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Intermediate-severity wind disturbance in mature temperate forests: legacy structure, carbon storage, and stand dynamics

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Abstract. Wind is one of the most important natural disturbances influencing forest structure, ecosystem function, and successional processes worldwide. This study quantifies the stand-scale effects of intermediate-severity windstorms (i.e., blowdowns) on (1) live and dead legacy structure, (2) aboveground carbon storage, and (3) tree regeneration and associated stand dynamics at four mature, mixed hardwood–conifer forest sites in the northeastern United States. We compare wind-affected forests to adjacent reference conditions (i.e., undisturbed portions of the same stands) 0–8 yr post-blowdown using parametric (ANOVA) and nonparametric (NMS ordination) analyses. We supplement inventory plots and downed coarse woody detritus (DCWD) transects with hemispherical photography to capture spatial variation in the light environment. Although recent blowdowns transferred a substantial proportion of live overstory trees to DCWD, residual live tree basal area was high (19–59% of reference areas). On average, the initial post-blowdown ratio of DCWD carbon to standing live tree carbon was 2.72 in blowdown stands and 0.18 in reference stands, indicating a large carbon transfer from live to dead pools. Despite these dramatic changes, structural complexity remained high in blowdown areas, as indicated by the size and species distributions of overstory trees, abundance of sound and rotten downed wood, spatial patterns of light availability, and variability of understory vegetation. Furthermore, tree species composition was similar between blowdown and reference areas at each site, with generally shade-tolerant species dominating across multiple canopy strata. Community response to intermediate-severity blowdown at these sites suggests a dynamic in which disturbance maintains late-successional species composition rather than providing a regeneration opportunity for shade-intolerant, pioneer species. Our findings suggest that intermediate-severity wind disturbances can contribute to stand-scale structural complexity as well as development toward late-successional species composition, at least when shade-tolerant regeneration is present pre-blowdown. Advance regeneration thus enhances structural and compositional resilience to this type of disturbance. This study provides a baseline for multi-cohort silvicultural systems designed to restore heterogeneity associated with natural disturbance dynamics.

Key words: biological legacies; blowdown; carbon storage; intermediate disturbance; northern hardwood–conifer forest; resilience; stand dynamics; structural complexity; windthrow.

Introduction

Forests play a fundamental role in the Earth system, but they are inherently dynamic, shaped by multiple natural and anthropogenic disturbances (Dale et al. 2001, Running 2008). In temperate forests, windstorms (i.e., blowdown events) are one of the most important natural disturbances worldwide (Everham and Brokaw 1996, Thom and Seidl 2016). Windstorms are also key indicators of global change, and blowdown frequency or severity may increase with changing climate, storm patterns, and land use (Foster and Boose 1992, Peterson 2000, Dale et al. 2001, Frelich and Reich 2010, Diffenbaugh et al. 2013, Kulakowski et al. 2016), contributing to positive feedbacks between intensifying disturbance regimes and the carbon cycle (Woodall et al. 2013, Seidl et al. 2014). In mature forests, blowdowns also may redirect or alter successional pathways, thereby acting as a strong control on late successional forest structure, composition (Foster 1988, Rich et al. 2007), and associated ecosystem services including carbon storage (Keeton et al. 2011, Gunn et al. 2014, Williams et al. 2016) and riparian function (Keeton et al. 2007, Bechtold et al. 2016). Although windstorms are widespread, key uncertainties remain regarding forest responses to blowdown events at the forest stand scale.

Wind disturbances impart a large range of stand-scale severity (i.e., tree mortality) while spanning multiple spatiotemporal scales, from frequent, small, gap-forming events (e.g., Frelich and Lorimer 1991, Lorimer and White 2003, Nagel et al. 2017) to infrequent, regional hurricane events with large extent but variable severity (e.g., Foster and Boose 1992, Sano et al. 2010, D'Amato et al. 2017). Previous studies typically have classified wind and other disturbances into two distinct groups at the endpoints of this spectrum (Seymour and White 2002). More recent studies suggest that such characterizations may have under-represented the importance of intermediate-severity blowdowns (Hanson and Lorimer 2007, North and Keeton 2008), which can strongly influence stand- and landscape-scale distributions of tree age, size, and species (Woods 2004, Martin and Ogden 2006, Stueve et al. 2011, Cowden et al. 2014, Janda et al. 2017). However, given the relatively small number of field-based studies that have assessed intermediate-severity wind disturbances, our understanding of their consequences

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for ecosystem dynamics, ecosystem services, and sustainable forest management remains incomplete. In this study, we investigate intermediate blowdown effects on legacy forest structure, carbon storage, and stand dynamics in mature temperate forests in the northeastern United States.

Blowdown severity stems from the interaction of multiple factors, including local storm meteorology, landscape characteristics, and forest structure and composition (Foster and Boose 1992, Mladenoff et al. 1993), and the interplay between these factors may be particularly important during intermediate-scale events. Here, we define intermediate-severity blowdowns as partial canopy disturbances that result from strong winds associated with thunderstorms, microbursts, macrobursts, *derechos*, and low-grade tornadoes (Hjelmfelt 2007, Cowden et al. 2014). At the forest stand scale, only a portion of the overstory tree canopy is killed or damaged (usually through uprooting or stem breakage), leaving biological legacies in the form of standing and downed, live and dead trees (e.g., Franklin et al. 2000, Christensen et al. 2005, Nagel et al. 2006, Svoboda et al. 2014). The variability of disturbance severity within a given stand sets the stage for multiple pathways of post-disturbance structural development, which depend on the abundance and composition of residual canopy trees, plant propagule availability, release effects, interspecific competition, climate variation during subsequent growing seasons, sub-canopy vegetation response, and interactions with other stressors and disturbance agents (Runkle 1982, Carlton and Bazzaz 1998, Beaudet et al. 2007, Donato et al. 2012, Lorimer and Halpin 2014, Stuart-Haëntjens et al. 2015, Janda et al. 2017, Meigs et al. 2017). By altering the distribution of standing and downed trees, intermediate-severity wind events also increase light availability and the spatial heterogeneity of residual dead and live structures, which are key components of ecological memory (i.e., material and information legacies; Johnstone et al. 2016). As disturbance regimes continue to change due to anthropogenic drivers from local to global scales (Seidl et al. 2011, Kulakowski et al. 2016), the biological legacies and ecological memory associated with windstorms may become increasingly important, especially their effects on forest structure, ecosystem services, and successional dynamics.

Forest structure is an integral attribute of within-stand heterogeneity (Fahey et al. 2015), structural resilience (Halpin and Lorimer 2016), and sustainable forest management (D'Amato et al. 2011, Lindenmayer et al. 2012). Due in part to increasing interest in forest management practices that foster rather than reduce complexity (Keeton 2006, Smith et al. 2008, Bauhus et al. 2009, Gustafsson et al. 2012, Puettmann et al. 2012), multiple structural complexity metrics have been developed (see review by McElhinny et al. 2005) and applied (e.g., Littlefield and Keeton 2012). These stand-scale complexity metrics, typically based on standing tree distributions, provide a way to quantify the biological legacies generated by disturbances like blowdown, particularly in combination with observations of downed wood, tree regeneration, and non-tree vegetation response (Franklin et al. 2000). Taken together, these building blocks of forest structure describe the overall architecture of a given stand, serving as a natural analog for stand-scale silvicultural prescriptions and directly influencing ecosystem services and functions.

Although disturbance-induced structural changes influence ecosystem services, these relationships are not necessarily direct (Thom and Seidl 2016). For example, blowdowns transfer live and dead trees to the forest floor, catalyzing biogenic carbon emissions, but they also open the canopy, creating opportunities for increased vegetation growth and associated carbon uptake (Stuart-Haëntjens et al. 2015, Gough et al. 2016). Thus, as with fire (Meigs et al. 2009), stand-scale carbon storage is dependent on the amount of live and dead biomass before and after wind disturbances. Unlike fire, however, there have been relatively few studies on the effects of wind disturbance on carbon pools and fluxes (Mayer et al. 2014, Williams et al. 2016). Given the importance of forests and forest management in the global carbon budget (McKinley et al. 2011, Pan et al. 2011), as well as the potential pervasiveness of partial canopy disturbances like intermediate blowdown (Stueve et al. 2011), a clearer understanding of disturbance effects on carbon storage at all points along the severity gradient is essential for forest policy and management (Running 2008).

As with ecosystem services, changes in stand structure may have differential effects on species composition and associated successional dynamics (Webb and Scanga 2001). In general, post-disturbance tree composition depends on pre-disturbance composition, species-specific mortality effects (Rich et al. 2007), pre- and post-disturbance regeneration (Macek et al. 2017), and environmental changes that confer a competitive advantage to particular species and/or tree strata (e.g., overstory vs. sapling vs. seedling). If blowdown-induced gaps are large enough to increase the availability of light, germination microsites (e.g., tip-up mounds), and other limiting factors in mature forests, then composition may shift toward locally present shade-intolerant species, as would be expected following large, stand-replacing disturbance (Romme et al. 1998). Alternatively, disturbances that disproportionately affect shade-intolerant overstory trees can accelerate succession toward shade-tolerant species if such species are locally abundant in the understory (Abrams and Scott 1989). Secondary northern hardwood and mixed hardwood–conifer forests in the northeastern United States include a variety of shade-tolerant, intermediate-tolerant, and intolerant species that mostly established following 19th-century agricultural abandonment, with subsequent stand development profoundly influenced by land-use history, introduced insects and pathogens (e.g., beech bark disease *[Neonectria faginata]*), and a range of timber harvest practices (Lorimer and White 2003, Keeton 2006, Giencke et al. 2014, Urbano and Keeton 2017). The phenomenon of dense American beech (*Fagus grandifolia*) understory thickets is an important management concern in the region (Wagner et al. 2010), highlighting the challenge of assessing successional dynamics in terms of both functional types (i.e., shade tolerance) and individual species. Indeed, empirical observations of blowdown effects on the composition of residual and regenerating trees in these forests will help inform management efforts intended to restore natural forest dynamics (Hanson and Lorimer 2007, Kern et al. 2017).

