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Disturbance history, species diversity, and structural complexity of a temperate deciduous forest

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Abstract Stand structural complexity enhancement is an increasingly popular management objective, especially on public lands. Complex stand structures are hypothesized to support a relatively high degree of native forest diversity and be more resistant and resilient to disturbances. Complex structures are characterized by the presence of deadwood and heterogeneity of tree-size classes and tree architecture. Relatively little is known about how discrete disturbance events affect structural complexity and compositional diversity in *Quercus*-dominated stands at fine spatial scales (i.e. neighborhoods). We established 20 0.05 ha fixed-radius plots on the Sipsey Wilderness of William B. Bankhead National Forest in northern Alabama to quantify woody plant species composition and structure. Trees were mapped on each plot to quantify overstory structural complexity and compositional diversity. We extracted two cores from all canopy *Quercus* spp. $\geq$ 5 cm diameter at breast height to quantify age, recruitment pulses, and reconstruct canopy disturbance history. Shannon species diversity in the sampled area was 1.75 for trees, 2.08 for saplings, and 1.69 for seedlings. *Quercus alba* had the greatest basal area, and *Ostrya virginiana* had the highest density. The stand exhibited a reverse J-shaped distribution with a q-factor of 1.72. The oldest *Quercus* dated to 1795, and the largest recruitment pulse occurred in the 1870s. The mean return interval for intermediate-severity disturbance was 38 years. Although we documented no relationships between disturbance frequency and compositional diversity at the neighborhood scale (0.05 ha), less frequent disturbance was associated with higher structural complexity (r^2 = 0.258, p = 0.026) at the neighborhood scale. We suggest that localized disturbance increases species diversity and structural complexity, but these processes are manifest at the stand level and not at the neighborhood scale. We conclude that the spatial variability (i.e. size, shape, orientation, microsite conditions) is likely more influential on diversity and complexity than the temporal variation (frequency) of these processes at the neighborhood scale.

Keywords Canopy gap · *Quercus* (oak) · Stand development · Succession

Abbreviations

dbh	Diameter at breast height
ha	Hectare
H'	Shannon–Weiner diversity index
J	Species evenness
M_i	Species mingling index
NOAA	National Oceanic and Atmospheric Administration

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Introduction

Throughout the temperate zone of the United States, multi-aged hardwood stands are often considered to be compositionally diverse and structurally complex (Tyrrell et al. 1998; Hale et al. 1999; McElhinny et al. 2005; Burrascano et al. 2013; O'Hara 2014). Complex forest structures typically exhibit heterogeneity of tree size classes, tree architecture, age structure, and the presence of deadwood in variable stages of decay and modes of death (McElhinny et al. 2005; Zenner and Peck 2018).

In this study, we define structural complexity as heterogeneity of tree diameter and the vertical distribution of foliage, as well as the presence of deadwood (McElhinny et al. 2005). Linkages between canopy disturbance events during stand development and their effects on composition and structure have been analyzed at the stand scale (e.g. Lorimer 1980; Nowacki and Abrams 1994; Hart and Grissino-Mayer 2008; Hart et al. 2012; Ford et al. 2017). Gap- and intermediate-severity disturbances have been found to increase the structural complexity of forests through the establishment of new cohorts with variable diameters and age classes. However, we know relatively little about the relationships between canopy disturbance events during development and compositional diversity and structural complexity at fine spatial scales (i.e. at sub-stand scales) (Zenner and Peck 2018).

Forest disturbances are typically classified along a severity gradient based on spatial extent, magnitude, and frequency and are broadly grouped into three categories: catastrophic events (those that remove most overstory individuals), gap-scale events (those that remove trees individually or in small groups), and intermediate-severity events (those that are not stand replacing, but exceed that of gap-scale disturbances) (Oliver and Larson 1996; Cowden et al. 2014). In most hardwood stands in the temperate zone, the canopy disturbance regime is dominated by gap-scale disturbances (Hart 2016). These events reorganize canopy structure and the vertical distribution of foliage and allow recruitment of additional species (Hart and Grissino-Mayer 2009; Hardiman et al. 2011). Richards and Hart (2011) found that 240 m^2 was the threshold beyond which canopy gaps typically closed from sub-canopy height growth in mature *Quercus* stands on the Cumberland Plateau.

By reconstructing the canopy disturbance history of a stand, we can link spatially explicit disturbance events to compositional and structural data to elucidate the relationships between canopy disturbance and stand conditions at fine spatial resolutions. This information is useful to improve our understanding of stand development and successional patterns and processes, and to inform silvicultural systems based on natural disturbances (Lorimer 1985; Coates and Burton 1997; Long 2009; O'Hara 2014).

Stand structural complexity enhancement is becoming increasingly popular, especially on public lands (Keeton 2006; O'Hara 2014). Gap- and intermediate-severity forest disturbances may increase structural complexity, and enhanced structural complexity is hypothesized to increase resistance and resilience to future perturbations, such as intermediate-severity wind events (White and Pickett 1985; Puettmann et al. 2009; O'Hara and Ramage 2013; Trotsiuk et al. 2014). Disturbance also results in biotic and abiotic legacies that depend on the spatial extent of the disturbance event, ranging from micro- (i.e. pit and mound microtopgraphy) to landscape-scales (i.e. stand-age distribution) (Jõgiste et al. 2017).

Increasing structural heterogeneity results in variation in tree species diversity, age, diameter, height, and vertical stratification, which broadens ecosystem services such as increased CO_2 uptake, erosion control, and aesthetics (Runkle 1981; Canham and Marks 1985; Phillips and Shure 1990; Richards and Hart 2011). Complex forest systems are also hypothesized to be more efficient at harvesting light than structurally homogenous forests, and therefore may have higher net primary production and C sequestration (Duursma and Mäkelä 2007; Hardiman et al. 2011). Because of these benefits, interest in managing for structural complexity is increasing, but the mechanisms that drive intra-stand structural complexity are still poorly understood.

The purpose of this study was to investigate the disturbance and developmental history of an upland *Quercus* stand and to examine neighborhood-scale relationships between local canopy disturbance, woody plant diversity, and structural complexity. The specific objectives of this study were to: (1) quantify species composition and vertical and horizontal stand structure in a mature *Quercus* stand; (2) reconstruct canopy disturbance history; (3) describe the compositional diversity and structural complexity at the neighborhood scale; and (4) examine potential relationships between species diversity and structural complexity metrics and known disturbance events. Our results provide insight for managers that wish to promote structural complexity in accord with natural disturbance processes in hardwood stands.

Materials and methods

Study site

This study was conducted in the Sipsey Wilderness Area; a 10,085 ha reserve established in 1975, within the Bankhead

National Forest in Winston and Lawrence Counties, Alabama, United States. The reserve is situated on the Cumberland Plateau section of the Appalachian Plateau physiographic province (Fenneman 1938) and the Southwestern Appalachians (level III) ecoregion (Griffith et al. 2001). The study site is within the Central Hardwood Forest Region (Fralish 2003). The region is geologically composed of the Pennsylvanian Pottsville formation, characterized by light gray, thick bedded to massive pebbly quartzose sandstone with shale, siltstone and thin discontinuous coal imbedded (GSA 2006). The topography is strongly dissected with steep slopes and narrow ridges and valleys so that it no longer resembles a tableland plateau (Smalley 1979).

The regional climate is classified as humid-mesothermal (Thornthwaite 1948). The last freeze generally occurs in late-April and the first freeze occurs late-October with a frost-free period between 160 and 200 days (Smalley 1979). Mean annual precipitation is 1401 mm with the highest mean monthly precipitation of 154.8 mm in March and the lowest mean monthly precipitation of 80.0 mm in October (PRISM 2016). Mean annual temperature at the study site is 16.0 °C with the highest mean monthly temperature of 26.0 °C in July and the lowest mean monthly temperature of 5.2 °C in January (PRISM 2016).

Braun (1950) described the region as a transition between the Mixed Mesophytic Forests to the north and mixed *Quercus–Pinus* Forests to the south. Zhang et al. (1999) described 14 unique ecological communities in the Sipsey Wilderness, and *Quercus* was the most dominant and widespread genus and occurred in almost every community type. Ridges and upper slope positions are often dominated by *Pinus taeda* and *Pinus echinata*. Hardwood dominance typically increases with decreased slope position and most mid-slopes are *Quercus* dominated. Lower slope positions may support mesophytic species, such as *Fagus grandifolia*, *Liriodendron tulipifera*, *Magnolia macrophylla*, and *Tsuga canadensis* L. (Zhang et al. 1999; Richards and Hart 2011; Parker and Hart 2014; Keasberry et al. 2016).

For management purposes, the Sipsey Wilderness has been divided into compartments and further subdivided into stands in accordance with the guidelines of the US Forest Service (USFS). Most *Quercus alba* stands in the Sipsey Wilderness established between 1890 and 1905. Prior to this, most of the BNF was harvested, and approximately 40% of the land base was vacated farmland (US Forest Service of Alabama 2003; Addor and Birkhoff 2004). The disturbance regime of these *Q. alba* stands is characterized by frequent gap-scale disturbances, and less frequent, intermediate-severity disturbances (Richards and Hart 2011; Cox et al. 2016).

Field methods

We targeted a *Q. alba* stand in the Sipsey Wilderness that had been utilized in prior research (Richards and Hart 2011; Cowden et al. 2014; White et al. 2015), but for which the canopy disturbance regime was yet to be described. To determine the stand description and location, USFS stand boundaries were overlaid in ArcGIS v. 10.3 (ESRI 2011). According to the USFS, the stand was dominated by *Q. alba* and originated prior to 1900. The stand was ca. 70 ha. Data were collected July–August 2016.

We established 20 fixed-radius plots that were 500-m^2 (0.05 ha) in size. To ensure adequate spatial coverage to ensure each sample plot was independent, plots were systematically placed 50 m apart along three transects, with seven plots on two transects and six on another. Plot size was chosen to analyze neighborhood-scale processes and was ca. double the mean size of canopy gaps in this and adjacent *Quercus*-dominated stands (Richards and Hart 2011). The spatial size of what constitutes neighborhood scale varies in the literature, but our classification of "neighborhoods" was between the ranges of Frelich et al. (1998) (10.0 m plot radius) and Boyden et al. (2012) (16.1 m radius plots). Transect locations were determined by choosing a starting point that was at least 50 m away from any roadway or other anthropogenic feature that may influence the composition and structure of the stand. Coordinate pairs were input into a GPS as waypoints for field navigation.

Trees were identified as live stems $\geq$ 5 cm diameter at breast height (dbh; 1.37 m from the ground). For all trees, we recorded species, dbh, and crown class. These measures were taken to quantify species composition and the vertical and diameter structure of the stand. We recorded the distance and azimuth of each tree from plot center to generate stem maps for horizontal structure metrics, using a Haglöf hypsometer and a sighting compass, respectively. Crown classes were based on the amount of intercepted light and were divided into four groups: dominant, co-dominant, intermediate, or overtopped (Oliver and Larson 1996).

