Forest Ecology and Management 444 (2019) 138–150

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Structural, compositional, and functional responses to tornado and salvage logging disturbance in southern New England hemlock-hardwood forests

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ARTICLE INFO

Keywords:
Natural disturbance
Tornados
Compound disturbance
Functional traits
Regeneration
Resilience

ABSTRACT

The frequency and severity of wind storms, such as hurricanes and tornados, are expected to increase in northeastern North America under climate change. As such, salvage logging is likely to become a more frequently-used post-disturbance management strategy; however, there is concern that the compound disturbance of wind followed by salvage logging could generate negative impacts on species composition, forest structure, and ecological resilience. These impacts are variable and uncertain, posing an opportunity for further research that considers differences in forest recovery following stand-replacing wind alone versus stand-replacing wind and salvage logging. We evaluated the short-term impacts of these singular (tornado) and interactive disturbance events (tornado + salvage logging) on the structure, composition, and function of a mature hemlock-hardwood forest in south-central Massachusetts. Specifically, we were interested in quantifying the impacts of salvage logging practices on forest recovery and resilience. Our analyses consider salvage logging impacts on forest overstory in addition to the regeneration layer (defined here as tree seedlings and saplings that make up the forest understory). We found that (i) delayed overstory mortality was highest on tornado-damaged sites, contributing additional material to dead wood pools, while salvaged sites lacked much of this material and associated structural legacies; (ii) tree regeneration layer diversity, as measured by Shannon's Index, was higher in the tornado-damaged sites than salvaged sites, but levels of sapling ($\geq$1.4 m in height and < 12.7 cm in dbh) density and richness were the same; and (iii) regeneration present on tornado-damaged sites was more functionally similar to that present on undisturbed control sites than to that on salvaged sites. Our results indicate that the compound disturbance created by salvage logging may have initially homogenized regeneration composition and pushed these areas toward disturbance-adapted species (e.g., *Acer rubrum* and *Betula lenta*) and traits (e.g., transitory on-site reproductive strategies). This shift in composition may have also been influenced by the removal of dead material and structural legacies at these sites. However, the high levels of regeneration density and richness found on both tornado-damaged and salvage-logged sites suggests that rapid forest recovery is occurring via multiple mechanisms of regeneration, such as vegetative reproduction, advance regeneration, and new seedlings. These findings highlight how post-disturbance management actions affect forest resilience and development after severe wind disturbances, and suggest that future salvage logging operations more explicitly integrate retention of structural legacies and protection of advance regeneration to enhance forest recovery.

1. Introduction

Disturbance is a central driver of forest successional and structural dynamics via its effects on resource availability through tree mortality and the subsequent influence on forest composition and structure at multiple temporal and spatial scales (Frelich, 2008; Lindenmayer et al., 2008; Lorimer and Frelich, 1994; Pickett and White, 1985). Variation in disturbance type, extent, and frequency greatly influences temporal and spatial patterns of forest composition and structure across a landscape (Foster et al., 1998; Seymour et al., 2002). Additionally, these events can vary in intensity, duration, severity, and heterogeneity, resulting in multiple potential post-disturbance pathways for ecosystem recovery (Dale et al., 2001; Turner et al., 1998) and resultant compositional and structural conditions at broad spatial scales.

Natural disturbance regimes in many temperate regions are dominated by localized wind events punctuated by infrequent, severe disturbances, such as hurricanes and tornados (Boose et al., 2001; Lorimer and White, 2003; Pickett and White, 1985). These disturbance regimes

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https://doi.org/10.1016/j.foreco.2019.04.039
Received 27 February 2019; Received in revised form 17 April 2019; Accepted 21 April 2019
Available online 28 April 2019
0378-1127/

historically maintained multi-cohort, mixed species forest conditions across many regions (Lorimer and White 2003). Given the prevalence of gap-scale disturbances created by small wind storms, much of our understanding of post-disturbance successional dynamics is following these events. However, climate change is predicted to increase the frequency and severity of large-scale wind disturbances in these areas (Dale et al., 2001; Hobbs et al., 2006), creating the potential for alterations to the extent and frequency of disturbances in these regions. There is a concomitant need for forest management to respond to these altered disturbance regimes (D'Amato et al., 2011a). Post-disturbance management strategies must therefore adaptively change to account for increased natural disturbance and promote ecosystem resilience (O'Hara and Ramage, 2013).

With an increasing occurrence of large disturbances around the globe, salvage logging has become a common yet controversial post-disturbance management response (Lindenmayer, 2006; Lindenmayer et al., 2008; Spittlehouse and Stewart, 2004). As such, there is concern that the compound disturbance of stand-replacing events followed by salvage logging could inhibit forest recovery by permanently altering species composition, forest structure, recovery capacity, and ecological resilience (Lindenmayer et al., 2008; Paine et al., 1998). However, the impacts of salvage logging on forest recovery are poorly understood and often variable due to numerous factors, including but not limited to heterogeneous disturbance severity, salvage logging intensity, and time since disturbance. A few studies (Elliott et al., 2002; Peterson and Leach, 2008a; Radeloff et al., 2000; Royo et al., 2016) have found minimal or neutral impacts of salvage logging on post-disturbance ecosystems; yet, most work highlights the negative ecological, social, and economic impacts stemming from the compound damage salvage logging generates on recently-disturbed sites (Fraver et al., 2011; Hutto, 2006; Lindenmayer, 2006; Lindenmayer and Noss, 2006; Waldron et al., 2014). Broadly, these potential impacts encompass lowered stand structural complexity, altered ecosystem processes and functions, homogenized landscapes, and shifts in species composition towards more disturbance-adapted species and lifeforms (Cooper-Ellis et al., 1999; D'Amato et al., 2011b; Foster et al., 1997; Fraver et al., 2017; Lindenmayer and Noss, 2006; Waldron et al., 2014). Despite the concerns surrounding this practice, salvage logging is a widespread management strategy following natural disturbance (Lindenmayer et al., 2008). Given that the impacts of this practice are variable, uncertain, and dependent on disturbance severity and type, current knowledge on salvaging impacts across diverse landscapes remains incomplete (Lindenmayer and Noss, 2006; Lindenmayer and Ough, 2006; Palik and Kastendick, 2009). As such, there is a continued need for research that evaluates this practice across diverse ecosystems and following a range of disturbance agents, including stand-replacing wind. Such examinations could serve to inform more robust strategies for post-disturbance management and policies to sustain ecosystem resilience in the future (Lindenmayer and Noss, 2006).

There are various aspects of the post-disturbance environment that can be affected by salvage logging that may lead to different ecological outcomes than those observed following a stand-replacing wind event alone, making it difficult to predict salvaging impacts *a priori*. For example, salvaging practices may impact the abundance of certain microsites (e.g., exposed mineral soil microsites and upturned root masses; Peterson and Leach, 2008a, Royo et al., 2016, Fraver et al., 2017) and structural legacies, which can impact seedling success and species diversity (Cooper-Ellis et al., 1999; D'Amato et al., 2011b; Foster et al., 1997; Sass et al., 2018b). These alterations to microsite and structural legacies have been suggested as the primary drivers of divergent post-disturbance successional trajectories of salvaged and unsalvaged areas in several studies examining salvage logging following wind (Lang et al., 2009; Palik and Kastendick, 2009; Royo et al., 2016; Sass et al., 2018b, 2018a). While many studies find that overstory composition converges between salvaged and unlogged treatments over the long term despite alterations to microsites, they also note that differences in understory composition and structural legacies persist (Lang et al., 2009; Sass et al., 2018a). These differences have important implications for species and functional diversity. Prior research has noted that surviving overstory trees and advance regeneration, as well as patterns of post-disturbance seedling establishment, act as the primary controls on post-disturbance forest development (Lang et al., 2009; Palik and Kastendick, 2009; Plotkin et al., 2013; Sass et al., 2018a). Additionally, salvage logging, in combination with past land use, has been shown to homogenize species composition in the regeneration layer and exacerbate environmental changes through soil scarification, increased light availability, and microsite alteration (Foster and Orwig, 2006). Therefore, forest resilience is strongly affected by overstory trees and regeneration that survive a given disturbance, two ecosystem attributes influenced by post-disturbance salvage logging. Moreover, since salvage logging impacts microsites and structural legacies important to forest regeneration, such as surviving trees and downed wood, this practice may result in altered forest recovery trajectories relative to unsalvaged sites.

