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Authors: Hales, Lucas P., Murray, Jacob, Goode, J. Davis, and Hart, Justin L.

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# Woody Plant Recovery in a Southern Appalachian *Quercus* Stand 12 Years after Wind Disturbance and Salvage Logging

**Lucas P. Hales,* Jacob Murray, J. Davis Goode, and Justin L. Hart**
Department of Geography and the Environment, University of Alabama, Tuscaloosa, Alabama 35487

## ABSTRACT

Compound forest disturbances may alter forest successional and developmental pathways differently than a single disturbance alone; however, this is not a certainty. We investigated effects of post-wind disturbance salvage logging, a common compound disturbance sequence, in an upland *Quercus* stand on the Alabama Cumberland Plateau 12 years after the events. We re-established 60 sample plots in undisturbed, wind-disturbed, and compound-disturbed (wind-disturbed and salvage logged) neighborhoods of a single stand that was first inventoried two years post-disturbance. Sapling density was greatest and seedling density was lowest on compound-disturbed plots. Over the 12 growing seasons since the wind disturbance and salvage logging events, the woody plant assemblages became more diverse and heterogeneous within disturbance categories. On wind-disturbed and compound-disturbed plots, we suspect this was related to reorganization of the woody plant assemblage and arrival of new propagules. On undisturbed plots, we speculated this pattern resulted from gap-scale disturbance processes as the *Quercus alba* stand approached the complex stage of development. In 2012, the wind-disturbed and compound-disturbed woody plant assemblages were distinct in ordination space, but by 2022 the wind-disturbed and compound-disturbed plots were no longer statistically distinct in ordination space. However, the sapling layer of compound-disturbed neighborhoods was heavily dominated by *Acer rubrum* and we hypothesized that the wind disturbance event accelerated succession of *Quercus*-to-*Acer* and that the salvage operation accelerated the composition shift.

**Key words:** *Acer rubrum*, compound disturbance, regeneration, succession, tornado

## INTRODUCTION

Projected increases in forest disturbances over the next century (Seidl et al. 2016) have catalyzed researchers to investigate the impacts of disturbance interactions on successional and stand developmental processes (Scheffer et al. 2001; Frelich 2002; Turner 2010; Cannon et al. 2014; Buma 2015; Cannon et al. 2019; Kleinman et al. 2019). Multiple disturbances that impact a stand in quick succession may be more influential than an isolated incident of the same intensity, as the first disturbance can increase the likelihood, intensity, or severity of a second disturbance and/or alter recovery (Folt et al. 1999; Buma 2015; Cannon et al. 2017; Cannon et al. 2019; Kleinman et al. 2019). Moreover, some compound disturbances have been found to drastically alter future disturbance behavior, reduce ecosystem adaptation potential, and result in stochastic, non-linear successional pathways (Paine et al. 1998; Frelich and Reich 1999; Scheffer et al. 2001; Buma and Wessman 2011; Buma 2015). These interactions can be buffered or amplified depending on factors such as the spatial arrangement of environmental variables and the number of life-history strategies retained as biological legacies (Johnstone et al. 2016; Cannon et al. 2017; Kleinman et al. 2019). Clearly, disturbance interactions are inherently complex and present a challenge for forest managers (Buma 2015).

*email address lphales@crimson.ua.edu
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In forests frequently impacted by canopy disturbances such as strong wind events (e.g. tornadoes, hurricanes), salvage logging is often used to recover economic losses, decrease fuel loads, and reduce the likelihood of subsequent disturbances (White et al. 2014; Kleinman 2019). However, the effects of windthrow followed by logging compared to windthrow alone have yet to be consistently examined. Differences in important factors such as the severity of the initial wind disturbance event, nature of the subsequent logging operation, time intervals between disturbances and observations, and response variables quantified (e.g. woody plants, forbs, fungi, soil compaction) hinder our ability to draw broad conclusions and provide impetus for additional research (Peterson and Leach 2008; Lang et al. 2009; Kleinman et al. 2017; Ford et al. 2018; Kleinman and Hart 2018; Kleinman et al. 2019; Oldfield and Peterson 2019; Kleinman et al. 2021). It is unclear if the quick application of a mechanized operation, intended in part to offset future risks, may alter stand structure and composition at short temporal scales compared to windthrow alone (Peterson and Leach 2008; Lang et al. 2009; White et al. 2014; Kleinman et al. 2017; Oldfield and Peterson 2019). For example, compound wind disturbance and salvage logging interactions have been found to: decrease microtopographic variability (Peterson and Leach 2008; Sass et al. 2018); reduce ground flora diversity, macrofungal richness, and propagule abundance (Ford et al. 2018; Kleinman and Hart 2018); increase soil compaction and homogenization (Lang et al. 2009); delay succession (Peterson and Leach 2008; Oldfield and Peterson 2019); and shift woody species composition in softwood and hardwood stands (Lang et al. 2009; White et al. 2014). Different recovery trajectories have been documented between sites that experienced wind disturbance alone and those that were subsequently salvage logged (Lang et al. 2009; White et al. 2014; Kleinman et al. 2019). Forest ecosystems that are less resilient may experience accelerated compositional and structural transitions in response to compound disturbances (Holling 1973; Walker et al. 2004; Peterson and Leach 2008).

For most *Quercus* stands in the Central Hardwood Region of the eastern United States, *Acer rubrum* and other shade-tolerant mesophytes dominate mid- and understory strata, suggesting an eventual shift in future canopy composition (Lorimer 1984; Abrams 2005; Nowacki and Abrams 2008; Hart et al. 2012; White et al. 2014). This widespread pattern has been attributed to interacting ecosystem drivers including climate change, fire suppression and other anthropogenic changes in disturbance regimes, the loss of foundation species, and population changes of browsing species (McEwan et al. 2011). The compounded effects of wind disturbance and salvage logging have been hypothesized to exacerbate this process. *Acer* mortality of stems <1 m in height was significantly less than *Quercus* mortality following a salvage logging operation in Kentucky (Stringer 2006), and the addition of a salvage operation amplified the *Quercus*-to-*Acer* transition just two growing seasons after implementation (White et al. 2014). However, few long-term studies have been conducted and, because initial post-disturbance regeneration has proven to be an unreliable indicator of successional trajectories (Oliver and Larson 1996; Gill et al. 2017), additional information is required to develop a better understanding of how wind disturbance and salvage logging interactions influence successional and developmental processes in *Quercus*-dominated stands.

Incorporating previously collected data from 2012 (reported in White et al. 2014), we examined the compound effects of wind disturbance and salvage logging on stand development and successional pathways 12 growing seasons post-disturbance in a *Quercus alba* stand. Our goals were to: (1) quantify species composition, structure, and diversity of the woody plant assemblage between disturbance categories (i.e., undisturbed, wind-disturbed, and compound-disturbed neighborhoods), and (2) document and compare post-disturbance successional trajectories.

## MATERIALS AND METHODS

### Study Area

The Bankhead National Forest (BNF) is located on the Cumberland Plateau at the southern terminus of the Appalachian Plateaus physiographic province (Fenneman 1938) in Alabama. The topography is thoroughly dissected, ranging in elevation from ca. 150–400 m, and is thus not characteristic

of a plateau tableland. The geology of the BNF consists primarily of the Pennsylvanian Pottsville Formation, composed of quartzose sandstone and conglomerate with interbedded shale, siltstone, and coal (Szabo et al. 1988). Soils are shallow, well-drained, and acidic (USDA 1959). The climate of the BNF is classified as humid mesothermal (Thornthwaite 1948), with hot, lengthy summers and short, mild winters. The mean annual temperature is 16°C, with a January mean of 5°C and a July mean of 26°C (Smalley 1979). Precipitation averages 1,390 mm annually and is evenly distributed throughout the year with no dry season (PRISM Climate Group 2013).

