

EFFECTS OF AN INTERMEDIATE-SCALE WIND EVENT ON FOREST COMPOSITION,
STRUCTURE, AND STRUCTURAL COMPLEXITY

by

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ABSTRACT

Forest disturbances alter environmental conditions, influence species composition and stand structure, and affect successional and developmental pathways. Natural disturbances differ in magnitude, severity, and return interval and range from frequent, gap-scale disturbances, to infrequent stand-replacing events. Disturbances at the gap and intermediate scale increase structural complexity and intra-stand heterogeneity. On 20 April 2011 in Lawrence County, AL, an EF1 tornado tracked 5 km, leaving a patchwork mosaic of disturbed areas. To analyze the intra-stand spatial patterns of tree mortality and biological legacies after an intermediate-scale wind disturbance, I established a 100×200 m (2 ha) rectangular plot perpendicular to the path of the storm within an affected *Quercus alba* stand. Based on the basal area removed by the wind event, I divided the plot into disturbance classes (minimal, light, and moderate) to compare compositional and structural attributes across areas of increasing disturbance severity. I analyzed species- and size-specific mortality trends within each disturbance class. In addition, I quantified the structural complexity of each disturbance class and described the effect of the intermediate-scale disturbance on stand development. Composition was not substantially affected by the disturbance, but large stems were disproportionately removed by the storm. Structural complexity increased as a result of the wind event. However, the spatial distribution of stems was more uniform after the disturbance. The intermediate-scale wind event altered the stand size class from a mature stand to a mature–sapling mosaic stand. This size class characterizes a stand in the mixed stage of development. Results from this thesis contribute to the understanding of the

compositional and structural attributes of upland *Quercus* stands after an intermediate-scale wind event. Quantitative descriptions of this stand may be used as references to inform silvicultural systems intended to enhance structural complexity and minimize the disparity between natural and managed stands

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CHAPTER 1

INTRODUCTION

1.1 Purpose

The purpose of this thesis is to describe the effects of an intermediate-scale wind disturbance on an upland *Quercus* stand. Results from this study will provide information on the composition and structure of a post-disturbance upland *Quercus* stand, and describe intra-stand spatial patterns of tree mortality and biological legacies after an intermediate-scale wind disturbance. Most studies on forest disturbance have focused on either stand-replacing disturbances or gap-scale disturbances. Unequivocally, more information is needed to describe the effects of intermediate-scale disturbances, as most eastern *Quercus* stands will experience an intermediate-scale disturbance during their lifespan. Although agents of intermediate-scale disturbance are variable, this thesis will describe the effects of wind, the most common influential natural disturbance agent in temperate forests. Knowledge of the effects of intermediate-scale disturbances is necessary for refining silvicultural systems which are intended to emulate the biological legacies of natural disturbances.

1.2 Influence of forest disturbance events on composition and structure

Forest disturbances alter environmental conditions, influence species composition and stand structure, and thus affect successional and developmental pathways (Lorimer 1980, White et al 1985, Foster et al. 1998, White and Jentsch 2001). These disturbances are often classified by their spatial extent and magnitude, and range from localized, gap-scale events to stand-wide,

catastrophic events (Oliver and Larson 1996). Along this disturbance severity gradient, intermediate-scale disturbances encompass events larger in extent than gap-scale disturbances and smaller than catastrophic events (Hanson and Lorimer 2007, Cowden et al. 2014, White et al. 2015). Similarly, intermediate-scale disturbances are more likely to occur more frequently than catastrophic events and less frequently than gap-scale disturbances (Frelich and Lorimer 1991, Mitchell 2013). Stand-wide disturbances (defined as 25% of canopy trees affected) occur every 30 to 50 years in the Central Hardwood Forest Region (Nowacki and Abrams 1997, Ruffner and Abrams 1998, Hart et al. 2012). Although the return interval of intermediate-scale disturbances is shorter than the life of canopy trees in the eastern United States (100–400 years; Lorimer 1989, 2001, Stueve et al. 2011, Di Filippo et al. 2015), most research on natural disturbance has focused on either extreme catastrophic disturbances or small gap-scale disturbances (Seymour et al. 2002).

Based on this disturbance classification scheme, the intermediate-scale disturbance category encompasses a large variation in magnitude, severity, and spatial patterns of tree mortality. For example, an intermediate-scale disturbance may remove canopy trees through a stand in a manner resembling many simultaneous gap-scale disturbances, or it may remove all canopy trees in a neighborhood (0.001–0.1 ha; Frelich et al. 1998), but not affect the remainder of the stand. Differing intermediate-scale disturbance agents may cause varying spatial patterns of tree mortality and resulting biological legacies. Natural disturbance agents of intermediate-scale disturbances include windthrow, fire, and insect outbreaks, among others (Oliver and Larson 1996). Larger stems with increased canopy volumes may be disproportionately removed by wind disturbances (Foster and Boose 1992, Peterson and Rebertus 1997, Canham et al. 2001, Peterson 2007, Rich et al. 2007), whereas smaller stems with relatively thin bark and fire-

intolerant species may be most susceptible to mortality after fire (Regelbrugge and Smith 1994, Brose et al. 2013) Thus, certain agents of intermediate-scale disturbance may also cause species-specific or size-specific tree mortality (Everham and Brokaw 1996, Canham et al. 2001, Peterson 2007, White et al. 2015). The variation among disturbance agent, severity, and spatial pattern of both impacted and surviving stems necessitates quantitative descriptions of different intermediate-scale disturbances to project subsequent successional and developmental trajectories.

1.3 Structural complexity

The enhancement and maintenance of stand structural complexity is an increasingly popular silvicultural objective, especially on multiple use lands (Franklin et al. 2002, Palik et al. 2002, Saunders and Wagner 2008, Puettmann et al. 2009, Puettmann 2011, O’Hara 2014). Complex structures with spatial heterogeneity are hypothesized to be more resistant and resilient to perturbations and typically support higher numbers of plant and animal communities, thus increasing biodiversity (Hansen et al. 1991, Pommerening 2002, Zenner 2004, Churchill et al. 2013, O’Hara 2014). Forest stand structures are described by horizontal and vertical arrangement of biomass in a stand and are often used as a proxy for managing stand function (Franklin et al. 2002). Complex structures are characterized by heterogeneity in stem size and canopy architecture, and the presence of deadwood (McElhinny et al. 2005, Donato et al. 2012). Zenner (2004) defined complex structures as those with different sized stems neighboring one another. The spatial distribution of stems within a stand often determines the light regime, regeneration patterns, and tree growth. In addition, the large differentiation in stem size may enhance

structural complexity and habitat availability, which affects the presence of certain animal and plant species (Emborg 1998, Spies 1998, Kint et al. 2003, Pommerening 2006).

As a result of the spatial variability of such disturbance events and the remaining biological legacies, stand structure must be studied with respect to the spatial aspects of a specific type of disturbance. Measurements such as stand density, basal area, and canopy cover are often used to describe stand structure, but these characterizations ignore the horizontal arrangement of individual trees, and thus do not describe stand structure with respect to spatial variability. Conversely, common spatial statistics and nearest neighbor analyses often ignore individual tree attributes and only account for the spatial patterns of stems. Structural complexity indices such as the diameter differentiation index and structural complexity index incorporate the spatial coordinates of individual trees and individual tree attributes (Fuldner 1995, Zenner and Hibbs 2000, McElhinny et al. 2005). The use of multiple structural metrics to describe the structural complexity of the stand is beneficial to minimizing limitations of any one metric (Neumann and Starlinger 2001, Aguirre et al. 2003, Kint et al. 2003, McElhinny et al. 2005, Zenner et al. 2015) and will contribute to the understanding of forest stand dynamics after an intermediate severity disturbance.

Relatively complex structures may be created or maintained by using natural disturbance-based management, as natural disturbances often enhance stand structural complexity (Spies 1998, White and Jentsch 2001, O'Hara and Ramage 2013). Natural disturbance-based silviculture attempts to emulate the biological legacies of naturally-occurring disturbance regimes and possibly multiple interacting disturbance regimes (e.g., wind disturbances and fire). The complexities of these legacy structures vary by disturbance type, magnitude, and severity (Franklin et al. 2002, Palik et al. 2002, Franklin et al. 2007, Long 2009). Because partial natural

disturbances may create multi-aged stands and increase structural complexity (O'Hara and Ramage 2013), analysis of biological legacies and spatial patterns created by intermediate-scale disturbances will contribute to the refinement of existing silvicultural systems that minimize the disparity between natural and managed stands. Importantly, a natural disturbance-based approach does not fundamentally change the desired future conditions of a stand, but rather the approach implemented to achieve these desired future conditions. Land managers determine the extent to which a natural disturbance-based approach is followed.

Stand developmental pathways after an intermediate disturbance event are complex and deviate from the linear pattern of classical models (Frelich and Lorimer 1991, Oliver and Larson 1996, Hanson and Lorimer 2007, Johnson et al. 2009, White et al. 2015). Johnson et al. (2009) hypothesized that intermediate-scale disturbances shift *Quercus* stands to a “mixed stage” of development. When a stand enters the mixed stage of development, the developmental trajectory becomes less certain. For example, a stand disturbed by a wind storm may move from the mixed stage to a later developmental stage in the absence of additional broad-scale events. In contrast, a mixed-severity fire may create a *Quercus* savanna, which may be maintained in the mixed stage of development with a frequent fire return interval. Quantitative descriptions of stands in the mixed stage of development will demonstrate the breadth of this developmental stage.

1.4 Hypotheses and objectives

This study addresses a gap in the understanding of the effects of intermediate-scale wind disturbance on intra-stand patterns of composition and structure. The overarching goals of this study are to describe post-disturbance composition and structure, determine species and size specific mortality patterns, describe the resultant structural complexity of the stand, and

document the current stage of development of the stand. I hypothesize that the composition of the stand will not differ from pre-disturbance conditions, but larger stems will be removed and alter the structure of the stand. I hypothesize that structural complexity will be highest in lightly disturbed portions of the stand because of the patchwork mosaic of disturbance created by the tornado.

1.5 Organization of thesis

The remainder of this thesis consists of five chapters. In Chapter 2, I provide description of the physical characteristics and land-use history of the study area. Chapter 3 outlines the field methods used to address the goals of this thesis. In Chapter 4, I describe the post-disturbance intra-stand spatial patterns of disturbance, composition, and structure. I also describe mortality trends based on individual tree attributes. Chapter 5 provides information on the structural complexity of the stand and information on the stage of development and developmental trajectory of the stand. In the concluding chapter (Chapter 6), findings are summarized and I make suggestions for future research needs.

CHAPTER 2

STUDY AREA

2.1 Physical description of study site

The Sipsey Wilderness, a 10,085 ha reserve established in 1975, is located in the William B. Bankhead National Forest in Lawrence and Winston Counties, Alabama. The reserve is situated on the Cumberland Plateau section of the Appalachian Plateau province (Fenneman 1938). The area is located within the Dissected Plateau ecoregion (level IV) of the Southwestern Appalachians (level III) ecoregion (Griffith et al. 2001). The topography of the region is complex, characterized by steep slopes and narrow ridges and valleys, no longer resembling a true plateau (Smalley 1979). The geology is primarily composed of the Pennsylvania Pottsville formation, which consists of quartzose sandstone with discontinuous layers of limestone, siltstone, and coal (Szabo 1988). Soils in the region are typically shallow, acidic, and well drained (USDA 1959). The regional climate is classified as humid mesothermal with short, mild winters and long, hot summers (Thorntwaite 1948). Mean annual temperature is 16° C with monthly means of 5° C and 26° C for January and July, respectively. The average growing season is 220 days and spans from late-March to early-November (Smalley 1979). Average annual precipitation is 1380 mm with monthly means of 138 mm and 113 mm for January and July, respectively (PRISM Climate Group 2015).

Braun (1950) classified this portion of the Cumberland Plateau as a transition zone between the Mixed Mesophytic Forest Region to the north and the *Quercus–Pinus* Forest Region to the south. Plant community composition in this area is largely influenced by topography

(Zhang et al. 1999) and soil-water availability (Hinkle 1989, Clatterbuck et al. 2006). *Quercus* spp. were included in most community types and *Quercus* was the most abundant genus of the 14 ecological community types identified by Zhang et al. (1999) in the Sipsey Wilderness within William B. Bankhead National Forest. These community types ranged from *Pinus virginiana*-dominated xeric sites to *Fagus grandifolia* and *Acer saccharum*-dominated mesic sites. Environmental gradients in this region are steep and species composition may change abruptly over relatively small changes in elevation. (Zhang et al. 1999, Parker and Hart 2014).

On 20 April 2011, an EF1 tornado embedded within a bow-echo affected the William B. Bankhead National Forest and multiple stands within portions of the Sipsey Wilderness, creating a mosaic of disturbed areas (Figure 2.1). The tornado produced winds up to 153 kph, accompanied by straight-line winds with speeds up to 145 kph (NWS 2011). Areas of highest disturbance severity were concentrated in the tornado path and severity decreased with distance from center of the path, creating a canopy disturbance severity gradient.