In 2011, an EF-3 rated tornado event generated significant blowdown in mixed oak hemlock-hardwood forests in central Massachusetts with subsequent salvage logging efforts generating a mosaic of salvaged and unlogged areas across the landscape. This disturbance event and associated salvage logging efforts provide an opportunity to expand our understanding of the impacts of stand-replacing wind and post-disturbance salvage logging on temperate forest systems, particularly in light of projections for increased frequency of such events in the future. We investigated the degree to which salvage logging affects forest recovery and alters successional dynamics compared to wind disturbance alone, and asked the following questions: after six years, does (i) overstory forest structure and composition; and (ii) tree regeneration abundance, composition, and functional structure differ between singular and compound disturbance treatments? We predict that salvage logging will have (i) decreased post-disturbance overstory mortality through removal of damaged trees while leaving less deadwood on-site; (ii) decreased regeneration density, richness, and diversity, and (iii) generated distinct patterns of species and functional composition relative to unsalvaged wind-disturbed sites and undisturbed controls. Overall, we expect the compound disturbance of salvage logging following tornado blowdown will have pushed the forest toward lower structural and compositional diversity and result in functional shifts toward response traits associated with high disturbance.

2. Materials and methods

2.1. Study area

The areas used for this study were centered on Brimfield State Forest (BSF), which is an approximately 784-hectare forested property managed by the Massachusetts Department of Conservation and Recreation (DCR) located in south-central Massachusetts (42.10° N, 72.23° W; 250–300 m above sea level). This area lies within the Central Uplands (Worcester-Monadnock Plateau, Ecoregion 221Ah) region, which is characterized by eastern broadleaf forests dominated by transition hardwoods (red oak, *Quercus rubra* L., red maple, *Acer rubrum* L., and black birch, *Betula lenta* L.) with a conifer component of white pine (*Pinus strobus* L.) and eastern hemlock (*Tsuga canadensis* L.) (Cleland et al., 2007; de la Crétaz et al., 2010; Omernik and Griffith, 2014; Westveld, 1956). Soils are derived from glacial till and are primarily composed of fine sandy loam, loamy sand, and rock outcrops. Forests in this landscape are generally second-growth systems recovering from a period of extensive land use in the 18th and 19th centuries, including logging and agricultural clearing and abandonment (Foster, 1992).

2.2. Experimental design

In 2012, approximately one year after the tornado event, 72

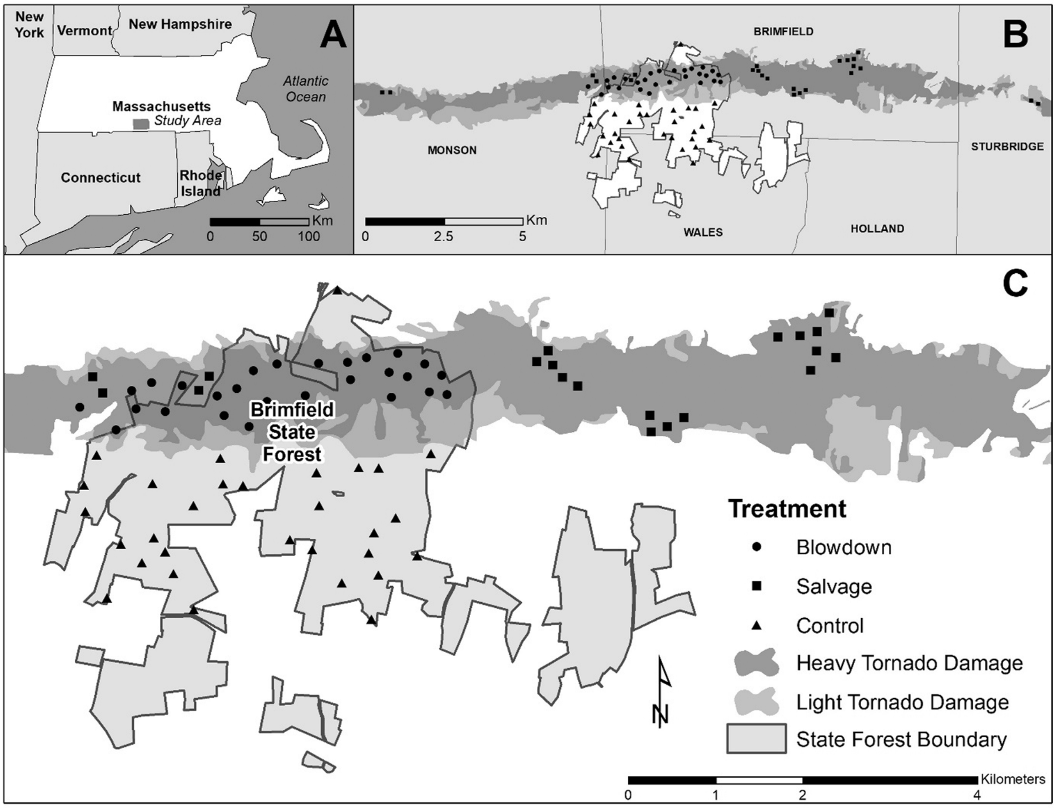

Fig. 1. Study site showing (A) the location of Brimfield State Forest and the 2011 tornado in south-central Massachusetts; (B) a portion of the tornado track as it went through Brimfield State Forest and the 81 plots set up to monitor post-tornado responses; and (C) the plot locations and treatment types distributed in and around Brimfield State Forest.

monitoring plots were established in and around BSF across three treatment types: blowdown, salvage, and control (Fig. 1). Blowdown sites were located in the path of the tornado and did not experience any post-disturbance management. Salvage sites were also located in the path of the tornado, but underwent salvage logging operations within one year of the tornado event. Control sites were undisturbed by the tornado and were selected to represent forest conditions similar to those areas impacted by the tornado and salvage logging. The majority of control plots were located to the south of the tornado path due to the location of the tornado with respect to BSF property boundaries. In the 2017 inventory, 9 additional salvage sites that were logged at the same time as the initial sites were added to the dataset for a total of 81 plots in the 2017 inventory. Salvage logging was generally carried out using tracked feller bunchers and forwarders in addition to rubber-tired grapple skidders; these operations were implemented according to Massachusetts Forest Cutting Regulations (William Hill and Douglas Hutcheson, personal communication). The majority of the salvage logging in the Brimfield area took place in the summer of 2011 through the winter of 2012. Due to the dominance of red oak in this community, the majority of salvaged material was comprised of red oak, especially in the mid to large size classes. More than 90% of the salvaged material was chipped, and the remaining volume was removed as firewood or sawlogs.

The breakdown of plots is: 27 blowdown, 24 salvage, and 30 control. Within each treatment, 800 m^2 circular plots were randomly established; however, in a limited number of cases, plots were purposely placed in the location of existing continuous forest inventory plots to allow for assessments of change from pre-disturbance conditions. Pre-disturbance site conditions and forest composition were similar across treatments (William Hill, personal communication). Plots within treatments were established on comparable stony terrain with similar elevation and aspect, and plots were divided between fine sandy loam, loamy fine sand, and rock outcrop-dominated soils (Soil Survey Staff, NRCS, 2006). Given the limited spatial extent of tornado disturbance in this area and associated salvage logging activities, we were not afforded the opportunity to establish independent replicates of each disturbance condition. Nonetheless, this experimental design, despite statistical limitations, provided the opportunity to document a rare sequence of disturbance events for this region.

2.3. Field sampling

Field data were collected in 2012 and 2017 at the same monitoring plots. Each plot consisted of a circular 800 m^2 overstory plot, two circular 10.5 m^2 nested regeneration layer plots, and one 30.5 m downed woody material (DWM) transect. On the 800 m^2 overstory plot, all standing live and dead trees (diameter at breast height [dbh] ≥ 12.7 cm) were tallied by species, diameter, and height. The regeneration layer, comprised of tree seedlings (≥7.6 cm and < 1.4 m in height) and saplings (≥1.4 m in height and < 12.7 cm in dbh), were measured on two nested 10.5 m^2 subplots located 7.9 m north and south of plot center. Tree regeneration, defined as the seedlings and saplings, was recorded by species and size. To estimate the volume of DWM on each plot, we established one 30.5 m transect per plot at a random azimuth starting at plot center. Random azimuths for the DWM transects were generated and recorded per plot in 2012 using a random number table and the same azimuths were used for the 2017 inventory. For each piece of DWM ≥ 7.6 cm in diameter and ≥ 0.9 m in length, we recorded diameter, length, and decay status using a decay class system with three classes (Parks et al., 1997). Volume of DWM was determined based on van Wagner (1968).