Forests on the Cumberland Plateau have high plant species richness and landscape-level diversity (Hinkle et al. 1993). Local plant communities are highly influenced by topography and limited by soil-water availability (Hinkle 1989; Clatterbuck and Kauffman 2006). Classified by Braun (1950) as a transitional zone between mixed mesophytic forests to the north and *Quercus-Pinus* forests to the south, this region typically supports mixed mesophytic communities in protected coves and riparian areas. Zhang et al. (1999) noted 14 different ecological communities, including barren communities, xeric *Pinus*-dominated sites, and mesic *Fagus*- and *Acer*-dominated sites within the region. *Quercus* species were a component of almost all community types, and *Quercus* was the most dominant genus in the Sipsey Wilderness Area (Zhang et al. 1999).

On 20 April 2011, the BNF was impacted by an EF1 tornado and received sustained winds of 130–145 kph (National Weather Service 2011). Most windthrow occurred in the tornado path, and storm damage severity decreased with distance from the path (Cowden et al. 2014, Keasberry et al. 2016, Cox et al. 2016). The USDA Forest Service contracted a salvage logging operation to mitigate financial losses and reduce fuel loads within the tornado swath. The operation was completed by November 2011 and yielded 1,973 tonnes of sawtimber and pulpwood.

### Field Methods

Our study occurred in a 49 ha *Quercus alba* stand delineated by the USDA Forest Service. According to inventory records, the stand was established in 1905. The stand was bisected by an unimproved road (Figure 1). Although the tornado resulted in damage through the stand, only portions of the stand north of the road were salvage logged. This provided the unique opportunity to examine the impacts of wind disturbance and subsequent salvage logging within neighborhoods of a single stand. All sampling plots occurred on the same land type according to Smalley's (1979) classification, and until the 2011 tornado, had the same disturbance and management history according to Forest Service records. Although these conditions precluded replicability, we objectively selected sites within the same stand so they would have comparable pre-disturbance conditions. Thus, we used a space-for-time substitution to provide insight on the impacts of catastrophic wind disturbance and salvage logging that would not otherwise be possible (Pickett 1989; Hargrove and Pickering 1992; Davies and Gray 2015).

Our sampling occurred in October 2022, 12 growing seasons after the wind disturbance and 10 years after the first inventory reported in White et al. (2014). Following the methods used in the 2012 inventory, we sampled 60 40 $m^2$ plots (20 plots in each of the three disturbance classes: undisturbed by the tornado, wind-disturbed, and compound-disturbedby both the tornado and salvage logging). Within each disturbance category, plots were established at 25 m intervals in a 4 x 5 plot grid (Figure 1). All plots had a minimum 25 m buffer from roads and adjacent disturbance classes to reduce edge effects. Within each fixed radius plot, all live woody stems were identified to species and tallied by size class. We considered all live woody stems less than 1.2 m height to be seedlings, all live woody stems ≥1.2 m height and <5 cm diameter at breast height (dbh) to be saplings, and all live stems ≥5 cm dbh to be trees. For all trees, we measured and recorded dbh.

### Analytical Methods

For the seedling and sapling size classes we calculated density (number of stems $ha^{-1}$), relative density (percentage of total stems), frequency (number of plots upon which the species occurred), relative frequency (percentage of plots on which species occurred), and relative importance (sum of

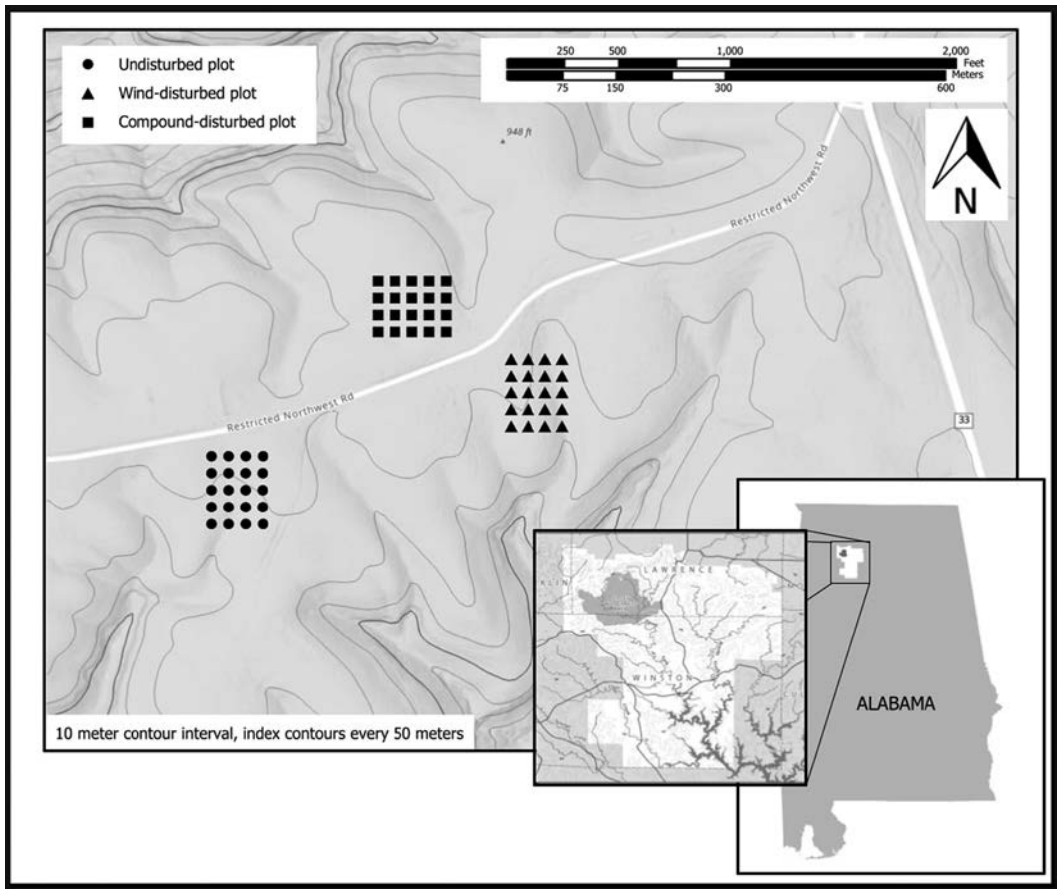


**Figure 1.** Plot locations within the Sipsey Wilderness Area and broader Bankhead National Forest on the Cumberland Plateau in Alabama, USA. Inset map shows location of Bankhead National Forest within the state of Alabama.

relative density and relative frequency) for each disturbance class. For the tree layer we calculated density (number of stems $ha^{-1}$), relative density (percentage of total stems), dominance (basal area as $m^2$ $ha^{-1}$), relative dominance (percentage of basal area), and relative importance (sum of relative density and relative dominance) for each disturbance class. We also calculated the following plot-level diversity measures: species richness (*S*), species evenness (*J*), and Shannon diversity (*H'*).

To illustrate differences in woody plant composition between disturbance categories, we conducted non-metric multidimensional scaling (NMS) in PC-ORD version 7 (McCune and Mefford 2016). Multivariate analyses were conducted separately based on woody plant density per plot collected for this study and by White et al. (2014). Woody plants with single-plot occurrences were excluded to reduce data sparsity. NMS scree plots were used to select the optimal number of axes in NMS solutions. The ordination was run 250 times with real data and relative Sørensen distance, and the final solution cross-checked for consistency with other solutions. To validate visualized compositional differences between treatments, one-way PerMANOVAs with relative Sørensen distance were conducted (McCune and Mefford 2016). To determine if woody plant assemblages became more or less variable between 2012 and 2022, values of mean dispersion were calculated from the 2012 and 2022 dissimilarity matrix and inferentially compared with a 3 x 2 mixed ANOVA.

