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Effects of intermediate-scale wind disturbance on composition, structure, and succession in *Quercus* stands: Implications for natural disturbance-based silviculture

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ABSTRACT

Forest disturbances are discrete events in space and time that disrupt the biophysical environment and impart lasting legacies on forest composition and structure. Disturbances are often classified along a gradient of spatial extent and magnitude that ranges from catastrophic events where most of the overstory is removed to gap-scale events that modify local environmental conditions only. Without question, a paucity of data is available on disturbance events of the intermediate scale (i.e. those events too localized to be classed as catastrophic and too widespread to be considered gap scale). The specific objectives of this study were to quantify and compare canopy structure, understory light regimes, woody species composition, and tree species diversity along a gradient of canopy disturbance caused by an EF1 tornado and to analyze the influence of intermediate-scale disturbance on the successional trajectory of an upland *Quercus* forest. Statistically significant differences in diversity measures between control (no storm damage), light, or moderate damage class plots were only found in the sapling layer. We documented significant differences ($P < 0.01$) in percent of intercepted PAR between the control and moderate damage classes and between moderate and light classes. Three growing seasons post-disturbance, the understory light regime had largely returned to pre-disturbance conditions. The disturbance event acted primarily as a release mechanism for advanced reproduction in the understory and for stems in the midstory. Our results provide quantitative information on disturbances of this extent and magnitude and can be used to guide silvicultural systems designed to emulate natural disturbance processes, which is an increasingly popular management approach especially on public lands.

1. Introduction

Forest disturbances are discrete events in space and time that disrupt the biophysical environment (White et al., 1985) and impart lasting legacies on forest composition, structure, and stand development patterns (Lorimer, 1980; Foster et al., 1998; White and Jentsch, 2001; Foster et al., 2002). Disturbances are often classified along a gradient of magnitude and spatial extent. This gradient spans from catastrophic, stand-replacing events to highly localized, gap-scale events (Oliver and Larson, 1996). The range between endpoints of this disturbance classification gradient is vast and makes quantifying disturbances that are too broad to be considered gap-scale and those too localized to be considered catastrophic difficult. Within this framework, disturbances can differ widely from each other yet have the same intermediate-scale classification.

Natural disturbance agents that often cause intermediate-scale damage include strong winds, ice storms, insect attacks, and pathogens (Oliver and Larson, 1996). In *Quercus*-dominated stands through the Central Hardwood Forest of the eastern US, the return interval of stand-wide canopy disturbances (events which remove at least 25% of canopy trees) ranges from ca. 30 to 50 years (Nowacki and Abrams, 1997; Ruffner and Abrams, 1998; Hart et al., 2012a). In the eastern US, the return interval for intermediate-scale disturbance is shorter than the life span of most canopy individuals, and much shorter than the return interval of catastrophic disturbances (Lorimer, 1989; Stueve et al., 2011; Lorimer, 2001). The effects of intermediate-scale disturbances range from the removal of significant portions of overstory vegetation, which initiates secondary succession, to the death of single

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canopy trees, which modifies fine-scale environmental conditions only (White, 1979; Christensen and Peet, 1981; Oliver, 1981). Regardless of the spatial extent, these canopy disturbance events remove canopy trees thereby altering the quantity, quality, and spatial distribution of light in the understory, which is typically the factor most limiting in forests of the eastern US (Canham and Loucks, 1984; Hanson and Lorimer, 2007; Grayson et al., 2012). Finally, intermediate-scale disturbances may increase stand heterogeneity and promote multi-aged structure (Hanson and Lorimer, 2007).

Approximately 1250 tornadoes occur in the USA annually, and 95% of these are classified as EF0, EF1, or EF2 events (NCDC, 2013). Tornadoes of this magnitude typically result in intermediate-scale disturbances. These storms are characterized by a central track associated with catastrophic damage, and damage severity typically decreases with increased distance from the main storm path. Consequently, forest damage from low intensity tornadoes varies spatially from zones of catastrophic damage, to zones with progressively less damage, and eventually to undamaged areas. Despite the high frequency of these intermediate-scale disturbances, there is a paucity of data available on the effects of these events on forest composition, biodiversity, and sub-canopy light regimes, especially when compared with gap-scale and catastrophic disturbances (Fujita, 1978; Foster and Boose, 1992; Trickel, 2002; Stueve et al., 2011).

The overarching goal of this study was to elucidate the effects of intermediate-scale wind disturbances on forest composition, structure, and succession. The specific objectives were to quantify and compare canopy structure, understory light regimes, woody species composition, and species diversity along a gradient of canopy disturbance and to analyze the influence of intermediate-scale disturbance on the successional trajectory of an upland hardwood forest. Successful implementation of a natural disturbance-based management approach requires quantitative information on natural disturbance processes (Long, 2009). Our results may be used to develop operational guidelines for the implementation of natural disturbance-based management (Seymour et al., 2002; Franklin et al., 2007) and lessons learned can be used to guide silvicultural treatments to achieve desired conditions.

2. Methods

2.1. Study area

This study was conducted in the Sipsey Wilderness on the William B. Bankhead National Forest in Lawrence and Winston counties of north Alabama (Fig. 1). The Sipsey Wilderness is a 10,085 ha portion of the National Wilderness Preservation System and occurs on the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman, 1938) and within the Southwestern Appalachian (level III) ecoregion (Griffith et al., 2001). The topography in this region consists of narrow ridges and valleys, steep slopes, and is so strongly dissected that it does not resemble a true plateau (Smalley, 1979). The geology is mainly composed of the Pennsylvania Pottsville formation, which consists of a gray conglomerate, fine to coarse grained sandstone, and is known to contain limestone, siltstone, and shale, as well as anthracite and bituminous coal (Szabo et al., 1988). The region contains soils that are acidic, shallow, and poorly drained (USDA SCS, 1959). The regional climate is humid mesothermal characterized by short, mild winters and long, hot summers (Thornthwaite, 1948). Mean annual temperature is 16 °C (January mean: 5 °C, July mean: 26 °C). The frost-free period is approximately 220 days in duration from late-March to early-November (Smalley, 1979). Mean annual precipitation is 1390 mm with monthly means of 135 and 113 mm for January and July, respectively (PRISM Climate Group, 2011). During winter most precipitation events are a result of frontal lifting, whereas summer precipitation may also be the result of convective storms (Smalley, 1979).

This area of the Cumberland Plateau is classified as a transitional region between the *Quercus–Pinus* Forest Region to the south and the Mixed Mesophytic Forest Region to the north (Braun, 1950). Species composition in this region varies locally based on topography (Zhang et al., 1999) and soil–water availability (Hinkle, 1989). Zhang et al. (1999) classified 14 ecological communities on the Sipsey Wilderness and found *Quercus* was the most abundant genus and occurred in the majority of the delineated community types. Ridges and upper slope positions are often dominated by *Pinus taeda* L. and *Pinus echinata* Mill. Over a distance of less than 100 m along a topographic gradient, stands may transition to support a stronger component of hardwood species (Zhang et al., 1999; Parker and Hart, 2014). Middle and lower slope positions are characterized by mesic hardwood stands that include strong components of *Fagus grandifolia* Ehrh., *Liriodendron tulipifera* L., and *Magnolia macrophylla* Michx. (Hardin and Lewis, 1980; Martin et al., 2008; Zhang et al., 1999; Richards and Hart, 2011; Parker and Hart, 2014).

On 20 April 2011 a long-lived, quasi-linear convective system developed in north-central Mississippi and tracked eastward through north Alabama (NCDC, 2012). A bow echo with a strong meso-vortex produced damaging straight-line winds across a five county region in north Alabama. The system also produced an EF1 tornado that tracked ca. 5 km and directly damaged portions of the Sipsey Wilderness. A wake low developed after the storms which produced a short period of damaging non-thunderstorm winds in the area. Wind gusts of 152 km hr^{-1} were recorded with the wake low system. These types of wind disturbances are representative of damage that occurs throughout the Eastern Deciduous Forest Formation; hence findings may be applicable to similar sites in the eastern US.

2.2. Field methods

Stands were surveyed during the third growing season post-disturbance. All stands selected were within the same biophysical setting according to Smalley's (1979) land classification system to ensure analogousness of results. The majority of *Quercus alba* L. stands within the Sipsey Wilderness established between 1890 and 1905 following anthropogenic clearing, and are at least 9 ha in size. The Sipsey Wilderness is divided into compartments and subdivided into stands, as is required by the USA Forest Service, and stand boundaries were consistent with those established by management personnel on the Bankhead National Forest. For this study, we conducted a comprehensive inventory of post-disturbance biophysical conditions across a gradient of disturbance in each stand. Undamaged neighborhoods within stands were considered the controls in this study, and we assumed that they were representative of pre-disturbance conditions using a space-for-time substitution.

