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Altered structural development and accelerated succession from intermediate-scale wind disturbance in *Quercus* stands on the Cumberland Plateau, USA

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ABSTRACT

Natural disturbances play important roles in shaping the structure and composition of all forest ecosystems and can be used to inform silvicultural practices. Canopy disturbances are often classified along a gradient ranging from highly localized, gap-scale events to stand-replacing events. Wind storms such as downbursts, derechos, and low intensity tornadoes typically result in disturbance that would fall near the center of this gradient and result in intermediate-scale disturbances. Despite their frequency and widespread occurrence, relatively little is known about how intermediate-scale disturbances influence stand development and succession. On 20 April 2011, the Sipsey Wilderness in Alabama was affected by an EF1 tornado with accompanying straight-line winds. In the third growing season after the disturbance, stands were sampled in a stratified subjective sampling design to evaluate the effects of intermediate-scale wind disturbance on structural and successional development of *Quercus* stands. We established 109 0.04 ha plots across a gradient of disturbance grouped into three classes, control (considered to represent pre-disturbance conditions using a space-for-time substitution), light, and moderate categories, to examine the effect of the intermediate-scale wind disturbance. Basal area was reduced from 25.7 m^2 ha^{-1} to 23.7 m^2 ha^{-1} and 15.3 m^2 ha^{-1} for light and moderate disturbance classes, respectively. Logistic regression revealed an increasing probability of mortality during wind disturbance with increasing tree diameter. This intermediate-scale disturbance increased intra-stand heterogeneity and altered the developmental pathway. The stands did not structurally resemble one of the four widely accepted stages of stand development. The disturbance also accelerated succession and released shade-tolerant taxa that were established in midstory and understory strata prior the event.

1. Introduction

All forest ecosystems are subject to disturbances that influence species composition and stand structure. Disturbances may therefore be strong controls on developmental and successional pathways in forest ecosystems. Canopy disturbances in forests are often classified according to their spatial extent and magnitude with discrete events falling along a gradient (Oliver and Larson, 1996). This disturbance classification gradient ranges from gap-scale events, highly localized disturbances that modify microenvironmental conditions only, at one endpoint to broad-scale and catastrophic events that result in stand replacement at the other (White and Pickett, 1985; Oliver and Larson, 1996; White and Jentsch, 2001). Disturbances that occur along the middle of the disturbance classification gradient, i.e. those that are too large to be labeled gap scale and too localized to be labeled broad scale, are considered to be intermediate-scale events (Cowden et al., 2014).

Interestingly, a dearth of research has been conducted to examine forest disturbances of the intermediate scale. As such, our understanding of the extreme events (i.e. those that occur near the endpoints of the disturbance classification gradient) and their impacts on forest ecosystems is advanced well beyond that of intermediary events (Seymour et al., 2002; Hanson and Lorimer, 2007. This paucity is notable because intermediate-scale disturbances occur more frequently than catastrophic events and disrupt larger portions of forest land than stand initiating or gap-scale disturbances (Fujita, 1978; Frelich and Lorimer, 1991; Foster and Boose, 1992; Jenkins, 1995; Trickel, 2002; Stueve et al., 2011). In the Eastern Deciduous Forest Formation of North America, the

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return interval of stand-wide canopy disturbance events ranges from ca. 30 to 50 years (Nowacki and Abrams, 1997; Ruffner and Abrams, 1998; Ziegler, 2002; Hart et al., 2012). The return interval for intermediate-scale disturbances is shorter than the lifespans of dominant taxa and much shorter than the return interval of catastrophic events in most temperate zone forests (Lorimer, 1989, 2001; D'Amato and Orwig, 2008; Stueve et al., 2011). Indeed, retrospective studies of old-growth forests in eastern North America have revealed that many of these systems experienced multiple intermediate-scale disturbances which had marked impacts on development and succession (e.g. Oliver and Stephens, 1977; Orwig et al., 2001; Fraver and White, 2005; Hart et al., 2008, 2012; Pederson et al., in press). Furthermore, research has indicated that the frequency of intermediate-scale disturbance in the Eastern Deciduous Forest Formation of North America may have declined over the past three centuries and this decline may in part explain widespread successional patterns throughout the region (Buchanan and Hart, 2012). Circumstantial evidence from the Northern Hardwood Forest of North America indicates that anthropogenic activity has diminished the ecological effects of these intermediate-scale disturbance events (Stueve et al., 2011).

Downbursts and tornadoes from convective storms, intense winds from cyclonic storms, topographically-induced windstorms, hurricanes, ice storms, insect attacks, and pathogens represent natural agents that may result in intermediate-scale disturbances in forest ecosystems (Canham and Loucks, 1984; Oliver and Larson, 1996; Peterson, 2000; Webb and Scanga, 2001; Lafon, 2006; Hjelmfelt, 2007; Hart et al., 2008). For example, approximately 1250 tornadoes occur annually in the USA alone, with 95% of these storms classed as EF0, EF1, or EF2 events (NCDC, 2013). These low intensity tornadoes are often not sufficiently powerful to result in catastrophic disturbance, but typically do remove more canopy trees than disturbance events classified as gap scale; thus, these storms often result in intermediate levels of disturbance (Peterson, 2007).

Unequivocally, the impacts of intermediate-scale disturbance on structural development and succession in deciduous forests are poorly understood (Seymour et al., 2002; Hanson and Lorimer, 2007; Fischer et al., 2013; Cowden et al., 2014). By quantifying the ways in which intermediate-scale disturbances modify species composition, stand structure, and developmental pathways, we can provide the information required to actively manage natural processes and to develop or refine silvicultural systems (Seymour et al., 2002; Franklin et al., 2007; Long, 2009). The overarching goal of our study was to examine the influence of intermediate-scale disturbance on the structural development and succession of a temperate deciduous forest. Specifically, our objectives were to: (1) quantify characteristics of stand structure and species composition across a gradient of storm damage that resulted in intermediate levels of forest disturbance, (2) evaluate the structural condition of the forest to determine if the disturbance resulted in acceleration or retrogression of stand development, and (3) document the impacts of the intermediate-scale disturbance on the successional status and trajectory of the forest. Our study on intermediate-scale wind disturbance may be used as a proxy for other top-down, intermediate-scale disturbances by using basal area reduction and percent canopy loss to quantify damage intensity and evaluate forest response.

2. Methods

2.1. Study area

This study was conducted on the Sipsey Wilderness within the William B. Bankhead National Forest in Alabama (34°20′N, 87°25′W; Fig. 1). The Sipsey Wilderness occurs on the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman, 1938). Topography is characterized by high relief with narrow ridges, steep slopes, and deep valleys (Smalley, 1979). The geology of the region is Pennsylvanian quartzose sandstone interspersed with layers of shale, siltstone, and coal (Szabo et al., 1988). Regionally, soils are strongly acidic, excessively drained, and somewhat shallow, ranging from 38 to 97 cm to bedrock (USDA SCS, 1959). The climate is classified as humid mesothermal (Thornthwaite, 1948) and is characterized by short, mild winters and long, hot summers. Mean annual precipitation is 149 cm with no distinct dry season (PRISM Climate Group, 2013). Mean temperatures for January and July are 5 °C and 26 °C, respectively. The average growing season is 220 days beginning in mid-March and ending in early-November.

