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# Composition, structure, and intra-stand spatial patterns along a disturbance severity gradient in a *Quercus* stand

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ABSTRACT

Natural forest disturbances, which drive succession and development, differ in extent, severity, and return interval and range from frequent, gap-scale disturbances, to infrequent stand-replacing events. Most studies have focused on natural disturbances near the ends of the disturbance severity gradient and relatively little quantitative information is available on intermediate-severity disturbance. On 20 April 2011, an EF1 tornado tracked 5 km through the Sipsey Wilderness in Alabama and resulted in a patchwork mosaic of disturbed areas. To analyze the effects of the intermediate-severity wind event on composition, structure, and intra-stand spatial patterns, we 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 (i.e. basal area of snags, snapped stems, or uprooted stems in decay class 1) by the wind event, we divided the plot into disturbance classes (minimal, light, and moderate) to compare compositional and structural attributes along a disturbance severity gradient. Composition varied little across the disturbance gradient, but diversity was highest in the moderately disturbed neighborhoods. Stems were relatively intermingled by species (i.e. each tree neighbored by trees of different species) in each disturbance severity class. However, some species, such as *Fagus grandifolia* and *Ostrya virginiana* exhibited less intermingling than *Quercus* spp. and stems classed in the "other spp." taxonomic group. Large stems were disproportionately removed by the storm in the light and moderate disturbance categories. In the light disturbance class, *O. virginiana* was significantly less likely to experience mortality from the storm, which may in part explain the relatively high density of *O. virginiana* stems in the plot.



## 1. Introduction

Forest disturbances alter species composition and stand structure and thus, direct successional and developmental pathways (Lorimer, 1980; White et al., 1985; Foster et al., 1998; White and Jentsch, 2001). Discrete forest disturbances are often classified by their spatial extent and severity, and range from localized, gap-scale events to stand-wide, catastrophic events (Oliver and Larson, 1996). Along this disturbance severity gradient, intermediate disturbances are those larger in extent than gap-scale disturbances and smaller than catastrophic events (Hanson and Lorimer, 2007; Cowden et al., 2014; White et al., 2015). An inverse relationship exists between the intensity (e.g. wind speed) and the return interval of a disturbance (Frelich and Lorimer, 1991; Mitchell, 2013). Stand-wide disturbances (defined here as 25% of canopy trees affected) occur every 30–50 years in the Central Hardwood Forest of the USA (Nowacki and Abrams, 1997; Ruffner and Abrams, 1998; Hart et al., 2012). Although the return interval of intermediate-severity disturbances in this region is shorter than the life of canopy trees (100–400 years; Lorimer, 1989, 2001; Stueve et al., 2011; Di Filippo et al., 2015), the vast majority of research on natural canopy disturbance has focused on either catastrophic or small gap-scale disturbances (Seymour et al., 2002). As such, relatively little quantitative information is available on natural intermediate forest disturbance processes.

The intermediate disturbance category of the disturbance gradient encompasses events that span a large range of severities and spatial patterns of tree mortality. For example, an intermediate-severity disturbance may remove canopy trees through a stand in a manner resembling many simultaneous gap-scale disturbances, or remove all canopy trees in a neighborhood (e.g. 0.001–0.1 ha; Frelich et al., 1998), but not affect the remainder of the stand. Natural intermediate-severity disturbance agents include

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windstorms, mixed severity fires, pathogens, and insect outbreaks among others (Oliver and Larson, 1996). Agents of intermediate-severity disturbance may result in size-specific or species-specific tree mortality (Everham and Brokaw, 1996; Canham et al., 2001; Peterson, 2007; White et al., 2015) and thus, cause unique spatial patterns of residual trees and biological legacies. For example, large trees, because of their relatively large canopy volumes, are disproportionately removed by strong wind events (Foster and Boose, 1992; Peterson and Rebertus, 1997; Peterson, 2007; Rich et al., 2007), whereas trees with relatively thin bark, to some degree a function of tree size, are most susceptible to mortality from fire (Regelbrugge and Smith, 1994; Brose et al., 2013) The variation amongst disturbance agent, severity, and spatial pattern of both killed and residual stems necessitates quantitative descriptions of different intermediate-severity disturbances to project subsequent successional and developmental trajectories.

The overarching goal of this study was to describe the effects of an intermediate-severity wind event on the composition, structure, and intra-stand spatial patterns of trees along a canopy disturbance severity gradient. Specifically, we aimed to (1) quantify the effects of an intermediate-severity wind disturbance on composition among neighborhoods of increasing disturbance severity, (2) describe the effects on stand structure among neighborhoods, (3) analyze the effects of an intermediate-severity disturbance on compositional diversity and species intermingling, and (4) investigate stem mortality trends based on size and species. Based on our preliminary observations and literature review, we hypothesized the wind disturbance disproportionately removed larger canopy trees and that the frequency of tree mortality was greatest near the center of the tornado track and decreased with increased distance from the path. Furthermore, we hypothesized species diversity and intermingling would be highest in areas where mortality was greatest and that these measures would decrease along the canopy disturbance severity gradient. Our findings provide information on tree mortality patterns and the biological legacies left by an intermediate-severity disturbance and may be used to guide natural disturbance-based silvicultural systems.

## 2. Methods

### 2.1. Study area

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, USA. The reserve is situated on the Cumberland Plateau section of the Appalachian Plateaus physiographic 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 et al., 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 (Thornthwaite, 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. 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 with relatively minor changes in slope position (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. 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.

### 2.2. Field methods

All field data were collected 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, we 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, we established a 2 ha ($100 \times 200$ 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. Elevation varied by 37 m within the plot and the contours were oriented perpendicular to the path of the 2011 storm so effects of wind disturbance were not confounded by topography. The plot was situated at least 25 m from the stand boundary to eliminate edge effects. A $5 \times 5$ m grid was superimposed over the 2 ha plot to divide the plot into disturbance severity subplots after sampling.