We overlaid shapefiles of stand boundaries, topography, and the tornado track using ArcGIS v. 10 in combination with aerial photographs and field reconnaissance to determine stands that would be included in the study. In each stand, we subjectively established sample points (plot locations) using GIS software to ensure adequate spatial coverage. These locations were inputted as waypoints into a handheld GPS device. In the field, we used a GPS receiver to navigate to the pre-determined waypoints. Plots that occurred in streams or on hiking trails were moved 15 m in one direction and the new coordinate pair for the plot was recorded. Plots were visually assigned to one of three damage classes based on the number of downed trees within or crossing through a plot and

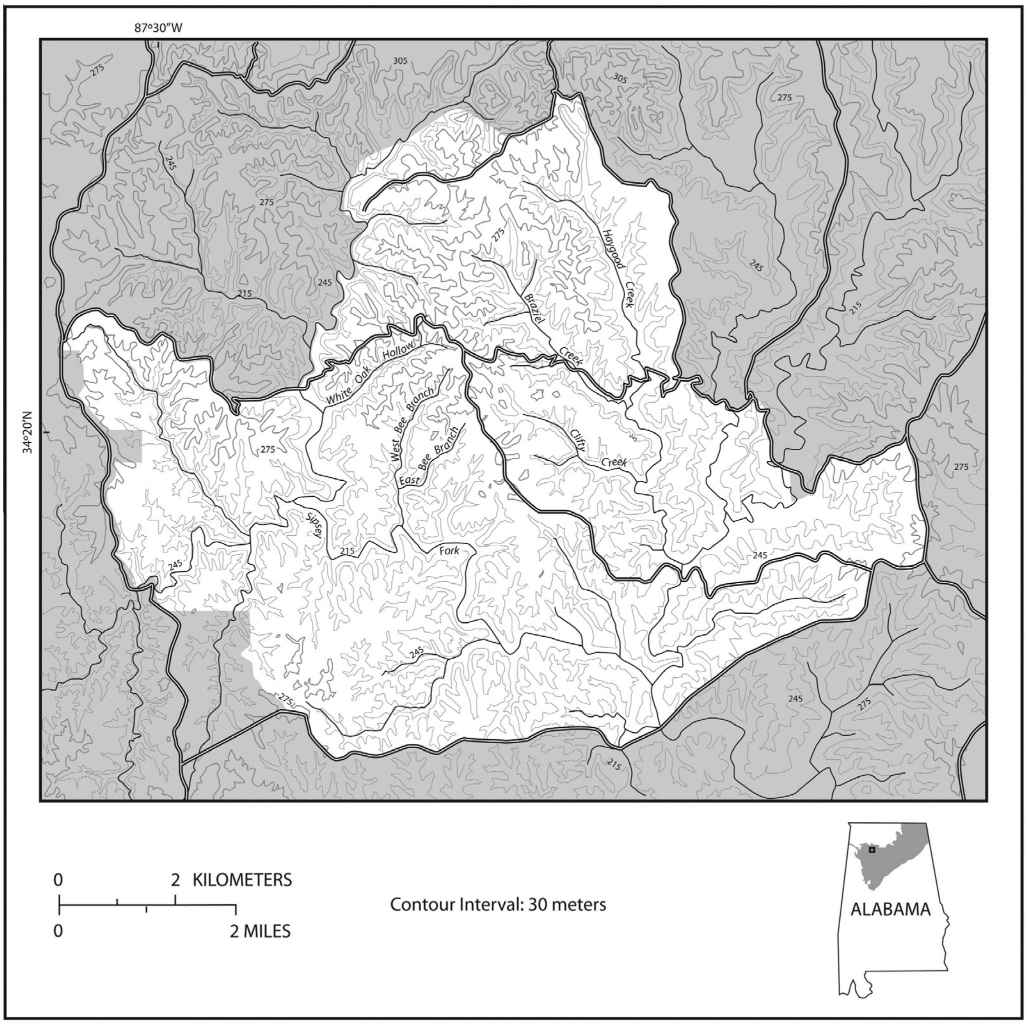

Fig. 1. Sipsey Wilderness on the Bankhead National Forest in Alabama, US. Shaded portion on Alabama inset map is the Cumberland Plateau physiographic section.

the proximity to the main storm tract thus, we used a combination of our maps and field observations to establish sampling points. Plots with three or more downed trees of ⩾20 cm dbh were classified as moderate damage (n = 37), and all other plots with visible wind damage (i.e. individuals were considered windthrown by the storm if they had been either uprooted so that the stem was less than 45° from the ground or if the bole had been broken below the crown, sensu Canham et al., 2001) were deemed to be light damage plots (n = 52). Control plots (n = 20) exhibited no visible evidence of damage from the storm. All plots were classified in the context of surrounding forest conditions. At each sample point, we established a 0.04 ha fixed-radius overstory vegetation plot in which we recorded the species, crown class, and diameter at breast height (dbh) of every woody stem, live or dead, >5 cm dbh. *Carya* spp. stems were only identified to the genus level. All live stems were classified as either undamaged or damaged (e.g. primary branch removed). Crown classification (dominant, co-dominant, intermediate, or overtopped) was based on the amount and direction of intercepted light (Oliver and Larson, 1996). Additionally, to provide more information on the structural diversity of the canopy and canopy damage, the intermediate class was divided into intermediate I (I1: 0–50% of total canopy height), intermediate II (I2: 50–75% of total canopy height), and intermediate III (I3: ⩾75% of total canopy height). Within each overstory plot, seedlings (stems < 1 m height) and saplings (stems ⩾ 1 m height, <5 cm dbh) were tallied by species within a 10 m^2 nested fixed-radius plot to quantify regeneration patterns.

All dead stems ⩾ 5 cm dbh within each overstory plot, were classified to the lowest taxonomic level possible and placed into one of four decay classes to examine species-specific mortality trends and overstory composition changes (Fraver et al., 2002). The four classes were defined as follows: decay class I (sound wood, bark intact, small to medium sized branches present); decay class II (sound to partially rotten wood, branch stubs firmly attached with only larger stubs present, some bark slippage); decay class III (substantially rotten wood, branch stubs easily pulled from softwood species, wood texture is soft and compacts when wet); or decay class IV (mostly rotten wood, branch stubs rotted down to log surface, bark no longer attached or absent, log is oval or flattened in shape). All dead stems ⩾ 5 cm dbh were classified as either: snag (standing dead tree with crown intact), snapped stem (bole broken below the crown), or uprooted stem (root network uplifted; Clinton et al., 1993; Yamamoto, 2000; Hart and Grissino-Mayer, 2009; Richards and Hart, 2011). Each dead tree was determined to have been killed by the wind event or already dead at the time of the intermediate stand-scale disturbance by assessing the level of decay. Based on time since the disturbance, we assumed that trees killed by the April 2011 storm event were in the decay class I category. The average amount of basal area removed (i.e. trees killed) from the natural mortality of individual trees (sensu Runkle, 1982) in the control plots was used as a surrogate for background mortality in study stands within the Sipsey Wilderness. To account for dead trees in decay class I that were not killed by the storm, we subtracted the background rate of mortality, which was calculated as the average basal area (m^2) lost from control plots, from the basal area lost in each wind damaged plot to estimate the basal area removed by the intermediate-scale disturbance event.

For each overstory plot, one hemispherical photograph was taken at plot center and a second photograph was taken 50 m away from plot center. All photographs were taken at breast height using a Panasonic Lumix (DMC-LX5) camera with a fish-eye lens attached to a self-leveling tripod using a Mid-OMount 10MP (Regent Instruments, 2011) during June and July. The aperture and shutter speed of the system used were set by the canopy analysis system distributor (Regent Instruments, 2011). We attempted to collect all images in morning or afternoon hours or during overcast conditions to reduce glare from direct sunlight, which can cause errors with image interpretation (Robison and McCarthy, 1999; Jonckheere et al., 2005). In the event that glare was unavoidable, we used a sun blocker device provided by the manufacturer to prevent direct sunlight from reaching the lens. The top of all images was oriented to true north. Finally, canopy interception of photosynthetically active radiation (PAR) ($\mu mol\ m^{-2}\ s^{-1}$) was quantified using two synchronized ceptometers (AccuPAR LP-80, Decagon Devices, US). One ceptometer was placed in full sunlight, while the second recorded PAR within each plot. Twenty recordings were taken in each cardinal direction from the center of each plot (80 total readings per plot). These readings were averaged together to determine one value per plot. These data were used to establish relationships between the percent of full sunlight and the level of canopy disturbance on a per plot basis.

