2017

Lasting Legacies of Hurricane, Harvesting, and Salvage Logging Disturbance on Succession and Structural Development in an Old-Growth Tsuga canadensis-Pinus strobus Forest

Emma Sass
University of Vermont

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LASTING LEGACIES OF HURRICANE, HARVESTING, AND SALVAGE LOGGING DISTURBANCE ON SUCCESSION AND STRUCTURAL DEVELOPMENT IN AN OLD-GROWTH TSUGA CANADENSIS-PINUS STROBUS FOREST

A Thesis Presented

by

Emma M. Sass

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The Faculty of the Graduate College

of

The University of Vermont

In Partial Fulfillment of the Requirements for the Degree of Master of Science Specializing in Natural Resources

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Abstraction

Disturbance events affect forest composition and structure across a range of spatial and temporal scales, and forest development may differ after natural, anthropogenic, or compound disturbances. Following large, natural disturbances, salvage logging is a common yet controversial management practice around the globe. While the short-term impacts of salvage logging have been studied in many systems, the long-term effects remain unclear. Further, while natural disturbances create many persistent and unique microsite conditions, little is known about the long-term influence of microsites on forest development. We capitalized on over eighty years of data on stand development following the 1938 hurricane in New England to provide the longest known evaluation of salvage logging impacts, as well as to highlight developmental trajectories for eastern hemlock (Tsuga canadensis)-white pine (Pinus strobus) forests under a variety of disturbance histories. Eight decades following disturbance, there were no differences in current overstory composition between areas that were logged, hurricane disturbed, or hurricane disturbed and salvage logged, but white pine declined across most sites. In contrast, structural characteristics remain distinct between the three management histories. In the unsalvaged area, the diversity of microsites and the coverage of uprootings and pits influenced overstory tree composition, diversity, and structural characteristics. These findings underscore the long-term influence of salvage logging on forest development and the importance of natural disturbance-mediated microsite conditions on tree species growth and survival. Future salvage logging efforts should consider these impacts and provide a greater range of unsalvaged areas across the landscape to maintain these important structural legacies over the long term.
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CHAPTER 1: INTRODUCTION

Disturbance events affect forest succession, structural development, and ecosystem dynamics across a range of spatial and temporal scales (Pickett and White 1985). The disturbance regime for forests in northeastern North America is generally viewed as being dominated by a combination of frequent, gap-scale disturbance events, including wind and ice storms, fire, insects, and pathogens (Lorimer and White 2003). In addition, regional, stand-replacing events have periodically impacted forests in the region over the past 500 years, exerting considerable influence on regional patterns in species composition, structure, and processes (Cline and Spurr 1942, Henry and Swan 1974, Foster 1988a, Boose et al. 2001). Hurricanes in 1788, 1815, and 1938 were particularly severe in central and southern New England, with heavy rains followed by intense wind (Brooks 1939, Foster 1988b, Boose et al. 2001). Given that hurricanes are projected to increase in intensity with climate change and warming ocean currents (Knutson and Tuleya 2004, Bender et al. 2010, Knutson et al. 2010, Mudd et al. 2014), understanding the historic role of these events in affecting forest dynamics will help with anticipating their future impacts.

Large, infrequent disturbances, such as hurricanes, can have lasting impacts on dynamics in forest composition and structural development (Foster et al. 1998). Nevertheless, most studies examining the impacts of these events have relied primarily on assessments of short-term vegetation response and understory plant survival to predict future composition and structure (Harcombe et al. 2009, Howard 2012). Multiple studies have called for more investigations into the long-term dynamics following wind
disturbance (Everham and Brokaw 1996, Turner et al. 1998); however, few opportunities exist for meaningful examinations spanning more than a few decades.

In northeastern forests, the primary source of information regarding long-term vegetation response to hurricanes comes from work examining the impacts of the 1938 hurricane, which is the most destructive hurricane in the modern record for this region. Work examining post-hurricane succession after the 1938 hurricane in transition hardwoods demonstrated that understory and overstory vegetation followed similar trajectories after the hurricane, with compositional conditions returning to those found prior to the hurricane within 53 years (Hibbs 1983, Mabry and Korsgren 1998). In northern hardwood ecosystems, tree growth rates in hurricane-damaged stands increased and remained above pre-1938 levels for at least 49 years (Merrens and Peart 1992). In addition, basal area was lower and stem density was higher in damaged areas, although species composition remained similar to undamaged old-growth stands (Merrens and Peart 1992). Similar structural results were found in Tsuga canadensis (eastern hemlock)-Pinus strobus (white pine) forests in New Hampshire, where damaged stands had lower basal area and higher stem density than pre-hurricane levels even 46 years after the hurricane (Foster 1988a). However, overstory species composition shifted dramatically from pre-hurricane conditions in these systems, with white pine essentially disappearing from these landscapes. Collectively, these results underscore the complexity in long-term recovery patterns as influenced by pre-disturbance forest composition and structure.

The effects of changes in future disturbance regimes on forest ecosystem composition and structure will be strongly influenced by the degree of post-disturbance
management in managed landscapes. Salvage logging, the removal of damaged and
downed trees after major natural disturbances, has been a common practice after
windstorms and fire for over a century (Lindenmayer et al. 2008). Recent studies have
demonstrated that salvage logging impacts may be even greater than the initial
disturbance given compounding effects on ecosystem structure and rates of recovery
(Lindenmayer et al. 2008). In most cases, this research has focused on the salvage
logging impacts after wildfires and over very short time periods (less than 10 years;
Lindenmayer et al. 2008, Lang et al. 2009) leaving key knowledge gaps regarding
impacts following other disturbances and over longer time frames. In particular, there has
been a call for studies that directly compare naturally disturbed and logged sites with
disturbed and unlogged sites over ecologically meaningful timeframes (Lindenmayer and

Areas within Pisgah State Park in southwest New Hampshire offer a unique,
direct comparison between old-growth forest stands that were logged prior to the 1938
hurricane, old-growth stands that were damaged by the 1938 hurricane, and stands that
were damaged by the hurricane and subsequently salvage logged (Branch et al. 1930,
NETSA 1943, Foster 1988a). Ongoing research before and after the hurricane provides a
rich history of the dynamics of dead and downed wood, the long-term development of the
vegetation community, and microsite dynamics and variability. Further, it offers an
opportunity for direct and long-term comparison of how forest harvesting, major natural
disturbance, and salvage logging affect species composition, forest structure, and detrital
dynamics over almost eight decades. This study presents the longest temporal evaluation
of the impacts of salvage logging to date. Long-term studies of the unsalvaged sites in this area also allow a uniquely detailed investigation of the influence of microsite conditions on the development of forest structural and compositional development in an old-growth forest impacted by severe wind disturbance.

Specifically, Chapter 2 focuses on the comparison of forest structure and composition of old-growth remnants with divergent disturbance histories: natural disturbance of the 1938 hurricane, pre-hurricane logging, and salvage logging following the hurricane. In particular, we examine three questions: How do different management regimes affect the long-term composition and structure of forest stands? Do stands under certain management regimes return to their pre-disturbance composition? Do salvaged stands return to the same composition and structure as naturally disturbed, non-salvaged stands?

Chapter 3 investigates the long-term forest dynamics following hurricane disturbance, focusing on the non-salvaged area within the Harvard Tract of Pisgah State Park 51 and 71 years after the 1938 hurricane. This study draws on composition, structure, and microsite data from repeated measures in a long-term study. Specifically, we ask: What are the patterns in live tree size distributions, mortality, and growth five and seven decades after disturbance? What role does microsite heterogeneity and the presence of different microsite structures, including pit-and-mound microtopography and coarse woody debris, play in the long-term development of a forest stand following a severe disturbance? How do pre-disturbance species composition, topography, and
microsite conditions interact to influence the vegetation composition in the post-disturbance stand?

Finally, Chapter 4 offers a general discussion of the findings from Chapters 2 and 3 in relation to our understanding of forest disturbance ecology, as well as consideration of the study’s limitations and concluding remarks on the potential applications of this research to management before and after large natural disturbance events.
CHAPTER 2: LASTING LEGACIES OF HISTORIC CLEARCUTTING, WIND AND SALVAGE LOGGING ON OLD-GROWTH *TSUGA CANADENSIS-PINUS STROBUS* FORESTS

2.1. Abstract

Disturbance events affect forest composition and structure across a range of spatial and temporal scales, and forest development may differ after natural, anthropogenic, or compound disturbances. Following large, natural disturbances, salvage logging is a common and often controversial management practice in many regions of the globe. Yet, while the short-term impacts of salvage logging have been studied in many systems, the long-term effects remain unclear. We capitalized on over eighty years of data following an old-growth *Tsuga canadensis-Pinus strobus* forest in southwestern New Hampshire, USA after the 1938 hurricane, which severely damaged forests across much of New England. To our knowledge, this study provides the longest evaluation of salvage logging impacts, and it highlights developmental trajectories for *Tsuga canadensis-Pinus strobus* forests under a variety of disturbance histories. Specifically, we examined development from an old-growth condition in 1930 through 2016 across three different disturbance histories: 1) clearcut logging prior to the 1938 hurricane that was subsequently damaged by the hurricane (“logged”), 2) severe damage from the 1938 hurricane (“hurricane”), and 3) severe damage from the hurricane followed by salvage logging (“salvaged”). There were no differences in current overstory composition between the different disturbance histories, as most areas shifted strongly away from pre-hurricane composition through nearly complete elimination of *P. strobus* and
corresponding increases in hardwoods (Betula and Acer spp.), while T. canadensis decreased but remained dominant. In contrast, eight decades later, structural characteristics remain distinct between logged, hurricane, and salvaged sites. Specifically, trees were larger in the logged and salvaged sites, and pit-and-mound microtopography were largest and most abundant in the hurricane site. Tree densities and coarse woody debris biomass was greater in the hurricane site than the logged site, but not significantly different from salvaged sites. These findings underscore the long-term influence of salvage logging on forest development, indicating convergence in overstory composition over time between logged, salvaged, and non-salvaged areas, but persistent structural differences, especially in microtopographic structures and live tree development. Future salvage logging efforts should consider these impacts and provide a greater range of unsalvaged areas across the landscape to maintain these important structural legacies over the long term.

