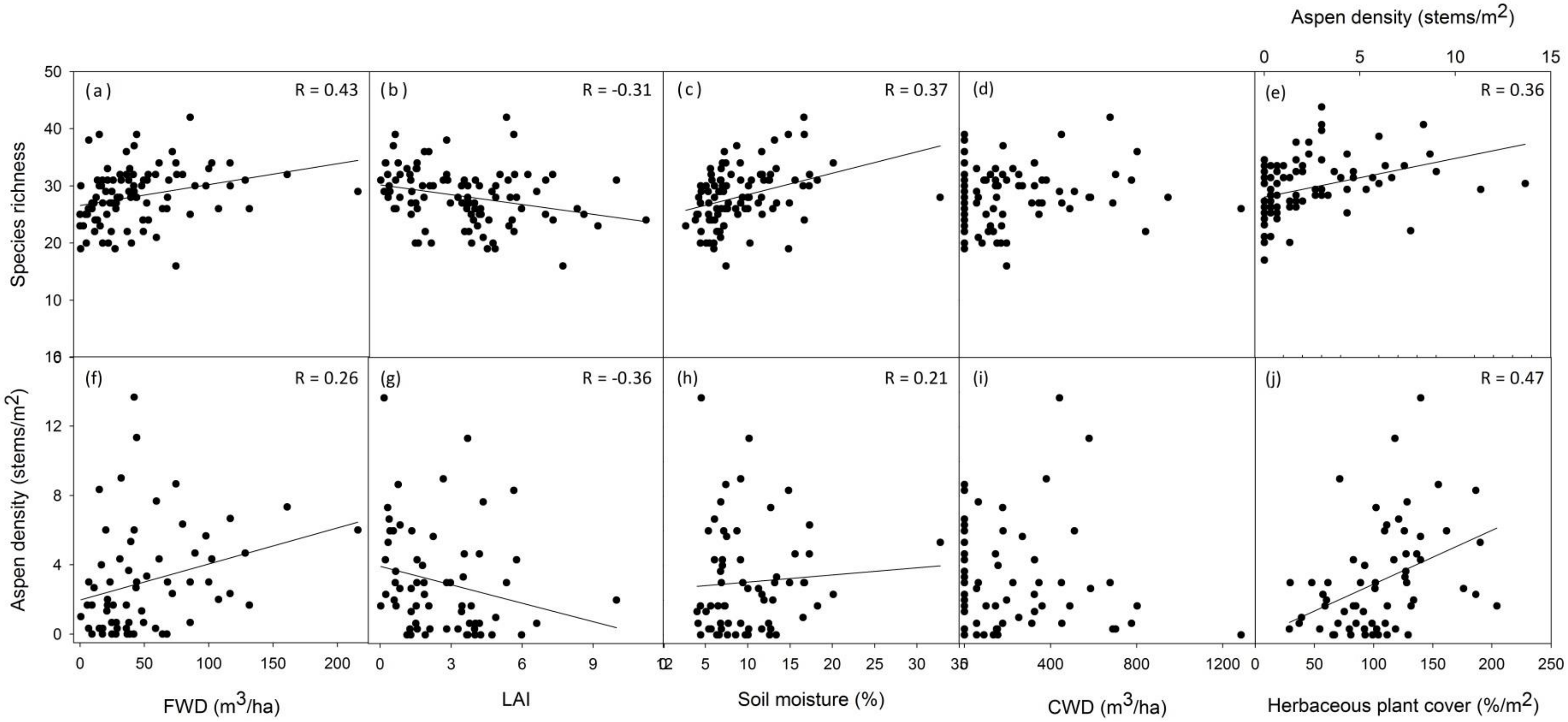

Figure 3.3 Scatterplots illustrating how species richness (a-e) and aspen density (f-j), relate to fine woody debris (FWD), leaf area index (LAI), soil moisture, coarse woody debris (CWD), herbaceous plant cover (aspen density only).The Pearson correlation coefficient, R, and mean functions are displayed where statistically significant ($p < 0.05$).