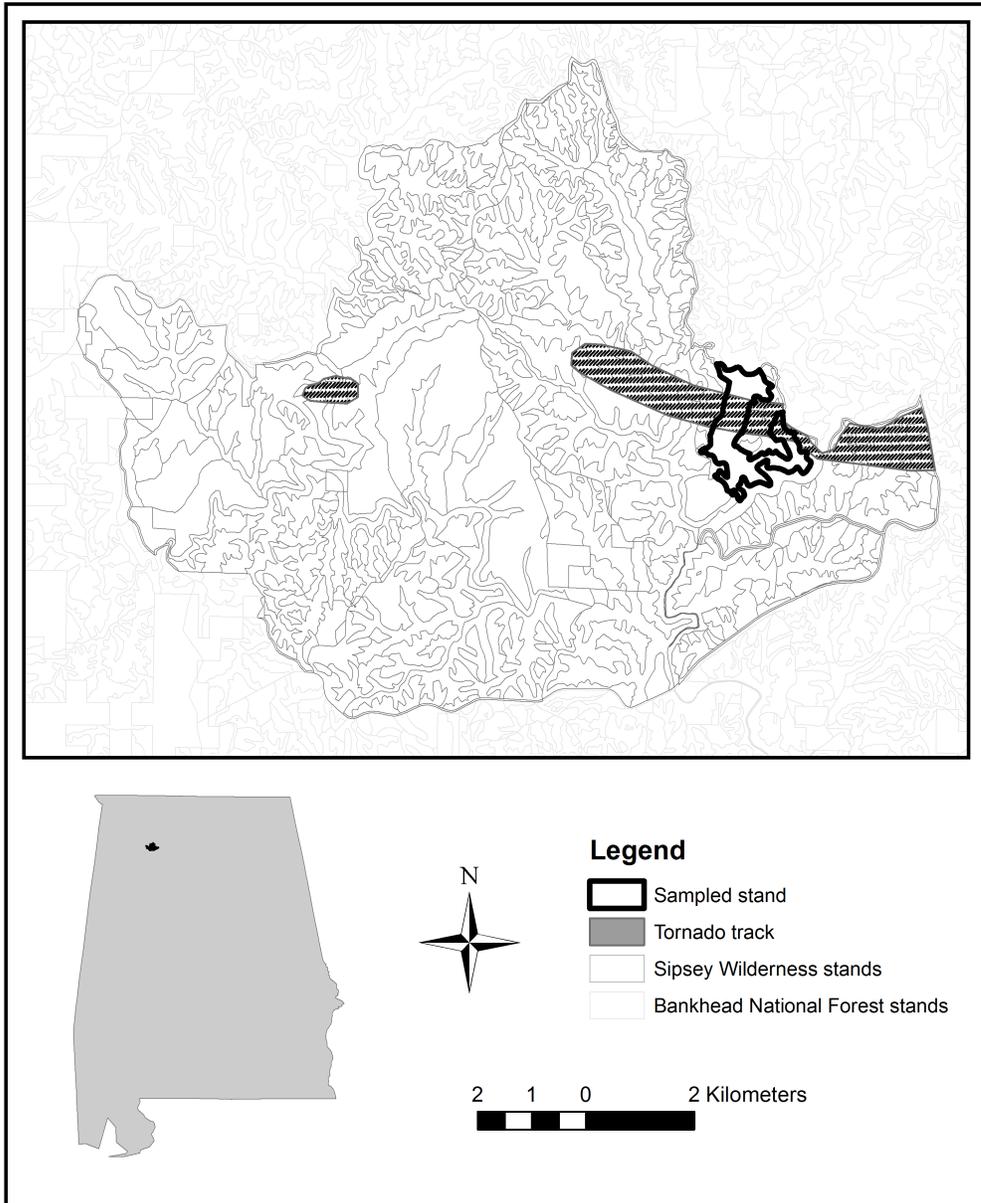


Figure 2.1 Sipsy Wilderness Area in William B. Bankhead National Forest, Alabama. Path of a 2011 EF1 tornado and the sampled *Q. alba* stand are indicated

2.2 Land-use history

The earliest documentation of Indian inhabitation of the Cumberland Plateau was found in Russell Cave in North Alabama and dates to 7,000 BCE. Indians of the Archaic period (8000–1000 BCE) were nomadic hunters and gatherers and often used caves as shelter (Manning 1999). Kinlock Rock Shelter, located in the Sipsey Wilderness, was occupied by Indians of this period and later used by Cherokee Indians. During the Woodland period (1000 BCE–1000 CE), the Oakville Indian mounds were constructed by the Copena Indians near present-day Moulton, Alabama. These mounds were used for burial and ceremonial purposes. The Oakville Indian mounds were also used by Mississippian Indians (1000 BCE–1540 CE), who began to rely on crops such as corn, beans, and squash. Bows used for hunting were commonly made of *Carya* spp, *Robinia pseudacacia* L., and *Platanus occidentalis* L.. The population of Mississippian Indians in north Alabama had declined by the arrival of DeSoto in 1540 CE (Rozema 2007). Moundville, a population center in Hale County, Alabama, was depopulated by 1300 CE (Blitz 2010).

During the 1700s, Cherokee and Chickasaw Indians moved westward because of European settlement in the eastern United States. Historically, Lawrence County was inhabited by the Creek Indians, whose northern boundary was delineated by the High Town Path (Walker 2011). The High Town Path was an Indian trail that spanned from Charleston, South Carolina to Memphis, Tennessee and was used by both Indians and settlers for trade and westward migration (Rozema 2007). This path transversed the present-day Sipsey Wilderness Area. As Cherokee and Chickasaw Indians migrated west, they established towns in North Alabama along the Tennessee River. During the 1780s, the Chickasaw and Creek Indians engaged in the Battle of Indian Tomb Hollow, located in William B. Bankhead National Forest. The Chickasaw Boundary Treaty

established the High Town Path as the southern boundary for Chickasaw Indians. Chief Doublehead, a Cherokee, established multiple villages and leased land in the area to European settlers until 1807. In the 16th–18th centuries, increased trade and land disputes occurred between local Indians and incoming European settlers. In 1814, President Andrew Jackson, with the assistance of Cherokee Indians, defeated the Creeks and acquired Creek territory south of the High Town Path in the Fort Jackson Treaty of 1814 (Walker 2011). The Turkey Town Treaty of 1816 ceded land south of the High Town Path to the federal government and compensated Chickasaw and Cherokee Indians for this territory (Rozema 2007, Walker 2011).

Lawrence County, Alabama was established in 1818 (Remington 2010). In 1838, Cherokee Indians were relocated under the Indian Removal Act of 1830 (Rozema 2007). The first recorded American establishment in the present-day Sipsey Wilderness was Kinlock Post Office, which operated from 1843–1866, 1868–1871, and 1874–1901. At least one gristmill was located within the present-day Sipsey Wilderness. Historical maps indicated that the gristmill was in operation in 1856 and in 1914, under new ownership (Remington 2010). Census data from 1900 indicated that the county seat of Moulton, AL, had a population of 290.

The U.S. Federal government purchased the land of the current Bankhead National Forest in 1914 to create the Alabama National Forest. Civilian Conservation Corps (CCC) camp F-3 was situated within the Alabama National Forest. Projects conducted by the CCC included road construction, timber stand improvement, and the construction of two bridges. Camp F-3 was in operation until 1937 (Pasquill 2008). In 1936, President Franklin D. Roosevelt changed the name of the forest to Black Warrior National Forest, and Congress later renamed it the William B. Bankhead National Forest in 1942. The Sipsey Wilderness Area was established in 1975 under the Eastern Wilderness Act of 1975 and was expanded to its current size in 1988. Although no

active management has occurred during the Sipsev Wilderness Area since 1975, the current forest conditions of the natural area have been influenced by prior anthropogenic activity.

CHAPTER 3

FIELD METHODS

All field data were collected in the summer of 2014, during the fourth growing season post-disturbance. Using a shapefile of Forest Service stand delineations and aerial photography in ArcMap v. 10.2 as reference, I selected a 182 ha *Quercus alba* stand that was contained completely within the Sipsey Wilderness, had no written records of previous broad-scale disturbances, and was partially disturbed by the 20 April 2011 EF1 tornado. Within this stand, I established a 2 ha (100 × 200 m) permanent, rectangular plot. The plot captured a gradient of disturbance, from severe disturbance at the center of the tornado path to neighborhoods of the stand that were seemingly unaffected by the wind event, based on visual reconnaissance. The average slope of the plot was 3.7%, with the contours running perpendicular to the path of the 2011 storm so effects of wind disturbance were not compounded by topography. The plot was situated at least 25 m from the stand boundary to eliminate edge effects. A 5 × 5 m grid was superimposed over the 2 ha plot to divide the plot into disturbance severity subplots after sampling.

Within each 5 × 5 m quadrat, all live stems ≥ 5 cm DBH were recorded for species, diameter at breast height (DBH), and height to record average stand characteristics. Heights were determined using a clinometer and ground tape. For all dead, woody stems ≥ 5 cm rooted within each quadrat, I identified the stem to the lowest taxonomic level possible, recorded the DBH and decay class, and classified each stem by mode of death. For uprooted stems, DBH was recorded at 1.4 m above the root collar, where the estimated standing DBH would have been measured.

Decay classes assigned to each dead stem include: decay class 1 (least decayed, sound wood, intact bark, branches present), decay class 2 (sound to somewhat rotten wood, bark may be intact, branch stubs firmly attached), decay class 3 (substantially rotten wood, bark slippage, branch stubs easily pulled from softwood species, wood texture is soft and compacts when wet), or decay class 4 (most decayed, mostly rotten wood, branch stubs rotted down to log surface, bark no longer attached or absent, log is oval or flattened in shape; Fraver et al. 2002). Modes of death included uprooted stem (overturned with root network uplifted), snapped stem (broken above ground and below crown), and snag (standing dead tree with crown mostly intact; Clinton et al. 1993, Hart and Grissino-Mayer 2009, Richards and Hart 2011, Weber et al. 2014). I recorded the location of every stem, both living and dead, within each 5 × 5 m quadrat by recording the distance and azimuth from the northwest corner of the quadrat.

CHAPTER 4

COMPOSITION, STRUCTURE, AND SPATIAL PATTERNS OF BIOLOGICAL LEGACIES

4.1 Introduction

The overarching goal of this study is to describe the effects of an intermediate-scale wind event on the composition, structure, and intra-stand spatial patterns of trees along a disturbance severity gradient. Specifically, I aim to 1) describe the effects of an intermediate-scale disturbance on composition among neighborhoods of increasing disturbance severity, 2) describe the effects on stand structure among neighborhoods, 3) describe the effects of an intermediate-scale disturbance on compositional diversity and species intermingling and 4) describe stem mortality trends based on size and species. The results will provide information on tree mortality patterns and the biological legacies left by a low severity wind event and provide information for natural disturbance-based silvicultural systems.

4.2 Data analyses

To analyze the effects of the intermediate-scale wind event, I assumed that stems classified as decay class 1 were those impacted by the storm and those resulting from background mortality shortly prior to and since the wind event (Cowden et al. 2014, White et al. 2015). I used percent background mortality from studies in adjacent stands (1.2% m² ha⁻¹ removed) to approximate background mortality and estimate the actual basal area removed by the 2011 wind event (Runkle 1982, Cowden et al. 2014, White et al. 2015). However, because of

the spatially explicit field sampling and data analysis, I did not differentiate between storm-killed decay class 1 stems and decay class 1 stems as a result of background mortality in data analyses.

I divided the plot into three disturbance severity classes (minimal, light, and moderate disturbance) to compare differences in stand composition and structure among neighborhoods of increasing disturbance severity. To determine boundaries of disturbance severity classes, I used simple kriging with a normal score transform of basal area of decay class 1 stems for 20×20 m quadrats within the 2 ha plot. This spatial scale corresponded to the approximate crown diameter of dominant *Q. alba* stems in the stand (Johnson et al. 2009) and was broad enough to determine general trends of basal area removed and remain unbiased by highly localized areas of disturbance (Zenner et al. 2015). Using contours created by the simple kriging, I defined disturbance severity class boundaries by following the borders of $5 \text{ m} \times 5 \text{ m}$ quadrat boundaries through the 2 ha plot (see plot establishment description). The minimum and maximum contour values were $0.0\text{--}2.3 \text{ m}^2 \text{ ha}^{-1}$ (0–8% basal area removed) for minimal disturbance, $2.3\text{--}6.4 \text{ m}^2 \text{ ha}^{-1}$ (8–24% basal area removed) for light disturbance, and $6.4\text{--}20.0 \text{ m}^2 \text{ ha}^{-1}$ (24–75% basal area removed) for moderate disturbance (Figure 4.1). These contour values related to percentages of basal area removed of disturbance classes in Hanson and Lorimer (2007). The minimal, light, and moderate disturbance classes were 0.570, 0.855, and 0.575 ha in size, respectively, and therefore were composed of multiple 0.001–0.1 ha neighborhoods.

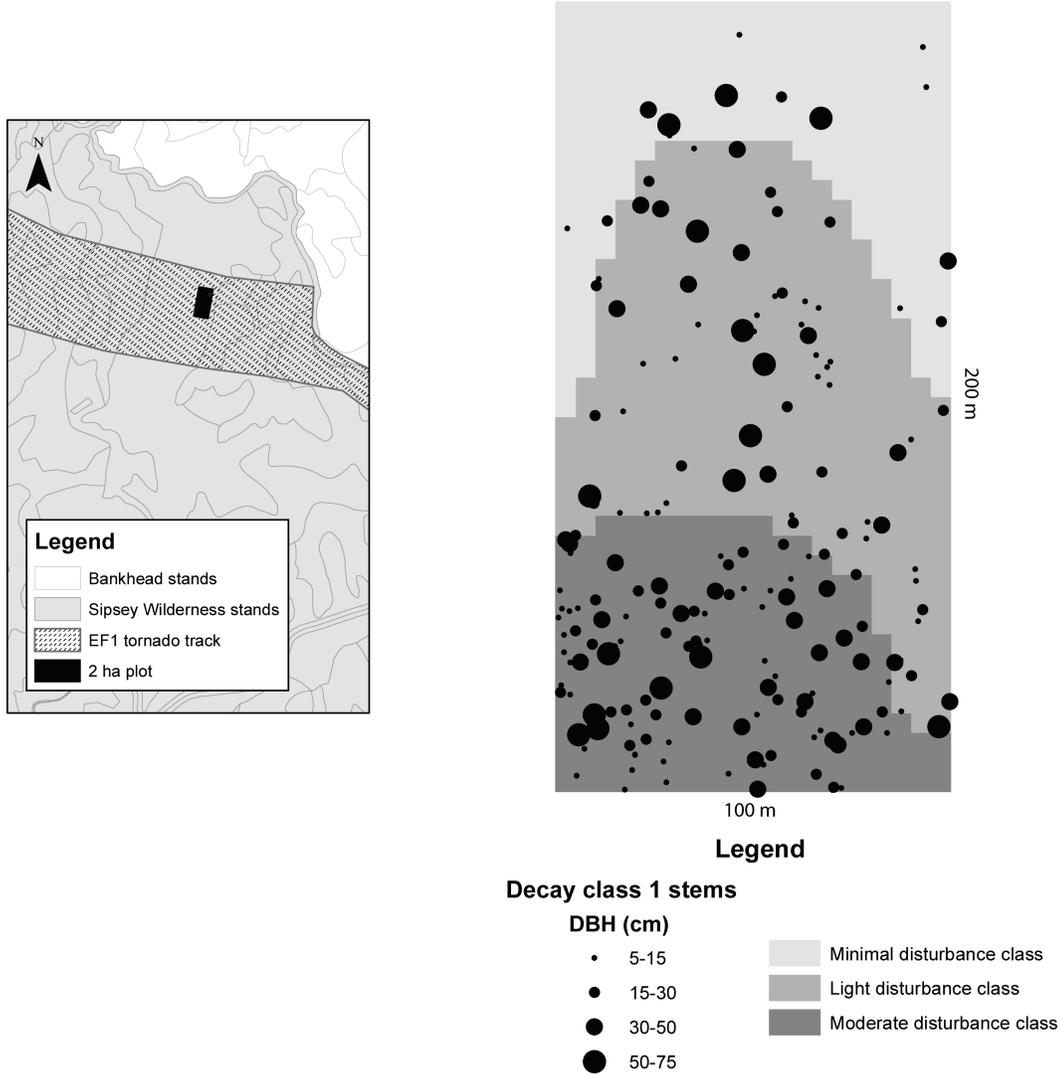


Figure 4.1 Contiguous 2 ha permanent plot established perpendicular to the track of an EF1 tornado in the Sipsey Wilderness, William B. Bankhead National Forest, Alabama. Disturbance severity classes, determined by basal area removed, are indicated by shading. Points representing stems are not to scale to better illustrate spatial patterns of residual trees.