Despite increasing focus on intermediate disturbances in the context of forest management (North and Keeton 2008, Cowden et al. 2014) and the recognition that wind is an important disturbance agent worldwide (Thom and Seidl 2016), critical knowledge gaps remain regarding the biological legacies associated with blowdown events. The primary objective of this study is to quantify the stand-scale effects of intermediate-severity blowdown on (1) live and dead legacy structure, (2) aboveground carbon storage, and (3) tree regeneration and associated stand dynamics. We hypothesize that (H_1) blowdowns transform forest structure and generate abundant biological legacies (live and dead trees) by transferring overstory trees to the forest floor; (H_2) blowdowns alter the distribution and abundance of live and dead carbon by reallocating biomass among aboveground pools; and (H_3) blowdowns reinforce late-successional, shade-tolerant species composition by providing resources and growth opportunities for advance regeneration in the understory. To test these hypotheses, we analyze field observations of wind disturbance effects in mature, mixed hardwood-conifer forests in the northeastern United States.

Methods

Study area and design

We surveyed intermediate-severity wind impacts at four recent blowdown areas in the states of New York and Vermont (Table 1, Fig. 1). These sites are representative of a range of conditions found more broadly throughout the northern forest region, including species composition, site productivity, and land use/management history. The four specific sites are (1) primary old growth (i.e., never cleared), mixed hardwood-conifer forest near Saranac Lake, New York (Melonberry, MB; Curzon and Keeton 2010); (2) naturally regenerated white pine (*Pinus strobus*) with codominant eastern hemlock (*Tsuga canadensis*) and northern hardwoods in Charlotte, Vermont (Williams Woods, WW); (3) naturally regenerated secondary northern hardwoods with codominant balsam fir (*Abies balsamea*) in Weston, Vermont (Weston, WS); (4) mature white pine plantation with sub-canopy northern hardwoods in Jericho, Vermont (University of Vermont Jericho Research Forest, JF).

Although species composition varies by site, dominant overstory tree species are generally shade-tolerant hardwoods (red maple [*Acer rubrum*], sugar maple [*Acer saccharum*], American beech) and conifers (balsam fir, eastern hemlock), with the exception of white pine, which exhibits intermediate shade tolerance (Appendix S1: Tables S1 and S2). Site elevations range from 48 to 609 m above sea level, and the climate is humid and continental, with mean annual temperature of 6.2°C and mean annual precipitation of 1,112 mm (Table 1). Land ownership varies among sites, but all four sites are managed primarily for conservation objectives and are publicly accessible (Table 1). The four blowdowns span a range of patch sizes from 0.22 to 13.0 ha (delineated using digital ortho-photos; Table 1).

All four blowdowns resulted from microbursts associated with low-pressure storm systems in late summer to early fall. The phenomena of microbursts are related to strong downdrafts, straight-line winds, and outflows <4 km long and can arise during hurricanes, convective storms, winter storms, and topographically induced downslope winds (Hjelmfelt 2007). Because these events occurred in different years and locations, we sampled them at different times since blowdown based on

Table 1. Characteristics of blowdown sites.

Site (abbreviation)	Year of blowdown	No. times sampled	No. plots in reference, by visit	No. plots in blowdown, by visit	Initial observation (yr since blowdown)	Second observation (yr since blowdown)	Latitude (°N)	Longitude (°W)	Elevation (m)	Patch size (ha)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Management agency (Ownership)
Jericho Forest (JF)	2010	2	2, 3	4, 3	1	4	44.4469	72.9920	188	0.22	7	1,040	University of Vermont (VT State)
Williams Woods (WW)	2007	2	9, 7	10, 8	0	6	44.2705	73.2527	48	0.45	8	920	The Nature Conservancy (Private)
Melonberry (MB)	2006	2	10, 8	8, 5	1	7, 8	44.2314	74.2462	609	2.91	5	1,079	Adirondack Park Agency (NY State)
Weston (WS)	2014	1	3	5	1		43.3635	72.7985	545	13.00	5	1,410	Green Mountain National Forest (USDA Forest Service)

Notes: Elevation derived from 30-m digital elevation model. Patch size delineated with digital ortho-photos in Google Earth, recognizing that blowdown areas do not necessarily have distinct edges. Annual temperature and precipitation data are 30-yr normals from the PRISM research group: http://prism.oregonstate.edu

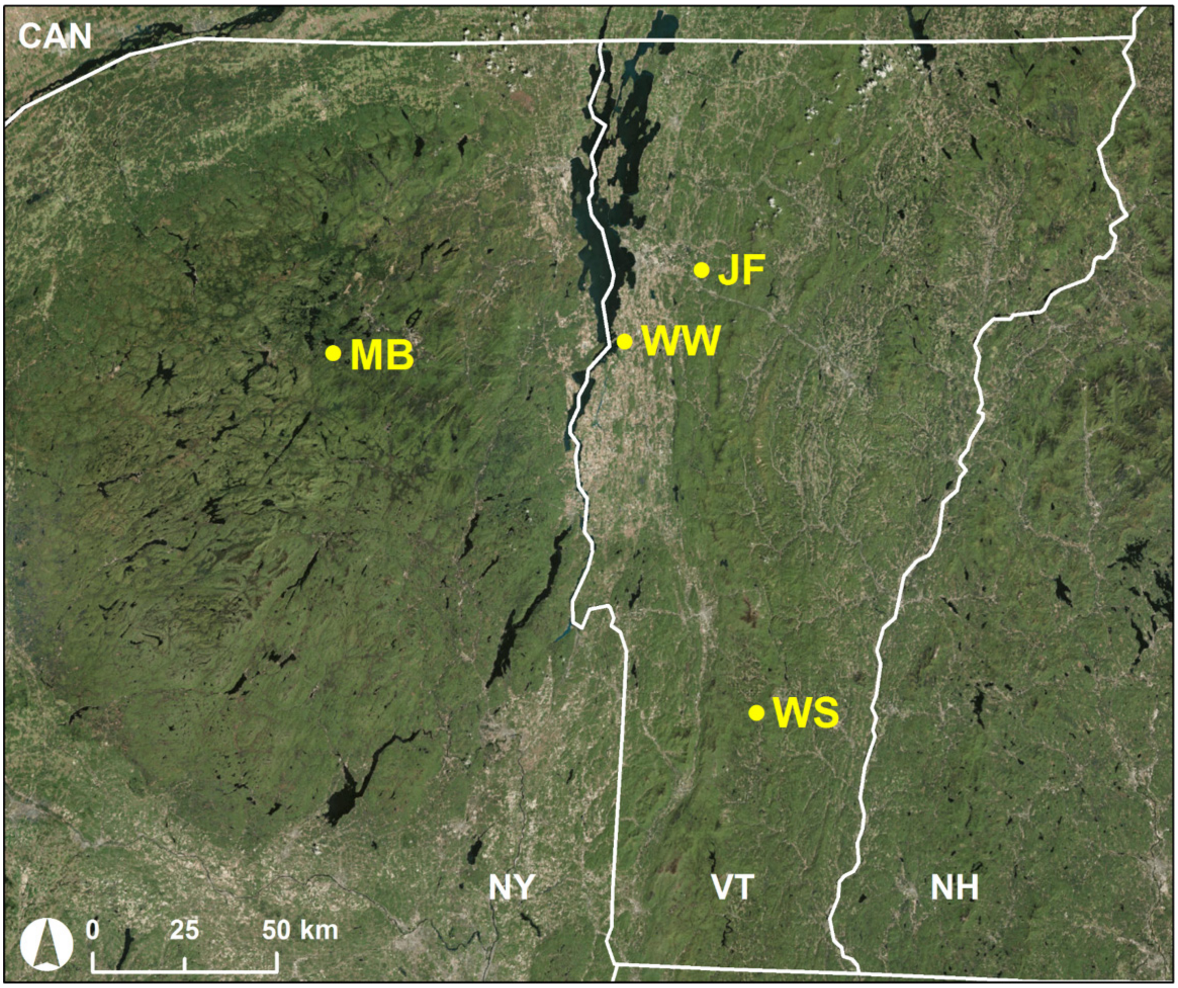

FIG. 1. Study site locations in the northern forest region of New York (NY) and Vermont (VT). Study site abbreviations are identified in Table 1. Generally forested land cover indicated by ESRI World Imagery basemap.

available resources. The two oldest blowdown events occurred in 2006 (MB) and 2007 (WW). At these sites, we sampled overstory trees and downed coarse woody detritus (DCWD) in 2007 (0–1 yr post-blowdown) and again in 2013/2014 (6–8 yr post blowdown; Table 1). During the second visit, we sampled overstory trees and DCWD at a different randomized set of plots and transects, and we also sampled saplings, seedlings, and understory vegetation cover. Because we randomized plot locations independently at the second observation rather than repeating observations at the original plot locations, we focus our analyses on stand-scale mean and variability (i.e., standard deviation). The two more recent blowdown events occurred in 2010 (JF) and 2014 (WS). Whereas we sampled JF twice (overstory and DCWD in 2010, 1 yr post-blowdown; all strata in 2014, 4 yr post-blowdown), our time since blowdown at WS was limited to one survey of all vegetation strata in 2015 (1 yr post-blowdown; Table 1).

We used a hierarchical, stratified random sampling design to compare variability within and among sites. At each site, we established inventory plots at random locations within the blowdown area (total $n = 43$) and the adjacent undisturbed area (total $n = 42$), which served as a reference condition. The sample size varied among sites and visits based on blowdown size, complexity, and available resources (Table 1). Blowdowns exhibited relatively distinct edges, and we located sample plots within a given blowdown or reference area rather than in edge areas. The paired design assumes that the blowdown and reference areas are part of the same general forest stand (i.e., that pre-disturbance structure and composition were equivalent). We evaluated the comparability of reference and blowdown areas using historical digital ortho-photos, documentary records, and field-based scouting to ensure similar species composition, tree age and size, and topographic position. The generally similar species composition between reference and blowdown stands also supports this assumption See subsection “Blowdown effects on tree regeneration and associated stand dynamics”).