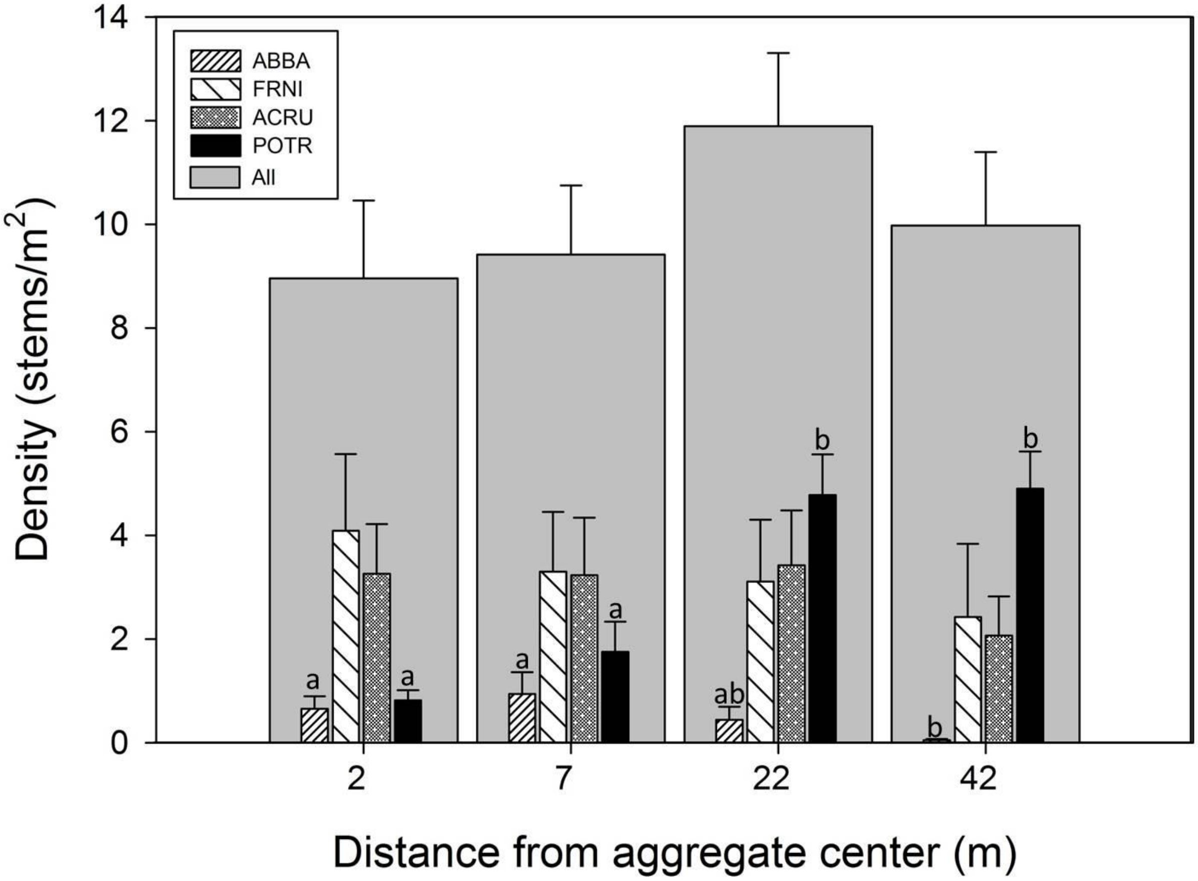

Figure 3.4 Density of seedlings at increasing distances from the center of aggregated overstory reserves ("aggregates"). Aggregates generally have radii of 18 m, so plots at 2 m and 7 m are within the aggregate, plots at 22 m are outside but near the edge, and plots at 42 m are in the open. Only those species making up > 1% of all seedlings are shown. Abbreviations are as follows: ABBA, *Abies balsamea;* FRsp, *Fraxinus nigra* or *F. pensylvanica;* ACRU, *Acer rubrum;* POTR, *Populus tremuloides*. The grey bars in the background represent total seedling densities. Error bars indicate standard error and lower-case letters indicate where significant differences in seedling densities (within the same species) exist between different distances ($p < 0.05$, ANOVA).

CHAPTER 4: CONCLUSIONS

Balancing objectives that include continuing to provide current forest products, meeting future resource demands, and maintaining ecosystem services given uncertainty surrounding future climate and disturbance regimes presents a formidable challenge to forest managers. In light of that challenge, the primary objective of this dissertation was to examine the ecological impacts of removing harvest residues for bioenergy production, an emerging management practice, in order to inform the development and refinement of related guidelines. Recognizing a disconnect between applied forest ecology and research conducted in more theoretical contexts, a secondary goal was to apply and evaluate proposed methods for quantifying and assessing functional diversity. The results presented here can inform future decision-making, regardless of objectives, particularly in forest ecosystems dominated by species that reproduce vegetatively. Additionally, while conclusions about direct impacts of residue removal on function are limited, this research highlights areas where further study is needed to improve quantification and interpretation of functional diversity while also providing a foundation on which further work can be based.

This research affirmed some broad concerns for productivity associated with removal of harvest residues like the importance of limiting soil disturbance (Chapter 1), but many impacts appeared to be specific to site conditions. Both Chapter 1 (15-year results) and Chapter 3 (2-year results) indicate that stem densities may not differ significantly between stem-only harvest (SOH) and whole-tree harvest (WTH) on fine-textured soils, although relativized 2-year aspen cover was greater for SOH. In contrast, density and standing biomass reductions did occur in association with WTH and the additional removal of the forest floor (FFR) on sandy soils. For this latter finding, the mechanism behind biomass reductions cannot be definitively determined, but results indicate that residues should be retained following harvest on similar sites.