Data were not recorded at these plots before the tornado event, so all data collected represent post-disturbance conditions. In 2012, overstory data collection only tallied live and dead standing trees, so windthrown trees from the tornado were only potentially recorded on the DWM transects.

2.4. Statistical analysis

We analyzed post-tornado forest change between 2012 and 2017 for overstory, regeneration, and DWM across the study site to determine the influence of tornado blowdown and salvage logging on forest composition and structure six years after the tornado event. One control plot was eliminated from the analysis due to complete overstory mortality resulting from flooding from a beaver dam after the 2012 inventory. Analyses were conducted in R version 3.3.2 (R Core Team, 2016).

2.4.1. Structural analyses

Components of post-disturbance forest structure, including post-tornado overstory basal area, mortality rates, and DWM volumes, were assessed with analysis of variance (ANOVA) based on treatment (blowdown, salvage, or control). ANOVAs were evaluated to ensure the assumptions of normally-distributed residuals and equal variances as determined by Levene's test were met at the 0.05 level; if they did not, data were transformed using log or square-root transformations in order to meet these assumptions. Because the objectives of this study are primarily to quantify differences between treatments and assess the impacts of post-disturbance salvage logging on this ecosystem, we focused on the multiple comparisons of means with 95% family-wise confidence level using post-hoc Tukey tests.

Plot-level mortality rates between 2012 and 2017 were calculated using a negative compound interest formula (Lorimer et al., 2001; Silver et al., 2013):

$$M = 1 - [(N_t/N_o)^{1/t}]$$

where M = mortality rate, t = time (here, 5 years between measurements), N_t = number of surviving trees during the 2017 remeasurement, and N_o = number of live trees at plot establishment in 2012. Mortality rates were calculated at the plot level and analyzed for all plots. ANOVAs were conducted to determine differences in mortality rates by treatment.

2.4.2. Compositional analyses

We analyzed post-disturbance forest composition, focusing on community diversity measures such as tree regeneration stem density, richness, and diversity. These measures were assessed with ANOVAs based on treatment. Since red oak is of particular ecological and economic importance in this forest, we analyzed differences in red oak regeneration by treatment to assess the recovery potential of this species on this landscape. Multiple comparisons of means were evaluated using post-hoc Tukey tests.

We performed linear models to examine the effects of treatment (blowdown and salvage) and DWM volume (used as a proxy for disturbance severity) on regeneration compositional characteristics, including diversity, density, and richness of seedlings and saplings. DWM volume was chosen as a proxy for disturbance severity (cf. Peterson and Leach, 2008a) because we lack pre-disturbance data, and thus cannot quantify levels of disturbance severity at the plot level. Lower DWM volumes indicate more severe disturbance due to salvage logging, which removed fallen trees generated from the tornado event from the landscape. Shannon's Diversity Index was calculated using the following formula (Kent and Coker, 1994; Shannon, 1948):

$$H' = -\Sigma p_i \ \log \ (p_i)$$

where p_i is the proportion of individuals found for the *i*th species and log is base 10. In addition, Sørensen's (Bray-Curtis) index of dissimilarity was calculated based on presence/absence of species (Kent and Coker, 1994). This index varies between 0 and 1, with values approaching zero indicating samples with completely overlapping species composition. Both Shannon's Diversity Index and Sørensen's dissimilarity were computed in the 'vegan' package in R (Oksanen et al., 2017).

2.4.3. Functional analyses

To assess the effects of blowdown and salvage logging on regeneration functional composition and associated potential successional dynamics, we used nonparametric multivariate approaches. The response of species and functional composition of the understory layer across treatments was examined using non-metric multidimensional scaling (NMS) ordination. Understory regeneration was analyzed to assess functional differences associated with post-disturbance recovery trajectories. Species included in these analyses are listed in the Appendix (Table A.1). NMS analyses considered only functional traits of those species that had greater than 10 occurrences across the dataset.

Eight plant functional traits were identified for use in this analysis (Table A.1). They included three response traits, which relate to plant responses to environmental factors, and five effect traits, which relate to plant effects on various ecosystem processes (Lavorel and Garnier, 2002). Response traits analyzed are shade tolerance, drought tolerance, and flood tolerance. Effect traits analyzed are wood specific gravity, leaf mass per area, maximum height at maturity, height at 20 years (as a proxy for growth rate), and seed mass. Species-specific trait means were collected from the literature (Table A.2; Wright et al., 2004, Niinemets and Valladares, 2006, Miles and Smith, 2009, Curzon et al., 2017). Due to intraspecific trait variation, these trait values have some uncertainty, which may impact the results. To compare traits and meet statistical assumptions for analyses, all trait values were standardized to unitless z-score for all species (Villéger et al., 2008). Community-weighted means (CWM) for all functional traits were calculated as:

$$CWM_{aj} = \Sigma(s_{ij} - t_i)$$

Where CWM_{aj} = mean for trait *a* in plot *j*, s_{ij} = relative abundance of species *i* in plot *j*, and t_i = trait value for species *i* (Lavorel et al., 2008). Functional diversity indices, including functional divergence, functional dispersion, functional richness, and functional evenness, were computed (Table 1) (Laliberté and Legendre, 2010; Villéger et al., 2008). CWMs and functional diversity indices were computed using the R 'FD' package (Laliberté et al., 2014).

Regeneration functional trait CWMs were compiled by plots for both the 2012 and 2017 inventories (rows) and species or functional trait CWMs (columns). A constant was added to all CWMs to force all values to be positive in order to use a Sørensen (Bray-Curtis) distance measure in NMS. All NMS analyses were performed in PC-ORD 6.0 using 250 runs with real data and 250 iterations per run (McCune and Mefford, 2011). Kendall correlations (tau) were calculated between the abundance of species or functional trait and the resulting axis scores. A Bonferroni correction was applied to tau p-values to correct for inflated Type 1 error. To evaluate species and functional trait compositional differences between treatment types, pair-wise PERMANOVA distance-based analyses of variance were computed in the R package 'vegan' and Bonferroni corrections were applied to output p-values (Oksanen et al., 2017). Indicator species analysis was performed using the R package 'indicspecies' (De Caceres and Legendre, 2009) in order to assess potential relationships between tree regeneration species abundance and treatment type to more accurately draw conclusions about the impacts of tornado and salvage logging on site characteristics and species composition.

In addition to broad plant functional traits, we quantified regenerating tree responses to disturbance within reproductive strategy-focused functional groups in order to more directly assess the effect of disturbance on predominance of a given regeneration strategy. We assigned regenerating tree species to one of four functional groups based on regeneration strategy and level of persistence on site (cf. Blair et al., 2016). Regeneration strategy was divided into seed dispersal type: blown-in seed, on-site seed, or seed/sprout. Level of persistence was

Table 1
Per-treatment means and standard errors (in parentheses) of community-level species and functional metrics for tree regeneration, live overstory, and dead overstory data in 2017.