I calculated density, relative density, dominance (basal area ($\text{m}^2 \text{ha}^{-1}$)), and relative dominance by species for each disturbance severity class to compare effects of the disturbance on composition and structure. Values were calculated for both living and decay class 1 stems. To analyze additional compositional patterns, trees were divided into the following taxonomic groups: *Acer-Fagus*, *Carya* spp., *Ostrya virginiana*, *Quercus* spp., and other species. Taxonomic groups were chosen based on taxa dominance across all disturbance severity classes. I included *Acer* and *Fagus* in one taxonomic group based on shade tolerance and successional trend in the Central Hardwood Forest Region (e.g. Rentch et al. 2003, Cowden et al. 2014). Trees within each taxonomic group were divided into 5 cm size bins and diameter distributions were created for each group (Nyland 2002). Diameter distribution shapes were assigned to each taxonomic group by disturbance class following Leak (1996) and Janowiak et al. (2008). Using ordinary least squares regression, I regressed the $\log_{10}(\text{stems ha}^{-1} + 1)$ in each DBH size class by all combinations of the DBH size class midpoint DBH, DBH^2 , and DBH^3 . The model used to determine the diameter distribution shape to each group was chosen by the highest adjusted R^2 value and the lowest root mean square error. I assigned the diameter distribution shape according to the sign (positive or negative) of significant DBH, DBH^2 , and DBH^3 coefficients ($p < 0.05$), following Janowiak et al. (2008). Because of a relative low sample size (9 stems ha^{-1}), I did not assign a diameter distribution shape to *Carya* spp. in the moderate disturbance class. To analyze size distributions of *O. virginiana* which had little differentiation among stem size, I created diameter distributions using 1 cm DBH size classes for each disturbance severity class. I did not assign shapes to these diameter distribution curves using polynomial regression.

I calculated the Gini coefficient (GC) for each taxonomic group and disturbance class (Gini 1912). This index was originally developed to describe inequities in income among

populations and has since been applied to describe the inequality of plant sizes (Weiner and Solbrig 1984). Lexerød and Eid (2006) determined that the GC most clearly differentiated between diameter distributions compared to multiple indices. Values for the GC range between 0 and 1; a value of 0 indicated that all stems had the same DBH, whereas a value of 1 indicated that all stems had dissimilar DBH (Lexerød and Eid 2006). The GC for other species was calculated three ways: other species including *O. virginiana*, *O. virginiana* alone, and other species excluding *O. virginiana*.

To describe the compositional diversity of trees, I calculated Shannon diversity (H') and evenness (J) for each disturbance class. I also calculated the Mingling index (M_i) to determine the degree of species intermingling (Gadow and Hui 2002). The M_i describes the level of interspersed distribution of species within a stand based on the species of the four nearest neighbors of each tree (Pommerening 2002, Kint et al. 2003, Saunders and Wagner 2008, Pastorella and Paletto 2013). The M_i is calculated for each tree within a group or stand and values range from 0 to 1 (0 for trees with all nearest neighbors of the same species; 1 for trees with no nearest neighbors of the same species). Stand M_i values are calculated by averaging tree M_i values. I also analyzed M_i values by species to determine species specific variation in interspersed distribution. For species-specific M_i values, low values indicated that stems of a the focal species are more likely to occur in groups of that species, whereas high values indicate that stems of the focal species tend to occur along. For stand averages of the M_i , low values may indicate low species diversity or a clumping of species within a stand, whereas high values may indicate high species diversity or a highly interspersed distribution of species (Graz 2004). For calculations of the M_i , I used a 5 m buffer edge correction within each irregularly shaped disturbance severity class to reduce edge-bias. (Pommerening and Stoyan, 2006)

To determine species- and size-specific mortality trends, I used multiple logistic regression analysis with tree mortality (live v. decay class 1) as the dependent variable and DBH and taxonomic groups (coded as dummy variables) as independent variables (Trexler and Travis 1993, Hanson and Lorimer 2007, Peterson 2007). I applied the Box–Tidwell transformation to verify the logit-transformation of tree mortality exhibited a linear relationship with DBH, the only continuous predictor variable (Menard 1995). Four multiple logistic regressions for tree mortality were conducted: one for all stems in the 2 ha plot, and one for stems in each disturbance severity class. Each model was built using the forward variable selection method with an entry threshold of $p < 0.05$ (Peterson 2007). I used the likelihood ratio χ^2 to test the significance of each model and the Wald χ^2 test to evaluate the significance of variables within the model (Trexler and Travis 1993, Hosmer and Lemeshow 2000, Peterson 2007). All statistical analyses were performed in SAS and all spatial analyses were performed in ArcMap v. 10.2 and R using the “spatstat package” (Baddeley and Turner, 2005).

4.3 Results

4.3.1 Effects on composition and structure

Live basal area for the minimal, light, and moderate disturbance severity classes was 23.5 $\text{m}^2 \text{ha}^{-1}$, 23.2 $\text{m}^2 \text{ha}^{-1}$, and 13.7 $\text{m}^2 \text{ha}^{-1}$, respectively. Basal area of decay class 1 stems was 2.1 $\text{m}^2 \text{ha}^{-1}$, 5.1 $\text{m}^2 \text{ha}^{-1}$, and 11.0 $\text{m}^2 \text{ha}^{-1}$, for minimal, light, and moderate disturbance classes, respectively. Removing estimated background mortality from decay class 1 basal area indicated that 1.8 $\text{m}^2 \text{ha}^{-1}$ (7%), 4.7 $\text{m}^2 \text{ha}^{-1}$ (17%), and 10.7 $\text{m}^2 \text{ha}^{-1}$ (43%) was removed by the 2011 wind event in the minimal, light, and moderate disturbance classes, respectively. In all disturbance

classes, *Q. alba* was the most dominant tree species and *O. virginiana* occurred at the highest density (Table 4.1). In the minimal disturbance class, *F. grandifolia* (14%) and *A. saccharum* (8%) were the second and third most dominant species, and *F. grandifolia* (19%) and *Q. alba* (17%) occurred second and third most commonly. In the light disturbance class, *O. virginiana* (7%) and *F. grandifolia* (4%) were the second and third most dominant species, and *Q. alba* (18%) and *C. florida* (7%) occurred second and third most commonly. In the moderate disturbance class, *O. virginiana* (11%) and *A. saccharum* (7%) were the second and third most dominant species, and *A. saccharum* (15%) and *Q. alba* (11%) occurred second and third most commonly. Among decay class 1 stems, the most dominant species in the minimal, light, and moderate disturbance classes was *Q. alba*. *Quercus alba* also had the highest density of decay class 1 stems in the minimal and light disturbance categories, whereas *O. virginiana* was the most commonly occurring species of decay class 1 stems in the moderate disturbance class (Table 4.2).

Table 4.1 Dominance ($m^2 ha^{-1}$) and density (stems ha^{-1}) measures for all live woody stems ≥ 5 cm DBH in the Sipsey Wilderness, William B. Bankhead National Forest, Alabama

	Dominance ($m^2 ha^{-1}$)			Relative Dominance (%)			Density (stems ha^{-1})			Relative Density (%)		
	Minimal	Light	Moderate	Minimal	Light	Moderate	Minimal	Light	Moderate	Minimal	Light	Moderate
<i>Acer rubrum</i> L.	0.1	0.1	–	0.3	0.4	–	7.0	16.4	–	1.0	1.9	–
<i>Acer saccharum</i> Marshall	1.9	0.5	1.0	8.1	2.2	7.3	80.7	29.2	85.2	11.9	3.5	14.5
<i>Carpinus caroliniana</i> Walter	–	0.0	0.1	–	0.2	0.4	–	8.2	12.2	–	1.0	2.1
<i>Carya glabra</i> (Mill.) Sweet	0.6	0.6	0.4	2.8	2.5	2.8	24.6	15.2	5.2	3.6	1.8	0.9
<i>Carya ovata</i> (Mill.) K. Koch	0.8	0.1	0.5	3.5	0.4	3.6	10.5	3.5	10.4	1.6	0.4	1.8
<i>Carya tomentosa</i> (Lam.) Nutt.	0.2	0.7	0.4	0.8	3.0	3.1	7.0	10.5	7.0	1.0	1.3	1.2
<i>Cercis canadensis</i> L.	0.0	–	0.1	0.0	–	0.7	1.8	–	24.3	0.3	–	4.2
<i>Cornus florida</i> L.	0.0	0.3	0.1	0.0	1.2	0.6	1.8	60.8	20.9	0.3	7.2	3.6
<i>Fagus grandifolia</i> Ehrh.	3.3	1.0	0.1	14.0	4.1	0.5	129.8	33.9	3.5	19.2	4.0	0.6
<i>Fraxinus americana</i> L.	0.4	0.3	0.8	1.9	1.5	5.9	14.0	9.4	5.2	2.1	1.1	0.9
<i>Fraxinus pennsylvanica</i> Marshall	0.0	0.0	0.1	0.2	0.1	1.0	3.5	1.2	5.2	0.5	0.1	0.9
<i>Juniperus virginiana</i> L.	0.1	0.1	0.0	0.2	0.6	0.1	3.5	5.8	3.5	0.5	0.7	0.6
<i>Liriodendron tulipifera</i> L.	0.4	0.7	–	1.8	3.1	–	7.0	2.3	–	1.0	0.3	–
<i>Magnolia acuminata</i> (L.) L.	0.4	0.1	0.0	1.8	0.3	0.1	21.1	8.2	1.7	3.1	1.0	0.3
<i>Magnolia macrophylla</i> Michx.	0.0	0.1	–	0.1	0.3	–	1.8	11.7	–	0.3	1.4	–
<i>Nyssa sylvatica</i> Marshall	0.3	0.6	0.1	1.3	2.5	0.5	28.1	55.0	3.5	4.1	6.5	0.6
<i>Ostrya virginiana</i> (Mill.) K. Koch	0.6	1.7	1.6	2.6	7.4	11.4	171.9	380.1	240.0	25.4	45.1	40.9
Other spp.*	0.0	0.1	0.0	0.1	0.4	0.2	1.8	12.9	10.4	0.3	1.5	1.8
<i>Pinus taeda</i> L.	0.0	0.9	–	0.1	4.0	–	1.8	3.5	–	0.3	0.4	–
<i>Quercus alba</i> L.	12.3	14.5	6.3	52.2	62.6	45.9	112.3	150.9	64.3	16.6	17.9	11.0
<i>Quercus falcata</i> Michx.	1.0	0.4	–	4.1	1.6	–	7.0	2.3	–	1.0	0.3	–
<i>Quercus mantana</i> Willd.	0.7	–	–	3.0	–	–	12.3	–	–	1.8	–	–
<i>Quercus muehlenbergii</i> Engelm.	–	–	0.6	–	–	4.1	–	–	12.2	–	–	2.1
<i>Quercus rubra</i> L.	0.0	–	0.2	0.0	–	1.2	1.8	–	3.5	0.3	–	0.6
<i>Tilia americana</i> L.	0.0	–	0.1	0.0	–	1.0	1.8	–	13.9	0.3	–	2.4
<i>Ulmus alata</i> Michx.	0.2	0.4	0.5	1.0	1.6	3.7	17.5	11.7	17.4	2.6	1.4	3.0
<i>Ulmus rubra</i> Muhl.	0.0	0.0	0.8	0.0	0.0	5.6	1.8	1.2	24.3	0.3	0.1	4.2
<i>Viburnum rufidulum</i> Raf.	0.0	0.0	0.1	0.1	0.1	0.4	5.3	8.2	12.2	0.8	1.0	2.1
Total	23.5	23.2	13.7	100.0	100.0	100.0	677.2	842.1	586.1	100.0	100.0	100.0

* Other spp. include species that had a relative importance value (i.e. sum of relative dominance and relative density) of < 1%. Species include *Asimina triloba* (L.) Dunal, *Celtis laevigata* Willd., *Frangula caroliniana* (Walter) A. Gray, *Ilex opaca* Aiton, *Ligustrum sinense* Lour., *Oxydendrum arboreum* (L.) DC., *Prunus serotina* Ehrh. and *Quercus stellata* Wangenh.

Table 4.2 Dominance (m² ha⁻¹) and density (stems ha⁻¹) measures for all decay class 1 stems ≥ 5 cm DBH in the Sipsey Wilderness, William B. Bankhead National Forest, Alabama

	Dominance (m ² ha ⁻¹)			Relative Dominance (%)			Density (stems ha ⁻¹)			Relative Density (%)		
	Minimal	Light	Moderate	Minimal	Light	Moderate	Minimal	Light	Moderate	Minimal	Light	Moderate
<i>Acer rubrum</i> L.	–	0.0	–	–	0.6	–	–	3.5	–	–	4.5	–
<i>Acer saccharum</i> Marshall	–	0.2	0.6	–	3.1	5.6	–	5.8	20.9	–	7.5	10.4
<i>Carpinus caroliniana</i> Walte	–	0.0	0.0	–	0.2	0.1	–	2.3	3.5	–	3.0	1.7
<i>Carya glabra</i> (Mill.) Sweet	0.0	0.3	0.3	0.4	6.2	2.7	1.8	3.5	1.7	7.1	4.5	0.9
<i>Carya ovata</i> (Mill.) K. Koch	–	0.2	2.2	–	4.9	20.2	–	1.2	19.1	–	1.5	9.6
<i>Carya</i> spp.	–	0.4	–	–	7.2	–	–	3.5	–	–	4.5	–
<i>Carya tomentosa</i> (Lam.) Nu	0.2	0.4	0.2	10.2	7.2	1.9	1.8	2.3	1.7	7.1	3.0	0.9
<i>Cercis canadensis</i> L.	–	–	0.0	–	–	0.3	–	–	3.5	–	–	1.7
<i>Cornus florida</i> L.	0.0	0.0	0.0	0.9	0.2	0.1	1.8	2.3	3.5	7.1	3.0	1.7
<i>Fagus grandifolia</i> Ehrh.	–	–	0.0	–	–	0.1	–	–	1.7	–	–	0.9
<i>Fraxinus americana</i> L.	–	0.0	0.8	–	0.1	6.9	–	1.2	10.4	–	1.5	5.2
<i>Fraxinus pennsylvanica</i> Ma	0.0	–	–	2.0	–	–	1.8	–	–	7.1	–	–
<i>Ilex opaca</i> Aiton	–	0.0	–	–	0.2	–	–	1.2	–	–	1.5	–
<i>Juglans nigra</i> L.	–	–	0.6	–	–	5.1	–	–	5.2	–	–	2.6
<i>Juniperus virginiana</i> L.	0.0	0.2	0.2	0.5	3.7	1.6	1.8	10.5	13.9	7.1	13.4	7.0
<i>Liriodendron tulipifera</i> L.	0.2	–	–	9.8	–	–	1.8	–	–	7.1	–	–
<i>Magnolia acuminata</i> (L.) L.	0.0	–	0.0	1.7	–	0.2	1.8	–	1.7	7.1	–	0.9
<i>Magnolia macrophylla</i> Micl	0.0	0.0	–	0.3	0.4	–	1.8	1.2	–	7.1	1.5	–
<i>Nyssa sylvatica</i> Marshall	–	0.0	–	–	0.3	–	–	2.3	–	–	3.0	–
<i>Ostrya virginiana</i> (Mill.) K. I	0.0	0.0	0.6	0.4	0.8	5.1	3.5	8.2	57.4	14.3	10.4	28.7
<i>Pinus echinata</i> Mill.	–	0.4	–	–	6.9	–	–	1.2	–	–	1.5	–
<i>Prunus serotina</i> Ehrh.	0.0	–	–	2.0	–	–	1.8	–	–	7.1	–	–
<i>Quercus alba</i> L.	1.5	2.8	3.5	71.8	54.2	31.7	5.3	25.7	36.5	21.4	32.8	18.3
<i>Quercus rubra</i> L.	–	0.2	1.4	–	3.9	12.5	–	2.3	7.0	–	3.0	3.5
<i>Tilia americana</i> L.	–	–	0.0	–	–	0.1	–	–	1.7	–	–	0.9
<i>Ulmus alata</i> Michx.	–	–	0.2	–	–	1.9	–	–	3.5	–	–	1.7
<i>Ulmus rubra</i> Muhl.	–	–	0.4	–	–	3.9	–	–	7.0	–	–	3.5
Total	2.1	5.1	11.0	100.0	100.0	100.0	24.6	78.4	200.0	100.0	100.0	100.0

