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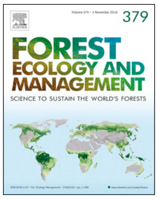

Lasting legacies of historical clearcutting, wind, and salvage logging on old-growth *Tsuga canadensis-Pinus strobus* forests

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ABSTRACT

Disturbance events affect forest composition and structure across a range of spatial and temporal scales, and subsequent 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 with some subsequent damage 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* 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 structures 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 sites, 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 important structural legacies over the long term.

1. 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 disturbances 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 historical role of these events in affecting forest dynamics within managed and natural landscapes will help anticipate their future impacts (Dale et al., 2001).

Severe windstorms, including hurricanes, affect forests around the world, but the impacts of hurricanes on forest development can vary considerably depending on forest conditions at the time of disturbance (Everham and Brokaw, 1996; Mitchell, 2013). While some hurricane-damaged forests return to their prior composition (Hibbs, 1983; Mabry

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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, 1988; Schwarz et al., 2001; Busing et al., 2009; Trammell et al., 2017). 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). Salvage logging 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). Salvage logging 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; Priewasser et al., 2013; Taylor et al., 2017), and pit-and-mound microtopography (Waldron et al., 2014; Fraver et al., 2017). CWD and pit-and-mound microtopography play an important role in many temperature forests through affecting patterns of nutrient cycling (Harmon et al., 1986; Schaetzl et al., 1988) and temperature and moisture (Gray and Spies, 1997; Peterson et al., 1990), as well as serving as an important substrate for germination of small-seeded and shade-intolerant tree species (Lyford and MacLean, 1966; Bolton and D'Amato, 2011; Chećko et al., 2015). 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 (Rumbaitis del Rio, 2006; Lindenmayer et al., 2008; Cobb et al., 2011; Blair et al., 2016; Lindenmayer et al., 2017). 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).

Northeastern North America has experienced several severe hurricanes in the last 500 years, with extensive salvage logging following the 1938 hurricane (NETSA, 1943), allowing us to investigate long-term forest trajectories following different management histories. Areas within Pisgah State Park in southwest New Hampshire offer a unique opportunity to directly compare old-growth forest stands that were: (1) logged prior to the 1938 hurricane before being damaged by the hurricane ("logged"), (2) damaged by the 1938 hurricane and never salvage logged ("hurricane"), and (3) damaged by the 1938 hurricane and subsequently salvage logged ("salvaged"; Branch et al., 1930; NETSA, 1943; Foster, 1988). Research conducted before the hurricane represents pre-disturbance condition (Cline and Spurr, 1942), and research following 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. 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 how the stands under different disturbance histories compare to the pre-disturbance composition. To our knowledge, this study represents the longest timeframe over which the impacts of salvage logging have been investigated.

2. Materials and methods

2.1. 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 to 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, 1988). By the 1880s, almost all but 300 ha of the forest had been logged, with additional logging occurring in the 1920s (Foster, 1988). 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, 1988). 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, 1988).

2.2. 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 surveyed 91 0.04 ha plots across the forested upland area in 1930: 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 (Branch et al., 1930; data available at harvardforest.fas.harvard.edu/harvard-forest-data-archive). At each old-growth plot, they recorded the species and diameter at breast height (DBH; 1.3 m) of each tree. In the logged plots, they identified the species and diameter of each stump, as well as the former measurements on the remaining, uncut trees. Foster (1988) used aerial photos from 1939 to determine the extent of the damage from the 1938 hurricane.

2.3. 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

Table 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, 1988).