2.2. Introduction

Disturbance affects forest succession, structural development, and ecosystem dynamics across a range of spatial and temporal scales (Pickett and White 1985). Understanding the impacts of disturbance on forest processes and development is critical for informing ecosystem modeling (Seidl et al. 2011) and forest management and conservation efforts (Seymour et al. 2002). Anthropogenic disturbance and land-use history have also strongly influenced forest dynamics and ecosystem processes across wide regions of the globe (Lorimer and White 2003) often simplifying forest conditions
relative to those observed in regions where only natural disturbance predominate (e.g. Mladenoff et al. 1993). Given that many disturbance regimes are predicted to shift in intensity and frequency under climate change, understanding the historic role of these events in affecting forest dynamics within managed and natural landscapes will help anticipate their future impacts (Dale et al. 2001).

In most regions of the globe, disturbance regimes are dominated by minor disturbances; however, large, infrequent disturbances can have a profound and long-term influence on forest conditions. These disturbances strongly influence patterns of stand initiation (Foster 1988a, Wells et al. 2001), compositional and structural development (Mladenoff and Pastor 1993, Oliver and Larson 1996), and large-scale patterns of heterogeneity (Turner et al. 1998, Turner 2010). In northeastern North America, the disturbance regime is dominated by a combination of frequent, gap-scale disturbance events, including wind and ice storms, fire, insects, and pathogens (Lorimer and White 2003). In addition, regional, stand-replacing wind events have periodically impacted this area over the past 500 years, exerting considerable influence on broad-scale patterns in species composition, structure, and ecosystem processes (Foster 1988a, Boose et al. 2001). Hurricanes in 1788, 1815, and 1938 were particularly severe in central and southern New England (Brooks 1939, Foster 1988b, Boose et al. 2001), generating lasting impacts on historic and contemporary forest development (Foster and Boose 1992, D’Amato and Orwig 2008).

The impacts of hurricanes on temperate forest development can vary considerably depending on forest conditions at the time of disturbance. While some hurricane-
damaged forests return to their prior composition (Hibbs 1983, Mabry and Korsgren 1998, Batista and Platt 2003), other studies show shifts away from the pre-hurricane condition depending on cohort structure and composition of the regeneration layer (Foster 1988a, Schwarz et al. 2001, Busing et al. 2009). Hurricane damage has also been shown to homogenize live-tree structural conditions across the landscape, relative to pre-disturbance condition (D'Amato et al. 2017). Given the complicated interactions of forest structure and composition with hurricane disturbance, there is an increasing need to better understand the long-term impacts of hurricanes on temperate forests, especially as hurricanes are expected to become more severe with climate change (Dale et al. 2001, Bender et al. 2010, Mudd et al. 2014).

The effects of changes in future disturbance regimes on forest ecosystem composition and structure will be strongly influenced by the degree of post-disturbance management in managed landscapes. Salvage logging, the removal of damaged and downed trees after major natural disturbances, has been a common practice after natural disturbances for over a century (Lindenmayer et al. 2008). Salvaging can have variable effects on forest composition, with stands undergoing more dramatic change if regeneration mechanisms are directly affected by management activities, such as through the removal of aerial seed banks (Buma and Wessman 2011), damage to shade-tolerant advance regeneration (Lang et al. 2009), or stimulation of vegetative reproduction (Palik and Kastendick 2009). Salvaging tends to decrease structural legacies, including live, damaged trees (Cooper-Ellis et al. 1999, Foster and Orwig 2006, Lindenmayer and Ough 2006), coarse woody debris (CWD; D'Amato et al. 2011), and pit-and-mound
microtopography (Fraver et al. 2017), and may increase the sprouting response of seedlings and shrubs (Sessions et al. 2004, D'Amato et al. 2011). Recent studies have demonstrated that salvage logging impacts may be even greater than the initial disturbance given compounding effects on ecosystem structure and rates of recovery (Lindenmayer et al. 2008). In most cases, previous research has focused on salvage logging impacts after wildfires and over very short time periods (i.e. less than 10 years; Lindenmayer et al. 2008, Lang et al. 2009) leaving key knowledge gaps regarding impacts following other disturbances and over longer time frames. In particular, there has been a call for studies that directly compare naturally disturbed and logged sites with disturbed and unlogged sites over ecologically meaningful timeframes to inform refinement of salvage logging guidelines (Lindenmayer and Noss 2006, Lindenmayer and Ough 2006).

Areas within Pisgah State Park in southwest New Hampshire offer a unique opportunity to address this key knowledge gap through direct comparisons among old-growth forest stands that were: 1) logged prior to the 1938 hurricane before being damaged by the hurricane, 2) damaged by the 1938 hurricane and never salvage logged, and 3) damaged by the 1938 hurricane and subsequently salvage logged (Branch et al. 1930, NETSA 1943, Foster 1988a). Ongoing research before and after the hurricane provides a rich historical account of dead and downed wood dynamics, long-term development of the vegetation community, and microsite dynamics, processes, and variability. Further, this area offers an opportunity for direct, long-term comparison of how forest harvesting, major natural disturbance, and salvage logging affect species
composition, forest structure, and detrital dynamics over almost eight decades. Specifically, we investigate how these three disturbance histories have affected the long-term composition and structure of forest stands, if there is convergence in the characteristics of the managed and the non-managed stands, and whether any of the disturbance histories have led to a return to pre-disturbance composition. To our knowledge, this study represents the longest timeframe over which the impacts of salvage logging have been investigated.

2.3. Methods

2.3.1 Study site

Pisgah State Park occupies 5300 ha in the southwest corner of New Hampshire in the town of Winchester, Cheshire County. The area is characterized by ridges running generally north to south with steep slopes and rocky outcrops from recent glaciation; elevations range from 215 m-400 m (Cline and Spurr 1942). The soil is podzolic, thin, and stony, with 5-10 cm of organic material at the surface over bedrock of schist, granite, and gneiss (Rosenberg 1989). This region receives about 100 cm of precipitation annually, evenly distributed throughout the year (U.S.D.A. 1941). Temperatures in this area range from an average high of 28.3°C in July to an average low of -0.6°C in January (U.S. Climate Data 2017), and the growing season is an average of 120 days (U.S.D.A. 1941). The site is located in the southern end of the Northern Hardwoods-Hemlock-White Pine region in the Worcester/Monadnock Plateau ecoregion (Westveldt et al. 1956, Griffith et al. 2009).
The forests in this region have historically been subject to a variety of frequent, small-scale disturbances, including windstorms, fire, and pathogens, and infrequent, large-scale disturbance by hurricanes (Foster 1988a). By the 1880s, almost all but 300 ha of the forest had been logged, with additional logging occurring in the 1920s (Foster 1988a). In 1927, Harvard Forest purchased 10 ha within the remaining unlogged area, known as the Harvard Tract, surrounded by land that became Pisgah State Park in 1972. The 1938 hurricane severely damaged roughly a quarter of the Pisgah area, moderately damaged about one half, and left one quarter undisturbed (Foster 1988a). Disturbance was highly heterogeneous across the landscape, but almost all of the mature trees on the Harvard Tract were severely damaged, with large areas completely windthrown (Cline and Spurr 1942). Much of the surrounding area affected by the hurricane was salvage logged as part of the largest timber salvage operation in U.S. history (NETSA 1943); however, the Harvard Tract was left untouched (Harvard Forest Archives, Foster 1988a).

2.3.2. Previous Research

This study takes advantage of and builds on substantial previous research collected across Pisgah State Park over the past 110 years. R.T. Fisher, the first director of the Harvard Forest, first documented remnant old-growth forest patches in 1905 and made multiple trips to characterize the composition and dynamics of these ‘natural’ forests (Harvard Forest Archives). Building on these initial trips, his students Branch, Daley, and Lotti (1930) surveyed 91 0.04 ha plots across the forested upland area: 68 in old-growth forest, where there was no evidence of human disturbance, and 23 in areas
that had been logged 9 months prior to their sampling. At each old-growth plot, they recorded the species, diameter at breast height (DBH; 1.3 m), and height of each tree, grouped by canopy class. In the logged plots, they identified the species and diameter of each stump, as well as the former measurements on the remaining, uncut trees. Cline and Spurr (1942) further analyzed these data by vegetation cover type, elevation, and stand history. Foster (1988a) determined the extent of the damage from the 1938 hurricane by overlaying aerial photos from 1939 on topographic maps across the site.

2.3.3. Plot selection

In the summer of 2016, study sites were located in the approximate position of Branch et al.’s (1930) plots to determine the change over time in plots that were logged prior to the hurricane (Branch et al.’s “Stump Plots”), plots that were salvage logged after the hurricane (Branch et al.’s “Old-growth Plots” outside of the Harvard Tract), and plots that were not logged or salvage logged, but were severely damaged by the 1938 Hurricane (Branch et al.’s “Old-growth Plots” inside the Harvard Tract; Branch et al. 1930, Foster 1988a). Study sites for the logged and salvaged plots were selected by similarity in composition to the Harvard Tract prior to the 1938 hurricane (Branch et al. 1930). Since the Harvard Tract was primarily hemlock (Tsuga canadensis)-pine (Pinus strobus) forest in 1930, only plots that were characterized as pine, hemlock, or hemlock-pine were included in the salvaged and logged treatments. Similarly, since the Harvard Tract was severely damaged by the 1938 hurricane, only plots in the salvaged areas that were severely damaged were selected. Topography and soil type were not explicitly
accounted for in the site selection process. From these criteria, 6 salvaged and 7 logged sites were selected, as well as one site that was hurricane-damaged but not salvaged (i.e. the Harvard Tract; Table 2-1, Figure 2-1).
Table 2-1. Study areas across disturbance histories in Pisgah State Park, NH. Study sites were selected based on vegetation classification (Branch et al. 1930) similar to the Harvard Tract and the extent of the 1938 hurricane damage (Foster 1988a). *Represent plots encompassed by Harvard Tract (includes Old-growth plots 1, 2, 3, 4, 14, 15, 16, 17, 18, 19, 20, 46, 47, 48).