## RESULTS

Seedling density in the compound-disturbed class was 5,938 stems $ha^{-1}$, much lower than the densities in the undisturbed and wind-disturbed classes (12,213 and 10,263 stems $ha^{-1}$ respectively, Table 1). Sapling density exhibited the opposite trend, with a density of 7,875 stems $ha^{-1}$ in the compound-disturbed class and only 1,263 and 3,188 stems $ha^{-1}$ in the undisturbed and wind-disturbed classes respectively (Table 2). Tree density was higher with increased disturbance severity, with 1,038, 1,238, and 1,563 stems $ha^{-1}$ in the undisturbed, wind-disturbed, and compound-disturbed classes respectively (Table 3). Basal area of the undisturbed neighborhood was 40.8 $m^2$ $ha^{-1}$. Basal area of the disturbed neighborhoods was lower, but we note that basal area in the wind-disturbed neighborhood was 57% greater than that of the compound-disturbed neighborhood. The average dbh of trees in the undisturbed class was 17.0 cm, with an average of 10.4 cm for the wind-disturbed and 7.2 cm for the compound-disturbed classes. The number of live woody plants documented on the study plots was similar across disturbance classes (14,514 for undisturbed, 14,689 for wind-disturbed, and 15,376 for salvaged), but those stems were differentially distributed across the size classes. In the undisturbed class, 84% of all stems were seedlings, 9% were saplings, and 7% were trees. In the wind-disturbed class, 70% of all stems were seedlings, 22% were saplings, and 8% were trees. In the salvaged class, 39% of all stems were seedlings, 51% were saplings, and 10% were trees.

For seedlings, *Quercus alba* was the most important species in the undisturbed class and *Acer rubrum* was most important in the wind-disturbed and compound-disturbed classes. In general, the most important species remained consistent across the disturbance gradient. *Quercus* comprised ca. 57% of all seedlings in undisturbed plots, 38% of all seedlings in wind-disturbed plots, and 39% of all seedlings in compound-disturbed plots. Seedlings of *Acer saccharum* and *Cornus florida* increased in importance from undisturbed to wind-disturbed but were not found in any compound-disturbed plots. Seedlings of *Liriodendron tulipifera* and *Pinus taeda* were not found in any undisturbed plots but increased in importance from wind-disturbed to compound-disturbed plots.

For saplings, *Acer rubrum* was the most important species in the undisturbed and compound-disturbed classes. *Acer rubrum* and *Frangula caroliniana* tied for most important in the wind-disturbed class. *Quercus* comprised 11% of all saplings in undisturbed plots, 27% of all saplings in wind-disturbed plots, and 12% of all saplings in compound-disturbed plots. *Acer* comprised 21% of all saplings on wind-disturbed plots and 49% of all saplings on compound-disturbed plots. For trees, *Pinus taeda* was the most important species in the undisturbed class, *Fagus grandifolia* was the most important species in the wind-disturbed class, and *P. taeda* was the most important species in the compound-disturbed class. Notably, *A. rubrum* dominance was highest on wind-disturbed plots, but density of the species was highest on compound-disturbed plots.

Species richness did not vary greatly by disturbance category, with the exception that richness of the seedling size class was much greater in wind-disturbed neighborhoods than the other disturbance categories (Table 4). For the tree and sapling size classes, Shannon diversity and evenness were lowest in the compound-disturbed neighborhood, but for the seedling size class the undisturbed plots had lower diversity and evenness.

The final three-dimensional NMS solution of the 2012 woody plant assemblages had a non-metric $r^2$ of 0.97 and a final stress of 17.2. The one-way PERMANOVA statistically confirmed visual differences in woody plant assemblages between disturbance categories ($p<0.001$). In the 2012 solution, wind-disturbed and compound-disturbed woody plant assemblages were completely segregated in ordination space, but both assemblages overlapped the undisturbed woody plant assemblage (Figure 2). The wind-disturbed plots were associated with the positive range of axis one, the undisturbed plots were associated with the positive range of axis two, and the compound-disturbed plots were associated with the mid-range of axis one and the positive range of axis two.

The final three-dimensional NMS solution of the 2022 woody plant assemblages had a non-metric $r^2$ of 0.98 and a final stress of 15.7. The one-way PERMANOVA statistically confirmed visual differences in woody plant assemblages between disturbance categories ($p<0.001$). In the 2022 solution, all three woody plant assemblages overlapped in ordination space. The wind-disturbed plots were

**Table 1. Density, relative density, frequency (number of plots present out of 20 sampled), relative frequency (percent of plots present out of 20 sampled), and relative importance (sum of relative density and relative frequency) for seedlings (<1.2 m ht) in adjacent undisturbed (UND), wind-disturbed (WIND), and compound (wind and salvage)-disturbed (SAL) portions of the Bankhead National Forest, Alabama, USA.**