Forest measurements and calculations

We inventoried stand-scale forest structure, aboveground carbon pools, and tree species composition using randomly placed variable radius prism plots for overstory trees and nested fixed-area plots for sub-canopy vegetation. We recorded species, diameter at breast height (DBH; 1.37 m), height (measured with an Impulse 200 laser rangefinder [Laser Technology, Inc., Centennial, Colorado, USA]), and vigor class/decay stage (1–9; Maser et al. 1979) for all live and dead overstory trees within a variable radius plot (2.3 metric basal area prism) centered on the same point as the nested fixed area plots. We sampled saplings (height ≥1 m, DBH ≤5 cm) within 7.98-m fixed radius circular plots (0.2 ha) and assumed that these trees were present prior to blowdown events. We sampled seedlings (height <1 m) within two transects per plot (15.96 × 1 m; 0.0032 ha) and assumed that these trees established post-blowdown. Because our primary focus was forest structure, we did not destructively sample understory trees, which would bolster these assumptions and clarify which, if any, saplings established post-blowdown, particularly at the less recently disturbed sites. Additionally, we recognize that our sample intensity may not have captured all rare species and that additional insight into regeneration dynamics would be possible with measurements of substrate microsites and relative differences in height and growth rates among shade tolerance classes. We sampled percent cover of woody plant (i.e., shrubs), herbaceous, moss, total vegetation, and DCWD ground cover in four quadrats (1 m^2 each) located at the ends of each seedling transect. Sampling intensity was consistent between sites, with the number of plots approximately proportionate to the size of each blowdown area. We connected inventory plots with line-intercept transects of random length and azimuth to sample DCWD volume and biomass for logs at least 10 cm and 1 m length at point of intercept, recording decay class (1–5) after Sollins et al. (1987). At the WW, MB, and WS sites, we also collected hemispherical photos along transects at 25 to 50 m intervals across the blowdowns and into adjacent reference areas to capture spatial variation in the light environment. We collected these photos separately from survey plots to provide supplemental data on overstory canopy conditions, placing a digital camera on a self-leveling tripod above understory vegetation. We processed photos using HemiView software (Version 2.1; Delta-T Devices 2012, Burwell, Cambridgeshire, UK) after Gottesman and Keeton (2017) to estimate proportion of visible sky (i.e., gap fraction) and leaf area index.

We summarized all field measurements at the plot scale and averaged plot estimates within blowdown and reference areas (i.e., stands) at each site. To explore multiple dimensions of structural complexity, we calculated a variety of structure metrics for overstory trees, understory trees, and DCWD (Table 2, Table 3), and we also computed overstory structural complexity indices. Although there are a variety of structural complexity indices, including some combining tree size and species (McElhinny et al. 2005, Littlefield and Keeton 2012), we calculated Shannon diversity among tree size classes and species (H_{DBH} and H_{spp}; D'Amato et al. 2011) to distinguish blowdown effects on structure vs. composition in two, readily interpretable indices. For understory trees, we calculated sapling and seedling abundance in terms of density (stems/ha) and species composition. We classified low, moderate, and high shade tolerance of all tree species with the USDA Forest Service Fire Effects Information System (Appendix S1: Tables S1 and S2; available online).[5] We estimated DCWD volume (m^3/ha) following Warren and Olsen (1964) and Harmon and Sexton (1996), converting volume to biomass (Mg/ha) using species-group- and decay class-specific density and carbon content values following Harmon et al. (2008). We defined sound DCWD as decay classes 1–3 and rotten DCWD as decay classes 4–5.

We quantified aboveground carbon pools by computing biomass and carbon for live trees, dead trees, and DCWD. In so doing, we focus on the largest and most dynamic aboveground pools that we expect wind to alter most substantially (D'Amato et al. 2011), recognizing (1) that non-tree and subcanopy vegetation can store small amounts of carbon yet contribute a large proportion of post-disturbance productivity (Meigs et al. 2009, Stuart-Haëntjens et al. 2015) and (2) that the forest floor and belowground soil pools contain substantial carbon (Fahey et al. 2010). We estimated live tree biomass with species-group-specific allometric equations from Jenkins et al. (2003) embedded in the Northeast Decision Model (NED-3; Twery and Thomasma 2014). Although different allometric equations can derive differing biomass estimates, especially for large trees of some species (Hoover and Smith 2016), our primary focus was on the relative difference between blowdown and reference areas rather than absolute values. We used a volumetric, component-ratio approach to estimate standing dead tree volume and biomass following the California Air Resources Board carbon inventory protocol (Climate Action Reserve 2014; Ford and Keeton 2017). Briefly, we calculated the proportion remaining of estimated full tree biomass based on live tree diameter-height regression equations specific to each site and tree type (conifer, hardwood; R^2 range: 0.53–0.87). We applied density reduction factors after Harmon et al. (2011) and assumed that carbon accounted for 50% of standing biomass.

Statistical analysis

We assessed components of residual (post-wind) structure, aboveground carbon storage, and shade tolerance with two-way ANOVAs based on site and condition, where site refers to the four field sites and condition refers to blowdown vs. reference areas. We assured that we met the assumptions of equal variance with Levene's test (Levene 1960), which indicated that data transformations were not necessary, and conducted ANOVAs in the R statistical environment (R Core Team 2017). Because our objective was to quantify the effect of blowdown and the sites exhibited key differences in composition and structure, we focused primarily on the interaction of site and condition. This interactive effect indicates site-specific pairwise differences between blowdown and reference conditions. For the shade tolerance analysis, we focused on the percentage of species with high shade tolerance and determined that arcsine square root transformations did not yield different results. We calculated 95% confidence intervals, interpreting $P < 0.05$ as strong evidence of differences and $P < 0.1$ as moderate evidence of differences after Meigs et al. (2015) to reduce potential Type II errors due to modest sample sizes and high natural variability. We also report standard deviations as a direct measure of variability within blowdown and reference areas.

We assessed blowdown effects on tree species composition and potential successional dynamics with multivariate,

[5] http://www.feis-crs.org/feis/faces/index.xhtml

Table 2. Overstory tree structural attributes in reference (Ref) and blowdown (Blow) conditions across four sites.

	Site (yr since blowdown)													
	JF (1)		WW (0)		MB (1)		WS (1)		JF (4)		WW (6)		MB (8/7)	
Forest structure variable (units)	Ref	Blow	Ref	Blow	Ref	Blow	Ref	Blow	Ref	Blow	Ref	Blow	Ref	Blow
Live tree density (stems/ha)														
Mean	**934.8**	**92.2**	**959.2**	**425.6**	792.3	457.9	553.5	626.1	908.2	123.2	1096.7	1232.0	539.6	614.5
SD	222.5	29.4	436.3	363.5	480.1	398.7	400.6	728.8	999.7	66.6	839.1	698.6	235.3	633.0
Dead tree density (stems/ha)														
Mean	170.1	22.7	97.3	118.0	**51.7**	**186.2**	156.4	82.1	230.7	92.5	27.8	23.0	125.2	178.0
SD	65.6	25.0	85.0	208.5	37.1	171.9	79.4	76.2	297.1	128.2	36.5	22.8	130.8	192.8
Total tree density (stems/ha)														
Mean	**1104.8**	**114.9**	**1056.5**	**543.6**	844.0	644.1	709.8	708.2	*1138.9*	*215.7*	1124.5	1255.0	664.8	792.5
SD	288.1	22.9	393.8	379.0	503.3	523.1	470.9	731.1	903.4	67.7	824.5	712.8	237.7	811.6
Live basal area (m^2/ha)														
Mean	**62.0**	**12.1**	**33.4**	**19.7**	**33.5**	**17.2**	**23.7**	**6.9**	*30.6*	*11.5*	**30.8**	**18.1**	**36.2**	**18.8**
SD	19.5	4.3	15.4	7.1	10.6	6.4	20.8	6.5	17.8	8.3	11.8	7.2	15.4	9.9
Dead basal area (m^2/ha)														
Mean	6.9	2.3	8.4	6.9	**7.1**	**12.1**	6.9	5.5	9.2	3.8	3.9	4.0	*6.0*	*10.6*
SD	0.0	1.9	3.4	5.3	3.7	5.2	2.3	4.5	8.0	2.7	4.9	4.0	4.2	3.5
Total basal area (m^2/ha)														
Mean	**68.9**	**14.3**	**41.8**	**26.6**	**40.6**	**29.3**	**30.6**	**12.4**	**39.8**	**15.3**	**34.8**	**22.1**	**42.2**	**29.4**
SD	19.5	2.9	16.6	8.0	11.5	9.3	18.6	8.1	13.5	6.6	12.0	8.3	12.6	9.9
Canopy closure† (%)														
Mean	**93.6**	**18.0**	**75.7**	**41.5**	**80.9**	**43.3**	**61.8**	**23.7**	**59.6**	**21.1**	**66.4**	**40.5**	**81.5**	**51.3**
SD	9.1	6.4	22.3	17.7	17.2	10.8	41.9	21.1	25.9	9.4	22.6	14.4	21.5	21.4
Large tree density (stems >50 cm DBH/ha)														
Mean	**42.4**	**5.4**	27.5	20.6	**47.3**	**23.6**	6.1	0.0	14.6	6.7	*34.7*	*7.5*	*57.7*	*29.8*
SD	0.4	6.2	26.0	15.5	20.4	15.8	5.6	0.0	12.7	11.7	26.8	8.4	39.8	27.2
Relative density‡ (%)														
Mean	**100.0**	**18.0**	**77.3**	**41.5**	**84.6**	**43.3**	**70.5**	**23.7**	*59.6*	*21.1*	**71.3**	**40.5**	**93.6**	**51.3**
SD	22.2	6.4	24.5	17.7	22.7	10.8	54.5	21.1	25.9	9.4	32.6	14.4	34.7	21.4
Quadratic mean diameter (cm)														
Mean	28.7	40.0	*22.8*	*29.4*	27.9	28.0	*24.6*	*14.0*	23.6	30.9	23.3	17.1	29.2	26.7
SD	7.8	2.7	3.6	10.4	9.1	8.7	8.4	9.5	5.9	11.0	8.8	6.9	6.0	10.4
Structural complexity (H_{DBH})														
Mean	1.6	1.3	1.5	1.5	1.4	1.4	1.4	0.8	1.5	1.3	**1.3**	**0.9**	**1.6**	**1.1**
SD	0.0	0.2	0.3	0.4	0.2	0.4	0.5	0.6	0.1	0.4	0.3	0.4	0.2	0.5
Compositional complexity (H_{spp})														
Mean	0.3	0.0	**1.3**	**1.0**	0.8	0.7	1.4	1.0	0.7	0.3	*1.1*	*0.8*	0.8	0.9
SD	0.2	0.0	0.3	0.3	0.4	0.2	0.4	0.6	0.0	0.3	0.2	0.4	0.4	0.2
Species richness														
Mean	2.5	1.0	**5.2**	**3.3**	3.7	3.4	*5.3*	*3.0*	**3.7**	**1.7**	**4.3**	**3.0**	3.3	3.6
SD	0.7	0.0	1.6	1.1	0.9	0.5	2.5	1.7	0.6	0.6	1.1	1.1	0.9	0.5

