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Catastrophic wind and salvage harvesting effects on woodland plants

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ABSTRACT

Compound disturbances may result in novel forest successional and developmental patterns. This study investigated effects of post-wind disturbance salvage harvesting, a unique compound disturbance of which the ecological consequences are unresolved, in fire-restored longleaf pine woodlands of the Alabama Fall Line Hills, a characteristically biodiverse and rare ecosystem. Plot-level data were collected May–June 2016 in areas undisturbed, wind-disturbed, and compound-disturbed (salvage harvested within seven months of an April 2011 EF3 tornado). Disturbance-mediated differences in (1) physical site conditions, (2) woody plant composition and structure, and (3) ground flora (herbaceous and woody plants ≤ 1 m in height) were assessed. Multivariate analyses revealed distinct differences in ground flora across disturbance categories. Biophysical drivers most correlated with differences in species assemblages included volume of coarse woody debris, sapling density, percent canopy cover, and basal area. Unharvested wind-disturbed plots had the greatest diversity of saplings and ground flora, and had indicator species with unique habitat requirements (specialists). Indicator species of compound-disturbed plots were mostly generalists that also had a relatively high frequency and abundance in the other disturbance categories. Reduced plant diversity on compound-disturbed plots was attributed to salvage harvest-mediated reductions in habitat heterogeneity and resource availability. Thus, leaving patches unharvested within salvaged stands is recommended to promote stand-scale plant diversity.

1. Introduction

Forest succession and development are influenced by disturbance agents, each with a unique frequency, severity, and spatial extent (Frelich, 2002; Oliver and Larson, 1996; White and Pickett, 1985). Variation in the spatiotemporal relationship and collective severity of disturbances results in distinct species assemblages and spatial arrangements (Roberts, 2004). Multiple disturbances in quick succession (i.e. compound disturbances) may have impacts beyond the scope of discrete disturbance events (Paine et al., 1998). As the frequency and severity of natural and human-induced disturbances intensify with global change and growing human demands, it is becoming increasingly relevant to study forest dynamics in the context of multiple interacting disturbances (Buma, 2015; Dale et al., 2001).

Longleaf pine (*Pinus palustris* P. Miller) ecosystems of the southeastern United States provide an excellent model for assessing effects of interacting disturbances, both natural and anthropogenic, because desirable conditions are clearly defined. Contrary to most temperate forests with complex woody plant assemblages and a broad range of conditions from desirable to degraded, proper-functioning longleaf pine ecosystems are relatively simple, approaching monospecific canopy strata situated above relatively open midstories. Degraded longleaf pine ecosystems that do not meet these criteria are easily recognized.

Continuity of longleaf pine dominated canopies and open midstories often requires surface fires to suppress small-statured woody competition coupled with canopy disturbances to facilitate canopy recruitment of longleaf pine (Gilliam et al., 2006; Platt et al., 1988). These fire-maintained conditions may also support some of the most species-rich assemblages of ground flora (woody and herbaceous plants ≤1 m height) in temperate forests of North America (Gilliam, 2007; Van Lear et al., 2005; Walker and Silletti, 2006). However, starting in the late 1800s, industrial-scale exploitation, land-use change, and fire suppression have made longleaf pine ecosystems one of the most endangered ecosystems in the United States (Frost, 1993, 2006; Noss et al., 1995), providing additional incentive to study contemporary disturbance effects on maintaining longleaf pine ecosystems.

Most wind disturbances enhance habitat heterogeneity and resource availability through canopy removal, generation of litter and debris associated with stripped leaves and broken stems, soil scarification, and creation of pit-and-mound microtopography (Beatty, 1984; Gardiner et al., 2016; Mitchell, 2013). Natural disturbance legacies (e.g. coarse woody debris) often support increased species diversity during early stages of development by providing suitable microclimatic conditions and resources (light, moisture, and nutrients) that were previously

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limited (Bartels and Chen, 2010; Swanson et al., 2011). Contrarily, salvage harvesting may be criticized for removing natural disturbance legacies, thereby diminishing species diversity and ecosystem functions (Lindenmayer et al., 2004; Lindenmayer and Noss, 2006). Furthermore, the interaction and collective severity of wind disturbance and salvage harvesting may result in novel forest recovery trajectories (Buma and Wessman, 2011). With the removal of wind-disturbance legacies, plants with prolific reproductive capabilities on heavily disturbed sites (i.e. invasive plants and other ruderal species) may outcompete those adapted to specific habitat requirements (Rumbaitis del Rio, 2006).

Biodiversity is closely linked to ecosystem processes and services that benefit human life, and human impacts on biodiversity have both direct and indirect effects on human well-being (Díaz et al., 2006; Millennium Ecosystem Assessment, 2005). Although some studies suggest salvage harvesting reduces biodiversity, Royo et al. (2016) and Waldron et al. (2014) posited that salvage harvesting can be conducted in ways that maintain or even enhance broad-scale species diversity, especially when some wind-disturbed patches are left unharvested. Because salvage harvesting is used globally to reclaim economic losses on damaged wood products and reduce risks of intense fire and insect outbreaks associated with wind-killed and weakened trees, there is need for a better understanding of salvage harvesting effects on forest recovery and biodiversity, especially ground flora diversity (Rumbaitis del Rio, 2006).

The overarching goal of this study was to assess the early response of a longleaf pine ecosystem to the collective impacts of catastrophic wind and salvage harvesting. Plot-level data were collected May–June 2016 in areas undisturbed, wind-disturbed, and compound-disturbed (salvage harvested within seven months of an April 2011 EF3 tornado) to compare disturbance-mediated differences in (1) physical site conditions, (2) woody plant composition and structure, and (3) ground flora. Results provide a reference condition for monitoring succession and development in this and other longleaf pine ecosystems, and highlight biophysical drivers and forest strata interactions associated with short-term recovery. This information may assist decision making on salvage harvesting in other forest types and enhance understanding of the role of disturbance in the maintenance of biodiversity.

2. Methods

2.1. Study area

This study was conducted on the Oakmulgee District of the Talladega National Forest in Bibb County, Alabama, USA (Fig. 1). The Oakmulgee District is located in the Fall Line Hills, a series of marine-deposited, sedimentary rock belts spanning the inland border of the Coastal Plain that have been carved by streams into steep slopes and ridges resembling the adjacent Appalachian Highlands (Fenneman, 1938; Griffith et al., 2001). Landforms in the study area are composed of the Late-Cretaceous Gordo Formation (GSA 2006). Soils in the Maubila series, which are common on hillslopes and ridges, are deep, moderately-well drained, and have a subangular blocky structure resulting in slow percolation of water (USDA NRCS 2008, 2016). Ironstone fragments occur throughout the soil profile, consisting of a sandy loam or loam surface layer to 10 cm deep situated on clay-based substrata over 200 cm deep to bedrock (USDA NRCS 2008).

The region has a humid mesothermal climate with year-round rainfall and a long, hot growing season (Thornthwaite, 1948). Annual precipitation averages 1376 mm (PRISM 2016). February has the highest mean monthly precipitation of 139 mm and October has the lowest mean monthly precipitation of 87 mm (PRISM 2016). Annual temperature of the study area averages 17 °C, with July having the highest mean monthly temperature of 27 °C and January having the lowest mean monthly temperature of 7 °C (PRISM 2016). The frost-free period spans ca. 230 days from March to November (USDA NRCS 2008).

Plant communities correspond to the Oak (*Quercus*)-Pine (*Pinus*) forest region of the southeastern United States (Braun, 1950). Harper (1943) distinguished these forests as the central longleaf pine belt of Alabama. Although longleaf pine dominates the canopy, loblolly pine (*Pinus taeda* Linnaeus), shortleaf pine (*P. echinata* P. Miller), and a diversity of hardwoods may also attain canopy and subcanopy positions (Beckett and Golden, 1982; Cox and Hart, 2015). Serving as a physiographic transition zone, the Fall Line Hills support species assemblages representative of the Coastal Plain and Appalachian Highlands (Shankman and Hart, 2007).

Harper (1943) speculated that longleaf pine ecosystems in the region "burned originally at least five years out of ten, but likely at irregular intervals." Following industrial-scale harvesting of longleaf pine coupled with an annual fire return interval in the early 1900s, many foresters incorrectly thought fire exclusion would protect these forests from further degradation (Harper, 1943; Reed, 1905). Since federal acquisition of the land in 1943, staff on the Oakmulgee District have prioritized longleaf pine restoration (Cox and Hart, 2015). Today, most restoration efforts are motivated by the intention to improve habitat for the federally endangered red-cockaded woodpecker (*Leuconotopicus borealis* Vieillot), which nests in living longleaf pine trees (Engstrom, 1993). Restoration efforts include regeneration harvests followed by site preparation and longleaf pine outplanting, tree and shrub density reductions in overstocked stands, and implementation of a two to five year prescribed fire rotation (USDA, 2005).