Within each $5 \times 5$ m quadrat, all live stems $\geqslant 5$ cm diameter at breast height (1.4 m above the surface, DBH) were recorded for species, DBH and crown class to record stand characteristics. Crown class was based on the amount of intercepted light and included overtopped, intermediate, codominant, and dominant stems (Oliver and Larson, 1996). We also noted whether the crown was visually damaged or undamaged (i.e., major branches removed, etc.). For all dead, woody stems $\geqslant 5$ cm rooted within each quadrat, we identified the stem to the lowest taxonomic level possible, recorded the DBH and decay class, and classified each stem by mode of death. 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). We 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.

### 2.3. Analytical methods

To analyze the effects of the intermediate-severity wind event, we 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). We used percent background mortality from studies in adjacent stands (1.2% $m^2\ ha^{-1}$ 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, we did not differentiate between storm-killed decay class 1 stems and decay class 1 stems as a result of background mortality in data analyses.

We divided the plot into three disturbance severity categories (minimal, light, and moderate disturbance classes) to compare differences in stand composition and structure among neighborhoods of increasing disturbance severity. To determine boundaries of disturbance severity classes, we 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 and was broad enough to determine general trends of basal area removed and remain unbiased by highly localized areas of disturbance (Johnson et al., 2009; Zenner et al., 2015). Using contours created by the simple kriging, we defined disturbance severity class boundaries by following the borders of 5 m × 5 m

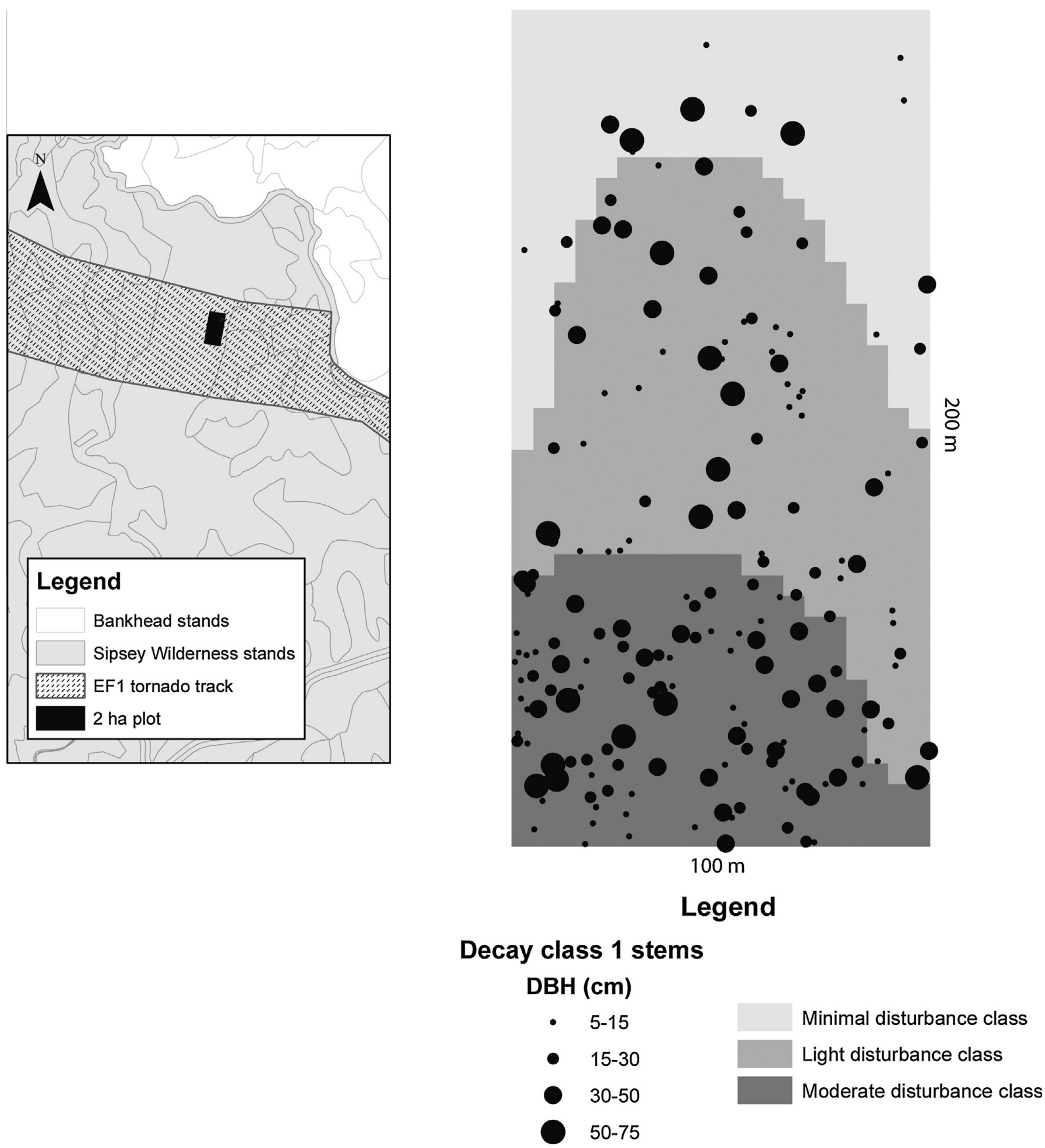


**Fig. 1.** Contiguous 2 ha permanent plot established perpendicular to the track of an EF1 tornado in the Sipsey Wilderness, William B. Bankhead National Forest, Alabama. Disturbance severity classes, determined by basal area removed, are indicated by shading. Points representing stems are not to scale to better illustrate spatial patterns of dead trees.

quadrat boundaries through the 2 ha plot (see plot establishment description). The minimum and maximum contour values were 0.0–2.3 $m^2\ ha^{-1}$ (0–8% basal area removed) for minimal disturbance, 2.3–6.4 $m^2\ ha^{-1}$ (8–24% basal area removed) for light disturbance, and 6.4–20.0 $m^2\ ha^{-1}$ (24–75% basal area removed) for moderate disturbance (Fig. 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.