Notes: Tree values refer to overstory trees. Sites are arranged by increasing blowdown patch size (Table 1) and time since blowdown. Mean and SD of plots within blowdown (Blow) and adjacent reference (Ref) areas at four sites sampled at different times post-blowdown. Boldface type indicates pairwise $P < 0.05$; italic type indicates pairwise $P < 0.1$ from two-way ANOVA based on site and blowdown condition. MB site was sampled seven years post-blowdown in the blowdown area and eight years post-blowdown in the reference area.

†Canopy closure based on live tree basal area calculations in Northeast Ecosystem Management Decision Model (NED-3; Twery and Thomasma 2014).

‡Relative density is based on tree-area ratios (Sollins et al. 1987). See Appendix S1: Table S3 for statistical details.

nonparametric community analyses. Specifically, we quantified the similarity of tree species composition among conditions, sites, and strata (overstory, sapling, seedling) using nonmetric multidimensional scaling (NMS ordination) and multi-response permutation procedures (MRPP). For this analysis, we focused on tree density values (stems/ha) because it was not practical to survey or estimate basal area for very small saplings and seedlings. We based both NMS and MRPP on Sørensen distance and implemented them in PC-ORD version 6.22 (McCune and Mefford 2011). NMS ordination arranges sites and strata in a similarity matrix, condensing an n-dimensional space based on the number of species into a reduced set of axes that minimizes stress (i.e., departure from monotonicity in the association between distances in the original species space and reduced ordination space; McCune and Grace 2002, D'Amato et al. 2011). We prepared the NMS

TABLE 3. Live and dead aboveground biomass/carbon pools in reference and blowdown conditions across four sites.

	Site (yr since blowdown)													
	JF (1)		WW (0)		MB (1)		WS (1)		JF (4)		WW (6)		MB (8/7)	
Biomass/carbon variable (units)	Ref	Blow	Ref	Blow	Ref	Blow	Ref	Blow	Ref	Blow	Ref	Blow	Ref	Blow
Live aboveground tree biomass (Mg/ha)														
Mean	**311.5**	**61.9**	**191.6**	**121.0**	**217.5**	**107.4**	**153.8**	**31.4**	154.5	60.2	**182.4**	**94.9**	**256.7**	**119.3**
SD	89.8	22.8	82.5	48.0	65.4	42.4	125.5	26.7	77.8	42.3	69.0	48.3	111.0	67.5
Dead aboveground tree biomass (Mg/ha)														
Mean	27.9	10.7	38.9	29.8	**35.7**	**67.0**	20.5	12.4	**32.3**	**7.5**	9.9	14.0	**13.5**	**36.2**
SD	0.9	8.7	18.3	26.5	21.7	32.0	9.6	8.6	28.0	1.6	12.1	14.6	12.1	15.6
Total aboveground tree biomass (Mg/ha)														
Mean	**339.4**	**72.7**	**230.5**	**150.8**	**253.2**	**174.4**	**174.3**	**43.8**	**186.8**	**67.7**	**192.3**	**108.8**	**270.3**	**155.5**
SD	88.8	15.6	84.4	51.8	65.1	57.9	118.5	31.0	61.9	41.0	65.3	50.5	100.7	62.5
Live aboveground tree carbon (Mg C/ha)														
Mean	**155.7**	**31.0**	**95.8**	**60.5**	**108.7**	**53.7**	**76.9**	**15.7**	77.2	30.1	**91.2**	**47.4**	**128.4**	**59.6**
SD	44.9	11.4	41.3	24.0	32.7	21.2	62.8	13.3	38.9	21.1	34.5	24.1	55.5	33.8
Dead aboveground tree carbon (Mg C/ha)														
Mean	14.0	5.4	19.4	14.9	**17.9**	**33.5**	10.3	6.2	**16.2**	**3.8**	5.0	7.0	**6.8**	**18.1**
SD	0.5	4.3	9.1	13.3	10.8	16.0	4.8	4.3	14.0	0.8	6.0	7.3	6.0	7.8
Total aboveground tree carbon (Mg C/ha)														
Mean	**169.7**	**36.3**	**115.2**	**75.4**	**126.6**	**87.2**	**87.1**	**21.9**	**93.4**	**33.8**	**96.1**	**54.4**	**135.1**	**77.7**
SD	44.4	7.8	42.2	25.9	32.6	28.9	59.3	15.5	30.9	20.5	32.6	25.3	50.4	31.3
Sound DCWD volume (m^3/ha)														
Mean	**104.9**	**453.7**	**38.9**	**941.0**	**153.5**	**353.6**	**64.2**	**284.2**	**69.7**	**413.9**	**166.1**	**329.8**	**91.6**	**261.2**
SD	123.6	49.2	25.9	288.2	136.0	83.1	31.8	176.8	54.9	257.3	72.4	115.1	57.5	50.1
Rotten DCWD volume (m^3/ha)														
Mean	2.1	25.4	53.5	21.9	78.5	87.6	59.1	23.2	26.4	57.4	22.6	104.0	91.7	86.3
SD	2.9	23.0	37.4	28.0	54.3	59.5	42.5	46.1	27.3	53.2	12.4	117.9	58.4	64.4
Total DCWD volume (m^3/ha)														
Mean	**106.9**	**479.2**	**92.4**	**962.9**	**232.0**	**441.2**	123.3	307.4	**96.0**	**471.2**	**188.8**	**433.7**	**183.3**	**347.5**
SD	126.5	63.1	62.4	311.7	154.4	111.0	71.6	164.3	82.2	310.5	69.4	132.0	81.7	99.0
Sound DCWD biomass (Mg/ha)														
Mean	**36.9**	**160.3**	**13.5**	**389.9**	**50.4**	**148.5**	**20.1**	**107.0**	**19.6**	**121.2**	**51.6**	**102.3**	**29.2**	**83.3**
SD	44.5	20.0	10.1	112.9	43.1	45.0	9.6	57.9	14.9	81.5	21.5	38.7	20.8	16.9
Rotten DCWD biomass (Mg/ha)														
Mean	0.3	4.3	9.5	4.0	13.2	14.5	9.8	3.8	4.5	9.7	3.9	18.0	14.7	14.1
SD	0.5	3.9	6.6	5.1	9.7	9.7	6.9	7.4	4.6	9.0	2.1	20.4	9.1	10.8
Total DCWD biomass (Mg/ha)														
Mean	**37.3**	**164.6**	**23.1**	**393.9**	**63.7**	**163.0**	**30.0**	**110.8**	**24.0**	**130.9**	**55.5**	**120.3**	**43.9**	**97.4**
SD	45.0	22.1	16.2	117.5	46.1	48.3	15.6	55.0	19.6	90.5	21.1	35.3	22.7	25.2
Sound DCWD carbon (Mg C/ha)														
Mean	**18.4**	**79.5**	**6.6**	**193.1**	**24.6**	**73.7**	**9.8**	**52.8**	**9.5**	**59.0**	**25.1**	**49.8**	**14.2**	**40.6**
SD	22.2	10.0	5.0	55.6	21.0	22.7	4.7	28.5	7.3	39.8	10.5	18.9	10.1	8.3
Rotten DCWD carbon (Mg C/ha)														
Mean	0.2	2.2	4.9	2.1	6.8	7.4	5.0	1.9	2.3	5.0	2.0	9.2	7.5	7.2
SD	0.3	2.0	3.4	2.7	5.0	5.0	3.5	3.7	2.4	4.7	1.1	10.5	4.6	5.5
Total DCWD carbon (Mg C/ha)														
Mean	**18.5**	**81.7**	**11.5**	**195.2**	**31.4**	**81.1**	**14.9**	**54.8**	**11.8**	**64.0**	**27.1**	**59.0**	**21.7**	**47.8**
SD	22.4	11.1	8.1	58.0	22.6	24.4	7.8	27.0	9.7	44.4	10.2	17.3	11.2	12.5
Dead : live tree carbon	0.09	0.17	0.20	0.25	0.16	0.62	0.13	0.40	0.21	0.12	0.05	0.15	0.05	0.30
DCWD : live tree carbon	0.12	2.64	0.12	3.23	0.29	1.51	0.19	3.49	0.15	2.13	0.30	1.24	0.17	0.80

Notes: Tree values refer to overstory trees. DCWD refers to downed coarse woody detritus. Sites are arranged by increasing blowdown patch size (Table 1) and time since blowdown. Mean and SD of plots within blowdown (Blow) and adjacent reference (Ref) areas at four sites sampled at different times post-blowdown. Boldface type indicates pairwise $P < 0.05$; italic type indicates pairwise $P < 0.1$ from two-way ANOVA based on site and blowdown condition. MB site was sampled seven years post-blowdown in the blowdown area and eight years post-blowdown in the reference area. See Appendix S1: Table S4 for statistical details.

species matrix by removing species with fewer than four occurrences and relativizing density values by row (parameter = 1). To aid interpretation of the primary axes, we overlaid the percent hardwood, conifer, and low, intermediate, and high shade tolerance. MRPP is a complementary comparison test that provides statistical evidence of significant differences among pre-determined groups using random permutations of the original data (McCune and Grace 2002).