| | Density (stems ha$^{-1}$) | | | Relative Density (%) | | | Frequency | | | Relative Frequency (%) | | | Relative Importance | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **UND** | **WIND** | **SAL** | **UND** | **WIND** | **SAL** | **UND** | **WIND** | **SAL** | **UND** | **WIND** | **SAL** | **UND** | **WIND** | **SAL** |
| *Acer rubrum* L. | 2100 | 2600 | 1500 | 17.2 | 25.3 | 25.3 | 19 | 18 | 18 | 95.0 | 90.0 | 90.0 | 112.2 | 115.3 | 115.3 |
| *Acer saccharum* Marshall | 13 | 88 | 0 | 0.1 | 0.9 | 0.0 | 1 | 3 | 0 | 5.0 | 15.0 | 0.0 | 5.1 | 15.9 | 0.0 |
| *Callicarpa americana* L. | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Carya* spp. | 1163 | 1138 | 613 | 9.5 | 11.1 | 10.3 | 18 | 15 | 16 | 90.0 | 75.0 | 80.0 | 99.5 | 86.1 | 90.3 |
| *Cercis canadensis* L. | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Celtis laevigata* Willd. | 0 | 13 | 0 | 0.0 | 0.1 | 0.0 | 0 | 1 | 0 | 0.0 | 5.0 | 0.0 | 0.0 | 5.1 | 0.0 |
| *Cornus alternifolia* L. | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Cornus florida* L. | 25 | 188 | 0 | 0.2 | 1.8 | 0.0 | 2 | 7 | 0 | 10.0 | 35.0 | 0.0 | 10.2 | 36.8 | 0.0 |
| *Crataegus* spp. | 38 | 25 | 50 | 0.3 | 0.2 | 0.8 | 3 | 1 | 3 | 15.0 | 5.0 | 15.0 | 15.3 | 5.2 | 15.8 |
| *Diospyros virginiana* L. | 75 | 25 | 25 | 0.6 | 0.2 | 0.4 | 6 | 2 | 1 | 30.0 | 10.0 | 5.0 | 30.6 | 10.2 | 5.4 |
| *Elaeagnus pungens* Thunb. | 25 | 13 | 0 | 0.2 | 0.1 | 0.0 | 2 | 1 | 0 | 10.0 | 5.0 | 0.0 | 10.2 | 5.1 | 0.0 |
| *Fagus grandifolia* Ehrh. | 50 | 275 | 88 | 0.4 | 2.7 | 1.5 | 4 | 7 | 5 | 20.0 | 35.0 | 25.0 | 20.4 | 37.7 | 26.5 |
| *Frangula caroliniana* (Walter) A. Gray | 125 | 475 | 113 | 1.0 | 4.6 | 1.9 | 5 | 10 | 3 | 25.0 | 50.0 | 15.0 | 26.0 | 54.6 | 16.9 |
| *Hamamelis virginiana* L. | 0 | 13 | 0 | 0.0 | 0.1 | 0.0 | 0 | 1 | 0 | 0.0 | 5.0 | 0.0 | 0.0 | 5.1 | 0.0 |
| *Ilex opaca* Aiton | 38 | 188 | 38 | 0.3 | 1.8 | 0.6 | 3 | 6 | 2 | 15.0 | 30.0 | 10.0 | 15.3 | 31.8 | 10.6 |
| *Juniperus virginiana* L. | 0 | 25 | 0 | 0.0 | 0.2 | 0.0 | 0 | 2 | 0 | 0.0 | 10.0 | 0.0 | 0.0 | 10.2 | 0.0 |
| *Liquidambar styraciflua* L. | 38 | 25 | 13 | 0.3 | 0.2 | 0.2 | 3 | 2 | 1 | 15.0 | 10.0 | 5.0 | 15.3 | 10.2 | 5.2 |
| *Liriodendron tulipifera* L. | 0 | 50 | 113 | 0.0 | 0.5 | 1.9 | 0 | 4 | 7 | 0.0 | 20.0 | 35.0 | 0.0 | 20.5 | 36.9 |
| *Magnolia macrophylla* Michx. | 13 | 38 | 13 | 0.1 | 0.4 | 0.2 | 1 | 2 | 1 | 5.0 | 10.0 | 5.0 | 5.1 | 10.4 | 5.2 |
| *Nyssa sylvatica* Marshall | 88 | 25 | 63 | 0.7 | 0.2 | 1.1 | 4 | 2 | 4 | 20.0 | 10.0 | 20.0 | 20.7 | 10.2 | 21.1 |
| *Oxydendrum arboreum* (L.)DC. | 25 | 50 | 25 | 0.2 | 0.5 | 0.4 | 1 | 3 | 2 | 5.0 | 15.0 | 10.0 | 5.2 | 15.5 | 10.4 |
| *Pinus echinata* Mill. | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Pinus taeda* L. | 0 | 75 | 563 | 0.0 | 0.7 | 9.5 | 0 | 1 | 4 | 0.0 | 5.0 | 20.0 | 0.0 | 5.7 | 29.5 |
| *Pinus virginiana* Mill. | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Prunus serotina* Ehrh. | 113 | 0 | 63 | 0.9 | 0.0 | 1.1 | 4 | 0 | 3 | 20.0 | 0.0 | 15.0 | 20.9 | 0.0 | 16.1 |
| *Quercus alba* L. var. *serotina* | 3225 | 1138 | 775 | 26.4 | 11.1 | 13.1 | 19 | 15 | 17 | 95.0 | 75.0 | 85.0 | 121.4 | 86.1 | 98.1 |
| *Quercus falcata* Michx. | 163 | 1025 | 213 | 1.3 | 10.0 | 3.6 | 8 | 17 | 6 | 40.0 | 85.0 | 30.0 | 41.3 | 95.0 | 33.6 |
| *Quercus montana* Willd. | 1800 | 325 | 300 | 14.7 | 3.2 | 5.1 | 13 | 9 | 7 | 65.0 | 45.0 | 35.0 | 79.7 | 48.2 | 40.1 |

**Table 1. continued**

| Species | Density (stems ha$^{-1}$) | | | Relative Density (%) | | | Frequency | | | Relative Frequency (%) | | | Relative Importance | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | UND | WIND | SAL | UND | WIND | SAL | UND | WIND | SAL | UND | WIND | SAL | UND | WIND | SAL |
| *Quercus nigra* L. | 0 | 13 | 0 | 0.0 | 0.1 | 0.0 | 0 | 1 | 0 | 0.0 | 5.0 | 0.0 | 0.0 | 5.1 | 0.0 |
| *Quercus rubra* L. | 775 | 713 | 563 | 6.3 | 6.9 | 9.5 | 17 | 12 | 10 | 85.0 | 60.0 | 50.0 | 91.3 | 66.9 | 59.5 |
| *Quercus velutina* Lam. | 963 | 650 | 450 | 7.9 | 6.3 | 7.6 | 16 | 9 | 14 | 80.0 | 45.0 | 70.0 | 87.9 | 51.3 | 77.6 |
| *Rhus copallinum* L. | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Robinia pseudococacia* L. | 0 | 13 | 13 | 0.0 | 0.1 | 0.2 | 0 | 1 | 1 | 0.0 | 5.0 | 5.0 | 0.0 | 5.1 | 5.2 |
| *Sassafras albidum* (Nutt.) Nees | 550 | 13 | 25 | 4.5 | 0.1 | 0.4 | 5 | 1 | 2 | 25.0 | 5.0 | 10.0 | 29.5 | 5.1 | 10.4 |
| *Symplocos tinctoria* (L.) L'Hér. | 0 | 13 | 0 | 0.0 | 0.1 | 0.0 | 0 | 1 | 0 | 0.0 | 5.0 | 0.0 | 0.0 | 5.1 | 0.0 |
| *Ulmus alata* Michx. | 25 | 113 | 125 | 0.2 | 1.1 | 2.1 | 1 | 3 | 3 | 5.0 | 15.0 | 15.0 | 5.2 | 16.1 | 17.1 |
| *Ulmus rubra* Muhl. | 25 | 63 | 25 | 0.2 | 0.6 | 0.4 | 1 | 3 | 2 | 5.0 | 15.0 | 10.0 | 5.2 | 15.6 | 10.4 |
| *Vaccinium arboreum* Marshall | 763 | 863 | 175 | 6.2 | 8.4 | 2.9 | 12 | 13 | 8 | 60.0 | 65.0 | 40.0 | 66.2 | 73.4 | 42.9 |
| **Total** | **12213** | **10263** | **5938** | **100.0** | **100.0** | **100.0** | – | – | – | – | – | – | – | – | – |

**Table 2. Density, relative density, frequency (number of plots present out of 20 sampled), relative frequency (percent of plots present out of 20 sampled), and relative importance (sum of relative density and relative frequency) for saplings (>1.2 m ht, <5 cm dbh) in adjacent undisturbed (UND), wind-disturbed (WIND), and compound (wind and salvage)-disturbed (SAL) portions of the Bankhead National Forest, Alabama, USA.**