Carya ovata and *L. tulipifera* were the second and third most dominant species of decay class 1 stems in the minimal disturbance class, and *O. virginiana* had the second highest density in the minimal disturbance class for decay class 1 stems. In the light disturbance class for decay class 1 stems, *C. tomentosa* and *P. echinata* were the second and third most dominant species, whereas *J. virginiana* and *O. virginiana* were the second and third most commonly occurring stems. In the moderate disturbance class, *C. ovata* and *Q. rubra* were the second and third most dominant decay class 1 stems whereas *Q. alba*, *C. glabra*, and *A. saccharum* were the second and third most commonly occurring decay class 1 stems.

Mean DBH for all live stems was 14.6 cm whereas mean DBH for decay class 1 stems was 22.6 cm. For taxonomic groups, mean DBH for live stems was 14.3 cm, 21.9 cm, 7.5 cm, 11.6 cm, and 32.7 cm, for live stems in *Acer-Fagus*, *Carya* spp., *O. virginiana*, other spp., and *Quercus* spp., respectively. Mean DBH for decay class 1 stems was 14.8, 36.2, 9.8, 17.7, and 35.5 cm for *Acer-Fagus*, *Carya* spp., *Ostrya virginiana*, other spp. and *Quercus* spp., respectively. Diameter distribution shapes varied among taxonomic groups and disturbance class (Figure 4.2). *Acer-Fagus* exhibited a concave shape in the minimal disturbance class, a negative exponential distribution in the light disturbance class, and a rotated sigmoid shape in the moderate disturbance class. *Carya* spp. was classified as negative exponential in the minimal disturbance class and increasing-q in the light disturbance class. *Quercus* stems exhibited a unimodal distribution across all disturbance severity classes. Other species were assigned a rotated sigmoid diameter distribution across all disturbance classes. For diameter distributions of *O. virginiana* stems using 1 cm diameter bins, the majority of stems in the minimal and light disturbance classes range from 5–7 cm DBH (Fig 4.3).

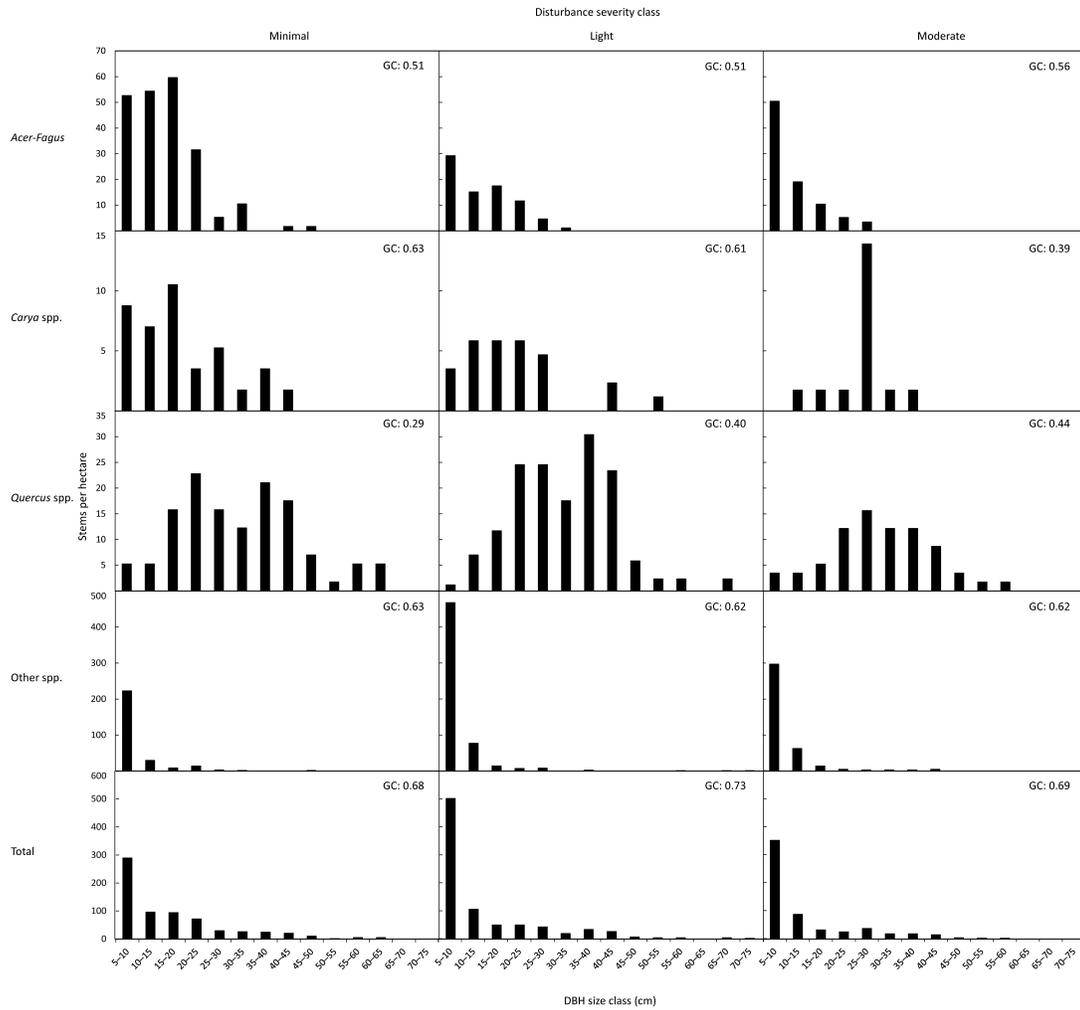


Figure 4.2 Density (stems ha⁻¹) for live stems ≥ 5 cm DBH by 5 cm diameter size class bins by taxonomic group across three disturbance severity classes in Sipse Wilderness, William B. Bankhead National Forest, Alabama. GC=Gini coefficient.

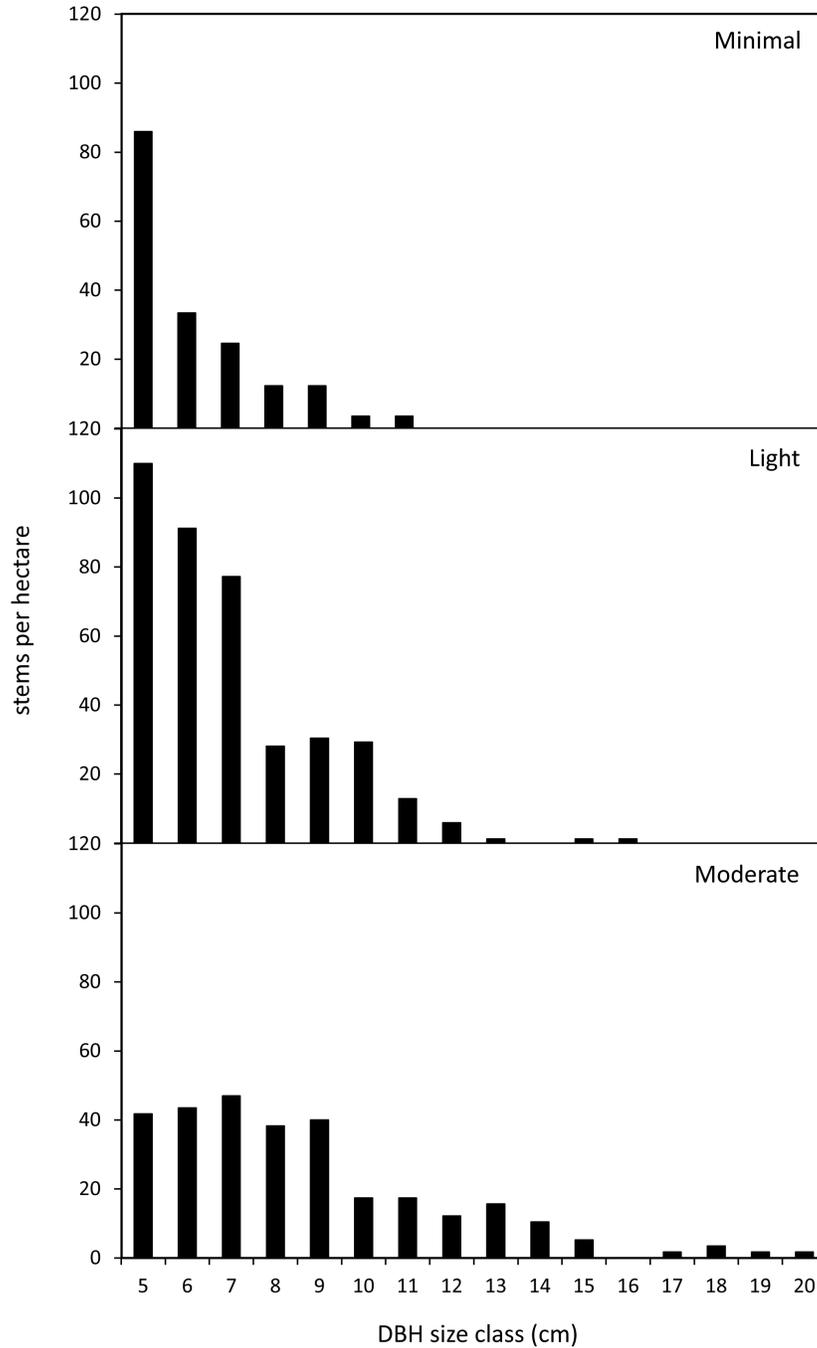


Figure 4.3 Density (stems ha⁻¹) for *O. virginiana* stems \geq 5 cm DBH in 1 cm diameter size class bins across three disturbance severity classes (minimal, light, moderate) in Sipsey Wilderness, William B. Bankhead National Forest, Alabama.

In the light disturbance class, 25 more *O. virginiana* stems ha⁻¹ are in the 5–6 cm diameter class than the minimal disturbance class. In the moderate disturbance class, 52 *O. virginiana* stems ha⁻¹ ≥ 12 cm DBH (8 *O. virginiana* stems ha⁻¹ ≥ 15 cm DBH) were present, whereas in the light disturbance class 9 *O. virginiana* stems ha⁻¹ ≥ 12 cm DBH were present. No *O. virginiana* stems ≥ 12 cm occurred in the minimal disturbance class.

GC values for *Quercus* were 0.29, 0.4, and 0.44 for minimal, light, and moderate disturbance classes, respectively, which are lower than overall disturbance class *GC* values of 0.68, 0.73, and 0.69 (Figure 4.2). *GC* for *O. virginiana*, excluding other species, were 0.25, 0.31, and 0.37, for minimal, light, and moderate disturbance. The *GC* for other species, excluding *O. virginiana*, were 0.65, 0.74, and 0.74, for minimal, light, and moderate disturbance.

Proportions of decay class 1 stems in 5 cm size classes indicated the removal of large *Quercus* stems. Taxa of small stems (5–25 cm DBH) in decay class 1 across all disturbance classes included *J. virginiana*, *O. virginiana*, *Magnolia* spp., *C. florida*, *Fraxinus* spp., *P. serotina*, *C. caroliniana*, *N. sylvatica*, *T. americana*, *C. canadensis*, and *Ulmus* spp. Taxa of large stems (> 25 cm) in decay class 1 included *L. tulipifera*, *P. echinata*, *Ulmus* spp., *Fraxinus* spp., and *J. nigra*. Stems of *J. nigra* only occurred in decay class 1 in the moderate disturbance class. Generally, highest proportions of decay class 1 stems of *Acer–Fagus* occurred in 5–30 cm size classes, *Carya* spp. in 30–50 cm size classes, and *Quercus* stems from 50–75 cm size classes.

4.3.2 Effects on diversity and species intermingling

I documented 36 unique species of both live and decay class 1 stems ≥ 5 cm DBH. Both the *H'* and *J* were highest in the moderate disturbance class (*H'*=2.0, *J*=0.63) and lowest in the

light disturbance class ($H'=1.6$, $J=0.55$). M_i values of live and decay class 1 stems (i.e. pre-disturbance conditions) were 0.75, 0.73, and 0.77 for minimal, light, and moderate disturbance classes, respectively. M_i values for live stems were 0.75, 0.69, and 0.75, which were lower than pre-disturbance values for the light and moderate disturbance classes.