Saplings were identified as live stems $>$ 1 m in height, but $<$ 5 cm in dbh within each 500-m^2 plot. Saplings were identified to species for composition and tallied for density. Seedlings were identified as woody plants $<$ 1 m in height and were inventoried in a 10-m^2 nested subplot at plot center. Deadwood ($\geq$ 5 cm diameter) in each 500-m^2 plot was tallied and classified as a snag (standing dead trees with crown fully intact), snapped stem, uprooted stem, or log. Deadwood was assigned one of five decay classes, following the guidelines of the Forest Inventory and Analysis program of the USFS (FIA 2005), with "1" indicating least decayed, and "5" indicating most decayed. Logs (without root plate) were measured for length and the

diameter ($\geq$ 5 cm) at the two ends of each individual within the plot or at the point where the log intersected the plot boundary. Uprooted stems (with root plate) were measured for diameter 1.37 m above the root collar. Deadwood lying outside of the plot was not included in the volume measurements. The dbh of snags and snapped stems was also measured.

All live stems $\geq$ 20 cm dbh were cored with an increment borer to determine age and radial growth patterns. All *Quercus* stems $\geq$ 5 cm dbh were cored twice to determine disturbance history via radial growth rate analysis (Buchanan and Hart 2011). Each tree was cored at breast height perpendicular to the slope to minimize the influence of reaction wood.

Laboratory methods

Disturbance history

Tree core samples were air-dried and glued to wooden mounts with the cells vertically aligned (Stokes and Smiley 1996). Each mount was sanded using a series of progressively finer grit abrasives to reveal the cellular structure of the wood surface (Orvis and Grissino-Mayer 2002). Once processed, tree rings were dated to the calendar year of formation. Pith estimators (Villalba and Veblen 1997) were used to estimate inner dates on ring series that did not contain pith but did show substantial ring curvature. Tree-ring series from overstory (dominant and codominant, sensu Oliver and Larson 1996) *Quercus* stems were used to reconstruct disturbance history because ring boundaries are clear, false and absent rings are uncommon, and the genus has been used extensively for disturbance history reconstructions (e.g. McCarthy and Bailey 1996; Nowacki and Abrams 1997; Rubino and McCarthy 2004; Hart and Grissino-Mayer 2008; Buchanan and Hart 2012).

To identify canopy disturbance events, raw ring-widths of every overstory *Quercus* individual (n = 176 ring series) were measured to the nearest 0.001 mm using a Velmex measuring system (Velmex Incorporated 2009) interfaced with the program Measure J2X (Voor Tech Consulting 2008). Each series was visually inspected and statistically analyzed using COFECHA (Grissino-Mayer 2001), a program that uses segmented time series correlation analysis to ensure each ring is assigned the proper calendar year of formation. Segments that fell below the predetermined significance threshold (r = 0.32, $p < 0.01$) were automatically flagged by the program (Holmes 1983; Grissino-Mayer 2001). Flagged series were re-inspected for possible dating errors and dates were adjusted if necessary.

When we were certain that all tree-ring series were accurately dated and each annual growth ring was measured, we used dendrochronological techniques to determine the frequency, magnitude, and spatial extent of canopy-disturbance events. The identification of release episodes in radial growth patterns of canopy trees is the most common dendrochronological technique to elucidate canopy disturbance events (Lorimer 1980; Abrams and Nowacki 1992; Fraver and White 2005; Hart et al. 2012).

We analyzed changes in raw ring-widths using a running mean of the previous and subsequent 10 years. Release events were identified as years where the mean annual growth of the subsequent 10 years was $\geq$ 50% (minor release) or $\geq$ 100% (major release) greater than the mean annual growth for the prior 10 years (Lorimer and Frelich 1989), sustained for at least 1 year. This technique provides quantification of disturbances that are discrete and localized at the neighborhood-scale, as well as canopy disturbances that persist on the landscape for a longer period and are theoretically larger in size. Intermediate-severity disturbance events were identified as release events detected in at least 25% of the plots (Nowacki and Abrams 1997; Hart et al. 2015).

Compositional diversity and structural complexity measures

Tree, sapling, and seedling layers were analyzed using standard descriptors. For trees, we calculated density (stems ha^{-1}); relative density (contribution to total trees); dominance (basal area, $m^2\ ha^{-1}$); relative dominance (contribution to total basal area); and relative importance (sum of relative density and relative dominance) for each species. All trees were placed into 5 cm dbh class bins to assess the diameter distribution of the stand. Size class bins of 5 cm dbh are most commonly used in structural analysis (Nyland 2002), but histogram shapes must be interpreted with caution because they are sensitive to size class interval (Pond and Froese 2015).

Trees were grouped into four categories (*Quercus-Carya*, *Acer-Fagus, Ostrya virginiana*, and "others") based on shade tolerance and successional trends in the Central Hardwood Forest Region (e.g. Rentch et al. 2003; Cowden et al. 2014; Cox et al. 2016) to analyze dbh and crown class distribution patterns. Canopy trees were defined as dominant and co-dominant stems and sub-canopy trees were defined as intermediate and overtopped stems [based on Oliver and Larson (1996) crown classes]. For seedlings and saplings, we calculated relative density. For all layers, we quantified species richness, Shannon diversity (H'), and species evenness (J; Ludwig and Reynolds 1988). Shannon diversity index is commonly used in ecological data sets to characterize the diversity of species in a community, to take into account the abundance and evenness of each species. However, this index was not originally intended for calculating the diversity of species

(Spellerberg and Fedor 2003), and thus can be transformed for other uses.

Species evenness is a measure of species-proportional representation and ranges from zero to one, with zero signifying no evenness and one signifying a complete evenness. Volume of downed logs (no root plate) was calculated using the method outlined by Fraver et al. (2007). Volume of uprooted trees (root plate intact) was calculated using species-specific allometric equations outlined by Woodall et al. (2011). Basal area was calculated for all standing deadwood (snags and snaps).

CRANCOD (Pommerening 2012) was used to quantify overstory compositional diversity and structural complexity. CRANCOD produces nearest-neighbor summary statistics and second-order characteristics using distance and azimuth data. We ran CRANCOD on each individual plot for neighborhood-scale complexity and all 20 plots together for stand-wide complexity. Compositional diversity indices were calculated using Mingling index (M_i) to determine the degree of overstory species intermingling and H' to determine compositional diversity of species in the overstory (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). M_i was calculated for each tree $\geq$ 5 cm dbh and automatically assigned values from 0 to 1 by the program (0 for trees with the four nearest neighbors of the same species, 1 for trees in which all four neighbors are of a different species).

To quantify structural complexity, we calculated M_i and H' with dbh size classes on a 5 cm interval (i.e. each five cm size class bin was analogous to a species) (Staudhammer and LeMay 2001). The treatment of edge trees can affect the estimation of neighborhood indices such as M_i (Pommerening and Stoyan 2006). For calculations of M_i, we used the nearest neighbor 1 (NN1) edge correction method because of our small sample size of trees per plot. NN1 was chosen because buffer zones are difficult to determine with a small sample size per plot (Pommerening and Stoyan 2006). Instead of a fixed buffer, NN1 accounts for the spatial arrangement of the trees nearest to plot edge.

Linking canopy history to compositional diversity and structural complexity

To statistically compare the compositional diversity and structural complexity measures with disturbance history, we derived a metric for the return interval of canopy disturbance for each plot. The return interval was calculated as a ratio of the age of the oldest tree per plot by the number of disturbance events on the plot. We used the disturbance return ratio metric to statistically determine how disturbance frequency correlated with pre-determined diversity metrics. The four metrics used to test correlation between canopy disturbance events and neighborhood-level compositional and structural diversity were (1) tree H', (2) tree M_i, (3) dbh H', and (4) dbh M_i.

To test for the assumptions of linear regression, we tested for normality using the Shapiro-Wilkes test and homoscedasticity using Levene's test for equality of variances. We log transformed disturbance return ratio and tree H' to obtain normality in SPSS v.22 (IBM corporation 2013). Tree M_i, dbh H', and dbh M_i were non-normal. We ran linear regression analysis using disturbance-return ratio and Pearson correlation for tree H' and Spearman ranking correlation for tree M_i, dbh H', and dbh M_i. Because of the lack of replications in this study, results from statistical analysis should not be further extrapolated.

To quantify the environment in which each *Quercus* stem was recruited into the canopy, each stem was categorized into one of three accession strategy classes: gap origin with no subsequent release, gap origin followed by a release, and understory origin followed by a release (Rentch et al. 2003; Hart et al. 2012). Canopy recruitment strategies were determined by comparing the average growth of the first 20 years to the average of the subsequent 20 years (Nowacki and Abrams 1997). If the radial growth of the first 20 years was less than that of the following 20 years, the tree was classified as establishing in the understory. If the first 20 years exceeded the growth of the subsequent 20-year period, the tree was classified as establishing in a gap environment. Residence time in the understory was calculated by the amount of time before the first release event was experienced for each canopy tree.

Results

Species composition

We documented 599 trees ha^{-1} and basal area of 23.85 m^2 ha^{-1}. Species richness of trees was 38, J was 0.79 and H' was 1.75. The most important species based on relative importance was *Q. alba* (20%) followed by *O. virginiana* (16%). The remaining species had a relative importance under 10% beginning with *F. grandifolia* at 9% and *Acer saccharum* at 6% (Table 1). The most important genus was *Quercus* (33% total relative importance and 50% total relative dominance).