Responses of species diversity and functional diversity to harvest-related disturbance severity varied widely (Chapters 2 and 3). The only common finding was no discernible difference in woody species richness over time (Chapter 2) or understory plant species richness shortly after harvest (Chapter 3) between SOH and WTH, regardless of site. The most interesting trends emerged from analyses of community composition. Short-term (2-year) results indicate the composition of regenerating communities diverged between SOH and WTH treatments, if only slightly (Chapter 3). Indicator species analysis suggested that WTH may favor species with potential to compete with aspen, the dominant overstory species. Additionally, many forbs also associated with SOH. These results suggest that it may be important for future productivity and diversity to retain at least a portion of residues following harvest. On both clayey and silty loam soils, compaction severity was the strongest driver of 15-year woody species composition (Chapter 2). Severe compaction combined with FFR on silty loam soils resulted in greater biomass allocation to the shrub community than to trees (Chapter 1) and indicator species analysis associated *Salix sp.* and *Rosa sp.* with severe compaction whereas aspen associated with C0 (Chapter 2).

A common theme in all three chapters and in ecosystem management, generally, is that of trade-offs: Regeneration or wood production versus biodiversity and structural complexity (Bradshaw 1992, Bradford and D’Amato 2012, Palik et al. 2014, Chapter 1, Chapter 2), and climate change mitigation versus adaptation (Millar et al. 2009, D’Amato et al. 2011, Chapter 2, Chapter 3). Results in Chapter 1 suggest that procuring bioenergy feedstocks from aspen forests on sandy soils might come at the expense of above-ground biomass production. On silty loam and clayey soils such a trade-off is not necessary as removing residues led to an increase in tree biomass; however, Chapter 2 indicates that residue removal and maximum stem production on finer-textured soils may coincide with reductions in species and functional diversity. In Chapter 3, retention aggregates increased structural and compositional complexity at the stand scale and appear to serve as refugia for some interior forest species, at least in the short term. These services were provided without any apparent trade-off in regeneration, although continued observations will be needed to confirm this finding over time. Recognizing, quantifying, interpreting, and communicating these sometimes nuanced trade-offs will better equip practitioners making management decisions.

Results in Chapter 2 indicate what might be a trade-off between maximized above-ground productivity and functional diversity. However, given that functional diversity increased in response to severe disturbance in some cases and that the increase might be attributed to an increased abundance in shrub species, it is possible that greater functional diversity is not always desirable. Just as it is imperative to discuss changes in species composition alongside species richness measures in order to account for any inflation in richness values due to an increase in non-native or invasive species, it is also key to accompany evaluations of functional diversity indices with some description of the specific species or traits that are contributing to changes in index values. Functional diversity may, in theory, increase ecosystem resilience in many cases (Folke et al. 2004), but only if that diversity is representative of the functions that have previously occurred within the ecosystem of study. Future work might use modeling techniques and other datasets associated with the LTSP study to more formally integrate findings from Chapters 1 and 2 and to better describe the relationships among disturbance severity, species diversity, functional diversity, community composition, structure, above-ground biomass, resilience and other attributes.

The LTSP study provides a rich dataset for exploring questions related to bioenergy feedstock removal and soil disturbance effects, and further work will more completely answer some of the questions still remaining. For example, understanding the mechanism behind the negative impacts of WTH and FFR to above-ground biomass and structural development on sandy soils is important for making appropriate management recommendations. While some level of calcium depletion was evident at 10 years post-harvest (Voldseth et al. 2011), it remains unclear whether productivity declines were in response to nutrient availability or moisture stress. If the retention of harvest residues with SOH benefited regeneration by ameliorating microenvironmental conditions, then supplementing soil nutrients would not be a viable option for preventing declines in above-ground productivity following WTH. The data collected so far only allow inference about the mechanisms driving reduced above-ground biomass at this site, but future work could use the existing study areas to explore this question further. Additionally, assessment of disturbance effects on species diversity and composition was limited to shrubs and trees. Woody species constitute the bulk of above-ground biomass in aspen-dominated forest and are thus expected to drive the majority of function per the biomass-ratio hypothesis (Grime 1998), but herbaceous plants in the understory also form an important component of these ecosystems. Composition and diversity of these species was not examined here, but could provide valuable information if studied in the future.

Current inferences from the short-term responses to harvest-related disturbance severity described in Chapter 3 are somewhat limited, given the variability observed and brief time since disturbance. The scale of this study (49 ha) was an advantage in the sense that it allowed the experiment to address questions relevant to management, but more subtle responses may have been lost due to increased variability. Many plant species occurred in fewer than 5% of plots which meant that they were necessarily excluded from analyses of composition to reduce noise. Additionally, while intact forest provided a control for comparison, the analyses of short-term understory response would be stronger if pre-treatment composition and abundance for the understory had been sampled. Despite these shortcomings, the changes in observed composition merit further investigation over time as they could result in future changes in function. Additionally, while the treatments implemented in the LTSP study do not represent the continuum of disturbance severity between SOH and WTH that is likely given variability in harvest operations and current recommendations for retaining at least some slash on site, the design of the study described in Chapter 3 will help fill this gap in knowledge over time.