We calculated density, relative density, dominance (basal area ($m^2\ ha^{-1}$)), 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*, *Quercus–Carya*, *Ostrya virginiana*, and other species. Taxonomic groups were chosen based on taxa dominance across all disturbance severity classes. We included *Acer* and *Fagus* in one taxonomic group and *Quercus* and *Carya* in a single taxonomic group based on shade tolerance and successional trends 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, we regressed the $\log_{10}((\text{stems ha}^{-1}) + 1)$ of each DBH size class bin by all combinations of the corresponding DBH size class midpoint (DBH), $DBH^2$, and $DBH^3$ (Janowiak et al., 2008; Keyser and Loftis, 2012). 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. We 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). To analyze size distributions of *O. virginiana* which had little differentiation among stem size, we created diameter distributions using 1 cm DBH size classes for each disturbance severity class. We did not assign shapes to the *O. virginiana* diameter distribution curves using polynomial regression.

To describe the distribution of stem size, we 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). To demonstrate the impact of *O. virginiana* on the diameter distribution for other species, 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 and compare these measures to analogous studies, we calculated Shannon diversity ($H'$) and evenness ($J$) for each disturbance class. Using the "vegan" package in R (Oksanen et al., 2016), we also calculated randomized species accumulation curves for each disturbance severity class to account for differences in sample size (Gotelli and Colwell, 2001). We calculated the Mingling index ($M_i$) to determine the degree of species intermingling (Pommerening, 2002). The $M_i$ describes the level of interspersion 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. We also analyzed $M_i$ values by species to determine species-specific variation in interspersion. For species-specific $M_i$ values, low values indicate that stems of the focal species are more likely to occur in spatial groups (i.e. neighborhoods of 5 stems), whereas high values indicate that stems of the focal species tend to occur alone (i.e. interspersed with other species). In addition, we created histograms of $M_i$ for each taxonomic group for the entire 2 ha plot regardless of disturbance class. 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 $M_i$, we 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, we 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). We 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). We used the likelihood ratio $\chi^2$ to test the significance of each model and the Wald $\chi^2$ 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 v.9.3 and all spatial analyses were performed in ArcMap v. 10.2 and R using the "spatstat package" (Baddeley and Turner, 2005).

## 3. Results

### 3.1. Effects on composition and structure

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

**Table 1**
Dominance ($m^2$ $ha^{-1}$) and density (stems $ha^{-1}$) measures for all live woody stems ⩾5 cm DBH for the 2 ha plot 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 |
| *Acer rubrum* L. | 0.1 | 0.1 | – | 0.3 | 0.4 | – | 7.0 | 16.4 | – | 1.0 | 1.9 | – |
| *Acer saccharum* 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 |
| *Carpinus caroliniana* Walter | – | 0.0 | 0.1 | – | 0.2 | 0.4 | – | 8.2 | 12.2 | – | 1.0 | 2.1 |
| *Carya glabra* (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 |
| *Carya ovata* (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 |
| *Carya tomentosa* (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 |
| *Cercis canadensis* L. | 0.0 | – | 0.1 | 0.0 | – | 0.7 | 1.8 | – | 24.3 | 0.3 | – | 4.2 |
| *Cornus florida* 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 |
| *Fagus grandifolia* 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 |
| *Fraxinus americana* 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 |
| *Fraxinus pennsylvanica* 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 |
| *Juniperus virginiana* 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 |
| *Liriodendron tulipifera* L. | 0.4 | 0.7 | – | 1.8 | 3.1 | – | 7.0 | 2.3 | – | 1.0 | 0.3 | – |
| *Magnolia acuminata* (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 |
| *Magnolia macrophylla* Michx. | 0.0 | 0.1 | – | 0.1 | 0.3 | – | 1.8 | 11.7 | – | 0.3 | 1.4 | – |
| *Nyssa sylvatica* 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 |
| *Ostrya virginiana* (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.[a] | 0.0 | 0.1 | 0.0 | 0.1 | 0.4 | 0.2 | 1.8 | 12.9 | 10.4 | 0.3 | 1.5 | 1.8 |
| *Pinus taeda* L. | 0.0 | 0.9 | – | 0.1 | 4.0 | – | 1.8 | 3.5 | – | 0.3 | 0.4 | – |
| *Quercus alba* 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 |
| *Quercus falcata* Michx. | 1.0 | 0.4 | – | 4.1 | 1.6 | – | 7.0 | 2.3 | – | 1.0 | 0.3 | – |
| *Quercus montana* Willd. | 0.7 | – | – | 3.0 | – | – | 12.3 | – | – | 1.8 | – | – |
| *Quercus muehlenbergii* Engelm. | – | – | 0.6 | – | – | 4.1 | – | – | 12.2 | – | – | 2.1 |
| *Quercus rubra* L. | 0.0 | – | 0.2 | 0.0 | – | 1.2 | 1.8 | – | 3.5 | 0.3 | – | 0.6 |
| *Tilia americana* L. | 0.0 | – | 0.1 | 0.0 | – | 1.0 | 1.8 | – | 13.9 | 0.3 | – | 2.4 |
| *Ulmus alata* 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 |
| *Ulmus rubra* 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 |
| *Viburnum rufidulum* 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 |

[a] 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.

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 abundant species of decay class 1 stems in the moderate disturbance class (Table 2). *Carya ovata* and *L. tulipifera* were