Plot in Branch et al. (1930)	2016 Site	Disturbance history	Lat. (W)	Long. (N)	1930 status	1930 forest type	Hurricane damage (1939)	Post-hurr. Mgmt	Sampling intensity (plots in 2016)
Multiple[a]	Hr	Hurricane	42.82936	72.43791	Old growth	Hem-Pine	Severe	None	2
Old-growth 5	Sl 5	Salvaged	42.84610	72.44983	Old growth	Hemlock	Severe	Salvaged	4
Old-growth 7	Sl 7	Salvaged	42.84418	72.44975	Old growth	Hemlock	Severe	Salvaged	4
Old-growth 13	Sl 13	Salvaged	42.84642	72.44579	Old growth	Hemlock	Severe	Salvaged	4
Old-growth 27	Sl 27	Salvaged	42.84775	72.44598	Old growth	Hemlock	Severe	Salvaged	3
Old-growth 28	Sl 28	Salvaged	42.84910	72.44715	Old growth	Hemlock	Severe	Salvaged	3
Old-growth 35	Sl 35	Salvaged	42.84484	72.44592	Old growth	Pine	Severe	Salvaged	4
Stump 7	Lg 7	Logged	42.83835	72.43760	Logged	Hemlock	Severe	None	3
Stump 12	Lg 12	Logged	42.81711	72.46576	Logged	Hemlock	Moderate	None	3
Stump 14	Lg 14	Logged	42.81831	72.46523	Logged	Hem-pine	Moderate	None	3
Stump 20	Lg 20	Logged	42.82590	72.47621	Logged	Hem-pine	Moderate	None	3
Stump 21	Lg 21	Logged	42.82743	72.47423	Logged	Hem-pine	Moderate	None	3
Stump 22	Lg 22	Logged	42.82665	72.47345	Logged	Hem-pine	Moderate	None	3
Stump 27	Lg 27	Logged	42.84070	72.44618	Logged	Pine	Severe	None	3

[a] Plots encompassed by Harvard Tract include Old-growth plots 1, 2, 3, 4, 14, 15, 16, 17, 18, 19, 20, 46, 47, 48 (Branch et al., 1930).

time. The Harvard Tract was severely damaged by the 1938 hurricane and was not salvaged; a study site there represented the trajectory of severe natural disturbance. Of the areas that were logged prior to the hurricane or salvage logged after the hurricane, we selected sites that had pre-disturbance composition similar to the Harvard Tract (i.e. dominated by hemlock or pine; Branch et al., 1930). Similarly, in order to control for natural disturbance severity between salvaged and non-salvaged treatments, we selected sites in the salvaged areas that were severely damaged by the hurricane (Foster, 1988). 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 (Table 1, Fig. 1). Prior to the 1938 hurricane, 14 plots were established in the Harvard Tract, which were remeasured as one site in 2016 given the relatively small size of the Tract.

2.4. 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 1930 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 (Sollins, 1982) 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 compass, clinometer, and GPS, respectively.

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:

$$V=\frac{\pi^2\sum d^2 r}{8L}$$

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 were based on snag height, basal area, and fragmentation class (Tyrrell and Crow, 1994).

Surrounding each site center we established 1-ha plots to quantify microtopography and to document 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 was measured as the difference between the top of the mound and the deepest part of the pit. For each stump, we recorded species, decay class, and angle from vertical; stumps frequently snap back following salvage logging (Fraver et al., 2017), and this study offered the opportunity to quantify the long-term decay and potential differences of these structures between disturbance histories.

2.5. 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 (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 (Appendix A). 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 (τ).

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, CWD 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 unsalvaged data from 2016 were excluded from the MRPP analysis due to the treatment sample size ($n = 1$).