The Oakmulgee District occurs in one of the most tornado-prone regions of the United States (Coleman and Dixon, 2014). Sometimes called Dixie Alley, the Gulf Coast experiences a disproportionately high number of tornadoes (NCDC 2016a). Indeed, Harper (1943) and Reed (1905) recognized Bibb County, Alabama for commonly experiencing high-intensity tornadoes. Since 1950, the National Climatic Data Center (NCDC 2016b) reported three high-intensity (EF3 and greater) tornadoes in Bibb County. Among these was a strong, long-tracked wedge tornado classified as EF3 that tracked across the Oakmulgee District on 27 April 2011 with estimated wind speeds of 233 km/h (NWS 2011). This tornado was one of 362 confirmed tornadoes during the 2011 Super Outbreak event from 25 to 28 April 2011.

The tornado was followed by a salvage harvesting operation July–November 2011. This operation was designed as a cost-effective strategy to mitigate risks of intense fire, smoke, insect outbreaks, and other safety hazards associated with an abundance of wind-damaged trees (Ragland, 2011). Operators were permitted to sever wind-damaged trees of all species and size classes with wheeled feller bunchers and chainsaws. Wheeled skidders were used to elevate logs and skid them to a ramp site for processing and loading by a stationary knuckleboom loader onto truck/trailer combinations for over-the-road transportation (Caylor, personal communication). Because the wood-products market was oversupplied with salvaged timber following the 2011 Super Outbreak, only the most accessible and merchantable stems were salvaged. Salvage harvesting occurred close to pre-existing road networks, leaving some wind-disturbed patches that were less accessible, but analogous from a biophysical perspective, unaffected by salvage harvesting. Combined with the presence of areas undisturbed by the tornado, these conditions provided the opportunity to compare undisturbed, wind-disturbed, and compound-disturbed (wind + salvage) sections of the Oakmulgee District (Fig. 2).

2.2. Field methods

Sites with similar pre-disturbance biophysical site characteristics were selected to distinguish disturbance-mediated differences in site conditions from differences resulting from environmental variation before the storm. Geospatial data provided by the USDA Forest Service were used to select sites characterized by longleaf pine dominance (FSVeg code 21) that established naturally prior to 1940. These second-growth sites occurred on upper and middle slope positions within a

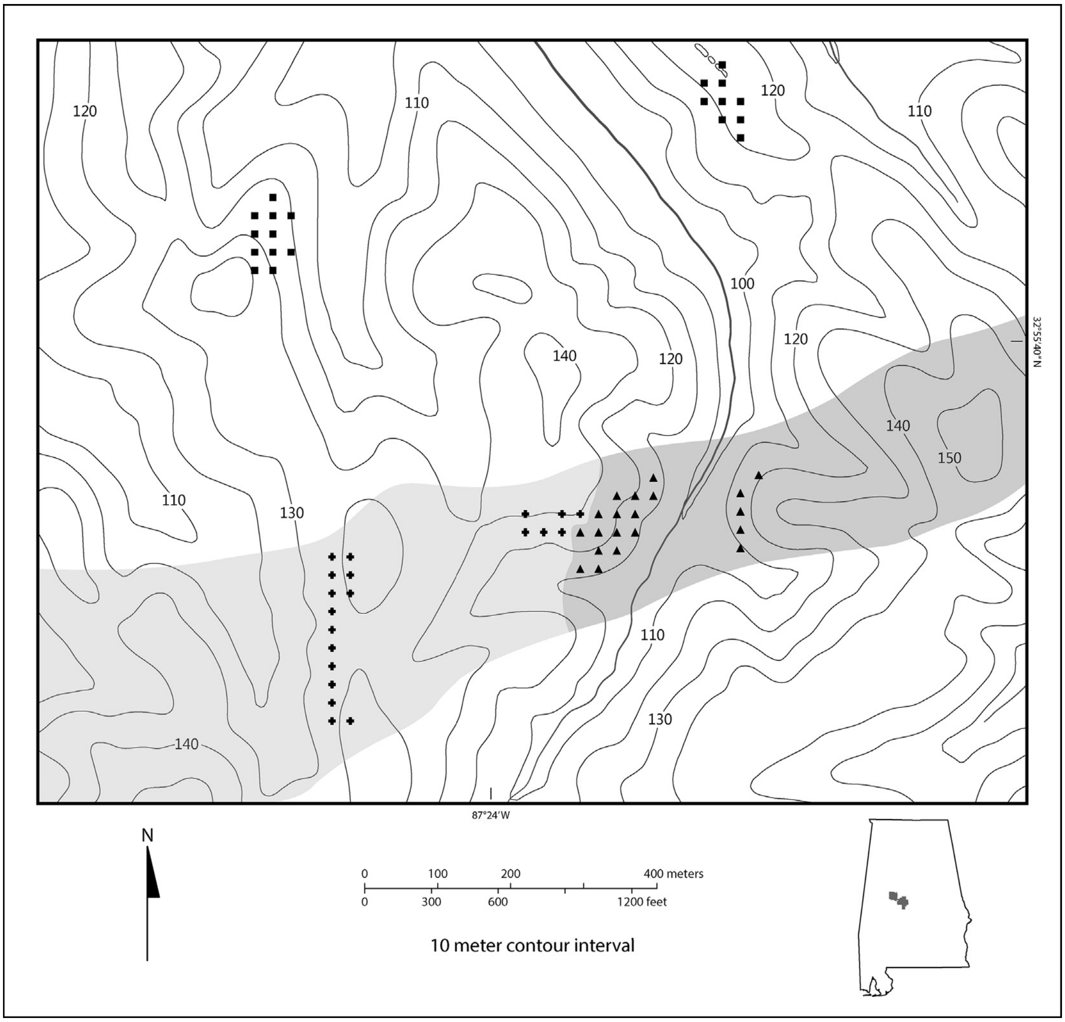

Fig. 1. Map of the study area on the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Path of the 27 April 2011 EF3 tornado is shaded with light shading representing compound-disturbed areas (wind disturbed and salvage harvested) and dark shading representing unharvested wind-disturbed areas. Symbols indicate the location of plots undisturbed (squares), wind-disturbed (triangles) and compound-disturbed (plus signs). The shaded area on the Alabama inset map represents the Oakmulgee Ranger District.

1 km^2 subsection of the same watershed. Web Soil Survey (USDA NRCS 2016) was used to select sites with the same soil series (Maubila series). Spatial proximity and occurrence within the same Forest Service-delineated compartment (burn unit) ensured that the sites experienced the same contemporary prescribed fire regime. At the time of sampling, May–July 2016, the two most recent burns were 5 May 2010 before the tornado and 12 April 2014 after the disturbance events. Thus, plots in all disturbance categories were superimposed over the same pre-existing fire regime.

Aerial photography and ground reconnaissance were used to delineate sections of the selected sites that were undisturbed, wind-disturbed, and compound-disturbed. The tornado had a direct path of impact spanning ca. 0.25–0.5 km wide through the study area. Compound-disturbed sites were distinguished from unharvested wind-disturbed sites by the presence of mechanically cut stems of which many were cut above uplifted root networks (uprooted stumps). ArcMap version 10.2 was used to superimpose a grid with 25 m spacing over the selected sites, and grid cell coordinates were used in the field as waypoints for plot locations. Sampling was only conducted on plots located $\geq$25 m within undisturbed and disturbed areas to reduce potential edge effects. In total, 20 plots in each disturbance category (n = 60) were sampled.