Quercus alba had the greatest basal area (7.15 m^2 ha^{-1}). The quadratic mean diameter for *Q. alba* was 40.7 cm, and the largest *Q. alba* stems was 70.5 cm dbh. *Fagus grandifolia* was the second most dominant species with a basal area of 2.44 m^2 ha^{-1}. The remaining

Table 1 Density (stems ha^{-1}) and dominance (m^2 ha^{-1}) of all live stems 5 cm dbh based on relative importance (relative density + relative dominance) in a *Quercus* stand on the Sipsey Wilderness, Alabama

Species	Density (stems ha^{-1})	Relative Density (%)	Dominance (m^2 ha^{-1})	Relative dominance (%)	Relative importance
Quercus alba L.	55	9.2	7.154	30.0	39.2
Ostrya virginiana (Mill.) K. Koch	163	27.2	1.050	4.4	31.6
Fagus grandifolia Ehrh.	45	7.5	2.437	10.2	17.7
Acer saccharum Marshall	41	6.8	1.091	4.6	11.4
Magnolia macrophylla Michx.	48	8.0	0.513	2.2	10.2
Quercus montana Willd.	18	3.0	0.951	4.0	7.0
Carya tomentosa (Lam.) Nutt.	14	2.3	0.999	4.2	6.5
Carya glabra (Mill.) Sweet	17	2.8	0.878	3.7	6.5
Quercus falcata Michx.	6	1.0	1.235	5.2	6.2
Cornus florida L.	29	4.8	0.166	0.7	5.5
Quercus coccinea Münchh.	4	0.7	1.114	4.7	5.3
Nyssa sylvatica Marshall	22	3.7	0.397	1.7	5.3
Fraxinus pennsylvanica Marshall	12	2.0	0.775	3.2	5.3
Other spp.[a]	18	3.0	0.540	2.3	5.2
Quercus muehlenbergii Engelm.	12	2.0	0.753	3.2	5.2
Liriodendron tulipifera L.	5	0.8	0.820	3.4	4.3
Carya ovata (Mill.) K. Koch	10	1.7	0.501	2.1	3.8
Ulmus rubra Muhl.	11	1.8	0.382	1.6	3.4
Oxydendrum arboreum (L.) DC.	13	2.2	0.205	0.9	3.0
Tilia americana L.	7	1.2	0.387	1.6	2.8
Juniperus virginiana L.	4	0.7	0.383	1.6	2.3
Cercis canadensis L.	10	1.7	0.037	0.2	1.8
Quercus michauxii Nutt.	3	0.5	0.275	1.2	1.7
Acer rubrum L.	9	1.5	0.034	0.1	1.6
Quercus stellata Wangenh.	3	0.5	0.251	1.1	1.6
Pinus echinata Mill.	2	0.3	0.282	1.2	1.5
Pinus virginiana Mill.	6	1.0	0.120	0.5	1.5
Carpinus caroliniana Walter	8	1.3	0.022	0.1	1.4
Prunus serotina Ehrh.	4	0.7	0.109	0.5	1.1
Totals	599	100.00	23.861	100.0	200.0

[a]Other species include species that had an importance value of $< 1\%$. Species include *Ulmus alata* Michx., *Quercus rubra* L., *Pinus taeda* L., *Sassafras albidum* (Nutt.) Nees, *Robinia psuedoacacia* L., *Celtis laevigata* Wild., *Acer negundo* L., *Juglans nigra* L., *Styrx grandifolia* Aiton, *Castanea dentata* (Marshal) Borkh, and *Vibernum rufidulum* Raf

species had dominance values under 2.00^2 ha^{-1} and relative dominance under 6%. *Ostrya virginiana* had a dominance of 1.05 m^2 ha^{-1} and a relative dominance of 4%.

Ostrya virginiana had the highest relative density with 163 stems ha^{-1} (27% relative density), nearly three times as abundant as any other species. *Quercus alba* exhibited the second highest relative density with 55 stems ha^{-1} (9%). *Ostrya virginiana* dbh ranged from 5.0 to 17.0 cm, with 117 individuals (72% of all *O. virginiana* stems) in the 5–10 cm size class. *Magnolia macrophylla* (48 stems ha^{-1}, 8%), *F. grandifolia* (45 stems ha^{-1}, 8%), and *Acer saccharum* (41 stems ha^{-1}, 7%) were the next three most abundant species. These five species represented 59% of all trees in the study area. No other species had more than 30 stems ha^{-1} or represented over 5% of total stems.

The canopy contained 131 trees ha^{-1} (dominant or codominant crown class). *Quercus* spp. and *Carya* spp. accounted for 67% of trees in canopy positions. The

intermediate crown position contained 117 stems ha^{-1}, with the "others" category (n = 61) having the highest abundance (Fig. 1). We documented 350 overtopped trees ha^{-1} with *O. virginiana* composing 46% of overtopped stems. In the *Acer-Fagus* taxonomic group, 20% of stems were in canopy positions, while 80% were in sub-canopy positions (intermediate or overtopped crown classes).

We also documented 3861 saplings ha^{-1} (Table 2). Sapling species richness was 51, J was 0.73, and H' was 2.07. *Ostrya virginiana* and *Acer rubrum* had the highest relative sapling abundances, representing 17 and 15% of all saplings, respectively. *Quercus* spp. composed 77 saplings ha^{-1}, representing 2% of saplings. We documented 4500 seedlings ha^{-1}. Seedling species richness was 45, J was 0.78, and H' was 1.68, which was the lowest of the three strata. *Vibernum acerfolium* composed 16% of seedling stems ha^{-1}, followed by *O. virginiana* (10%). *Quercus* spp. composed 335 seedling stems ha^{-1}, including 110 *Q. alba* stems ha^{-1}.

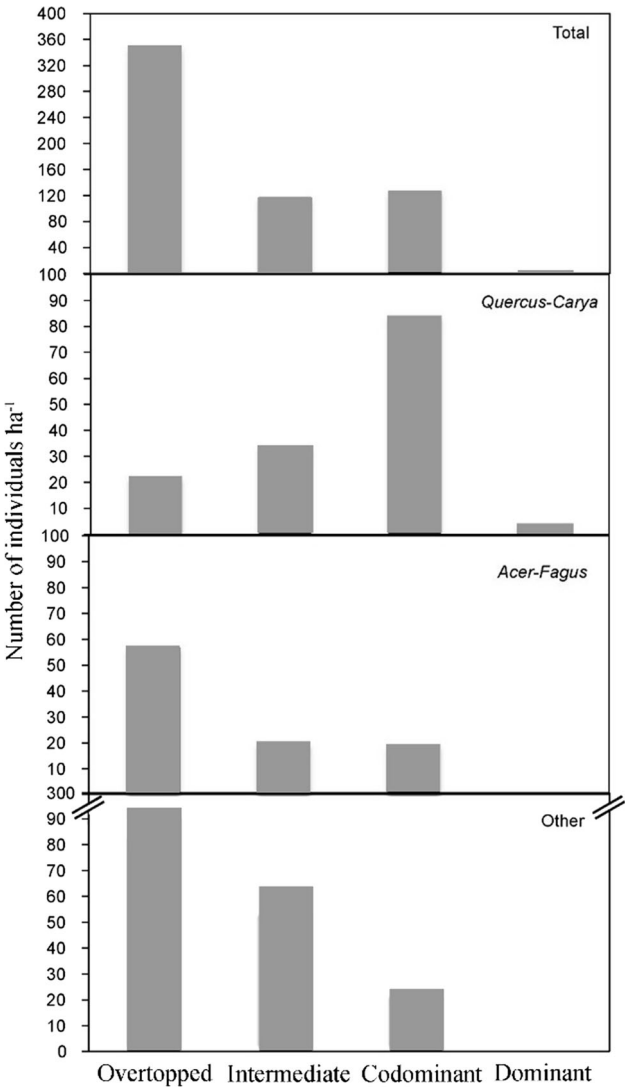

Fig. 1 Crown class distributions per hectare by taxonomic group. Crown classes are based on the amount of intercepted light (overtopped, intermediate, codominant, dominant) (Oliver and Larson 1996). Note the broken y-axis in the "others" group. See Table 1 for species in the "others" group

Stand structure

Tree diameter distribution exhibited a reverse J-shape from small to large size classes, with the highest density of trees in the 5 cm size class (Fig. 2). The Q factor for trees was 1.72. All taxonomic groups had stems in the smallest size class. *O. virginiana* had the highest density of stems in the 5–10 cm size class with 116 stems but had no stems $>$ 20 cm dbh. The diameter distributions of the *Acer-Fagus* group and the "others" group both exhibited a reverse J-shape. The *Quercus-Carya* group exhibited a unimodal distribution, with the highest stem density in the 20–25 cm size class. Only one tree (*Q. alba*) was $\geq$ 70 cm dbh.

The oldest recorded tree (*Carya tomentosa*) established in 1755 and had a dbh of 39.0 cm. The next oldest tree was a *Q. alba* with an inner date of 1796 and a dbh of 45.0 cm. Of the 99 trees that established before 1900 (17% of total trees), 76% were either in the genus *Quercus* or *Carya*. Of the 19 *O. virginiana* stems cored, the oldest had an inner date of 1881 and a dbh of 12.9 cm, and the youngest dated to 1990 and was 5.8 cm dbh. The tree with the largest dbh (*Q. alba*, 70.5 cm dbh) established in 1825 followed by another *Q. alba* with a dbh of 68.7 cm that established in 1918. The relationship between age and diameter was r^2 = 0.25 ($p < 0.001$) for all trees in the *Quercus* genus, r^2 = 0.20 ($p < 0.01$) for trees in the *Carya* genus, r^2 = 0.35 ($p < 0.01$) for trees in the *Acer* genus, r^2 = 0.55 ($p < 0.001$) for *F. grandifolia*, and r^2 = 0.60 ($p < 0.001$) for *O. virginiana* (Fig. 3).

The biggest establishment pulse for *Quercus* and *Carya* occurred in the 1870s and 1880s, with 42% of stems establishing in this 20-year period (Fig. 3). *Quercus* establishment started ca. 1800 and continued with declining establishment beginning in the early 1900s, corresponding with establishment pulses of *Acer* spp. and *F. grandifolia. Acer saccharum* had the largest establishment pulses in the 1900s, and *F. grandifolia* experienced its greatest establishment between 1870 and 1920. *Ostrya virginiana* experienced its largest establishment pulse in 1950, but six individuals established in the 1930s. *Ostrya virginiana* continued to show declining regeneration into the 1990s.

Deadwood composition

We recorded 71 downed logs ha^{-1} and 35 uprooted stems ha^{-1} that together had a total volume of 18.81 m^3 ha^{-1}.

Table 2 Density measures for live stems 1 m height and 5 cm dbh and live stems 1 m height in a *Quercus* stand on the Sipsey Wilderness, Alabama

Sapling	Sapling density	Relative density (%)	Seedling density	Seedling rel. density (%)
Ostrya virginiana	669	17.33	435	9.67
Acer rubrum	586	15.18	120	2.67
Forestiera ligustrina (Michx.) Poir.	298	7.72	140	3.11
Acer saccharum	294	7.61	355	7.89
Cornus florida	222	5.75	155	3.44
Viburnum acerifolium L.	200	5.18	710	15.78
Styrax grandifolia	148	3.83	105	2.33
Sassafras albidum	134	3.47	150	3.33
Lindera benzoin (L.) Blume	130	3.37	260	5.78
Fraxinus pennsylvanica	123	3.19	220	4.89
Asimina triloba (L.) Dunal	113	2.93	245	5.44
Ulmus spp.	86	2.23	240	5.33
Fagus grandifolia	77	1.99	140	3.11
Carpinus caroliniana	64	1.66	55	1.22
Cercis canadensis	59	1.53	100	2.22
Juniperus virginiana	58	1.50	5	0.11
Viburnum rufidulum	53	1.37	15	0.33
Magnolia macrophylla	52	1.35	10	0.22
Crataegus spp.	43	1.11	10	0.22
Frangula caroliniana (Walter) A. Gray	41	1.06	25	0.56
Aesculus pavia L.	38	0.98		
Vaccinium spp.	33	0.85	195	4.33
Carya glabra	30	0.78	75	1.67
Nyssa sylvatica	29	0.75	25	0.56
Carya tomentosa	28	0.73	80	1.78
Prunus serotina	27	0.70	70	1.56
Hypericum prolificum L.	22	0.57	10	0.22
Quercus alba	18	0.47	110	2.44
Quercus muehlenbergii	18	0.47	90	2.00
Quercus rubra	16	0.41	90	2.00
Betula lenta L.	15	0.39		
Quercus montana	15	0.39	15	0.33
Pinus spp.	14	0.36	15	0.33
Acer negundo	12	0.31	35	0.78
Magnolia acuminata (L.) L.	12	0.31	5	0.11
Castanea dentata	11	0.28		
Tilia americana	10	0.26	25	0.56
Amelanchier arborea (Michx. f.) Fernald	9	0.23		
Ilex opaca Aiton	7	0.18	10	0.22
Quercus falcata	7	0.18	10	0.22
Chionanthus virginicus L.	6	0.16		
Morus rubra L.	6	0.16		
Oxydendrum arboreum	6	0.16		
Liriodendron tulipifera	5	0.13	40	0.89
Celtis laevigata	4	0.10	5	0.11
Diospyros virginiana L.	3	0.08	15	0.33
Hamamelis virginiana L.	3	0.08	15	0.33
Quercus velutina Lam.	3	0.08	20	0.44