Plant communities on the Cumberland Plateau are influenced largely by topography and factors associated with soil–water availability (Hinkle, 1989; Clatterbuck et al., 2006). Cumberland Plateau forests are recognized for having high plant species richness and landscape-level diversity (Hinkle et al., 1993). Braun (1950) classified this region as a transition zone between the Mixed Mesophytic Forest to the north and the *Quercus–Pinus* Forest to the south. However, true mixed mesophytic communities occur only in shaded coves and riparian areas. Stands may contain taxa that typically dominate at both higher and lower latitudes, and environmental gradients are steep (Hardin and Lewis, 1980; Richards and Hart, 2011; Parker and Hart, 2014). Zhang et al. (1999) developed a classification scheme that included 14 different ecological communities on the Sipsey Wilderness portion within the national forest. These community types ranged from xeric sites dominated by *Pinus virginiana* to mesic sites dominated by *Fagus grandifolia* and *Acer saccharum* to barren communities. *Quercus* was the most dominant genus in the Sipsey Wilderness and was a component of almost all community types (Hardin and Lewis, 1980; Zhang et al., 1999).

On 20 April 2011, an EF1 tornado embedded in a bow echo system affected Bankhead National Forest, damaging a number of stands in the Sipsey Wilderness. The tornado produced a recorded maximum 3 s wind gust of 153 kph and was accompanied by other straight-line winds with bursts between 130 and 145 kph (NWS, 2011). The most severe damage was concentrated in the path of the tornado and decreased in intensity with distance from the center of the storm. Within the Sipsey Wilderness, damage was sporadic and created a patchwork mosaic of blowdown areas.

2.2. Field methods

Field sampling was conducted June–July 2013 during the third growing season following the disturbance. Our sampling followed a stratified subjective scheme to adequately capture wind disturbed areas within the Sipsey Wilderness. To select study stands we created a map in ArcMap v. 10.0 from geo-referenced data provided by the USDA Forest Service that included quantitative information on stands (species composition and establishment year), compartments, the tornado damage path, roads, and established trails. Geo-referenced aerial photographs and USGS quadrangles were imported as basemaps and used to identify terrain features such as slope and aspect. Using this information and field reconnaissance, we subjectively selected stands that met the following criteria: (1) were *Quercus alba* dominated, (2) between 100 and 120 years of age, (3) fully contained within the Sipsey Wilderness, (4) directly affected by the 2011 tornado, (5) on generally west-facing slopes (which subjected them to the full range of wind damage from this storm), and (6) without an official record or noticeable indications of a prior broad-scale exogenous disturbance during stand development. We then determined the land type of the

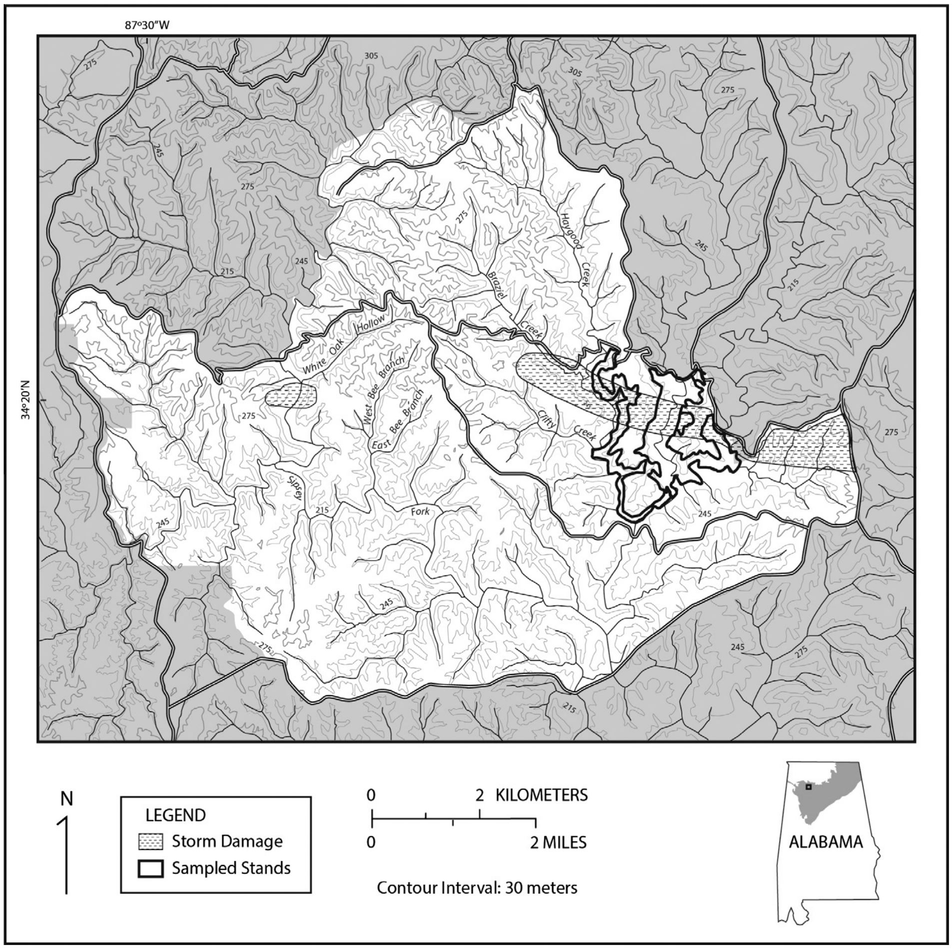

Fig. 1. Map of the Sipsey Wilderness, Alabama. The damage from the 2011 EF1 tornado is only shown for the Sipsey Wilderness and not the adjoining Bankhead National Forest. Shaded portion on Alabama inset map is the Cumberland Plateau physiographic province.

potential stands using the land classification system developed by Smalley (1979) to ensure that all sampled stands had the same biophysical setting. Within the selected stands we conducted a comprehensive inventory to quantify composition and structural conditions across the disturbance gradient. Undisturbed neighborhoods within each stand were considered controls, and we assumed that they represented pre-disturbance conditions using a space-for-time substitution. Plot centerpoints were established in the selected stands across one of three disturbance classes (control, light disturbance, or moderate disturbance) to ensure adequate spatial coverage and an even sampling distribution within stand boundaries using ArcMap. The waypoints were then entered into a handheld GPS receiver. In the field, we navigated to the pre-determined waypoints and assessed each plot in the context of surrounding stand conditions for the number of downed trees within or crossing through the plot and the proximity to the tornado path. Thus, we used a combination computer mapping and field observation to establish sampling points. Plots with three or more windthrown trees (i.e. individuals were considered windthrown if they were either uprooted so that the stem was less than 45° from the ground or if the bole was broken below the crown, sensu Canham et al., 2001) of ⩾20 cm dbh were classified as moderate disturbance ($n = 37$), and all other plots with visible wind damage were deemed to be light disturbance plots ($n = 52$). Control plots ($n = 20$) exhibited no visible evidence of disturbance from the storm.

A fixed-radius 0.04 ha overstory plot was placed at each pre-determined waypoint. All live stems ⩾5 cm diameter at breast height (dbh, 1.37 m high) were measured for dbh, recorded to species (except for *Carya*), and labeled as belonging to one of four crown classes: dominant, codominant, intermediate, or overtopped. Crown class was based on the amount of intercepted light and height in relation to the adjacent canopy (Oliver and Larson, 1996). The intermediate crown class was further subdivided for additional stand structural analyses: intermediate 1 (I1: <50% the height of residual canopy trees), intermediate 2 (I2: 50–75% the height of residual canopy trees), or intermediate 3 (I3: ⩾75% of residual canopy trees). Within the overstory plot, all dead woody stems ⩾5 cm dbh rooted within the plot were measured for diameter at 1.37 m above the root collar (estimated standing dbh), identified to the lowest possible taxonomic level, and classified as one of the following: an uprooted stem (dead stem with root network uplifted), a snapped stem (dead stem with bole broken below the crown), or a snag (standing dead stem with crown largely intact; Clinton et al., 1993; Yamamoto, 2000; Richards and Hart, 2011). Dead stems were also placed in one of four decay classes: class 1 (sound wood, bark intact, small to medium sized branches present); class 2 (sound to partially rotten wood, branch stubs firmly attached with only larger stubs present, some bark slippage); class 3 (substantially rotten wood, branch stubs easily pulled from softwood species, soft wood texture and would compact when wet); or class 4 (mostly rotten wood, branch stubs rotted down to log surface, bark no longer attached or absent, log oval or flattened in shape; adapted from Fraver et al., 2002). A single 10 m^2 regeneration plot was nested within each overstory plot at plot center where all stems <5 cm dbh were tallied, identified to the lowest taxonomic level, and classified as seedling (<1 m tall) or sapling (⩾1 m tall and >5 cm dbh).