At each plot location, a nested design was used to quantify and compare ecological variables at sampling unit sizes appropriate to characterize the variables of interest. The largest sampling unit was a 400-m^2 (0.04-ha) fixed-radius plot used to measure all dead stems $\geq$10 cm diameter and all live stems > 1 m in height. Ground flora (woody and herbaceous plants $\leq$1 m in height) and ground surface

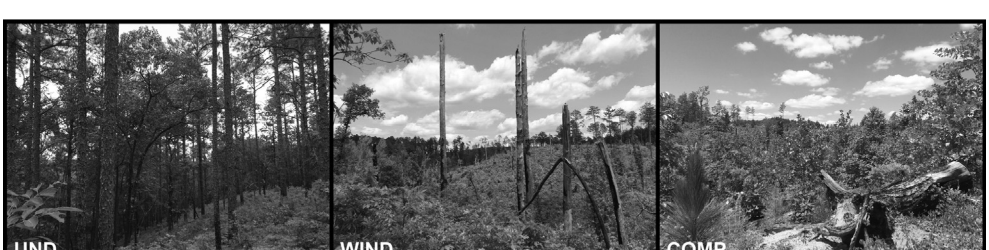

Fig. 2. Photographs of the disturbance categories assessed in this study: undisturbed (UND), wind-disturbed (WIND), and compound-disturbed (COMP) areas of the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Compound-disturbed areas were distinguished by the presence of stems mechanically cut above uplifted root networks.

cover were measured in ten 1 × 1 m quadrats (10 m^2) nested inside each 400-m^2 plot. The center quadrat was positioned at the center of the 400-m^2 plot, and the other nine quadrats were spaced evenly along the 0°, 120°, and 240° azimuths from plot center. Canopy cover was measured as a proxy for canopy light interception, and was quantified with five densitometer readings taken in each 400-m^2 plot: one at plot center and one in each cardinal direction 5 m from plot center.

Dead stems ≥10 cm diameter were broadly identified as hardwood or pine, and ranked from decay class I to V according to increasing degree of decay (USDA 2016). Dead stems disconnected from their roots were categorized as logs. Rooted dead stems were categorized as snags (standing dead stems with crown intact), snapped stems (standing dead stems broken above 1.37 m from root plate), stumps (standing dead stems broken or severed less than 1.37 m from root plate), uprooted stems (stems with uplifted root network), and uprooted stumps (uprooted stems severed less than 1.37 m from root plate). The 1.37 m benchmark was used to facilitate comparison with live trees measured for diameter at this height, and the diameter of dead stems was recorded at this distance from root plate when possible. Logs were measured for diameter at both ends. Coarse woody debris in the study area consisted of logs and uprooted stems (c.f. USDA 2016). Thus, the length of logs and uprooted stems were measured in addition to diameter to include in calculations of course woody debris volume.

Trees were defined as live woody stems ≥5 cm diameter at 1.37 m above root collar (diameter at breast height, dbh) and saplings as live woody stems < 5 cm dbh and > 1 m in height. Trees and saplings were identified to species to characterize their composition and tallied to quantify their density. Tree dbh measurements were recorded to quantify basal area ($m^2\,ha^{-1}$) and dominance (species-specific basal area). The crown classes of trees were recorded to characterize their vertical stratification. Crown classes included dominant, codominant, intermediate, and overtopped, and were based on crown height and amount of light interception compared to adjacent trees (Oliver and Larson, 1996).

With the exception of grasses (Poaceae), which were not identified beyond family, ground flora was identified to the lowest taxonomic level possible given existing reproductive structures. Voucher specimens and photographs were taken when necessary, and sites were visited repeatedly every other week May–July 2016 to refine identification of plants that were not fully developed at the time of initial documentation. Botanical nomenclature was adopted from Weakley (2015) and common names follow The Alabama Plant Atlas (Keener et al., 2017).

The percent cover of ground flora was estimated using panels sized to cover 1% and 5% of each 1 m^2 quadrat as guides. Percent cover estimations were ranked from 1 to 10 on each quadrat using the North Carolina Vegetation Survey (NCVS) protocol where 1 = solitary or few, 2 = 0–1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95%, and 10 = 95–100% (Peet et al., 1998). Seedlings were distinguished as woody plants ≤1 m in height, and tallied for frequency on each quadrat to quantify their density in addition to their percent cover. The percent cover of ground surface substrate was estimated on each quadrat and assigned a Daubenmire class from 1 to 6 where 1 = 0–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–95%, and 6 = 95–100% (Daubenmire, 1959). Ground surface categories were adapted from the USDA (2016) and the Wentworth (1922) grade scale, and included fine woody debris (woody material < 10 cm diameter and disconnected from coarse woody debris), litter (dead, non-woody material, e.g. dead grass, pine needles, broadleaves, and pieces of bark), bare ground, moss, gravel (sediments < 6.4 cm diameter), and rocks (sediments > 6.4 cm diameter).

2.3. Analytical methods

Canopy cover, the volume of coarse woody debris, and the density of rooted dead stems were compared across disturbance categories to assess the abiotic legacies of the disturbance events. Densiometer readings were averaged per plot and multiplied by 1.04 to calculate percent canopy cover (Lemmon, 1957), and compared with a one-way analysis of variance (ANOVA) and Tukey honest significant difference (HSD) test. The volume of logs was calculated with a conic paraboloid equation (Fraver et al., 2007), and the volume of uprooted stems was calculated with species-specific allometric equations (Parker and Hart, 2014; Woodall et al., 2011). The volume of coarse woody debris (logs and uprooted stems) per plot was cube root transformed to meet assumptions of homoscedasticity, and compared across disturbance categories with a one-way ANOVA and Tukey HSD test. The taxonomic composition of coarse woody debris was assessed to compare the relative contributions of pines and hardwoods to dead woody material on or near the ground. The density of rooted dead stems per plot was compared across disturbance categories with a one-way ANOVA and Tukey HSD test. Rooted dead stems in decay class II (structurally sound with partially rotten sapwood and peeling park c.f. USDA 2016) were distinguished as those that died in temporal proximity to the tornado based on decay dynamics of species in the study area (Russell et al., 2014). The structural composition of rooted dead stems in decay class II was evaluated to describe disturbance-mediated differences in the amount and quality of wind-killed trees. The volume of coarse woody debris and the density of rooted stems in decay class II on undisturbed plots were considered background mortality and subtracted from wind-disturbed and compound-disturbed plots to distinguish salvage harvest-specific reductions in dead woody material.

Live tree density and basal area per plot were compared across disturbance categories with one-way ANOVAs and Tukey HSD tests to quantify and assess the severity of the disturbance events. The density, relative density (percent of total trees), dominance (species-specific basal area), relative dominance (percent of total basal area), and importance (average of relative density and dominance) of individual tree species were quantified to assess the relative contribution of individual species and taxonomic groups to the tree stratum across disturbance categories. Taxonomic groups were used for descriptive purposes, not inferential statistics, and were selected based on similar life-history traits and management considerations. They included pines (all *Pinus* species), oaks (all *Quercus* species), and hardwoods (all non-*Pinus* species including oaks). Trees in undisturbed plots were grouped by crown class to characterize their vertical stratification. Sapling density per plot was compared across disturbance categories with a one-way ANOVA and Tukey HSD test, and individual sapling species and taxonomic groups (pines, oaks, and hardwoods) were ranked by density and relative density to assess their contribution to the sapling stratum across disturbance categories. The species richness and Shannon diversity of tree and sapling species per plot were compared across disturbance categories with one-way ANOVAs and Tukey HSD tests.

Seedling density was summed across quadrats for plot-level densities. Seedling densities were standardized to the hectare level and compared by individual species and taxonomic groups (pines and oaks) for comparison across vertical strata and disturbance categories. To calculate plot-level abundance values for all ground flora, quadrat-level NCVS rankings of woody and herbaceous plants were converted to their corresponding range midpoints, averaged per plot, and reconverted back to corresponding NCVS cover classes (Peet et al., 1998). Plot-level species richness and abundance-based values of Shannon diversity for ground flora were summarized with PC-ORD version 6 (McCune and Mefford, 2011), and compared across disturbance categories with one-way ANOVAs and Tukey HSD tests. Similarly, Daubenmire cover classes of ground surface substrate were converted to their corresponding range midpoints, averaged per plot, converted back to a corresponding Daubenmire value per plot, and compared across disturbance categories with one-way ANOVAs and Tukey HSD tests.