2.3. Laboratory methods

All hemispherical photographs were analyzed using the WinSCANOPY program v. 2010a (Regent Instruments, 2011). WinSCANOPY is a forest canopy analysis software that uses fisheye photographs to describe canopy structure, map and quantify radiation microclimate beneath canopies, and estimate radiation indices (Breda, 2003; Macfarlane et al., 2007; Regent Instruments, 2011). The software was used to analyze changes in canopy openness at breast height and disturbance effects on subcanopy solar radiation. All photos were analyzed by one individual, eliminating user bias and ensuring all images could be directly compared (Canham et al., 1990). Each image underwent 'pixel classification', or the process of classifying image pixels into two groups, canopy or sky, based on their gray levels (Regent Instruments, 2011). In photographs where we used the sun blocker device, a 'mask' defined within the software was delineated that excluded that portion from analysis. WinSCANOPY was used to calculate gap fraction, a measure of canopy openness, and leaf area index (LAI) (Wulder, 1998; Regent Instruments, 2011). Percent of full sunlight was calculated from ceptometer readings as the ratio between the PAR readings in each plot and the corresponding readings in open sunlight during the same time of day. This allowed us to neutralize slight changes in cloud cover or incidental differences in PAR.

All statistical analyses were performed in SAS v. 9.3. All plot-level data used to compare means between the three damage classes were statistically analyzed and visually checked for normality and homogeneity of variance, and variables that did not meet the test assumptions were log-, square root- or rank-transformed. To compare means among the three damage types, one-way analysis of variance (ANOVA) was performed for species richness (S), abundance, evenness, Shannon diversity (H'), gap fraction, canopy openness at breast height, percent of full sunlight, LAI, and basal area (total, live, DI) for seedlings, saplings, trees, seedlings and saplings combined, and all stems combined. If a statistically significant difference was found among the three damage classes ($P \leqslant 0.05$), a Scheffe post-hoc test was conducted to identify which groups were different. A Pearson correlation test was used to assess the relationships between percent of full sunlight and the number of seedlings and saplings in each damage class. To test for differences in the likelihood of a decay class 1 stem to be uprooted, snapped, or remain standing as a snag, we used Pearson chi square with a significance threshold of $P \leqslant 0.05$ to detect trends.

3. Results

3.1. Effects on composition and biodiversity

Mean basal area of the tree layer was 25.6, 23.7, and 15.3 $m^2\ ha^{-1}$ for control, light, and moderate damage classes, respectively, and values were significantly different between control and moderate classes and between light and moderate classes. Density of stems > 5 cm dbh for control, light, and moderate classes was 771, 666, and 531 ha^{-1}. The quadratic mean diameter (QMD) for each damage class was 20.6 cm for control, 21.3 cm for light, and 19.2 cm for moderate. QMD was statistically different between light and moderate classes. Species richness of the tree layer (stems $\geqslant$ 5 cm dbh) was 32, 37, and 33 for control, light and moderate damage classes, respectively, and was 40 for all treatments combined. Mean sapling richness per plot was statistically different between control (mean $S = 3.4\ plot^{-1}$) and moderate ($S = 5.0\ plot^{-1}$) classes, and between light ($S = 3.6\ plot^{-1}$) and moderate classes. Species richness was not significantly different between any damage categories in the seedling or tree layers, when seedling and sapling layers were combined, or when all woody stems were combined. Abundance statistically differed between all three classes of the tree layer (stems $\geqslant$ 5 cm dbh), and within the sapling layer between the control and moderate damage classes and between the light and moderate classes. We documented no statistically significant differences in species evenness between damage classes. Mean Shannon diversity for the tree layer of control plots was 1.80 ± 0.06 (SE), for light damage plots was 1.85 ± 0.04, and moderate damage plots was, 1.70 ± 0.07. We found no significant statistical differences in Shannon diversity except in the sapling layer between light and moderate damage classes, for which mean values per plot were 1.02 ± 0.07 and 1.32 ± 0.08 ($P = 0.012$), respectively.

Average live basal area per 0.04 ha plot was 1.00, 0.96, and 0.61 m^2 for control, light, and moderate classes, respectively, and these values were not significantly different. Average basal area lost (removed by the storm) per plot was 0.01, 0.26, and 0.56 m^2 control, light, and moderate damage classes, respectively. Mean percent basal area lost in each damage class was 2%, 21%, and 48%, for control, light, and moderate classes, respectively, and these values were significantly different ($P < 0.05$). The mean dbh for all trees in the decay 1 class was 24.1 cm. The mean dbh of *Q. alba* individuals damaged during the storm was 38 cm, and the mean dbh of all *Quercus* individuals damaged was 38 cm. The mean dbh of *Carya* individuals was 29 cm, and the mean branch size measured was 23 cm dbh. Of stems within the decay class 1 category, 17% were snags, 53% were snapped stems, and 30% were uprooted stems. Stems were more likely to be snapped than either to be uprooted or to remain standing as snags ($P < 0.001$).

For the control plot trees >5 cm dbh, *Ostrya virginiana* (Mill.) K. Koch, *Q. alba*, *Acer saccharum* Marsh., and *Carya* spp. occurred in the highest densities. The species with the highest densities on light damage class plots were *O. virginiana*, *Q. alba*, *F. grandifolia*, and *Magnolia macrophylla* Michx. *Ostrya virginiana*, *Q. alba*, *M. macrophylla*, and *A. saccharum* were present in the highest densities on moderate damage class plots (Table 1). The five most dominant taxa based on basal area contribution within the control class were *Q. alba*, *Carya* spp., *A. saccharum*, *Quercus rubra* L. and *L. tulipifera*. The five most dominant taxa on light damage plots were *Q. alba*, *Carya* spp., *L. tulipifera*, and *Quercus prinus* L. and *Q. rubra*. Similarly, the taxa with the highest relative dominance on moderate plots were *Q. alba*, *Carya* spp., *P. taeda*, and *F. grandifolia* (Table 1). The most common species damaged within the control plots, which represented expected background mortality, based on relative densities were *A. saccharum*, *Q. alba*, *Cercis canadensis* L., and *M. macrophylla* (Table 2). Within the light disturbance plots, *Q. alba*, *Carya* spp., *O. virginiana*, and *Q. prinus* were damaged in the highest densities. Taxa with the highest rates (based on density) of mortality on moderate damaged plots were *O. virginiana*, *Carya* spp., *Q. alba*, and *M. macrophylla*.

We documented 14 canopy dominant trees ha^{-1} in control plots, 13 ha^{-1} in light damage plots, and 5 ha^{-1} in moderate damage plots (Fig. 2). The density of canopy co-dominant trees ranged from 129 ha^{-1} in control plots to 64 ha^{-1} on moderate damage plots. Across all damage classes, the canopy was dominated by *Quercus* and *Carya* species. We did not document any *Acer* species or *F. grandifolia* stems with dominant positions in the canopy and these taxa represented minor contributions to the canopy co-dominant stratum. Density of overtopped stems in control plots far exceeded the abundance of such stems in light and moderate damage plots (119% more overtopped stems in control plots than in moderate damage plots). *Quercus* and *Carya* represented a small component of overtopped stems across all damage categories. *Acer* species and *F. grandifolia* were better represented than the *Quercus–Carya* group in the overtopped stratum. Interestingly, the overtopped layer contained an abundance of *O. virginiana* as this species represented 41%, 28%, and 48% of such stems in control, light, and moderate damage plots, respectively. *Magnolia macrophylla* was also abundant in the overtopped category. In the intermediate layer, the representation of taxonomic groups was similar across the damage categories.

3.2. Effects on sub-canopy light regimes

Percent of full sunlight for control class plots was 9% ± 3, for light damage class plots was 12% ± 2, and for moderate damage class plots was 22% ± 4 (Fig. 3). Percent of full sunlight was significantly different between control and moderate damage classes and between light and moderate damage classes. Three growing seasons post-disturbance, percent light reduction in the understory (measured at 1.4 m above the surface) for control, light, and moderate damage classes was 91%, 89%, and 78%, respectively (Table 3). Percent canopy cover ranged from 95% to 92% with increasing damage. Gap fraction (i.e. the proportion of unobscured

Table 1
Density and dominance measures for all live stems ⩾5 cm dbh in the Sipsey Wilderness, Alabama. Species are ranked according to relative dominance in control plots.