	Regeneration			Live Overstory			Dead Overstory		
	Control	Blowdown	Salvage	Control	Blowdown	Salvage	Control	Blowdown	Salvage
Functional Richness	5.6 (0.70)	8.7 (1.07)	12.6 (1.54)	7.7 (0.70)	5.1 (0.72)	6.5 (1.7)	3.4 (0.69)	6.2 (0.71)	5.1 (1.18)
Functional Evenness	0.67 (0.03)	0.68 (0.03)	0.67 (0.04)	0.70 (0.03)	0.77 (0.03)	0.79 (0.07)	0.74 (0.04)	0.68 (0.04)	0.73 (0.07)
Functional Dispersion	2.2 (0.15)	2.3 (0.16)	2.6 (0.17)	2.1 (0.09)	1.9 (0.16)	1.2 (0.35)	1.6 (0.15)	1.9 (0.13)	1.6 (0.26)
Functional Divergence	0.68 (0.04)	0.59 (0.04)	0.71 (0.04)	0.78 (0.03)	0.83 (0.02)	0.82 (0.04)	0.75 (0.03)	0.83 (0.02)	0.82 (0.04)
Species Richness	14.7 (0.80)	14.8 (0.92)	17.9 (1.0)	5.4 (0.25)	3.0 (0.23)	2.3 (0.41)	3.1 (0.23)	3.2 (0.27)	1.8 (0.23)
Species Evenness	0.40 (0.02)	0.49 (0.02)	0.31 (0.02)	0.69 (0.02)	0.89 (0.06)	0.39 (0.04)	0.43 (0.02)	0.95 (0.05)	0.36 (0.08)
Species Diversity (Shannon)	1.1 (0.06)	1.3 (0.06)	0.89 (0.07)	1.1 (0.04)	0.91 (0.06)	0.29 (0.07)	0.45 (0.04)	0.96 (0.06)	0.20 (0.04)
Species Dissimilarity (Sørensen)	0.33 (0.01)	0.59 (0.01)	0.36 (0.01)	0.30 (0.01)	0.52 (0.01)	0.19 (0.01)	0.20 (0.01)	0.49 (0.01)	0.17 (0.02)

divided into transitory (ruderal species that appear soon after disturbance events) or persistent (remains on site with or without additional disturbance). The groups were: (1) Transitory, blown-in seed; (2) Transitory, on-site seed; (3) Persistent, blown-in seed; and (4) Persistent, seed/sprout (see Table A.3. in Appendix A). We assigned regenerating tree species to these categories by field observation and consultation with the USDA PLANTS Database. Per-group differences were assessed statistically with ANOVAs.

3. Results

3.1. Structural conditions

Compound disturbance via salvage logging influenced the post-disturbance abundance of live and dead standing trees in addition to DWM (Fig. 2a). As expected, the blowdown treatment had the highest volume of DWM compared to other treatments (Fig. 2b). Additionally, the control treatment had the highest amount of live-tree basal area (ANOVA; $p < 0.001$) while the blowdown treatment had the highest amount of standing dead and downed dead basal area (ANOVA; $p < 0.001$; i.e. trees that were standing dead in the 2012 inventory and had fallen by the 2017 inventory) (Fig. 2a). There was no difference between blowdown and salvage treatments in terms of live-tree basal area (ANOVA; $p = 0.61$), and no difference between control and salvage treatments in terms of standing dead and downed dead basal area (ANOVA; $p = 0.63$).

Based on multiple comparisons of means, blowdown (mean = 0.26; se = 0.05) plots had higher post-disturbance mortality rates than control and salvage plots (ANOVA; $p < 0.001$). There was no difference in overstory mortality rates between salvage (mean = 0.03; se = 0.02) and control (mean = 0.02; se = 0.004) plots. Much of the mortality in blowdown plots was due to loss of large red oaks (6.0 m^2 ha^{-1} lost), eastern hemlock (0.66 m^2 ha^{-1} lost), and red maple (0.7 m^2 ha^{-1} lost) from the tornado event, whereas mortality in salvage plots was associated with loss of hemlock left on-site during salvage operations. Mortality in control plots was mostly from large red and white oak (*Quercus alba* L.).

Volume of DWM was significantly different between treatments (ANOVA; $p < 0.001$), with blowdown plots containing higher volumes of DWM than salvage ($p < 0.001$) and control ($p < 0.001$) plots, and salvage plots containing higher DWM volume than control ($p = 0.007$) plots. A majority of the DWM logs measured in blowdown plots were red oaks (northern red, black, and scarlet), whereas eastern hemlock, red maple, and white pine were the primary deadwood species in salvage plots (Fig. 3). Red maple and red oak were the primary deadwood species in control plots.

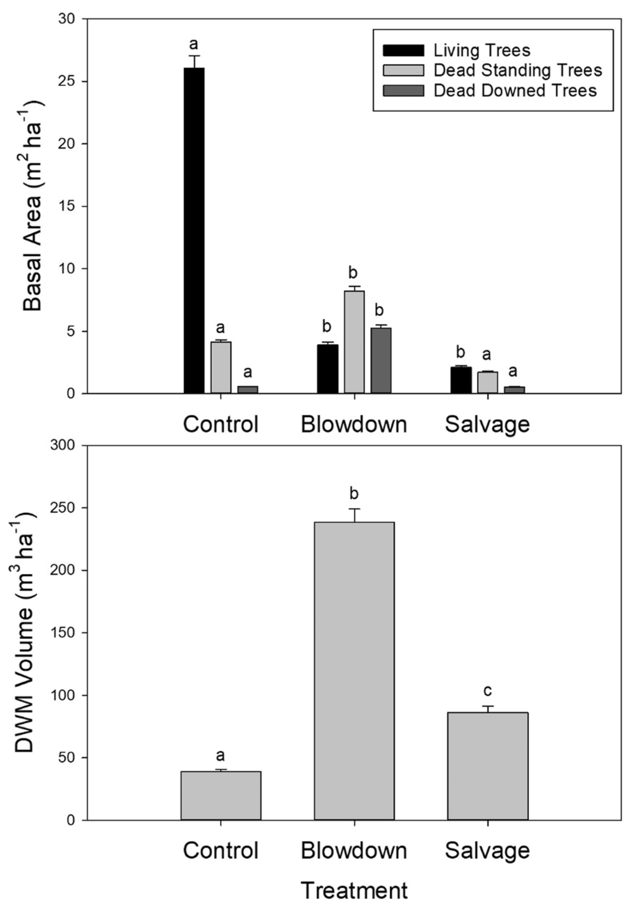

Fig. 2. (a) Tree basal area per hectare and (b) volume of downed woody material (DWM) per treatment in 2017. Error bars represent 95% confidence intervals. Statistical significance between like groups is assessed at the $p < 0.05$ level.

3.2. Compositional results

3.2.1. Overstory composition

Forest overstory conditions prior to the tornado were dominated by a mix of red oaks (*Quercus Lobatae*; including red; black, *Q. velutina* Lam.; and scarlet, *Q. coccinea* Münchh.) and red maple with understory and midstory components of black birch and eastern hemlock. After the

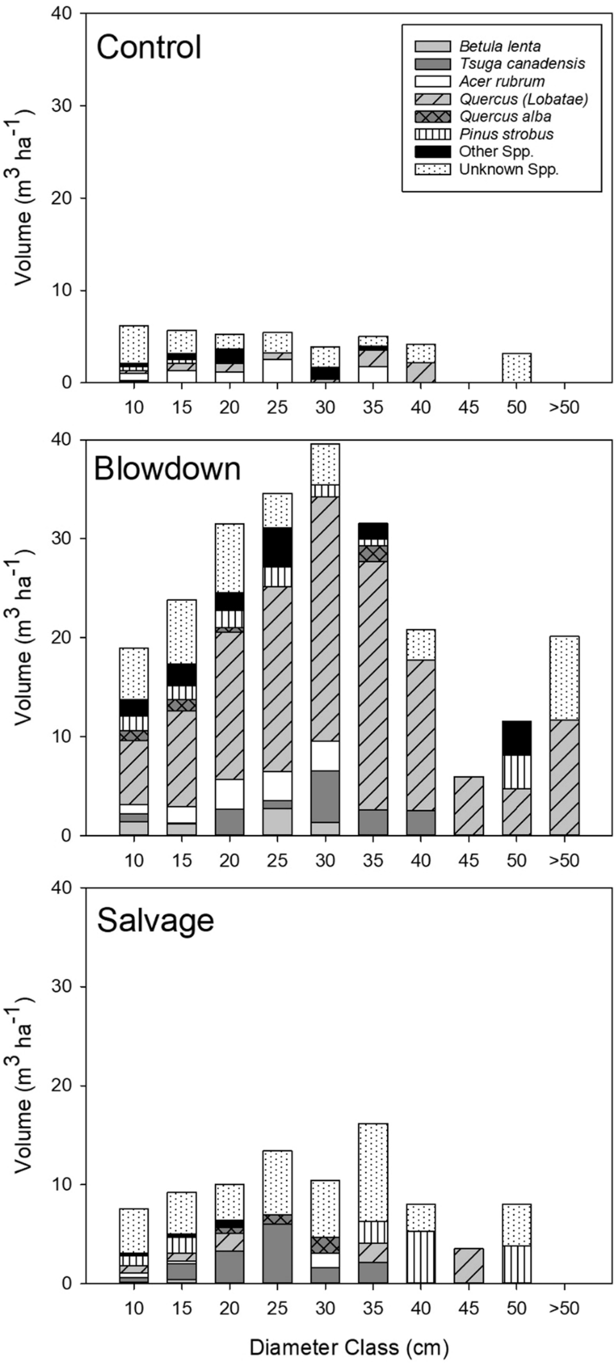

Fig. 3. Diameter distribution of DWM by species and treatment measured in 2017. Diameters are recorded in 5 cm bins. Species were classified as unknown if they were decayed past the point of identification.