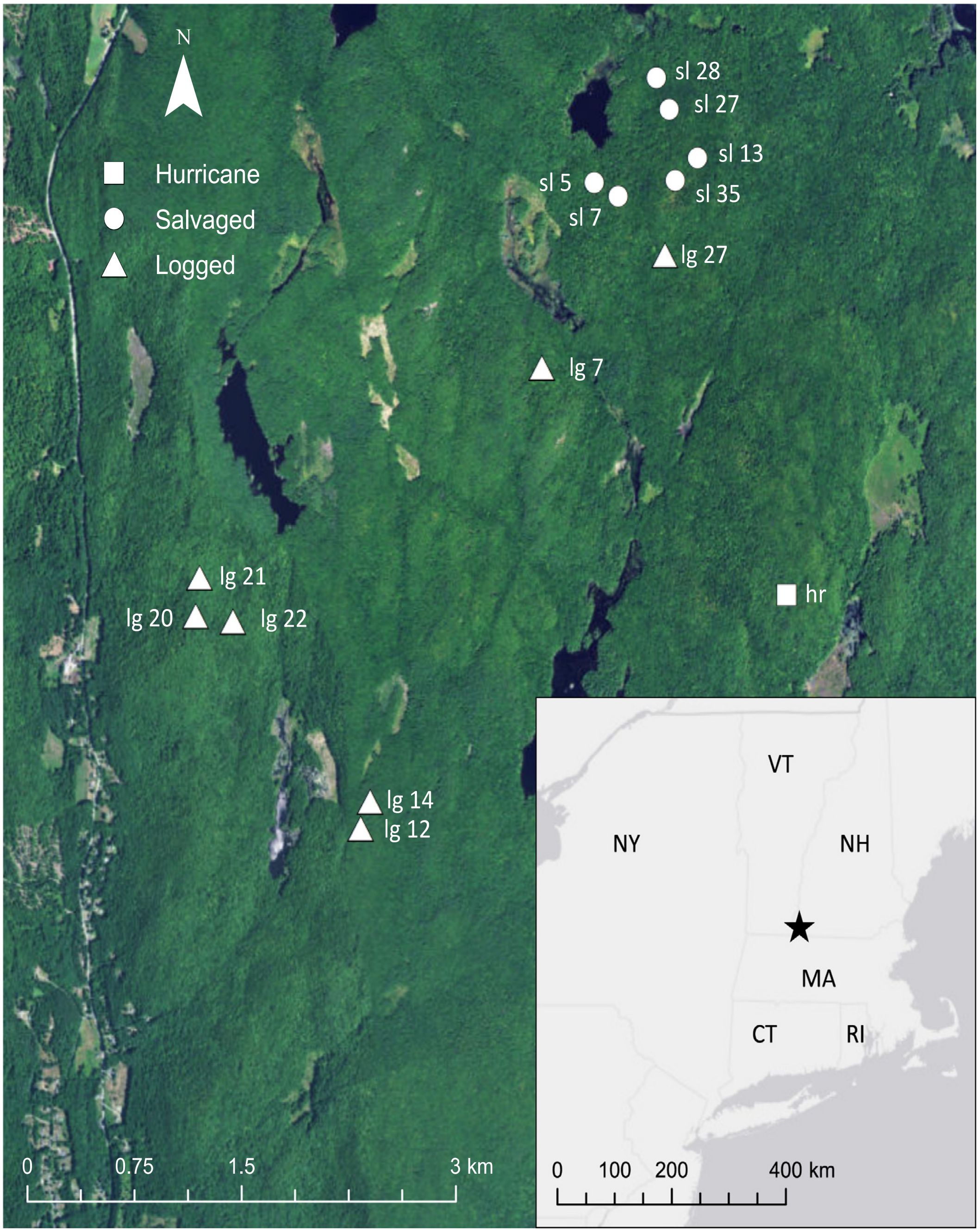

Fig. 1. Map of study sites within Pisgah State Park, including areas logged prior to the 1938 hurricane ("Logged"), damaged by the 1938 hurricane but never salvaged logged ("Hurricane"), and damaged by the 1938 hurricane and subsequently salvage logged ("Salvaged"). See Table 1 for details on plot disturbance histories. Basemap sources: ESRI, DigitalGlobe, GeoEye, i-cubed, USDA, FSA, USGS, AFX, Getmapping, Aerogrid, IGN, IGP, swisstopo, DeLorme, HERE, MapmyIndia, and the GIS User Community.