| | Density (stems ha$^{-1}$) | | | Relative Density (%) | | | Frequency | | | Relative Frequency (%) | | | Relative Importance | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **UND** | **WIND** | **SAL** | **UND** | **WIND** | **SAL** | **UND** | **WIND** | **SAL** | **UND** | **WIND** | **SAL** | **UND** | **WIND** | **SAL** |
| *Acer rubrum* L. | 513 | 575 | 3863 | 40.6 | 18.0 | 49.0 | 15 | 12 | 19 | 75.0 | 60.0 | 95.0 | 115.6 | 78.0 | 144.0 |
| *Acer saccharum* Marshall | 0 | 100 | 13 | 0.0 | 3.1 | 0.2 | 0 | 3 | 1 | 0.0 | 15.0 | 5.0 | 0.0 | 18.1 | 5.2 |
| *Callicarpa americana* L. | 0 | 0 | 13 | 0.0 | 0.0 | 0.2 | 0 | 0 | 1 | 0.0 | 0.0 | 5.0 | 0.0 | 0.0 | 5.2 |
| *Carya* spp. | 38 | 263 | 200 | 3.0 | 8.2 | 2.5 | 3 | 11 | 7 | 15.0 | 55.0 | 35.0 | 18.0 | 63.2 | 37.5 |
| *Cercis canadensis* L. | 38 | 13 | 0 | 3.0 | 0.4 | 0.0 | 2 | 1 | 0 | 10.0 | 5.0 | 0.0 | 13.0 | 5.4 | 0.0 |
| *Celtis laevigata* Willd. | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Cornus alternifolia* L. | 0 | 0 | 38 | 0.0 | 0.0 | 0.5 | 0 | 0 | 1 | 0.0 | 0.0 | 5.0 | 0.0 | 0.0 | 5.5 |
| *Cornus florida* L. | 0 | 50 | 38 | 0.0 | 1.6 | 0.5 | 0 | 3 | 3 | 0.0 | 15.0 | 15.0 | 0.0 | 16.6 | 15.5 |
| *Crataegus* spp. | 0 | 0 | 13 | 0.0 | 0.0 | 0.2 | 0 | 0 | 1 | 0.0 | 0.0 | 5.0 | 0.0 | 0.0 | 5.2 |
| *Diospyros virginiana* L. | 13 | 25 | 0 | 1.0 | 0.8 | 0.0 | 1 | 2 | 0 | 5.0 | 10.0 | 0.0 | 6.0 | 10.8 | 0.0 |
| *Elaeagnus pungens* Thunb. | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Fagus grandifolia* Ehrh. | 38 | 275 | 175 | 3.0 | 8.6 | 2.2 | 3 | 6 | 5 | 15.0 | 30.0 | 25.0 | 18.0 | 38.6 | 27.2 |
| *Frangula caroliniana* (Walter) A. Gray | 150 | 575 | 413 | 11.9 | 18.0 | 5.2 | 7 | 12 | 8 | 35.0 | 60.0 | 40.0 | 46.9 | 78.0 | 4 5 . 2 |
| *Hamamelis virginiana* L. | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Ilex opaca* Aiton | 38 | 38 | 75 | 3.0 | 1.2 | 1.0 | 3 | 3 | 2 | 15.0 | 15.0 | 10.0 | 18.0 | 16.2 | 11.0 |
| *Juniperus virginiana* L. | 25 | 25 | 25 | 2.0 | 0.8 | 0.3 | 2 | 2 | 1 | 10.0 | 10.0 | 5.0 | 12.0 | 10.8 | 5.3 |
| *Liquidambar styraciflua* L. | 0 | 38 | 0 | 0.0 | 1.2 | 0.0 | 0 | 2 | 0 | 0.0 | 10.0 | 0.0 | 0.0 | 11.2 | 0.0 |
| *Liriodendron tulipifera* L. | 0 | 38 | 475 | 0.0 | 1.2 | 6.0 | 0 | 3 | 9 | 0.0 | 15.0 | 45.0 | 0.0 | 16.2 | 51.0 |
| *Magnolia macrophylla* Michx. | 13 | 125 | 88 | 1.0 | 3.9 | 1.1 | 1 | 6 | 2 | 5.0 | 30.0 | 10.0 | 6.0 | 33.9 | 1 1 . 1 |
| *Nyssa sylvatica* Marshall | 0 | 38 | 350 | 0.0 | 1.2 | 4.4 | 0 | 3 | 9 | 0.0 | 15.0 | 45.0 | 0.0 | 16.2 | 49.4 |
| *Oxydendrum arboreum* (L.) DC. | 38 | 38 | 0 | 3.0 | 1.2 | 0.0 | 1 | 3 | 0 | 5.0 | 15.0 | 0.0 | 8.0 | 16.2 | 0.0 |
| *Pinus echinata* Mill. | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Pinus taeda* L. | 0 | 13 | 788 | 0.0 | 0.4 | 10.0 | 0 | 1 | 8 | 0.0 | 5.0 | 40.0 | 0.0 | 5.4 | 50.0 |
| *Pinus virginiana* Mill. | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Prunus serotina* Ehrh. var. *serotina* | 0 | 38 | 188 | 0.0 | 1.2 | 2.4 | 0 | 3 | 12 | 0.0 | 15.0 | 60.0 | 0.0 | 16.2 | 62.4 |
| *Quercus alba* L. | 50 | 388 | 238 | 4.0 | 12.2 | 3.0 | 3 | 11 | 12 | 15.0 | 55.0 | 60.0 | 19.0 | 67.2 | 63.0 |
| *Quercus falcata* Michx. | 0 | 100 | 75 | 0.0 | 3.1 | 1.0 | 0 | 5 | 3 | 0.0 | 25.0 | 15.0 | 0.0 | 28.1 | 16.0 |
| *Quercus montana* Willd. | 25 | 50 | 138 | 2.0 | 1.6 | 1.7 | 2 | 4 | 7 | 10.0 | 20.0 | 35.0 | 12.0 | 21.6 | 36.7 |

**Table 2. continued**

| Species | Density (stems ha$^{-1}$) | | | Relative Density (%) | | | Frequency | | | Relative Frequency (%) | | | Relative Importance | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | UND | WIND | SAL | UND | WIND | SAL | UND | WIND | SAL | UND | WIND | SAL | UND | WIND | SAL |
| *Quercus nigra* L. | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Quercus rubra* L. | 50 | 275 | 163 | 4.0 | 8.6 | 2.1 | 3 | 10 | 9 | 15.0 | 50.0 | 45.0 | 19.0 | 58.6 | 47.1 |
| *Quercus velutina* Lam. | 13 | 63 | 338 | 1.0 | 2.0 | 4.3 | 1 | 5 | 10 | 5.0 | 25.0 | 50.0 | 6.0 | 27.0 | 54.3 |
| *Rhus copallinum* L. | 0 | 0 | 38 | 0.0 | 0.0 | 0.5 | 0 | 0 | 3 | 0.0 | 0.0 | 15.0 | 0.0 | 0.0 | 15.5 |
| *Robinia pseudococacia* L. | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Sassafras albidum* (Nutt.) Nees | 113 | 13 | 13 | 8.9 | 0.4 | 0.2 | 3 | 1 | 1 | 15.0 | 5.0 | 5.0 | 23.9 | 5.4 | 5.2 |
| *Symplocos tinctoria* (L.) L'Hér. | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Ulmus alata* Michx. | 0 | 0 | 63 | 0.0 | 0.0 | 0.8 | 0 | 0 | 2 | 0.0 | 0.0 | 10.0 | 0.0 | 0.0 | 10.8 |
| *Ulmus rubra* Muhl. | 0 | 13 | 63 | 0.0 | 0.4 | 0.8 | 0 | 1 | 3 | 0.0 | 5.0 | 15.0 | 0.0 | 5.4 | 15.8 |
| *Vaccinium arboreum* Marshall | 113 | 25 | 0 | 8.9 | 0.8 | 0.0 | 6 | 2 | 0 | 30.0 | 10.0 | 0.0 | 38.9 | 10.8 | 0.0 |
| **Total** | **1263** | **3188** | **7875** | **100.0** | **100.0** | **100.0** | – | – | – | – | – | – | – | – | – |