2.3. Laboratory methods

Stems ⩾5 cm dbh were analyzed by standard descriptors of density (stems ha^{-1}), relative density (contribution to total stems), dominance ($m^2\ ha^{-1}$), relative dominance (contribution to total basal area), and relative importance (relative density + relative dominance). Seedlings and saplings were analyzed by density, relative density, frequency (number of plots on which the species occurred), and relative frequency (percent of plots the species occurred). Trees were categorized and tallied into 5 cm dbh classes and q-factors were calculated to evaluate the structural distribution of stems across disturbance classes (Nyland, 2002). To analyze additional regeneration and recruitment patterns, species were clustered into one of four taxonomic groups based on function: *Acer–Fagus*, *Quercus* spp., *Liriodendron tulipifera*, and others.

We used the decay classification of each dead tree to evaluate the effect of the intermediate-scale disturbance on stand basal area. Based on time since the disturbance, we assumed that trees killed by the April 2011 storm event were in the decay class 1 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 1 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 2011 storm event.

To determine if the intermediate-scale disturbance resulted in structural acceleration or regression, we used the methods of Hanson and Lorimer (2007) and classified the neighborhoods in each disturbance category of all sampled stands into one of four stand-size classes using the distribution of trees and basal area in four size classes (small trees (5–14.9 cm dbh), pole trees (15–29.9 cm dbh), sawtimber trees (30–44.9 cm dbh), or large sawtimber trees (⩾45 cm dbh) following the USDA Forest Inventory and Analysis guidelines (Bechtold and Patterson, 2005). Structural regression was defined as moving the structural distribution of a stand back to a prior stage of development (e.g. a sawtimber stand to a poletimber stand; Hanson and Lorimer, 2007). Structural acceleration was defined as advancing the structural distribution of a stand to a later stage of development.

Statistical comparisons were performed in SAS v. 9.3. One way analysis of variance (ANOVA) was used to detect differences in means across disturbance classes for all analyses. A Scheffe post hoc test was used to distinguish means when significance ($P < 0.05$) was found. Data were tested for normality using a Kolmogorov–Smirnov test and through histograms. When distributions did not conform to normal distributions and homoscedasticity, data were log-, square root-, or rank-transformed to meet the assumptions for ANOVA. Logistic regression was used to predict stem mortality in both wind disturbance classes by comparing dbh for live stems to dbh for dead stems in decay class 1.

3. Results

3.1. Structural analysis

Basal area for control, light, and moderate disturbance classes was 25.7, 23.7, and 15.3 $m^2\ ha^{-1}$, respectively (Table 1). Moderate mean plot basal area was significantly lower than the other two classes ($P < 0.001$ for both comparisons), with no difference between control and light disturbance classes. The control class had the highest density of stems ⩾5 cm dbh with 771 stems ha^{-1} followed by light and then moderate classes with 666 and 531 stems ha^{-1}, respectively.

The size distribution resembled a reverse J shape in control, light and moderate classes with mean q-factors of 1.7, 1.5, and 1.7, respectively (Fig. 2). The *Acer–Fagus* and others groups exhibited the reverse J shape, indicating continuous regeneration and recruitment into larger diameter classes. *Quercus* spp. was the only group to display the uni-modal distribution that typifies a failure to regenerate.

Total basal area of large woody debris (all dead stems ⩾5 cm dbh) for control, light, and moderate classes was 3.9, 9.6, and 17.1 $m^2\ ha^{-1}$, respectively (Table 2). Overall densities for large woody debris were 89, 142, and 250 stems ha^{-1} for control, light, and moderate classes, respectively. Decay class 1 basal area was 0.33, 6.44, and 14.08 $m^2\ ha^{-1}$ for control, light, and moderate classes, respectively. When classes were tested on a plot basis, ANOVA revealed that the mean basal area per plot was unique to each class (Table 3). Quadratic mean diameter (QMD) for decay class 1 was 13, 33, and 30 cm for control, light, and moderate classes, respectively. An ANOVA test revealed significant differences in means per plot between all classes. The median diameter for control, light, and moderate damage categories was 10, 11, and 9 cm, respectively. Trees from all size classes were removed by the storm in both disturbance categories, but a higher proportion of stems came from larger size classes (Fig. 2). Logistic regression of tree fate (live stems v. dead stems in decay class 1) revealed an increasing probability of mortality with diameter for both disturbance classes and results were significant ($P < 0.001$; Fig. 3). In the light disturbance category, the storm reduced basal area from 30.4 to 24.0 $m^2\ ha^{-1}$ (a 21% reduction). Basal area was reduced from 29.4 to 15.3 $m^2\ ha^{-1}$ in the moderate category, a 48% reduction. Basal area lost (i.e. removed by the storm) was significantly different ($P < 0.05$) between all disturbance classes (Table 3). When divided into product classes, the sawtimber tree class showed the greatest change in density, from 93 stems ha^{-1} in control to 33 stems ha^{-1} in the moderate disturbance class (a 65% reduction; Fig. 4). Also, basal area of the sawtimber tree class of the moderate damage category was reduced 75% compared to the control category, which was the greatest of any class (Fig. 4). Despite these changes, all neighborhoods in all stands still met the criteria for the sawtimber stand classification. Thus, the storm event did not change the stand-size classification, which we used to test for acceleration or regression of structural development stage.

Most stems killed by the storm were snapped; the light and moderate category had 53% and 55% of decay class 1 stems snapped, respectively (Fig. 5). Modes of death in decay class 1 in the control class were 74% snag, 16% snapped, and 11% uprooted. The light disturbance class had 53% snapped, 23% snag, and 23% uprooted stems in decay class 1. The moderate disturbance class had 55% snapped, 35% uprooted, and 10% snag stems in decay class 1.

3.2. Compositional analysis

In all three disturbance classes, the most important taxa were *Q. alba*, *Ostrya virginiana*, and *Carya* spp. *O. virginiana* ranked first in relative density in all disturbance classes representing 27%, 19%, and 27% of all stems for control, light and moderate classes, respectively (Table 1). *A. saccharum* decreased in importance in both wind damaged classes when compared to the control class. Total *Quercus* importance decreased with increasing storm damage: control, light, and moderate importance of *Quercus* was 75.6%, 69.8%, and 57.6%, respectively. *F. grandifolia* increased following light disturbance from 8.0% to 17.2%, but decreased slightly with moderate disturbance.

Table 1
Density, relative density, dominance, relative dominance, and relative importance (relative density + relative dominance) measures for all live stems ⩾5 cm dbh across three disturbance classes in a *Quercus alba* forest on the Sipsey Wilderness, Alabama.