A number of studies have compared the effectiveness of using species richness versus functional richness (or other functional diversity measures) at predicting above-ground biomass with varying results (Vila et al. 2007, Flynn et al. 2009, Chillo et al. 2011, and Ziter et al. 2013). While the predictive power of species and functional diversity indices were not evaluated here, neither group of metrics called attention to a shift in community composition and structure (and reduction in above-ground biomass) that occurred with FFR and C2 on silty loam soils. The indices available for measuring and assessing functional diversity continue to evolve, and they are only as reliable as the data used to calculate them. The findings reported here for functional diversity and trait responses were influenced by the suite of traits selected for analyses. While decisions were based on the best information available, these methods will become more exacting as additional data for traits are compiled and further research demonstrates which traits are most important to quantify and monitor.

As objectives and methods for managing forests evolve, it will be valuable to return to these studies and continue evaluating ecosystem health and response to disturbance. Species richness is a common and easily compared metric, but it does not account for abundance which is important for community development and dynamics as well as function (Grime 1998), nor does it capture potentially undesirable changes in composition (i.e. increases in invasive species or shifts in dominant species or guilds). While functional diversity metrics have their own drawbacks, they offer a different approach for quantifying, evaluating, and comparing communities. Much work at refining these techniques and building trait databases to widen their applicability remains, but this research demonstrated both their utility in an applied setting as well as some shortcomings. Future work could build off findings from the functional diversity and functional trait analyses presented here and relate them to specific ecosystem services that interest landowners, managers, policy-makers, conservationists, and other practitioners. For example, findings presented in Chapter 2 suggest that harvest operations that increase soil compaction may decrease the drought tolerance of a regenerating forest stand on clayey soils. Empirical evidence that demonstrates whether compaction levels correspond to drought response (potentially quantified with annual growth in overstory trees) would be a logical future direction for research in these areas and would provide practical information for practitioners and other stakeholders. At the same time, such a study would further demonstrate the utility behind using analyses like the fourth corner method that relate management actions to functional trait expression.

Management implications

Overall, results indicate that productivity, diversity, and functional responses to varying disturbance severities associated with harvest residue removal differ among sites, even when dominated by the same overstory species. On fine-textured soils, removal of residues does not appear to reduce aspen densities or total above-ground biomass, but there is potential for changes in species diversity and composition even when some incidental woody debris remains. Additionally, care should be taken to avoid soil disturbance on these soils as it could prompt a shift to shrub-dominated communities. On sandy soils, observed reductions in above-ground biomass suggest that WTH should be avoided and harvest residues retained on site. Lastly, initial results suggest that small aggregates of overstory reserves (0.1 ha) may accomplish ecological objectives such as ‘lifeboating’ some interior forest species and increasing structural complexity without compromising regeneration objectives.

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APPENDIX A: RESULTS FROM POST-HOC COMPARISONS OF FACTOR COMBINATIONS

Table A.1 Tukey-adjusted pairwise comparisons that correspond to interactions between to the two main factors (OMR X CPT) for those variables where OMR X CPT was a significant effect (p<0.05; Tables 3.1, 3.2) at the Chippewa (CH), Huron-Manistee (HM), and Ottawa (OT) National Forests, USA. Values in bold are significant with p< 0.05.

Factor held constant	Total above-ground biomass (CH)				Total above-ground biomass (HM)				Total above-ground biomass (OT)			
	Comparison			p-value	Comparison			p-value	Comparison			p-value
SOH	**SOH/C0**	>	**SOH/C1**	**p<0.0001**	SOH/C0	=	SOH/C1	p=0.4442	SOH/C0	=	SOH/C1	p=0.9899
	SOH/C0	>	**SOH/C2**	**p<0.0001**	SOH/C0	=	SOH/C2	p=0.9984	SOH/C0	>	SOH/C2	p=0.0762
	SOH/C1	=	SOH/C2	p=0.999	SOH/C1	=	SOH/C2	p=0.8715	SOH/C1	=	SOH/C2	p=0.4443
WTH	**WTH/C0**	>	**WTH/C1**	**p=0.0453**	WTH/C0	=	WTH/C1	p=0.8588	WTH/C0	=	WTH/C1	p=0.7532
	WTH/C0	>	**WTH/C2**	**p<0.0001**	WTH/C0	=	WTH/C2	p=0.2357	WTH/C0	=	WTH/C2	p=0.9734
	WTH/C1	>	WTH/C2	p=0.1137	WTH/C1	=	WTH/C2	p=0.9775	WTH/C1	=	WTH/C2	p=0.9998
FFR	FFR/C0	=	FFR/C1	p=0.9322	FFR/C0	=	FFR/C1	p=0.9504	**FFR/C0**	>	**FFR/C1**	**p=0.0487**
	FFR/C0	>	**FFR/C2**	**p=0.0017**	FFR/C0	=	FFR/C1	p=0.9167	FFR/C0	>	FFR/C2	p=0.0775
	FFR/C1	=	FFR/C2	p=0.1337	FFR/C1	=	FFR/C2	p=0.2344	FFR/C1	=	FFR/C2	p=1.000
C0	SOH/C0	=	WTH/C0	p=0.9946	SOH/C0	=	WTH/C0	p=0.8035	SOH/C0	=	WTH/C0	p=1.000
	SOH/C0	=	FFR/C0	p=0.9938	SOH/C0	=	FFR/C0	p=0.9172	SOH/C0	=	FFR/C0	p=0.9906
	WTH/C0	=	FFR/C0	p=0.7350	WTH/C0	=	FFR/C0	p=1.000	WTH/C0	=	FFR/C0	p=0.9965
C1	**SOH/C1**	<	**WTH/C1**	**p=0.0720**	SOH/C1	=	WTH/C1	p=0.3738	SOH/C1	=	WTH/C1	p=0.2794
	SOH/C1	<	**FFR/C1**	**p=0.0354**	**SOH/C1**	>	**FFR/C1**	**p=0.0006**	SOH/C1	=	FFR/C1	p=0.9965
	WTH/C1	=	FFR/C1	p=1.000	WTH/C1	=	FFR/C1	p=0.2886	**WTH/C1**	>	**FFR/C1**	**p=0.0053**
C2	SOH/C2	=	WTH/C2	p=0.9975	SOH/C2	=	WTH/C2	p=1.000	SOH/C2	na	WTH/C2	na
	SOH/C2	=	FFR/C2	p=0.9976	SOH/C2	=	FFR/C2	p=0.9984	SOH/C2	na	FFR/C2	na
	WTH/C2	=	FFR/C2	p=1.000	WTH/C2	=	FFR/C2	p=0.9889	**WTH/C2**	>	**FFR/C2**	**p=0.0401**