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<th>2016 Site</th>
<th>Disturbance history</th>
<th>Lat. (W)</th>
<th>Long. (N)</th>
<th>1930 status</th>
<th>1930 forest type</th>
<th>Hurricane damage (1939)</th>
<th>Post-hurr. Mgmt</th>
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<td>72.437917</td>
<td>Old growth</td>
<td>Hem-Pine</td>
<td>Severe</td>
<td>None</td>
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<td>Old-growth 5</td>
<td>Sl 5</td>
<td>Salvaged</td>
<td>42.846104</td>
<td>72.449833</td>
<td>Old growth</td>
<td>Hemlock</td>
<td>Severe</td>
<td>Salvaged</td>
</tr>
<tr>
<td>Old-growth 7</td>
<td>Sl 7</td>
<td>Salvaged</td>
<td>42.844183</td>
<td>72.449754</td>
<td>Old growth</td>
<td>Hemlock</td>
<td>Severe</td>
<td>Salvaged</td>
</tr>
<tr>
<td>Old-growth 13</td>
<td>Sl 13</td>
<td>Salvaged</td>
<td>42.846429</td>
<td>72.445796</td>
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<td>Hemlock</td>
<td>Severe</td>
<td>Salvaged</td>
</tr>
<tr>
<td>Old-growth 27</td>
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<td>72.445983</td>
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<td>Hemlock</td>
<td>Severe</td>
<td>Salvaged</td>
</tr>
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<td>Sl 28</td>
<td>Salvaged</td>
<td>42.849100</td>
<td>72.447150</td>
<td>Old growth</td>
<td>Hemlock</td>
<td>Severe</td>
<td>Salvaged</td>
</tr>
<tr>
<td>Old-growth 35</td>
<td>Sl 35</td>
<td>Salvaged</td>
<td>42.844842</td>
<td>72.445925</td>
<td>Old growth</td>
<td>Pine</td>
<td>Severe</td>
<td>Salvaged</td>
</tr>
<tr>
<td>Stump 7</td>
<td>Lg 7</td>
<td>Logged</td>
<td>42.838350</td>
<td>72.437600</td>
<td>Logged</td>
<td>Hemlock</td>
<td>Severe</td>
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<tr>
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<td>Lg 12</td>
<td>Logged</td>
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<td>72.465767</td>
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<td>Hemlock</td>
<td>Moderate</td>
<td>None</td>
</tr>
<tr>
<td>Stump 14</td>
<td>Lg 14</td>
<td>Logged</td>
<td>42.818317</td>
<td>72.465233</td>
<td>Logged</td>
<td>Hem-pine</td>
<td>Moderate</td>
<td>None</td>
</tr>
<tr>
<td>Plot in Branch et al. (1930) study</td>
<td>2016 Site</td>
<td>Disturbance history</td>
<td>Lat. (W)</td>
<td>Long. (N)</td>
<td>1930 status</td>
<td>1930 forest type</td>
<td>Hurricane damage (1939)</td>
<td>Post-hurr. Mgmt</td>
</tr>
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<tr>
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<td>Lg 20</td>
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<td>42.825900</td>
<td>72.476217</td>
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<td>Hem-pine</td>
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<tr>
<td>Stump 21</td>
<td>Lg 21</td>
<td>Logged</td>
<td>42.827433</td>
<td>72.474233</td>
<td>Logged</td>
<td>Hem-pine</td>
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</tr>
<tr>
<td>Stump 22</td>
<td>Lg 22</td>
<td>Logged</td>
<td>42.826650</td>
<td>72.473450</td>
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<td>Hem-pine</td>
<td>Moderate</td>
<td>None</td>
</tr>
<tr>
<td>Stump 27</td>
<td>Lg 27</td>
<td>Logged</td>
<td>42.840700</td>
<td>72.446183</td>
<td>Logged</td>
<td>Pine</td>
<td>Severe</td>
<td>None</td>
</tr>
</tbody>
</table>
Figure 2-1. Map of study sites within Pisgah State Park, including areas logged prior to the 1938 hurricane (“Logged”), damaged by the 1938 hurricane but never salvaged logged (“Hurricane”), and damaged by the 1938 hurricane and subsequently salvage logged (“Salvaged”). See Table 2-1 for details on plot disturbance histories.

2.3.4. Plot measurements

At each site, 2-4 0.05 ha plots were evenly distributed 25 m from the site center, which was determined as the point closest to the original plots established in the 1929 surveys (Branch et al. 1930). At each plot, DBH and species were recorded for all live trees over 10 cm DBH. For stumps (height < 1.3 m), diameter at the tallest solid point was taken and decay class was recorded. Decay classification followed USDA Forest
Inventory and Analysis guidelines (Woodall 2011) using a 5-class system, primarily determined by structural integrity, branch and twig presence, and level of rot and invading roots. For snags (height ≥ 1.3 m), DBH, height, and fragmentation class were recorded (Tyrrell and Crow 1994). Live and dead trees were identified to species or to the lowest taxonomic rank when species was unidentifiable. At each plot, aspect, slope, and elevation were recorded using a clinometer and GPS.

Downed CWD ≥10 cm in diameter was measured using the line intersect method with three 34 m transects established radiating from the site center at 0°, 120°, and 240° (Harmon and Sexton 1996). Diameter, species, and decay class were noted for all intersected pieces. CWD volume was determined using the following formula:

\[ V = \left( \pi \sum d^2 \cdot r / 8L \right) \cdot 10,000 \text{ m}^2/\text{ha} \]

where \( V \) is the volume of CWD (m\(^3\)/ha), \( d \) is the diameter of each CWD piece (m), \( r \) is the reduction factor if decay class is 4 or 5, and \( L \) is the length of the transect (m) (van Wagner 1968). Species-specific reduction factors were applied for CWD pieces in decay classes 4 and 5 (Fraver et al. 2013). CWD biomass was calculated from species- and decay class-specific wood density values (Harmon et al. 2008). Snag volume calculations followed Tyrrell and Crow (1994) and were based on snag height, basal area, and fragmentation class.

In addition to the abovementioned plot-based measurements, 1-ha plots were established around each site center for quantifying microtopography and documenting evidence of pre-hurricane logging and post-hurricane salvage logging. These larger plots encompassed all 0.05 ha plots within a site and were systematically surveyed along
adjacent transects to ensure coverage of the entire ha; stumps, pit and mound structures, and all boles associated with these structures were tallied. The height of pit and mound structures, measured as the difference between the top of the mound and the deepest part of the pit; the species, angle from vertical, and decay class of all stumps; and the species, azimuth of fall, and decay class of all boles were recorded in this larger plot.

2.3.5. Statistical analysis

To examine gradients in species composition across different land-use histories and over time, we used non-metric multidimensional scaling (NMS) ordination on species importance values in PC-ORD Version 6.0 (McCune and Mefford 2011). Data were averaged per site, and species were grouped at the genus or order level to avoid including excessive independent variables in the analysis, except for eastern hemlock, white pine, and American beech (*Fagus grandifolia*), which were abundant enough to count separately (Table 2-2). Individual species’ contributions to the ordination solution were determined by examining the correlation between axis scores and species importance values across sites based on Kendall’s tau ($\tau$).

Similarly, structural characteristics were averaged at the site level, and gradients in variation were examined using NMS. Nine structural attributes, including live trees per ha, live tree quadratic mean diameter (QMD), snags per ha, snag QMD, stumps per ha, coarse woody debris biomass, pit and mound structures per ha, average pit and mound size, and average stump angle, were included in the analysis. Structural data were
relativized by the maximum value of each structural characteristic to avoid bias from differing units (i.e. each variable ranged from 0 to 1).

Differences in composition and structure between disturbance histories were determined using multi-response permutation procedures (MRPP; McCune and Mefford 2011). For the composition data, inventory data from 1930 was included as “old growth” and compared to the contemporary (2016) composition of sites that developed after logging or salvage logging. Structural characteristics of the logged and salvaged areas in 2016 were also analyzed using MRPP. In both cases, the post-hurricane Harvard Tract data (from 2016) were excluded from the MRPP analysis due to the treatment sample size (n = 1).

Several of the structural attributes were also compared between logged and salvaged logged areas using parametric and non-parametric (where necessary; Wilcoxon rank sum test) t-tests. The live-tree diameter distributions between disturbance histories were compared using Kolmogorov-Smirnov tests. Logging intensity at plots logged in 1929 was determined by calculating the proportion of the basal area that was cut (taking the diameter at stump height as the DBH, since stump height was unknown) compared to the basal area of trees that were still standing at the time of the Branch et al. (1930) study. Levels of harvest for white pine and hemlock were calculated separately, and were compared across sites using Wilcoxon rank sum tests. Bonferroni correction with alpha = 0.05 was applied to all tests.
Table 2-2. Species were condensed to genus or order, depending on prevalence, in order to reduce the factors included in the ordination.