PC-ORD was used to conduct nonmetric multidimensional scaling (NMS), distance-based multivariate analysis of variance (PerMANOVA), and indicator species analysis. These multivariate analyses utilized the same modified data set, and were designed to explain variation in the composition and abundance of ground flora in relation to variation in biophysical conditions across disturbance categories. Species that occurred on only one plot were removed from the data set to prioritize describing what species represented the unique plant assemblages observed over distinguishing unique groups based on single-species occurrences. Plot-level NCVS values were relativized to their maximum potential (i.e. proportion of maximum cover class documented for each species respectively) to reduce the influence of species with naturally large growth forms (e.g. bracken fern, *Pteridium latiusculum* (Desvaux) Hieronymus ex Fries = {syn: *P. aquilinum*}) compared to more diminutive species on directing perceived differences in species assemblages (Peck, 2016). NMS was used to graphically interpret trends in the composition and abundance of ground flora on each plot in relation to ten environmental variables: (1) disturbance category, (2) transformed slope aspect (Beers et al., 1966), (3) percent slope, (4) percent canopy cover, (5) volume of coarse woody debris, (6) density of dead pine stems, (7) density of dead hardwood stems, (8) live tree density, (9) basal area, and (10) sapling density. An NMS scree plot was generated to determine the optimal number of axes in the final solution (Peck, 2016). The NMS ordination chosen for interpretation utilized Sørensen (Bray-Curtis) distance, 250 runs with real data, and was checked for consistency of interpretation with other solutions. A biplot overlay was used to assess the correlation between environmental variables and ordination axes with an r^2 cutoff of 0.4. A one-way PerMANOVA with Sørensen distance was used to evaluate the statistical significance of observed differences in species assemblages across disturbance categories. Indicator species analysis was used to summarize and compare the average relative frequency and relative abundance (Indicator Value, IV) of each species (single occurrences excluded) per disturbance category to identify species most strongly associated with differences in ground flora detected with PerMANOVA (Dufrêne and Legendre, 1997; Peck, 2016). To aid interpretation of the indicator species analysis, indicator species were grouped by herbaceous and woody growth forms, and categorized as generalists and specialists. A generalist was subjectively defined as a species that had a mean relative frequency and abundance across all plots (Indicator Value for all disturbance categories) that exceeded half of the Indicator Value for its associated disturbance category. Thus, generalists were differentiated from specialists that only had a relatively high frequency and abundance on plots in a particular disturbance category.

3. Results

3.1. Abiotic legacies

The wind disturbance and subsequent salvage harvesting operation had distinct impacts on the abiotic environment. Canopy cover was different in each disturbance category ($p < 0.01$), averaging 90% ± 1% (standard error, SE) on undisturbed plots, 14% ± 2% (SE) on wind-disturbed plots, and 5% ± 2% (SE) on compound-disturbed plots. Differences were also detected between each disturbance category in the volume of coarse woody debris ($p < 0.001$). The volume of coarse woody debris was greatest on wind-disturbed plots (179.0 ± 23.0 (SE) $m^3\ ha^{-1}$), followed by compound-disturbed plots (19.9 ± 2.5 (SE) $m^3\ ha^{-1}$) and undisturbed plots (5.7 ± 2.5 (SE) $m^3\ ha^{-1}$), and was composed primarily of pines in all disturbance categories (Fig. 3). The density of rooted dead stems in decay class II was greater on wind- and compound-disturbed plots compared to undisturbed plots ($p < 0.05$), and varied substantially by structural composition across disturbance categories (Fig. 4). Undisturbed plots had 26.3 ± 7.8 (SE) decay class II stems ha^{-1}, wind-disturbed plots had 226.3 ± 40.7 (SE) decay class II stems ha^{-1}, and compound-disturbed plots had 137.5 ± 25.1 (SE) decay class II stems ha^{-1}. On wind-disturbed plots, the majority of rooted dead stems in decay class II were uprooted (58% ± 11% (SE)), and the remainder were snapped

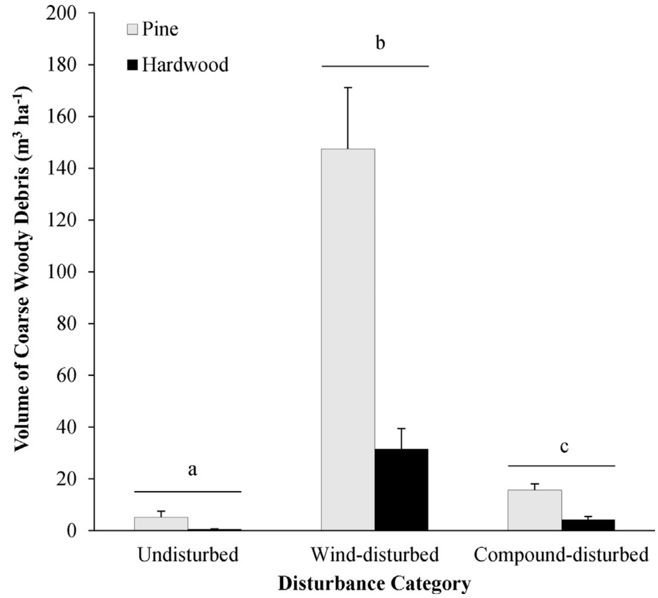

Fig. 3. Volume ($m^3\ ha^{-1}$) of coarse woody debris (dead stems ≥ 10 cm diameter lying ≤ 45° from the ground) composed of pines (light grey bars) and hardwoods (black bars). Letters indicate significant differences at $p < 0.05$ in the volume of all coarse woody debris (pine- and hardwood-composed) documented in undisturbed, wind-disturbed, and compound-disturbed plots on the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA.

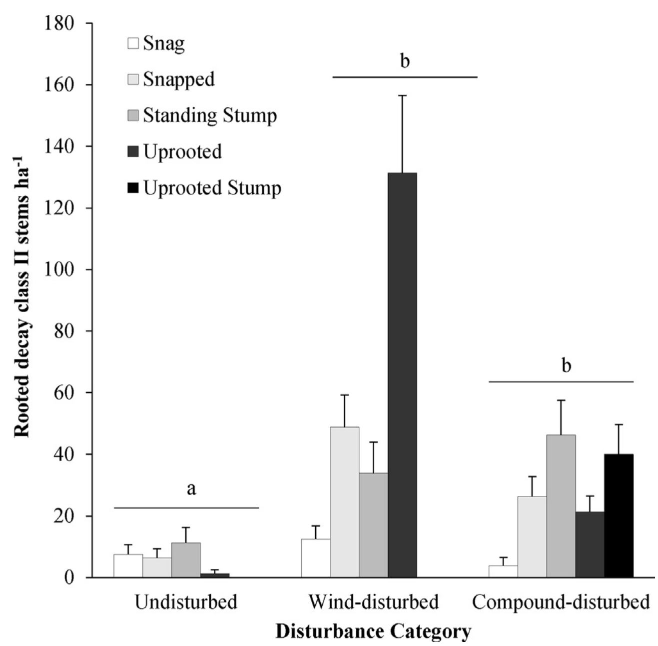

Fig. 4. Density (stems ha^{-1}) of rooted dead stems ≥ 10 cm diameter 1.37 m above root collar in decay class II categorized as snags (white bars), snapped (light grey bars), standing stumps (grey bars), uprooted (dark grey bars), and uprooted stumps (black bar). Letters indicate significant differences at $p < 0.05$ in the density of rooted dead stems in all structural categories between undisturbed, wind-disturbed, and compound-disturbed plots on the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA.

(22% ± 5% (SE)), standing stumps (15% ± 4% (SE)), and snags (5% ± 2% (SE)). On compound-disturbed plots, most rooted dead stems in decay class II were uprooted stumps (29% ± 7% (SE)) and standing stumps (34% ± 8% (SE)), and the remainder were snapped (19% ± 5% (SE)), uprooted (15% ± 4% (SE)), and snags (3% ± 2% (SE)). Considering dead stems on undisturbed plots background mortality, a 91% reduction in the volume of coarse woody debris and a 43% reduction in the density of rooted dead stems in decay class II were

Table 1
Density (stems ha^{-1}), relative density (%), dominance ($m^2\ ha^{-1}$), relative dominance (%), and relative importance (mean relative density and relative dominance) of trees (live stems ≥ 5 cm dbh) documented on undisturbed (UND), wind-disturbed (WIND), and compound-disturbed (COMP) plots on the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Species are ranked by importance in undisturbed plots.