**Table 3. Density, relative density, dominance ($m^2$ $ha^{-1}$) relative dominance (percent of total basal area) and relative importance (sum of relative density and relative dominance) for trees (>5 cm dbh) in adjacent undisturbed (UND), wind-disturbed (WIND), and compound (wind and salvage)-disturbed (SAL) portions of the Bankhead National Forest, Alabama, USA.**

| | Density (stems $ha^{-1}$) | | | Relative Density (%) | | | Frequency | | | Relative Frequency (%) | | | Relative Importance | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **UND** | **WIND** | **SAL** | **UND** | **WIND** | **SAL** | **UND** | **WIND** | **SAL** | **UND** | **WIND** | **SAL** | **UND** | **WIND** | **SAL** |
| *Acer rubrum* L. | 213 | 213 | 338 | 20.5 | 17.2 | 21.6 | 1.8 | 3.1 | 1.5 | 4.5 | 16.4 | 12.4 | 25.0 | 33.6 | 34.0 |
| *Carya* spp. | 50 | 13 | 13 | 4.8 | 1.0 | 0.8 | 3.8 | 0.4 | 0.1 | 9.3 | 2.3 | 0.8 | 14.2 | 3.3 | 1.6 |
| *Cercis canadensis* L. | 13 | 0 | 0 | 1.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 1.3 | 0.0 | 0.0 |
| *Cornus florida* L. | 38 | 88 | 25 | 3.6 | 7.1 | 1.6 | 0.2 | 0.8 | 0.2 | 0.5 | 4.5 | 2.0 | 4.2 | 11.6 | 3.6 |
| *Diospyros virginiana* L. | 13 | 0 | 0 | 1.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 1.3 | 0.0 | 0.0 |
| *Fagus grandifolia* Ehrh. | 125 | 313 | 0 | 12.0 | 25.2 | 0.0 | 1.3 | 3.7 | 0.0 | 3.1 | 19.5 | 0.0 | 15.1 | 44.7 | 0.0 |
| *Frangula caroliniana* (Walter) A. Gray | 13 | 138 | 38 | 1.2 | 11.1 | 2.4 | 0.0 | 0.4 | 0.1 | 0.1 | 2.2 | 0.7 | 1.3 | 13.3 | 3.1 |
| *Ilex opaca* Aiton | 0 | 13 | 0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.9 | 0.0 | 0.0 | 1.9 | 0.0 |
| *Liquidambar styraciflua* L. | 0 | 13 | 0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 1.2 | 0.0 |
| *Liriodendron tulipifera* L. | 25 | 38 | 488 | 2.4 | 3.0 | 31.2 | 2.6 | 3.1 | 2.9 | 6.4 | 16.5 | 24.1 | 8.8 | 19.6 | 55.3 |
| *Magnolia macrophylla* Michx. | 13 | 150 | 75 | 1.2 | 12.1 | 4.8 | 0.4 | 1.8 | 0.5 | 1.0 | 9.4 | 4.1 | 2.2 | 21.5 | 8.9 |
| *Nyssa sylvatica* Marshall | 25 | 113 | 13 | 2.4 | 9.1 | 0.8 | 2.9 | 1.7 | 0.4 | 7.2 | 8.9 | 3.6 | 9.6 | 18.0 | 4.3 |
| *Oxydendrum arboreum* (L.) DC. | 0 | 25 | 13 | 0.0 | 2.0 | 0.8 | 0.0 | 0.3 | 0.1 | 0.0 | 1.8 | 0.5 | 0.0 | 3.9 | 1.3 |
| *Pinus echinata* Mill. | 38 | 0 | 0 | 3.6 | 0.0 | 0.0 | 2.5 | 0.0 | 0.0 | 6.0 | 0.0 | 0.0 | 9.6 | 0.0 | 0.0 |
| *Pinus taeda* L. | 175 | 25 | 400 | 16.9 | 2.0 | 25.6 | 14.1 | 2.9 | 5.7 | 34.7 | 15.5 | 47.5 | 51.5 | 17.5 | 73.1 |
| *Pinus virginiana* Mill. | 38 | 0 | 13 | 3.6 | 0.0 | 0.8 | 2.1 | 0.0 | 0.0 | 5.2 | 0.0 | 0.3 | 8.9 | 0.0 | 1.1 |
| *Prunus serotina* Ehrh. var. *serotina* | 25 | 13 | 88 | 2.4 | 1.0 | 5.6 | 0.3 | 0.0 | 0.2 | 0.8 | 0.1 | 2.0 | 3.2 | 1.1 | 7.6 |
| *Quercus alba* L. | 138 | 13 | 25 | 13.2 | 1.0 | 1.6 | 5.5 | 0.0 | 0.1 | 13.4 | 0.3 | 0.9 | 26.6 | 1.3 | 2.5 |
| *Quercus falcata* Michx. | 13 | 0 | 0 | 1.2 | 0.0 | 0.0 | 0.8 | 0.0 | 0.0 | 1.9 | 0.0 | 0.0 | 3.1 | 0.0 | 0.0 |
| *Quercus montana* Willd. | 63 | 38 | 0 | 6.0 | 3.0 | 0.0 | 2.0 | 0.2 | 0.0 | 5.0 | 1.0 | 0.0 | 11.0 | 4.1 | 0.0 |
| *Quercus rubra* L. | 0 | 25 | 0 | 0.0 | 2.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.4 | 0.0 | 0.0 | 2.4 | 0.0 |
| *Quercus velutina* Lam. | 0 | 13 | 13 | 0.0 | 1.0 | 0.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.4 | 0.0 | 1.1 | 1.2 |
| *Sassafras albidum* (Nutt.) Nees | 25 | 0 | 0 | 2.4 | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 | 0.7 | 0.0 | 0.0 | 3.1 | 0.0 | 0.0 |
| *Ulmus rubra* Muhl. | 0 | 0 | 25 | 0.0 | 0.0 | 1.6 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.7 | 0.0 | 0.0 | 2.3 |
| **Total** | **1038** | **1238** | **1563** | **100.0** | **100.0** | **100.0** | **40.8** | **18.8** | **12.0** | **100.0** | **100.0** | **100.0** | **–** | **–** | **–** |

**Table 4. Diversity, structural, and compositional measures of seedlings (<1.2 m ht), saplings (≥1.2 m ht, <5 cm dbh), and trees (≥5 cm dbh) in adjacent undisturbed (UND), wind-disturbed (WIND), and compound (wind and salvage)-disturbed (SAL) portions of the Bankhead National Forest, Alabama, USA.**

| | Layer | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Tree | | | Sapling | | | Seedling | | |
| Parameter | UND | WIND | SAL | UND | WIND | SAL | UND | WIND | SAL |
| Density (stems $ha^{-1}$) | 1038 | 1238 | 1563 | 1301 | 3451 | 8075 | 13376 | 11401 | 6551 |
| Basal area ($m^2$ $ha^{-1}$) | 40.8 | 18.8 | 12.0 | – | – | – | – | – | – |
| Species richness (*S*) | 18 | 17 | 14 | 17 | 27 | 26 | 26 | 33 | 25 |
| Shannon diversity (*H'*) | 2.45 | 2.28 | 1.83 | 2.23 | 2.79 | 2.14 | 2.45 | 2.78 | 2.69 |
| Evenness (*J*) | 0.85 | 0.81 | 0.69 | 0.79 | 0.85 | 0.66 | 0.75 | 0.80 | 0.84 |

associated with the mid-range of axes one and two, the undisturbed plots were associated with negative range of axes one and two, and the compound-disturbed plot were associated with the positive range of axis two (Figure 2).

The dispersion of plots in ordination space was impacted by the interaction of disturbance and time ($p<0.001$). Between 2012 and 2022, mean dispersion increased across treatments and between time (Figure 3). In 2012, woody plant assemblages on compound-disturbed plots had the greatest mean dispersion, followed by wind-disturbed and undisturbed plots. Woody plant assemblages on wind-disturbed plots had the greatest increase in variability over the 10-year sampling interval. In 2022, both wind-disturbed and compound-disturbed plots had the same mean dissimilarity, although the increase in magnitude was less in compound-disturbed than wind-disturbed plots.