<table>
<thead>
<tr>
<th>Category for ordination</th>
<th>Component species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eastern hemlock</td>
<td><em>Tsuga canadensis</em></td>
</tr>
<tr>
<td>White pine</td>
<td><em>Pinus strobus</em></td>
</tr>
<tr>
<td>American beech</td>
<td><em>Fagus grandifolia</em></td>
</tr>
<tr>
<td>Birch</td>
<td><em>Betula alleghaniensis</em></td>
</tr>
<tr>
<td></td>
<td><em>B. lenta</em></td>
</tr>
<tr>
<td></td>
<td><em>B. papyrifera</em></td>
</tr>
<tr>
<td>Maple</td>
<td><em>Acer rubrum</em></td>
</tr>
<tr>
<td></td>
<td><em>A. saccharum</em></td>
</tr>
<tr>
<td>Oak</td>
<td><em>Quercus alba</em></td>
</tr>
<tr>
<td></td>
<td><em>Q. rubra</em></td>
</tr>
<tr>
<td>Other conifer</td>
<td><em>Picea rubens</em></td>
</tr>
<tr>
<td>Other hardwood</td>
<td><em>Fraxinus americana</em></td>
</tr>
<tr>
<td></td>
<td><em>Ostrya virginiana</em></td>
</tr>
<tr>
<td></td>
<td><em>Prunus serotina</em></td>
</tr>
<tr>
<td></td>
<td><em>Ulmus Americana</em></td>
</tr>
</tbody>
</table>
2.4. Results

2.4.1. Overstory composition

Hemlock was the most abundant species within these old-growth stands prior to the hurricane based on basal area (BA; 12.3±2.8 m²/ha) and stem density (123±24 trees/ha), followed by white pine (BA = 7.7±2.1 m²/ha; density = 66±15 trees/ha) and American beech (BA = 0.5±0.2 m²/ha; density = 22±8 trees/ha; Figure 2-2). Seventy-eight years after the 1938 hurricane, white pine was absent from the hurricane-damaged site, while hemlock increased to 860 trees/ha and 46.4 m²/ha BA and beech increased to 250 trees/ha and 11.7 m²/ha BA. In the areas that were salvaged, white pine decreased to 2±2 trees/ha and 0.05±0.05 m²/ha BA, while its density decreased to 32±24 trees/ha in logged areas, with 1.5±1.1 m²/ha BA (Figure 2-2); this was likely driven by one outlying logged site (site lg12 pine density = 173 stems/ha). In the stands that were logged in 1929, a higher proportion of white pine was cut than hemlock (Wilcoxon rank sum test, n = 18, W = 274, p < 0.001).

There was a significant shift in species composition within disturbance histories over time towards increasing maple (Acer spp.), birch (Betula spp.), beech, and oak (Quercus spp.) abundance (logged sites T = -3.084, A = 0.073, p = 0.013; salvaged sites T = -4.503, A = 0.111, p = 0.002; Figure 2-3). These differences were supported by the NMS ordination (stress = 10.98, instability = 0.000), which explained 93% of the variation in species composition along two axes. Most of the variation (51%) was explained by axis 1, which was positively related to hemlock (τ = 0.873, p < 0.001) and negatively related to beech abundance (τ = -0.444, p < 0.001). Axis 2 represented 42% of
the variation in species composition, and was positively related to white pine (τ = 0.669, p < 0.001) and negatively related to birch abundance (τ = -0.563, p < 0.001) and maple (τ = -0.521, p < 0.001). There was no difference in species composition between disturbance histories (MRPP, T = 0.134, A = -0.005, p = 0.461), but most plots decreased on both axes over time, from hemlock and pine towards greater amounts of beech, birch, and maple (Figure 2-3).

![Figure 2-2. Diameter distribution of live trees by species of old-growth plots (a) measured in 1930, and measured in 2016 following (b) hurricane disturbance, (c) salvage logging, and (d) logging prior to the hurricane. Data from 1930 were recorded in irregular bins and are graphed as the bin mean; data from 2016 are binned in 4 cm size classes.](image-url)
2.4.2. Structural characteristics

The hurricane-disturbed site had a higher live tree density (1520 tree/ha) than salvage logged sites after 78 years (838±98 trees/ha; Wilcoxon rank sum test, n = 6, V = 0, p = 0.016) but was not significantly different from sites that were logged prior to the 1938 hurricane (829±43 trees/ha; Wilcoxon rank sum test, n = 7, V = 0, p = 0.031). Live tree QMD at the hurricane-damaged site (19.1 cm) was lower than the other two disturbance histories, which did not differ from each other (salvaged QMD = 24.9±0.9
cm, t-test $t = 3.598$, df = 5, $p = 0.016$; logged QMD = 24.6±1.5 cm; $t = 6.366$, df = 6, $p < 0.001$). Similarly, the distribution of live tree sizes at the hurricane-damaged site differed from those in the other two disturbance histories (Kolmogorov-Smirnov for hurricane-damaged and salvaged sites: $D = 0.187$, $p < 0.001$; for hurricane-damaged and logged sites: $D = 0.176$, $p < 0.001$) and had a greater number of trees in smaller size classes and fewer in larger classes. There was no difference in live-tree size distributions between the salvaged and logged sites ($D = 0.051$, $p = 0.213$; Figure 2-2). Live-tree size distributions were more diverse in logged sites than the hurricane-damaged sites, when binned in 5 cm classes (Shannon’s diversity index, hurricane damaged $H = 1.44$, logged $H = 1.84±0.056$; Wilcoxon rank sum test $V = 28$, $p = 0.016$), but there was no difference in size-class diversity between these disturbance histories and the salvaged areas ($H = 1.81±0.10$, $p > 0.017$, the cutoff for alpha with Bonferroni correction). The hurricane-damaged site had significantly more CWD biomass than the logged sites (Wilcoxon sign rank, $V = 0$, $p = 0.016$) but not the salvaged sites ($V = 0$, $p = 0.031$). All the pieces at the hurricane-damaged site were in decay classes 4 and 5, while all decay classes were present in the salvaged and logged plots (Figure 2-4).

The three disturbance histories were structurally distinct based on nine attributes of live and dead trees and microtopographic structures (MRPP, $T = -3.82$, $p = 0.004$; Table 2-3). This was demonstrated by the separation of plots based on disturbance history in the NMS ordination (stress = 11.6, instability = 0.000), which explained 87% of the variation in structural attributes measured in 2016. Axis 1 captured 56% of the variation in the data and was positively related to live tree QMD ($\tau = 0.661$, $p = 0.010$) and
negatively related to pit and mound density (τ = -0.500, p = 0.016) and stump angle different from vertical (τ = -0.884, p < 0.001); axis 2 explained 31% of the variation in structural characteristics and was negatively correlated with density of pit and mound structures (τ = -0.597, p = 0.004) and pit and mound size (τ = -0.516, p = 0.012). Logged sites generally had more stumps and larger live trees; salvaged plots had intermediate-sized pit and mound structures and stumps that had the highest angle from vertical (Figure 2-5); and the hurricane-damaged site had the most and largest pit and mound structures, and a large amount of CWD (Figure 2-6).

Figure 2-4. Coarse woody debris biomass per hectare, averaged across each disturbance history. Decay classes follow Woodall (2011).
Figure 2-5. Salvage logged sites showed evidence of stumps snapping partway back when the bole was removed. Stump in photo is from *Pinus strobus.*
Figure 2-6. Nonmetric multidimensional scaling ordination based on structural characteristics of hurricane-damaged, logged, and salvage logged sites measured in 2016, 78 years following the 1938 hurricane, with convex hulls delineating treatments.
Table 2-3. Structural characteristics of each site measured in 2016. Pit and mound size was measured as the height from the deepest part of the pit to the top of the mound. (*) denotes characteristics not included in structural ordination.

<table>
<thead>
<tr>
<th>Site</th>
<th>Disturbance</th>
<th>Trees /ha</th>
<th>Live QMD (cm)</th>
<th>Snags /ha</th>
<th>Snag QMD (cm)</th>
<th>Stumps /ha</th>
<th>CWD volume (m$^3$/ha)</th>
<th>CWD biomass (Mg/ha)</th>
<th>Pit and mound size (cm)</th>
<th>Pit and mound /ha</th>
<th>Stump angle (°)</th>
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</thead>
<tbody>
<tr>
<td>HT</td>
<td>Hurricane</td>
<td>1520</td>
<td>19.1</td>
<td>120</td>
<td>22.4</td>
<td>70</td>
<td>75.4</td>
<td>12.02</td>
<td>115</td>
<td>64</td>
<td>10</td>
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<tr>
<td>Lg 12</td>
<td>Logged</td>
<td>880</td>
<td>23.4</td>
<td>87</td>
<td>24.2</td>
<td>200</td>
<td>18.4</td>
<td>3.70</td>
<td>11</td>
<td>53</td>
<td>6</td>
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<tr>
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<td>29.4</td>
<td>47</td>
<td>23.4</td>
<td>160</td>
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<td>3.95</td>
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<td>73</td>
<td>13.0</td>
<td>2.12</td>
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<tr>
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<td>160</td>
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<td>93</td>
<td>23.5</td>
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<td>0</td>
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<td>113</td>
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<td>67</td>
<td>9.8</td>
<td>3.16</td>
<td>3</td>
<td>47</td>
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<tr>
<td>Lg 27</td>
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<td>1000</td>
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<td>126</td>
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<td>7.48</td>
<td>18</td>
<td>48</td>
<td>7</td>
</tr>
<tr>
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<td>26.9</td>
<td>60</td>
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<td>15.4</td>
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<td>21</td>
<td>43</td>
<td>8</td>
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<tr>
<td>Sl 13</td>
<td>Salvaged</td>
<td>705</td>
<td>26.0</td>
<td>165</td>
<td>18.9</td>
<td>35</td>
<td>22.6</td>
<td>4.45</td>
<td>98</td>
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<td>19.4</td>
<td>100</td>
<td>17.0</td>
<td>80</td>
<td>6.7</td>
<td>1.25</td>
<td>118</td>
<td>51</td>
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<tr>
<td>Site</td>
<td>Disturbance</td>
<td>Trees /ha</td>
<td>Live QMD (cm)</td>
<td>Snags /ha</td>
<td>Snag QMD (cm)</td>
<td>Stumps /ha</td>
<td>CWD volume (m³/ha)*</td>
<td>CWD biomass (Mg/ha)</td>
<td>Pit and mound /ha</td>
<td>Pit and mound size (cm)</td>
<td>Stump angle (°)</td>
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</tr>
<tr>
<td>Sl 28</td>
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<td>33</td>
<td>13.6</td>
<td>2.67</td>
<td>75</td>
<td>46</td>
<td>35</td>
</tr>
<tr>
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<td>Salvaged</td>
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<td>120</td>
<td>17.0</td>
<td>30</td>
<td>4.0</td>
<td>0.98</td>
<td>61</td>
<td>48</td>
<td>20</td>
</tr>
<tr>
<td>Sl 5</td>
<td>Salvaged</td>
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<td>29.1</td>
<td>75</td>
<td>27.5</td>
<td>45</td>
<td>53.7</td>
<td>14.12</td>
<td>31</td>
<td>47</td>
<td>6</td>
</tr>
<tr>
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<td>Salvaged</td>
<td>590</td>
<td>27.8</td>
<td>65</td>
<td>30.2</td>
<td>70</td>
<td>33.8</td>
<td>7.62</td>
<td>53</td>
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</table>
2.5. Discussion