tornado, structure and composition in the blowdown plots reflected a combination of surviving trees (primarily red oaks, red maple, and eastern hemlock) and a new cohort dominated by red maple, black birch, yellow birch (*Betula alleghaniensis* Britton), black cherry (*Prunus serotina* Ehrh.), and American chestnut (*Castanea dentata* (Marshall) Borkh.) stump sprouts (Fig. 4). Salvage plots we composed mostly of eastern hemlock and red maple, and a new cohort dominated by black birch, red maple, and pin cherry (*Prunus pensylvanica* L. f.).

3.2.2. Understory composition

Disturbance type significantly affected regeneration species diversity as measured by Shannon's Index (ANOVA; $p < 0.001$). Species diversity was significantly higher on blowdown plots compared to control ($p < 0.001$) and salvage ($p < 0.001$) plots, but there was no significant difference between control and salvage plots ($p = 0.723$).

Disturbance type was not a significant predictor of tree regeneration density when all size classes were combined in the analysis (ANOVA; $p = 0.1955$); however, it was a significant predictor of both seedling regeneration density (ANOVA; $p = 0.005$) and sapling regeneration density (ANOVA; $p < 0.001$). Seedling density was higher on control plots compared to blowdown plots ($p = 0.004$), and sapling density was lower on control plots compared to salvage plots ($p < 0.001$) and blowdown plots ($p = 0.0003$). Overall, control treatments had the highest densities of seedlings, while salvage and blowdown treatments had the highest densities of saplings. Additionally, red oak regeneration densities differed by treatment (ANOVA; $p = 0.002$), with control plots containing significantly higher red oak regeneration compared to blowdown plots ($p = 0.0014$) and salvage plots ($p = 0.049$). Blowdown and salvage plots did not have significantly different densities of red oak regeneration ($p = 0.51$).

Treatment was not a significant predictor of regeneration species richness when all size classes were combined in the analysis (ANOVA; $p = 0.092$); however, seedling richness showed significant differences between treatment types (ANOVA; $p = 0.011$). Control treatments showed significantly higher seedling richness than blowdown plots ($p = 0.013$), but there were no significant differences between control and salvage treatments ($p = 0.061$) or blowdown and salvage treatments ($p = 0.868$). Treatment was also a significant predictor of sapling richness (ANOVA; $p < 0.001$). Control plots had significantly lower sapling richness compared to blowdown plots ($p < 0.001$) and salvage plots ($p < 0.001$), but there was no significant difference in sapling richness between blowdown and salvage plots ($p = 0.586$). Similar to regeneration species densities, control treatments had the highest species richness values for seedlings, but blowdown and salvage treatments had the highest species richness values for saplings.

In general, patterns of species diversity did not significantly differ between blowdown and salvage treatments when considering DWM volume (Fig. 5). Individually, treatment ($p = 0.003$) and DWM volume ($p = 0.002$) were significant predictors of regeneration diversity based on a linear model, but the interaction was not significant. There was no significant relationship between regeneration density or species richness and DWM volume.

3.3. Understory species and functional composition

PERMANOVA results analyzing effects of treatment and year indicated that only treatment was a significant predictor of species composition. Given this result, pair-wise PERMANOVA results for treatment pairs analyzed separately indicated that all treatment pairs were statistically significant for species composition (Table 2). Additionally, indicator species analysis was performed to assess regeneration species associations with treatment as an indication of successional dynamics across sites (De Caceres and Legendre, 2009). In 2012, black cherry, eastern hemlock, and gray birch (*Betula populifolia* Marshall) regeneration were significantly associated with salvage treatments, while black birch regeneration was significantly associated with both salvage and blowdown treatments. In 2017, yellow birch regeneration was significantly associated with blowdown treatments, while pin cherry and gray birch regeneration were significantly associated with salvage treatments.

The PERMANOVA analysis was repeated for community functional trait composition and found similar results: only treatment was a significant predictor of functional trait composition, and pair-wise PERMANOVA tests indicated that all treatment pairs were statistically significant (Table 2). From the disturbance perspective, this indicates that salvage treatments exhibited statistically different community functional trait and species compositions from blowdown and control treatments one and six years after the tornado event.

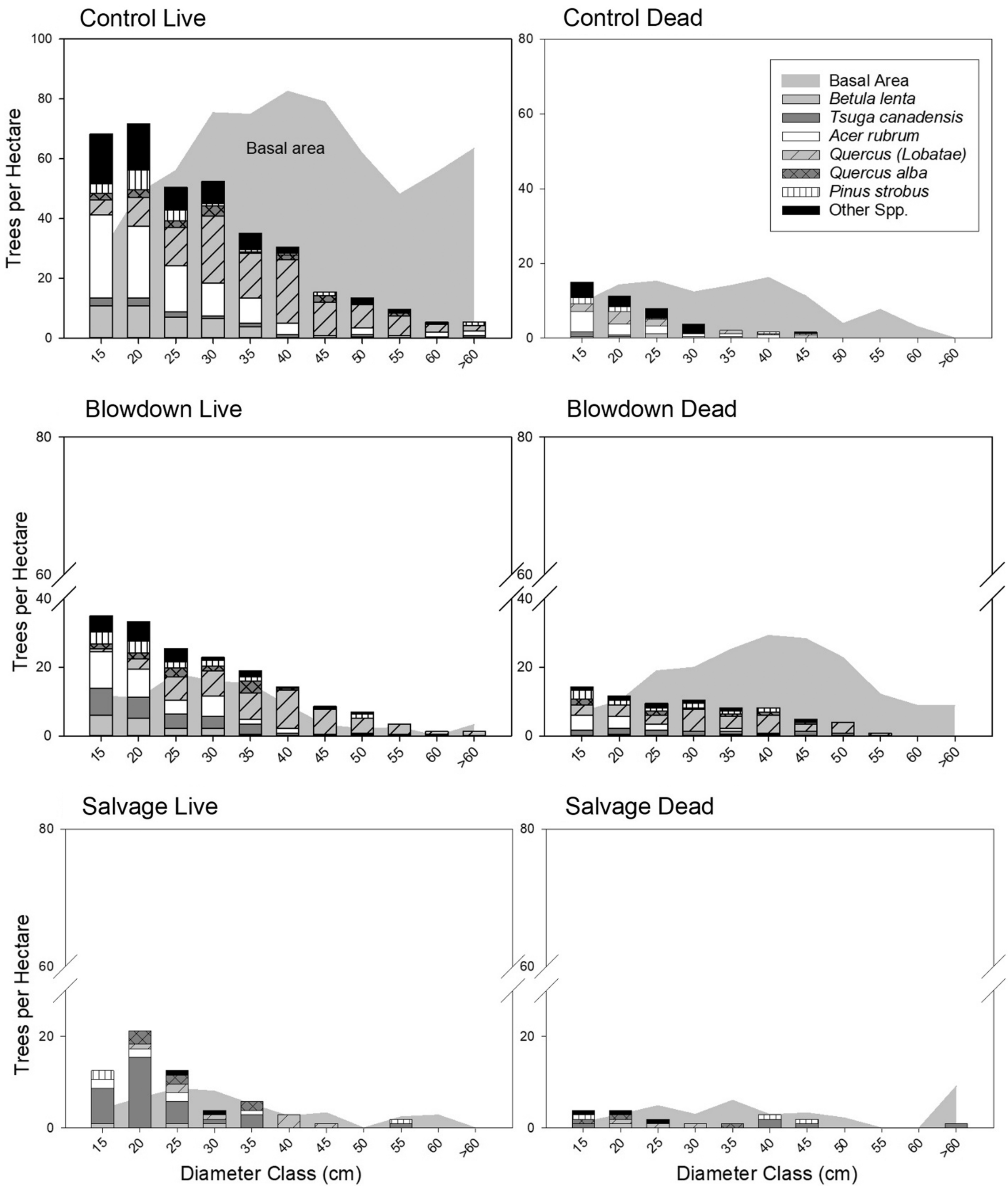

Fig. 4. Diameter distribution of standing live (left column) and standing dead (right column) overstory trees per treatment for major species measured in 2017. Basal area by size class is shown in the shaded gray backdrop. Diameters are recorded in 5 cm bins.