Results

Blowdown effects on residual live and dead forest structure

Blowdown effects on stand structure were highly variable within and among sites, generally leaving a complex pattern of residual standing live and dead trees, both dispersed and clustered in small patches (Appendix S2: Fig. S1). Within the first year following intermediate-severity wind events, live tree basal area in blowdowns ranged from 19% to 59% of adjacent reference areas, indicating substantial residual live structure (Table 2, Fig. 2). Standing dead tree basal area was not significantly higher or lower in blowdown areas at JF, WW, and WS ($P > 0.1$), but it did increase at MB ($P < 0.05$), potentially reflecting delayed mortality effects. Thus, declines in total overstory basal area, and density at some sites, were due primarily to changes in live trees (Table 2). In addition, although blowdowns lowered the ratio of live to dead tree density and basal area, these ratios remained above one in all cases (i.e., live trees were more prevalent than dead trees following each of these blowdown events; Table 2, Fig. 2).

Blowdowns also induced significant changes in other overstory tree attributes ($P < 0.1$; Table 2). Canopy closure and relative density were lower in blowdown areas at all sites. Whereas large live tree density was lower following blowdown at most sites, changes in quadratic mean diameter were site-specific, exhibiting decreases, increases, and no significant differences. Each site also exhibited distinct changes in tree size distributions at the initial observation following blowdown (Fig. 3). Although the stand structural complexity index based on overstory tree size distributions (H_{DBH}) was lower in blowdown areas at the WW (time 1) and MB (time 2) sites, blowdown events did not alter H_{DBH} in most cases (Fig. 4, Table 2). Similarly, the complexity index based on overstory tree species composition (H_{spp}) was lower at the WW blowdown site only; H_{spp} was not significantly different between reference and blowdown areas in all other combinations of site and timing (Fig. 4). The variability in these plot-based estimates of forest structure also was evident in the gap fraction and leaf area index estimates derived from hemispherical photos, which showed high fluctuations across space within and among sites (Appendix S2: Fig. S1). Gap fraction (canopy openness) ranged from 8% to 64%, and LAI ranged from zero to 3.1 (Appendix S2: Fig. S1).

Concurrent with the changes in overstory tree structure, initial mean DCWD volume and biomass were significantly higher in blowdown areas ($P < 0.05$), but differences varied substantially among sites (Table 3, Fig. 5). For example, initial total DCWD volume was 4.5, 10.4, 1.9, and 2.5 times higher in blowdown vs. reference areas at the JF, WW, MB, and WS sites, respectively. Blowdown effects were particularly pronounced for sound (fresh or poorly decayed) DCWD (Fig. 5), and there were no significant differences for rotten DCWD (Table 3), reflecting relatively low levels of old DCWD in the pre-blowdown stand.

Blowdown effects on aboveground carbon storage

The blowdown-induced structural changes described above translate to important changes in aboveground carbon pools. Total aboveground tree biomass and carbon were significantly lower in blowdowns than in reference areas ($P < 0.1$), reflecting large reductions in overstory live tree biomass (Table 3). As with basal area, however, retention of live tree carbon was substantial following blowdowns (blowdown range: 15.7–60.5 Mg C/ha; reference range 76.9–155.7 Mg C/ha), and standing dead tree carbon was similar between blowdown and reference areas (Tables 2 and 3).

Because standing live tree carbon declined but dead tree carbon did not change significantly, the initial mean ratio of dead to live tree carbon was higher in blowdown areas (0.36) than in reference areas (0.15; Table 3). This initial ratio was generally well less than one but varied substantially among blowdown areas (0. 17, 0.25, 0.62, and 0.40 at JF, WW, MB, and WS, respectively) and to a lesser degree in

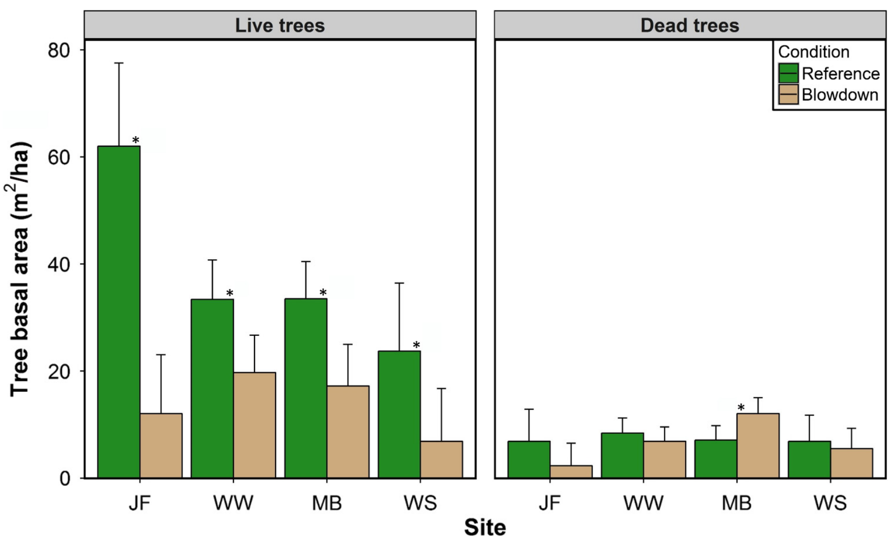

Fig. 2. Initial overstory live and dead tree basal area at each site (mean and 95% confidence intervals). Asterisks (*$P < 0.05$) indicate significant pairwise differences (interaction of site and condition from two-way ANOVA). See Table 2 for summary of all structural variables and Appendix S1: Table S3 for statistical details.

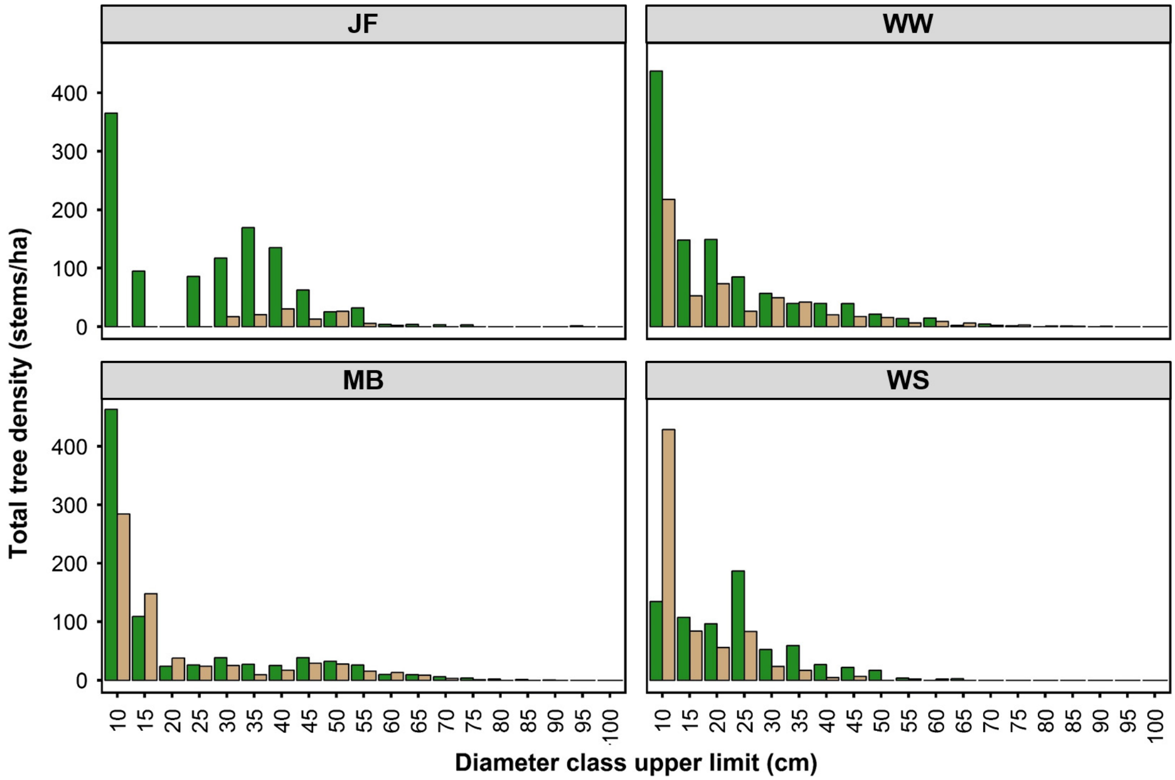

FIG. 3. Mean initial overstory tree size distributions for reference (dark green) and blowdown (light brown) conditions at each site.

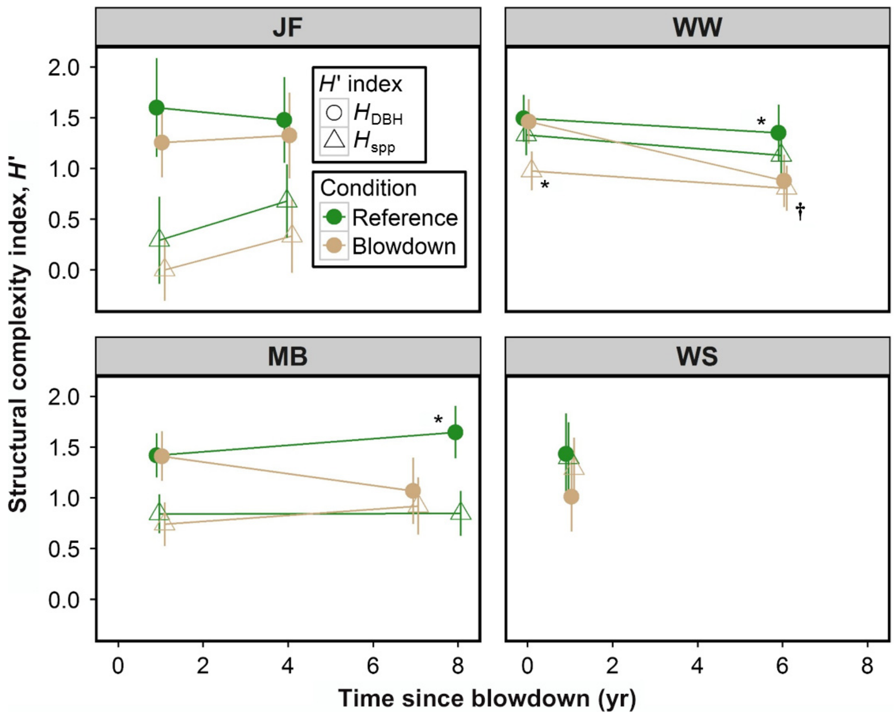

FIG. 4. Stand complexity indices comparing reference and blowdown conditions at each site over time (mean and 95% confidence intervals). Symbols (*$P < 0.05$; †$P < 0.1$) above means indicate significant pairwise differences in H_{DBH}; symbols below means indicate differences in H_{spp} (interaction of site and condition from two-way ANOVA). H'_{DBH} is based on distribution of tree density across size classes, and H'_{spp} is based on distribution of tree species across size classes (see *Methods*). See Table 2 for summary of all structural variables and Appendix S1: Table S3 for statistical details.