Species	Density (stems ⩾ 5 cm dbh/ha)			Relative density (%)			Dominance (m^2/ha)			Relative dominance (%)		
	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate
Quercus alba	105.00	95.19	52.70	13.6	14.3	9.9	10.62	9.04	5.42	41.4	38.2	35.4
Carya spp.	65.00	51.44	40.54	8.4	7.7	7.6	3.68	2.52	2.21	14.3	10.7	14.4
Acer saccharum	95.00	43.27	45.95	12.3	6.5	8.7	2.00	0.96	0.76	7.8	4.1	5.0
Quercus rubra	7.50	5.77	1.35	1.0	0.9	0.3	1.40	1.19	0.10	5.4	5.0	0.6
Liriodendron tulipifera	11.25	14.42	7.43	1.5	2.2	1.4	1.22	1.91	0.31	4.8	8.0	2.1
Ostrya virginiana	208.75	124.04	141.89	27.1	18.6	26.7	1.17	0.69	0.70	4.6	2.9	4.6
Quercus muehlenbergii	20.00	2.40	4.05	2.6	0.4	0.8	1.16	0.13	0.26	4.5	0.5	1.7
Quercus prinus	15.00	20.19	4.73	1.9	3.0	0.9	0.79	1.17	0.43	3.1	5.0	2.8
Fagus grandifolia	43.75	64.90	37.84	5.7	9.7	7.1	0.60	1.76	0.77	2.3	7.4	5.1
Pinus taeda	1.25	5.29	5.41	0.2	0.8	1.0	0.50	0.42	1.66	2.0	1.8	10.8
Nyssa sylvatica	33.75	44.71	27.70	4.4	6.7	5.2	0.34	0.48	0.40	1.3	2.0	2.6
Magnolia acuminata	8.75	11.06	9.46	1.1	1.7	1.8	0.32	0.35	0.24	1.2	1.5	1.5
Quercus falcata	2.50	3.85	4.05	0.3	0.6	0.8	0.31	0.36	0.59	1.2	1.5	3.8
Juglans nigra	3.75	0.48	–	0.5	0.1	–	0.27	0.07	–	1.0	0.3	–
Fraxinus americana	12.50	7.69	10.81	1.6	1.2	2.0	0.22	0.47	0.29	0.8	2.0	1.9
Cornus florida	31.25	33.65	17.57	4.1	5.1	3.3	0.15	0.16	0.08	0.6	0.7	0.5
Ulmus rubra	7.50	1.44	1.35	1.0	0.2	0.3	0.14	0.01	0.02	0.5	0.0	0.1
Juniperus virginiana	5.00	6.25	1.35	0.6	0.9	0.3	0.13	0.31	0.04	0.5	1.3	0.3
Ulmus alata	10.00	4.81	10.14	1.3	0.7	1.9	0.12	0.14	0.07	0.5	0.6	0.4
Cercis canadensis	22.50	4.81	10.81	2.9	0.7	2.0	0.12	0.02	0.04	0.5	0.1	0.2
Quercus stellata	1.25	1.44	0.68	0.2	0.2	0.1	0.10	0.06	0.07	0.4	0.3	0.5
Magnolia macrophylla	17.50	61.06	49.32	2.3	9.2	9.3	0.09	0.48	0.39	0.4	2.0	2.5
Acer rubrum	8.75	15.38	12.16	1.1	2.3	2.3	0.07	0.10	0.06	0.3	0.4	0.4
Frangula caroliniana	11.25	0.48	1.35	1.5	0.1	0.3	0.04	0.00	0.00	0.2	0.0	0.0
Oxydendrum arboreum	3.75	15.87	5.41	0.5	2.4	1.0	0.04	0.24	0.12	0.2	1.0	0.8
Carpinus caroliniana	7.50	5.77	16.22	1.0	–	3.1	0.04	0.03	0.06	0.2	0.1	0.4
Prunus serotina	3.75	8.17	2.03	0.5	1.2	0.4	0.04	0.06	0.05	0.2	0.3	0.3
Rhamnus cathartica	2.50	0.48	1.35	0.3	0.1	0.3	0.01	0.00	0.00	0.0	0.0	0.0
Acer negundo	1.25	–	–	0.2	–	–	0.00	–	–	0.0	–	–
Amelanchier arborea	1.25	0.96	–	0.2	0.1	–	0.00	0.00	–	0.0	0.0	–
Aesculus pavia	1.25	0.48	–	0.0	0.1	0.1	0.00	0.00	–	0.0	0.0	–
Asimina triloba	1.25	–	–	0.2	0.9	–	0.00	–	–	0.0	–	–
Morus rubra	–	0.48	0.68	–	0.1	0.1	–	0.00	0.01	0.0	0.0	0.0
Pinus echinata	–	1.44	–	–	0.2	–	–	0.17	–	–	0.7	–
Tilia americana	–	0.96	2.03	–	0.1	0.4	–	0.12	0.03	–	0.5	0.2
Ulmus americana	–	1.92	2.03	–	0.3	0.4	–	0.11	0.13	–	0.5	0.8
Pinus viriginiana	–	1.44	–	–	0.2	–	–	0.10	–	–	0.4	–
Sassafras albidum	–	2.88	1.35	–	0.4	0.3	–	0.05	0.00	–	0.2	0.0
Ilex opaca	–	0.96	0.68	–	0.1	0.1	–	0.01	0.00	–	0.0	0.0
Betula lenta	–	–	0.68	0.2	–	–	–	–	0.01	–	–	0.1
Total	771.25	665.87	531.08	100.0	100.0	100.0	25.68	23.67	15.32	100.0	100.0	100.0

Table 2
Density and dominance measures for all decay class 1 stems ⩾5 cm dbh in the Sipsey Wilderness, Alabama. Species are ranked according to relative dominance in control plots.

Species	Density (stems/ha)			Relative Density (%)			Dominance (m^2/ha)			Relative Dominance (%)		
	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate
Quercus alba	3.75	15.87	29.73	15.8	20.4	14.6	0.10	2.34	4.27	31.0	36.2	30.1
Acer sacharum	5.00	2.40	14.19	21.1	3.1	7.0	0.05	0.06	0.42	16.3	0.9	3.0
Magnolia macrophylla	2.50	2.88	16.22	10.5	3.7	8.0	0.05	0.02	0.17	14.5	0.4	1.2
Quercus muehlenbergii	1.25	0.96	1.35	5.3	1.2	0.7	0.04	0.05	0.04	13.1	0.7	0.3
Carya spp.	1.25	14.90	30.41	5.3	19.1	15.0	0.03	1.15	2.63	9.6	17.7	18.5
Fraxinus americana	1.25	–	4.73	5.3	–	2.3	0.02	–	0.31	4.6	–	2.2
Ostrya virginiana	1.25	6.25	36.49	5.3	8.0	17.9	0.01	0.03	0.21	2.7	0.4	1.5
Cercis canadensis	2.50	0.96	3.38	10.5	1.2	1.7	0.01	0.01	0.03	2.5	0.1	0.2
Liriodendron tulipifera	1.25	2.88	5.41	5.3	3.7	2.7	0.01	0.32	1.03	1.9	4.9	7.2
Frangula caroliniana	1.25	–	–	5.3	–	–	0.00	–	–	1.3	–	–
Fagus grandifolia	1.25	2.88	5.41	5.3	3.7	2.7	0.00	0.65	0.63	1.1	10.1	4.4
Cornus florida	1.25	3.37	5.41	5.3	4.3	2.7	0.00	0.02	0.03	1.0	0.2	0.2
Juniperus virginiana	0.00	2.88	2.70	0.0	3.7	1.3	0.00	0.06	0.08	0.0	1.0	0.6
Nyssa sylvatica	0.00	3.37	8.11	0.0	4.3	4.0	0.00	0.04	0.14	0.0	0.6	1.0
Pinus taeda	0.00	0.00	3.38	0.0	0.0	1.7	0.00	0.00	0.95	0.0	0.0	6.7
Pinus virginiana	0.00	3.37	0.68	0.0	4.3	0.3	0.00	0.44	0.08	0.0	6.8	0.6
Prunus serotina	0.00	1.92	0.68	0.0	2.5	0.3	0.00	0.01	0.03	0.0	0.1	0.2
Quercus falcata	0.00	0.96	4.73	0.0	1.2	2.3	0.00	0.12	0.42	0.0	1.8	3.0
Quercus prinus	0.00	4.81	4.73	0.0	6.2	2.3	0.00	0.47	0.87	0.0	7.2	6.1
Quercus rubra	0.00	2.88	8.11	0.0	3.7	4.0	0.00	0.62	1.27	0.0	9.6	8.9
Sassafrass albidum	–	0.48	0.00	–	0.6	0.0	–	0.00	0.00	–	0.0	0.0
Magnolia acuminata	–	0.48	4.05	0.0	0.6	2.0	–	0.01	0.18	–	0.1	1.3
Acer rubrum	–	1.92	0.68	–	2.5	0.3	–	0.01	0.00	–	0.1	0.0
Oxydendron arboreum	–	0.96	3.38	0.0	1.2	1.7	–	0.02	0.21	–	0.3	1.5
Quercus stellata	–	0.48	0.68	–	0.6	0.3	–	0.04	0.03	–	0.7	0.2
Juglans nigra	–	–	0.68	–	–	0.3		–	0.08	–	–	0.5
Ulmus alata	–	–	2.03	–	–	1.0	–	–	0.06	–	–	0.4
Tilia americana	–	–	0.68	–	–	0.3	–	–	0.02	–	–	0.1
Carpinus caroliniana	–	–	3.38	–	–	1.7	–	–	0.01	–	–	0.1
Betula lenta	–	–	0.68	–	–	0.3	–	–	0.01	–	–	0.1
Amelanchier arborea	–	–	1.35	0.0	0.0	0.7	–	–	0.00	–	–	0.0
Vaccinium arboreum	–	–	0.00	–	–	0.0	–	–	0.00	–	–	0.0
Total	23.75	77.88	203.38	100.0	100.0	100.0	0.33	6.47	14.22	100.0	100.0	100.0

sky commonly used to describe canopy structure) is important because it influences solar radiation in the sub-canopy. It increased with increasing storm damage from 5% to over 8%, but differences among damage classes were not significant. Hemispherical photographs were used to calculate percent openness above breast height (i.e. the fraction of open sky in a specified region of the real canopy above the lens), which was 5%, 6%, and 9% for control, light, and moderate damage classes, respectively. Leaf area index was 3.24 ± 0.07, 3.21 ± 0.07, 3.04 ± 0.12 for control, light, and moderate damage class plots, respectively.