Species	Density (stems/ha)			Relative density (%)			Dominance (m²/ha)			Relative dominance (%)			Relative importance (%)		
	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate
Acer rubrum L.	9	15	12	1.1	2.3	2.3	0.1	0.1	0.1	0.3	0.4	0.4	1.4	2.7	2.7
Acer saccharum Marshall	95	43	46	12.3	6.5	8.7	2.0	1.0	0.8	7.8	4.1	5.0	20.1	10.6	13.6
Carpinus caroliniana Walter	8	6	16	1.0	0.0	3.1	0.0	0.0	0.1	0.2	0.1	0.4	1.1	–	3.5
Carya spp. Nutt.	65	51	41	8.4	7.7	7.6	3.7	2.5	2.2	14.3	10.7	14.4	22.8	18.4	22.1
Cercis canadensis L.	23	5	11	2.9	0.7	2.0	0.1	0.0	0.0	0.5	0.1	0.2	3.4	0.8	2.3
Cornus florida L.	31	34	18	4.1	5.1	3.3	0.1	0.2	0.1	0.6	0.7	0.5	4.6	5.7	3.8
Fagus grandifolia Ehrh.	44	65	38	5.7	9.7	7.1	0.6	1.8	0.8	2.3	7.4	5.1	8.0	17.2	12.2
Frangula caroliniana (Walter) A. Gray	11	0	1	1.5	0.1	0.3	0.0	0.0	0.0	0.2	0.0	0.0	1.6	0.1	0.3
Fraxinus americana L.	13	8	11	1.6	1.2	2.0	0.2	0.5	0.3	0.8	2.0	1.9	2.5	3.1	3.9
Juglans nigra L.	4	0	–	0.5	0.1	–	0.3	0.1	–	1.0	0.3	–	1.5	0.4	–
Juniperus virginiana L.	5	6	1	0.6	0.9	0.3	0.1	0.3	0.0	0.5	1.3	0.3	1.1	2.2	0.5
Liriodendron tulipifera L.	11	14	7	1.5	2.2	1.4	1.2	1.9	0.3	4.8	8.0	2.1	6.2	10.2	3.5
Magnolia acuminata (L.) L.	9	11	9	1.1	1.7	1.8	0.3	0.3	0.2	1.2	1.5	1.5	2.4	3.1	3.3
Magnolia macrophylla Michx.	18	61	49	2.3	9.2	9.3	0.1	0.5	0.4	0.4	2.0	2.5	2.6	11.2	11.8
Nyssa sylvatica Marshall	34	45	28	4.4	6.7	5.2	0.3	0.5	0.4	1.3	2.0	2.6	5.7	8.8	7.8
Ostrya virginiana (Mill.) K. Koch	209	124	142	27.1	18.6	26.7	1.2	0.7	0.7	4.6	2.9	4.6	31.6	21.5	31.3
Others[1]	8	3	3	1.0	1.4	0.6	0.0	0.0	0.0	0.1	0.1	0.2	0.9	0.6	0.6
Oxydendrum arboreum (L.) DC.	4	16	5	0.5	2.4	1.0	0.0	0.2	0.1	0.2	1.0	0.8	0.6	3.4	1.8
Pinus echinata Mill.	–	1	–	–	0.2	–	–	0.2	–	–	0.7	–	–	0.9	–
Pinus taeda L.	1	5	5	0.2	0.8	1.0	0.5	0.4	1.7	2.0	1.8	10.8	2.1	2.6	11.8
Pinus viriginiana Mill.	–	1	–	–	0.2	–	–	0.1	–	–	0.4	–	–	0.6	–
Prunus serotina Ehrh.	4	8	2	0.5	1.2	0.4	0.0	0.1	0.0	0.2	0.3	0.3	0.6	1.5	0.7
Quercus alba L.	105	95	53	13.6	14.3	9.9	10.6	9.0	5.4	41.4	38.2	35.4	55.0	52.5	45.3
Quercus falcata Michx.	3	4	4	0.3	0.6	0.8	0.3	0.4	0.6	1.2	1.5	3.8	1.5	2.1	4.6
Quercus muehlenbergii Engelm.	20	2	4	2.6	0.4	0.8	1.2	0.1	0.3	4.5	0.5	1.7	7.1	0.9	2.5
Quercus prinus L.	15	20	5	1.9	3.0	0.9	0.8	1.2	0.4	3.1	5.0	2.8	5.0	8.0	3.7
Quercus rubra L.	8	6	1	1.0	0.9	0.3	1.4	1.2	0.1	5.4	5.0	0.6	6.4	5.9	0.9
Quercus stellata Wangenh.	1	1	1	0.2	0.2	0.1	0.1	0.1	0.1	0.4	0.3	0.5	0.5	0.5	0.6
Sassafras albidum (Nutt.) Nees	–	3	1	–	0.4	0.3	–	0.1	0.0	–	0.2	0.0	–	0.7	0.3
Tilia americana L.	–	1	2	–	0.1	0.4	–	0.1	0.0	–	0.5	0.2	–	0.6	0.6
Ulmus alata Michx.	10	5	10	1.3	0.7	1.9	0.1	0.1	0.1	0.5	0.6	0.4	1.8	1.3	2.4
Ulmus americana L.	–	2	2	–	0.3	0.4	–	0.1	0.1	–	0.5	0.8	–	0.8	1.2
Ulmus rubra Muhl.	8	1	1	1.0	0.2	0.3	0.1	0.0	0.0	0.5	0.0	0.1	1.5	0.2	0.4
Total	771	666	531	100.0	100.0	100.0	25.7	23.7	15.3	100.0	100.0	100.0	200.0	200.0	200.0

[1] Others category consists of species with all importance values less than 0.05% and includes *Rhamnus cathartica* L., *Morus rubra* L., *Ilex opaca* Aiton, *Aesculus pavia* L., *Amelanchier arborea* (Michx. f.) Fernald, *Asimina triloba* (L.) Dunal, *Betula lenta* L., and *Acer negundo* L.

Q. alba had the highest large woody debris relative density and relative dominance in all three disturbance classes. In the control class, the highest relative densities in large woody debris were *Q. alba*, *Juniperus virginiana*, and *Quercus rubra*. The highest relative dominances in large woody debris were *Q. alba*, *Q. rubra*, and *L. tulipifera*. In the light disturbance class, *Q. alba*, *Carya* spp., and *P. virginiana* had the highest relative densities of large woody debris. *Q. alba*, *O. virginiana*, and *Carya* spp. had the highest relative densities of large woody debris in the moderate disturbance class. The light and moderate categories were similar in rankings for relative dominance: *Q. alba* ranked the highest, followed by *Carya* spp. and *Q. rubra*. No shade-tolerant species had a relative density or relative dominance over 8%, with the exception of *O. virginiana* in the moderate class (15%).

In decay class 1, *Quercus* spp. comprised a larger proportion of stems in the light disturbance (34%) than in moderate disturbance (24%). Similarly, *L. tulipifera* percentages slightly declined with increasing disturbance with 4% and 3% for light and moderate classes, respectively. *Quercus* and *Carya* increased in overall density in decay class 1, but *Acer*/*Fagus* were not as well represented comparatively (Fig. 6).

3.3. Regeneration

Seedling density was 18,250 ha^{-1} in control, 17,883 ha^{-1} in light, and 16,678 ha^{-1} in moderate disturbance classes (Table 4). In the control class, the species with the highest relative density were *A. saccharum* and *Fraxinus americana*, followed by *Q. alba*, *Acer rubrum*, and *Q. rubra*. In the light damage class, *Q. alba* had the highest seedling density followed by *A. saccharum* and *A. rubrum*. In moderate damage, *Viburnum acerfolium*, *A. saccharum*, and *Ligustrum sinense* had the highest seedling densities. The most frequently occurring seedling species on both control and moderate damage plots was *A. saccharum*, whereas *A. rubrum* was most frequent on light damage plots. *Q. alba* seedlings occurred on 60%, 58%, and 46% of plots in control, light, and moderate classes, respectively.