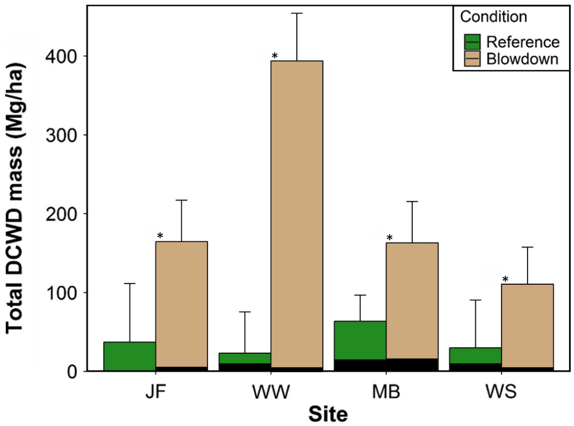

Fig. 5. Initial downed coarse woody detritus (DCWD) biomass for reference and blowdown conditions at each site (mean and 95% confidence intervals for total biomass). Black sections of bars correspond to rotten DCWD; colored sections correspond to sound DCWD. Asterisks (*P < 0.05) indicate significant pairwise differences (interaction of site and condition from two-way ANOVA). See Table 3 for summary of biomass variables and Appendix S1: Table S4 for statistical details.

the reference areas (0.09, 0.20, 0.16, and 0.13 at JF, WW, MB, and WS, respectively; Table 3). Reflecting the dominant wind-induced structural changes, the initial post-blowdown ratio of DCWD carbon to standing live tree carbon exhibited more pronounced blowdown effects (blowdown: 2.72; reference: 0.18; Table 3). Like the standing tree carbon ratio, this DCWD : standing live tree ratio varied among sites, especially in blowdown areas (2.64, 3.23, 1.51, and 3.49 at JF, WW, MB, and WS, respectively; Table 3).

Blowdown effects on tree regeneration and associated stand dynamics

Tree regeneration and sub-canopy tree density in the sapling and seedling canopy strata were generally abundant in both blowdown and reference areas. Due to high within-stand variability, there were no significant pairwise differences in total abundance (stems/ha) between blowdown and reference areas for either saplings (i.e., advance regeneration present before blowdowns) or seedlings (P > 0.1; Table 4, Fig. 6). Although there were no consistent differences for specific understory non-tree vegetation groups (shrub, herbaceous, moss), total understory vegetation cover was significantly higher in blowdown areas (P < 0.1; Table 4).

In nearly all combinations of site and canopy stratum, the majority of tree stems exhibited high shade tolerance; tree species with low shade tolerance accounted for <5% of tree density in all but two cases (Fig. 6, Appendix S1: Table S2). At the WW, MB, and WS sites, overstory species composition was dominated by generally late-successional, shade-tolerant species in both blowdown and reference areas (Fig. 6, Appendix S1: Table S2). At JF, the overstory was primarily eastern white pine, a species with intermediate shade tolerance (Fig. 6, Appendix S1: Tables S1 and S2). In contrast to the overstory, the sapling and seedling strata exhibited a somewhat higher proportion of species with intermediate shade tolerance, particularly at MB, where yellow birch (*Betula alleghaniensis*) competed with American beech

Table 4. Understory tree and non-tree vegetation in reference and blowdown conditions across four sites.

	Site (yr since blowdown)							
	JF (4)		WW (6)		MB (8/7)		WS (1)	
Understory vegetation variable (units)	Ref	Blow	Ref	Blow	Ref	Blow	Ref	Blow
Sapling density (stems/ha)								
Mean	2,200	467	1,579	1,894	1,825	2,700	2,900	1,330
SD	1,659	301	739	659	2,428	2,110	1,213	562
Seedling density (stems/ha)								
Mean	28,229	2,396	7,991	10,508	47,411	46,938	44,479	28,750
SD	11,076	361	4578	12,652	31,669	29,617	29,139	15,368
Shrub cover (%)								
Mean	8	7	0	6	**0**	**11**	na	na
SD	9	5	1	12	1	11	na	na
Herbaceous cover (%)								
Mean	**8**	**53**	9	16	8	6	21	10
SD	4	22	6	11	4	5	19	7
Moss cover (%)								
Mean	0	4	*8*	*16*	**9**	**20**	6	1
SD	1	5	6	16	6	6	3	1
Total understory cover (%)								
Mean	**17**	**64**	**17**	**39**	**17**	**37**	*27*	*11*
SD	6	23	7	18	4	12	19	7

Notes: Sites are arranged by increasing spatial extent. Mean (SD) of plots within blowdown (Blow) and adjacent reference (Ref) areas at four sites sampled at different times post-blowdown. Total understory cover is the sum of shrub, herbaceous, and moss cover. Boldface type indicates pairwise P < 0.05; italic type indicates pairwise P < 0.1 from two-way ANOVA based on site and blowdown condition; na, not applicable. MB site was sampled seven years post-blowdown in the blowdown area and eight years post-blowdown in the reference area. See Appendix S1: Table S5 for statistical details.

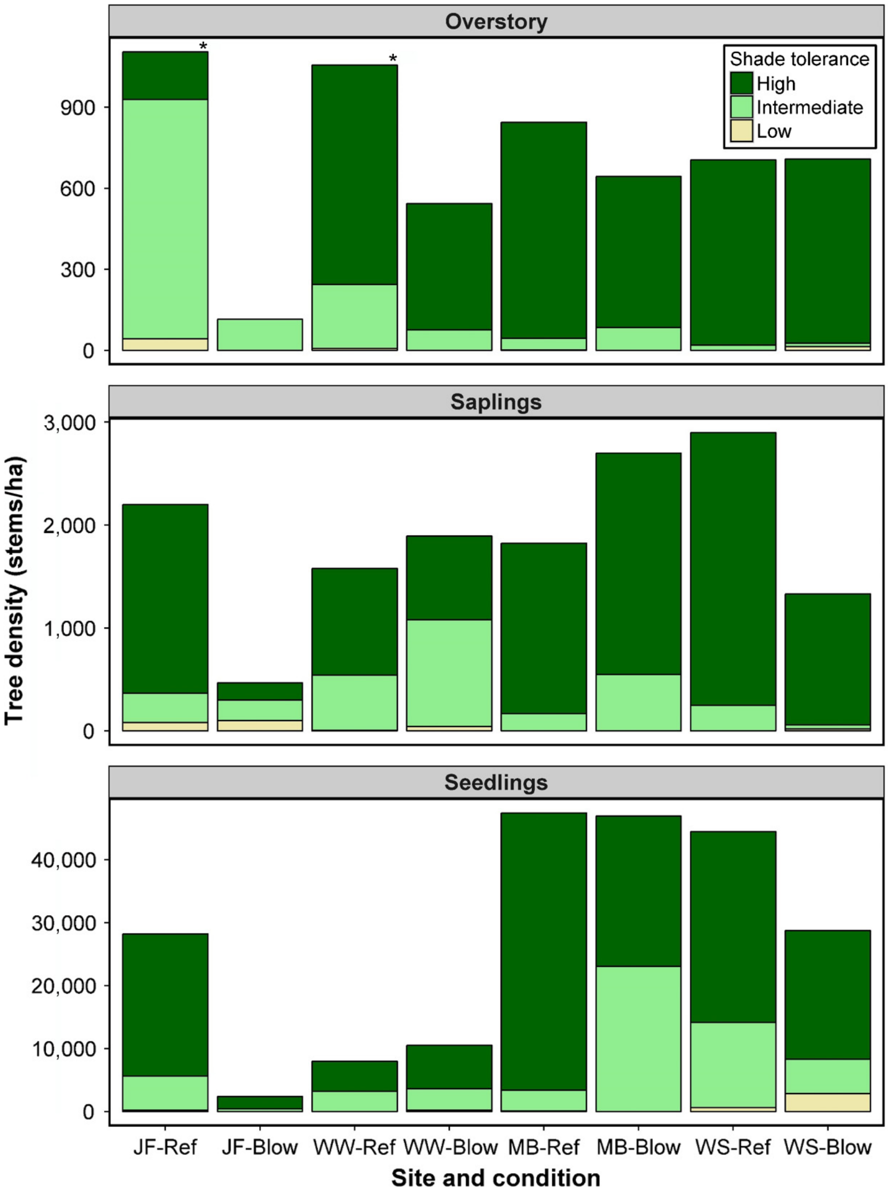

Fig. 6. Mean tree density by shade tolerance classes in three canopy strata (overstory, saplings, seedlings) at each site. Asterisks (*P < 0.05) indicate significant pairwise differences (interaction of site and condition [ref, reference; blow, blowdown] from two-way ANOVA) of total density in each stratum. Initial post-blowdown overstory total tree density was lower at the JF and WW sites, but there were no significant pairwise differences for the sapling and seedling strata. See Appendix S1: Table S2 for species composition, Table 2 for overstory structural variables, Table 4 for sapling and seedling abundance, Appendix S1: Table S1 for shade tolerance of all tree species, and Appendix S1: Table S5 for assessment of shade tolerance.