3.3. Effects on the regeneration layer

We documented 53 unique species throughout the seedling (stems < 1 m) layer of the three damage classes (Table 4). Within the control plots, *A. saccharum*, *Fraxinus americana* L., *Q. alba*, and *Acer rubrum* L. had the highest relative densities. Species with the highest relative densities on light damage class plots were *Q. alba*, *A. sacharrum*, *A. rubrum*, and *Viburnum acerifolium* L., *Viburnum acerifolium*, *A. saccharum*, *Ligustrum sinense* Lour., and *Q. alba* exhibited the highest relative densities in the seedling layer on moderate damage class plots. *Acer saccharum*, *Q. rubra*, *A. rubrum*, and *Q. alba* were each present on at least 10% of control plots. *Acer rubrum*, *O. virginiana*, *Q. alba*, and *Carya* spp. occurred on at least 20% of light damage class plots. Species that were recorded on at least 15% of moderate damage class plots were *A. saccharum*, *Carya* spp., *O. virginiana*, *F. americana*, and *Q. alba*. We documented two alien species in the seedling layer, *L. sinense* and *Rhamnus cathartica* L. *Ligustrum sinense* represented 3%, 1%, and 8% of total seedling layer stems in the control, light, and moderate classes, respectively.

Within the sapling layer (stems > 1 m, <5 cm dbh), which included 45 unique species, the species with the highest relative densities were *A. rubrum*, *O. virginiana*, *L. sinense*, and *F. grandifolia* across the control plots (Table 5). Within the light damage class, the four most abundant species were *O. virginiana*, *A. rubrum*, *A. saccharum*, and *Lindera benzoin* (L.) Blume. The species with the highest relative densities in the moderate damage class were *A. saccharum*, O. *virginiana*, *A. rubrum*, and *C. florida*. Species that were present on greater than 5% of control plots were *A. rubrum*, *O. virginiana*, *F. americana*, and *A. saccharum*. *Ostrya virginiana*, *A. rubrum*, *A. saccharum*, and *F. grandifolia* each occurred on greater than 10% of light damage class plots. On moderate damage plots, *A. saccharum*, *O. virginiana*, *A. rubrum*, *Cornus florida* L., and *F. americana* were the five species that were found on greater than 10% of plots. Notably, *Q. rubra* was the only *Quercus* sapling species that occurred on more than five plots, the majority of which were present in the moderate damage class. *Quercus alba*, which occurred in relatively high densities in the seedling layer, was only present as a sapling on one control plot, two light plots, and one moderate plot. The two alien species that occurred in the seedling layer also occurred in the sapling layer. Notably, *L. sinense* represented 14%, 3%, and 6% of total sapling layer stems on control, light, and moderate plots, respectively. Only two *Quercus* species, *Q. prinus* and *Q. rubra*, had relative densities above 1% in any of the three sapling damage classes (Table 5).

4. Discussion

4.1. Light regimes

The majority of variables we tested to characterize understory light regimes following an intermediate-scale disturbance had returned to pre-disturbance conditions after three growing seasons. However, there were significant differences in percent of full

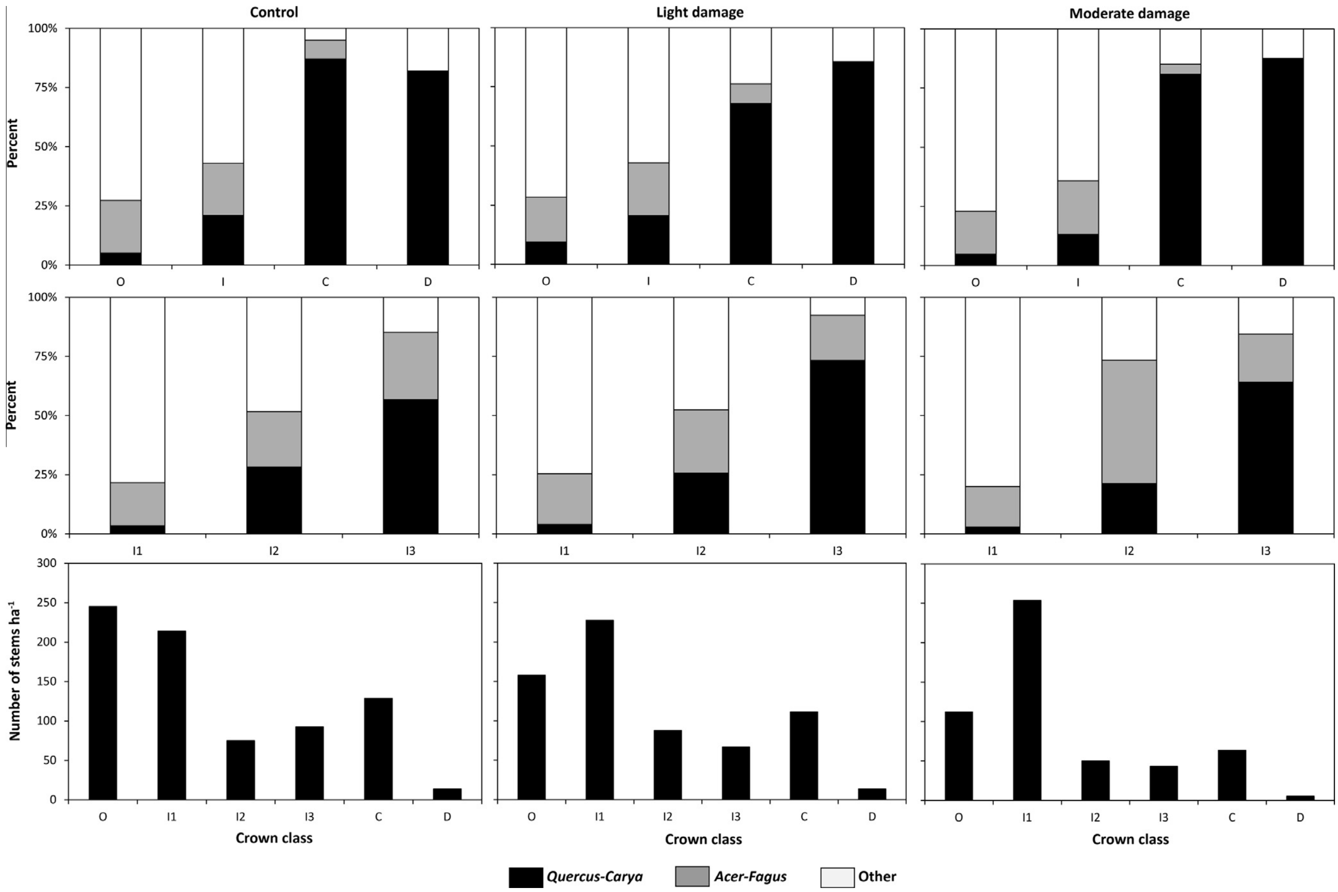

Fig. 2. Crown class percentages by taxonomic group and tree (stems ⩾ 5 cm dbh) density by crown class for control, light, and moderate damage plots in the Sipsey Wilderness, Alabama. For a list of species in the "other" category see Table 1. Crown class categories are based on the amount and direction of intercepted light (Oliver and Larson (1996)). O: overtopped, I: intermediate, C: co-dominant, D: dominant, I1: 0–50% of total canopy height, I2: 50–75% of total canopy height, I3: ⩾75% of total canopy height.