Table A.1, continued

Factor held constant	maxBD (CH)				maxBD (OT)				maxBD (HM)			
	Comparison			p-value	Comparison			p-value	Comparison			p-value
SOH	**SOH/C0**	>	**SOH/C1**	**p=0.0006**	SOH/C0	=	SOH/C1	p=0.9996	SOH/C0	=	SOH/C1	p=0.4714
	SOH/C0	>	**SOH/C2**	**p=0.0006**	SOH/C0	=	SOH/C2	na	SOH/C0	=	SOH/C2	p=1.000
	SOH/C1	=	SOH/C2	p=1.000	SOH/C1	=	SOH/C2	na	SOH/C1	=	SOH/C2	p=0.5275
WTH	WTH/C0	=	WTH/C1	p=1.000	WTH/C0	=	WTH/C1	p=1.000	WTH/C0	=	WTH/C1	p=1.000
	WTH/C0	=	WTH/C2	p=0.1211	WTH/C0	=	WTH/C2	p=0.9993	WTH/C0	=	WTH/C2	p=1.000
	WTH/C1	=	WTH/C2	p=0.2010	WTH/C1	=	WTH/C2	p=1.000	WTH/C1	=	WTH/C2	p=1.000
FFR	FFR/C0	=	FFR/C1	p=0.9751	FFR/C0	=	FFR/C1	p=0.3194	FFR/C0	=	FFR/C1	p=0.1378
	FFR/C0	>	**FFR/C2**	**p=0.0017**	FFR/C0	=	FFR/C2	p=0.7393	FFR/C0	=	FFR/C2	p=1.000
	FFR/C1	>	**FFR/C2**	**p=0.0414**	FFR/C1	=	FFR/C2	p=0.9990	FFR/C1	=	FFR/C2	p=0.2801
C0	SOH/C0	=	WTH/C0	p=0.9992	SOH/C0	=	WTH/C0	p=0.9924	SOH/C0	=	WTH/C0	p=0.9529
	SOH/C0	=	FFR/C0	p=0.8124	SOH/C0	=	FFR/C0	p=1.000	SOH/C0	=	FFR/C0	p=1.000
	WTH/C0	=	FFR/C0	p=0.9903	WTH/C0	=	FFR/C0	p=0.9808	WTH/C0	=	FFR/C0	p=0.9954
C1	**SOH/C1**	<	**WTH/C1**	**p=0.0109**	SOH/C1	=	WTH/C1	p=1.000	**SOH/C1**	>	**WTH/C1**	**p=0.0396**
	SOH/C1	=	FFR/C1	p=0.5307	SOH/C1	=	FFR/C1	p=0.1462	**SOH/C1**	>	**FFR/C1**	**p<0.0001**
	WTH/C1	=	FFR/C1	p=0.7048	WTH/C1	>	FFR/C1	p=0.0622	WTH/C1	=	FFR/C1	p=0.5640
C2	SOH/C2	=	WTH/C2	p=0.9564	SOH/C2	na	WTH/C2	na	SOH/C2	=	WTH/C2	p=0.7814
	SOH/C2	=	FFR/C2	p=0.9384	SOH/C2	na	FFR/C2	na	SOH/C2	=	FFR/C2	p=0.9958
	WTH/C2	=	FFR/C2	p=0.2834	WTH/C2	=	FFR/C2	p=0.5099	WTH/C2	=	FFR/C2	p=0.9958