**Table 2**
Dominance ($m^2$ $ha^{-1}$) 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 (m2 $ha^{-1}$) | | | Relative dominance (%) | | | Density (stems $ha^{-1}$) | | | Relative density (%) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Minimal | Light | Moderate | Minimal | Light | Moderate | Minimal | Light | Moderate | Minimal | Light | Moderate |
| *Acer rubrum* L. | – | 0.0 | – | – | 0.6 | – | – | 3.5 | – | – | 4.5 | – |
| *Acer saccharum* Marshall | – | 0.2 | 0.6 | – | 3.1 | 5.6 | – | 5.8 | 20.9 | – | 7.5 | 10.4 |
| *Carpinus caroliniana* Walter | – | 0.0 | 0.0 | – | 0.2 | 0.1 | – | 2.3 | 3.5 | – | 3.0 | 1.7 |
| *Carya glabra* (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 |
| *Carya ovata* (Mill.) K. Koch | – | 0.2 | 2.2 | – | 4.9 | 20.2 | – | 1.2 | 19.1 | – | 1.5 | 9.6 |
| *Carya* spp. | – | 0.4 | – | – | 7.2 | – | – | 3.5 | – | – | 4.5 | – |
| *Carya tomentosa* (Lam.) Nutt. | 0.2 | 0.4 | 0.2 | 10.2 | 7.2 | 1.9 | 1.8 | 2.3 | 1.7 | 7.1 | 3.0 | 0.9 |
| *Cercis canadensis* L. | – | – | 0.0 | – | – | 0.3 | – | – | 3.5 | – | – | 1.7 |
| *Cornus florida* 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 |
| *Fagus grandifolia* Ehrh. | – | – | 0.0 | – | – | 0.1 | – | – | 1.7 | – | – | 0.9 |
| *Fraxinus americana* L. | – | 0.0 | 0.8 | – | 0.1 | 6.9 | – | 1.2 | 10.4 | – | 1.5 | 5.2 |
| *Fraxinus pennsylvanica* Marshall | 0.0 | – | – | 2.0 | – | – | 1.8 | – | – | 7.1 | – | – |
| *Ilex opaca* Aiton | – | 0.0 | – | – | 0.2 | – | – | 1.2 | – | – | 1.5 | – |
| *Juglans nigra* L. | – | – | 0.6 | – | – | 5.1 | – | – | 5.2 | – | – | 2.6 |
| *Juniperus virginiana* 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 |
| *Liriodendron tulipifera* L. | 0.2 | – | – | 9.8 | – | – | 1.8 | – | – | 7.1 | – | – |
| *Magnolia acuminata* (L.) L. | 0.0 | – | 0.0 | 1.7 | – | 0.2 | 1.8 | – | 1.7 | 7.1 | – | 0.9 |
| *Magnolia macrophylla* Michx. | 0.0 | 0.0 | – | 0.3 | 0.4 | – | 1.8 | 1.2 | – | 7.1 | 1.5 | – |
| *Nyssa sylvatica* Marshall | – | 0.0 | – | – | 0.3 | – | – | 2.3 | – | – | 3.0 | – |
| *Ostrya virginiana* (Mill.) K. Koch | 0.0 | 0.0 | 0.6 | 0.4 | 0.8 | 5.1 | 3.5 | 8.2 | 57.4 | 14.3 | 10.4 | 28.7 |
| *Pinus echinata* Mill. | – | 0.4 | – | – | 6.9 | – | – | 1.2 | – | – | 1.5 | – |
| *Prunus serotina* Ehrh. | 0.0 | – | – | 2.0 | – | – | 1.8 | – | – | 7.1 | – | – |
| *Quercus alba* 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 |
| *Quercus rubra* L. | – | 0.2 | 1.4 | – | 3.9 | 12.5 | – | 2.3 | 7.0 | – | 3.0 | 3.5 |
| *Tilia americana* L. | – | – | 0.0 | – | – | 0.1 | – | – | 1.7 | – | – | 0.9 |
| *Ulmus alata* Michx. | – | – | 0.2 | – | – | 1.9 | – | – | 3.5 | – | – | 1.7 |
| *Ulmus rubra* 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 |