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 of the three disturbance histories in 2016 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.

2.6. *Spatial autocorrelation*

Due to the opportunistic nature of the original measurements in 1930 (Branch et al.), sites were not located randomly nor evenly distributed across the landscape (Fig. 1). Mantel tests were used to determine potential autocorrelation between site location and composition in 1930, composition in 2016, and structural characteristics in 2016. Distance matrices were created for species importance values and structural characteristics to test the influence of location on composition and structure; distance matrices were also created for individual species groups and individual structural characteristics. Mantel tests were calculated in R (Dray and Dufour, 2007). The direction of the correlation was determined through a correlogram matrix of latitude and longitude with compositional and structural factors (Wright, 2015).

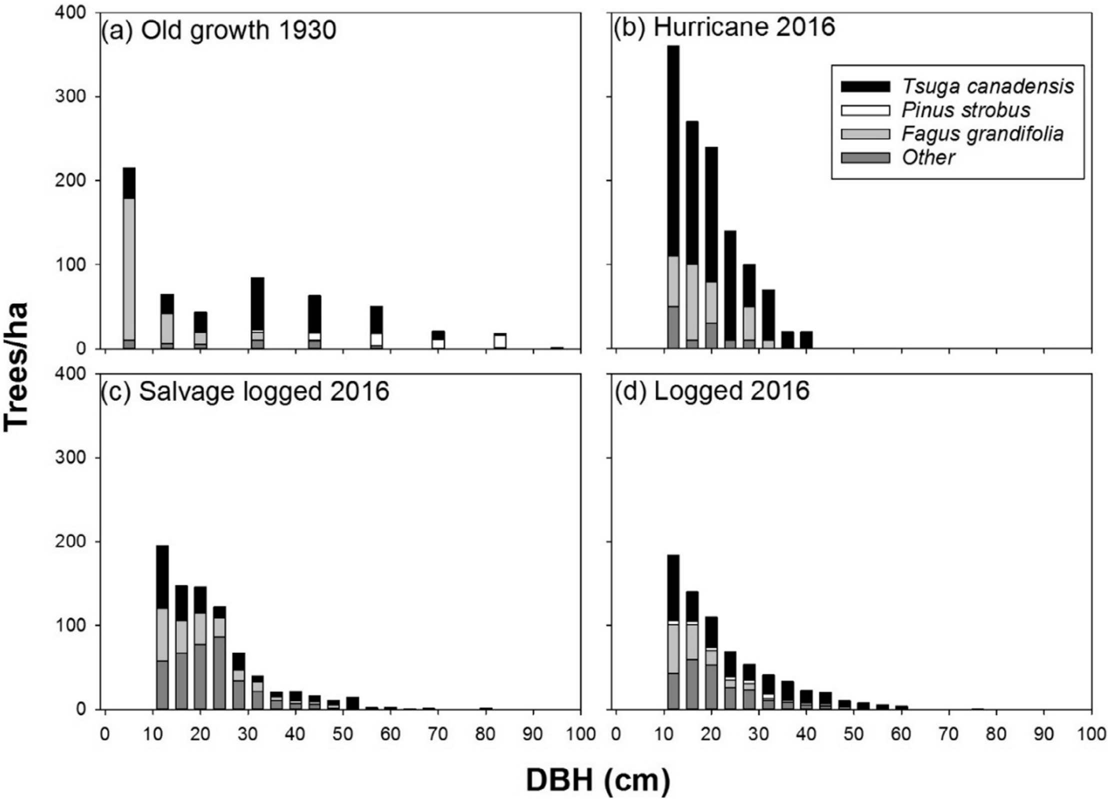

Fig. 2. Diameter distribution of live trees by species of old-growth plots (a) measured in 1930, and measured in 2016 following (b) hurricane disturbance, (c) salvage logging, and (d) logging prior to the hurricane. Data from 1930 were recorded in irregular diameter-class bins and are graphed as the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