Total sapling density was 5890, 6922, 10,461 ha^{-1} for control, light, and moderate classes, respectively (Table 5). Unlike seedlings, sapling densities increased with disturbance intensity. The highest relative densities in the control were *Acer rubrum* and *O. virginiana*, followed by *L. sinense* and *F. grandifolia*. In the light disturbance class, *O. virginiana* had the highest relative density followed by *A. rubrum* and *A. saccharum*. In the moderate disturbance class, *O. virginiana* and *A. saccharum* tied for the highest relative density followed by *A. rubrum* and *Cornus florida*. Few *Quercus* individuals were present in the sapling size class for all disturbance categories. Relative frequency values for *Quercus* spp. were also low, as all *Quercus* spp. occurred on less than 6.0% of plots except for *Q. rubra* in the moderate damage class.

4. Discussion

4.1. Structural analysis

The relationship between size classes (q-factor) was not altered between control and moderate disturbance classes. The q-factor was only slightly lower in the light disturbance class compared

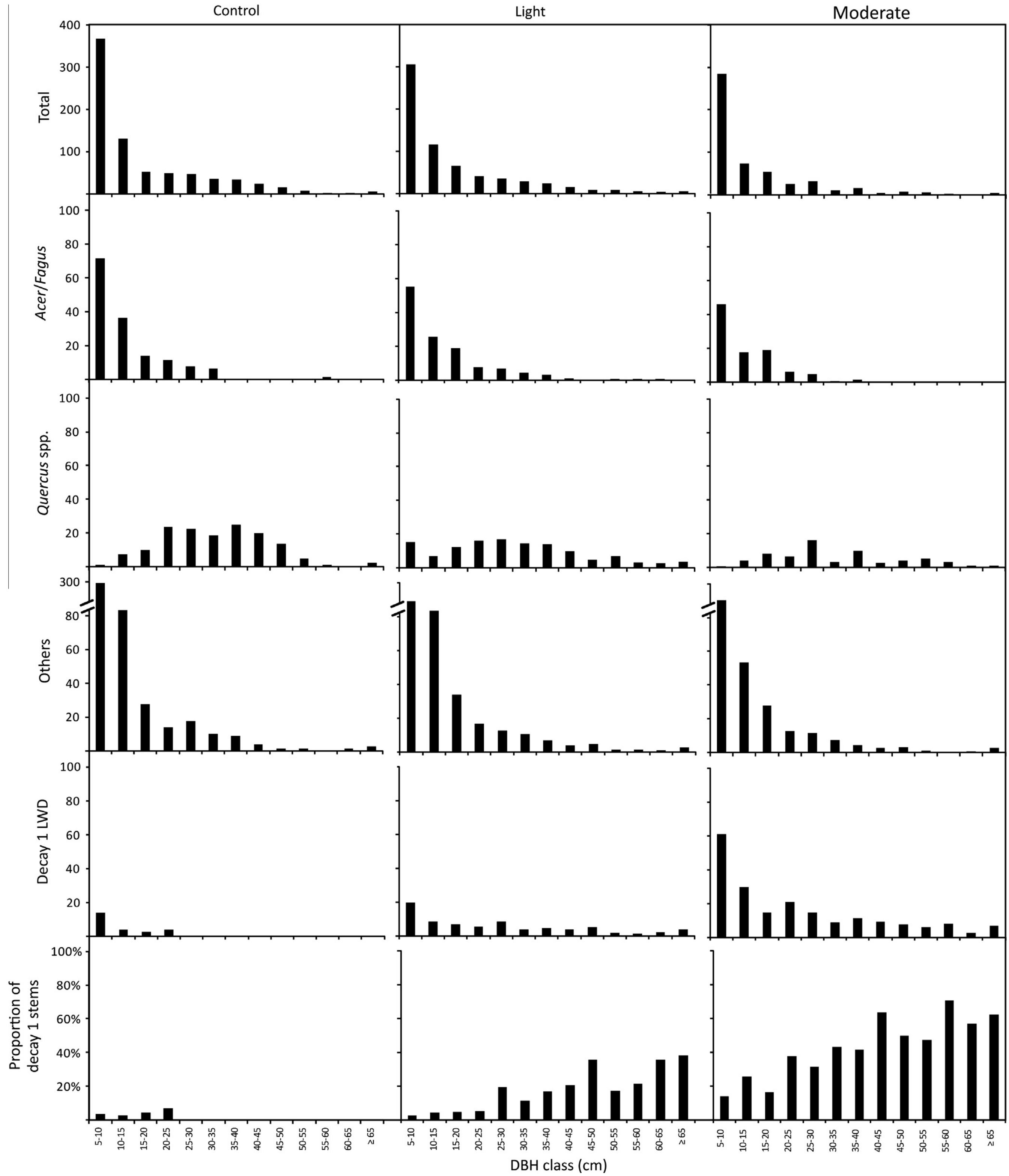

Fig. 2. Density of stems ha^{-1} in 5 cm diameter bins across three disturbance classes in a *Quercus alba* forest on the Sipsey Wilderness, Alabama. Proportion of dead stems ⩾5 cm dbh in decay class 1 was determined by comparing decay class 1 density to total density in each respective class.

to the control category. Trees from all size classes were removed by the storm in both disturbance categories, but larger size classes exhibited higher rates of mortality compared to smaller size classes. This pattern was also noted following an intermediate-scale disturbance in the Northern Hardwood Forest (Hanson and Lorimer, 2007). Although we documented significant relationships between tree diameter and mortality, the actual drivers of wind-induced removal were likely tree height and crown volume. Increased canopy height and crown volume result in increased wind drag, which can uproot or snap trees if a critical threshold is exceeded (Foster and Boose, 1992; Peterson and Rebertus, 1997; Peterson, 2000; Rich et al., 2007). Thus, we hypothesized

Table 2
Density, relative density, dominance, and relative dominance for all large woody debris (⩾5 cm estimated standing dbh) across three disturbance classes in a *Quercus alba* forest on the Sipsey Wilderness, Alabama.