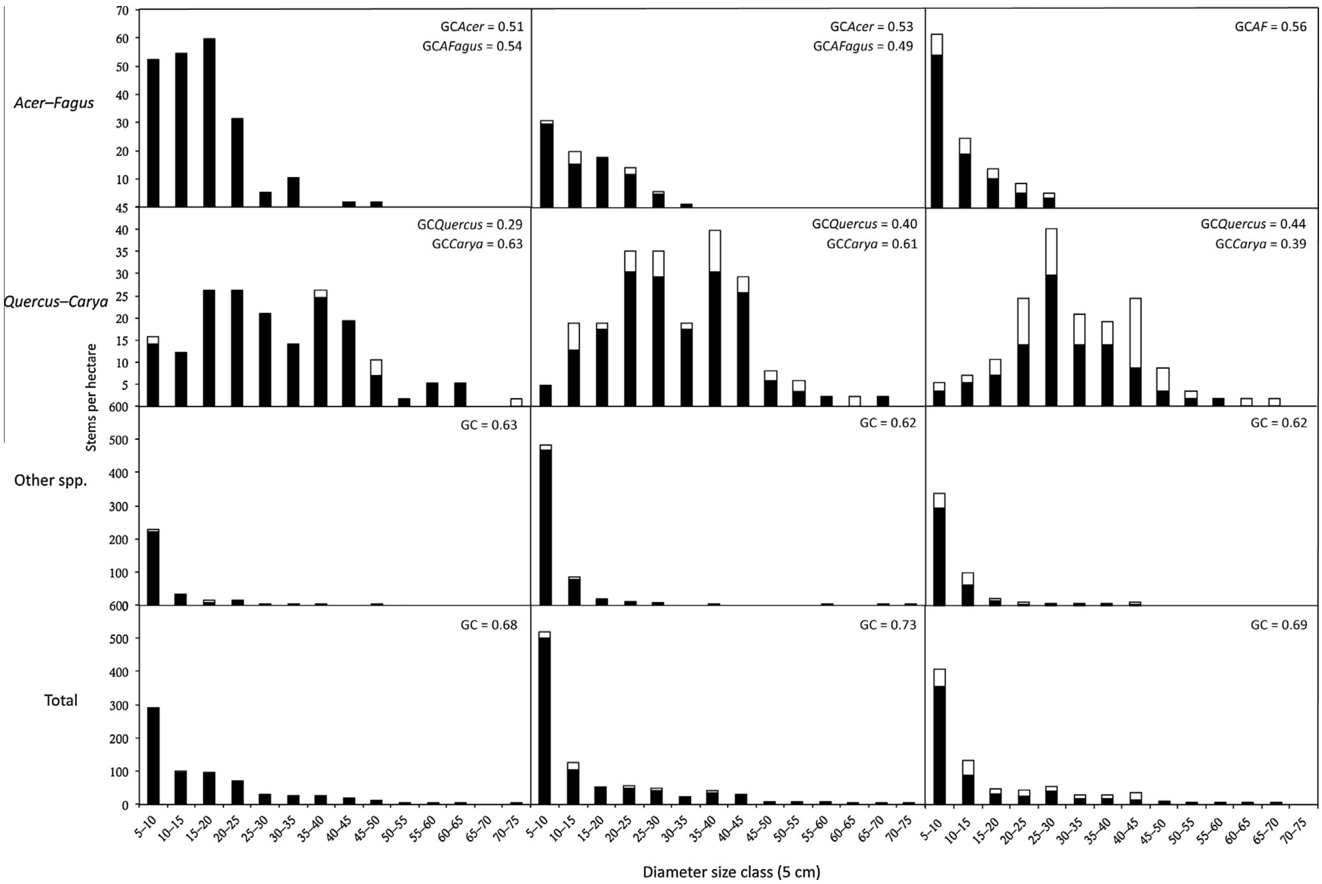


**Fig. 2.** Density (stems ha$^{-1}$) for stems ⩾5 cm DBH by 5 cm diameter size class bins and taxonomic group across three disturbance severity classes in Sipsey Wilderness, William B. Bankhead National Forest, Alabama. Black bars indicate density of live stems; white bars indicate density of decay class 1 stems. *GC* = Gini coefficient. Because of low sample size for *F. grandifolia* in the moderate disturbance class, we only calculated the *GC* for all *Acer-Fagus* stems.

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 species. 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 15 cm whereas mean DBH for decay class 1 stems was 23 cm DBH. Mean DBH for live stems was 14 cm, 31 cm, 8 cm, and 12 cm for the *Acer–Fagus*, *Quercus–Carya*, *O. virginiana*, and other spp. taxonomic groups, respectively. Mean DBH for decay class 1 stems was 15 cm, 36 cm, 10 cm, and 18 cm for *Acer–Fagus*, *Quercus–Carya*, *Ostrya virginiana*, and other spp. groups, respectively. Diameter distribution shapes varied among taxonomic groups and disturbance class (Fig. 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. *Quercus–Carya* 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 ranged from 5 to 7 cm DBH (Fig. 3). In the moderate disturbance class, 52 *O. virginiana* stems ha$^{-1}$ ⩾12 cm DBH (eight *O. virginiana* stems ha$^{-1}$ ⩾15 cm DBH) were present, whereas in the light disturbance class nine *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, 0.40, and 0.44 for minimal, light, and moderate disturbance classes, respectively, which were lower than overall disturbance class *GC* values of 0.68, 0.73, and 0.69 (Fig. 2). *GC* for *O. virginiana* was 0.25, 0.31, and 0.37, for minimal, light, and moderate disturbance classes. The *GC* values for the other species category, excluding *O. virginiana*, were 0.65, 0.74, and 0.74, for minimal, light, and moderate disturbance classes.

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 in the "other species" category were *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) of "other species" 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, the 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 to 75 cm size classes.

### 3.2. Effects on diversity and species intermingling

We documented 36 unique species of both live and decay class 1 stems ⩾5 cm DBH. Both $H'$ 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). Based on randomized species