Species	Density (stems ≥ 5 cm dbh ha^{-1})			Relative density (%)			Dominance ($m^2\ ha^{-1}$)			Relative dominance (%)			Importance (%)		
	UND	WIND	COMP	UND	WIND	COMP	UND	WIND	COMP	UND	WIND	COMP	UND	WIND	COMP
Pinus palustris P. Miller	153.75	10.00	13.75	47.31	32.00	44.00	16.21	0.49	0.27	74.77	44.90	47.64	61.04	38.45	45.82
Pinus taeda Linnaeus	62.50	5.00	16.25	19.23	16.00	52.00	2.11	0.08	0.23	9.73	7.06	39.74	14.48	11.53	45.87
Quercus marilandica Muenchhausen	21.25	1.25	–	6.54	4.00	–	0.59	0.06	–	2.72	5.71	–	4.63	4.85	–
Quercus falcata Michaux	15.00	–	–	4.62	–	–	0.87	–	–	4.01	–	–	4.31	–	–
Cornus florida Linnaeus	20.00	–	–	6.15	–	–	0.23	–	–	1.06	–	–	3.61	–	–
Nyssa sylvatica Marshall	15.00	–	–	4.62	–	–	0.35	–	–	1.63	–	–	3.12	–	–
Quercus stellata Wangenheim	12.50	6.25	–	3.85	20.00	–	0.22	0.13	–	1.01	11.57	–	2.43	15.78	–
Pinus echinata P. Miller	6.25	2.50	–	1.92	8.00	–	0.53	0.18	–	2.44	16.39	–	2.18	12.19	–
Oxydendrum arboreum (Linnaeus) A.P. de Candolle	7.50	–	–	2.31	–	–	0.22	–	–	1.00	–	–	1.66	–	–
Quercus alba Linnaeus	5.00	2.50	–	1.54	8.00	–	0.08	0.12	–	0.37	11.09	–	0.95	9.55	–
Quercus velutina Lamarck	1.25	–	–	0.38	–	–	0.12	–	–	0.56	–	–	0.47	–	–
Liriodendron tulipifera Linnaeus	1.25	–	–	0.38	–	–	0.11	–	–	0.52	–	–	0.45	–	–
Diospyros virginiana Linnaeus	1.25	–	–	0.38	–	–	0.02	–	–	0.11	–	–	0.25	–	–
Liquidambar styraciflua Linnaeus	1.25	2.50	–	0.38	8.00	–	0.01	0.03	–	0.04	2.82	–	0.21	5.41	–
Fagus grandifolia Ehrhart	1.25	–	–	0.38	–	–	0.01	–	–	0.03	–	–	0.21	–	–
Quercus coccinea Muenchhausen	–	–	1.25	–	–	4.00	–	–	0.07	–	–	12.62	–	–	8.31
Quercus montana Willdenow	–	1.25	–	–	4.00	–	–	0.01	–	–	0.47	–	–	2.23	–
Total	325.00	31.25	31.25	100.00	100.00	100.00	21.69	1.09	0.57	100.00	100.00	100.00	100.00	100.00	100.00

documented from wind-disturbed to compound-disturbed plots, which was attributed primarily to salvage harvesting.

The contribution of fine woody debris, litter, and bare ground to ground surface cover was different in undisturbed plots compared to wind- and compound-disturbed plots ($p < 0.05$). The mean Daubenmire class of fine woody debris was 1.1 ± 0.1 (SE) on undisturbed plots, 1.4 ± 0.1 (SE) on wind-disturbed plots, and 1.5 ± 0.1 (SE) on compound-disturbed plots. The mean Daubenmire class of litter was 5.5 ± 0.1 (SE) on undisturbed plots, 4.3 ± 0.2 (SE) on wind-disturbed plots, and 4.0 ± 0.2 (SE) on compound-disturbed plots. The mean Daubenmire class of bare ground was 1.0 ± 0.0 (SE) on undisturbed plots and 1.7 ± 0.1 (SE) on wind-disturbed and compound disturbed plots. The contributions of moss, gravel, and rock to ground surface cover were not significantly different across disturbance categories.

3.2. Woody plants

Live tree density and basal area were greatest on undisturbed plots ($p < 0.001$), and reduced by over 90% on wind- and compound-disturbed plots (Table 1). Undisturbed plots had 325 ± 26.8 (SE) trees ha^{-1}, wind-disturbed plots had 31 ± 8.1 (SE) trees ha^{-1}, and compound-disturbed plots had 31 ± 14.5 (SE) trees ha^{-1}. Basal area was 21.7 ± 1.0 (SE) $m^2\ ha^{-1}$ on undisturbed plots, 1.1 ± 0.4 (SE) $m^2\ ha^{-1}$ on wind-disturbed plots, and 0.6 ± 0.3 (SE) $m^2\ ha^{-1}$ on compound-disturbed plots. Seventeen tree species were documented in plots across all disturbance categories. Tree species richness was greatest on undisturbed plots ($p < 0.001$), averaging 4.3 ± 0.5 (SE) species compared to 1.1 ± 0.3 (SE) species on wind-disturbed plots and 0.4 ± 0.1 (SE) species on compound-disturbed plots (Fig. 5). Shannon diversity of tree species was also greatest on undisturbed plots ($p < 0.001$), averaging 1.1 ± 0.1 (SE) compared to 0.3 ± 0.1 (SE) on wind-disturbed plots and 0.4 ± 0.1 (SE) on compound-disturbed plots.

The majority of trees documented were pines, of which longleaf pine was the most common, followed by loblolly pine and shortleaf pine. In undisturbed plots, the canopy stratum was composed primarily of pine species, with longleaf pine composing the only dominant trees recorded (5 trees ha^{-1}). Pine species composed 126 of 130 codominant trees ha^{-1} on undisturbed plots of which 104 were longleaf pine. The midstory of undisturbed plots contained more hardwood species, especially oaks. Hardwood species composed 61 of 118 intermediate trees ha^{-1} of which 36 were oaks, and 38 of 73 overtopped trees ha^{-1} of which 16 were oaks.

Sapling density was greatest on wind-disturbed plots ($p < 0.001$), but all disturbance categories had relatively high sapling densities (Table 2). Undisturbed plots had 3360 ± 566 (SE) saplings ha^{-1}, wind-disturbed plots had 7661 ± 418 (SE) saplings ha^{-1}, and compound-disturbed plots had 4425 ± 449 (SE) saplings ha^{-1}. Species richness of saplings was greatest on wind-disturbed plots, reduced on compound-disturbed plots, and lowest on undisturbed plots ($p < 0.05$). Undisturbed plots averaged 9.6 ± 1.0 (SE) sapling species, wind-disturbed plots averaged 19.6 ± 0.7 (SE) sapling species, and compound-disturbed plots averaged 16.3 ± 0.7 (SE) sapling species (Fig. 5). Shannon diversity of saplings was lowest on undisturbed plots ($p < 0.001$), averaging 1.2 ± 0.1 (SE), compared to 2.3 ± 0.1 (SE) on wind-disturbed plots and 2.1 ± 0.1 (SE) on compound-disturbed plots. On undisturbed plots, 29 sapling species were documented of which one was unique to the undisturbed category; 42 sapling species were documented on wind-disturbed plots of which six were unique to the wind-disturbed category; and 39 sapling species were documented on compound-disturbed plots of which two were unique to the compound-disturbed category. Of the 46 sapling species documented, 27 were common to all disturbance categories.

Sparkleberry (*Vaccinium arboreum* Marshall) had the greatest single-species sapling densities in undisturbed plots (1448 saplings ha^{-1}) and