## DISCUSSION

Sapling density was greatest and seedling density was lowest on compound-disturbed plots. Along the disturbance severity gradient, increased severity, caused by compounded disturbances, may have constituted a more influential release event and facilitated recruitment of stems from the seedling to sapling size class. We suspect this pattern was related to increased light availability along the disturbance severity gradient associated with fewer residual trees and less coarse woody debris that would restrict light near the forest floor. Interestingly, in 2012, the wind-disturbed plots had almost twice the density of saplings as the compound-disturbed plots (White et al. 2014). In 2022, the compound-disturbed plots contained 147% more saplings and 26% more trees than the wind-disturbed plots. Although some saplings documented in 2012 undoubtedly recruited to the tree size class, based on tree density, we propose that sapling mortality in wind-disturbed neighborhoods was relatively high. Perhaps the presence of residual trees limited growing space in the sapling layer (Liu et al. 2022).

Notably, of the 7,875 saplings $ha^{-1}$ in the compound-disturbed neighborhood, 49% of them were *Acer rubrum*. This relative density of *A. rubrum* saplings on compound-disturbed plots approximates that of undisturbed neighborhoods. However, the actual density of *A. rubrum* in the sapling layer was similar for undisturbed and wind-disturbed plots. In contrast to undisturbed and compound-disturbed plots, the sapling layer of the wind-disturbed neighborhood was not solely dominated by *A. rubrum*. *Acer rubrum* abundance in sapling and small tree size classes has been widely reported from *Quercus* stands across the eastern United States on all but the most xeric sites (McEwan et al. 2011; Dey et al. 2019). This species is more shade-tolerant than co-occurring *Quercus* and *Carya* species and can persist in the understory for extended periods and then positively respond to increased resources (Fei and Steiner 2009; Hart et al. 2012). On wind-disturbed sites, the relative density of *A. rubrum* in the sapling size class decreased from 33% in 2012 to 18% in 2022, while relative density of the species increased from 41% to 49% during this time on compound-disturbed sites (White et al. 2014). White et al. (2014) hypothesized that the wind disturbance accelerated succession toward

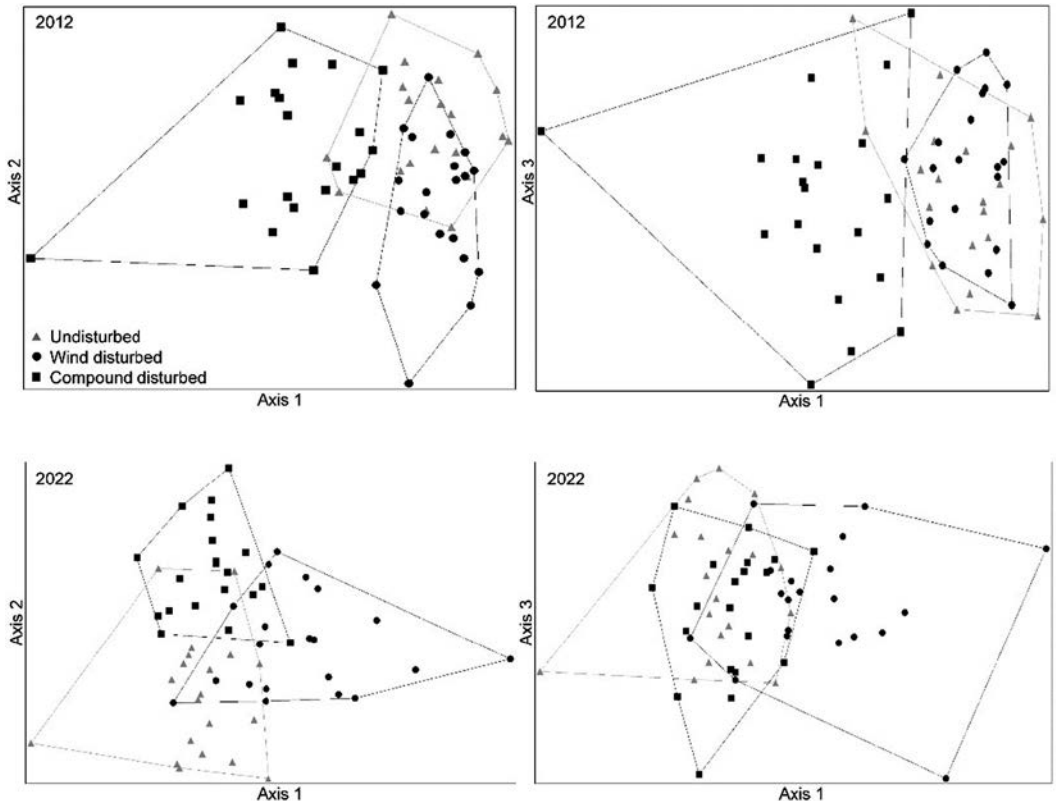


**Figure 2.** Three-dimensional non-metric multidimensional scaling (NMS) ordination of woody plant assemblages (stems plot$^{-1}$) across disturbance categories (undisturbed, wind-disturbed, and compound-disturbed) and between time (2012 and 2022) in a *Quercus* stand on the Bankhead National Forest, Alabama.

increased *A. rubrum* dominance and that this pattern was exacerbated by the salvage operation. Although we acknowledge that density during the stand initiation phase of development is a poor predictor of future dominance (Oliver and Larson 1996), we suspect that *A. rubrum* will be more dominant in compound-disturbed neighborhoods in subsequent stages of stand development. We do note that most of the *A. rubrum* stems were sprouts and that intra-specific competition and density-dependent mortality will likely be high.

Despite the abundance of *Acer rubrum*, especially on compound-disturbed plots, the relative density of *Quercus* saplings increased across all disturbance categories from 2012 to 2022. *Quercus* relative density in the sapling layer was highest on wind-disturbed plots. On compound-disturbed plots, *Quercus* sapling density increased by 376%. However, with the abundance of *A. rubrum*, *Quercus* species represented just ca. 12% of all saplings on compound-disturbed plots. We note that *Quercus* was well stocked in wind- and compound-disturbed neighborhoods and that seedling and sapling densities of *Quercus* were similar across both disturbance classes. White et al. (2014) observed a decline in *Quercus* seedling density across the disturbance gradient, as *Quercus* seedlings comprised 54% of all seedlings on undisturbed plots, 41% on wind-disturbed plots, and 28% on compound-disturbed plots. This trend dissipated over the past decade.