The importance of natural, anthropogenic, and compound disturbances in shaping forest successional dynamics and structural development has been widely recognized (Paine et al. 1998, Foster and Orwig 2006, Lindenmayer and Noss 2006, D'Amato et al. 2011). There is concern that the compounding effects of post-disturbance management regimes, such as salvage logging, following natural disturbances may push ecosystems past a threshold of resilience and lead to alternate stable states (Peterson and Leach 2008, Buma and Wessman 2011). To address these concerns, this study took advantage of a unique long-term record of forest recovery following three disturbance histories—logging, hurricane disturbance, and salvage logging—to evaluate the persistence of their effects on old-growth hemlock-pine forests in New England. Generally, we found that overstory composition did not differ between the logged, salvaged, and unmanaged sites, but there was a shift over time away from the pre-disturbance old-growth composition for all three disturbance histories. We also saw long-term reductions in deadwood abundance and microhabitat heterogeneity in salvage logged areas; a result that expands the temporal scale of previously documented short-term effects of this practice (Peterson and Leach 2008, Lang et al. 2009, D'Amato et al. 2011). The long-term persistence of these impacts are particularly important to consider in light of projected increases in disturbance severity and frequency under climate change and associated calls for future applications of salvage logging, as the forest structure and composition will affect its ability to resist and respond to these disturbance (Millar et al. 2007).
Overall, the logged, hurricane-disturbed, and salvage-logged sites in these forests followed similar long-term trajectories in overstory composition. The primary change observed in forest composition over time (1930-2016), regardless of disturbance history, was from hemlock-white pine- to hemlock-hardwood-dominated conditions. Hardwood species were likely successful following each disturbance type due to their ability to sprout (Cooper-Ellis et al. 1999, Barker Plotkin et al. 2012), whereas the shade-tolerant hemlock likely existed as advance regeneration prior to these disturbances and was subsequently released by the mortality of overstory trees (Hibbs 1983). White pine lacks similar regeneration mechanisms and therefore was effectively eliminated from these sites following the mortality of overstory trees either through logging or windthrow.

Factors contributing to the historic dominance of white pine in these forests are unclear (Baiser et al. 2014); however, the conditions following the disturbance examined in this study did not create the regeneration conditions necessary to recruit a new cohort.

The lack of recovery to pre-disturbance compositional conditions we documented following the 1938 hurricane diverges from other studies of hurricanes and severe windstorms that found stands returning to their pre-storm composition (Merrens and Peart 1992, Mabry and Korsgren 1998). This may be driven by the prior composition and developmental stage of the forest. Windstorms favor recovery mechanisms of sprouting and advance regeneration (Peterson and Pickett 1995, Oliver and Larson 1996), allowing forests where those species are dominant to self-replace (Putz and Sharitz 1991, Merrens and Peart 1992, Batista and Platt 2003, Barker Plotkin et al. 2012). Similarly, stands disturbed during early developmental stages often lack shade-tolerant advance
regeneration in the understory, so canopy disturbance is more likely to favor pre-disturbance overstory species when growing space and resources are released (Hibbs 1983, Peterson and Pickett 1995), especially if the stand is severely damaged (Everham and Brokaw 1996, Peterson 2000). In contrast, disturbance may shift forest composition away from pre-disturbance conditions when shade-tolerant advance regeneration of other species is present in the pre-disturbance community (Glitzenstein and Harcombe 1988, Veblen et al. 1991, Holzmueller et al. 2012), a developmental pathway observed in the forests we examined.

The effects of salvage logging on post-disturbance composition have varied in previous studies depending on disturbance type and severity, forest structure and composition prior to the disturbance, and intensity and timing of salvage (Lindenmayer and Noss 2006, Peterson and Leach 2008, Griffin et al. 2013, Royo et al. 2016). Although variable, the short-term impacts of salvage logging on forest composition often include decreasing conifer regeneration, increased sprouting of hardwoods, and invasion of non-forest species due to damage by mechanical disturbance (Van Nieuwstadt et al. 2001, Donato et al. 2006, Greene et al. 2006, Lindenmayer and Ough 2006; but see Peterson and Leach 2008). Our long-term evaluation of salvage logging indicated overstory composition did not differ between salvaged and unsalvaged areas after 78 years. Instead, the abundance of pine declined in both salvaged and unsalvaged areas, which is consistent with the decrease in conifers observed in other work examining wind and salvage logging in hemlock-dominated forests in the Great Lakes Region, USA (Lang et al. 2009).
The importance of structural diversity has been recognized for decades for its influence on forest development and biodiversity (Franklin et al. 2000, Franklin et al. 2002). In our study, logged, hurricane-damaged, and salvaged stands were each characterized by distinct structural conditions more than 75 years after the initial disturbance. This supports other studies that have found that logging and salvage logging alter stand structure with potentially long-term ramifications, including the persistence of pit and mound structures (Kuuluvainen and Laiho 2004, Lang et al. 2009), the presence of snags and downed wood (Kenefic and Nyland 2007, D'Amato et al. 2011, Gustafusson et al. 2012), and live tree dynamics (Palik and Kastendick 2009, Nyland 2016). These structural differences could further influence forest functioning and development. For example, pits and mounds can influence the forest floor microclimate, including temperature and moisture gradients, nutrient cycling, and soil formation, and tree species establishment and success (Carlton and Bazzaz 1998a, b, Ulanova 2000). Pit and mound structures can persist for centuries (Oliver and Stephens 1977, Ulanova 2000), but if they are removed from the landscape they can take decades to centuries to return, as larger trees create larger pit and mounds structures with greater residence times (Sobhani et al. 2014, Barker Plotkin et al. in prep).

Structurally, there appeared to be a tradeoff between live-tree development and microsite heterogeneity from CWD and pit and mound structures. The hurricane-damaged, unsalvaged plot had a high density of small trees, indicative of the stem exclusion phase, whereas sites that were logged prior to the hurricane or salvage logged following the hurricane had larger trees and a more diverse tree distribution, typical of a
more advanced developmental stage (Oliver and Larson 1996). It is possible that the large influx of CWD from the 1938 hurricane (Foster 1988a) and the persistence of damaged and dying trees impeded the development of advance regeneration and new seedlings (Figure 2-7). Much of the CWD consisted of large pine and hemlock boles (Foster 1988a) that decay very slowly (Harmon et al. 1986) and likely occupied space on the ground for extended periods in these forests. Further, poor quality trees that were damaged in the hurricane would have been removed from the salvaged areas, but in the unsalvaged area these trees may have grown more slowly and potentially died after a number of years (Tanner et al. 2014). As a result, released advance regeneration and establishing tree seedlings grew more quickly in logged and salvaged sites relative to unsalvaged areas, resulting in more developed contemporary overstory conditions.

The hurricane-damaged site had the largest volume of CWD, followed by the salvaged areas, while the logged sites had the least (Table 2-3). Although the hurricane site received only one major pulse of deadwood roughly 78 years ago, abundance of coarse wood in this area approaches levels found in old-growth hemlock-dominated systems (Tyrrell and Crow 1994, Ziegler 2000, Gora et al. 2014, D'Amato et al. 2017). All of the CWD at the hurricane-damaged site was well decayed (Figure 2-4), and much of it was from the 1938 hurricane (Foster 1988a). The less-decayed CWD in the salvaged and logged sites, especially of more rapidly decaying hardwood species, implies that these inputs are from more recent disturbances, likely gap-scale events including windthrow, lightning strikes, disease, and self-thinning (E. Sass pers. obs.). This is supported by the larger average log diameter in the Harvard Tract (31.8 cm) compared to
that of the salvaged (20.2 cm) or logged areas (17.8 cm). White pine composed 55% of the CWD volume at the hurricane-damaged site, as opposed to 20% in the salvaged areas. This reduction was even more dramatic in the logged sites, in which white pine comprised only 5% of the CWD volume. Since none of the disturbance scenarios created the conditions necessary to establish a new cohort of white pine, removal of pine by salvaging and logging severely decreased this species’ contribution to contemporary forests in these areas. Moreover, it will be decades before live trees on salvaged sites approach the dimensions of those constituting the deadwood pools in unsalvaged areas, highlighting the long-term impacts of this practice on large deadwood legacies in these forests.