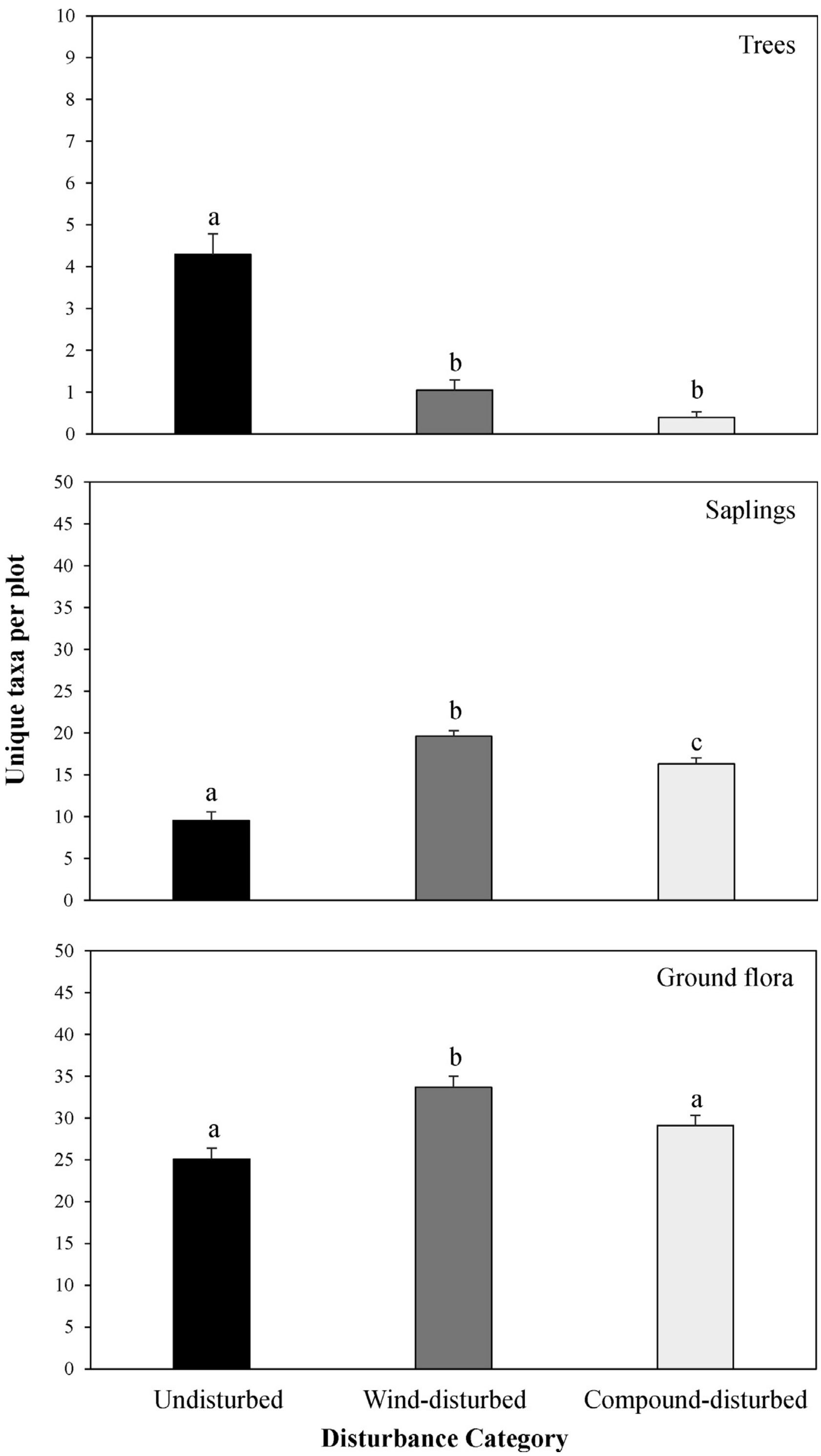

Fig. 5. Species richness (unique taxa per plot) of trees (stems > 5 cm dbh surveyed in 400 m^2 plots), saplings (stems > 1 m height and < 5 cm dbh surveyed in 400 m^2 plots), and ground flora (vascular plants ≤ 1 m height surveyed in 10 m^2 plots). Letters indicate significant differences at $p < 0.05$ in undisturbed (black bars), wind-disturbed (dark grey bars), and compound-disturbed (light grey bars) plots on the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA.

compound-disturbed plots (1325 saplings ha^{-1}), but was outnumbered in wind-disturbed plots (1203 saplings ha^{-1}) by winged sumac (*Rhus copallinum* Linnaeus, 1366 saplings ha^{-1}). Winged sumac was the third-most abundant sapling species in undisturbed plots (380 saplings ha^{-1}) after red maple (*Acer rubrum* Linnaeus, 649 saplings ha^{-1}) and sparkleberry, and the second-most abundant saplings species on compound-disturbed plots (500 saplings ha^{-1}) after sparkleberry. Oak species combined had greater sapling densities than sparkleberry on wind-disturbed plots (2433 saplings ha^{-1}) and compound-disturbed plots (1555 saplings ha^{-1}), but remained outnumbered by sparkleberry, red maple, and winged-sumac on undisturbed plots (260 saplings ha^{-1}). Contrary to the tree stratum, pine saplings were markedly outnumbered by hardwoods in all disturbance categories, and exhibited increased densities with increased disturbance severity. Most pine saplings documented were longleaf pine, composing 30 of 44 pine saplings ha^{-1} on undisturbed plots, 34 of 59 pine saplings ha^{-1} on wind-disturbed plots, and 75 of 110 pine saplings ha^{-1} on compound-disturbed plots.

3.3. Ground flora

The species richness of ground flora was greatest on wind-disturbed plots ($p < 0.05$) averaging 33.7 ± 1.3 (SE) taxa, but was not

Table 2
Density (stems ha^{-1}) and relative density (%) of saplings (live woody stems > 1 m in height and < 5 cm dbh) documented in undisturbed (UND), wind-disturbed (WIND), and compound-disturbed (COMP) plots on the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Species are ranked by relative density in undisturbed plots.

Species	Sapling stem density (stems ha^{-1})			Sapling stem relative density (%)		
	UND	WIND	COMP	UND	WIND	COMP
Vaccinium arboreum Marshall	1447.50	1202.50	1325.00	43.08	15.70	29.94
Acer rubrum Linnaeus	648.75	248.75	181.25	19.31	3.25	4.10
Rhus copallinum Linnaeus	380.00	1366.25	500.00	11.31	17.83	11.30
Diospyros virginiana	157.50	323.75	108.75	4.69	4.23	2.46
Oxydendrum arboreum	143.75	570.00	102.50	4.28	7.44	2.32
Liquidambar styraciflua	113.75	541.25	253.75	3.39	7.06	5.73
Quercus falcata	60.00	442.50	430.00	1.79	5.78	9.72
Callicarpa americana Linnaeus	60.00	26.25	7.50	1.79	0.34	0.17
Cornus florida	53.75	7.50	42.50	1.60	0.10	0.96
Quercus coccinea	47.50	543.75	87.50	1.41	7.10	1.98
Quercus marilandica	42.50	37.50	235.00	1.26	0.49	5.31
Quercus alba	33.75	388.75	51.25	1.00	5.07	1.16
Pinus palustris	30.00	33.75	75.00	0.89	0.44	1.69
Quercus stellata	28.75	115.00	96.25	0.86	1.50	2.18
Quercus velutina	18.75	291.25	75.00	0.56	3.80	1.69
Carya tomentosa (Lamarck) Nuttall	18.75	130.00	31.25	0.56	1.70	0.71
Pinus taeda	13.75	21.25	35.00	0.41	0.28	0.79
Vaccinium elliottii Chapman	13.75	1.25	22.50	0.41	0.02	0.51
Quercus margarettae W.W. Ashe ex Small	8.75	47.50	93.75	0.26	0.62	2.12
Quercus nigra Linnaeus	7.50	468.75	378.75	0.22	6.12	8.56
Quercus laevis Walter	6.25	16.25	61.25	0.19	0.21	1.38
Castanea pumila (Linnaeus) P. Miller	5.00	–	3.75	0.15	–	0.08
Carya glabra (P. Miller) Sweet	3.75	166.25	8.75	0.11	2.17	0.20
Vaccinium stamineum Linnaeus	3.75	28.75	22.50	0.11	0.38	0.51
Quercus incana Bartram	3.75	8.75	23.75	0.11	0.11	0.54
Sassafras albidum (Nuttall) Nees	2.50	23.75	45.00	0.07	0.31	1.02
Nyssa sylvatica	2.50	10.00	65.00	0.07	0.13	1.47
Quercus rubra Linnaeus	2.50	3.75	3.75	0.07	0.05	0.08
Fagus grandifolia	1.25	–	–	0.04	–	–
Symplocos tinctoria (Linnaeus) L'Heritier	–	216.25	10.00	–	2.82	0.23
Styrax grandifolius Aiton	–	146.25	2.50	–	1.91	0.06
Hamamelis virginiana Linnaeus	–	57.50	1.25	–	0.75	0.03
Quercus montana	–	50.00	1.25	–	0.65	0.03
Acer floridanum (Chapman) Pax	–	48.75	–	–	0.64	–
Rhus glabra Linnaeus	–	25.00	2.50	–	0.33	0.06
Quercus hemisphaerica Bartram ex Willdenow	–	18.75	17.50	–	0.24	0.40
Magnolia macrophylla Michaux	–	10.00	5.00	–	0.13	0.11
Vaccinium pallidum Aiton	–	8.75	–	–	0.11	–
Asimina parviflora (Michaux) Dunal	–	5.00	–	–	0.07	–
Pinus echinata	–	3.75	–	–	0.05	–
Prunus serotina Ehrhart *var. serotina*	–	2.50	1.25	–	0.03	0.03
Liriodendron tulipifera	–	1.25	11.25	–	0.02	0.25
Acer saccharum Marshall	–	1.25	–	–	0.02	–
Aesculus pavia Linnaeus var. *pavia*	–	1.25	–	–	0.02	–
Magnolia virginiana Linnaeus	–	–	5.00	–	–	0.11
Ilex opaca Aiton	–	–	1.25	–	–	0.03
TOTAL	3360.00	7661.25	4425.00	100.00	100.00	100.00

significantly different between undisturbed and compound-disturbed plots, which averaged 25.1 ± 1.3 (SE) and 29.1 ± 1.2 (SE) taxa respectively (Fig. 5). Likewise, Shannon-diversity of ground flora was greatest on wind-disturbed plots ($p < 0.05$) averaging 3.3 ± 0.0 (SE), but was not significantly different between undisturbed and compound-disturbed plots, which had average Shannon-diversity values of 3.0 ± 0.1 (SE) and 3.1 ± 0.0 (SE) respectively. On undisturbed plots, 75 species were documented as ground flora of which 11 were unique to the undisturbed category; 115 species were documented as ground flora on wind-disturbed plots of which 33 were unique to the wind-disturbed category; and 90 species were documented on compound-disturbed plots of which 13 were unique to the compound-disturbed category. Of the 140 species documented as ground flora on plots, 101 occurred on two or more plots of which 57 were common to all disturbance categories.