4.3.3 Mortality related to species and size

Across all disturbance classes, larger diameter classes exhibited higher proportions of basal area removed than smaller diameter classes (Figure 4.4). Results from the tree mortality logistic regression for all stems in the 2 ha plot revealed DBH and the interaction between DBH and *Carya* stems were significant main effects ($\chi^2_{\text{wald}}=36.0$, $p<0.0001$; $\chi^2_{\text{wald}}=7.6$, $p=0.006$). Coefficients for both diameter and the interaction between *Carya* and diameter were positive, indicating an increased probability of mortality with increased tree diameter. For stems in the minimal disturbance class, logistic regression did not indicate any significant effects associated with stems mortality. In the light disturbance class, *O. virginiana* and the interaction between DBH and *Carya* stems were significant main effects ($\chi^2_{\text{wald}}=14.3$, $p=.0002$; $\chi^2_{\text{wald}}=4.3$, $p=0.039$). The coefficient for *O. virginiana* was negative, indicating a decreased probability of mortality for *O. virginiana* stems. Conversely, the coefficient for the interaction between DBH and *Carya* was positive, indicating an increased probability of mortality for *Carya* stems that increased with increasing DBH. In the moderate disturbance class, DBH was the only significant effect ($\chi^2_{\text{wald}}=32.9$, $p<0.0001$) and had a positive coefficient, indicating an increased probability of mortality with increasing DBH.

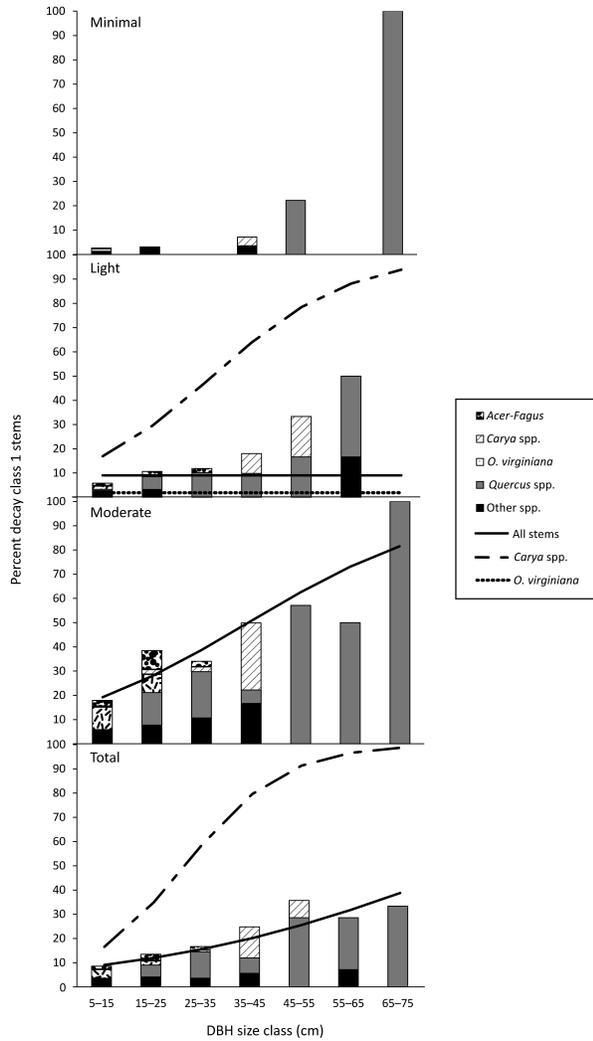


Figure 4.4 Observed percentages of decay class 1 stems in 10 cm diameter size class bins in a *Q. alba* stand in the Sipsey Wilderness, William B. Bankhead National Forest, Alabama. Percentages are divided by taxonomic group within each diameter bin. Lines are logistic regression equations for predicted stem mortality by disturbance severity class

In all disturbance classes, most decay class 1 stems were snapped (57% in minimal, 55% in light, 47% in moderate). In light and moderate disturbance classes, more stems were uprooted (30%, 42%, respectively) than snags (15%, 11%, respectively), whereas in the minimal disturbance classes, more snags (29%) were present. Most snags were *Quercus* spp. stems in all disturbance classes. In the moderate disturbance class, more *O. virginiana* and stems of the “other species” group were uprooted than snapped (Figure 4.5).

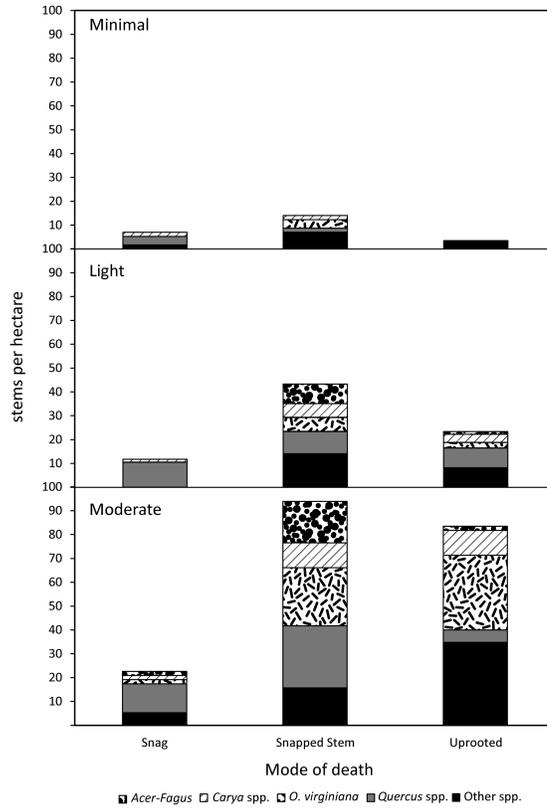


Figure 4.5 Density (stems ha⁻¹) of decay class 1 stems by mode of death (snag, snapped stem, uprooted stem) across three disturbance severity classes on the Sipsey Wilderness, William B. Bankhead National Forest, Alabama. Stems are divided by taxonomic group

4.4 Discussion

4.4.1 Effects on composition and structure

Although the return interval of intermediate-scale disturbances is shorter than the lifespan of most temperate forest species, data on the effects of such disturbances is lacking (Foster and Boose 1992, Seymour et al. 2002, Stueve et al. 2011). Four growing season after an intermediate-scale wind event in an upland *Q. alba* stand, species composition remained similar across disturbance severity neighborhoods. In the light and moderate size classes, *Acer* spp. and *Fagus* spp. did not exhibit higher relative density or dominance than in the minimal disturbance class. However, the diameter distributions for *Acer–Fagus* in all disturbance classes indicated that these taxa were regenerating and had relatively large densities of stems in small size classes. Conversely, the unimodal diameter distributions for *Quercus* stems in all disturbance classes indicated that *Quercus* stems are less likely to maintain dominance and more shade tolerant stems may gain dominance as larger *Quercus* stems senesce. The shape of *Carya* diameter distributions indicated some regeneration in low densities occurring. However, these occur in relatively low densities compared to *Acer–Fagus* stems. Although *Quercus* has maintained its dominance after the disturbance, the removal of large *Quercus* stems in conjunction with the lack of small *Quercus* stems in the understory has hastened the *Quercus* to *Acer* transition (i.e. disturbance-mediated accelerated succession), as is prevalent in *Quercus* stands in the Central Hardwood Forest Region (Lorimer 1984, Abrams 1989, Abrams 2005, Fei et al. 2011, McEwan et al 2011, Hart et al 2012, Holzmueller et al. 2012).

Density of *O. virginiana* stems was greater in the light and moderate than in the minimal disturbance class. Because of the higher density of *O. virginiana* in the light disturbance class,

total density was greater in the light disturbance class than in the minimal disturbance class. The largest stems of *O. virginiana* were located in the moderate disturbance class and stem size decreased with decreasing disturbance severity. These stems likely established first and may have served as a seed source that populated smaller size classes in the minimal and light disturbance classes, as *O. virginiana* stems are prolific seeders and produce seeds that are lightweight and easily dispersed. Batista and Platt (2003) classified *O. virginiana* as an ‘usurper’ species, which are relatively undamaged by wind disturbance and respond with increased growth after the disturbance, as described by Bellingham et al. (1995). Batista and Platt (2003) found that *O. virginiana* had significantly more saplings present post-disturbance than pre-disturbance and that the mean DBH growth rate of *O. virginiana* was significantly higher after hurricane disturbance than prior to disturbance. Kwit and Platt (2003) found that relative growth rates of *O. virginiana* increased after the occurrence of a hurricane and was highest for four years after disturbance. The tendency of *O. virginiana* to respond positively to disturbance in both recruitment and diameter growth in conjunction with a low probability of mortality because of its relatively small DBH and height may explain the higher density of *O. virginiana* stems ≥ 5 cm DBH in the light disturbance class.

4.4.2 Effects on diversity and species intermingling

Measures of diversity were similar across disturbance severity classes. However, values for H' and J were consistently highest for the moderate disturbance class and lowest for the light disturbance class. Cowden et al. (2014) found no significant difference in H' values among canopy disturbance severity classes for trees in the same region. Differences in these findings may be the result of field sampling approaches. The contiguous plot used in my analysis captured

the intra-stand heterogeneity that may have been masked by a stratified subjective sampling method used by Cowden et al. (2014). In addition, the moderate disturbance class described by Cowden et al. (2014) did not include neighborhoods of catastrophic disturbance, which were embedded in the contiguous moderate disturbance class of the 2 ha plot. Thus, patterns of increased tree diversity may only be apparent when considering neighborhoods of severe disturbance. Puettmann et al. (2009) suggested the use of spatially explicit field methods to document patterns of intra-stand heterogeneity at the neighborhood scale, as stand averages assume stand homogeneity. Because species richness is scale dependent and neighborhoods varied in size, I could not conclude definitive differences in species richness.

Values of evenness and diversity describe the contribution of a species to the diversity of a stand, but neither considers the spatial distribution of species within a stand. The distribution of species among each other (i.e. interspersed or mingling of species) elucidates diversity at a finer scale and describes intra-stand patterns of composition (Graz 2004). Prior to disturbance, M_i values were higher across all disturbance classes than post-disturbance values, consistent with studies in managed stands (Saunders and Wagner 2008). Therefore, the removal of stems resulted in a less dispersed distribution of species and more “clumps” of similar species. However, the distribution of the post-disturbance M_i indicated that most stems of a species occur alone rather than in groups. The M_i of individual species across all disturbance classes revealed that *F. grandifolia* and *O. virginiana* had the lowest species-specific M_i , indicating that these species are more likely to occur in groups. *Fagus grandifolia* tends to produce root sprouts and grow in groups close to a parent tree (Jones and Raynal 1986). However, the low M_i for *O. virginiana* may be a result of high densities and therefore a higher likelihood of occurring next to one another.

4.4.3 Mortality related to species and size

Larger stems were disproportionately removed by the intermediate-scale disturbance, which is consistent with other findings (Foster and Boose 1992, Peterson 2007, Rich et al. 2007, White et al. 2015). However, logistic regression analysis revealed certain taxonomic trends as well. No significant effects were present in the minimal disturbance class. However, the light disturbance class revealed *O. virginiana* and the interaction of *Carya* and DBH were significant effects. *Ostrya virginiana* was inversely related with tree mortality and thus had a lower probability of being affected by the storm. Likewise, Batista and Platt (2003) documented that *O. virginiana* were not as susceptible to mortality by a hurricane. Although no interaction between *O. virginiana* and DBH was not a significant effect, the canopy position of *O. virginiana* stems may have contributed to a lower probability of stems being affected by the storm. Interestingly, *Carya* stems exhibited an increased probability of mortality. Peterson and Rebertus (1997) and Peterson (2007) did not find a statistically increased probability for *Carya* spp. However, Peterson and Rebertus (1997) reported 42% mortality for *C. lacinosa* Michx. f.. Notably, *Carya* was never a significant effect separate from DBH. In the moderate disturbance class, DBH was the only significant effect. This was consistent with other studies that have shown that increased disturbance intensity tends to result in fewer species-specific effects and only will reveal diameter or tree size as a factor in tree mortality (Peterson 2000, Peterson 2007). For overall tree mortality within the 2 ha plot, both DBH and the interaction of *Carya* and DBH were included in the logistic regression model, likely because of the higher proportion of midsized decay class 1 *Carya* stems, as was consistent with trends in the light disturbance class. The increased mortality of *Carya* is contradictory to its status as windfirm, characterized by strong wood and a large taproot. However, *Carya* may have been impacted more because of the density of the wood

(Phillips 1973). With increased swaying, momentum may have caused the stem to break or uproot (Frelich 2002). *Carya* stems were almost equally snapped or uprooted and did not exhibit trends toward either mode of death by disturbance class. Half of *Carya* stems were removed in the moderate disturbance class, compared to 31% in the light disturbance class and 11% in the minimal disturbance class. Over the entire plot, 30% of *Carya* stems were classified as decay class 1. Although *Carya* was disproportionately removed by the storm, the relatively low density of *Carya* stems within the entire plot may impact the significance of the effect in the logistic regression model. Studies in adjacent stands did not note the disproportionate removal of any species (White et al. 2015).

Although only 7% of *O. virginiana* stems were classified as decay class 1, *O. virginiana* composed 21% of decay class 1 stems, the majority of which were snapped or uprooted (Figure 4.5). In the light disturbance class, 71% of decay class 1 *O. virginiana* stems were snapped, whereas 42% of stems in the moderate disturbance class were snapped. *O. virginiana* stems were most commonly uprooted in the moderate disturbance class (54%). Because of the sheltered position of small *O. virginiana* stems, the majority of uprooted *O. virginiana* stems were not uprooted as a single uprooted stem, but rather were uplifted in a rootball of another uprooted stem, especially in the moderate disturbance class. Likewise, snapped *O. virginiana* stems may have been affected by other downed stems rather than by wind disturbance alone. These hypotheses are supported by the average distances from uprooted and snapped *O. virginiana* stems to the nearest uprooted or snapped stem. The average distance of an uprooted *O. virginiana* stem to the nearest uprooted stem was 0.76 ± 1.06 m, which was shorter than the average distance of a snapped *O. virginiana* stem to the nearest snapped stem (2.02 ± 1.29 m) or uprooted stem (3.04 ± 1.69 m).

Species-scale analyses of mortality trends across all disturbance classes revealed that *C. ovata*, *J. virginiana*, and *Q. rubra* were disproportionately removed by the storm. These species were identified based on the ratio of percent decay class 1 stems to percent of live stems. The higher occurrence of *C. ovata* stems classified as decay class 1 reflected the interaction of diameter and *Carya* spp. in the logistic regression models. Peterson (2007) documented a wind disturbed stand with high density of *J. virginiana* and *J. virginiana* exhibited intermediate vulnerability to wind disturbance. This may be a function of wood strength or rooting habit (Peterson 2007). *J. virginiana* stems tend to have very fibrous roots when grown in rocky soils. In the light disturbance class, the majority of *J. virginiana* stems were snapped, whereas in the moderate disturbance class the majority of stems were uprooted. Unlike *O. virginiana* stems, the average distance of decay class 1 *J. virginiana* stems to the nearest uprooted or snapped stem was > 2 m. Thus, *J. virginiana* stems may have been affected by other snapped and uprooted stems, but were most likely not uplifted in a rootball with another stem. A relatively large proportion of *Q. rubra* stems were in decay class 1, similar to Cooper-Ellis et al. (1999) and Peterson (2007). Peterson (2007) noted that although *Q. rubra* has relatively flexible wood, more *Q. rubra* stems were damaged than *Q. alba* stems.