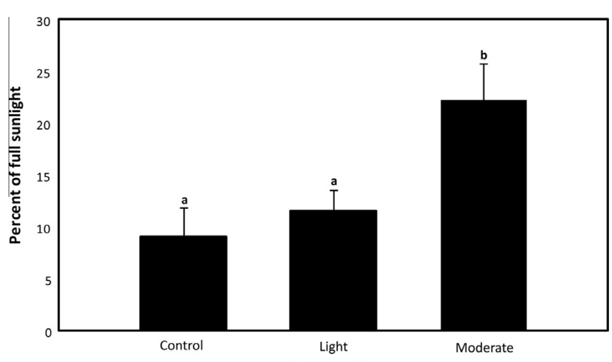

Fig. 3. Mean (with standard error) percent of full sunlight values for control, light, and moderate damage classes for stands in the Sipsey Wilderness, Alabama. Bars with different letters are significantly different ($P < 0.05$).

sunlight between control and moderate damage plots and light and moderate damage plots; based on measures of light at breast height. We did not find significant differences in measures from our hemispherical photographs. The difference between percent of full sunlight on control v. light damage plots was not discernible, which does not necessarily mean canopy gaps had been completely filled, but rather that well-developed individuals in the midstory increased sufficiently in height and crown volume to negate the increases in light from canopy gaps. Although the canopy was still open at our sampling, midstory stems restricted light to the seedling and sapling layers. Consequently, even though the mean percent of full sunlight in the moderate plots fell within the 20–50% range required for understory *Quercus* stems (Dey, 2002), light levels below breast height (i.e. light level in the regeneration layer) were insufficient for *Quercus* recruitment.

Percent of full sunlight on control and light damage plots, which best represented actual understory light levels at breast height, were comparable to those from the region (Canham et al., 1990; Schweitzer and Dey, 2011). Schweitzer and Dey (2011) quantified forest response to different levels of regeneration harvests in north Alabama and the levels of canopy openness and gap fraction they documented after three growing seasons were comparable to those found in this study after the same time since disturbance. The stage of stand development is particularly important when evaluating the effects of intermediate-scale disturbances on understory light levels. The majority of stems disturbed by the wind event were canopy trees, and during the understory reinitiation stage the midstory in these forest systems is well-developed. Thus, rather than creating new opportunities for the establishment of new stems, the disturbance served largely as a mechanism to release stems already present in the midstory. Consequently, the resultant changes in the light regime at breast height were ephemeral and lasted only a few growing seasons.

4.2. Effects on composition and biodiversity

Trees with larger diameters were disproportionately killed by the storm event. This is consistent with the results from other studies on wind disturbance (Foster and Boose, 1992; Peterson

Table 3
Comparisons of diversity and structural measures of managed stands in Jackson County, Alabama (light: 75% basal area retention, moderate: 50% basal area retention harvests) versus naturally disturbed stands in Lawrence County, Alabama. Both sites were located on the Cumberland Plateau.

	Jackson Co., Alabama[a]			Lawrence Co., Alabama		
	Control	Light	Moderate	Control	Light	Moderate
Diversity (H')	2.2	2.1	2.1	1.8	1.9	1.7
Basal area retention (m^2/ha)	23.1	26.3	10.1	25.6	25.4	15.3
Percent canopy cover	98.8	96.2	71.9	95.0	94.0	91.6
Percent light reduction	97.0	93.7	73.3	91.0	88.5	77.8

[a] Data from Schweitzer and Dey (2011).

Table 4
Density and frequency (number of plots on which each species occurred by damage class) measures for all seedlings (<1 m height, ⩽5 cm dbh) in the Sipsey Wilderness, Alabama. Species were ranked based on relative density in control plots.

Species	Density (stems/ha)			Relative density (%)			Frequency (# plots)			Relative frequency (%)		
	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate
Acer saccharum	2400	1942	1946	13.2	10.9	11.7	16	27	28	80.0	51.9	75.7
Fraxinus americana	2400	1038	892	13.2	5.8	5.3	8	17	17	40.0	32.7	45.9
Quercus alba	1950	2154	1162	10.7	12.0	7.0	12	30	17	60.0	57.7	45.9
Acer rubrum	1450	1885	919	7.9	10.5	5.5	12	38	19	60.0	73.1	51.4
Quercus rubra	1400	538	649	7.7	3.0	3.9	13	18	12	65.0	34.6	32.4
Viburnum acerifolium	1100	1615	2135	6.0	9.0	12.8	5	18	15	25.0	34.6	40.5
Ostrya virginiana	900	1192	892	4.9	6.7	5.3	10	31	18	50.0	59.6	48.6
Fagus grandifolia	750	462	270	4.1	2.6	1.6	3	12	7	15.0	23.1	18.9
Carya spp.	650	1250	892	3.6	7.0	5.3	7	29	18	35.0	55.8	48.6
Ulmus rubra	650	308	216	3.6	1.7	1.3	5	7	6	25.0	13.5	16.2
Ligustrum sinense	600	212	1351	3.3	1.2	8.1	7	6	5	35.0	11.5	13.5
Cercis canadensis	550	423	351	3.0	2.4	2.1	6	14	10	30.0	26.9	27.0
Prunus serotina	500	423	324	2.7	2.4	1.9	6	17	11	30.0	32.7	29.7
Frangula caroliniana	450	96	81	2.5	0.5	0.5	3	5	2	15.0	9.6	5.4
Ulmus alata	350	77	243	1.9	0.4	1.5	7	3	8	35.0	5.8	21.6
Aralia spinosa	250	38	81	1.4	0.2	0.5	2	2	2	10.0	3.8	5.4
Lindera benzoin	250	115	–	1.4	0.6	–	1	3	–	5.0	5.8	–
Nyssa sylvatica	200	404	703	1.1	2.3	4.2	4	16	15	20.0	30.8	40.5
Vaccinium arboreum	200	769	162	1.1	4.3	1.0	1	15	4	5.0	28.8	10.8
Amelanchier arborea	150	115	81	0.8	0.6	0.5	2	2	3	10.0	3.8	8.1
Asimina triloba	150	154	216	0.8	0.9	1.3	3	5	3	15.0	9.6	8.1
Carpinus caroliniana	150	115	135	0.8	0.6	0.8	2	5	4	10.0	9.6	10.8
Magnolia acuminata	150	77	81	0.8	0.4	0.5	3	4	3	15.0	7.7	8.1
Quercus muehlenbergii	150	77	–	0.8	0.4	–	3	1	–	15.0	1.9	–
Juniperus virginiana	100	115	54	0.5	0.6	0.3	2	6	2	10.0	11.5	5.4
Quercus prinus	100	250	135	0.5	1.4	0.8	1	7	3	5.0	13.5	8.1
Styrax grandifolius	100	38	81	0.5	0.2	0.5	1	2	2	5.0	3.8	5.4
Aesculus pavia	50	135	–	0.3	0.8	–	1	3	–	5.0	5.8	–
Celtis occidentalis	50	19	–	0.3	0.1	–	1	1	–	5.0	1.9	–
Cornus florida	50	538	460	0.3	3.0	2.8	1	14	11	5.0	26.9	29.7
Quercus falcata	50	38	27	0.3	0.2	0.2	1	2	1	5.0	3.8	2.7
Liriodendron tulipifera	–	481	243	–	2.7	1.5	–	3	5	–	5.8	13.5
Pinus taeda	–	192	432	–	1.1	2.6	–	5	7	–	9.6	18.9
Sassafras albidum	–	96	649	–	0.5	3.9	–	3	3	–	5.8	8.1
Oxydendrum arboreum	–	77	–	–	0.4	–	–	1	–	–	1.9	–
Quercus velutina	–	77	108	–	0.4	0.6	–	3	3	–	5.8	8.1
Rhododendron catawbiense	–	77	162	–	0.4	1.0	–	4	1	–	7.7	2.7
Magnolia macrophylla	–	58	243	–	0.3	1.5	–	3	8	–	5.8	21.6
Pinus virginiana	–	58	81	–	0.3	0.5	–	2	2	–	3.8	5.4
Crataegus phaenopyrum	–	38	–	–	0.2	–	–	2	–	–	3.8	–
Rhamnus cathartica	–	38	–	–	0.2	–	–	2	–	–	3.8	–
Betula lenta	–	19	–	–	0.1	–	–	1	–	–	1.9	–
Ilex opaca	–	19	–	–	0.1	–	–	1	–	–	1.9	–
Kalmia latifolia	–	19	–	–	0.1	–	–	1	–	–	1.9	–
Morus rubra	–	19	–	–	0.1	–	–	1	–	–	1.9	–
Pinus echinata	–	–	54	–	–	0.3	–	–	2	–	–	5.4
Ulmus americana	–	–	54	–	–	0.3	–	–	1	–	–	2.7
Diospyros virginiana	–	–	27	–	–	0.2	–	–	1	–	–	2.7
Juglans nigra	–	–	27	–	–	0.2	–	–	1	–	–	2.7
Quercus stellata	–	–	27	–	–	0.2	–	–	1	–	–	2.7
Tilia americana	–	–	27	–	–	0.2	–	–	1	–	–	2.7
Total	18,250	17,883	16,678	100.0	100.0	100.0	–	–	–	–	–	–

and Rebertus, 1997; Canham et al., 2001). We did not detect species-specific mortality patterns among canopy trees and canopy tree diversity was not significantly different across the three damage classes. In all overstory damage classes, *Q. alba* was a major component of the canopy and consequently, it was the species most consistently killed across both damage classes. *Quercus alba* represented 30% of the 1617 stems within the intermediate 3 (I3) crown class. This is the crown class that we hypothesized would

Table 5
Density and frequency (number of plots on which each species occurred by damage class) measures for all saplings (⩾1 m height, ⩽5 cm dbh) in the Sipsey Wilderness, Alabama. Species were ranked based on relative density in control plots.