Species	Density (stems/ha)			Relative density (%)			Dominance (m^2/ha)			Relative dominance (%)		
	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate	Control	Light	Moderate
Acer rubrum	–	2.4	0.7	–	1.7	0.3	–	0.0	0.0	–	0.1	0.0
Acer saccharum	6.3	2.4	14.9	7.0	1.7	6.0	0.1	0.1	0.4	1.9	0.6	2.5
Amelanchier arborea	–	–	1.4	–	–	0.5	–	–	0.0	–	–	0.0
Betula lenta	–	–	0.7	–	–	0.3	–	–	0.0	–	–	0.0
Carpinus caroliniana	–	–	3.4	–	–	1.3	–	–	0.0	–	–	0.1
Carya spp.	5.0	17.3	36.0	5.6	12.2	14.4	0.3	1.3	2.9	8.1	13.4	16.7
Cercis canadensis	3.8	3.4	3.4	4.2	2.4	1.3	0.0	0.0	0.0	0.4	0.2	0.2
Cornus florida	1.3	7.2	5.4	1.4	5.1	2.2	0.0	0.0	0.0	0.1	0.4	0.2
Fagus grandifolia	1.3	3.8	5.4	1.4	2.7	2.2	0.0	0.8	0.6	0.1	8.3	3.7
Frangula caroliniana	1.3	–	–	1.4	–	–	0.0	–	–	0.1	–	–
Fraxinus americana	2.5	–	4.7	2.8	–	1.9	0.0	–	0.3	0.5	–	1.8
Juglans nigra	–	–	0.7	–	–	0.3	–	–	0.1	–	–	0.4
Juniperus virginiana	12.5	10.6	11.8	14.1	7.4	4.7	0.3	0.2	0.3	8.4	2.1	1.6
Liriodendron tulipifera	5.0	4.8	6.1	5.6	3.4	2.4	0.6	0.4	1.0	14.5	3.6	6.1
Magnolia acuminata	–	0.5	4.1	–	0.3	1.6	–	0.0	0.2	–	0.1	1.1
Magnolia macrophylla	5.0	3.8	16.9	5.6	2.7	6.7	0.1	0.0	0.2	2.5	0.3	1.0
Nyssa sylvatica	1.3	3.8	8.8	1.4	2.7	3.5	0.0	0.0	0.2	0.8	0.5	0.9
Ostrya virginiana	2.5	6.7	37.9	2.8	4.7	15.1	0.0	0.0	0.2	0.4	0.3	1.3
Oxydendrum arboreum	–	4.8	4.1	–	3.4	1.6	–	0.1	0.2	–	0.6	1.5
Pinus taeda	5.0	10.1	6.1	5.6	7.1	2.4	0.2	0.7	1.6	4.4	7.2	9.4
Pinus virginiana	1.3	11.5	0.7	1.4	8.1	0.3	0.0	0.8	0.1	0.5	8.5	0.5
Prunus serotina	1.3	2.9	1.4	1.4	2.0	0.5	0.0	0.0	0.1	0.5	0.5	0.3
Quercus alba	18.8	27.9	44.2	21.1	19.6	17.6	1.1	3.3	5.3	29.2	33.9	31.1
Quercus falcata	2.5	1.0	4.7	2.8	0.7	1.9	0.1	0.1	0.4	3.2	1.2	2.5
Quercus muehlenbergii	2.5	1.0	1.4	2.8	0.7	0.5	0.1	0.0	0.0	2.2	0.5	0.2
Quercus prinus	2.5	6.7	4.7	2.8	4.7	1.9	0.0	0.6	0.9	1.2	5.8	5.1
Quercus rubra	7.5	6.7	14.4	8.5	4.7	5.8	0.8	1.0	1.7	21.0	10.5	9.9
Quercus stellata	–	1.4	0.7	–	1.0	0.3	–	0.1	0.0	–	0.8	0.2
Quercus unidentified	–	1.0	2.0	–	0.7	0.8	–	0.0	0.2	–	0.4	1.0
Sassafras albidum	–	0.5	0.7	–	0.3	0.3	–	0.0	0.0	–	0.0	0.0
Tilia americana	–	–	0.7	–	–	0.3	–	–	0.0	–	–	0.1
Ulmus alata	–	–	2.0	–	–	0.8	–	–	0.1	–	–	0.3
Vaccinium arboreum Marshall	–	–	0.7	–	–	0.3	–	–	0.0	–	–	0.0
Total	88.8	142.3	250.5	100.0	100.0	100.0	3.9	9.6	17.1	100.0	100.0	100.0

Table 3
Mean basal area measures and quadratic mean diameter ± SE across three disturbance classes in a *Quercus alba* forest on the Sipsey Wilderness, Alabama. Values with different letters indicate differences at $P < 0.05$.

Parameter	Control	Disturbance class	
		Light	Moderate
Live BA (m^2 0.04 ha $plot^{-1}$)	1.02 ± 0.06 a	0.96 ± 0.04 a	0.61 ± 0.06 b
Live BA (m^2 ha^{-1})	25.6	24.0	15.3
Decay class I BA (m^2 0.04 ha $plot^{-1}$)	0.01 ± 0.00 a	0.26 ± 0.02 b	0.56 ± 0.05 c
Decay class I BA (m^2 ha^{-1})	0.33	6.44	14.08
% BA removed in decay class 1	1.49 ± 0.40 a	21.06 ± 1.90 b	48.07 ± 3.16 c
Quadratic mean diameter (cm) of live trees	20.75 ± 0.76 ab	21.59 ± 0.61 a	18.77 ± 0.67 b
Quadratic mean diameter (cm) of decay class I	8.23 ± 1.67	33.37 ± 1.91	30.06 ± 1.34

diameter was only related to mortality because of the autocorrelation between diameter and tree height and crown volume (Peterson, 2000).

The percentage of stems removed decreased by crown class; dominant trees were the most susceptible to wind damage, followed by codominant, I3, I2, I1, and finally overtopped classes. We speculated that wind damage will blow down trees in the canopy first then affect lower strata of the stand as overstory layers are removed and subcanopy trees are exposed to damaging winds and falling overstory trees. Indeed, logistic regression of mortality compared to diameter exhibited a sharp increase in mortality until ca. 20 cm dbh. This value approximates the mean diameter of the I3 crown class. Thus, we noted that canopy trees were more likely to be damaged than intermediate stems and that the likelihood of mortality increased abruptly between intermediate and canopy crown positions. QMD of moderate and light disturbance classes differed significantly, but neither of the wind disturbed classes was significantly different from the control. The larger QMD in the light disturbance class may indicate that larger trees are the most prone to blow down in low to moderate windstorms, but we speculated that such a small difference in diameter is not meaningful although statistically significant (ca. 2 cm difference).

The size distributions of all trees in each disturbance category resembled the reverse J shape, indicating continuous regeneration and recruitment of smaller size classes. When divided into taxonomic groups, the diameter distributions were quite different. In the control class, *Quercus* spp. exhibited a bell-shaped frequency distribution, therefore density of small stems was likely insufficient to maintain *Quercus* dominance. In contrast, the *Acer*/*Fagus* group was well represented in the small sizes and displayed the reverse J shape distribution. This pattern is typical of *Quercus* stands throughout the Central Hardwood Forest (McEwan et al., 2011; Hart et al., 2012). Indeed, *Quercus* stands across the eastern United States appear to be transitioning to dominance by more

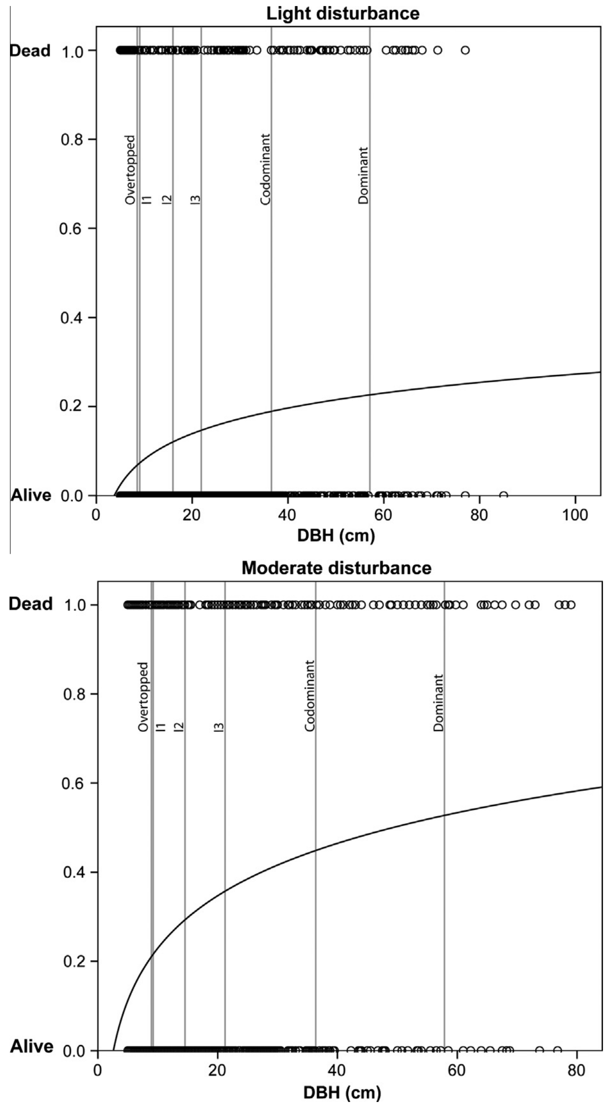

Fig. 3. Logistic regression of mortality for all live stems (alive) and all dead stems in decay class 1 (dead) ⩾5 cm dbh in light and moderate disturbance classes of wind damaged areas on the Sipsey Wilderness, Alabama. Gray vertical lines illustrate the mean diameter of living trees in each crown class category.