Within the ground flora stratum, 69,150 ± 7206 (SE) seedlings ha^{-1} were documented on undisturbed plots, 72,550 ± 8154 (SE) seedlings ha^{-1} were documented on wind-disturbed plots, and 52,500 ± 5458 (SE) seedlings ha^{-1} were documented on compound-disturbed plots. Although seedling density was not significantly different across disturbance categories, the species composition of seedlings was noticeably different. Longleaf pine had the greatest single-species seedling density on undisturbed plots, but was outnumbered by other species, especially sparkleberry, on wind-disturbed and compound-disturbed plots. Longleaf pine composed 18,100 of 24,350 pine seedlings ha^{-1} on undisturbed plots, 4050 of 6200 pine seedlings ha^{-1} on wind-disturbed plots, and 6500 of 14,500 pine seedlings ha^{-1} on compound-disturbed plots. Sparkleberry composed 15,950 seedlings ha^{-1} on undisturbed plots, and had the greatest single-species seedling densities on wind-disturbed and compound-disturbed plots, composing 18,800 seedlings ha^{-1} and 9950 seedlings ha^{-1} respectively. On undisturbed plots, oak species combined (9400 seedlings ha^{-1}) ranked third to longleaf pine and sparkleberry, followed by loblolly and shortleaf pine (combined 6250 seedlings ha^{-1}), dwarf huckleberry (*Gaylussacia dumosa* (Andrews) Torrey & A. Gray, 4500 seedlings ha^{-1}), and blackgum (*Nyssa sylvatica* Marshall, 3300 seedlings ha^{-1}). On wind-disturbed plots, oak species combined (9600 seedlings ha^{-1}) ranked second to sparkleberry, followed by winged sumac (8900

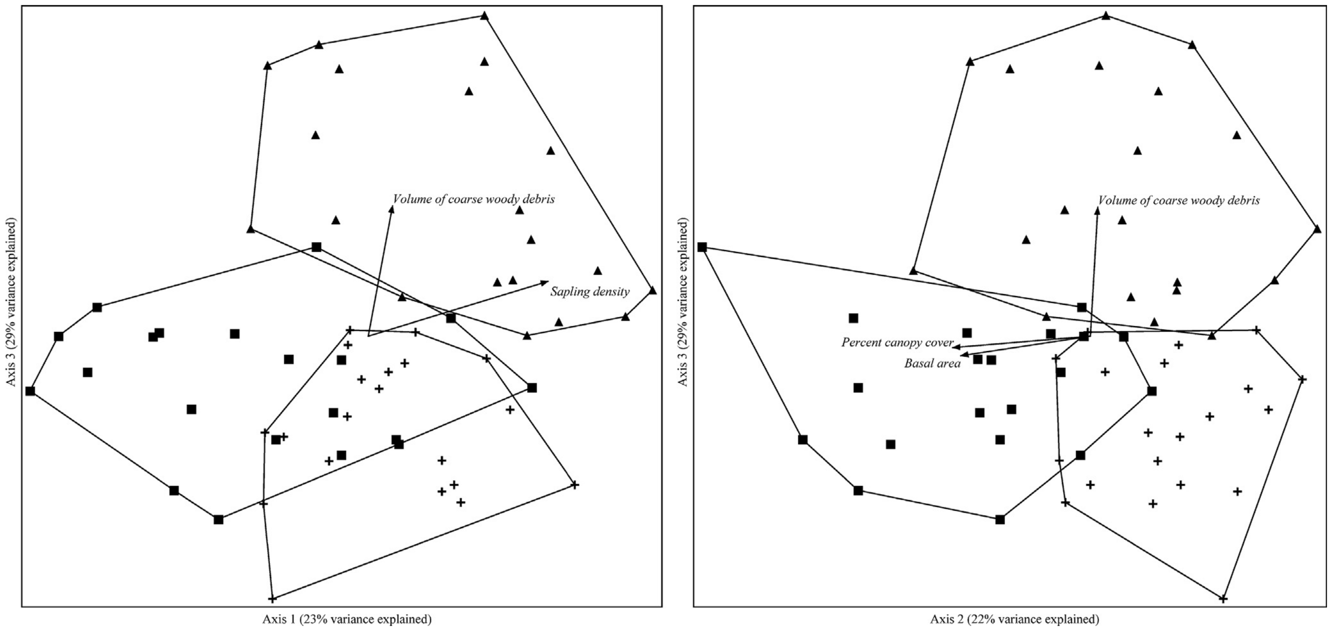

Fig. 6. Three-dimensional non-metric multidimensional scaling solution based on the abundance of ground flora (vascular plants ≤ 1 m height) in plots undisturbed (squares), wind-disturbed (triangles), and compound-disturbed (plus signs) on the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Loops (convex hulls) connect plots in the same disturbance category, and arrows (biplots) show the strength (length of arrow) and direction of correlations ($r^2 \geq 0.4$) between biophysical factors and ordination axes.

seedlings ha^{-1}), bigleaf snowbell (*Styrax grandifolius* Aiton, 7950 seedlings ha^{-1}), horse sugar (*Symplocos tinctoria* (Linnaeus) L'Heritier, 4600 seedlings ha^{-1}), and black gum (4300 seedlings ha^{-1}). On compound-disturbed plots, 7050 oak seedlings ha^{-1} were documented, which was less than sparkleberry, dwarf huckleberry (8700 seedlings ha^{-1}), and loblolly and shortleaf pine (combined 8000 seedlings ha^{-1}), but greater than longleaf pine and winged sumac (4500 seedlings ha^{-1}).

A three-dimensional NMS solution (Fig. 6) and one-way PerMANOVA revealed distinct differences in the composition and abundance of the 101 species of ground flora that occurred on two or more plots across disturbance categories ($p < 0.001$). Axis 1 explained 23% of variance in the NMS solution, and was positively correlated with sapling density ($r^2 = 58\%$). Axis 2 explained 22% of variance in the NMS solution, and was negatively associated with percent canopy cover ($r^2 = 45\%$), basal area ($r^2 = 42\%$), and tree density ($r^2 = 31\%$, not pictured). Axis 3 explained 29% of variance in the NMS solution, and was positively associated with volume of coarse woody debris ($r^2 = 42\%$) and density of dead hardwood stems ($r^2 = 34\%$, not pictured). Undisturbed plots were generally located on the lower left portion of the NMS graphs, corresponding to the negative ranges of Axis 1, Axis 2, and Axis 3. Wind-disturbed plots were generally located on the upper right portion of the NMS graphs, corresponding to the positive ranges of Axis 1, Axis 2, and Axis 3. Compound-disturbed plots were generally located on the lower right portion of the NMS graphs, corresponding to the positive ranges of Axis 1 and Axis 2, and the negative range of Axis 3.

Thirty-four significant indicator species ($p < 0.05$) were documented in the study area (Table 3). Two occurred on undisturbed plots, of which both were woody generalists: red maple (IV = 35.3) and flowering dogwood (*Cornus florida* Linnaues, IV = 31). Indicator species of wind-disturbed plots included one herbaceous generalist: *Symphyotrichum* spp. Nees (IV = 41.7); eight herbaceous specialists: tall lettuce (*Lactuca canadensis* Linnaeus, IV = 68), common horseweed (*Conyza canadensis* (Linnaeus) Cronquist, IV = 60.8), dog fennel (*Eupatorium capillifolium* (Lamarck) Small, IV = 25), pokeweed (*Phytolacca americana* Linnaeus, IV = 20), hairy skullcap (*Scutellaria elliptica* Muhlenberg ex Sprengel var. *elliptica*, IV = 20), Virginia creeper (*Parthenocissus quinquefolia* (Linnaeus) Planchon, IV = 20), lance leaf

Table 3
Indicator species of undisturbed (UND), wind-disturbed (WIND), and compound-disturbed (COMP) longleaf pine woodlands of the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Species are ranked by indicator significance (* = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$) and presence (bullets) in associated disturbance categories.