Table 2 continued

Sapling	Sapling density	Relative density (%)	Seedling density	Seedling rel. density (%)
Hydrangea quercifolia W. Bartram	2	0.05	15	0.33
Euonymus americanus L.	1	0.03		
Fraxinus americana L.	1	0.03	20	0.44
Acer floridanum (Chapm.) Pax			5	0.11
Ligustrum sinense Lour.			10	0.22
Total	3861	100.00	4500	100.00

The majority of downed logs were in decay classes II (n = 55) and III (n = 39), and decay class I and IV had 3 and 4 downed logs, respectively. We identified 20% of logs to species and 22% to genus. The remaining 58% were classified as hardwood or pine because they were in advanced stages of decay and could not be identified to species with confidence. Of the downed logs, 88% were hardwood and 12% were pine (identified to lowest taxonomic class possible).

We recorded 29 standing snapped stems and 3 snags. Of the 32 snaps and snags recorded, 28 were in decay class II, 4 in decay class I, and 1 in decay class IV for a total basal area of 1.41 m^2, and dbh range of 11–45 cm. The highest density of dead stems occurred in the 10–15 cm size class (n = 9) with decreasing density in the larger size classes, revealing a reverse J-shape. All dead stems were recorded to lowest taxonomic class possible, with 72% identified to species, 22% to genus, and the remaining 6% were identified as either hardwood or pine.

Canopy disturbance history

Of the 103 *Quercus* stems analyzed for age structure, 66 were in canopy dominant or co-dominant crown positions and were used to reconstruct canopy disturbance history. From the tree-ring series of these 66 individuals, we documented 96 release events, with 58 (88%) of the individuals showing at least one release. Of the trees assessed, 36 (55%) exhibited two or more release events. The average length of release was 8.0 ± 0.5 (SE) years. The longest release occurred over a 22-year period in a *Q. alba* individual. Of the 96 release events, 33 (34%) were classified as major, and 63 (66%) were classified as minor. The mean time before experiencing a release for understory origin-gap release trees was 44.8 years. The mean interval between release events for the sampled area was 2.4 years ± 0.4 (SE), years with consecutive releases were common. Mean return interval of intermediate-severity disturbance was 37.8 years ± 4.2 (SE).

We documented three intermediate-severity disturbance events occurring from 1911 to 1913 (30% of plots), 1949–1951 (30% of plots), and 1962–1964 (25% of plots). Two of four *Quercus* stems over 10 years old at the time showed a release in the decade of 1850 (Fig. 4). A release event was experienced by 26% of sampled trees in the 1910 decade. Between 1940 and 1960, 39% of trees at least 10 years old experienced a release (n = 26). The distribution of decadal release based on sample size showed a sinusoidal pattern of decadal recruitment between 1900 and 2000 (Fig. 5).

Canopy *Quercus* stems exhibited three recruitment strategies: gap origin-gap release, gap origin-no release, and understory origin-gap release (Fig. 6). The understory origin-gap release recruitment strategy was documented in 58% (n = 38) of dominant and codominant *Quercus* stems. Of the dominant and codominant *Quercus* individuals, 30% (n = 20) exhibited a gap origin-gap release recruitment strategy. The gap origin-no release strategy was documented in 12% (n = 9) dominant and codominant *Quercus* stems. The mean residence time in the understory was 44.8 years for gap origin-gap release trees and 26.9 years for understory origin- gap release. The canopy *Quercus* stems that established in an understory environment (58%) resided for an average of 27 years before being released into the canopy, whereas the canopy *Quercus* stems that established in a gap (30%) resided for an average of 45 years before a subsequent canopy disturbance allowed the stem to recruit into the canopy. The return interval for intermediate-severity disturbance was 11 years greater than the residence time for canopy trees that established in the understory and 7 years less than the residence time for canopy trees that established in a gap.

Linking canopy disturbance to compositional diversity and structural complexity

Stand-wide species M_i was 0.77 with plot-scale values ranging from 0.25 to 1.00. Stand-wide overstory H' was

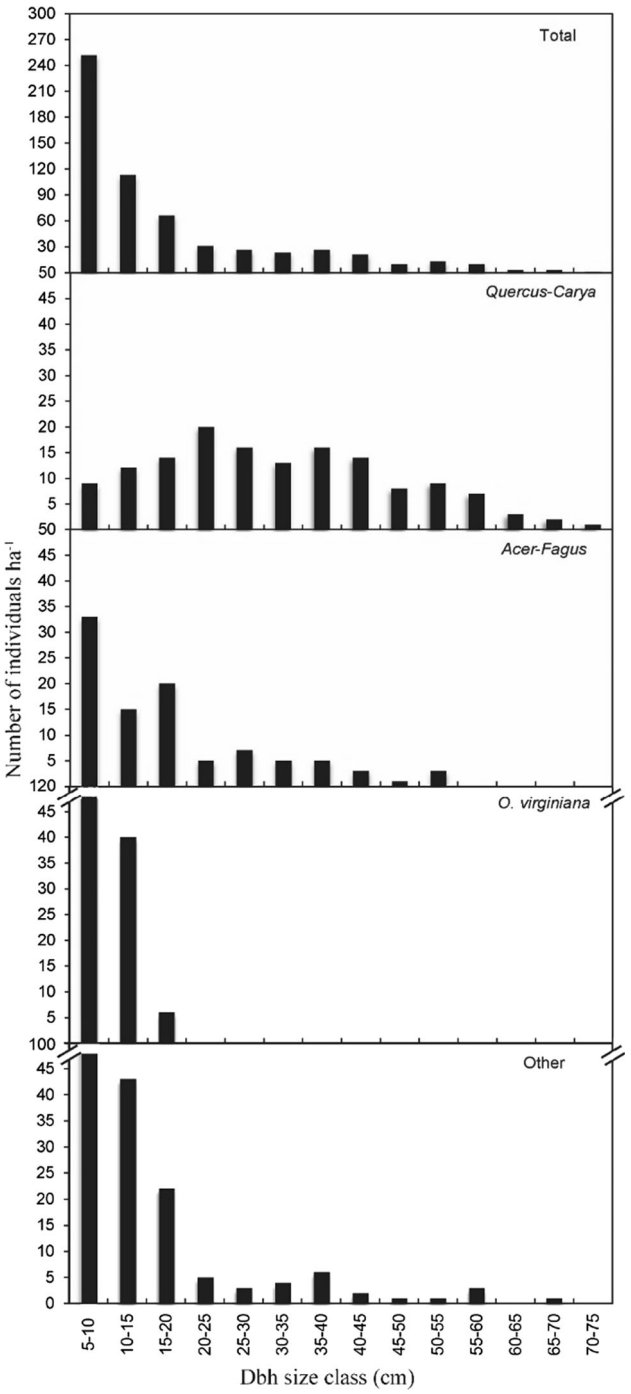

Fig. 2 Number of trees (≥ 5 cm dbh) per hectare for all species, divided into four taxonomic groups in a *Quercus* stand on Sipsey Wilderness, Alabama

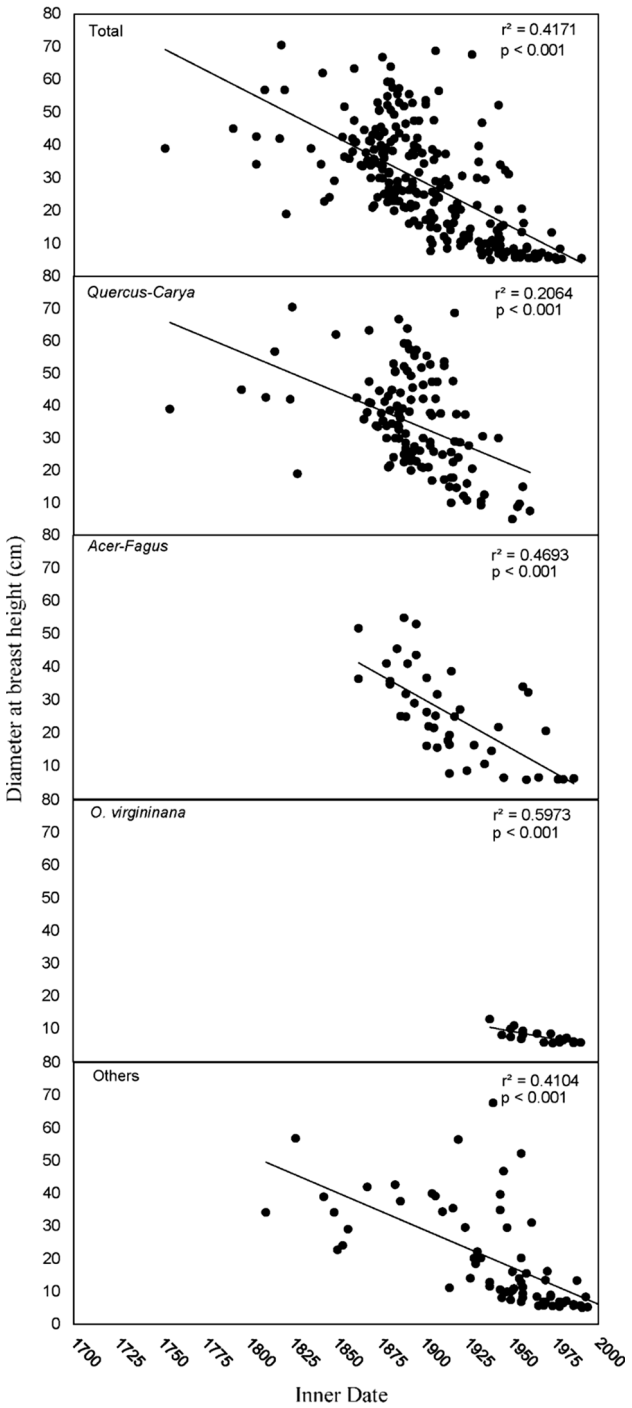

Fig. 3 Diameter-age relationships for all cored trees in our 20 sample plots in a *Quercus* stand on the Sipsey Wilderness, Alabama

1.77, with a plot-scale range of 0.59–2.27. Stand-wide dbh M_i was 0.71, with plot-scale values ranging from 0.09 to 0.91. Stand-wide dbh H' was 1.70, with plot dbh H' values ranging from 1.29 to 2.18 (Table 3). We found a significant relationship between the log-transformed dbh size class H' and log-transformed disturbance frequency using Pearson correlation ($r^2 = 0.26$, $p = 0.03$). All other metrics were non-normal and yielded non-significant values ($p > 0.05$) for Spearman's rank correlation with disturbance frequency.