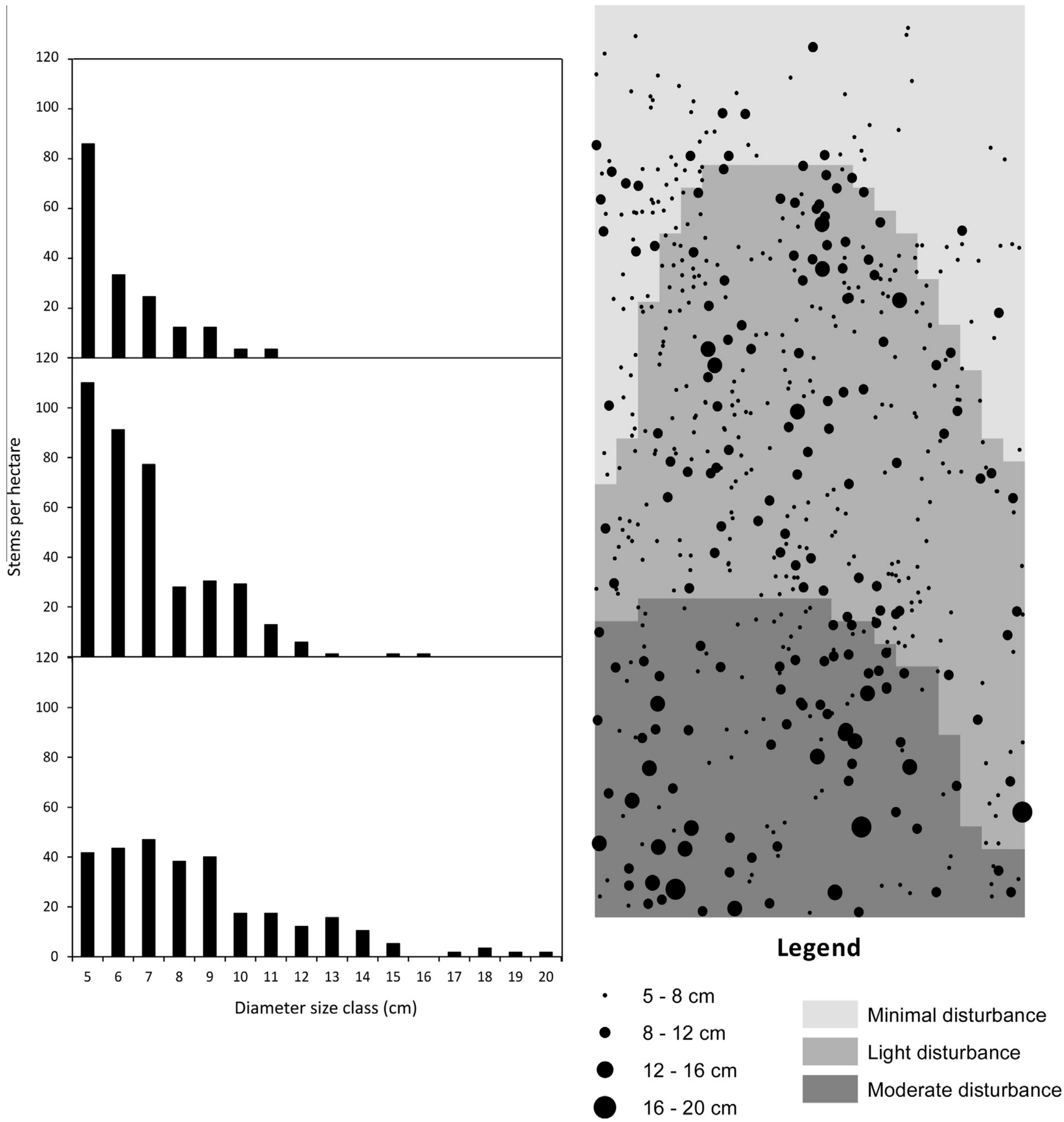


**Fig. 3.** Density (stems $ha^{-1}$) for *O. virginiana* stems ⩾5 cm DBH in 1 cm diameter size class bins across three disturbance severity classes in Sipsey Wilderness, William B. Bankhead National Forest, Alabama and map of a 2 ha contiguous plot. Shading on map corresponds to disturbance classes based on basal area removed by the storm. Points representing stems are not to scale.

accumulation curves, species richness was highest for the minimal disturbance class, followed by the moderate and light disturbance severity classes, respectively. Species accumulated the most rapidly in the moderate severity class, followed by the minimal and light severity classes (Fig. 4). $M_i$ 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. The $M_i$ value for *Carya* (0.94), *Acer* (0.84), *Quercus* (0.83) and species classed in the others category (0.88) were relatively high (Fig. 5). *Ostrya virginiana* had a relatively low $M_i$ value (0.52).

### 3.3. Mortality related to species and size

Across all disturbance categories, larger tree diameter classes exhibited higher proportions of basal area removed than smaller diameter classes (Fig. 6). Results from the tree mortality logistic regression for all stems in the 2 ha plot revealed DBH was the only significant main effect ($\chi^2_{Wald} = 58.6$, $p < 0.0001$). The coefficient for diameter was 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 stem mortality. In the light disturbance class, DBH and *O. virginiana* were the significant main effects ($\chi^2_{Wald} = 7.4$, $p = 0.006$; $\chi^2_{Wald} = 14.0$, $p = 0.0002$). The coefficient for *O. virginiana*

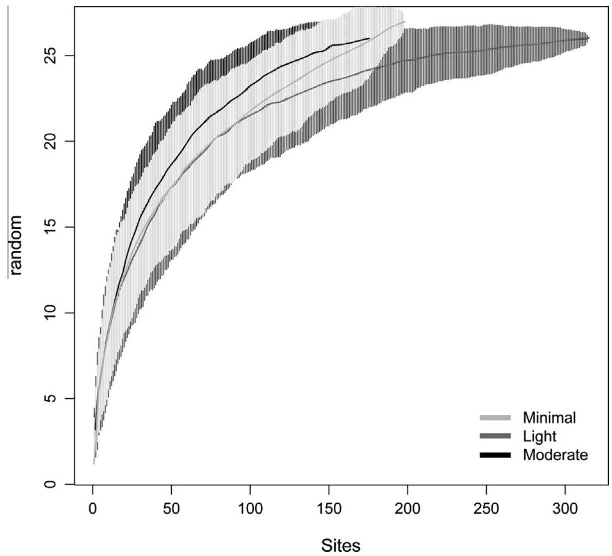


**Fig. 4.** Species accumulation curves for minimal, light, and moderate disturbance classes in a *Q. alba* stand in the Sipsey Wilderness, William B. Bankhead National Forest, Alabama.

was negative, indicating a decreased probability of mortality for *O. virginiana* stems. Conversely, the coefficient for DBH was positive. In the moderate disturbance class, DBH was the only significant effect ($\chi^2_{\mathrm{Wald}} = 32.9$, $p < 0.0001$) and had a positive coefficient.

In all disturbance classes, snapped stems represented the most common mode of death for decay class 1 stems (57% in minimal, 55% in light, 47% in moderate disturbance). In light and moderate disturbance classes, stem uprooting was a more common mode of death for decay class I stems (30%, 42%, respectively) than snags (15%, 11%, respectively). Conversely, in the minimal disturbance class, snags (29%) were more common than uprooted trees. *Quercus* spp. stems were the most common snags in all disturbance classes. In the moderate disturbance class, more *O. virginiana* and stems of the "other species" group were uprooted than snapped (Fig. 7).

## 4. Discussion

### 4.1. Effects on composition and structure

Although the return interval of intermediate-severity 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 seasons after an intermediate-severity wind event in an upland *Q. alba* stand, species composition remained similar across disturbance severity neighborhoods. In the light and moderate severity 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 as they 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 were 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 tree establishment, but at a relatively low rate compared to *Acer–Fagus*. Although *Quercus* maintained dominance after the wind 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); a shift