The NMS ordination of regeneration functional composition over the two inventory periods had a two-dimensional solution with the first axis explaining 49.5% of the variation and the second axis explaining 20.4% of the variation (Fig. 6). Axis 1 ranged from control and blowdown treatments in the negative portions to the salvage treatment in the positive portion. Salvage treatments moved toward more positive portions of Axis 1 and 2 in the 2017 measurement, reflecting an increase in regeneration with higher wood specific gravity and shade tolerance (Table 3). The distance separating salvage treatment points between time periods suggests that compound disturbance increased the amount of functional change compared to blowdown treatments alone.

The abundance of one reproductive strategy evaluated also differed between treatments. Transitory, on-site seed species (pin cherry) had significantly higher ($p = 0.03$) abundance in salvage plots than blowdown (Fig. 7). None of these species were found in control plots. There were no significant differences between treatments for transitory, blown-in seed strategies and persistent, seed/sprout strategies.

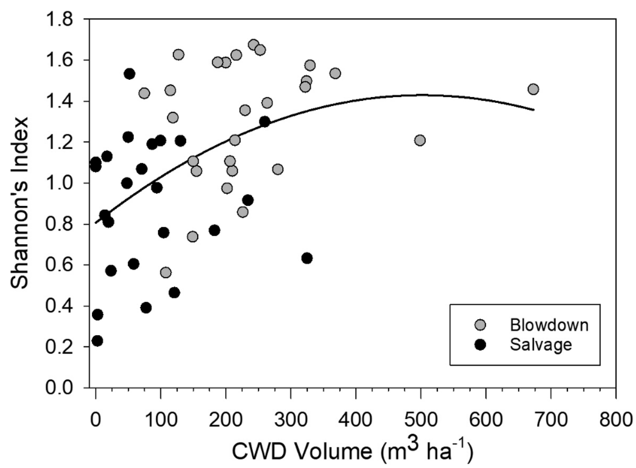

Fig. 5. Comparison of species diversity, as measured by Shannon's Index, of tree regeneration to DWM volume in wind-damaged (blowdown and salvage) plots. A second-order polynomial trendline was fit to the data (R^2 = 0.2263).

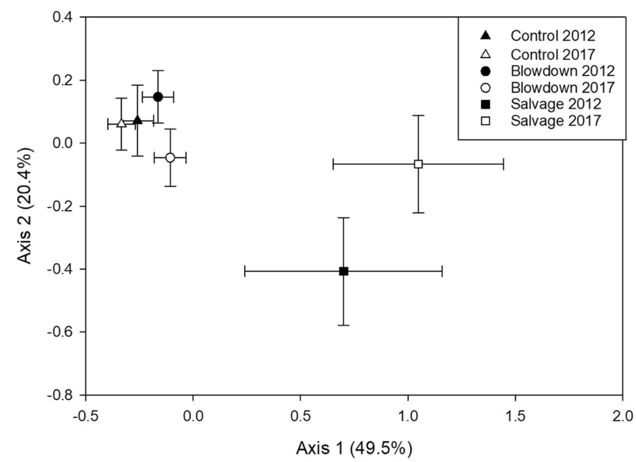

Fig. 6. NMS ordination of regeneration tree functional traits (mean of treatment ± standard error) by treatment in 2012 (filled points) and 2017 (open points), which corresponds to 1- and 6-years post-tornado event in south-central Massachusetts.

Table 2
Pair-wise PERMANOVA results for species composition (left) and functional trait composition (right) by treatment pairs for regenerating tree species. Significant values (*) are based on Bonferroni-corrected p-values (α = 0.05) to correct for inflated Type 1 error.

	Species Composition			Functional Composition		
Treatment Pairs	F Statistic	R^2	p-value	F Statistic	R^2	p-value
Blowdown vs. Control	2.454	0.023	0.002*	2.799	0.026	0.034*
Blowdown vs. Salvage	5.415	0.065	0.001*	18.268	0.190	0.001*
Control vs. Salvage	6.371	0.077	0.001*	22.360	0.227	0.001*

Table 3
Functional traits with significant correlations with the two-axis NMS ordination of tree regeneration in 1- and 6-year post-tornado event sampling. Significant values (*) are based on Bonferroni-corrected p-values (α = 0.05) to correct for inflated Type 1 error.

	Axis 1		Axis 2	
Functional Trait	Kendall's τ	p-value	Kendall's τ	p-value
Shade Tolerance	−0.3968	$p < 0.0001$*	0.4864	0*
Drought Tolerance	0.0497	0.4009	−0.7230	0*
Flood Tolerance	−0.4480	$p < 0.0001$*	0.5593	0*
Wood Specific Gravity ($g\,cm^{-3}$)	0.3091	$p < 0.0001$*	−0.3548	$p < 0.0001$*
Seed Mass (mg)	−0.1976	0.000791*	−0.2550	$p < 0.0001$*
Maximum Height (m)	−0.5292	$p < 0.0001$*	0.2281	0.000106*
Height at 20 Years (m)	−0.5941	0*	0.2401	$p < 0.0001$*
Leaf Mass per Area ($g\,m^{-2}$)	−0.4526	$p < 0.0001$*	0.5750	0*

4. Discussion

This study documented the short-term responses of hemlock-hardwood forests to severe wind disturbance and associated salvage logging, and generally supports the findings of previous work demonstrating the altered, short-term successional dynamics following salvage logging relative to recovery trajectories after natural disturbance (Cooper-Ellis et al., 1999; Foster et al., 1997; Lang et al., 2009; Lindenmayer and Ough, 2006). In particular, our findings suggest post-disturbance salvage logging operations may functionally and compositionally alter the successional dynamics of hemlock-hardwood forests to a greater extent than standing-replacing wind alone by pushing short-term successional trajectories toward more disturbance-adapted species and traits, with the potential to generate lasting effects on ecosystem recovery and biodiversity (Lindenmayer and Noss, 2006; Palik and Kastendick, 2009). Despite dramatic sustained damage to and structural reorganization of this ecosystem after singular and compound disturbances, tornado-damaged areas remained similar to control sites in certain aspects. In light of projected increases of disturbance frequency and severity in this region, it is critical to consider how post-disturbance management activities will affect structural, compositional, and functional conditions and the long-term ability of these systems to respond to future disturbances (Millar et al., 2007).