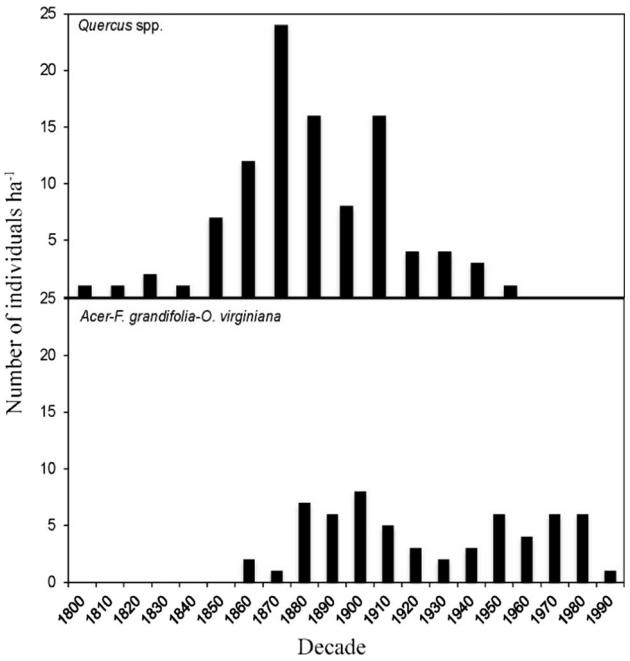

Fig. 4 Decadal recruitment of trees in a *Quercus* stand on the Sipsey Wilderness, Alabama

Discussion

Species composition

The most important tree genus was *Quercus*, however, it was underrepresented in the sapling and seedling layers relative to shade-tolerant species. The lack of *Quercus* and the abundance of shade-tolerant species in the understory (i.e. *O. virginiana* and *A. saccharum*) has been observed in *Quercus* stands throughout the Central Hardwood Forest Region of the United States (McCarthy et al. 2001; Nowacki and Abrams 2008; McEwan et al. 2011; Hart et al. 2012).

Indeed, one of the most pressing issues for the management of *Quercus* stands in the Central Hardwood Forest Region is *Quercus* regeneration failure. Based on their relative abundance, shade-tolerant species had the greatest probability of recruiting from saplings to tree-size classes under the current disturbance regime because of their ability to persist in the understory until a gap-forming disturbance (Hart and Grissino-Mayer 2009; Hart et al. 2012). In the 5–10 cm dbh size class, the abundance of *O. virginiana* (39% of all such stems; nearly three times more than any other species) and *Acer* spp. (18% of all such stems) contributed to the lower diversity (H') of trees relative to saplings and seedlings. The sapling layer was the most diverse ($H' = 2.08$) and species rich ($S = 51$) stratum, but it had the lowest evenness value ($J = 0.73$).

We attributed the richness of this layer to a diversity of sexually mature trees in the stand and the relatively high frequency of canopy disturbances, which may allow seedlings to recruit to > 1 m in height. We attributed the comparatively low evenness value to the abundance of *O. virginiana* and *A. rubrum* as these two species composed over 30% of all saplings. However, we also noted that sapling-layer evenness, although lower than tree and seedling strata, was still relatively high for upland *Quercus* stands in the region (Hart and Grissino-Mayer 2008; Schweitzer and Dey 2011). The lack of *Quercus* spp. in small diameter size classes was likely a result of the abundance of shade-tolerant individuals inhibiting the recruitment of *Quercus* saplings.

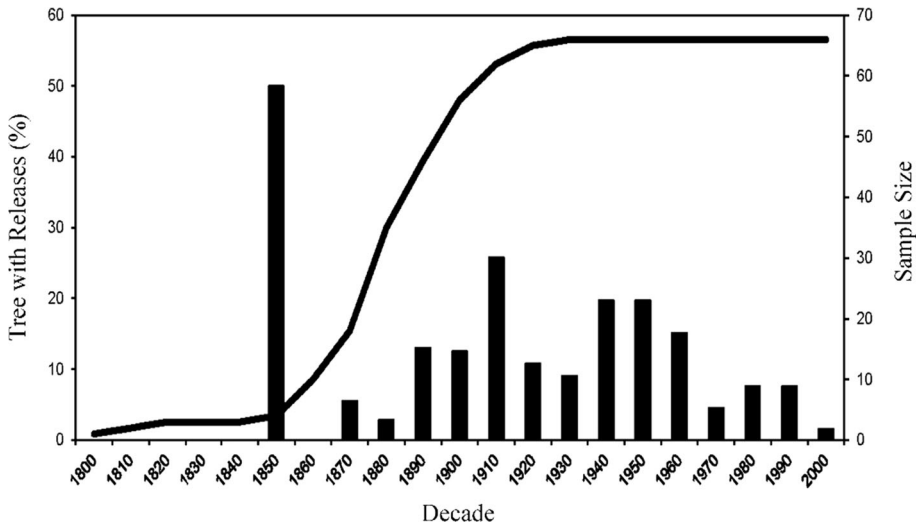

Fig. 5 Release to sample depth ratio (%) by decade. Release events were identified as years where the mean annual growth of the subsequent 10 years was at least 50% greater than the mean annual growth for the prior 10 years. (Lorimer and Frelich 1989). Sample depth is trees at least 10 years old at the time

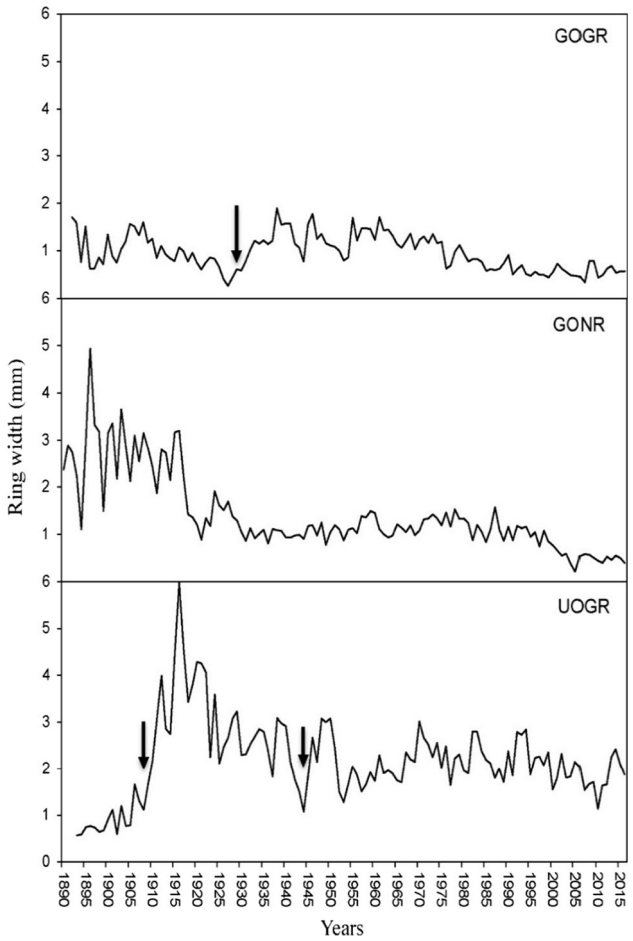

Fig. 6 Line graphs of three different strategies of recruitment into the canopy for trees in Sipsey Wilderness, Alabama. GOGR is gap origin-gap release, GONR is gap origin-no release, and UOGR is understory origin-gap release

Stand structure

The diameter distribution for all *Quercus* spp. was unimodal, with the highest density of *Quercus* stems in the 20–25 cm size class. Similar results have been recorded in other studies that also used 5 cm dbh size class bins (Hart and Grissino-Mayer 2008; Hart et al. 2012, 2015), further indicating that *Quercus* stems are failing to establish and then recruit to larger size classes. We note that comparison of categorical classification of diameter distributions should be made with caution (Pond and Froese 2015). Only 110 *Quercus* seedlings ha^{-1} and 77 saplings ha^{-1} were documented and combined with the lack of *Quercus* stems in the small tree size classes, the results indicate *Quercus* regeneration failure.

Although *A. rubrum* was not a common overstory species, it was abundant in the sapling layer (669 stems ha^{-1}). Shade-tolerant stems (e.g. *A. rubrum, O. virginiana*) revealed a reverse J-shaped diameter distribution, indicating regeneration and possible recruitment into canopy positions following canopy disturbance. We noted a relatively high density of *O. virginiana*, which was documented in other studies in the Sipsey Wilderness (Cowden et al. 2014; White et al. 2015; Cox et al. 2016). Batista and Platt (2003) noted relatively high canopy post-disturbance densities of *O. virginiana*. *Ostrya virginiana* commonly grows in mature stands under low-light conditions, and rarely recruits to canopy positions (Metzger et al. 1990). The ability of *O. virginiana* to persist in the sub-canopy may inhibit certain species (notably *Quercus* spp.) from regenerating. The establishment of *O. virginiana* and *Acer* spp. could be a result of fire exclusion or changes in grazing, or other land use, but that information is unknown.

The diameter distribution for stems $\geq$ 5 cm resembled a reverse J shape with a q-factor of 1.72, which was influenced by 253 stems in the 5–10 cm dbh class, 2.26 times the amount in the 10–15 cm size class. This change from the smallest dbh size class to the next larger can partially be credited to the abundance of *O. virginiana*, with 117 individuals in the 5–10 size class (46%). The q-factor in our stand was similar to what has been reported in other mulit-aged *Quercus* stands (Lowenstein et al. 2000; Rentch 2001). The pulse of individuals in the 35–40 cm size class was credited to the abundance of *Quercus* and *Carya* in this category [16 individuals out of the 26 (62%)].