3. Results

3.1. 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 m^2/ha) and stem density (123 ± 24 trees/ha), followed by white pine (BA = 7.7 ± 2.1 m^2/ha; density = 66 ± 15 trees/ha) and American beech (BA = 0.5 ± 0.2 m^2/ha; density = 22 ± 8 trees/ha; Fig. 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 m^2/ha BA and beech increased to 250 trees/ha and 11.7 m^2/ha BA. In the areas that were salvaged, white pine decreased to 2 ± 2 trees/ha and 0.05 ± 0.05 m^2/ha BA, while its density decreased to 32 ± 24 trees/ha and 1.5 ± 1.1 m^2/ha BA in logged areas (Fig. 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 (MRPP, logged sites $T = -3.084$, $A = 0.073$, $p = 0.013$; salvaged sites $T = -4.503$, $A = 0.111$, $p = 0.002$; Fig. 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 ($\tau = 0.873$, $p < 0.001$) and negatively related to beech abundance ($\tau = -0.444$, $p < 0.001$). Axis 2 represented 42% of the variation in species composition, and was positively related to white pine ($\tau = 0.669$, $p < 0.001$) and negatively related to birch ($\tau = -0.563$, $p < 0.001$) and maple abundance ($\tau = -0.521$, $p < 0.001$). 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 (Fig. 3).

3.2. 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 ($D = 0.051$, $p = 0.213$; Fig. 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 $H = 1.84 \pm 0.056$; 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 ($H = 1.81 \pm 0.10$, $p > 0.017$, 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

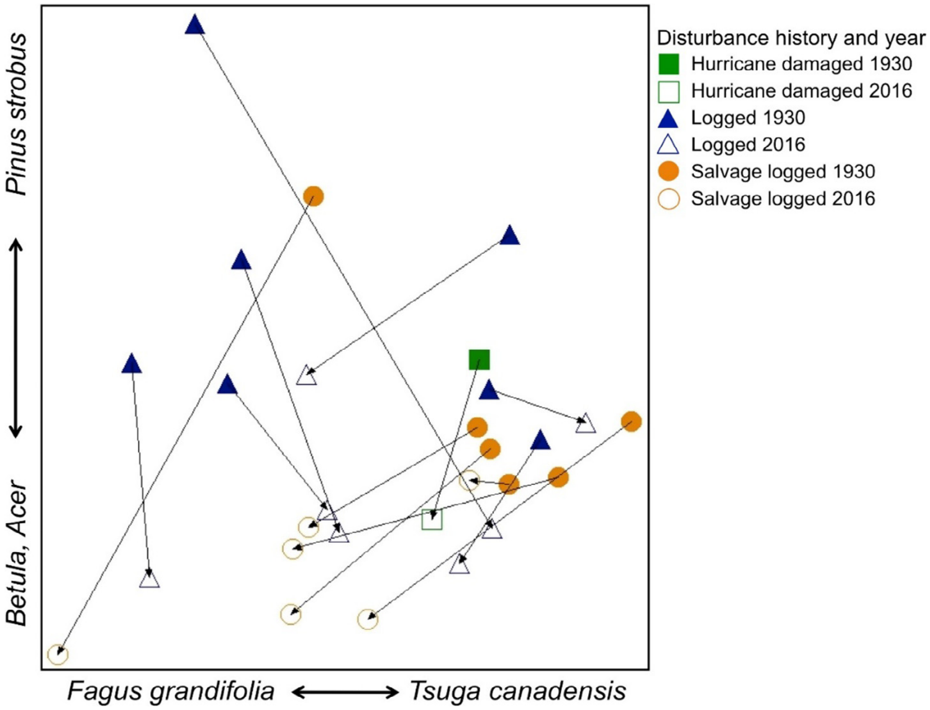

Fig. 3. Nonmetric multidimensional scaling (NMS) ordination of species importance values along two main axes for plots that were damaged by the 1938 hurricane, logged prior to the hurricane, and salvaged following hurricane damage. Filled symbols represent initial measurements taken in 1930 in old-growth hemlock-pine forest prior to disturbance; lines connect plots that were remeasured in 2016.