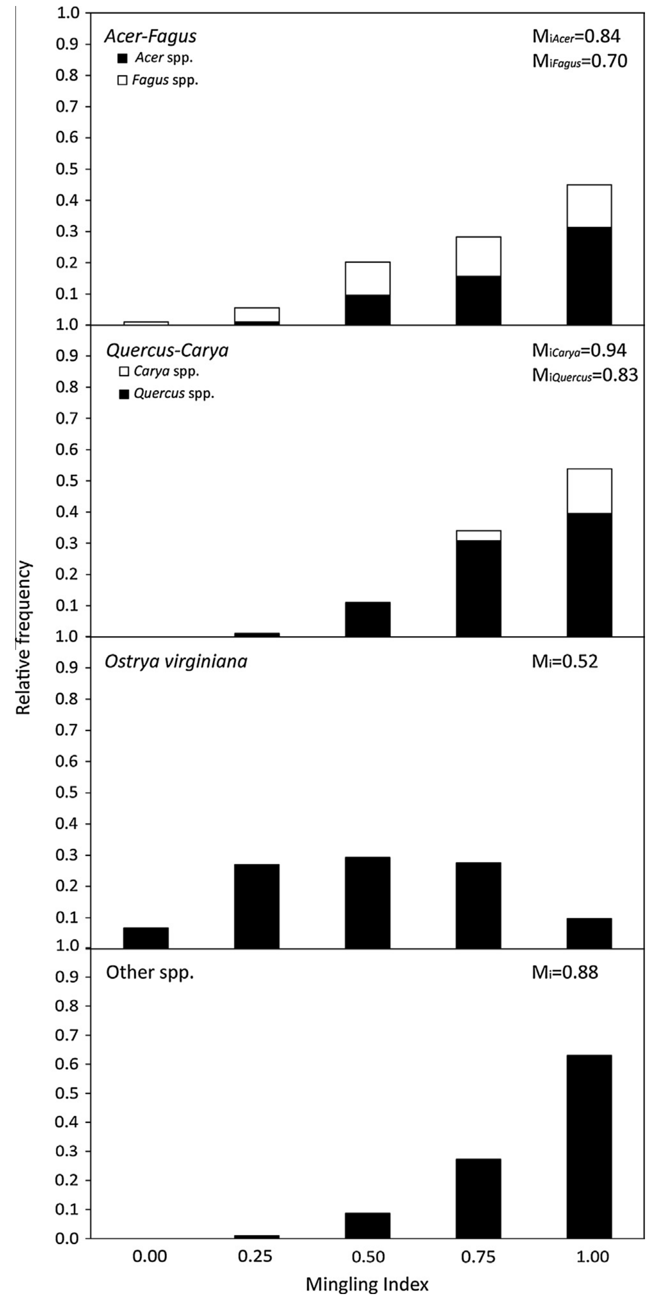


**Fig. 5.** Histograms of mingling index values ($M_i$) by taxomomic group. A $M_i$ value of 1 indicates four nearest neighbors of the focal stem are different species from the focal stem. A $M_i$value of 0 indicates the four nearest neighbors are the same species as the focal stem.

that is prevalent in *Quercus* stands throughout the Central Hardwood Forest Region (Lorimer, 1984; Abrams and Scott, 1989; Abrams, 2005; Fei et al., 2011; Holzmueller et al., 2012).

Density of *O. virginiana* stems was greater in the light and moderate disturbance classes than in the minimal disturbance class. Total stem density in the light disturbance class was higher than in the minimal disturbance class and we attributed this largely to the abundance of *O. virginiana*. The largest *O. virginiana* trees were located in the moderate disturbance class neighborhood and stem size generally decreased with decreasing disturbance severity. These large stems were likely the oldest in the plot and may have served as a seed source that populated smaller size classes in the minimally and lightly disturbed neighborhoods, as

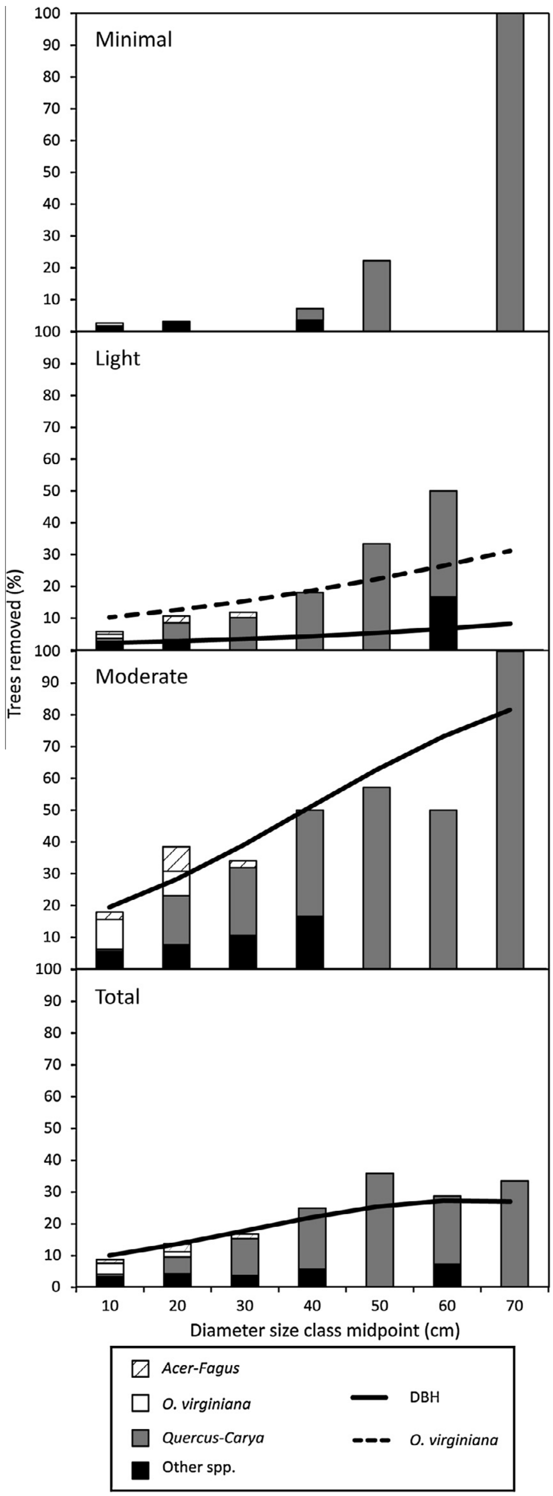


**Fig. 6.** Observed percentages of decay class 1 stems in 10 cm diameter size class bins in a *Q. alba* stand in the Sipsey Wilderness, William B. Bankhead National Forest, Alabama. Percentages are divided by taxonomic group within each diameter bin. Lines are logistic regression equations for predicted stem mortality by disturbance severity class.