Table 3 Plot-level summary statistics of compositional diversity and structural complexity metrics

	Composition		Structure			
	Tree H'	Tree M_i	Dbh H'	Dbh M_i	BA	Trees $Plot^{-1}$
Mean	1.78	0.77	1.70	0.71	1.19	29.95
St. Dev.	0.40	0.17	0.21	0.20	0.30	6.37
Variance	0.16	0.03	0.04	0.04	0.09	40.58
Median	1.87	0.81	1.69	0.72	1.19	30.5
Max	2.27	1.00	2.18	0.91	1.85	39.0
Min	0.59	0.25	1.29	0.09	0.75	18.00

H' Shannon diversity, M_i mingling index, *BA* basal area

Deadwood structure

We documented a low density of snags relative to other studies on the Cumberland Plateau in specific and Central Hardwood Forest Region in general (McComb and Muller 1983; Parker 1989; Richards and Hart 2011; Hart et al. 2012). Of the 32 standing dead stems ha^{-1}, 29 were snapped and the remaining three were snags. Martin (1992) suggested that characteristic old-growth forests typically have at least 10 snags $\geq$ 30 cm dbh ha^{-1}; Parker (1989) reported a range of 19–44 snags ($\geq$ 30 cm dbh) ha^{-1}. Hart et al. (2012) documented 130 snags ha^{-1} $\geq$ 5 cm dbh in an old-growth *Quercus* forest on the Cumberland Plateau. Of the 32 standing dead stems, we recorded four *Q. alba*, one *Pinus,* and one *Carya* stem $\geq$ 30 cm dbh, with the remaining standing dead stems $<$ 30 cm dbh. Over half (52%) of standing deadwood was in the genus *Quercus*, representative of the dominant overstory genus.

Interestingly, McComb and Muller (1983) found that snag densities were higher on secondary-growth sites rather than old-growth sites on the Cumberland Plateau. Of the three snags recorded, only one was representative of the dominant overstory genus (a 24 cm dbh *Q. montana*). In 2011, an EF-1 tornado tracked through the Sipsey Wilderness, producing wind speeds up to 153 kph and was accompanied by fast straight-line winds (NOAA 2016). This resulted in an intermediate-severity disturbance event that may have removed snags from the canopy. Perhaps some of the documented snapped stems were originally snags that were snapped during this event. Over half of the downed woody debris was identified as hardwood (58%) and could not be identified further because of advanced decay. Based on overstory composition, we speculate that a relatively large component of the downed and decayed hardwood stems was *Quercus*.

Canopy disturbance history

Only 11 of the canopy *Quercus* trees on our plots established prior to 1850, and 145 established prior to land acquisition in 1918. Of all stems that established before 1918, 59% were *Quercus* and 34% of such stems were *Q. alba*. The decade with the largest recruitment of *Quercus* was the 1870s. These stands initiated after timber harvesting and older trees were those that were not cut during this event, likely because they were of low quality or too small to be marketable at that time.

We acknowledge that inner dates may have been different if cores were extracted from nearer the root collar rather than at breast height (Larsen and Johnson 1998). However, the height of core extraction did not influence the chronology for reconstructing the disturbance history. The disturbance history reconstruction indicated that the canopy disturbance regime for this stand was characterized by infrequent intermediate-severity events superimposed over frequent gap-scale events. Indeed, this disturbance regime is characteristic of most *Quercus* stands in the eastern United States (Hart and Cox 2017).

Of the 97 release events recorded, 78% were localized events (i.e. asynchronous) likely involving the mortality of a single tree or small cluster of canopy trees (Nowacki and Abrams 1997; Hart et al. 2012), which influenced the surrounding microenvironment only. The remaining 22% were classed as intermediate-severity disturbance events because of synchronous detection in multiple *Quercus* individuals across the stand. These disturbances likely consisted of a high frequency of small-canopy gaps because the individuals that experienced a release were spread throughout the stand (i.e. not geographically clustered), with unaffected residual stems documented (Hart 2016).

Intermediate-severity disturbances were detected in the years 1911, 1949, and 1962. The intermediate-severity disturbances of 1949 directly altered stand structure and provided enough light and growing space to be filled from the understory (canopy tree recruitment) rather than being filled by adjacent branching, commonly the case with the more frequent yet smaller gap-scale disturbances (Richards and Hart 2011), as evidenced by the individuals not experiencing another release after 1949. The 1911 and 1962 intermediate-severity events likely resulted in numerous smaller canopy gaps, evidenced by individuals experiencing a release in years following the intermediate-severity disturbance. These three events were not severe enough to be stand-initiating, as evidenced by surviving residual trees that did not experience releases. The mean residence time for 98% (2% of *Quercus* established in the understory and never experienced a release yet still made it to the canopy) of canopy *Quercus* stems was 36 years, similar to the 38-year return interval of intermediate-severity disturbances.

As a result of the three intermediate-severity disturbance events, 32% of sampled canopy *Quercus* stems ascended to the canopy. We speculate that the 1911 intermediate-severity disturbance event was caused by selective harvesting, which would have occurred prior to federal acquisition in 1918. We are uncertain of the agents responsible for the other intermediate-severity disturbance events. However, we know that the region experienced three tornado outbreaks in 1949, with one EF-4 tornado approximately 100 km southeast of the stand, which may have resulted in wind damage to the stand (NWS 2017). In 1948, two extratropical depressions tracked through western Mississippi and central Alabama, possibly resulting in damaging winds that may have impacted the stand. The 1962 release event was likely caused by a localized

disturbance that was not of sufficient severity to appear in the NWS (2017) severe weather reports. Unknown for this stand is the history of fire and grazing.

Fire is hypothesized to have been a common disturbance process in *Quercus* stands of the eastern United States (Nowacki and Abrams 2008). Prior to federal land acquisition, European settlers may have burned this stand in connection with grazing, and *Quercus* canopy dominance may have been associated with these disturbances or land uses. Regardless of the history, we know that fire has not been a common disturbance agent since federal ownership and we contend that the contemporary canopy disturbance regime is analogous to that of earlier stages of stand development.

Canopy disturbance, species diversity, and structural complexity

One objective of this study was to determine if canopy gap frequency influenced species diversity and structural complexity at a fine spatial scale (i.e. neighborhood scale). We found no significant relationships between plot-level canopy disturbance frequency and compositional diversity. We documented a high degree of variation in compositional diversity at the neighborhood scale in relation to canopy disturbance frequency. We suspect the compositional H' and M_i values were more likely influenced by the stochastic spatial nature of gap-scale disturbances, rather than the frequency of disturbance. We suggest that the frequency of gap-scale disturbances does not necessarily influence plot-level diversity, but rather stand-level diversity.

The formation of a single canopy gap may not increase alpha diversity, but at the stand level, the presence of canopy gaps from a wide range of sizes and shapes formed at different intervals across heterogenous site conditions should increase gamma diversity (Hart and Grissino-Mayer 2009). Also, a release event detected in the radial growth trends may have had a greater impact on microenvironmental conditions outside of our plots.

Conversely, diversity and complexity values may have been influenced by canopy disturbances that occurred outside, but adjacent to our plots and therefore unrecorded in our radial growth analysis. At this latitude (ca. 34.5 N), a gap located to the south of a plot may have allowed increased light to reach the understory whereas, gaps that formed in our plots may have increased insolation to the north of the plot (Poulson and Platt 1989). The lack of high compositional diversity in frequently disturbed plots could also be attributed to the documented abundance of *O. virginiana* and its ability to persist in the understory and inhibit recruitment. Gap recruitment is often influenced by species composition prior to formation rather than the characteristics of the gap itself, which may cause compositional diversity from gaps to be variable because of the patchy nature of propagule dispersion in many landscapes (Midgley et al. 1995; Brown and Jennings 1998; Weber et al. 2014).

The relationship between plot-level structural complexity and disturbance frequency was more conclusive. We documented a significant negative relationship between structural complexity (dbh H') and disturbance frequency. We speculated this pattern was attributed to the presence of large canopy trees and the presence of shade-tolerant stems in sapling and small tree size classes. Large trees have a greater probability of being removed in canopy disturbance events (Peterson 2007; White et al. 2015; Cox et al. 2016) and therefore, should be present on sites that have not experienced canopy disturbance. Also, small and shade-tolerant stems growing in neighborhoods with relatively few canopy disturbances have had relatively few opportunities to recruit to larger size classes.

Therefore, we speculate that a low frequency of canopy disturbance in mature *Quercus* stands may increase structural complexity at the neighborhood scale by retention of large canopy trees and suppression of small shade-tolerant stems that would recruit to larger size classes following canopy disturbance. In the understory re-initiation stage of development, a high frequency of canopy disturbance at the plot scale may actually reduce the range of tree size classes by removing larger canopy trees that are more susceptible to canopy disturbance and releasing small-sized stems. However, we note that at the stand scale, the creation of localized canopy disturbances should increase structural complexity by creating a wide range of tree size classes and horizontal and vertical arrangements of stems and foliage. Although neighborhood-level complexity may decrease, complexity between neighborhoods may increase which would increase stand-level structural complexity (Hart and Cox 2017).

Conclusions

The stand studied here was dominated by *Q. alba* and established as the result of selective harvesting that occurred prior to federal land acquisition in 1918. The dominant overstory taxa (*Quercus* and *Carya*), established starting in 1860, experienced the greatest establishment pulse in the 1870s, with declining establishment until the 1920s. The disturbance regimes of most temperate deciduous forests are characterized by a high frequency of localized and asynchronous gap-scale events, with intermediate-severity disturbance events occurring every 20–50 years (Nowacki and Abrams 1997; Hart et al. 2012; Hart and Cox 2017).

We documented three intermediate-severity canopy disturbance events that occurred in 1911, 1949, and 1962. The return interval of these intermediate-severity events was 38 years and the return interval of localized gap-scale events was ca. 2 years. Our analysis linking disturbance frequency to compositional diversity did not yield a significant relationship. However, we did document a significant negative relationship between canopy disturbance frequency and structural complexity (dbh H') at the neighborhood scale.

Based on these results, we speculate that a high frequency of localized canopy disturbances may have minimal influence on species diversity and may lower structural complexity at the neighborhood scale. However, a high frequency of localized canopy disturbances likely creates heterogeneous structures and species composition at the stand scale. Canopy gaps that vary in size, shape, and age throughout a stand create a patchwork mosaic of neighborhoods with variable structure and composition. Less frequent disturbance allows shade-tolerant individuals to persist in the understory and grow in a suppressed state, allowing more structural variability between the canopy and sub-canopy stems at the neighborhood scale.

Gap-scale disturbances are stochastic processes that vary through space and time. We suggest that localized disturbance increases species diversity and structural complexity, but these processes are manifest at the stand level and not at the neighborhood scale. The spatial variability (i.e. size, shape, orientation, and microsite conditions) of these canopy gaps likely has a greater effect on diversity and complexity than the frequency (temporal variability) of these events at the neighborhood scale. Increasingly, managers are interested in emulating natural disturbance processes in silvicultural systems (Franklin et al. 2007; Long 2009). *Quercus* stands in the Central Hardwood Forest Region are often managed using an even-aged system that treats entire stands uniformly. Our findings, and those of other disturbance history studies in *Quercus* stands, demonstrate that the disturbance regime is characterized by a high frequency of gap-scale disturbance with intermediate-severity canopy disturbances occurring at 20–50 year intervals (Hart and Cox 2017).