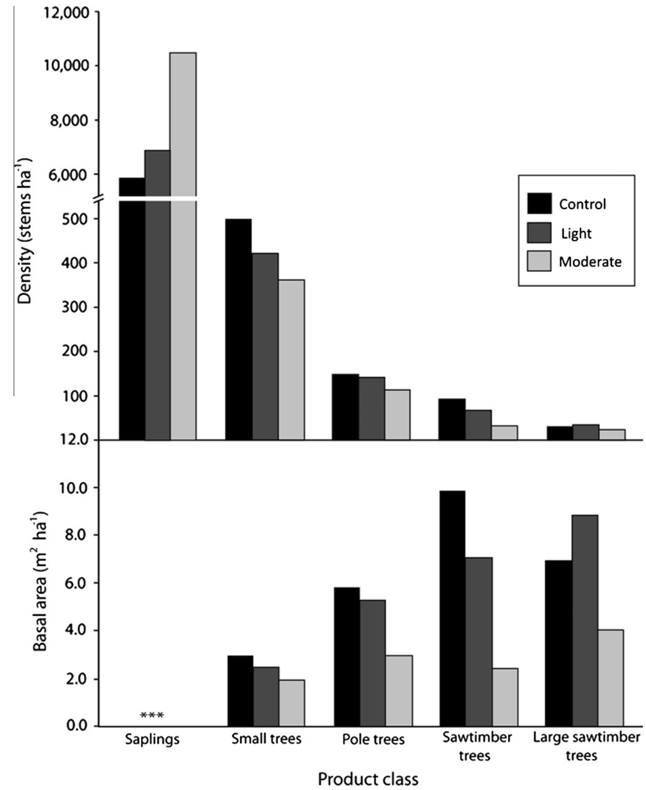

Fig. 4. Density and basal area for saplings (⩾1 m tall and >5 cm dbh), small trees (5–15 cm dbh), pole trees (15–30 cm dbh), sawtimber (30–45 cm dbh), and large sawtimber (⩾45 cm dbh) in three disturbance classes on the Sipsey Wilderness, Alabama. ***Saplings were not measured for basal area.

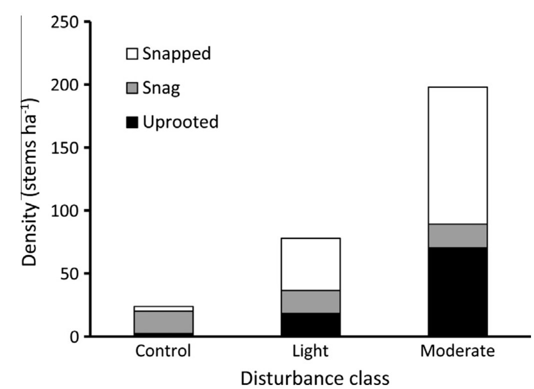

Fig. 5. Mode of death and density of dead stems ⩾5 cm dbh in decay class 1 in three disturbance classes on the Sipsey Wilderness, Alabama.

shade tolerant taxa, principally *Acer* spp. (i.e. the *Quercus*-to-*Acer* phenomenon; Lorimer, 1984; Abrams, 2005; Nowacki and Abrams, 2008; Fei et al., 2011; McEwan et al., 2011; Hart et al., 2012).

Despite the sawtimber tree product class being removed at the greatest proportion, the wind damage did not result in a reclassification of any stands to a category other than sawtimber (Bechtold and Patterson, 2005). This may be primarily explained by the nature of high-intensity wind events as such storms may result in a mosaic of blowdown areas of varying patch sizes within each stand. Although we did not note significant differences in most structural parameters evaluated along the disturbance gradient, the storm event did increase intra-stand structural heterogeneity (O'Hara and Nagel, 2013). Each stand affected by the storm contained an array of damage including patch blowdowns with few standing trees, single and multi-treefall gaps, and clusters of undamaged trees within the broader matrix of disturbance. At the stand scale, the non-uniform distribution of damage led us to conclude the resultant stand structures were outside of the four distinct stages of stand development as described by Oliver and Larson (1996) and Johnson et al. (2009). We suggest the intermediate-scale disturbance did not regress or advance the stands along the linear model of development, but rather created unique structural conditions that do not fit within one of the four stages of development. The "mixed stage" of stand development depicted by Johnson et al. (2009) following an incomplete stand-scale disturbance best embodies the structural state of the resultant stands affected by this wind disturbance.

New research is needed to analyze the spatial dynamics of damage resulting from windstorms that allows for intra-stand analyses so that variability can be captured at a sub-stand scale. Stands in the "mixed stage" may follow alternate developmental pathways, and thus warrant further research to quantify the structural development following this stage. Because natural disturbances are

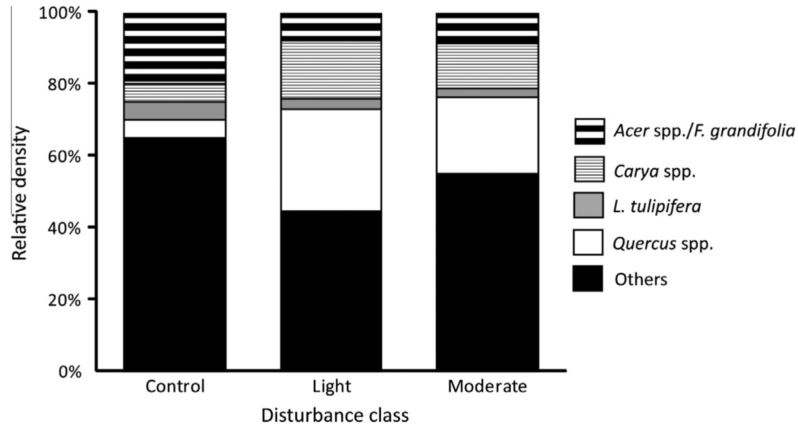

Fig. 6. Relative density of dead stems ⩾5 cm dbh in decay class 1 in three disturbance classes on the Sipsey Wilderness, Alabama.

stochastic, an undefined endpoint may be more suitable than a linear model of development; that is to say, a web-based model with interconnected stages may describe the development of stands in the "mixed stage" better than a deterministic linear model. Further quantification and characterization of the "mixed stage" and its development through time is needed to determine if such stands will return to the traditional model of development, and therefore be placed into one of the four discrete stages, or if such stands will remain entrenched in the altered pathway.