Table A.1, continued

Factor held constant	Diameter, QMD (OT)				Stem density (OT)				Herbaceous biomass (CH)			
	Comparison			p-value	Comparison			p-value	Comparison			p-value
SOH	SOH/C0	=	SOH/C1	p=0.9999	SOH/C0	=	SOH/C1	p=0.9998	**SOH/C0**	<	**SOH/C1**	**p<0.0001**
	SOH/C0	=	SOH/C2	p=0.3054	SOH/C0	=	SOH/C2	p=0.9011	**SOH/C0**	<	**SOH/C2**	**p<0.0001**
	SOH/C1	=	SOH/C2	p=0.9980	SOH/C1	=	SOH/C2	p=0.7443	SOH/C1	=	SOH/C2	p=0.8671
WTH	WTH/C0	=	WTH/C1	p=0.9406	WTH/C0	=	WTH/C1	p=0.5654	**WTH/C0**	<	**WTH/C1**	**p<0.0001**
	WTH/C0	=	WTH/C2	p=0.9937	WTH/C0	=	WTH/C2	p=0.6322	**WTH/C0**	<	**WTH/C2**	**p<0.0001**
	WTH/C1	=	WTH/C2	p=1.000	WTH/C1	=	WTH/C2	p=1.000	WTH/C1	=	WTH/C2	p=0.2996
FFR	**FFR/C0**	>	**FFR/C1**	**p=0.0436**	FFR/C0	=	FFR/C1	p=0.5927	FFR/C0	<	FFR/C1	p=0.0593
	FFR/C0	>	**FFR/C2**	**p=0.9523**	FFR/C0	=	FFR/C2	p=0.9999	**FFR/C0**	<	**FFR/C2**	**p=0.0002**
	FFR/C1	=	FFR/C2	p=0.9353	FFR/C1	=	FFR/C2	p=0.5813	FFR/C1	=	FFR/C2	p=0.99989
C0	SOH/C0	=	WTH/C0	p=0.9980	SOH/C0	=	WTH/C0	p=1.000	SOH/C0	=	WTH/C0	p=1.000
	SOH/C0	=	FFR/C0	p=1.000	SOH/C0	=	FFR/C0	p=0.2491	SOH/C0	=	FFR/C0	p=0.4143
	WTH/C0	=	FFR/C0	p=1.000	WTH/C0	=	FFR/C0	p=0.1455	WTH/C0	=	FFR/C0	p=0.3872
C1	SOH/C1	=	WTH/C1	p=0.9736	SOH/C1	=	WTH/C1	p=0.4405	SOH/C1	=	WTH/C1	p=0.9151
	SOH/C1	>	FFR/C1	p=0.0883	SOH/C1	<	FFR/C1	p=0.0503	SOH/C1	=	FFR/C1	p=0.5442
	WTH/C1	>	**FFR/C1**	**p=0.0007**	WTH/C1	=	FFR/C1	p=0.9523	WTH/C1	=	FFR/C1	p=0.9990
C2	SOH/C2	na	WTH/C2	na	SOH/C2	na	WTH/C2	na	SOH/C2	=	WTH/C2	p=1.000
	SOH/C2	na	FFR/C2	na	SOH/C2	na	FFR/C2	na	SOH/C2	=	FFR/C2	p=0.7675
	WTH/C2	>	FFR/C2	p=0.0782	WTH/C2	=	FFR/C2	p=0.9991	WTH/C2	=	FFR/C2	p=0.9379

APPENDIX B

MEANS FOR STEM DENSITY AND DIAMETER OVER TIME

Table B.1 Treatment means for structural attributes by organic matter removal and compaction treatment at sampling periods 5, 10, and 15 years following disturbance at the Chippewa (CH), Huron-Manistee (HM), and Ottawa (OT) National Forests, USA. Standard error is indicated in parentheses. BD indicates basal diameter, measured at 15 cm height. All stems > 15 cm in height are included.