Species	Density (stems/ha)			Relative density (%)			Frequency (# plots)			Relative frequency (%)		
	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate
Acer rubrum	900	1115	1135	15.3	16.1	10.9	9	23	16	45.0	44.2	43.2
Ostrya virginiana	900	1192	1324	15.3	17.2	12.7	8	28	22	40.0	53.8	59.5
Ligustrum sinense	850	192	649	14.4	2.8	6.2	5	5	4	25.0	9.6	10.8
Fagus grandifolia	500	462	189	8.5	6.7	1.8	4	11	4	20.0	21.2	10.8
Acer saccharum	400	692	1324	6.8	10.0	12.7	6	20	22	30.0	38.5	59.5
Fraxinus americana	400	346	432	6.8	5.0	4.1	7	9	12	35.0	17.3	32.4
Styrax grandifolius	200	–	108	3.4	–	1.0	1	–	2	5.0	–	5.4
Aesculus pavia	150	269	–	2.5	3.9	–	1	4	–	5.0	7.7	–
Carpinus caroliniana	150	192	540	2.5	2.8	5.2	3	5	8	15.0	9.6	21.6
Cercis canadensis	150	58	351	2.5	0.8	3.4	3	2	7	15.0	3.8	18.9
Quercus prinus	150	–	54	2.5	–	0.5	1	–	1	5.0	–	2.7
Viburnum acerifolium	150	404	297	2.5	5.8	2.8	2	10	4	10.0	19.2	10.8
Frangula caroliniana	100	19	135	1.7	0.3	1.3	2	1	3	10.0	1.9	8.1
Juniperus virginiana	100	38	54	1.7	0.6	0.5	2	2	2	10.0	3.8	5.4
Rhamnus cathartica	100	–	–	1.7	–	–	1	–	–	5.0	–	–
Tilia americana	100	–	–	1.7	–	–	1	–	–	5.0	–	–
Ulmus alata	100	38	108	1.7	0.6	1.0	2	2	4	10.0	3.8	10.8
Lindera benzoin	90	500	–	1.5	7.2	–	2	2	–	10.0	3.8	–
Cornus florida	50	289	676	0.8	4.2	6.5	1	10	14	5.0	19.2	37.8
Magnolia macrophylla	50	38	324	0.8	0.6	3.1	1	2	6	5.0	3.8	16.2
Nyssa sylvatica	50	135	540	0.8	1.9	5.2	1	6	9	5.0	11.5	24.3
Prunus serotina	50	58	135	0.8	0.8	1.3	1	3	5	5.0	5.8	13.5
Quercus alba	50	58	54	0.8	0.8	0.5	1	2	1	5.0	3.8	2.7
Quercus rubra	50	58	189	0.8	0.8	1.8	1	3	6	5.0	5.8	16.2
Ulmus rubra	50	38	81	0.8	0.6	0.8	1	1	3	5.0	1.9	8.1
Vaccinium arboreum	50	–	81	0.8	–	0.8	1	–	2	5.0	–	5.4
Carya spp.	–	192	216	–	2.8	2.1	–	10	4	–	19.2	10.8
Magnolia acuminata	–	96	135	–	1.4	1.3	–	4	4	–	7.7	10.8
Asimina triloba	–	77	189	–	1.1	1.8	–	4	2	–	7.7	5.4
Amelanchier arborea	–	58	–	–	0.8	–	–	–	–	–	–	–
Celtis occidentalis	–	38	–	–	0.6	–	–	2	–	–	3.8	–
Diospyros virginiana	–	38	81	–	0.6	0.8	–	2	3	–	3.8	8.1
Rhododendron catawbiense	–	38	–	–	0.6	–	–	1	–	–	1.9	–
Betula lenta	–	19	–	–	0.3	–	–	1	–	–	1.9	–
Castanea dentata	–	19	27	–	0.3	0.3	–	1	1	–	1.9	2.7
Liriodendron tulipifera	–	19	81	–	0.3	0.8	–	1	3	–	1.9	8.1
Morus rubra	–	19	–	–	0.3	–	–	1	–	–	1.9	–
Oxydendrum arboreum	–	19	27	–	0.3	0.3	–	1	1	–	1.9	2.7
Pinus taeda	–	19	81	–	0.3	0.8	–	1	1	–	1.9	2.7
Quercus falcata	–	19	–	–	0.3	–	–	1	–	–	1.9	–
Quercus velutina	–	19	–	–	0.3	–	–	1	–	–	1.9	–
Sassafras albidum	–	19	406	–	0.3	3.9	–	1	2	–	1.9	5.4
Ulmus americana	–	19	–	–	0.3	–	–	1	–	–	1.9	–
Arundinaria tecta	–	–	406	–	–	3.9	–	–	1	–	–	2.7
Quercus muehlenbergii	–	–	27	–	–	0.3	–	–	1	–	–	2.7
Total	5890	6922	10,461	100.0	100.0	100.0	–	–	–	–	–	–

have the greatest potential to recruit to the canopy in the future (i.e. fill canopy space that is available after current dominant and co-dominant trees are removed), as these were the tallest and most developed stems within the intermediate crown class. Likewise, the genus *Quercus* and the group *Quercus–Carya* represented 43% and 65% of total I3 stems, respectively. Additionally, it is important to note that not only will I3 stems rapidly capture canopy positions after disturbances, but that they are also less susceptible to wind damage because of their size. If these stems are able to fill canopy positions created by the mortality of current dominant and co-dominant trees, this forest could remain dominated by *Quercus–Carya* (Xi and Peet, 2011) until the point when shade-tolerant stems, in particular *Acer* spp., begin to fill the majority of canopy openings. *Acer* saplings accounted for 42% of all sapling layer stems. Based on the preponderance of the *Acer* genus in the well-developed understory and midstory and its ability to capture canopy gaps (Hart et al., 2012b), we hypothesized that these species will succeed a majority of canopy trees as the canopy is subsequently disturbed and the forest moves toward the complex stage of development (Barden, 1979, 1980; White et al., 1985; Yamamoto and Nishimura, 1999).

In developing secondary stands that have not reached the complex stage of development, gaps created by the death of canopy trees are relatively small and typically close by lateral crown expansion rather than by height growth of sub-canopy stems (Hart and Grissino-Mayer, 2009; Hart et al., 2011; Richards and Hart, 2011). In contrast, the spacing between canopy trees increases and each canopy tree crown represents a larger portion of the main forest canopy as stands age. When one of these large canopy trees is removed, it creates a relatively large gap. These large gaps are typically filled by the height growth of sub-canopy individuals (Clebsch and Busing, 1989; Busing, 1995). The majority of forest stands in the eastern US are second growth (i.e. not primeval), less than 100 years old, and established after being harvested (Cowell, 1998; Rebertus and Meier, 2001). Prior to European settlement of the eastern US, it is estimated that a larger percentage of the landscape supported stands in the complex stage of development (Whitney, 1994; Lorimer, 2001). A change in stand structure from pre-European settlement to the present may have influenced canopy disturbance regimes, especially canopy gap size. Contemporary forests with relatively small canopy gaps that more often fill by lateral crown expansion may have had significant impacts on regeneration of *Quercus*. In the forest studied here, which was in the understory reinitiation stage of development, canopy disturbances acted as a top-down control on competition and served only to release midstory (largely *Quercus* spp. and *Carya* spp.) and understory (largely *Acer* spp.) stems. Intermediate-scale disturbances during this stage of development, without competition control measures, provided the proper amount of insolation to recruit *Quercus* spp. from seedling to sapling or sapling to small tree size classes, but did not provide the mechanism for *Quercus* reproduction to outcompete shade-tolerant mesophytes that were already present in the sapling layer. *Acer* spp. and *F. grandifolia* and trees that lack canopy potential such as *O. virginiana* and *M. macrophylla* in the small size classes effectively formed a "recalcitrant understory layer" that altered succession following canopy disturbance (Royo and Carson, 2006).