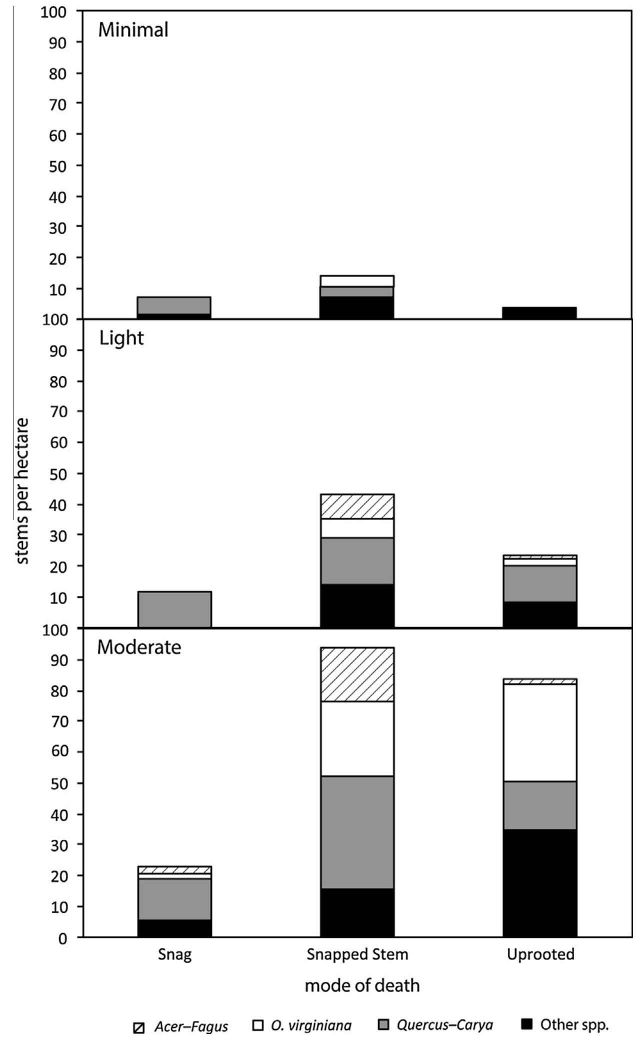


**Fig. 7.** Density (stems ha$^{-1}$) of decay class 1 stems by mode of death (snag, snapped stem, uprooted stem) across three disturbance severity classes on the Sipsey Wilderness, William B. Bankhead National Forest, Alabama. Stems are divided by taxonomic group.

*O. virginiana* are prolific seeders and produce seeds that are lightweight and easily dispersed. Thus, the pre-disturbance presence of *O. virginiana* stems may be reflected in post-disturbance results. Batista and Platt (2003) classified *O. virginiana* as a '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 (see Keasberry et al., 2016) and that the mean radial growth rate of *O. virginiana* was significantly higher after hurricane disturbance than prior to disturbance. Similarly, Kwit and Platt (2003) found that relative growth rates of *O. virginiana* increased after the occurrence of a hurricane and growth peaked 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 from strong wind events because of its relatively small stature may explain the higher density of *O. virginiana* stems ⩾5 cm DBH in the light disturbance class.

### 4.2. Effects on diversity and species intermingling

Although measures of diversity were relatively similar across disturbance severity classes, values for $H'$ and $J$ were consistently highest for the moderate disturbance class and lowest for the light disturbance class neighborhoods. Species accumulation curves revealed that species richness was slightly higher in the minimal disturbance class compared to the light and moderate disturbance classes, but that species accumulated more rapidly in the moderate disturbance class. Cowden et al. (2014) found no significant difference in $H'$ values among canopy disturbance severity classes for the tree layer in the same region. Differences in these findings may be the result of field sampling approaches. The contiguous plot used in our 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 included 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. Species accumulation curves revealed that species richness was slightly higher in the minimal disturbance class compared to the light and moderate disturbance classes.

Diversity indices and species accumulation curves describe the composition of a stand, but such indices do not consider the spatial distribution of species within a stand. The interspersion of species (i.e. intermingling) reflects fine-scale diversity. The distribution of $M_i$ values by species may indicate stand compositional heterogeneity at the stand scale and is indicative of stand compositional heterogeneity (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 wind event resulted in more trees being situated near trees of the same species (i.e. more "clumps" of similar species) compared to the pre-disturbance condition. The distribution of $M_i$ by individual species across all disturbance classes revealed that *F. grandifolia* and *O. virginiana* had the lowest species-specific $M_i$, indicating that these species were 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). 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.

### 4.3. Mortality related to species and size

Larger stems were disproportionately removed by the intermediate-severity 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 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. Notably, studies in adjacent stands did not note the disproportionate removal of any canopy species either (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 (Fig. 7). 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 (i.e. the tip-up mounds contained multiple of *O. virginiana* trees). 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. 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). *Juniperus virginiana* stems tend to have 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 root network 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 following a strong wind event.

*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 US (Abrams, 2007).

## 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 inherently 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; Fischer 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 this study indicate that the intermediate-severity 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. An irregular group shelterwood with reserves or group selection are silvicultural systems that may yield structures similar to the biological legacies left by a low severity tornado. Throughout the study area, basal area removed ranged from 8% to 45%, with 22% removed on average. Thus, we recommend that stand-wide basal area retention remain between 40% and 80% when applying a treatment patterned after a natural intermediate-severity wind event, but treatments should be applied in groups. We recommend that initial group sizes range from 0.01 to 0.5 ha based on our findings. Although this may homogenize neighborhoods, the structural heterogeneity at the stand scale would increase (Boyden et al., 2012). Managers may wish to vary sizes of group openings to promote regeneration of stems of various shade tolerance (*sensu* Lhotka, 2013). To emulate patterns of the wind event, managers would 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 likely need to make concessions on emulating structures resulting from natural disturbance. Without such concessions, an entry patterned after a natural intermediate-severity wind event would likely accelerate succession. Shelterwood systems are most commonly used to regenerate *Quercus* (Loftis, 1990; Stringer, 2006; Schweitzer and Dey, 2011), but preparatory and final harvests are typically implemented uniformly throughout a stand. To promote *Quercus* regeneration and more closely emulate the legacy structure left by an intermediate-severity wind disturbance compared to a two-phase shelterwood, managers may implement group selection harvests around existing patches of advanced *Quercus* reproduction (i.e. stems $\geqslant$1.4 m in height). Surrounding the gap, a midstory removal preparatory cut may be used to reduce competition of more shade tolerant 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 growth of *Quercus* reproduction (Marquis, 1965; Dey, 2002). In subsequent entries, managers may create new gaps or expand existing gaps. However, to increase edge effects, expanded gaps may be situated tangentially rather than concentrically in relation to the initial gap. Based on specific management objectives, managers must weigh the importance placed on timber revenue and the importance of following a close-to-nature management approach.

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