Fagus grandifolia and *N. sylvatica* were disproportionately retained. A higher density and dominance of *F. grandifolia* occurred in the minimal disturbance class, which may be a result of its natural clumping from root suckers (Jones and Raynal 1986). Thus, the pre-disturbance condition may have influenced the species' retention. Peterson (2007) found that *Fagus grandifolia* had higher probability of mortality in larger diameter classes. However, because of the relatively high density of *F. grandifolia* stems in small diameter classes compared to large diameter classes, fewer stems were affected by the storm. Additionally, *F. grandifolia*

tend to have compact crowns that are less susceptible to windthrow (Carpenter 1974, Rich et al. 2007). *Nyssa sylvatica* is resistant to many disturbance types, including fire, wind, flood, and drought, and may remain in the understory stratum for two centuries (Abrams 2007). Batista and Platt (2003) described *N. sylvatica* as persistent after a hurricane, which is similar to the response of *N. sylvatica* after a low severity tornado. Although *N. sylvatica* is resistant to various disturbances, stems of this species rarely benefit as a result of disturbance and are among the slowest growing in the eastern United States (Abrams 2007).

4.5 Management implications

Natural disturbance-based silviculture, which attempts to emulate the effects of a natural disturbance, is an increasingly popular management strategy, especially on public lands (Long 2009, Franklin and Johnson 2012). The purpose of natural disturbance-based silviculture is not to mimic the process of a natural disturbance, but rather to mimic the biological legacies left by the disturbance (Franklin et al. 2002). This management approach is hypothesized to maintain ecosystem function and promote resilience and native species diversity (Long 2009). The extent to which managers emulate these biological legacies is dependent upon individual management objectives and adoption of a natural disturbance-based approach does not necessitate a change in desired stand conditions. Wind is the most common and perhaps the most influential disturbance in temperate forests and thus, may be used as a reference for natural disturbance based-management (Runkle 1985, 1996, Fisher et al. 2013). However, to successfully implement natural disturbance-based silvicultural practices, quantitative descriptions of naturally disturbed stands are required as references of biological legacies (Seymour et al. 2002, Franklin et al. 2007).

Results from my study indicate that the intermediate-scale wind event resulted in increased intra-stand structural and compositional heterogeneity. By analyzing the spatial patterns of composition and structure, intra-stand patterns revealed that the storm decreased species interspersion, i.e. surviving stems occurred more frequently in groups of the same species, whereas stems occurred more frequently in groups of differing species prior to the disturbance. Throughout the study area, basal area removed ranged from 8% to 45%, with 22% removed on average. I recommend that stand-wide basal area retention remain between 40–80%, but treatments to remove basal area should be applied in groups. An irregular group shelterwood with reserves or a group selection system are options for silvicultural systems that may yield structures similar to the biological legacies left by a low severity tornado. I recommend that initial group sizes range from 0.01 to 0.5 ha. Though this may homogenize neighborhoods, the structural heterogeneity at the stand scale would increase (Boyden et al. 2012). Managers may wish to vary sizes of these groups to promote regeneration of stems of various shade tolerance (*sensu* Lhotka 2013). To emulate patterns of the wind event, managers should preferentially remove large stems (> 30 cm DBH).

Quercus regeneration failure has been documented in the Central Hardwood Forest Region (Abrams 1992, Lorimer 1993, Nowacki and Abrams 2008, McEwan et al. 2011). Managers that wish to maintain *Quercus* in stands with a pre-existing shade-tolerant component in the midstory may need to make concessions on emulating structures resulting from natural disturbance. Shelterwood systems are most commonly used to regenerate *Quercus* (Loftis 1990, Stringer 2006, Schweitzer and Dey 2011), but preparatory and final harvests are implemented evenly throughout a stand. To promote *Quercus* regeneration and more closely emulate the legacy structure left by an intermediate-scale wind disturbance compared to a two-phase

shelterwood, managers may implement group selection harvests around existing patches of advanced *Quercus* regeneration (i.e. stems ≥ 1.4 m in height). Surrounding the gap, a midstory removal preparatory cut may be used to reduce competition of mesophytic species and promote growth of *Quercus* seedlings around the gap edge, as *Quercus* reproduction responds positively to edge effects of clearings (Lhotka and Stringer 2013). The diameter of initial gaps should be at minimum equal to the height of surrounding trees to achieve adequate light levels (20–50% full sunlight) for *Quercus* reproduction growth (Marquis 1965, Dey 2002). In subsequent entries, managers may create new gaps or expand existing gaps. However, to increase edge effects, expanded gaps should be situated tangentially rather than concentrically in relation to the initial gap. Based on specific management objectives, managers must consider the importance of timber revenue and the importance of following a close-to-nature management approach. Ultimately, managers must decide to what extent concessions should be made to implement a natural disturbance-based management approach.

CHAPTER 5

STRUCTURAL COMPLEXITY AND DEVELOPMENTAL TRAJECTORY

5.1 Introduction

The overarching goal of this study is to describe the structural complexity and development of an upland *Quercus* stand after a moderate severity wind event based on structural characteristics and the spatial pattern of individual stems. My specific objectives are to: 1) describe the effect of an intermediate-scale wind event on the structure of neighborhoods within a stand, 2) describe the structural complexity of neighborhoods of increasing disturbance severity, and 3) relate structural complexity to the stages of development to project the developmental trajectory of the stand. The results from this study will provide a comprehensive understanding of structural attributes in upland *Quercus* stands after an intermediate-scale wind event and may be used to refine silvicultural systems intended to enhance structural complexity and minimize the disparity between natural and managed stands.

5.2 Data Analysis

To compare patterns of structural complexity among disturbance severity classes, I divided the 2 ha plot into three disturbance classes (minimal, light, and moderate) based on decay class 1 basal area (see Chapter 4.2). Within each disturbance severity class, trees were divided into 5 cm size bins to create diameter distributions. Q-factors were calculated for each disturbance class (Nyland, 2002). Diameter distribution shapes were determined following

methods of Leak (1996) and Janowiak et al (2008) (see Chapter 4.2). To compare the effects of the storm on the structure of each disturbance severity class, I calculated the quadratic mean diameter (QMD) and standard deviation of DBH for each disturbance class.

To describe the structural complexity of each disturbance class, I calculated values for the Gini coefficient, Clark–Evans aggregation index, diameter differentiation index, and structural complexity index. The Gini coefficient (*GC*) may describe how evenly basal area is distributed among stems on a scale from 0 to 1 (Gini 1912, Weiner and Solbrig 1984). A *GC* value of 0 indicates that the basal area is evenly distributed among stems; a *GC* value of 1 indicates the basal area is completely unevenly distributed among stems. The Clark–Evans aggregation index (*R*) characterizes the spatial distribution of stems within a designated area (clustered, random, or uniform; Clark and Evans, 1954). The diameter distribution index (*DT*; Fuldner 1995) quantifies the difference in tree size based on the diameter of each tree within a plot and the four nearest neighbors of the focal tree. This metric describes the distribution of stem size in neighborhoods of five individuals, rather than other metrics such as the standard deviation of diameters and the *GC*, which focus on the distribution of diameter values around the mean diameter and the entire plot. Values range from 0 to 1, with 0 representing neighborhoods within a plot that have no size differentiation and 1 representing neighborhoods within a plot that have maximum size differentiation. Pommerening (2002) specified *DT* values of 0–0.3 to represent small differentiation, 0.3–0.5 to represent average differentiation, 0.5–0.7 to represent large differentiation, and 0.7–1 to represent very large differentiation. Unlike other spatial structural metrics, the structural complexity index (*SCI*; Zenner and Hibbs 2000) is spatially explicit and describes stands with three-dimensional structural characteristics. The *SCI* uses x,y coordinates of stem-mapped trees and incorporates a third variable for each tree to spatially analyze the stand

on an individual tree basis rather than using summary statistics. This third variable can be any numerical attribute for the tree such as DBH or height. This method creates a Delaunay triangular network that connects neighboring points without overlap. The *SCI* is calculated from the ratio of the surface area of the triangulation network formed by the z-values to the area sampled. I calculated the *SCI* for each disturbance class using both height (SCI_{height}) and DBH (SCI_{DBH}) as structural attributes. For the *GC*, *R*, *DT*, and SCI_{DBH} , I calculated both the value for living trees (i.e. post-disturbance condition) and the value for living and decay class 1 stems (i.e. pre-disturbance condition).

To describe the patterns of mortality within each disturbance class, I determined the *R* value for decay class 1 stems. I also used an extension of the M_i to analyze the interspersion of decay class 1 stems among live stems (deadwood Mingling index (M_d); Laarmann et al. 2009). To calculate the M_d value for each disturbance class, I coded each stem as either living or decay class 1, rather than by species (see Chapter 4.2, Pommerening 2002). For calculations of *GC*, *R*, *DT*, *SCI*, and M_d , I used a 5 m buffer zone for each irregularly shaped disturbance severity class to reduce edge-bias (Pommerening and Stoyan 2006).

To describe the stand size class and stage of development of the stand, I classified the neighborhoods in each disturbance class by the percent basal area in each of the following categories: small trees (5–12.4 cm DBH), pole trees (12.5–27.4 cm DBH), sawtimber trees (27.5–44.9 cm DBH), and large sawtimber trees (≥ 45 cm DBH; Bechtold and Patterson 2005, White et al. 2015). To determine the stand size class of each neighborhood, I modified the decision tree outlined in Lorimer and Halpin (2014) to fit basal area values for mature *Quercus* stands on the Cumberland Plateau and adjacent regions (Figure 5.1; Parker 1989, Martin 1992, Hart et al. 2012, Hart et al. 2015). For a stand to be classified as mature or old growth, Lorimer

and Halpin (2014) required that the basal area of mature and large stems be $\geq 20 \text{ m}^2 \text{ ha}^{-1}$. For a stand to be classified as mature-sapling mosaic, basal area of mature and large stems must be $\geq 10 \text{ m}^2 \text{ ha}^{-1}$ and to be classified as a pole stand, basal area of pole, mature, and large stems must be $10 \text{ m}^2 \text{ ha}^{-1}$ and pole basal area must be $\geq 30\%$ of the total. However, because the basal area range of mature and old growth northern hardwood stands ($37\text{--}48 \text{ m}^2 \text{ ha}^{-1}$, Lorimer and Halpin 2014) is greater than the range of old growth stands in the Central Hardwood Forest Region ($25\text{--}35 \text{ m}^2 \text{ ha}^{-1}$, Parker 1989, Martin 1992), I altered basal area requirements from $20 \text{ m}^2 \text{ ha}^{-1}$ to $12 \text{ m}^2 \text{ ha}^{-1}$ and from $10 \text{ m}^2 \text{ ha}^{-1}$ to $6 \text{ m}^2 \text{ ha}^{-1}$ for the mature-old growth and mature-sapling mosaic classes, respectively (Figure 5.1). The term “old growth” in Figure 5.1 is taken from Lorimer and Halpin (2014); I acknowledge that this term implies a relationship between structure and age that may not be apparent in stand size classifications. The stand size classes relate to stages of development outlined by Johnson et al. (2009) (i.e. stand initiation, stem exclusion, understory reinitiation, and complex) and include a mature-sapling mosaic stand size class which corresponds to the mixed stage of development.

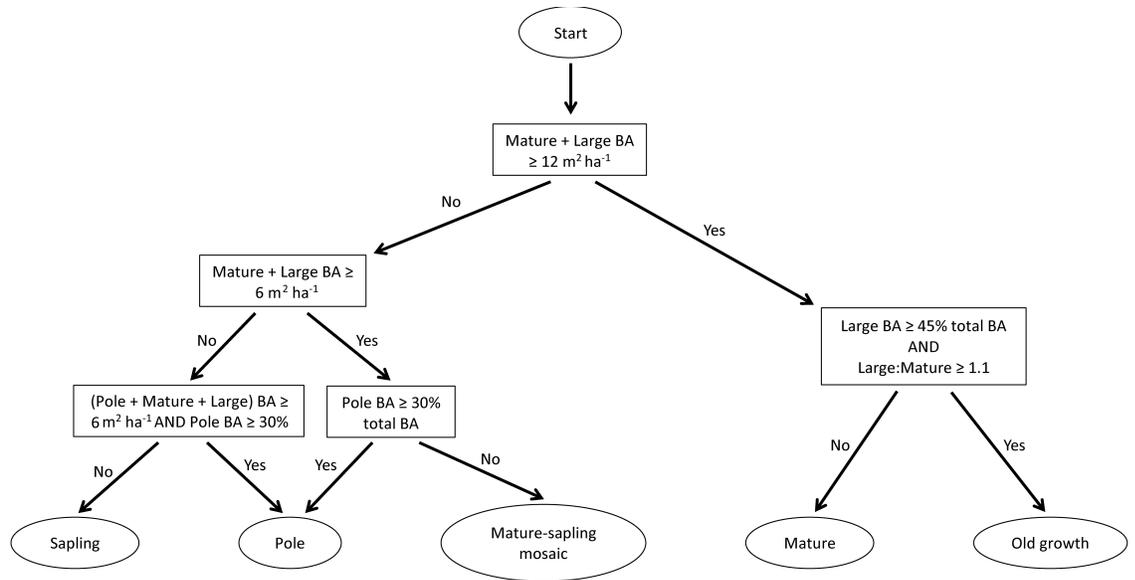


Figure 5.1 Decision tree for classifying stand size class for *Quercus* stands in the Central Hardwood Forest Region. Stem size classes include: sapling (5–12.4 cm DBH), pole (12.5–27.4 cm DBH), mature (27.5–44.9 cm DBH), and large trees (≥ 45 cm DBH)

5.3 Results

5.3.1 Effects on neighborhood structure

Basal area of live stems in minimal, light, and moderate disturbance classes was 23.5 m^2ha^{-1} , 23.2 m^2ha^{-1} , and 13.7 m^2ha^{-1} , whereas basal area in decay class 1 for each disturbance class was 2.1 m^2ha^{-1} , 5.1 m^2ha^{-1} , and 11 m^2ha^{-1} . Including background mortality rate for adjacent upland *Quercus* stands reported in Cowden et al. (2014) and White et al. (2015), basal area of decay class 1 removed by the April 2011 tornado was 1.8 m^2ha^{-1} , 4.7 m^2ha^{-1} , and 10.7 m^2ha^{-1} for the minimal, light, and moderate disturbance class. Thus, basal area was reduced by 7%, 17%, and 43% for the minimal, light, and moderate disturbance class, respectively. The light disturbance class had the highest density of stems with 212 stems with 5–10 cm DBH more than the minimal disturbance class. Density of decay class 1 stems was 24.5 stems ha^{-1} , 78.4 stems ha^{-1} , and 200 stems ha^{-1} for minimal, light, and moderate disturbance classes, respectively. QMD for live stems was 21, 19, and 17 for minimal, light, and moderate disturbance classes, whereas QMD for decay class 1 stems was 44, 31, and 35, for minimal, light, and moderate disturbance classes. The diameter distribution for all disturbance classes were classified as negative exponential shapes with q-factors of 1.6, 1.7, and 1.4 for the minimal, light, and moderate disturbance classes, respectively (Figure 5.2).