4.2. Compositional analysis

The storm did not allow for recruitment of moderately shade-tolerant species to larger size classes, but favored later-successional, shade-tolerant individuals already established in midstory and understory positions. Following intermediate-scale wind disturbance, *Acer* increased in dominance and *Quercus* declined thus hastening the *Quercus*-to-*Acer* transition. No species-specific mortality trends were noted in our study. Some authors have noted species-specific mortality trends following wind disturbance (Everham and Brokaw, 1996; Canham et al., 2001), but others have found the probability of blowdown to be more dependent upon canopy position rather than species (Peterson, 2007; Rich et al., 2007), which appeared to be the case in the forest studied here. *A. saccharum* large woody debris was not common despite its high live-stem importance value. We suggest this may be a function of height, as *A. saccharum* was not found in a dominant canopy position in any control plot. Similarly, we did not find any shade-tolerant, mesophytic species to be more important in large woody debris than in the live trees except for *Cercis canadensis*. In a tandem study, Cowden et al. (2014) found that PAR levels increased in the midstory and understory following the canopy disturbance and individuals in those strata were released. The successional trajectory of a stand may be strongly influenced by its stage of development. During the understory reinitiation phase of development, the understory of *Quercus*-dominated stands often contain a high density of shade-tolerant mesophytic species and low densities of *Quercus* advanced reproduction. The intermediate-scale wind disturbance documented here removed canopy individuals and released those in midstory and understory positions, therefore accelerating succession. These findings are consistent with the disturbance-mediated accelerated succession scenario proposed by Abrams and Scott (1989) that stated a disturbance event, whether natural or anthropogenic, occurring during understory reinitiation will favor a composition of shade-tolerant taxa in the stand.

Successional acceleration following wind disturbance has been found in other studies, for example, Arevalo et al. (2000) for *Pinus strobus* L. and *Quercus ellipsoidallis* E.J. Hill stands in central Minnesota, Holzmueller et al. (2012) for mixed *Quercus* stands in southern Illinois, and Hanson and Lorimer (2007) evaluated *Tsuga Canadensis* (L.) Carr.-northern hardwoods stands in northern Wisconsin. Disturbance during different stages of stand development may affect differently the successional trajectory of the stand. The stands sampled in this study were in the understory reinitiation phase of stand development, which is typical of most *Quercus* stands in the Central Hardwood Forest. This disturbance killed canopy individuals (mostly *Quercus*) while releasing understory and midstory individuals (mostly *Acer*). We posit the wind disturbance affected the stand based on its structural assemblage, not based on differential susceptibility to wind damage.

4.3. Regeneration

The seedling and saplings layers were comprised mostly of shade-tolerant species, primarily *O. virginiana* and *Acer* spp. The canopy disturbance did not create sufficient light in the understory for the establishment or recruitment of shade-intolerant or moderately shade-tolerant taxa such as *Quercus* and *Carya* (Cowden et al., 2014). Indeed, widespread *Quercus* regeneration failure has been noted across the Central Hardwood Region (Lorimer, 1984; Abrams, 2005; Nowacki and Abrams, 2008; Fei et al., 2011; Hart et al., 2012). *Quercus* saplings occurred in low density and frequency, despite the high density and relative frequency of *Quercus* seedlings in all classes. The failure of *Quercus* seedlings to recruit into the sapling size class has been widely documented and coined the "*Quercus* bottleneck." Abundant shade-tolerant seedlings and saplings such as *Acer* spp. and *O. virginiana* were documented in the stands studied here, likely resulting in low *Quercus* sapling density and inhibition of *Quercus* recruitment from seedling to sapling size classes (Lorimer et al., 1994). Thus, *Quercus* are not in competitive positions to take advantage of newly available growing space that resulted from canopy disturbance. This disturbance affected primarily canopy individuals, and therefore made available new growing space for the recruitment of individuals established in the midstory and understory.

Low *Quercus* densities in small diameter classes are primarily attributed to competition from shade-tolerant seedlings and saplings (Lorimer et al., 1994). Recruitment of subcanopy *Quercus* to canopy positions typically requires that the gap size be at least as large as the surrounding canopy trees are tall (Dey, 2002). Gap-scale disturbances in secondary *Quercus* stands often do not meet this 1:1 ratio (Hart and Grissino-Mayer, 2009; Richards and Hart, 2011). In the third growing season following disturbance in

Table 4
Density, relative density, frequency, and relative frequency for all seedlings (<1 m height, ⩽5 cm dbh) in three disturbance classes on the Sipsey Wilderness, Alabama. Frequency is the number of plots on which each species occurred by disturbance class, and relative frequency is the percent of plots on which each species occurred by disturbance class.

Species	Density			Relative density			Frequency			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 L.	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 Lour.	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 Marshall	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 Aiton	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 Michx.	–	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 (L. f.) Medik.	–	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 L.	–	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 L.	–	–	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	—	—	—	—	—	—

these stands, Cowden et al. (2014) found that understory PAR percentages were below the 20–50% thresholds required for *Quercus* (Dey, 2002), despite basal area reductions being within these bounds for both light and moderate disturbance classes. We hypothesized the increased light was captured by a growth release of shade-tolerant individuals that were established in midstory and understory positions following the canopy disturbance (Lorimer et al., 1994). Additionally, we attribute the lack of *Quercus* saplings to increased competition from established shade-tolerant individuals in the understory, preventing recruitment from seedlings to saplings. The successional trajectory of a stand may be significantly impacted by the stage of stand structural development in conjunction with the type of disturbance. In this study, primarily canopy individuals were killed by the storm, but advanced reproduction in subcanopy strata were able to respond to increased sunlight which precluded establishment of new seedlings. Thus, a top-down disturbance during the understory reinitiation phase might be only able to accelerate the *Quercus*-to-*Acer* transition in the Central Hardwood Forest.

5. Management implications

Forest managers, especially those of public lands, are increasingly interested in the use of silvicultural practices that emulate the effects of natural disturbances (O'Hara, 2001; Seymour et al., 2002; Franklin et al., 2007; Long, 2009; O'Hara and Nagel, 2013). The natural disturbance-based approach to forest management seeks to satisfy objectives by implementing silvicultural systems that are based to some extent on natural disturbance processes,

Table 5
Density, relative density, frequency, and relative frequency for all saplings (>1 m height, ⩽5 cm dbh) in three disturbance classes on the Sipsey Wilderness, Alabama. Frequency is the number of plots on which each species occurred by disturbance class, and relative frequency is the percent of plots on which each species occurred by disturbance class.

Species	Density			Relative density			Frequency			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 (Marshall) Borkh.	–	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 (Walter) Muhl.	–	–	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	—	—	—	—	—	—

the degree of which may vary depending upon management goals. The rationale is that emulation of natural disturbance processes is hypothesized to restore or maintain ecosystem resilience, ecosystem function, and native forest biodiversity (Long, 2009). This approach does not imply a change in desired conditions, but rather a change in the approach used to achieve those conditions. For example, the size of a regeneration harvest may be modified to approximate the size of a natural disturbance event. The success of this approach requires quantitative information on natural disturbance regimes and population and community responses (Seymour et al., 2002; Franklin et al., 2007). Wind is the most common and likely the most influential natural disturbance agent in most temperate deciduous forests (Runkle, 1985, 1996; MacDonald, 2003; Fischer et al., 2013). Thus, quantitative data on the impacts of wind disturbance, such as those provided in our study, may help guide silviculturists in the development of prescriptions that will achieve desired conditions, but that also mimic natural disturbance events. For example, the wind damage documented in this study did not affect any of the sampled stands uniformly, but rather increased intra-stand heterogeneity in regards to stem densities, vertical stratification of foliage, and species composition. The storm resulted in stands with distinct neighborhoods that varied in structure and composition. Thus, a silvicultural system that emulates the effects of this type of wind event might utilize an even-aged approach where entries were made in groupings within a stand, rather than uniformly, to create multi-aged structures at the stand-scale.

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