Managers that wish to enhance native forest diversity, maintain ecosystem functions, and promote stand resiliency using a natural disturbance-based silviculture approach, may consider implementing even-aged treatments in groups rather than uniformly through stands. The return interval of harvest entries could be based upon the return interval of natural intermediate-severity disturbances in these systems (20–50 years). The group openings could contain reserve trees at variable densities to emulate variability of natural disturbance. Group shelterwoods with reserves at 20–50 year stand entries would seem to resemble the disturbance regime that was documented in this *Q. alba* stand and other *Quercus* stands in the Central Hardwood Forest Region (Hart and Cox 2017).

A primary concern for mangers of *Quercus* stands throughout the temperate zone is *Quercus* regeneration failure. This is a widespread phenomenon that will have direct and negative implications for a range of ecosystem goods and services (Abrams and Nowacki 1992; Lorimer 1993; Nowacki and Abrams 2008; McEwan et al. 2011; Dey 2014). Managers that wish to maintain *Quercus* in stands with an abundance of shade-tolerant stems in the seedling, sapling, and small-tree size classes may not be able to adhere strictly to natural disturbance patterns in their silvicultural systems. Indeed, canopy disturbance in successional *Quercus* stands will likely serve to accelerate succession toward mesophyte dominance without some form of competition control.

Managers of *Quercus* stands in this condition might focus harvest-created openings around patches of advanced *Quercus* reproduction and consider intra-stand heterogeneity in species composition and structure. Regeneration harvests should be timed in conjunction with competition-reduction measures such as fire and/or herbicide application (Schweitzer and Dey 2011; Hutchinson et al. 2012; Brose et al. 2013). The use of herbicide, and perhaps fire, may not have been historically part of the disturbance regimes of *Quercus* stands, but in stands with an abundance of shade-tolerant stems in the regeneration layer, these treatments are likely needed to maintain *Quercus* dominance.

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Author's contributions JDG, CRB, and JLH conceived and designed the study. JDG and CRB led field data collection and data analysis. JDG, CRB, JLH, and DCD wrote the paper.

References

Abrams MD, Nowacki GJ (1992) Historical variation in fire, oak recruitment, and post-logging accelerates succession in central Pennsylvania. J Torrey Bot Soc 119(1):19–28. https://doi.org/10.2307/2996916

Addor ML, Birkhoff J (2004) Bankhead National Forest health & restoration initiative: final report. NCSU Extension. https://projects.ncsu.edu/nrli/decision-making/archive/documents/BankheadFinalReport1.23.04.pdf

Batista WB, Platt WJ (2003) Tree population responses to hurricane disturbance: syndromes in a south-eastern USA old-growth forest. J Ecol 91(2):197–212

Boyden S, Montgomery R, Reich PB, Palik B (2012) Seeing the forest for the heterogeneous trees: stand-scale resource distributions emerge from tree-scale structure. Ecol Appl 22(5):1578–1588

Braun EL (1950) Deciduous forests of eastern North America. Deciduous forests of Eastern North America

Brose PH, Dey DC, Phillips RJ, Waldrop TA (2013) A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak reproduction in eastern North America. For Sci 59(3):322–334

Brown ND, Jennings S (1998) Gap-size niche differentiation by tropical rainforest trees: a testable hypothesis or a broken-down bandwagon. Dynamics of tropical communities. Blackwell, Oxford, pp 79–94

Buchanan ML, Hart JL (2011) A methodological analysis of canopy disturbance reconstructions using *Quercus alba*. Can J For Res 41(6):1359–1367. https://doi.org/10.1139/x11-057

Buchanan ML, Hart JL (2012) Canopy disturbance history of old-growth *Quercus alba* sites in the eastern United States: examination of long-term trends and broad-scale patterns. For Ecol Manag 267:28–39. https://doi.org/10.1016/j.foreco.2011.11.034

Burrascano S, Keeton WS, Sabatini FM, Blasi C (2013) Commonality and variability in the structural attributes of moist temperate old-growth forests: a global review. For Ecol Manag 291:458–479. https://doi.org/10.1016/j.foreco.2012.11.020

Canham CD, Marks PL (1985) The response of woody plants to disturbance patterns of establishment and growth. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, San Diego, pp 197–216

Coates KD, Burton PJ (1997) A gap-based approach for development of silvicultural systems to address ecosystem management objectives. For Ecol Manag 99(3):337–354. https://doi.org/10.1016/S0378-1127(97)00113-8

Cowden MM, Hart JL, Schweitzer CJ, Dey DC (2014) Effects of intermediate-severity wind disturbance on composition, structure, and succession in *Quercus* stands: implications for natural disturbance-based silviculture. For Ecol Manag 330:240–251. https://doi.org/10.1016/j.foreco.2014.07.003

Cox LE, Hart JL, Dey DC, Schweitzer CJ (2016) Composition, structure, and intra-stand spatial patterns along a disturbance severity gradient in a *Quercus* stand. For Ecol Manag 381:305–317. https://doi.org/10.1016/j.foreco.2016.09.040

Dey DC (2014) Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. For Sci 60(5):926–942

Duursma RA, Mäkelä A (2007) Summary models for light interception and light-use efficiency of non-homogeneous canopies. Tree Physiol 27(6):859–870. https://doi.org/10.1093/treephys/27.6.859

ESRI (2011) ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands

Fenneman NM (1938) Physiography of eastern United States. McGraw-Hill Book Company Inc, New York

Ford SA, Kleinman JS, Hart JL (2017) Spatial patterns of canopy disturbance, structure, and species composition in a multi-cohort hardwood stand. Forests 8(3):93. https://doi.org/10.3390/f8030093

Forest Inventory and Analysis (FIA) National Program (2005) 3.0 Phase 3 Field Guide Down Woody Materials, pp 1–38

Fralish JS (2003) The central hardwood forest: its boundaries and physiographic provinces. In: Van Sambeek JW, Dawson JO, Ponder F Jr., Loewenstein EF, Fralish JS (eds) Proceedings, 13th Central Hardwood forest conference; 2002 April 1–3; Urbana, IL. General Technical Report NC-234. US Department of Agriculture, Forest Service, North Central Research Station, St. Paul

Franklin JF, Mitchell RJ, Palik B (2007) Natural disturbance and stand development principles for ecological forestry. US Department of Agriculture, Forest Service, Northern Research Station, Washington, p 44

Fraver S, White AS (2005) Identifying growth releases in dendrochronological studies of forest disturbance. Can J For Res 35(7):1648–1656. https://doi.org/10.1139/x05-092

Fraver S, Ringvall A, Jonsson BG (2007) Refining volume estimates of down woody debris. Can J For Res 37(3):627–633. https://doi.org/10.1139/X06-269

Frelich LE, Sugita S, Reich PB, Davis MB, Friedman SK (1998) Neighbourhood effects in forests: implications for within-stand patch structure. J Ecol 86(1):149–161

Geological Survey of Alabama (GSA) (2006) Geologic map of Alabama, digital version 1.0: Alabama Geological Survey Special Map 220A [adapted from Szabo MW, Osborne WE, Copeland CW, Neathery TL, (1988) Geologic map of Alabama (1:250, 000): Alabama Geological Survey Special Map 220

Griffith GE, Omernik JM, Comstock JA, Lawrence S, Martin G, Goddard A, Hulcher VJ, Foster T (2001) Ecoregions of Alabama and Georgia (Color Poster with Map, Descriptive Text, Summary Tables, and Photographs; Map Scale 1:1,7000,000). US Geological Survey, Reston

Grissino-Mayer HD (2001) Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Res 57:205–221

Hale CM, Pastor J, Rusterholz KA (1999) Comparison of structural and compositional characteristics in old-growth and mature, managed hardwood forests of Minnesota, USA. Can J For Res 29(10):1479–1489. https://doi.org/10.1139/x99-076

Hardiman BS, Bohrer G, Gough CM, Vogel CS, Curtis PS (2011) The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. Ecology 92(9):1818–1827. https://doi.org/10.1890/10-2192.1

Hart JL (2016) Gap-scale disturbances in central hardwood forests with implications for management. In: Greenberg CH, Collins BS (eds) Natural disturbances and historic range of variation: type, frequency, severity, and post-disturbance structure in central hardwood forests USA. Springer, Basel

Hart JL, Cox LE (2017) Incorporating intermediate-severity disturbances in oak stand development. Forests 8(8):284. https://doi.org/10.3390/f8080284

Hart JL, Grissino-Mayer HD (2008) Vegetation patterns and dendroecology of a mixed hardwood forest on the Cumberland Plateau: implications for stand development. For Ecol Manag 255(5):1960–1975. https://doi.org/10.1016/j.foreco.2007.12.018

Hart JL, Grissino-Mayer HD (2009) Gap-scale disturbance processes in secondary hardwood stands on the Cumberland Plateau, Tennessee, USA. Plant Ecol 201(1):131–146. https://doi.org/10.1007/s11258-008-9488-9

Hart JL, Clark SL, Torreano SJ, Buchanan ML (2012) Composition, structure, and dendroecology of an old-growth *Quercus* forest on the tablelands of the Cumberland Plateau, USA. For Ecol Manag 266:11–24. https://doi.org/10.1016/j.foreco.2011.11.001

Hart JL, Cowden MM, Torreano SJ, Vestal PR (2015) Disturbance, succession, and structural development of an upland hardwood forest on the Interior Low Plateau, Tennessee. Nat Areas J 35(4):557–573. https://doi.org/10.3375/043.036.0102

Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bull 43:69–78

Hutchinson TF, Long RP, Rebbeck J, Sutherland EK, Yaussy DA (2012) Repeated prescribed fires alter gap-phase regeneration in mixed-oak forests. Can J For Res 42(2):303–314

International Business Machines Corp (IBM). Released 2013. IBM SPSS Statistics for Windows, Version 22.0. IBM Corp, Armonk