4.1. Effects of disturbance on stand structure

Large, infrequent disturbances have been shown to influence ecosystem processes over the long term by generating enduring biological and structural legacies (Foster et al., 1998). In particular, wind events such as hurricanes and tornados alter the trajectory of forest structural development through the creation of numerous biological legacies such as dead and downed woody material, snags, pit and mound structures, and residual live trees (D'Amato et al., 2011b; Fraver et al., 2017; Meigs and Keeton, 2018; Sass et al., 2018a; Spies, 1998). In our study, structural legacies differed based on treatment, which was a function of singular and compound disturbance. As expected, the effects of salvage logging on tornado-damaged sites resulted in a lower volume of snags and DWM, since salvage logging practices typically aim to remove these legacies from the landscape (Lindenmayer et al., 2008). The removal of this dead material and associated open-canopy conditions in salvaged areas may have important ecological implications for forest recovery. The retention of snags, downed logs, and structural legacies such as tip-up mounds have been shown to augment regeneration recovery following natural disturbances by mitigating extreme (i.e. dry, compacted soil) conditions that may inhibit growth (D'Amato et al., 2011b; Palik and Kastendick, 2009; Sass et al., 2018b). Although not specifically examined in this study, additional impacts of the loss of standing and downed dead wood include biodiversity declines (Lindenmayer and Ough, 2006; Thorn et al., 2018), including loss of deadwood-dependent organisms (Spies, 1998), and decreased establishment or recruitment failure of key species in this ecosystem (yellow birch, eastern hemlock)

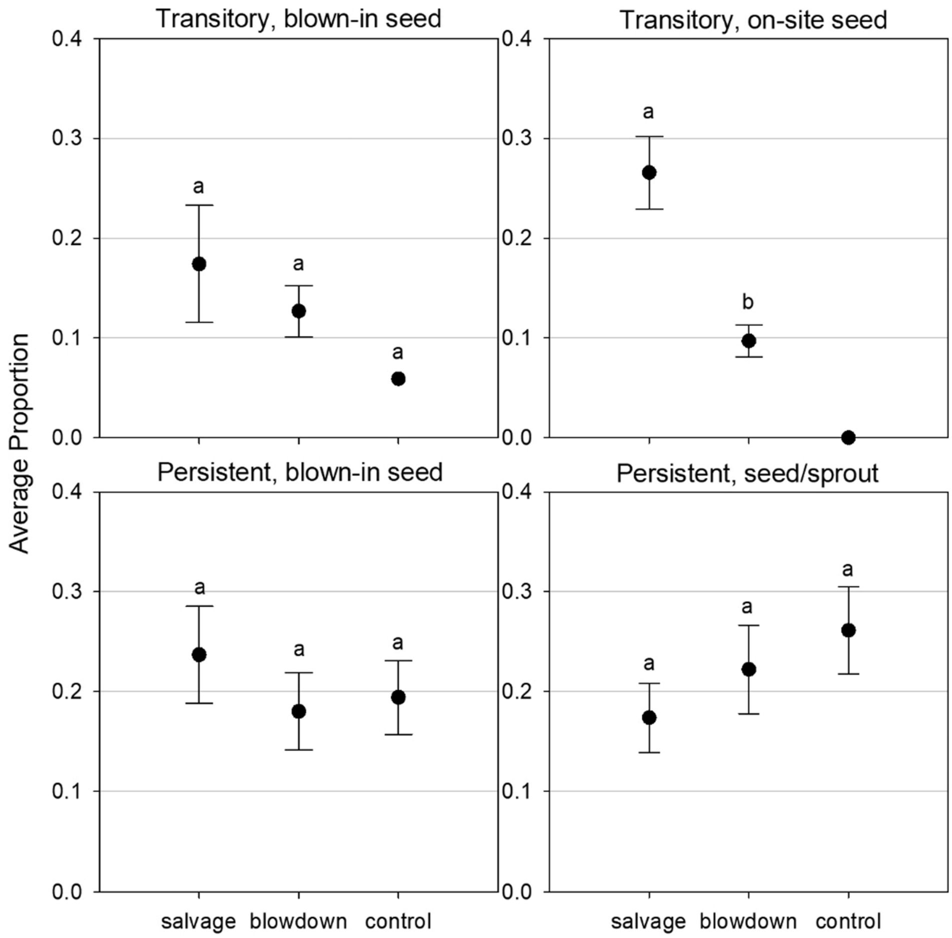

Fig. 7. Average proportion of tree species in regeneration functional strategy group by treatment in 2017. Error bars represent 95% confidence intervals. Statistical significance between like groups is assessed at the $p < 0.05$ level.

due to lack of structural legacies necessary for germination and establishment (Caspersen and Saprunoff, 2005).

4.2. Effects of disturbance on stand composition

Post-disturbance overstory mortality in salvage plots was lower than blowdown plots and similar to background levels of senescence in undisturbed control plots, supporting our first hypothesis. The higher rates of post-disturbance mortality in blowdown treatments can be attributed to the initial survival of wind-damaged (leaning, snapped, and uprooted) trees in 2012 that died due to damage before remeasurement in 2017. Such individuals were likely removed in salvaged areas. In all treatments, red oak was a major component of the overstory, and consequently, it was the species that suffered the highest losses, as individuals in upper canopy positions generally experience greater rates of post-windthrow mortality (Foster, 1988; Peterson, 2007; Rich et al., 2007). Eastern hemlock and black birch exhibited higher survival rates in blowdown plots over time, potentially due to smaller size and lower levels of canopy dominance at the time of the tornado (cf. Rich et al., 2007). These surviving species will likely constitute a greater component of post-disturbance stand conditions over time, a dynamic observed following stand-replacing wind in many other studies (e.g. Spurr, 1956, Lang et al., 2009, D'Amato et al., 2017). The differences observed in post-disturbance mortality may have also reflected differential susceptibility of pre-disturbance stand conditions to disturbance impacts (cf. Foster, 1988); however, biophysical settings and forest conditions were similar across plots evaluated suggesting observed patterns in mortality and survival were driven by disturbance impacts.

4.3. Effects of disturbance on understory trees and successional trajectories

We documented rapid recovery of tornado-damaged plots (blowdown and salvage) over the short time frame of this study, likely through multiple mechanisms including seedling establishment, sprouting of damaged trees, and advance regeneration (Plotkin et al., 2013). The tornado event served to release advance regeneration, as well as create conditions suitable for recruitment of new seedlings, as indicated by the significantly higher sapling densities and richness in both blowdown and salvage treatments compared to the control. However, salvage logging tended to homogenize the tree regeneration communities, as evident in the comparatively low species diversity and dissimilarity values for these plots (Table 1). These results are consistent with other work examining post-salvage logging plant communities (D'Amato et al., 2011b) and may be due to the higher disturbance severity associated with dead wood removal in salvage sites, which may damage or kill existing woody species regeneration and favor early-successional, disturbance-adapted species (Blair et al., 2016; Lindenmayer and Ough, 2006; Peterson and Leach, 2008b; Thorn et al., 2018).

Salvage logging had a negative impact on regeneration diversity and positive impact on sapling density and richness compared to undisturbed forest, thus only partially supporting our second hypotheses.

Other studies examining salvage logging responses have observed similar results (Elliott et al., 2002; Peterson and Leach, 2008a; Taylor et al., 2017). These findings may be explained by the more open canopy conditions and possible additional exposure of mineral soil resulting from salvage operations removing residual overstory and DWM which may have created seedbed conditions that favored rapid establishment by disturbance-adapted species (Lang et al., 2009; Taylor et al., 2017) in areas not occupied by surviving advance regeneration and stump sprouts, which dominated recovering communities (Plotkin et al., 2013). By reducing competing vegetation, salvage logging has been shown on some sites to enhance the establishment of a wider range of species (Royo et al., 2016), which is confirmed in our study since salvage logged sites exhibited the highest treatment-wide regeneration species and functional richness values (Table 1). However, the low species diversity and dissimilarity values observed on salvage plots suggest that the compound disturbance of salvage logging tended to homogenize understory regeneration in comparison to blowdown treatments.

Red oak regeneration densities were lower in blowdown and salvage treatments than control treatments, potentially indicating a lower abundance of this species over time on these sites. One post-tornado study in an oak-dominated forest in Alabama noted that both wind disturbance and salvage logging accelerated succession towards shade-tolerant species in the regeneration layer, notably shifting away from oaks and towards red maple (White et al., 2014). This acceleration was more pronounced in the salvaged sites. Longer-term work in New England, however, highlights that survivors of disturbance, not new seedlings germinating in response to disturbance, control the structure and composition of the recovering disturbed forest (Plotkin et al., 2013). Thus, the lower densities of red oak regeneration in blowdown and salvage plots may not be as concerning. Moreover, regeneration abundance in control plots may represent a proxy for pre-disturbance conditions, which indicate a portion of the sapling layer currently present in blowdown and salvage plots may be from advance regeneration. However, survival of red oak in the overstory of tornado-damaged plots is low after taking 2017 post-disturbance mortality into account, comprising only 15–25% of total overstory basal area compared to nearly 50% in control plots. These analyses indicate that red oak regeneration may be outcompeted by other species in blowdown and salvage plots, hindering its ability to recover basal area in the future, and potentially shifting this forest away from a red oak dominated forest. Continued remeasurement will help to determine the future of red oak in these ecosystems.