Interpretation of the tree layer is complex because the size class includes residual stems that survived the disturbance or disturbances and those that recruited to this size class post-disturbance. For example, *Liriodendron tulipifera* exhibited a more-than-twelvefold increase in density

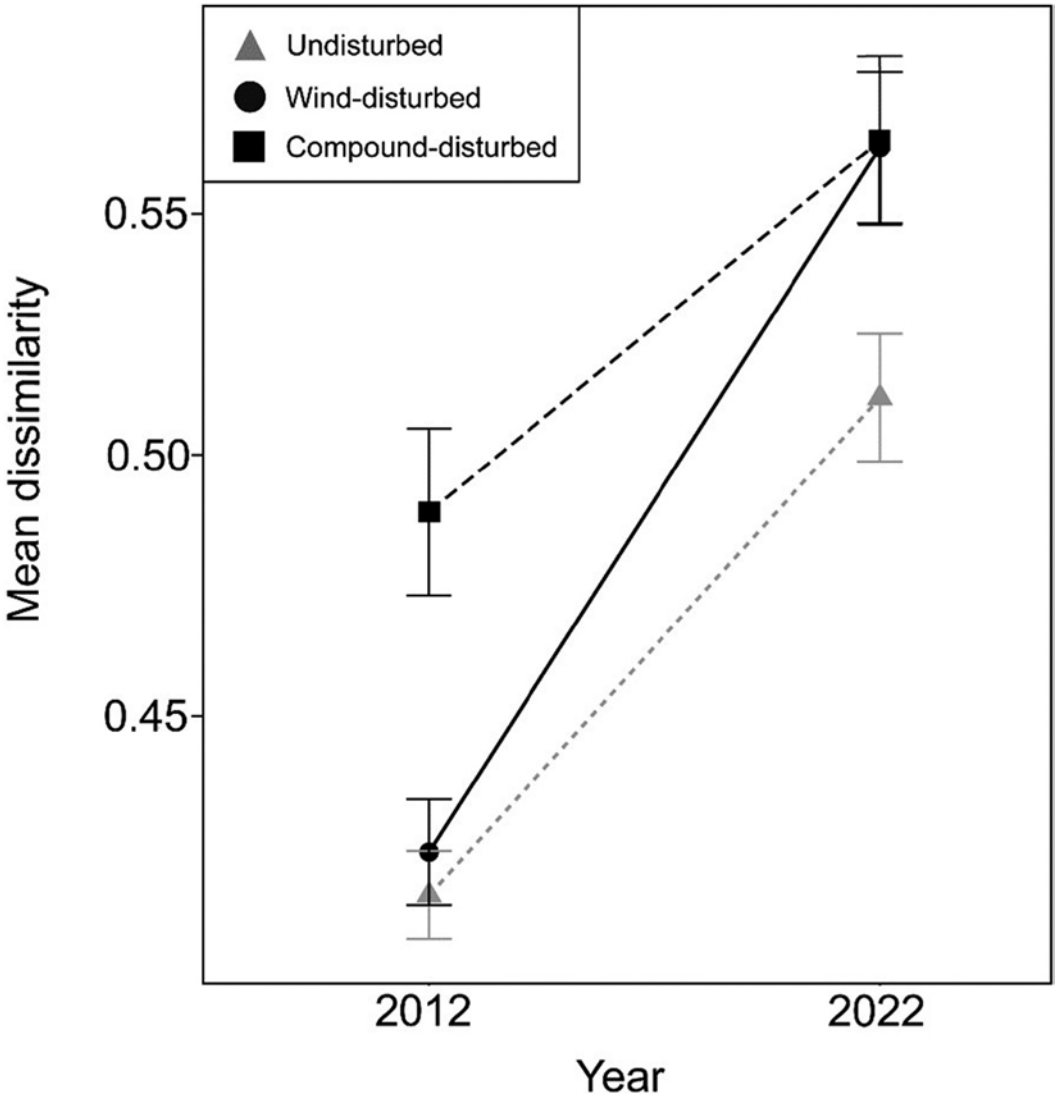


**Figure 3.** Disturbance and time had a significant interaction ($p<0.001$) on the mean dissimilarity (i.e., dispersion) of woody plant assemblages across treatments (undisturbed, wind-disturbed, and compound-disturbed) and between time (2012 and 2022).

between wind-disturbed and compound-disturbed categories but constituted less basal area in the compound-disturbed class. This indicates that the abundance of *L. tulipifera* trees in the compound-disturbed neighborhood were young, small stems that recruited to this size class since the wind disturbance, whereas the few *L. tulipifera* in the wind-disturbed neighborhood were older, larger stems that were legacies from pre-disturbance conditions. The abundance of many young *L. tulipifera* on compound-disturbed plots, which had more of the canopy removed, is consistent with the fast-growing and shade-intolerant characteristics of this species. *Pinus* species appear to have been severely impacted by the wind disturbance, but many small *Pinus taeda* trees were found on compound-disturbed plots. Much like *L. tulipifera*, *P. taeda* is fast-growing and we suspect these

stems were able to reach the tree size class since the disturbance attributed to increased light availability consistent with compound disturbance.

Ordination results indicated that the woody plant assemblages of the three disturbance categories become more similar over the last decade. Notably, the wind- and compound-disturbed assemblages were distinct in 2012 but overlapped in ordination space in 2022. In *Tsuga canadensis*-northern hardwood stands, Lang et al. (2009) found that after 25 years woody plant metrics including tree basal area, sapling density, shrub layer density, and seedling cover had converged between wind-disturbed and compound-disturbed sites. Similarly, Sass et al. (2018) found convergence in the tree layer in *T. canadensis-Pinus strobus* stands 78 years after the events. The woody plant assemblages of disturbed neighborhoods in our study area also seem to be converging.

Although the woody plant assemblages of the three disturbance categories seemed to converge over the past decade, dispersion of plots in each category increased, and this is especially true for the wind-disturbed plots. Thus, over the past 10 years, the woody plant assemblage of plots within each disturbance category became more dissimilar one to the next. Species diversity metrics also increased since the 2012 survey (White et al. 2014). We suspect this is a product of the timing of community reorganization post-disturbance. The 2012 sampling was conducted during the second growing season after the disturbance or disturbances. Thus, some stems documented in the 2022 survey likely originated from propagules that had not yet arrived on the site. Although many of the hardwood stems existed as seedlings or saplings before the disturbance or were of sprout origin, we suspect that some woody stems documented in 2022 did indeed originate from seed that arrived on the site shortly after the disturbance. This may in part explain increased dissimilarity and diversity within the woody plant assemblages. Interestingly, even undisturbed plots exhibited greater species diversity and dissimilarity of the woody plant assemblage. We suspect this was simply related to natural gap-scale disturbance processes in the mature stand and associated responses in the seedling and sapling size classes (Hart and Kupfer 2011; Richards and Hart 2011). The *Quercus alba* stand in which the study occurred established in 1905 and at that stage of development, localized canopy disturbances are common (Hart 2016). We note that we did not quantify the herb layer and other studies have observed that herb layer assemblages differed between wind- and compound-disturbed sites even after 25 years (Lang et al. 2009) and multiple prescribed fires (Kleinman et al. 2021). Oldfield and Peterson (2019) found no significant difference in Shannon diversity between wind-disturbed and salvaged plots 6 years post-disturbance in mixed conifer-hardwood stands in north Georgia, but did find that tree and sapling species composition varied by disturbance category. Thus, they suggested that salvage logging did not impact tree species diversity but did alter species composition. Their findings are consistent with those documented here.

## Conclusion

In the 12 years since the wind disturbance and salvage logging events, the woody plant assemblages became more diverse and heterogenous within disturbance categories. On wind-disturbed and compound-disturbed plots, we attributed this to reorganization of the woody plant assemblage and the arrival of new propagules to the sites. On the undisturbed plots, we speculated this pattern resulted from gap-scale disturbance processes as the *Quercus alba* stand studied approached the complex stage of development. In 2012, the wind-disturbed and compound-disturbed woody plant assemblages were distinct in ordination space, but by 2022 the assemblages converged so that they overlapped in ordination space. Although the wind-disturbed and compound-disturbed plots were no longer visually distinct in ordination space, the sapling layer of compound-disturbed neighborhoods was heavily dominated by *Acer rubrum*. Based on the 2012 inventory, White et al. (2014) suggested that the wind disturbance event accelerated succession of *Quercus*-to-*Acer* and that the salvage operation exacerbated the composition shift. Based on the 2022 survey, we suggest that this pattern was still evident 12 years post-disturbance. Continued monitoring is important to document long-term succession and development patterns in this compound-disturbed *Q. alba* stand.

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