	Structural attributes								
	Stem density (no./ha)			QMD (cm)			BD (cm, 99th percentile)		
Treatment	5 years	10 years	15 years	5 years	10 years	15 years	5 years	10 years	15 years
CH (loamy)									
SOH	25750 (8067)	14506 (4089)	9555 (2891)	1.268 (0.171)	2.777 (0.244)	4.942 (0.332)	2.789 (0.518)	6.778 (0.552)	11.667 (0.877)
TTH	33750 (7666)	14703 (4306)	10913 (3269)	1.550 (0.137)	3.501 (0.338)	4.993 (0.381)	3.411 (0.366)	8.011 (0.621)	12.533 (0.823)
FFR	36361 (9020)	18679 (4290)	13555 (2932)	1.219 (0.129)	2.562 (0.169)	3.717 (0.279)	2.844 (0.340)	6.333 (0.377)	10.078 (0.514)
C0	60222 (6306)	28913 (4069)	19172 (3351)	1.821 (0.076)	3.468 (0.259)	4.695 (0.417)	4.322 (0.226)	8.111 (0.369)	11.667 (0.884)
C1	23444 (2703)	13172 (1805)	10197 (1924)	1.240 (0.123)	3.066 (0.226)	4.754 (0.321)	2.711 (0.343)	7.189 (0.519)	12.000 (0.933)
C2	12194 (2836)	5802 (637)	4654 (573)	0.975 (0.070)	2.307 (0.239)	4.202 (0.404)	2.011 (0.167)	5.822 (0.534)	10.611 (0.561)
HM (sandy)									
SOH	79580 (12347)	47172 (7757)	53049 (8715)	1.298 (0.096)	2.104 (0.196)	2.637 (0.317)	3.711 (0.186)	6.678 (0.254)	9.322 (0.549)
TTH	95185 (14586)	61135 (11629)	53790 (7805)	1.087 (0.121)	1.721 (0.215)	5.822 (0.438)	3.133 (0.243)	5.822 (0.438)	8.394 (0.694)
FFR	84703 (15517)	48160 (8221)	49802 (9136)	1.118 (0.107)	1.786 (0.188)	2.316 (0.303)	3.200 (0.220)	5.944 (0.432)	8.406 (0.574)
C0	89987 (15598)	45654 (6567)	48172 (7790)	1.103 (0.147)	1.841 (0.259)	2.394 (0.377)	3.322 (0.283)	6.200 (0.438)	8.906 (0.796)
C1	91790 (12305)	55864 (8975)	57172 (9735)	1.137 (0.087)	1.802 (0.162)	2.394 (0.377)	3.200 (0.174)	5.789 (0.303)	8.422 (0.466)
C2	77691 (14573)	54950 (12105)	51296 (7797)	1.263 (0.087)	1.969 (0.187)	2.479 (0.287)	3.522 (0.222)	6.456 (0.430)	8.794 (0.564)
OT (clay)									
SOH	21166 (4482)	10833 (1257)	7907 (1881)	1.088 (0.109)	2.120 (0.235)	3.860 (0.416)	2.200 (0.286)	4.783 (0.533)	8.558 (0.775)
TTH	26500 (2977)	11232 (1473)	9373 (1036)	1.180 (0.071)	2.549 (0.175)	3.877 (0.268)	2.491 (0.184)	5.545 (0.231)	8.664 (0.251)
FFR	32555 (3304)	15851 (1240)	8814 (1251)	0.925 (0.079)	1.854 (0.217)	3.485 (0.283)	2.033 (0.243)	4.256 (0.308)	7.911 (0.414)
C0	22181 (3156)	12545 (1457)	10020 (947)	1.165 (0.080)	2.303 (0.179)	3.636 (0.219)	2.454 (0.221)	5.218 (0.179)	8.805 (0.380)
C1	31750 (3585)	12819 (1541)	8236 (1183)	1.013 (0.085)	2.302 (0.286)	4.013 (0.409)	2.225 (0.210)	4.913 (0.447)	8.425 (0.501)
C2	30500 (3489)	12952 (1974)	7682 (1829)	0.990 (0.098)	1.957 (0.227)	3.582 (0.317)	2.014 (0.257)	4.471 (0.457)	7.657 (0.334)

APPENDIX C: SPECIES TRAITS

Table C.1 Raw trait values used for functional diversity analyses in Chapter 2. For those plants only identified to genus, values for the species most likely to occur at the sites were averaged. Values in bold are based on a closely related species within the same genus.

	Traits										
Species	Drought tolerance	Flood tolerance	Shade tolerancee	Rooting depth (cm)	Seed mass (mg)	Height (m)	Leaf lifespan (months)	Specific gravity	Leaf mass per area	N mass	P mass
Abies balsamea	1.00	2.00	5.01	50.80	8.60	18.28	109.95	0.34	151.00	1.66	0.17
Acer rubrum	1.84	3.08	3.44	76.20	21.01	27.43	5.57	0.49	71.09	1.91	0.30
Acer saccharum	2.25	1.09	4.76	101.60	66.02	30.48	5.50	0.56	70.63	1.83	0.30
Acer spicatum	2.00	2.00	3.31	81.28	21.01	9.14	5.00	0.44	27.11	2.23	0.34
Alnus sp.	2.00	2.85	1.00	60.96	1.42	7.62	4.80	0.37	67.14	2.98	0.21
Amelanchier sp.	2.38	3.50	4.33	50.80	6.50	15.24	5.00	0.66	78.86	1.82	0.32
Betula alleghaniensis	3.00	2.00	3.17	76.20	1.02	30.48	5.50	0.58	46.08	2.20	**0.24**
Betula papyrifera	2.02	1.25	1.54	60.96	1.33	21.34	3.60	0.48	77.88	2.31	0.24
Carpinus carolinia	2.02	2.30	4.58	50.80	14.00	12.19	7.70	0.58	49.05	2.15	0.18
Corylus sp.	2.88	1.27	3.00	40.64	14.01	3.65	5.00	0.50	27.20	2.01	0.27
Cornus sericea	2.48	2.12	2.86	50.80	1.00	3.65	5.00	0.61	81.45	**1.94**	**0.32**
Diervilla lonicera	4.00	0.00	2.50	40.60	19.30	0.73	5.00	0.46	87.35	1.89	0.22
Dirca palustris	1.00	1.00	4.00	50.00	23.34	1.70	5.00	0.33	60.00	1.88	0.34
Fraxinus nigra	2.00	3.50	2.96	101.60	59.03	24.38	5.00	0.45	71.94	2.10	0.34
Fraxinus pensylvanica	3.85	2.98	3.11	101.60	31.68	21.34	5.00	0.53	87.72	1.90	0.34
Ostrya virginiana	3.25	1.07	4.58	40.60	16.01	13.71	5.00	0.63	37.04	2.20	0.23
Picea glauca	2.88	1.02	4.15	76.00	3.15	30.48	50.00	0.35	302.86	1.28	0.18
Pinus strobus	2.29	1.03	3.21	101.00	17.99	45.72	20.01	0.36	121.92	1.42	0.16