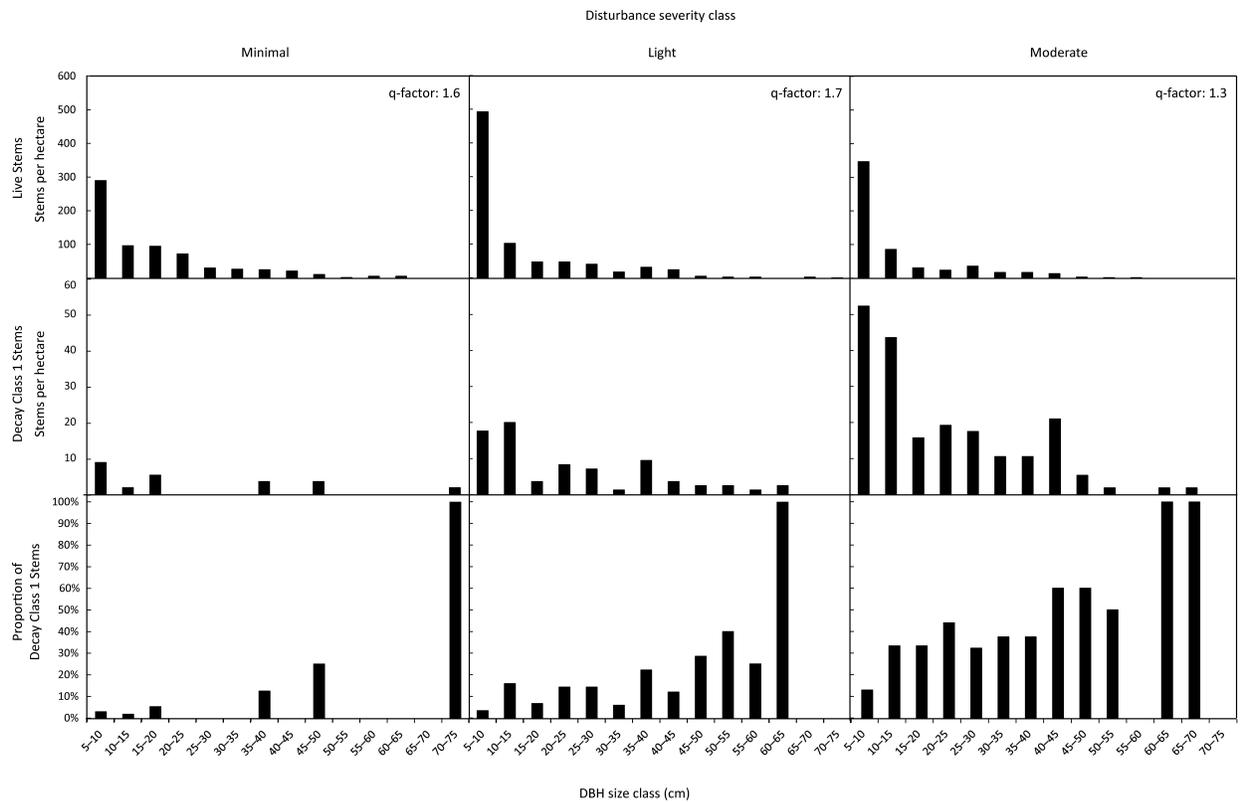


Figure 5.2 Density (stems ha⁻¹) of live trees (stems ≥ 5 cm DBH) by 5 cm diameter size class bins across three disturbance severity classes on the Sipsey Wilderness, William B. Bankhead National Forest, Alabama. Proportion of decay class 1 stems was calculated for each diameter size bin within each disturbance size class

For live stems, *GC* values were 0.68, 0.73, and 0.69 for the minimal, light, and moderate disturbance classes, respectively. For pre-disturbance conditions, *GC* values were 0.68, 0.72, and 0.69 for the minimal, light, and moderate disturbance classes, respectively. Trees were removed from all size classes in each disturbance class, but larger stems were removed in larger proportions (see Chapter 4.3).

Most decay class 1 stems were snapped (51% across all disturbance classes; Figure 5.3). In the minimal disturbance class, 29% decay class 1 stems were snags, 57% were snapped, and 14% were uprooted. In the light disturbance class, 15% were snags, 55% were snapped, and 30% were uprooted. In the moderate disturbance class, 11% decay class 1 stems were snags, 47% were snapped, and 42% were uprooted.

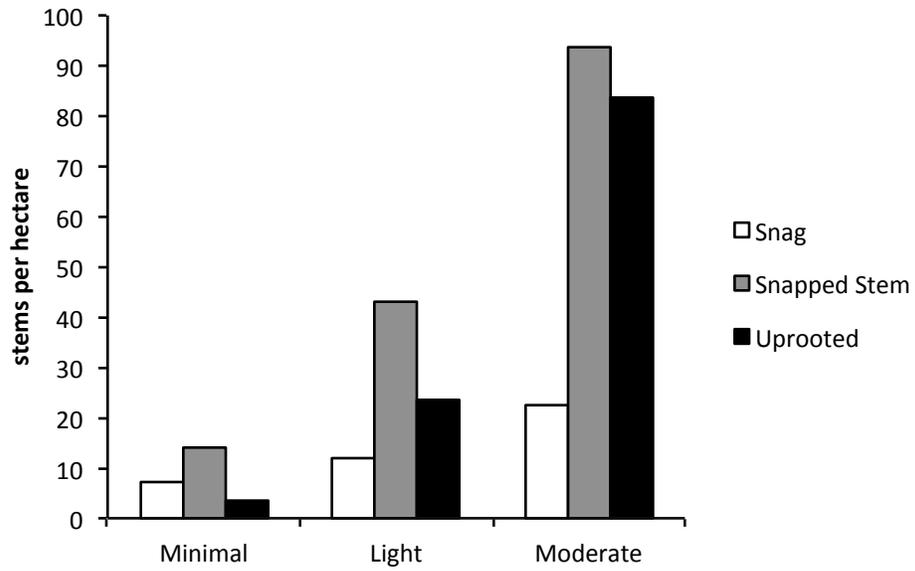


Figure 5.3 Mode of death and density (stems ha⁻¹ for decay class 1 stems across three disturbance severity classes (minimal, light, moderate) on the Sipsey Wilderness, William B. Bankhead National Forest, Alabama

5.3.2 Structural complexity

Based on the Clark-Evans aggregation index, live stems were regularly distributed in the minimal and light disturbance classes ($R=1.14, 1.07$) and randomly distributed in the moderate disturbance class ($R=0.97$). Decay class 1 stems were regularly distributed in the minimal disturbance class ($R=1.88$), randomly distributed in the light disturbance class ($R=0.97$), and clustered in the moderate disturbance class ($R=0.66$). As such, the patterns of stem mortality resulted in a more uniform distribution of living stems post-disturbance. M_d values for live and decay class 1 stems were 0.11, 0.16, and 0.34 for minimal, light, and moderate disturbance classes, respectively. The values for DT for the minimal, light, and moderate disturbance classes were 0.46, 0.43, and 0.43, respectively. Values for diameter differentiation indices for both live and decay class 1 stems were 0.47, 0.43, and 0.46.

Based on the SCI , the light disturbance class was the most structurally complex ($SCI_{height}=3.70, SCI_{DBH}=5.33$). The SCI_{height} of minimal and moderate disturbance classes were 2.96 and 2.76, respectively. The SCI_{DBH} of minimal and moderate disturbance classes were 4.76 and 3.50, respectively. The SCI_{DBH} including both live and decay class 1 stems was 1.37, 1.34, and 1.49 for the minimal, light, and moderate disturbance classes, respectively (Table 5.1).

Table 5.1 Complexity indices for three disturbance severity classes (minimal, light, moderate) on the Sipsey Wilderness, William B. Bankhead National Forest, Alabama. “Pre” values indicate index values for live and decay class 1 stems. “Post” values indicate index values for live stems only. *GC*=Gini coefficient; *R*=Clark–Evans aggregation index; *DT*=diameter differentiation index; *SCI_{DBH}*=structural complexity index using DBH; *SCI_{height}*=structural complexity index using tree height; *M_d*=deadwood mingling index.

Index	Minimal		Light		Moderate	
	Pre	Post	Pre	Post	Pre	Post
<i>GC</i>	0.68	0.68	0.72	0.72	0.69	0.69
<i>R</i>	Uniform	Uniform	Random	Uniform	Random	Random
<i>DT</i>	0.47	0.46	0.43	0.43	0.46	0.43
<i>SCI_{DBH}</i>	1.37	4.76	1.34	5.34	1.49	3.5
<i>SCI_{height}</i>	–	2.96	–	3.7	–	2.76
<i>M_d</i>	–	0.07	–	0.15	–	0.34

5.3.3 *Developmental trajectory of stand*

Among product classes, large trees were reduced by the largest percent (53%) in density, from 29.8 stems ha⁻¹ to 13.9 stems ha⁻¹, between the minimal and moderate disturbance class (Figure 5.4). Large trees also exhibited the largest percent decrease (62%) in basal area, from 7.6 m²ha⁻¹ to 2.9 m²ha⁻¹, between the minimal and moderate disturbance class. All disturbance severity neighborhoods were categorized as mature–sapling mosaic stand size classes. The minimal disturbance class had 15.3 m²ha⁻¹ of combined mature trees and large trees basal area and pole basal area contributed 29% to total basal area. The light disturbance class had 15.6 m²ha⁻¹ of combined mature tree and large tree basal area; pole basal area contributed 21% to total basal area. The moderate disturbance class had 8.3 m²ha⁻¹ of combined mature and large tree basal area and pole basal area contributed 26% to total basal area.

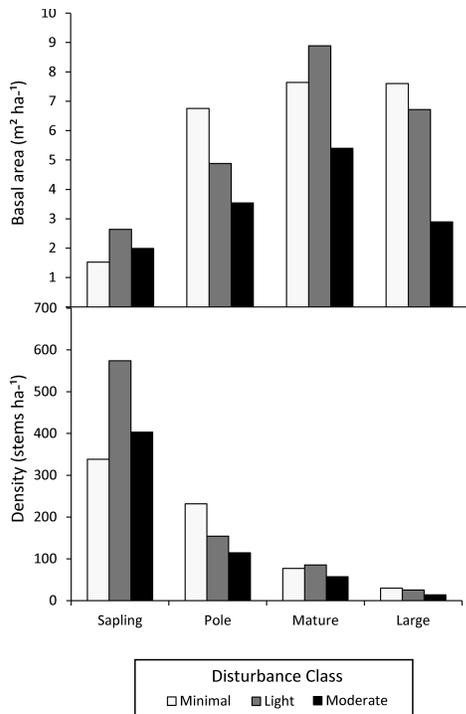


Figure 5.4 Basal area (m²ha⁻¹) and density (stems ha⁻¹) of stems in product size classes across three disturbance severity classes on the Sipsey Wilderness, William B. Bankhead National Forest, Alabama. Size classes include: saplings (5–12.4 cm DBH), pole (12.5–27.4 cm DBH), mature (27.5–44.9 cm DBH), and large trees (≥ 45 cm DBH).

5.4 Discussion

5.4.1 Structural effects

The q-factor and diameter distribution shape were similar across each disturbance severity class (Figure 5.2). All disturbance severity classes exhibited a negative exponential diameter distribution shape, indicative of uneven-sized structure (Rubin et al. 2006). Interestingly, the minimal disturbance class had the largest live QMD and decay class 1 QMD. The largest decay class 1 stem (75 cm snapped stem) was situated in the minimal disturbance class; in conjunction with the relatively few decay class 1 stems in the minimal disturbance class, the QMD for decay class 1 stems for the minimal disturbance class was high. The decay class 1 QMD was higher in the moderate disturbance class than the light disturbance class, which is consistent with the increased probability of larger stems being removed by increased wind intensity (see Chapter 4; Foster and Boose 1992, Peterson 2007).

Unexpected variations in structure among disturbance severity classes, such as the large QMD for decay class 1 stems in the minimal disturbance class and the high density of stems in the light disturbance class, may be a result of the field sampling design and division of the plot into contiguous disturbance severity classes. Had the disturbance severity classes been chosen using 20×20 m quadrats without concern for contiguity, neighborhoods within the minimal disturbance class may have been considered light disturbance, whereas neighborhoods in the light disturbance class may have been considered minimal or moderate disturbance. Indeed, some neighborhoods within the 2 ha plot were undisturbed and may have represented pre-disturbance conditions and served as a “control.” Patterns of disturbance are scale-dependent (Wiens 1989) and the spatial resolution at which data is analyzed is dependent upon the

disturbance type (Zenner et al. 2015b). For management-focused analyses of wind disturbance, stand-scale observations may be appropriate for determining basal area removed. Fine-scale data analyses are needed to determine neighborhood scale-structural effects that may inform stand-scale structural heterogeneity.

5.4.2 Structural complexity

Spatial patterns of tree mortality revealed that decay class 1 stems were clustered in the moderate disturbance class, random in the light disturbance class, and uniform in the minimal disturbance class. Because of these differing patterns of stem mortality among neighborhoods, the spatial distribution of living stems within each neighborhood were more uniform as a result of the disturbance. Similarly, Myster and Malahy (2010) found that spatial patterns of stems exhibited a more uniform distribution after an EF1 tornado affected a *Quercus stellata* stand. Xi et al. (2008) found that spatial patterns of stem mortality were uniform at finer resolutions and clustered at broader resolutions, reiterating the scale-dependence of disturbance patterns. Similarly, mortality within the entire stand was clustered near the path of the tornado and appeared to be uniform at finer spatial scales. These differing patterns in stem mortality by disturbance class neighborhood may be the result of varying wind intensities, where highest intensities likely occurred at the center of the tornado track and generally decreased with distance from the center of the track (Battan 1984). Decay class 1 stems were more interspersed within the moderate disturbance class compared to the minimal disturbance class. Although the values may increase based on increased density of decay class 1 stems alone, M_d values indicated more aggregated patches of dead stems in the light and moderate disturbance classes. Laarmann et al. (2009) suggested that M_d values could be used to determine if a stand had recently experienced a

large disturbance; in sampled stands, the M_d value of stands that were recently disturbed was 0.29. The implementation of such spatial indices elucidates fine-scale structural heterogeneity. Differences in spatial patterns at different spatial scales highlight the need to consider intra-stand heterogeneity when making managerial decisions at the stand level (O'Hara and Nagel, 2013).