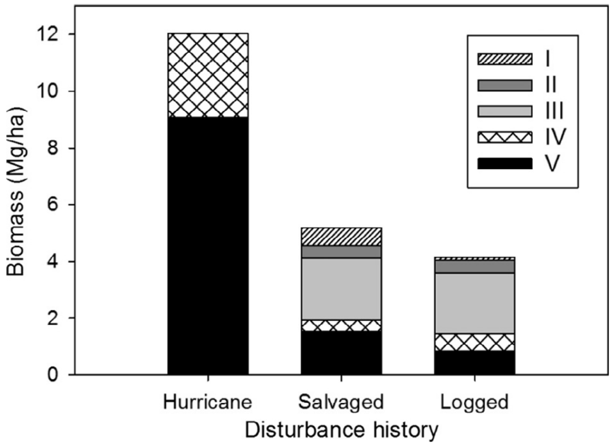

Fig. 4. Coarse woody debris biomass per hectare, averaged across each disturbance history. Decay classes follow Sollins (1982).

in the salvaged and logged plots (Fig. 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). 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 ($\tau = -0.500$, $p = 0.016$) and stump angle different from vertical ($\tau = -0.884$, $p < 0.001$); axis 2 explained 31% of the variation in structural characteristics and was negatively correlated with density of pit and mound structures ($\tau = -0.597$, $p = 0.004$) and pit and mound size ($\tau = -0.516$, $p = 0.012$). 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 (Fig. 5); and the hurricane-damaged site had the most and largest pit and mound structures, and a large amount of CWD (Fig. 6).

3.3. Spatial autocorrelation

The overall species composition was not correlated with the geographic distribution of study sites in either 1930 or 2016 (Mantel test, $r = -0.03$, $p = 0.58$). When species were considered separately, only *Quercus* importance values in 2016 showed a significant spatial pattern ($r = 0.41$, $p = 0.01$). *Quercus* importance was positively correlated with longitude ($r = 0.63$) and negatively correlated with latitude ($r = -0.70$; i.e. higher *Quercus* importance to the southeast portions of the study landscape). Similarly, there was no correlation between structural characteristics and site location (Mantel test $r = 0.05$, $p = 0.42$). However, the density of pit and mound structures ($r = 0.31$, $p = 0.01$), size of pit and mound structures ($r = 0.27$, $p = 0.01$), and density of stumps ($r = 0.35$, $p = 0.01$) were correlated with site location. Pit and mound density was higher to the northwest ($r = 0.58$ with latitude; $r = -0.67$ with longitude), and pit and mound size was higher to the west ($r = 0.22$ with latitude; $r = -0.59$ with longitude). Stump density was higher to the south ($r = -0.78$ with latitude; $r = 0.51$ with longitude).

4. Discussion

Generally, we saw persistent 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; Priewasser et al., 2013; Waldron et al., 2013, 2014). 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. The long-term persistence of these structural and compositional 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).

The importance of structural diversity has been recognized for decades for its influence on forest development and biodiversity

Table 2
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. Site average is shown, followed by plot-level minimum and maximum values.