(Fig. 6, Appendix S1: Table S2). Yellow birch also was an important component of the understory at JF and WW (Appendix S1: Table S2). Despite the prevalence of species with high shade tolerance, the percentage of sapling and seedlings with high shade tolerance was lower in blowdown than in reference areas in some cases (Fig. 6, Appendix S1: Tables S2 and S6).

Overall, species composition was similar between blowdown and reference areas within a given site and stratum, indicating that wind disturbance did not have a pronounced effect on tree species composition (Fig. 6, Appendix S1: Table S2). NMS ordination (three-dimensional solution with minimum stress of 11.403, final instability <0.00001) indicated that species composition was more similar between reference and blowdown stands within a given combination of site and stratum than among strata and sites (Fig. 7). In addition, species composition was not significantly different between reference and blowdown conditions within a given site at three of four sites (MRPP pairwise A < 0.06; P > 0.13; Table 5; WS was the exception likely because it was sampled only one year post-blowdown). In contrast, all sites were significantly different from each other in the multivariate species space (MRPP pairwise A > 0.09; P < 0.009; Table 5; strata and condition combined at site level). Collectively, the relative dominance of shade-tolerant species in multiple strata and similarity between reference and blowdown areas demonstrate that

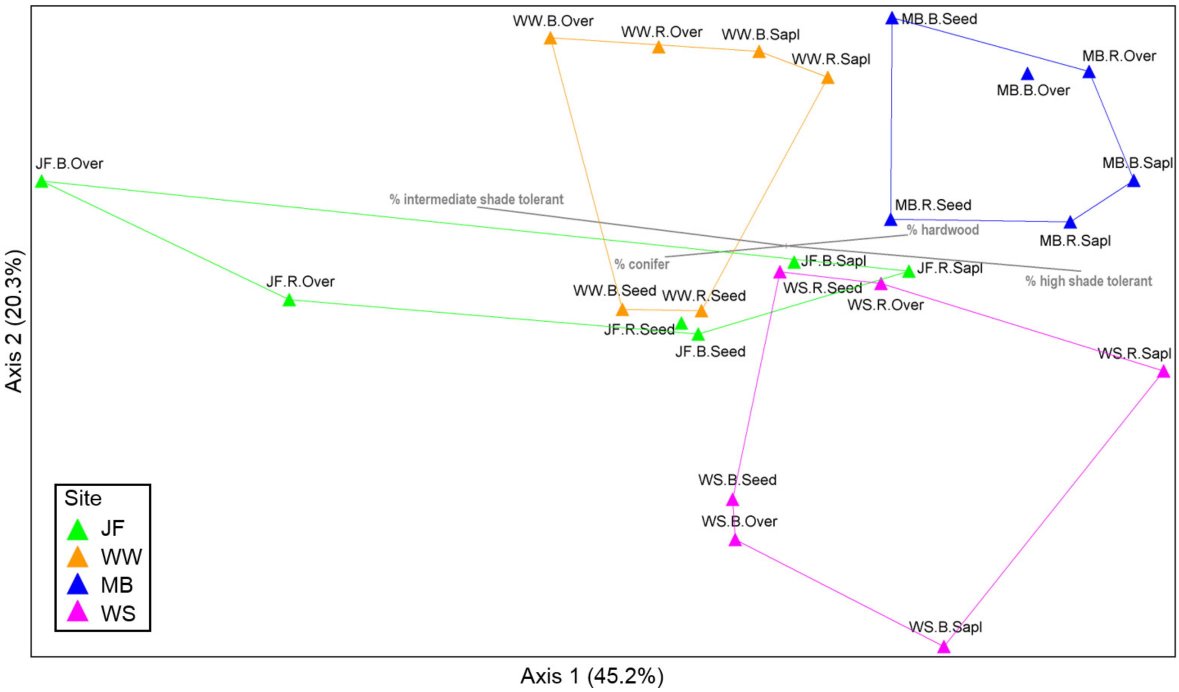

Fig. 7. Nonmetric multidimensional scaling (NMS) ordination indicating similarity among reference and blowdown areas, tree strata, and sites in multivariate species space. Colors indicate sites. R indicates reference, B indicates blowdown, Over indicates overstory stratum, Sapl indicates sapling stratum, and Seed indicates seedling stratum. Gray lines in biplot indicate species attributes. The values in parentheses correspond to the variance represented by the two axes (based on comparison between points in the ordination space and distances in the original space; McCune and Grace 2002). Note that each site occupies a relatively distinct species space and that the reference and blowdown conditions are more similar within a given stratum and site than among strata and sites. See associated multi-response permutation procedures (MRPP) statistics in Table 5.

Table 5. Multi-response permutation procedure (MRPP) comparison of tree species composition among sites and conditions (blowdown vs. reference).

	MRPP statistics		
Grouping variable	*T*	*A*	*P*
Site overall	−7.00858	0.16604	3.9×10^{-7}
Site pairwise			
JF vs. WW	−2.7117	0.092043	0.009786
JF vs. MB	−3.6158	0.12657	0.001501
JF vs. WS	−3.0472	0.10018	0.003786
WW vs. MB	−4.9564	0.14535	0.000591
WW vs. WS	−4.0297	0.12333	0.002541
MB vs. WS	−4.2278	0.14624	0.002552
Site × Condition overall	−4.6192	0.18690	0.00011
Site × Condition pairwise			
JF Ref vs. JF Blow	0.8377	−0.11079	0.79466
WW Ref vs. WW Blow	−0.4566	0.031377	0.34760
MB Ref vs. MB Blow	−1.0033	0.058169	0.13908
WS Ref vs. WS Blow	−2.1698	0.14995	0.02860

Notes: MRPP comparisons correspond to distances among groups in nonmetric multidimensional scaling (NMS) ordination of based on species composition of overstory, sapling, and seedling trees (Fig. 7). *T* statistic is the primary test statistic. *A* is the chance-corrected within-group agreement; $A = 0$ when heterogeneity within groups equals expectation by change, and $A = 1$ when all items are identical within groups. $P < 0.05$ indicates significant difference among groups based on permutation of the original data matrix (McCune and Grace 2002).

blowdown events released advance regeneration that was present prior to disturbance.

Although American beech was an important part of the species mix at all four sites, beech sapling and seedling densities were generally lower in blowdowns than in adjacent reference areas. Specifically, beech accounted for 0–31% of sapling density in blowdowns and 7–55% in reference areas (Appendix S1: Table S2). Beech was less prevalent in the seedling stratum, with all sites exhibiting <10% relative abundance (Appendix S1: Table S2).

Discussion

Influence of wind disturbance on forest structure, carbon storage, and stand dynamics

Whereas previous studies typically have documented wind and other disturbance effects at the two ends of the disturbance frequency/severity gradient (e.g., Romme et al. 1998, Seymour and White 2002, Sano et al. 2010), recent research has highlighted the role of intermediate disturbances like blowdowns, ice storms, insect outbreaks, pathogens, and mixed-severity fire (Martin and Ogden 2006, North and Keeton 2008, Cowden et al. 2014, Dunn and Bailey 2016, Reilly and Spies 2016, Janda et al. 2017, Nagel et al. 2017). Our study adds to a growing body of literature showing that intermediate-severity disturbances contribute to stand- and landscape-scale heterogeneity and associated values prioritized by many contemporary forest policies (e.g., wildlife habitat, ecosystem services; Turner et al. 2013). By opening otherwise closed-canopy conditions, intermediate disturbances are particularly important in forested landscapes like the northeastern United States, which are dominated by young to mature secondary forests that grew following 19th-century agricultural abandonment (Lorimer and White 2003, Urbano and Keeton 2017). These secondary forests are relatively homogeneous over large, contiguous expanses, having less patch complexity compared to historic, pre-European settlement landscapes (Mladenoff et al. 1993, Rhemtulla et al. 2009). In this context, intermediate-severity disturbances represent a subsidy to the system, enhancing the availability of otherwise under-represented spatial patterns and habitat features, such as gaps and canopy openings of irregular shape, size, and within-patch residual structure (Kneeshaw and Prevost 2007, Kern et al. 2013, 2017).

In the present study, recent blowdown events altered or enhanced important aspects of stand-scale forest structure and carbon storage but did not appear to redirect or alter late successional development substantially. Our empirical observations support the first hypothesis that intermediate-severity blowdowns generate abundant live and dead biological legacies, both standing and downed, despite substantial structural changes (H_1). However, because these forests were generally mature or old-growth with a history of no (MB, WW) or only light (JF, WS) recent silvicultural management, stand-level structural complexity was relatively high already, as indicated by reference values of the overstory live and dead tree attributes, overstory tree structural complexity indices (Table 2), DCWD (Table 3), and understory tree and non-tree vegetation (Table 4). Nevertheless, blowdown events induced substantial within-stand variability in canopy openness (Appendix S2: Fig. S1) and other structural attributes, including residual live and dead overstory structure and large volumes of downed CWD, a fundamental component of habitat complexity in late successional forests (Franklin et al. 2002, Burrascano et al. 2013). These results highlight the variable structural conditions that intermediate- or moderate-severity disturbances can create at the forest stand scale, which, in turn, have direct implications for ecosystem processes such as primary production and structural development (Stuart-Haëntjens et al. 2015, Meigs et al. 2017). Our study also provides field-based evidence of the structural resilience demonstrated recently with simulation modeling by Halpin and Lorimer (2016), wherein partial canopy disturbances accelerated the development of complex forest structure.