Figure 2-7. The Harvard Tract in Pisgah State Park experienced an influx of large white pine and hemlock CWD following the 1938 hurricane that likely delayed regeneration development in areas with large accumulations of these materials. Photo: S. H. Spurr, 1942.
2.6. Conclusion

Salvage logging remains a controversial practice given the potential for this compounding disturbance to impact forests through shifts in species assemblages, changes in stand structure, and alterations to ecosystem processes (Lindenmayer and Noss 2006). To our knowledge, this study represents the longest investigation into the persistence of salvage logging impacts compared to natural disturbance and pre-disturbance logging on overstory composition and stand structure. While there was no difference in tree species composition between the different disturbance histories, there was a significant shift over time from white pine and eastern hemlock towards birch, beech, and maple.

In contrast to overstory composition, there were still structural differences between disturbance histories after more than 75 years since the hurricane, especially in live tree size, pit and mound density and size, stump angle, and CWD abundance and piece size. These structural differences highlighted a tradeoff between the impacts of salvage logging on the complexity of ground structures and live tree development, with salvaged areas having larger and more diverse tree sizes, but less CWD and fewer pit and mound structures than unsalvaged plots. The value of this tradeoff will depend on the economic, aesthetic, and ecological goals. As hurricanes and other natural disturbances are predicted to become more intense (Dale et al. 2001), some aspects of forest ecosystems may shift regardless of management treatment, like the loss of white pine in these forests. However, other outcomes, such as the persistence of structures on the
landscape and the rate of stand development, may be impacted by management decisions for many decades.

Salvage logging has significantly altered the development of the Pisgah landscape, and structural differences are still noticeable more than 75 years after the initial disturbance. Integrating and retaining disturbance legacies is important to maintain critical ecosystem functioning; preserving a mosaic of unsalvaged and less intensely savaged areas can help increase the resilience and functioning of natural forest systems (Lindenmayer and Noss 2006, O'Hara and Ramage 2013).
CHAPTER 3: LONG-TERM INFLUENCE OF MICROSITE LEGACIES
FOLLOWING HURRICANE DISTURBANCE ON FOREST STRUCTURAL
AND COMPOSITIONAL DEVELOPMENT

3.1. Abstract

Wind disturbance generates heterogeneous patterns of certain microsite structures, including downed logs, uprootings, and pit-and-mound microtopography. While some of these structures provide documented opportunities for regeneration of certain tree species, the long-term influence of microsites and microsite heterogeneity on forest development has not been quantified. We used long-term measurements of an old-growth *Tsuga canadensis*-*Pinus strobus* forest severely damaged by the 1938 hurricane to quantify the long-term impact of the microsite conditions on overstory composition and structure. Specifically, we asked 1) what are the patterns in live-tree size distributions, growth, and mortality five and seven decades after disturbance, 2) what role does microsite heterogeneity and the presence of disturbance-generated structures play in long-term forest development following a severe disturbance; and 3) how do pre-disturbance species composition, topography, and microsite conditions interact to influence post-disturbance vegetation composition? We found that microsite diversity, as well as the density of uprootings and pits, were related to species composition five decades after disturbance with positive correlations with *Betula* spp. and negative correlations with *Fagus grandifolia* abundance, although these relationships did not persist seven decades after the hurricane. Further, microsite diversity was positively correlated with overstory species diversity and stem density and negatively correlated with average tree size both
five and seven decades after the hurricane. These persistent relationships expand our understanding of the importance of microsite conditions in affecting forest development after severe disturbances. Management practices that compromise the creation or persistence of these structures should take into account the long-term ramifications of changes to microsite presence and associated tree species diversity.

3.2. Introduction

Disturbance is a key driver of forest vegetation and structural dynamics (Pickett and White 1985). Forest disturbances are typically quantified by the amount of vegetation killed (i.e., disturbance severity; Oliver and Larson 1996) given its influence on resource availability for species establishment or release following a disturbance event. In many cases, different disturbance agents (e.g., wind, fire) may have dramatically different impacts on forest floor conditions, despite being of comparable severity. Given the importance of forest floor conditions in affecting patterns of recruitment and development, there has been an increasing emphasis on accounting for the long-term influence of post-disturbance microsites on forest development and patterns of diversity (Roberts 2004).

Large, infrequent disturbances often leave unique and heterogeneous patterns of post-disturbance legacies across the landscape (Turner 2010). In temperate forests of northeastern North America, these disturbances are primarily in the form of hurricanes, which have a return interval of 85 to 380 years for hurricanes of F2 or higher severity (Fujita 1971, Boose et al. 2001) and often leave a mosaic of surviving, windthrown and
broken trees (Putz and Sharitz 1991, Foster and Boose 1992, Everham and Brokaw 1996, Prengaman et al. 2008). Pit-and-mound microtopography that is created by uprooting of large trees during these and other wind events can persist for decades to centuries (Oliver and Stephens 1977, Ulanova 2000), with some age estimates exceeding 1000 years old (Schaetzl and Follmer 1990). These structures influence tree establishment patterns, with trees tending to grow on mounds and avoid pits (Lyford and MacLean 1966). Several species preferentially establish on mounds due to exposed mineral soil seedbed conditions and reduced competition from advance regeneration found in undisturbed forest floor areas (Carlton and Bazzaz 1998a, Barker Plotkin et al. in prep). Pit-and-mound microtopography can further shift forest succession through moderation of temperature and moisture gradients on the forest floor and retention of lower leaf litter and greater snow depths (Beatty 1984, Carlton and Bazzaz 1998a, b, Ulanova 2000). They also increase microhabitat heterogeneity, which is thought to result in a greater diversity of regeneration niches, and subsequently higher species diversity (Grubb 1977, Jonsson and Esseen 1990).

Large volumes of coarse woody debris (CWD) are also often generated during hurricanes from windthrow or snapping and can persist for decades (McFee and Stone 1966, Harmon et al. 1986). In some systems, CWD has been shown to support higher seedling establishment rates than other substrates, especially larger diameter pieces in advanced stages of decay (Robert et al. 2012, Chečko et al. 2015). Certain species preferentially regenerate on CWD, particularly smaller-seeded species like *Picea* and *Betula*. (Simard et al. 1998, Marx and Walters 2008, Bolton and D'Amato 2011, Chečko
et al. 2015). The presence of CWD on a site can also moderate temperature and moisture conditions experienced by seedlings following disturbance, as well as potentially protect them from herbivory, allowing higher survival of sheltered seedlings (Gray and Spies 1997). However, high volumes of CWD on the forest floor following extensive windthrow may also inhibit early stages of post-disturbance seedling development by restricting access to space and light (Sass et al. in review).

Despite the documented importance of post-disturbance microsite legacies on seedling establishment, little is known about how patterns in microtopography affect long-term development of stand structure and composition. This study takes advantage of a unique, long-term dataset that follows the development of an old-growth *Tsuga canadensis* (eastern hemlock)-*Pinus strobus* (white pine) forest seven decades following a stand-replacing hurricane in the northeastern US. Specifically, we ask: What are the patterns in live tree size distributions, mortality, and growth five and seven decades after disturbance? What role does microsite heterogeneity and the presence of different structures play in the long-term development of a forest stand following severe disturbance? How do pre-disturbance species composition, topography, and microsite conditions interact to influence current vegetation composition? To our knowledge, this is the first study to directly analyze the effect of microsite variability on long-term forest stand development.
3.3. Methods

3.3.1. Field site

The Harvard Tract is located within Pisgah State Park in southwestern New Hampshire, USA, within the Northern Hardwoods-Hemlock-White Pine region (Westveldt et al. 1956, Griffith et al. 2009; Figure 3-1a). This area had been dominated by old-growth mixed eastern hemlock and white pine forests at the time it was acquired by Harvard University in 1929 (Cline and Spurr 1942, Foster 1988a); however, much of this landscape was severely impacted by the 1938 hurricane and subsequently developed into contemporary forests dominated by hemlock with lesser amounts of red maple, black birch, and American beech (D'Amato et al. 2017). The site is bisected by a north-south trending ridge and ranges in elevation from about 200 to 400 m (Cline and Spurr 1942), which is representative of the surrounding area. For more detail on the Pisgah region and land-use history, see Chapter 2.

3.3.2. Field methods

Data were collected from two east-west transects within the Harvard Tract in order to capture forest conditions across the topographic variability of the site. From 1985 to 1989, Schoonmaker (1992) collected intensive data on live and dead trees, microsites, site topography, and downed dead wood across these transects, which are 10 m x 270 m and 10 m x 300 m and spaced 20 m apart (Figure 3-1b). Each transect is divided into contiguous 10 x 10 m plots that are further subdivided into 1 x 1 m grids for quantifying fine-scale variability in microsite conditions (Schoonmaker 1992; Figure 3-1c). Within
each plot, species, diameter at breast height (DBH), canopy class, and substrate were recorded for all live trees ≥ 2 cm DBH in 1989; plots were remeasured in 2009 (Schoonmaker 1992, D'Amato et al. 2017). Substrate was divided into 8 categories: mounds, pits, uprootings, logs, stumps, thin soil, and bare rock, with areal coverage of each of these categories measured and mapped on the 1 x 1 m grid. Area not in these categories was categorized as undisturbed ground. Bare rock was not included in the analyses for this chapter given that the focus of this work was on evaluating disturbance-mediated substrate conditions, and the occurrence of this substrate type was directly related to topographic position (i.e., on the ridge tops). Pre-1938 vegetation was also reconstructed across each transect based on measurement and analysis of downed wood (Schoonmaker 1992). Specifically, measurements of piece length, diameter at base and tip, estimated DBH, fall orientation, and cause of fall (i.e., snap, windthrow) were used to determine pre-hurricane forest structural and compositional conditions.
Figure 3-1. (a) The Harvard Tract is located in southwestern New Hampshire. (b) In 1989, two transects running east-west were laid out across the Harvard Tract. Each red square represents a 10 x 10 m plot within the transect. (c) At each 10 x 10 m plot, microsites and live and dead trees were mapped onto a 1 x 1 m grid.
3.3.3. Data manipulation

Microsite diversity, species diversity, and tree size diversity were calculated using Shannon’s diversity index \( H \) at the plot level (10 x 10 m). For tree size diversity, individual trees were grouped into 4 cm bins. Average tree size was based on quadratic mean diameter (QMD). Biomass was calculated by converting tree volume estimates based on Honer (1967) and Honer et al. (1983) to biomass based on species-specific wood density values (Harmon et al. 2008). Net growth increment was defined at the plot level as the total live-tree biomass gained between 1989 and 2009. Mortality rate was determined at the plot level and by diameter class for all trees present in 1989 (Sheil and May 1996, Silver et al. 2013). Slope and aspect were manually extracted from the linear cross-section of the transects (Schoonmaker 1992, D'Amato et al. 2017). Slope per plot was classified as flat, moderate, or steep; aspect was classified as flat, west, or east.