Site	Disturb. history	Trees/ha	Live QMD (cm)	Snags/ha	Snag QMD (cm)	Stumps/ha	CWD volume (m^3/ha)[a]	CWD biomass (Mg/ha)	Pit and mounds/ha	Pit and mound size (cm)	Stump angle (°)	Mean CWD diameter (cm)[a]
HT	Hurricane	1520 (1440–1600)	19.1 (18.6–19.6)	120 (20–220)	22.4 (12.9–64.6)	70	75.4	12.02	115	64	10	33.3
Lg 12	Logged	880 (600–1300)	23.4 (20.4–28.4)	87 (40–140)	24.2 (13.8–37.2)	200	18.4	3.70	11	53	6	25.2
Lg 14	Logged	720 (540–920)	29.4 (27.0–31.8)	47 (40–60)	23.4 (11.2–27.3)	160	19.1	3.95	5	42	5	17.8
Lg 20	Logged	740 (600–880)	25.0 (23.0–29.3)	113 (80–140)	16.7 (16.0–17.3)	73	13.0	2.12	18	33	11	15.7
Lg 21	Logged	706 (700–720)	22.7 (20.7–24.8)	160 (100–200)	19.5 (14.2–24.2)	93	23.5	6.25	0	0	8	15.1
Lg 22	Logged	860 (660–1020)	23.2 (20.0–25.4)	113 (20–200)	15.4 (14.6–15.8)	67	9.8	3.16	3	47	8	13.4
Lg 27	Logged	1000 (860–1120)	23.8 (22.9–25.0)	126 (20–240)	28.2 (10.6–32.0)	80	23.6	7.48	18	48	7	21.9
Lg 7	Logged	826 (800–880)	26.9 (25.8–28.9)	60 (20–120)	19.3 (16.6–20.7)	33	15.4	2.34	21	43	8	22.7
Sl 13	Salvaged	705 (580–860)	26.0 (22.8–27.2)	165 (120–220)	18.9 (16.9–19.0)	35	22.6	4.45	98	48	21	26.1
Sl 27	Salvaged	1193 (880–1540)	19.4 (18.9–19.7)	100 (40–180)	17.0 (13.9–18.3)	80	6.7	1.25	118	51	23	12.0
Sl 28	Salvaged	1053 (420–1580)	22.0 (19.0–33.2)	93 (80–100)	23.5 (15.6–32.8)	33	13.6	2.67	75	46	35	18.6
Sl 35	Salvaged	840 (700–1000)	23.1 (19.7–26.7)	120 (60–180)	17.0 (16.1–18.8)	30	4.0	0.98	61	48	20	14.4
Sl 5	Salvaged	645 (420–900)	29.1 (24.9–39.0)	75 (60–100)	27.5 (18.2–31.7)	45	53.7	14.12	31	47	6	24.7
Sl 7	Salvaged	590 (360–940)	27.8 (20.9–40.5)	65 (40–100)	30.2 (15.8–61.1)	70	33.8	7.62	53	49	5	22.5

[a] Denotes characteristics not included in structural ordination.

Fig. 5. Angled stump at salvage logged site reflective of stump snapping partway back when the bole was removed. Stump in photo is from *Pinus strobus.*

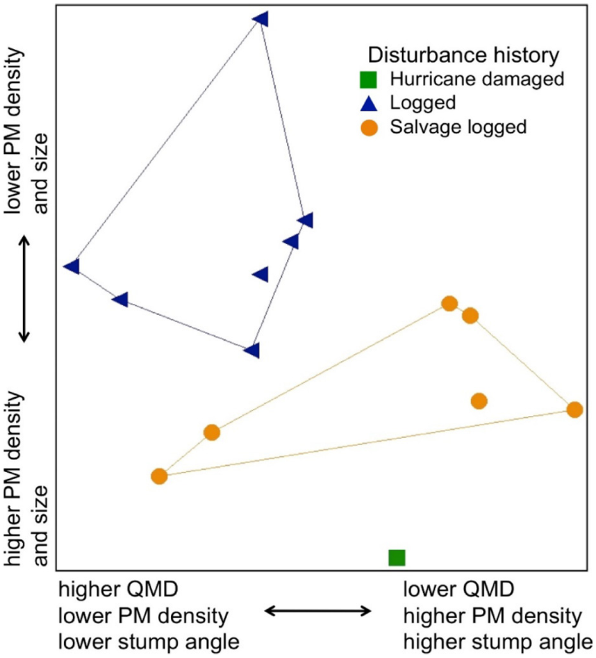

Fig. 6. Nonmetric multidimensional scaling ordination based on structural characteristics of hurricane-damaged, logged, and salvage logged sites measured in 2016, 78 years following the 1938 hurricane, with convex hulls delineating treatments. PM = Pit and mound structures; QMD = quadratic mean diameter.