Our findings support the second hypothesis that intermediate-severity blowdowns alter the distribution and abundance of aboveground carbon pools (H_2), but the relatively high levels of residual live and dead structure and stand complexity dampen these effects. By inducing numerous structural changes (Table 2), recent blowdowns have changed the short-term balance between live and dead carbon, as indicated by the two ratio metrics (Table 3). We characterize these changes as carbon transfers rather than losses, given that the total amount of standing and downed tree carbon on site is similar in reference and blowdown areas. We recognize that long-term carbon storage and emissions will depend on the balance between lagged dead wood decomposition, post-disturbance vegetation growth, and interactions with ungulate browsing and forest management (Meigs et al. 2009, Mayer et al. 2014, Williams et al. 2016, D'Amato et al. 2017). Specifically, dead carbon in DCWD generated by recent blowdowns will be released over one to several decades, depending on the degree of dead wood incorporation into soil organic matter pools (Johnson and Curtis 2001, Buchholz et al. 2014) and differential decay rates associated with local climate variability, species, and log size (Woodall et al. 2015, Dunn and Bailey 2016). Carbon in large standing trees (live and dead), especially the old conifers present at all four sites, is likely to be a relatively persistent and stable pool for multiple decades (Woodall et al. 2015). In addition to the lagged decomposition and emissions from dead carbon pools, net ecosystem carbon balance will depend on post-disturbance vegetation growth (Chapin et al. 2006, McKinley et al. 2011, Gough et al. 2016), which may be enhanced by the release of advance regeneration at our sites.

In addition, our parametric (ANOVA; Fig. 6, Appendix S1: Table S2) and nonparametric analyses (NMS ordination, MRPP; Table 5; Fig. 7) generally support the third hypothesis that intermediate-severity blowdowns reinforce late-successional, shade-tolerant species composition (H_3). Indeed, these blowdown events provided an opportunity for shade-tolerant regeneration present prior to the disturbances (Foster 1988, Foster and Boose 1992). Rather than affecting tree species differentially (Woods 2004, Rich et al. 2007, Frelich and Reich 2010), blowdown at our sites reinforced or maintained pre-disturbance hierarchies of species dominance, consistent with prior studies (Abrams and Scott 1989, Webb and Scanga 2001, Nagel et al. 2006, 2014, Beaudet et al. 2007). In this way, the regeneration response to intermediate blowdown in these generally mature, shade-tolerant forests is more analogous to fine-scale canopy gap dynamics, highlighting the importance for stand dynamics of live tree legacies associated with partial disturbances (Woods 2004, Lorimer and Halpin 2014). At the same time, the relative reduction of species with high shade tolerance in some cases, particularly in the sapling stratum, indicates a moderate response of less shade-tolerant species (e.g., yellow birch) to the post-blowdown environment. If this pattern of a more even distribution among shade tolerance classes persists, then blowdowns could increase the diversity of species composition and stand development trajectories over time. Further studies that are able to sample understory trees destructively to determine the precise timing of pre- and post-disturbance establishment, as well as those covering a longer time since blowdown (e.g., Nagel et al. 2014, D'Amato et al. 2017), would further elucidate the interactions among species with varying shade tolerance and life history strategies.

Taken together, our results indicate that intermediate-severity disturbance events can enhance structural complexity without substantially altering or redirecting successional trajectories occurring pre-disturbance. This dynamic likely reflects the generally shade-tolerant overstory composition as well as the abundance of shade-tolerant advance regeneration (Fig. 6), which rapidly exploited available growing space across the full range of residual canopy closure we investigated. From this perspective, we suggest that advance regeneration of shade-tolerant species contribute to both structural resilience (Halpin and Lorimer 2016) and compositional resilience to this particular type and severity of disturbance. There are important site-specific nuances to consider with less shade-tolerant species, especially yellow birch, whose capacity to survive in the understory and attain overstory codominance over longer time scales likely depends on light from partial canopy disturbances (e.g., Beaudet and Messier 1998). Nevertheless, intermediate-severity blowdown at our sites generally released advance regeneration without recruiting a cohort of early-successional, pioneer species, although such effects depend on the pre-disturbance structure, composition, and successional condition (e.g., Gough et al. 2016).

Due to widespread forest health and management concerns related to beech bark disease and associated thickets (Nyland et al. 2006, Wagner et al. 2010, Giencke et al. 2014), the advance shade-tolerant regeneration at these sites could be problematic if beech root-suckers are dominating post-blowdown species composition. However, our findings indicate that the relative abundance of beech saplings and seedlings generally is lower in blowdowns areas (Appendix S1: Table S2). Other common tree species, such as sugar maple, red maple, yellow birch, and balsam fir, exhibited robust regeneration at the different sites, contributing to the high site-to-site variability in species composition (Fig. 7, Appendix S1: Table S2). Moreover, because total sapling and seedling abundance did not differ significantly between reference and blowdown areas at a given site (Table 4), successional trajectories do not appear to have changed despite dramatic structural changes, consistent with Beaudet et al. (2007). Our findings differ from observations of beech release following ice storms (Covey et al. 2015), although the generally shade-tolerant overstory at three of our four sites represents a different pre-disturbance condition than the less tolerant *Quercus* in that study. Given that one disturbance event may not induce enough change to alter beech development patterns (Beaudet et al. 2007), the issue of beech competition and health remains an important management concern.

Management implications of intermediate wind disturbance

Our findings have key implications for stand-scale silvicultural approaches intended to emulate natural disturbance processes (Franklin et al. 2002, Seymour and White 2002, Seymour 2005, Keeton 2006, North and Keeton 2008, Smith et al. 2008) and/or retain ecologically important elements of stand structure (Gustafsson et al. 2012, Puettmann et al. 2012). Two of our central findings were the relatively robust density and abundance of standing live tree legacies within blowdown areas and the spatial variability in residual canopy cover evident in the hemispherical photos (Appendix S2: Fig. S1), both of which have direct applications to sustainable forestry. First, they are consistent with other recent studies (e.g., Woods 2004, Hanson and Lorimer 2007, Lorimer and Halpin 2014, Svoboda et al. 2014) in suggesting that multi-cohort silvicultural systems, such as irregular shelterwood (Raymond et al. 2009), as well as other retention harvesting systems (Lindenmayer et al. 2012, Mori and Kitagawa 2014), are analogous in some respects to intermediate wind disturbance. In the irregular shelterwood system, for instance, legacy trees may be retained at each entry, with some portion of these maintained over two or three rotations or even permanently (Seymour 2005), producing a discontinuous or multi-aged structure. In addition, the horizontal pattern evident in the hemispherical photos, residual live overstory cover persisting over a sub-canopy of intermediate trees, saplings, and seedlings, was notably similar to stands managed for multicohort structure.

Second, our findings suggest that intermediate-severity disturbances could contribute to patch diversity at larger spatial scales, particularly in landscapes mostly dominated by closed-canopy secondary forests, such as the U.S. Northeast (Kern et al. 2013). However, intermediate blowdowns differ from harvesting systems, such as patch cuts, commonly used to produce early-successional habitats (King et al. 2001, DeGraaf and Yamasaki 2003) in that substantial live basal area (19–59%) remained standing at our wind-disturbed sites, and very high levels of DCWD (mean initial post-blowdown volume = 548 m^3/ha; Table 3) constituted a significant increase in habitat complexity on the forest floor. In this sense, intermediate blowdowns produce distinct stand structures that add to the complexity of patch mosaics at landscape scales. Management activities that emulate intermediate disturbances at stand and landscape scales might facilitate forest adaptation and resilience under ongoing climate and land use change (Seidl et al. 2011, Turner et al. 2013, Thom and Seidl 2016). Future studies could explore spatial patterning further by comparing stand- and landscape-scale complexity across landscapes with differing amounts and configurations of recent wind disturbance and management activities, especially over longer time scales. In addition, because blowdown events can increase forest structural complexity without altering late successional dynamics, they may be compatible with multi-functional management approaches specifically promoting late successional forest structure and function (Abrams and Scott 1989, Smith et al. 2008 Bauhus et al. 2009, Ford and Keeton 2017).

Our results also have direct applications to carbon forestry. Forest carbon management under existing carbon market protocols emphasize retention harvesting and extended rotations to maintain high levels of stocking in managed forests (Nunery and Keeton 2010, McKinley et al. 2011, Kerchner and Keeton 2015). For this reason, multi-cohort silvicultural systems that are analogous to intermediate-severity wind effects have great potential for carbon management in northern hardwood–conifer forests. We found a relatively high level of initial carbon storage in residual live (mean = 40.2 Mg C/ha) and dead (mean = 15.0 Mg C/ha) standing trees as well as DCWD pools (mean = 103.2 Mg C/ha) in blowdown areas. If timber harvests incorporated similar post-harvest carbon stocking across multiple pools, they would be incentivized under many current market-based "improved forest management" protocols (e.g., Climate Action Reserve 2014; Verified Carbon Standard, *available online*).[6] Therefore, disturbance-based forestry approaches emulating intermediate blowdown events may offer further opportunities for integrated management of carbon, timber, and wildlife habitat (Schwenk et al. 2012).

[6] http://www.v-c-s.org/project/vcs-program/

Conclusion

This study of recent wind disturbance in the northeastern United States documents important biological legacies following intermediate-severity blowdown events, including relatively high residual live and dead overstory tree abundance, moderate structural complexity in both reference and blowdown areas, abundant sound and rotten downed wood, and abundant yet variable tree regeneration density up to eight years post blowdown. Our findings suggest that intermediate wind disturbances can contribute to structural complexity and carbon storage without substantially altering late-successional stand dynamics. Specifically, recent blowdowns contributed to within-stand structural variability and dead wood biomass, critical elements of late successional forest structure that contemporary forest management activities aim to restore. In addition, although windstorms altered the balance between live and dead aboveground carbon pools, long-term carbon storage will depend on lagged dead wood decomposition and post-disturbance vegetation growth. Moreover, intermediate-severity blowdown at our sites released advance regeneration of shade-tolerant trees but did not recruit a new cohort of shade-intolerant trees, suggesting a dynamic in which disturbance initially sustains or advances late-successional species composition rather than providing a regeneration opportunity for pioneer species. Advance regeneration thus enhances structural and compositional resilience to this type of disturbance. Finally, this study underscores how partial canopy disturbances like wind can create heterogeneity that forest managers can integrate into adaptive management plans addressing current and projected global change.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1691/full

Data Availability

Data available from the Forest Ecosystem Monitoring Cooperative (FEMC) Repository: https://www.uvm.edu/femc/data/archive/project/cdlwinddisturbance.