4.4. Effects of singular and compound disturbance on functional differences

Singular and compound disturbances generated functional shifts in this forest with implications for future change. Control and blowdown regeneration functional trait CWMs were similar based on our ordinations, whereas the distance of salvage treatments from these treatments suggests a greater amount of functional difference (Fig. 6). Both blowdown and control sites exhibited high correlation with shade tolerance, maximum height, and seed mass, which are typical characteristics of mature forests (Wilfahrt et al., 2014). However, given that blowdown sites have little red oak regeneration, these sites may be skewed toward high seed mass due to the prevalence of American chestnut stump sprouts, which are unlikely to persist in the mature forest. Additionally, control and blowdown sites had similar reproductive strategy-focused functional groups, especially in terms of persistent species, whereas salvage plots had a greater presence of transitory, on-site seeded species (i.e. pin cherry) (Fig. 7). These results emphasize the resilience of northern hardwood-hemlock forests to singular natural disturbance, and are consistent with other studies that noted similar species and functional composition between blowdown and control sites (D'Amato et al., 2011b; Lang et al., 2009; Meigs and Keeton, 2018; Palik and Kastendick, 2009; Spurr, 1956). As documented in other studies, it is likely that the tornado event acted as a top-down release for advance regeneration at these sites, which may explain the similarity of regeneration function, composition, and reproductive strategy to that of control sites (Cowden et al., 2014; Plotkin et al., 2013; Spurr, 1956) (Table 3).

5. Conclusions and management implications

Overall, our study found that the primary impacts of post-tornado salvage logging were a reduction in structural legacies, namely DWM, and general homogenization of tree regeneration composition. These latter results may be due to a combination of advance regeneration killed by salvage logging operations and creation of favorable site conditions (i.e. compacted soil, open canopy) for disturbance-adapted species. The significance of gray birch and pin cherry on salvaged sites based on indicator species analysis confirms this finding, and suggests that compound disturbance may ultimately generate differences in community structure and composition as compared to unlogged blowdown sites. These impacts were also reflected in the shifts in species and functional composition of the regeneration layer in northern hemlock-hardwood forests toward disturbance-adapted species and traits following salvage logging. Because the observed trends were only recorded for two time periods, we cannot yet say if salvage logging permanently redirects successional trajectories away from blowdown or undamaged control plots, but future monitoring efforts at the site may be able to detect those trends.

While there are many human benefits to salvage logging (i.e. aesthetics, reduced fire risk, economic recovery - Lindenmayer et al., 2008), our results show that it also has immediate and likely lasting impacts on forest communities, especially relating to the removal of DWM and structural legacies that influence recovery. However, salvage logging operations are unlikely to cease entirely, so developing salvage logging management guidelines to preserve these structures on the landscape is a priority. Because structural legacies are important in aiding the recovery of diverse species, management actions should focus on retaining these structures during salvage logging operations to create landscape heterogeneity. Designating unlogged "leave islands" while logging other areas contributes to a patchy mosaic of structural retention and landscape diversity, which in turn emulates the historical patterns of disturbance and encourages continued structural and spatial diversity in the recovering forest.

Acknowledgments

We thank Lydia Kiewra, Danelle Laflower, and Dan Wright for assistance with field work, Cliff Kipper for initial plot establishment and inventory in 2012, and William Hill for assistance with data delivery and sampling logistics. Thanks to the Massachusetts Department of Conservation and Recreation for assistance with this project.

Funding

This work was supported by the USDA NIFA McIntire-Stennis Cooperative Forestry Program, USDA Forest Service Northern Research Station, University of Vermont, and Department of Interior Northeast Climate Adaptation Science Center.

Declarations of interest

None.

Appendix A

See Tables A1–A3.

Table A.1
List of species evaluated and their functional traits. (*) denotes that the species was only considered in the regeneration dataset, not the overstory.

Species	Shade tolerance	Drought tolerance	Flood tolerance	Wood specific gravity ($g\,cm^{-3}$)	Seed mass (mg)	Maximum height (m)	Height at 20 years (m)	Leaf mass per area ($g\,m^{-2}$)
Acer rubrum	3.44	1.84	3.08	0.54	21.01	27.43	10.67	104.71
Acer saccharum	4.76	2.25	1.09	0.63	66.02	30.48	6.10	102.33
Betula alleghaniensis	3.17	3.00	2.00	0.62	1.02	30.48	7.62	45.71
Betula lenta	2.58	3.00	1.00	0.65	0.70	18.29	4.57	58.88
Betula papyrifera *	1.54	2.02	1.25	0.55	1.33	21.34	12.19	100.00
Betula populifolia *	1.50	2.34	1.00	0.45	0.11	7.62	7.62	58.88
Carya spp.	2.20	3.00	1.26	0.75	2267.96	24.38	9.14	52.48
Castanea dentata *	3.06	3.00	1.00	0.43	4535.92	35.05	10.67	57.54
Fraxinus americana	2.46	2.38	2.59	0.60	45.35	27.43	12.19	91.20
Pinus strobus	3.21	2.29	1.03	0.35	17.99	45.72	12.19	134.90
Prunus pensylvanica *	1.00	1.50	1.50	0.47	31.94	9.14	7.62	50.12
Prunus serotina *	2.46	3.02	1.06	0.50	95.01	24.30	15.24	56.23
Quercus alba	2.85	3.56	1.43	0.68	3543.69	30.48	7.62	100.00
Quercus rubra	2.51	3.29	1.06	0.64	3630.04	25.37	10.97	109.65
Tsuga canadensis	4.83	1.00	1.25	0.40	2.42	32.00	6.71	123.03

Table A.2
Sources for functional trait values.

Trait	Primary source	Additional sources
Shade Tolerance	(Niinemets and Valladares, 2006)	USDA Plants Database
Drought Tolerance	(Niinemets and Valladares, 2006)	USDA Plants Database
Flood Tolerance	(Niinemets and Valladares, 2006)	USDA Plants Database
Wood Specific Gravity	(Miles and Smith, 2009)	
Seed Mass	USDA Plants Database	
Maximum Height	USDA Plants Database	(Paquette and Messier, 2011)
Height at 20 Years	USDA Plants Database	
Leaf Mass per Area	(Wright et al., 2004)*	(Curzon et al., 2017; Paquette and Messier, 2011)

* Datasets used: Bassow & Bazzaz (Petersham, Massachusetts, USA), Ricklefs (Ontario, Canada), Reichetal (North Carolina, USA), and Small (Ottawa, Ontario, Canada).

Table A.3
List of regeneration tree species present in the study site in 2017 with their regeneration strategy functional group and occurrence by treatment. Regeneration strategy functional groups include (1) Transitory; blown-in seed, (2) Transitory; on-site seed, (3) Persistent; blown-in seed, and (4) Persistent; seed/sprout. Note that treatments have different numbers of plots measured.

Species	Functional group (reproductive strategy)	Blowdown	Salvage	Control
Acer rubrum	(4) Persistent, seed/sprout	382	235	375
Acer saccharum	(4) Persistent, seed/sprout	22	10	32
Betula alleghaniensis	(3) Persistent, blown-in seed	83	26	21
Betula lenta	(3) Persistent, blown-in seed	116	342	136
Betula papyrifera	(1) Transitory, blown-in seed	19	19	1
Betula populifolia	(1) Transitory, blown-in seed	13	30	0
Carya spp.	(4) Persistent, seed/sprout	13	4	13
Castanea dentata	(4) Persistent, seed/sprout	92	11	33
Fraxinus americana	(3) Persistent, blown-in seed	1	0	20
Pinus strobus	(3) Persistent, blown-in seed	36	80	71
Prunus pensylvanica	(2) Transitory, on-site seed	15	149	0
Prunus serotina	(3) Persistent, blown-in seed	39	33	78
Quercus alba	(4) Persistent, seed/sprout	16	20	12
Quercus rubra	(4) Persistent, seed/sprout	32	61	157
Tsuga canadensis	(4) Persistent, seed/sprout	10	33	2
Totals	**Overall**	**889**	**1053**	**951**
	(1) Transitory, blown-in seed	32	49	1
	(2) Transitory, on-site seed	15	149	0
	(3) Persistent, blown-in seed	275	481	326
	(4) Persistent, seed/sprout	567	374	624

Appendix B. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.04.039.

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