(Franklin et al., 2000, 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

Fig. 7. The Harvard Tract in Pisgah State Park experienced an influx of large white pine and hemlock coarse woody debris following the 1938 hurricane. Photo: S.H. Spurr, 1942.

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).

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 site 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 size 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, 1988) and the persistence of damaged and dying trees impeded the development of advance regeneration and new seedlings (Fig. 7). Much of the CWD consisted of large pine and hemlock boles (Foster, 1988) 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 may have grown more quickly in logged and salvaged sites relative to unsalvaged areas, resulting in more developed contemporary overstory conditions. Historical accounts from all stand histories indicated abundant eastern hemlock advance regeneration in these areas prior to disturbance, suggesting these contemporary differences in structural development were not due to differing pre-disturbance regeneration conditions. However, dense hemlock advance regeneration and slow self-thinning could have contributed to the stand structure seen at the Harvard Tract, as well as the other sites. The hurricane-damaged site had the largest volume of CWD, followed by the salvaged areas, while the logged sites had the least (Table 2). 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 (Fig. 4), and much of it was from the 1938 hurricane (Foster, 1988). 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 (33.3 cm) compared to that of the salvaged (20.2 cm) or logged areas (17.8 cm; Table 2). 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 logging and salvaging 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 salvage logging on large deadwood legacies in these forests.

Pit and mound density and size, as well as stump density, were correlated with site location, emphasizing the importance of topography in influencing these disturbance-created characteristics (Foster and Boose, 1992). It is important to note that while structural characteristics overall were not correlated with location, the skewed geographic distribution of stumps and pit and mound structures may have influenced the differences we saw between disturbance histories. Similarly, the lack of replication of the hurricane-damaged disturbance history prevents statistical comparison to the other treatments and control for confounding factors.

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; Lain et al., 2008; 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; Taylor et al., 2017). White pine lacks similar regeneration mechanisms and was effectively eliminated from these sites following the mortality of overstory trees either through logging or windthrow. Factors contributing to the historical dominance of white pine in these forests are unclear (Foster, 2014); however, the conditions following the disturbances examined in this study did not create the regeneration conditions necessary to recruit a new cohort.

Forests have diverse outcomes following hurricanes and other wind events, from complete return to pre-storm species (Merrens and Peart, 1992; Mabry and Korsgren, 1998) to maintaining a significantly altered species composition (Mitchell, 2013; Trammell et al., 2017), as seen in this study. 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; Mitchell, 2013), 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 decreased 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 mixed conifer-hardwood stands (Lang et al., 2009; Trammell et al., 2017).

5. 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 on overstory composition and stand structure. While there was no difference in tree species composition between the different disturbance histories, there was a 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.

Declarations of interest

None.

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Appendix A

Species were condensed to species, genus, or order, depending on prevalence, in order to reduce the factors included in the ordination.

Category for ordination	Component species
Eastern hemlock	*Tsuga canadensis*
White pine	*Pinus strobus*
American beech	*Fagus grandifolia*
Birch	*Betula alleghaniensis* *B. lenta* *B. papyrifera*
Maple	*Acer rubrum* *A. saccharum*
Oak	*Quercus alba* *Q. rubra*
Other conifer	*Picea rubens*
Other hardwood	*Fraxinus americana* *Ostrya virginiana,* *Prunus serotina* *Ulmus americana*

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