The distribution of basal area among stems was not altered by the intermediate-scale wind event. Studies from managed stands have found GC to remain constant after treatment (McGown et al 2015; D'Amato et al 2011). However, D'Amato et al. (2011) only found this trend in stands that were thinned from above; stands that were thinned from below exhibited a decreased GC followed by an increased GC over time. The disproportionate removal of large stems by the wind event was more similar to a thin from above, thus the lack of change in GC was consistent with similar treatments. GC values from the *Q. alba* stand were similar to those in old-growth *Fagus orientalis* Lipsky stands ($GC=0.7$; Zenner et al., 2015a). DT values decreased in the moderate disturbance severity class because of the disproportionate removal of stems. The largest DT occurred in the minimal disturbance class; however, all neighborhoods were considered to have average diameter differentiation (Pommerening 2002). Based on values of the GC and DT index, I was not able to differentiate between disturbance severity classes.

The light disturbance class consistently had the highest SCI value for both DBH and height, whereas the moderate disturbance class was the least structurally complex. However, both disturbance classes exhibited an increase in structural complexity compared to pre-disturbance conditions. Interestingly, based on SCI_{DBH} values that included live and decay class 1 stems, the moderate disturbance class was the most structurally complex prior to the wind event, whereas the light disturbance class had the lowest structural complexity prior to the disturbance. As such, based on SCI_{DBH} values, the complexity of the moderate disturbance neighborhood

increased the least, whereas the complexity of the light disturbance class increased the most. The differences in SCI_{DBH} values for surviving stems between the light and moderate disturbance class were likely because of the disproportionate removal of large stems in the moderate disturbance class compared to the light disturbance class. Mortality in the light disturbance class was randomly distributed and therefore resulted in a relatively high frequency of small gaps rather than relatively low frequency of large gaps, as in the moderate disturbance class. Zenner (2004) consistently found that the SCI was highest for old growth stands in the Pacific Northwest U.S.A. In contrast, *F. orientalis* stands in northern Iran in the initial stage of development were the most structurally complex (Zenner 2015a). However, these *F. orientalis* stands were largely monospecific. Structural complexity in Acadian “mixedwood” stands was highest in natural areas over a 30 year period followed by stands with a five year single tree selection harvest (Saunders and Wagner 2008). The SCI has not been applied to *Quercus* stands in the temperate zone, thus I was only able to compare relative trends in SCI values.

Compared to pre-disturbance values across all disturbance severity classes, R , GC , and DT all indicated a decrease in structural complexity, characterized by an increased uniformity of stem spatial patterns and increased equality in the distribution of basal area among stems. Conversely, M_d and SCI increased as a result of the disturbance. I hypothesize that the decreased R and DT values are primarily a result of a decreased number of stems resulting in a more uniform spatial distribution and the disproportionate removal of large stems. At the stand scale, the intermediate-scale disturbance increased the structural heterogeneity of the stand, as indicated by differences in disturbance severity classes. However, neighborhoods within the stand may have decreased in structural complexity (Boyden et al. 2012, Fahey et al. 2015). Patterns of structural heterogeneity manifest at different spatial scales (Wiens 1989). The

intermediate-scale wind event resulted in a matrix of small, homogeneous neighborhoods situated adjacent to different yet homogenous neighborhoods. Thus, at the stand scale, structural heterogeneity increased.

5.4.3 Developmental trajectory of stand

Although mature trees were disproportionately removed in the moderate disturbance class, all disturbance severity neighborhoods were classified as a mature–sapling mosaic size class (Lorimer and Halpin 2014). When decay class 1 stems were included to estimate pre-disturbance stand conditions, all neighborhoods were classified as a mature stand size class. The mature stand size class corresponds to the understory reinitiation stage of development as defined by Oliver and Larson (1996) and Johnson et al. (2009). Therefore the intermediate-scale disturbance altered the structure of each disturbance severity class, which resulted in different stand size classifications. Prior to the disturbance, approximately 30% of basal area was distributed among large trees across all disturbance classes. The sapling size class represented approximately 9% of total basal area across all disturbance classes. However, after the disturbance, 20% of basal area in the moderate disturbance class was distributed among large trees, compared to 29% in the light disturbance class and 32% in the minimal disturbance class. The percent basal area distributed among saplings was 11% in the light disturbance class and 14% in the moderate disturbance class. Shifts in basal area distributed among size classes highlights the change in stand structure and subsequently, the developmental trajectory.

The mature-sapling mosaic is described as any stand size class that does not meet criteria for sapling, pole, mature, or old growth stands; these stands are those that have been affected by a moderate disturbance or are in a transitional phase (Frelich and Lorimer 1991, Hanson and

Lorimer 2007, Lorimer and Halpin 2014). This stand size class corresponds to the mixed stage of *Quercus* development described by Johnson et al. (2009). Johnson et al. (2009) described the mixed stage of development as the state of a stand after an incomplete-stand disturbance that does not result in the stand initiation stage of development. This definition encompasses a myriad of possible stand structures that vary based on the disturbance type, intensity, and magnitude, including *Quercus* savannas, high-graded stands, and stands affected by intermediate-scale wind disturbances. Indeed, Johnson et al. (2009) stated that because of this encompassing definition, *Quercus* stands in the mixed stage of development are “ubiquitous.” Because of the breadth of the mixed stage of development, quantitative descriptions are needed to describe variability of stand structure in this stage. Long-term data collection is needed to project developmental trajectories of stands in the mixed stage.

Intermediate-scale disturbances vary in magnitude, intensity, and, importantly, spatial pattern. For example, an ice storm may result in similar basal area removal as a low intensity tornado, but basal area removal may be distributed evenly throughout the stand after the ice storm whereas mortality from a tornado disturbance may be concentrated close to the storm track. The path of the 2011 storm affected approximately 438 ha of the Sipsey Wilderness and transected the sampled *Q. alba* stand (see Figure 2.1). The tornado affected 44 ha (24%) of the 182 ha stand. As such, the effects of the disturbance were concentrated at the center of the path, i.e. the moderate disturbance severity class. With increasing distance from the center of the path, patterns of disturbed areas were patchy, characterized by single and multi-treefall gaps interspersed in undamaged groups of stems (Cowden et al. 2014, White et al. 2015). This disturbance severity gradient extending from the center of the tornado path increased intra-stand structural heterogeneity.

5.5 Management implications

The creation and maintenance of structural heterogeneity is an increasingly popular management objective, especially on multiple use lands (Franklin et al. 2002, Palik et al. 2002, Saunders and Wagner 2008, Puettmann 2011, O'Hara and Ramage 2013, O'Hara 2014). Natural disturbances often increase structural heterogeneity (Spies 1998, White and Jentsch 2001). As natural disturbance-based silviculture attempts to emulate the residual structure after a natural disturbance event (Franklin et al. 2002, Franklin et al. 2007), this management approach may be implemented to achieve increased structural complexity. Notably, complex stand structures may also be created through approaches other than natural disturbance-based management.

Based on the patchiness of tree mortality after the intermediate-scale wind event, I recommend for managers who wish to emulate natural disturbance to consider applying treatments to neighborhoods within a stand rather than distributing treatments evenly throughout a stand. Silvicultural systems such as the group selection system or irregular shelterwood may increase structural complexity and simultaneously emulate the biological legacies of an intermediate-scale wind event. As shelterwood systems are commonly implemented to promote *Quercus* regeneration, a variation of the regular shelterwood system may be an appropriate choice to incorporate a natural disturbance-based approach to regenerate *Quercus*. Unlike a regular shelterwood system, an irregular shelterwood retains overstory trees for a longer rotation and allows new cohorts to have a longer regeneration period (Hannah 1988). Raymond et al. (2009) specified three variations of the irregular shelterwood system: expanding-gap, continuous cover, and extended. The expanding-gap irregular shelterwood regenerates cohorts by enlarging groups until the stand is removed (Spurr 1956, Seymour 2005). The continuous cover shelterwood allows for freely spaced and timed cuttings and is based on the autecology of

existing species and site type (Spurr 1956). The extended regular shelterwood delays the final removal of the overstory by more than 20% of the rotation period (Nyland 2002). A variation of the expanding-gap irregular shelterwood is the irregular group shelterwood with reserves. However, this system does not require the expansion of initial gaps.

I recommend implementing the irregular group shelterwood with reserves to increase the structural complexity and intra-stand heterogeneity of a stand. Initial gaps created may vary in size from 0.01 to 0.5 ha, similar to the gaps resulting from the intermediate-scale wind disturbance. Managers may alter the initial gap size of the irregular group shelterwood based on the light requirements of desired species (Lhotka et al. 2013). Reserves may be left in variable densities to promote certain wildlife habitat or retain desired structural legacies. Additionally, variable density thinning within a stand may enhance structural complexity (Franklin et al. 1997, Mitchell and Beese 2011, Gustaffson et al. 2012). Guidelines for the creation and maintenance of structurally complex stands should be adaptive to pre-existing stand conditions. Managers should be creative when choosing silvicultural systems and may choose to combine practices of multiple systems (i.e. “freestyle silviculture”; Boncina 2011, O’Hara 2014) to achieve desired management objectives.

CHAPTER 6

CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE RESEARCH

The purpose of this thesis was to describe the effects of an intermediate-scale wind disturbance on the composition, structure, and stem spatial patterns in an upland *Quercus* stand. A paucity of research has been conducted on the effects of intermediate-scale wind disturbances in temperate forests, despite their relatively short return interval (ca. 30–50 years). In particular, most studies on intermediate disturbances have not investigated the spatial patterns of tree mortality and biological legacies. This research addresses the need for spatially explicit compositional and structural data on stands affected by an intermediate-scale disturbance. In this chapter, I summarize major results from this thesis and make recommendations for future research.

6.1 Composition, structure, and spatial patterns of biological legacies

1. The size distribution of stems differed among taxonomic group in the minimal, light, and moderate disturbance class.

Diameter distributions for *Acer-Fagus* revealed the species are regenerating in the stand. Unimodal distribution of *Quercus* individuals in all disturbance classes indicated a lack of regeneration. This trend is common in stands of the Central Hardwood Forest Region and demonstrates the documented *Acer-to-Quercus* transition.

2. Large stems, especially *Carya* spp., are more likely to be affected by wind disturbance.

Logistic regression of tree mortality indicated that large stems had a higher probability of being killed by the wind event. In the light disturbance class logistic regression model, *O. virginiana* stems exhibited a decreased probability of mortality, and the interaction between *Carya* spp. and DBH exhibited an increased likelihood of mortality. In the moderate disturbance class, DBH was the only factor that influenced the probability of stem mortality. The size-specific trend is consistent with other studies and is most likely because large stems have larger crown volumes that increase wind drag.

3. Spatially explicit data elucidates intra-stand heterogeneity and explains unexpected trends in density and dominance among disturbance classes.

The contiguity of disturbance severity classes emphasized spatial patterns of tree mortality. The minimal disturbance class had the largest QMD for decay class 1 stems, likely because of few relatively large decay class 1 stems and no small decay class 1 stems as were present in the light and moderate disturbance classes. The minimal disturbance class also had the lowest density of *O. virginiana* stems. However, the largest *O. virginiana* stems were located in the moderate disturbance class and may have served as a seed source for the numerous stems in the light disturbance class and relatively fewer *O. virginiana* stems in the minimal disturbance class.

6.2 Structural complexity and developmental trajectory

1. Stems affected by the storm were clustered in the moderate disturbance class, randomly distributed in the light disturbance class, and uniformly distributed in the minimal

disturbance class. Surviving stems exhibited a more uniform pattern compared to pre-disturbance conditions in each disturbance severity class.

Patterns of tree mortality exhibited increased clustering with increased disturbance severity. Within each disturbance severity class, the spatial pattern of tree mortality differed. However, at the stand scale, tree mortality was clustered near the tornado track. The differences in stem spatial patterns at different scales emphasizes the importance of investigating both stand-scale and neighborhood-scale patterns.

2. Structural complexity was highest in the light disturbance class.

The light disturbance class was characterized by various single- and multi-tree gaps. The variety in tree mortality pattern likely contributed to the enhanced structural complexity of the light disturbance class. However, all disturbance classes exhibited increased structural complexity as a result of the disturbance.

3. After an intermediate-scale disturbance, the stand was classified as a mature-sapling mosaic stand, corresponding to the mixed stage of development.

Prior to the disturbance, each disturbance severity class was classified as a mature stand size class. However, the disturbance resulted in all disturbance severity classes being reclassified as mature-sapling mosaic stand size classes. Thus, this *Q. alba* stand represents a stand in the mixed stage of development. Because of the breadth of the mixed stage, developmental trajectories are not well understood. Further research is needed to project the developmental trajectory of this stand in relation to other stands in the mixed stage of development.

6.3 Recommendations for future research

Results from this research indicate the importance of spatially explicit forest inventory data for describing the effects of intermediate scale disturbances that enhance intra-stand heterogeneity. However, additional research is necessary to more fully understand the lasting effects of intermediate-scale disturbances. Future research question suggestions include (1) the effects of intermediate-scale disturbance by other disturbance agents and (2) developmental patterns of stands affected by an intermediate-scale disturbance.

Intermediate-scale disturbances vary in magnitude, severity, and return interval. In addition, the spatial patterns of tree mortality after an intermediate-scale disturbance, and subsequent biological legacies, are influenced by the disturbance agent. As such, quantitative descriptions of an intermediate-scale wind event may not be comparable to intermediate-scale disturbances caused by fire or pests. This necessitates further research on the effects of intermediate-scale disturbances caused by various agents. Specifically, information is needed on the composition, structure, and spatial pattern of live and dead stems. Because of the intra-stand scale of intermediate disturbance, spatially explicit studies will elucidate fine-scale patterns of disturbance that may have lasting effects on the developmental trajectories of affected stands.

The majority of research conducted on intermediate-scale disturbances has fine-scale temporal resolutions. More data with broad-scale temporal resolution and fine-scale spatial resolution are needed to document the development of stands affected by intermediate-scale disturbances. The mixed stage of development is broad and includes many stand structures. Thus, the developmental trajectories of stands in the mixed stage must also be broad. These developmental trajectories are understudied and more information is needed to fully describe the mixed stage of development.

In conclusion, this study described the effects of an intermediate-scale wind disturbance on an upland *Quercus* stand. Four growing seasons after the disturbance, composition remained similar to pre-disturbance conditions, structural complexity increased because of the disturbance, and the developmental trajectory was altered as a result of the disturbance. Further research is needed to describe the effects of intermediate-scale disturbances by various disturbance agents and to quantify the development of stands after a natural intermediate-scale disturbance.

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