Significant differences in species richness and Shannon diversity were found in the sapling layer, but not seedling or tree strata or when seedling and saplings or all stems were analyzed. Thus, the sapling layer was the only stratum where we observed possible influences of the disturbance on woody plant diversity. Mean species richness of saplings per plot was significantly higher in the moderate damage class than in the control or light damage classes. Similarly, mean Shannon diversity of saplings per plot was significantly higher in the moderate v. the light damage class, although neither damage class was significantly different from the control. We speculated this finding was a function of the amount of time that elapsed since the storm. During three growing seasons, seedlings present at the time of the event were able to recruit to sapling size classes. Likewise, propagules in the seedbed at the time of the disturbance and those that arrived shortly afterward were able to germinate and recruit to sapling size classes. The intermediate disturbance hypothesis proposed by Connell (1978), posits that intermediate levels of disturbance, both in spatial and temporal extent, maintain the highest levels of biodiversity. This hypothesis has been intensely criticized (e.g. Wilkinson, 1999; Bongers et al., 2009; Fox, 2013a, b). At the sapling layer our results seem to support the hypothesis, however, we found no evidence that biodiversity was enhanced by the intermediate scale disturbance across other woody plant size classes. In fact, Shannon diversity of all woody stems was lowest in the moderate damage class.

We hypothesized that Shannon diversity would increase with increasing disturbance intensity because in the most damaged plots both residual stems and new germinants that colonized the disturbed areas would be present. Furthermore, we hypothesized new germinants in disturbed neighborhoods would include some shade-intolerant species that occurred on the site as established trees (e.g. *L. tulipifera*), but were not present in the understory prior to the canopy disturbance event. The canopy disturbance event we studied largely served to release stems in the well-developed midstory and understory strata which were comprised primarily of shade-tolerant and moderately-tolerant species rather than create new niche space for the colonization of early seral species; i.e. disturbance-mediated accelerated succession (Abrams and Scott, 1989; Holzmueller et al., 2012). We did document some species in the regeneration layer of disturbed plots that were absent on control plots thus, total woody plant species richness was higher in the disturbance classes relative to the control. However, species richness is scale-dependent and our sample size varied by disturbance category. Thus, we were not able make conclusions based on general species richness patterns. Based on our results, we suggest that intermediate levels of disturbance may promote woody plant diversity in *Quercus* stands, but this diversity may be restricted to sapling or small tree size classes and thus, may be ephemeral. Alternatively, the intermediate scale disturbance hypothesis may not hold for stands in the understory reinitiation stage of development with dissimilar vertical strata (i.e. in successional stands). We agree with authors (e.g. Sheil and Burslem, 2003, 2012) that have called for the hypothesis to be more narrowly defined rather than discounted and abandoned. We speculated that a more intense disturbance than what occurred at our study site would be required to allow shade-intolerant and moderately-tolerant taxa to compete with the well-established shade-tolerant stems in the sapling and small tree size classes. It may be that a disturbance regime characterized by wind damage, including some severe events, and periodic fire may maximize diversity in *Quercus* systems rather than a regime characterized by fine- to intermediate-scale wind events alone.

4.3. Effects on regeneration and succession

Wind storms such as those documented here result in damage to seedlings and saplings through fallen canopy trees crushing only patches of small reproduction that may be able to quickly recover by sprouting. Consequently, wind disturbances may serve as top-down controls on regeneration by releasing overtopped and intermediate trees from competition. In this specific case, the canopy gaps caused by the tornado largely released *Acer* stems in the understory and midstory and further widened the disparity between the presence of *Acer* spp., *F. grandifolia*, and other shade-tolerant species and *Quercus* advanced reproduction. Hart and Grissino-Mayer (2009) found that in *Quercus* individuals, the increase in resources from a canopy opening would generally not be sustained in canopy trees for more than four years, which may also be true for *Quercus* stems in the regeneration layer. Notably, we documented minimal amounts of shade-intolerant *L. tulipifera* in the understory, despite the fact that mature trees occurred in the stands and the species is a noted gap opportunist (Boring et al., 1981; Phillips and Shure, 1990; Busing, 1995). Our findings illustrate the complexity of sub-canopy conditions that are present in the understory reinitiation phase of stand development and further emphasize why *Quercus* individuals are not able to outcompete shade-tolerant mesophytes in the regeneration layer.

5. Management Implications

In recent decades, there has been a fundamental philosophical change in the management of forest resources. Increasingly, managers, especially on public lands, are utilizing approaches that emulate natural ecological processes including natural disturbance events (O'Hara, 2001; Long, 2009; Franklin and Johnson, 2012; Hanson et al., 2012; Franklin and Johnson, 2013). When implementing a natural disturbance-based approach to forest management, natural disturbance patterns (e.g. scale, frequency, and magnitude of natural disturbance events) are emulated in silvicultural entries. For example, the size of a harvest created opening may be adjusted to approximate the size of a natural canopy disturbance event. The goal of natural disturbance-based management is not to mimic the actual disturbance event (i.e. trees are not typically felled by winching to emulate the effects of strong winds), but rather to use the effects of such events (e.g. the altered light regime) as models for individual and cumulative silvicultural treatments. Emulation of natural disturbance regimes is thought to restore or maintain ecosystem resilience, ecosystem function, and native forest biodiversity (Long, 2009). The success of this management approach requires clear and tangible guidelines that are based on quantitative data from stands that are situated in similar biophysical settings and are therefore appropriate analogues (Seymour et al., 2002; Franklin et al., 2007).

Intermediate treatments and regeneration treatments may be patterned after intermediate-scale wind events. The intermediate-scale disturbance documented in our study did not result in regeneration, but our results can be used to help design intermediate stand entries that emulate natural processes. For example, based on the quantitative data collected and analyzed here, we recommend managers that wish to mimic the effects of intermediate-scale wind disturbances aim to create canopy gaps that provide light levels of ca. 20% of full sunlight in the understory. Additionally, although canopy openness and gap fraction values were influenced by individuals in the midstory, to create conditions similar to those found at breast height a value of approximately 8–10% of full sunlight would be appropriate. The average percent basal area removed by the wind event in our study was 48%, so basal area retention of 35–50% would approximate the natural pattern. Mortality rates were highest for the genus *Quercus*, but this genus was the most abundant canopy tree and therefore, managers that wish to mimic a natural wind event should remove trees based on size and markets more than attempting to bias against certain taxa. This trend should allow managers to marry ecological goals with economic constraints based on market fluctuations more easily. Intermediate-scale wind disturbances do not affect stands uniformly, so rather than an even distribution of treatments throughout a stand in a regular pattern, managers may implement various even-aged treatments in patches thereby creating two or more age classes within a stand. To emulate spatial patterns of natural wind disturbance, managers might apply treatments in patches that exhibit different gradients of damage. Group selections, which serve as release and regeneration treatments and may include temporary or permanent leave trees, may be implemented in linear fashions if the goal is mimic tornado damage. Such an approach may take advantage of existing road networks (Seymour, 2005). A silvicultural system that manipulates neighborhoods rather than entire stands in a single entry may challenge the concept that silviculture is conducted at the stand scale; however, the stand should still be the logical operational unit of natural disturbance-based management (O'Hara and Nagel, 2013).

It is important to emphasize that it was not natural disturbance processes that created many of the contemporary *Quercus*-dominated stands that occur throughout the Central Hardwood Forest of the eastern US (Cowell, 1998; Foster et al., 2002). Thus, managers that wish to maintain *Quercus* dominance and adhere to a natural disturbance-based management approach will likely need to make concessions rather than following a true close-to-nature approach. Regeneration failure of *Quercus* has been widely reported across all but the most xeric site types throughout the Central Hardwood Forest (Abrams, 1992; Lorimer, 1993; Nowacki and Abrams, 2008; McEwan et al., 2011). Although variability exists at the species-level, *Quercus* are generally considered only moderately tolerant of shade and canopy disturbance events that increase insolation in the understory are required for regeneration (Dey, 2002). These canopy disturbances must be sufficiently large to provide adequate light levels, but not so large that they allow for the establishment of shade-intolerant species that can outcompete *Quercus* in high light environments (Runkle, 1985; Grayson et al., 2012). The natural intermediate-scale canopy disturbance event documented in this study was not sufficient to regenerate *Quercus* and other taxa moderately tolerant of shade. Similarly, Schweitzer and Dey (2011) noted that various intensities of regeneration treatments only ephemerally increased light levels in the understory for three years before pre-disturbance light levels returned. We hypothesized this was a function of the high density of shade-tolerant individuals in understory and midstory strata in stands in the understory reinitiation stage of development. Thus, in stands with a significant component of shade-tolerant mesophytes in the understory and where the management objective is to maintain *Quercus*, regeneration harvests should be implemented in conjunction with competition reduction measures such as fire or herbicide application (Loftis, 1990; Schweitzer and Dey, 2011; Hutchinson et al., 2012; Brose et al., 2013). Although competition removal may fall outside the historical range of variation, these actions may be essential to maintain *Quercus* dominance. In such instances, the natural disturbance events may be used to guide silvicultural treatments, but concessions would be made to ensure adequate *Quercus* stocking.

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