Jõgiste K, Korjus H, Stanturf JA, Frelich LE, Baders E, Donis J, Jansons A, Kangur A, Köster K, Laarmann D, Maaten T, Marozas V, Metslaid M, Nigul K, Polyachenko O, Randveer T, Vodde F (2017) Hemiboreal forest: natural disturbances and the

importance of ecosystem legacies to management. Ecosphere. https://doi.org/10.1002/ecs2.1706
Keasberry AM, Hart JL, Dey DC, Schweitzer CJ (2016) Spatial patterns of irradiance and advanced reproduction along a canopy disturbance severity gradient in an upland hardwood stand. Forests 7(4):73. https://doi.org/10.3390/f7040073
Keeton WS (2006) Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. For Ecol Manag 235(1):129–142. https://doi.org/10.1016/j.foreco.2006.08.005
Kint V, Van Meirvenne M, Nachtergale L, Geudens G, Lust N (2003) Spatial methods for quantifying forest stand structure development: a comparison between nearest-neighbor indices and variogram analysis. For Sci 49(1):36–49
Larsen DR, Johnson PS (1998) Linking the ecology of natural oak regeneration to silviculture. For Ecol Manag 106(1):1–7
Long JN (2009) Emulating natural disturbance regimes as a basis for forest management: a North American view. For Ecol Manag 257(9):1868–1873. https://doi.org/10.1016/j.foreco.2008.12.019
Lorimer CG (1980) Age structure and disturbance history of a southern Appalachian virgin forest. Ecology 61(5):1169–1184. https://doi.org/10.2307/1936836
Lorimer CG (1985) Methodological considerations in the analysis of forest disturbance history. Can J For Res 15(1):200–213. https://doi.org/10.1139/x85-038
Lorimer CG (1993) Causes of the oak regeneration problem. In: Oak regeneration: serious problems, practical recommendations. USDA Forest Service General Technical Report SE-84, Southeastern Forest Experiment Station, Asheville, NC, pp 14–39
Lorimer CH, Frelich LE (1989) A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Can J For Res 19(5):651–663. https://doi.org/10.1139/x89-102
Lowenstein EF, Johnson PS, Garrett HE (2000) Age and diameter structure of a managed uneven-aged oak forest. Can J For Res 30:1060–1070
Ludwig JA, Reynolds JF (1988) Statistical ecology: a primer on methods and computing. Wiley, New York
Martin WH (1992) Characteristics of old-growth mixed mesophytic forests. Nat Areas J 12(3):127
McCarthy BC, Bailey DR (1996) Composition, structure, and disturbance history of Crabtree Woods: an old-growth forest f western Maryland. Bull Torrey Bot Club 124(4):350–365. https://doi.org/10.2307/2996783
McCarthy BC, Small CJ, Rubino DL (2001) Composition, structure and dynamics of Dysart Woods, an old-growth mixed mesophytic forest of southeastern Ohio. For Ecol Manag 140(2):193–213. https://doi.org/10.1016/S0378-1127(00)00280-2
McComb WC, Muller RN (1983) Snag densities in old-growth and second-growth Appalachian forests. J Wildl Manag 47(2):376–382. https://doi.org/10.2307/3808510
McElhinny C, Gibbons P, Brack C, Bauhus J (2005) Forest and woodland stand structural complexity: its definition and measurement. For Ecol Manag 218(1):1–24. https://doi.org/10.1016/j.foreco.2005.08.034
McEwan RW, Dyer JM, Pederson N (2011) Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. Ecography 34(2):234–256. https://doi.org/10.1111/j.1600-0587.2010.06390.x
Metzger FT, Burns RM, Honkala BH (1990) *Ostrya virginiana* (Mill.) K. Koch. In: Burns RM, Honkala BH (eds) Silvics of North America, vol 2. United States Department of Agriculture, Washington, DC
Midgley JJ, Cameron MC, Bond WJ (1995) Gap characteristics and replacement patterns in the Knysna Forest, South Africa. J Veg Sci 6(1):29–36. https://doi.org/10.2307/3236253
National Oceanic and Atmospheric Administration (NOAA) Storm Events Database—Event Details | National Centers for Environmental Information (2016) Ncdc.noaa.gov. Retrieved 25 Aug 2017 from https://www.ncdc.noaa.gov/stormevents/eventdetails.jsp?id=309220
National Weather Service (NWS) (2017) Alabama tornado database. https://www.weather.gov/bmx/tornadodb_main. Accessed 21 Sept 2017
Nowacki GJ, Abrams MD (1994) Forest composition, structure, and disturbance history of the Alan Seeger Natural Area, Huntington County, Pennsylvania. Bull Torrey Bot Club 121(3):277–291. https://doi.org/10.2307/2997182
Nowacki GJ, Abrams MD (1997) Radial growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. Ecol Monogr 67(2):225–249. https://doi.org/10.1890/0012-9615(1997)067
Nowacki GJ, Abrams MD (2008) The demise of fire and ''mesophication'' of forests in the eastern United States. Bioscience 58(2):123–138. https://doi.org/10.1641/B580207
Nyland RD (2002) Silviculture: concepts and applications. Waveland Press Inc., Long Grove
O'Hara KL, Ramage BS (2013) Silviculture in an uncertain world: Utilizing multi-aged management systems to integrate disturbance. Forestry 86(4):401–410. https://doi.org/10.1093/forestry/cpt012
O'Hara KL (2014) Multiaged silviculture: managing for complex forest stand structures. Oxford University Press, Oxford
Oliver CD, Larson BC (1996) Forest stand dynamics: updated edition. Wiley, New York
Orvis KH, Grissino-Mayer HD (2002) Standardizing the reporting of abrasive papers used to surface tree–ring samples. Tree-Ring Res 58(1/2):47–50
Parker GR (1989) Old–growth forests of the central hardwood region. Nat Areas J 9(1):5–11
Parker RP, Hart JL (2014) Patterns of riparian and in–stream large woody debris across a chronosequence of southern Appalachian hardwood stands. Nat Areas J 34:65–78. https://doi.org/10.3375/043.034.0108
Pastorella F, Paletto A (2013) Stand structure indices as tools to support forest management: an application in Trentino forests (Italy). J For Sci 59(4):159–168
Peterson CJ (2007) Consistent influence of tree diameter and species on damage in nine eastern North America tornado blowdowns. For Ecol Manag 250(1):96–108. https://doi.org/10.1016/j.foreco.2007.03.013
Phillips DL, Shure DJ (1990) Patch size effects on early succession in southern Appalachian forests. Ecology 71(1):204–212. https://doi.org/10.2307/1940260
Pommerening A (2002) Approaches to quantifying forest structures. Forestry 75(3):306–324. https://doi.org/10.1093/forestry/75.3.305
Pommerening A (2012) CRANCOD: a program for the analysis and reconstruction of spatial forest structure. Bern University of Applied Sciences, Bern
Pommerening A, Stoyan D (2006) Edge–correction needs in estimating indices of spatial forest structure. Can J For Res 36(7):1723–1739. https://doi.org/10.1139/x06-060
Pond NC, Froese RE (2015) Interpreting stand structure through diameter distributions. For Sci 61(3):429–437
Poulson TL, Platt WJ (1989) Gap light regimes influence canopy tree diversity. Ecology 70(3):553–555. https://doi.org/10.2307/1940202
PRISM Climate Group (2016) http://www.prism.oregonstate.edu/. Accessed 11 Nov 2016
Puettmann KJ, Coates KD, Messier C (2009) A critique of silviculture: managing for complexity. Island Press, Washington, p 38

Rentch JS (2001) Stand dynamics and disturbance history of five oak–dominated old–growth stands in the Unglaciated Appalachian Plateau. Ph.D. Dissertation, West Virginia University, Morgantown

Rentch JS, Fajvan MA, Hicks RR (2003) Oak establishment and canopy accession strategies in five old–growth stands in the central hardwood forest region. For Ecol Manag 184(1):285–297. https://doi.org/10.1016/S0378-1127(03),00155-5

Richards JD, Hart JL (2011) Canopy gap dynamics and development patterns in secondary *Quercus* stands on the Cumberland Plateau, Alabama, USA. For Ecol Manag 262(12):2229–2239. https://doi.org/10.1016/j.foreco.2011.08.015

Rubino DL, McCarthy BC (2004) Comparative analysis of dendroecological methods used to assess disturbance events. Dendrochronologia 21(3):97–115. https://doi.org/10.1078/1125.7865.00047

Runkle JR (1981) Gap regeneration in some old-growth forests of the eastern United States. Ecology 62(4):1041–1051. https://doi.org/10.2307/1937003

Saunders MR, Wagner RG (2008) Long–term spatial and structural dynamics in Acadian mixedwood stands managed under various silvicultural systems. Can J For Res 38(3):498–517. https://doi.org/10.1139/X07-155

Schweitzer CJ, Dey DC (2011) Forest structure, composition, and tree diversity response to a gradient of regeneration harvests in the mid–Cumberland Plateau escarpment region, USA. For Ecol Manag 262(9):1729–1741. https://doi.org/10.1016/j.foreco.2011.07.020

Smalley GW (1979) Classification and evaluation for forest sites on the southern Cumberland Plateau. USDA, Forest Service, Southern Forest Experiment Station, GTR SO–23, New Orleans

Spellerberg IF, Fedor PJ (2003) A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon–Wiener' Index. Glob Ecol Biogeogr 12(3):177–179

Staudhammer CL, LeMay VM (2001) Introduction and evaluation of possible indices of stand structural diversity. Can J For Res 31(7):1105–1115

Stokes MA, Smiley TL (1996) An introduction to Tree–ring Dating. University of Arizona Press, Tucson

Thornthwaite CW (1948) An approach toward a rational classification of climate. Geogr Rev 38(1):55–94. https://doi.org/10.2307/210739

Trotsiuk V, Svoboda M, Janda P, Mikolas M, Bace R, Rejzek J, Samonil P, Chaskovskyy O, Korol M, Myklush S (2014) A mixed severity disturbance regime in the primary *Picea abies* (L.) Karst. forests of the Ukrainian Carpathians. For Ecol Manag 334:144–153. https://doi.org/10.1016/j.foreco.2014.09.005

Tyrrell LE, Nowacki GJ, Buckley DS, Nauertz EA, Niese JN, Rollinger JL, Zasada JC (1998) Information about old growth for selected forest type groups in the eastern United States. US Forest Service General Technical Report

US Forest Service of Alabama (2003) History of National Forests in Alabama. http://www.southernregion.fs.fed.us/alabama/forests/forest–history.htm

Velmex Inc. (2009) Velmex Measurement System

Villalba R, Veblen TT (1997) Improving estimates of total tree ages based on increment core samples. Ecoscience 4(4):534–542

Voor Tech Consulting (2008) Measure J2X

Weber TA, Hart JL, Schweitzer CJ, Dey DC (2014) Influence of gap–scale disturbance on developmental and successional pathways in Quercus-Pinus stands. For Ecol Manag 331:60–70. https://doi.org/10.1016/j.foreco.2014.08.006

White PS, Pickett STA (1985) Natural disturbance and patch dynamics: An introduction. In: Pickett STA, White PS (eds) The ecology and natural disturbance and patch dynamics. Academic Press, Cambridge, pp 3–13

White SA, Hart JL, Schweitzer CJ, Dey DC (2015) Altered structural development and accelerated succession from intermediate-scale wind disturbance in *Quercus* stands on the Cumberland Plateau, USA. For Ecol Manag 336:52–64. https://doi.org/10.1016/j.foreco.2014.10.013

Woodall CW, Heath LS, Domke GM, Nichols MC (2011) Methods and equations for estimating aboveground volume, biomass, and carbon for trees in the US forest inventory; 2010

Zenner EK, Peck JE (2018) Floating neighborhoods reveal contribution of individual trees to high sub-stand scale heterogeneity. For Ecol Manag 412:29–40. https://doi.org/10.1016/j.foreco.2018.01.054

Zhang LJ, Oswald BP, Green TH (1999) Relationships between overstory species and community classification of the Sipsey Wilderness, Alabama. For Ecol Manag 114(2):337–383. https://doi.org/10.1016/S0378-1127(98),00368-5