3.3.4. Analyses

The influence of microsite diversity \( H \) on forest structural and compositional development was examined using linear mixed effects models in R (R Core Team 2014) with the package lme (Pinheiro et al. 2017). Separate models were developed predicting tree species \( H \), QMD, tree size \( H \), stem density, and total basal area as a function of microsite diversity, with year (1989 and 2009) as a random effect. Normal distributions and Gaussian families were selected for each regression. The relationship between microsite \( H \) and mortality rate, and microsite \( H \) and growth increment were examined using generalized linear models (R Core Team 2014), since there was only one metric for each plot across the 20 years of the study. The shape of diameter distributions were
quantified following Janowiak et al. (2008) using the corrected Akaike’s Information Criterion (AICc) to compare models, with the best model determined as the simplest model within 10 \( \Delta \text{AIC}_c \) units of the lowest AICc score.

Nonmetric multidimensional scaling (NMS) ordination scores calculated in PC-ORD were used to reduce the dimensionality of tree species composition and microtopographic structure data (McCune and Mefford 2011). The species composition importance values, a metric combining stem density and size, were condensed into eight categories before being input into the ordination: *Acer* spp. (*Acer saccharum* and *A. rubrum*), *Betula* (*Betula alleghaniensis*, *B. lenta*, and *B. papyrifera*), and other hardwood (*Fraxinus americana*, *Ostrya virginiana*, *Prunus serotina*, and *Ulmus americana*), while *Fagus americana*, *Quercus rubra*, *Picea rubens*, *Pinus strobus*, and *Tsuga canadensis* were included individually. Species scores were compared to secondary matrices of 1938 reconstructed species composition importance values, microsite structures by area, slope, and aspect. Levels of significance for the relationships between the axis scores and input and secondary variables were calculated in R (R Core Team 2014), using Bonferroni’s correction to adjust cutoffs for significance with multiple comparisons. Composition data from 1989 and 2009 were run separately to account for potential shifts in community organization over time and to examine the influence of microsite conditions in affecting these patterns over time based on the strength of correlations with secondary variables.
3.4. Results

Across all the transects, 1581 trees were measured in 1989 and 974 were measured in 2009. Live tree QMD averaged 14.0±0.6 cm 51 years after the hurricane (in 1989, range = 7.2 - 27.9 cm) and increased to 18.0±0.6 cm after 71 years (in 2009, range = 9.8 to 31.7 cm). Basal area after 51 years averaged 36±1 m²/ha (range = 13 - 55 m²/ha) and increased to 42±2 m²/ha 71 years after the hurricane (range = 16 - 67 m²/ha). Stem density 51 years post-hurricane (1989) ranged from 300 to 6800 stems/ha, averaging 2770±180 across all plots; 71 years post-hurricane (2009) densities decreased to 1710±100 stems/ha (range = 300 to 3700). The diameter distribution after 51 years followed a negative exponential curve (Figure 3-2a; the distribution followed an increasing-γ shape after 71 years (Figure 3-2b).
Figure 3-2. Live-tree diameter distribution a) 51 and b) 71 years after hurricane disturbance (1989 and 2009, respectively) at the Harvard Tract in Pisgah State Park, NH. Trees are binned in 4 cm diameter classes. Lines and shading represent smoothed conditional means ± standard error for best approximating curve.

Plot-level mortality rates averaged 2.2±0.1 trees/ha/year and ranged from no mortality to 47 trees/ha/year. Mortality was highest for trees in the smallest size classes and generally descended monotonically with increasing size until the largest size classes,
although there was high variability between plots (Figure 3-3). This pattern held for both shade-tolerant and -intolerant species groups (data not shown). Growth increment averaged 2.19±0.10 Mg/ha/year and ranged from 0.74 to 3.90 Mg/ha/year across all plots.

Over half of the area in the transects was undisturbed ground, with the seven measured structures comprising 38% of the transect area (Figure 3-4). Microsite diversity, as measured by Shannon’s diversity index (H), was positively correlated with tree species H (slope estimate = 0.421±0.107, t=3.921, p = 0.0002; Figure 3-5a) and tree density (lme estimate = 0.421±0.107, t = 3.921, p = 0.0002; Figure 3-5b) and negatively correlated with QMD (lme estimate = -4.573±1.341, t = -3.411, p = 0.0009; Figure 3-5c). There was no relationship between microsite H and live-tree size H, mortality rate, basal area, or growth increment (p > 0.05).

Tree species importance values 51 years after the hurricane were best described by two axes in the NMS ordination (stress = 16.7, instability = 0.0000). Axis 1 explained 34.3% of the variability and was positively correlated with birch abundance (τ = 0.511, p < 0.0001) and negatively correlated with beech (τ = -0.608, p < 0.0001). Axis 2 described 51.6% of the variability and was driven by increasing hemlock abundance (τ = 0.166, p < 0.0001) in the positive portions and increasing maple (τ = -0.093, p < 0.0001) in the negative portions. Microsite diversity was positively correlated with Axis 1 (τ = 0.378, p < 0.0001), as was the area in uprootings (τ = 0.332, p = 0.0003) and pits (τ = 0.403, p < 0.0001; Figure 3-6a).

Similarly, 71 years after the hurricane, species composition was also described by two axes (stress = 12.6, instability = 0.0000), with 59.7% of the variability explained by
Axis 1 and 32.6% explained by Axis 2. Axis 1 was positively correlated with hemlock abundance ($\tau = 0.815$, $p < 0.0001$) and negatively correlated with birch ($\tau = -0.281$, $p = 0.002$) and beech abundance ($\tau = -0.518$, $p < 0.0001$). Axis 2 was correlated with increasing birch ($\tau = 0.350$, $p = 0.0001$) and hemlock ($\tau = 0.306$, $p = 0.0008$) in the positive portions and increasing maple abundance in the negative portions ($\tau = -0.778$, $p < 0.0001$). There were no significant correlations between either axis and any of the secondary variables ($p > 0.0019$; Figure 3-6b).
Figure 3-3. Mortality rate by diameter class of all trees alive 51 years after the hurricane (1989) and remeasured 71 years after the hurricane (2009); trees are binned in 4 cm size classes. Boxes represent variability in plot-level mortality. Numbers at the base of each bar represent trees present in each size class 51 years after the hurricane.
Figure 3-4. Percent cover of seven microsite categories measured 51 years after the hurricane disturbance (1989) averaged over all plots and both transects. Area not in the seven listed categories was undisturbed ground. Note that area in rock was excluded from subsequent analyses.
Figure 3-5. Microsite diversity (H) as measured 51 years after the 1938 hurricane (i.e. in 1989) was correlated with a) tree species diversity, b) stem density, and c) average tree size both 51 and 71 years after the hurricane (in 1989 and 2009, respectively). Grey shading indicates 95% confidence interval.
Figure 3-6. Ordination based on species importance values a) 51 years after the hurricane disturbance (in 1989) and b) 71 years after the hurricane (in 2009), with four-letter codes showing locations of highest species’ importance. ACER = Acer spp.; BETULA = Betula spp.; FAGR = Fagus grandifolia; HDWD = other hardwood spp. including Fraxinus americana, Ostrya virginiana, Prunus serotina, Quercus rubra, and Ulmus americana; PIRU = Picea rubens; PIST = Pinus strobus; TSCA = Tsuga canadensis. Slope, pits, uprootings, and diversity of microtopographic structures (microH) had an $r^2 > 0.10$ in 1989; slope, aspect, and microH had an $r^2 > 0.05$ in 2009; lines show direction of correlation for each variable.
3.5. Discussion

Microsite conditions generated by disturbances affect succession and structural development, but our understanding of the influence of microsite patterns, including variability, on forest development has generally been limited to the first few years following disturbance. This study takes advantage of a long-term dataset following an old-growth hemlock-pine stand that was severely damaged in the 1938 hurricane to determine the influence of microsite variability and conditions on post-disturbance stand development over seven decades. Areas with greater microsite diversity supported a higher diversity of tree species 51 and 71 years following the hurricane, which is consistent with short-term findings from other work and long-term predictions based on general niche theory (Grubb 1977). Structural development, as quantified by QMD and stem density, was less advanced in areas with greater microsite diversity, likely reflecting greater levels of species packing in these areas (Ishii and Asano 2010). However, higher microsite diversity was not correlated with productivity (i.e. growth increment), potentially due to greater mortality on uprootings decreasing gross biomass accumulation. We also saw that microsite diversity as well as certain structures (i.e. pits and uprootings) were significantly correlated with overstory tree composition 51 years after the hurricane, but this influence decreased by 71 years likely due to the limited longevity of some of the species that preferentially established on certain microsites (e.g., *Betula papyrifera*; Barker Plotkin et al. in review). Collectively, these results reinforce the importance of disturbance legacies, namely microsite structures and forest floor
heterogeneity, in affecting patterns of development following severe disturbance events, particularly in relation to patterns of tree diversity and forest structural development.