Species	**Traits**										
	Drought tolerance	Flood tolerance	Shade tolerancee	Rooting depth (cm)	Seed mass (mg)	Height (m)	Leaf lifespan (months)	Specific gravity	Leaf mass per area	N mass	P mass
Populus balsamifera	1.77	2.63	1.27	76.00	1.30	24.38	3.60	0.37	83.46	1.95	0.29
Populus grandidentata	2.50	2.00	1.21	50.00	1.18	19.80	5.00	0.39	70.45	2.50	0.26
Populus tremuloides	1.77	1.77	1.21	81.00	1.15	19.80	4.86	0.37	82.02	2.16	0.43
Prunus pensylvanica	1.50	1.50	1.00	50.00	33.02	7.62	5.00	0.36	50.00	2.40	0.37
Prunus serotina	2.50	0.00	1.00	91.00	95.01	24.30	5.50	0.47	72.30	2.48	0.31
Prunus virginiana	2.80	1.11	2.59	50.00	92.02	7.62	5.00	0.36	84.03	2.80	0.37
Quercus alba	3.56	1.43	2.85	121.00	3540.42	30.40	5.00	0.60	81.21	2.39	0.18
Quercus macrocarpa	3.85	1.82	2.71	71.00	6051.13	30.40	6.00	0.58	92.74	2.27	0.27
Quercus rubra	2.88	1.12	2.75	91.00	3630.04	30.40	6.00	0.56	84.20	2.06	0.23
Ribes sp.	2.50	2.00	2.00	35.00	27.94	1.52	4.96	0.50	58.80	1.59	0.33
Rosa sp.	2.50	2.50	1.50	15.00	4.14	1.21	5.00	0.43	84.70	1.81	0.31
Salix sp.	1.50	3.50	1.25	40.00	1.20	3.65	4.20	0.36	83.10	2.50	0.18
Tilia americana	2.88	1.26	3.98	76.00	16.01	39.60	5.00	0.32	60.81	2.94	0.31
Viburnum sp.	2.00	2.50	4.00	35.50	7.92	1.82	5.00	0.73	52.60	1.19	0.25
Crataegus sp.	4.98	1.27	1.67	76.20	92.02	7.62	5.00	0.53	96.34	1.70	0.11
Cornus drummondii	1.77	1.02	4.00	50.80	28.89	14.63	5.00	0.64	**39.81**	1.93	0.32
Lonicera canadensis	1.00	2.00	4.00	**50.00**	**24.60**	0.61	5.00	**0.48**	**62.63**	1.68	0.28
Fraxinus americana	2.38	2.59	2.46	101.60	45.35	27.43	5.70	0.55	76.75	2.12	**0.34**
Cornus alternifolia	1.77	1.02	4.00	50.80	56.69	7.50	5.00	0.64	39.81	1.90	0.33
Pinus resinosa	3.00	1.00	1.89	152.40	9.70	24.38	36.02	0.39	294.12	1.13	0.15
Pinus banksiana	4.00	1.00	1.36	88.90	4.50	24.38	27.00	0.42	243.90	1.19	0.12
Ulmus americana	2.92	2.46	3.14	106.68	6.67	36.58	5.90	0.46	79.47	2.56	0.41

Table C.2 Sources for species trait values.

Trait	Main Source	Additional sources
Drought tolerance	Niinemets et al. (2009)	USDA Plant Atlas
Flood tolerance	Niinemets et al. (2009)	USDA Plant Atlas
Shade tolerance	Niinemets et al. (2009)	USDA Plant Atlas
Rooting depth	USDA Plant Atlas	Schulz (pers. Comm.)
Seed mass	Paquette and Messier (2011)	USDA, Waller (unpublished data), Burns and Honkala (1990)
Height at maturity	USDA Plant Atlas	Smith 2008
Leaf longevity	Reich et al. (1998), Niinemets and Lukjanova (2003)	When not available, 5 months was used following Paquette and Messier (2011)
Specific gravity	Miles et al. (2009)	Waller (unpublished data)
N mass	Paquette and Messier (2011)	Henry (1973), Waller (unpublished data)
P mass	Henry (1973)	Niinemets and Kull (2003), Waller (unpublished data)

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