The changes in forest structure 51 to 71 years after the 1938 hurricane followed general post-disturbance patterns described elsewhere, with increasing average tree size, increasing basal area, and decreasing stem density over time (Bormann and Likens 1979). We also saw a shift in diameter distribution, from negative exponential to increasing-$q$, as smaller trees grew or died and were not replaced by ingrowth into those size classes. This is consistent with other studies following even-aged cohorts after stand-replacing events (Goff and West 1975, Schwartz et al. 2005, Zenner 2005, Janowiak et al. 2008).

Although the stands examined in the present study were in an uneven-aged, old-growth condition prior to the 1938 hurricane, the near-complete removal of overstory trees by the 1938 hurricane (Foster 1988a) functionally generated a single-cohort stand through the release of advance regeneration and establishment of new seedlings.

Mortality rate was variable, with trees in the smallest size classes comprising the highest levels of mortality, similar to the size-mortality relationships seen in other single-cohort, self-thinning temperate forests (Lorimer et al. 2001, Coomes and Allen 2006). Mortality rates for shade-tolerant trees followed a descending monotonically relationship with diameter, similar to patterns found by Lorimer et al. (2001); however, the intolerant species in this system also followed this pattern, which is potentially due to their representation being low relative to the beech, hemlock, and red maple that dominated after the 1938 hurricane. In addition, work examining mortality patterns on different microsites at this site demonstrated that mortality over this period was higher on mounds.
and pits, where intolerant and mid-tolerant species largely recruited after the 1938 hurricane, whereas shade-tolerant species recruiting prior to 1938 were on other substrates (e.g., forest floor; Barker Plotkin et al. in prep).

The distribution and abundance of microsites created by the 1938 hurricane remained an important driver of patterns of forest compositional and structural conditions five and seven decades after this event. Microsite diversity was related to the first axis of the species composition ordination 51 years after the hurricane (in 1989), which was also associated with birch abundance, a genus requiring either exposed mineral soil or decayed wood microsites (Hutnik 1952, Smallidge and Leopold 1994, Carlton and Bazzaz 1998a), and it was negatively associated with beech abundance, a species largely establishing from advance regeneration or sprouting. Similarly, the density of uprootings was correlated with this axis, emphasizing the documented benefit of these structures for birch (Hutnik 1952, Henry and Swan 1974, Carlton and Bazzaz 1998a, Kuuluvainen and Pauli 1998). The positive correlation of pits with that axis was probably due to the close proximity in which these features occur to uprootings and the scale at which we quantified microsites (i.e. an uprooting is usually associated with a pit). However, these correlations were not seen 71 years after the hurricane (in 2009), likely due to mortality of many of the smaller trees (Figure 3-3), especially those on mounds, which were predominantly birch (Barker Plotkin et al. in prep).

Microsite diversity also had lasting impacts on species diversity, with plots with higher microsite diversity having more diverse overstory composition. Other studies have demonstrated the importance of particular microsite structures that promote coexistence
of species that would otherwise disappear from a stand, as well as a range of microsite conditions for maintaining species diversity (Jonsson and Esseen 1990, Carlton and Bazzaz 1998a, von Oheimb et al. 2007, Marx and Walters 2008, Chećko et al. 2015). In the more microsite-diverse plots, the tree species mixture was likely stratified, with a smaller, tolerant understory below the more intolerant overstory. Stratification was supported by the positive relationship between microsite diversity and stem density and the negative relationship between microsite diversity and plot-level QMD. Despite the positive relationships between microsite diversity and tree density, we did not see any evidence of higher productivity in these plots, as has been observed in studies of other stratified mixtures (Kelty 1989). Much of the regeneration at the Harvard Tract following the hurricane established prior to this event (Foster 1988a), emphasizing the importance of these disturbance-mediated microsites for establishment and persistence of other species in these forests.

3.6. Conclusion

This study expands our understanding of the long-term development of temperate forest ecosystems following stand-replacing wind and the influence of microsite structures and diversity on forest structure and composition. As has been observed with other short-term examinations, certain structures, namely tip-up mounds, play a critical role in the maintenance of small-seeded, less tolerant tree species in these forests due to favorable seedbed conditions and an absence of advance regeneration from more tolerant species. Moreover, the diversity of microsites in a given area has a strong influence on
long-term patterns in species diversity, stand density, and average tree size. These disturbance-mediated structures can persist for decades or centuries, but if removed can take as long to develop. Understanding the long-term ramifications of management practices that alter or remove microsite structures or decrease microsite diversity will be important for achieving species diversity and structural development goals.
CHAPTER 4: SUMMARY

4.1. Conclusions and implications

The goal of this study was to further our understanding of how forests develop after severe natural, anthropogenic, and compound disturbances, and how tree species composition and overstory and forest floor structure vary many decades after the initial disturbance. We found that *Pinus strobus*, a large component of the pre-disturbance overstory, was largely removed across all three management histories. In old-growth areas that were severely damaged by the hurricane but were not salvage logged, post-disturbance legacies including uprootings, coarse woody debris (CWD), and snags (Foster 1988a) persisted eight decades after the hurricane. These complex microsite conditions potentially contributed to species diversity and modern species composition, with plots with higher microsite diversity tending towards a higher birch component and a lower beech component five decades following disturbance. However, species composition was not significantly different in the sites that were logged prior to or salvaged logged following the hurricane, which may reflect the strong dominance of all these areas by hemlock released by each disturbance event. In logged sites and hurricane-damaged, salvaged sites, trees tended to be larger and tree density lower than in the hurricane-damaged site, indicating that the hurricane-damaged site was in a less advanced stage of stand development than the managed sites.

The decrease in white pine across all sites, regardless of management history, represents the dramatic influence disturbance can have on compositional development, with or without human interference. It is not clear what originally led to the dominance of...
white pine in these previously unmanaged areas (Baiser et al. 2014). White pine can
thrive on a range of soil types, and in the pre-settlement forests it tended to dominate in
areas with sandy soils and frequent disturbance and was especially prevalent in pockets in
2002). In the 1800s, old-field abandonment also led to the dominance of white pine in
many sites across the northeast (Abrams 2001). Our study site was in the old-growth
condition prior to the logging and hurricane disturbances, but the susceptibility of white
pine to each disturbance type (Foster 1988b) and white pine’s absence from the current
overstory indicates that composition may shift if sufficient regeneration does not
establish and survive. It is possible that the lack of white pine regeneration was due to the
lack of available seed source, and if there had been a mast year prior to the hurricane
there would have been substantial white pine regeneration. Further, in logged and
salvage-logged sites, the large standing white pine and large white pine CWD that was
removed from the forest system will not be replaced for centuries.

We also saw differences in the structural characteristics between sites with
different management histories eight years following major disturbance, as well as
variability within the hurricane-damaged plots. While some studies have shown that
certain biological legacies (i.e. remnant old-growth trees) enhance the rate of stand
development following disturbance (Keeton and Franklin 2005, Seidl et al. 2014), this
study presents evidence that other legacies, including large volumes of CWD and higher
microsite variability, may lead to slower stand reinitiation and development. Specifically,
stands that were not salvaged appeared developmentally younger, and plots with higher
microsite diversity had smaller average stem size and a higher density of stems. This is likely due to the huge influx of dead and dying trees that potentially inhibited regeneration through their occupation of space and shading of the understory. While the salvaged stands arguably experienced the most severe disturbance in this system (Buma and Wessman 2011) given that the severe hurricane disturbance was followed by deadwood removal and associated ground disturbance, the deadwood removal appears to have led to stand development trajectories similar to the stands that were logged prior to the hurricane. In addition, we quantified stand development by average tree size, stem density, and compositional conditions multiple decades after the disturbance, as opposed to by the rate of seedling establishment of certain species or by carbon sequestration rates (Keeton and Franklin 2005, Bradford et al. 2012, Seidl et al. 2014).

While this study provides the longest analysis, to date, of the impact of salvage logging and the role of microsite variability in forest development, there are several limitations that should be considered and further explored. This study encompasses a relatively small geographic area, and one of our management histories is represented by only one site, so extrapolation to region-wide dynamics is restricted. Also, a true, undisturbed control treatment was lacking, which would have allowed direct comparison to the three different disturbance histories and allowed us to differentiate the effects of the different disturbances from undisturbed forest development. We measured tree DBH, but directly determining tree age by extracting tree increment cores would enable a more detailed history of establishment and release and their relationship with disturbance events. Finally, this study only investigated the effects and interactions of disturbance
history on overstory and ground structures. Further study into the dynamics of understory plants, regeneration, and other communities (e.g. microbial, soil fungi, etc.) would enhance our understanding of the long-term influence of disturbance history on forest ecosystem development and functioning.

Based on the long-term influence of management history and of microsite conditions on forest structural and compositional development, it is important to incorporate these impacts into management options such as salvage logging. Specifically, salvaging within a mosaic of intensities, with some areas completely excluded from salvage, will enhance the persistence of disturbance legacies, including pit-and-mound microtopography, large CWD, snags, and microsite variability to maintain ecosystem functioning across the landscape (Lindenmayer and Noss 2006, O'Hara and Ramage 2013). Further, retention of old-growth characteristics such as large trees will encourage the subsequent development of large uprootings, snags, and CWD (Keeton 2006). Treatments that promote the creation of microsite diversity will potentially increase the available regeneration niches and the species diversity, supporting the forest’s resilience to stressors that may be increasing with climate change (Millar et al. 2007). As natural disturbances, including hurricanes, are predicted to become more frequent and more intense (Dale et al. 2001), it is important to understand how these disturbances interact with management decisions to alter forest development in the long-term.
REFERENCES

Abrams, M. D. 2001. Eastern white pine versatility in the presettlement forest: this eastern giant exhibited vast ecological breadth in the original forest but has been on the decline with subsequent land-use changes. BioScience 51:967-979.