Species	UND	WIND	COMP
Acer rubrum	*	•	•
Cornus florida	*	•	•
Quercus alba	•	***	•
Vaccinium stamineum	•	***	•
Conyza canadensis (Linnaeus) Cronquist		***	•
Lactuca canadensis Linnaeus		***	•
Styrax grandifolius		***	•
Carya glabra	•	**	•
Quercus coccinea	•	**	•
Quercus velutina	•	**	•
Rhus copallinum	•	**	•
Eupatorium capillifolium (Lamarck) Small		**	•
Symplocos tinctoria		**	•
Liquidambar styraciflua	•	*	•
Liriodendron tulipifera	•	*	•
Nyssa sylvatica	•	*	•
Symphyotrichum Nees	•	*	•
Osmundastrum cinnamomeum (Linnaeus) C. Presl		*	•
Parthenocissus quinquefolia (Linnaeus) Planchon		*	•
Smilax smallii Morong		*	•
Phytolacca americana Linnaeus		*	
Scutellaria elliptica Muhlenberg ex Sprengel *var. elliptica*		*	
Agalinis purpurea (Linnaeus) Pennell	•	•	***
Gelsemium sempervirens (Linnaeus) St. Hilaire	•	•	***
Tephrosia virginiana (Linnaeus) Persoon	•	•	***
Poaceae	•	•	**
Coreopsis major Walter	•	•	**
Quercus nigra	•	•	**
Gaylussacia dumosa (Andrews) Torrey & A. Gray	•	•	*
Hypericum gentianoides (Linnaeus) Britton	•	•	*
Quercus falcata	•	•	*
Tragia smallii Shinners	•	•	*
Diodella teres (Walter) Small		•	*
Stylisma humistrata (Walter) Chapman		•	*

greenbriar (*Smilax smallii* Morong, IV = 20), and cinnamon fern (*Osmundastrum cinnamomeum* (Linnaeus) C. Presl, IV = 20); four woody generalists: winged sumac (IV = 45.1), black gum (IV = 40.4), black oak (*Quercus velutina* Lamarck, IV = 38), and sweet gum (*Liquidambar styraciflua* Linnaeus, IV = 30.3); and seven woody specialists: northern white oak (*Quercus alba* Linnaeus, IV = 52.4), common deerberry (*Vaccinium stamineum* Linnaeus, IV = 51.2), bigleaf snowbell (IV = 39.8), scarlet oak (IV = 39.7), pignut hickory (*Carya glabra* (P. Miller) Sweet, IV = 36.8), horse sugar (IV = 30.7), and tulip poplar (*Liriodendron tulipifera* Linnaeus, IV = 20). Indicator species of compound-disturbed plots included five herbaceous generalists: goat's rue (*Tephrosia virginiana* (Linnaeus) Persoon, IV = 54.4), yellow jessamine (*Gelsemium sempervirens* (Linnaeus) St. Hilaire, IV = 45.6), grass (Poaceae family, IV = 43.3), greater tickseed (*Coreopsis major* Walter, IV = 42.5), and Gulf Coast noseburn (*Tragia smallii* Shinners, IV = 33.9); four herbaceous specialists: purple false foxglove (*Agalinis purpurea* (Linnaeus) Pennell, IV = 61.8), poor joe (*Diodella teres* (Walter) Small, IV = 26.3), pineweed (*Hypericum gentianoides* (Linnaeus) Britton, IV = 24.5), and southern dawnflower (*Stylisma humistrata* (Walter) Chapman, IV = 22.5); three woody generalists: water oak (*Quercus nigra* Linnaeus, IV = 47), southern red oak (*Quercus falcata* Michaux, IV = 41.8), and southern dwarf huckleberry (IV = 35); and no woody specialists.

4. Discussion

4.1. Abiotic legacies

Canopy cover was almost completely removed by the catastrophic wind event. Compound-disturbed plots had lower canopy cover than wind-disturbed plots that were not salvaged, which was attributed to removal of leaning dead stems and reduced sapling densities. Canopy tree removal allows more solar radiation to reach the ground, thereby increasing surface temperature and light availability, and promoting the recruitment and growth of shade-intolerant species (Carlton and Bazzaz, 1998; Fernandez and Fetcher, 1991; Geiger, 1965; Hanson and Lorimer, 2007). Sapling density may be more influential than tree density and basal area on filtering light availability closer to the ground (Montgomery and Chazdon, 2001), and is linked with variation in the composition and distribution of tree seedlings and other ground flora (Denslow et al., 1991).

Plant recovery after wind disturbance is also influenced by availability of suitable growing substrate and microclimatic conditions associated with variation in the abundance and spatial arrangement of coarse woody debris, fine woody debris, litter, and exposed mineral soil generated by wind-disturbed trees (Franklin et al., 2002; Peterson and Pickett, 1995). Salvage harvesting operations are epitomized by a reduction in coarse woody debris, which was clearly exhibited on compound-disturbed plots in the study area. Pine composed the majority of coarse woody debris in all disturbance categories, which was attributed to pine dominance in the canopy before the storm and increased susceptibility of larger trees to wind-induced mortality (Foster and Boose, 1992; Peterson, 2007; White et al., 2015; Xi et al., 2008). However, a greater proportion of hardwood-composed coarse woody debris was documented in wind-disturbed plots, which may have resulted from preferential harvesting of hardwoods during the salvage harvesting operation. This discrepancy in coarse woody debris composition may have influenced observed differences in plant assemblages because pine- and hardwood-composed debris contribute differentially to carbon and nitrogen pools upon decomposition (Currie and Nadelhoffer, 2002).

Based on the density and structural composition of rooted dead stems in decay class II, approximately half of wind-killed trees were uprooted, of which salvage harvesting converted most to uprooted stumps. Interestingly, the sum of uprooted stems and uprooted stumps in compound-disturbed plots was less than half the density of uprooted stems in wind-disturbed plots. Some uplifted root networks may have hinged back to their original position when their associated stems were mechanically severed or were pushed back into place by salvage harvest operators, thereby converting some uprooted stems to standing stumps (Fraver et al., 2017). The salvage harvesting operation also converted many standing snags and snapped stems into standing stumps, which might have affected wildlife that use these structural disturbance legacies as habitat (Franklin et al., 2002; Goodburn and Lorimer, 1998).

Compared to wind- and compound-disturbed plots, the surface of undisturbed plots was covered by more litter and less fine woody debris and bare ground. The litter on undisturbed plots was composed primarily of pine needles, which were not differentiated from the broadleaf litter, bark, and dead grass that composed most litter on wind- and compound-disturbed plots (personal observation). Future research should differentiate pine litter, which regulates the growth and survival of ground flora differently than broadleaf litter (Peterson and Pickett, 2000). Consistent with Fraver et al. (2017), the salvage harvesting operation did not alter the amount of fine woody debris, which likely resulted from preferential harvesting of larger, more merchantable pieces of wood. Although the discarded pieces of wood had less economic value, fine woody debris is an important regulator of soil temperature following canopy removal (Slesak, 2013), and provides microhabitat required by plants and animals (Franklin et al., 2002; Swanson et al., 2011). Like fine woody debris, the wind event increased the amount of bare ground exposed on wind- and compound-disturbed plots, which was unaltered by salvage harvesting. Increased cover of bare ground on these plots likely influenced observed differences in plant assemblages because some species require bare mineral soil to germinate (Peterson and Pickett, 2000).

4.2. Woody plants

Live tree density and basal area were reduced on wind- and compound-disturbed plots, as were tree species richness and diversity, which were relatively low on undisturbed plots and reduced further on wind- and compound-disturbed plots. In longleaf pine ecosystems, it is desirable to have low species richness in the canopy stratum where longleaf pine co-occurs with few other scattered species (Varner et al., 2005). Undisturbed plots exhibited this condition; pines composed the majority of canopy trees and the midstory contained more hardwoods, especially oaks. Thus, the composition and structure of undisturbed plots epitomized longleaf pine woodlands of the region (Beckett and Golden, 1982; Teague et al., 2014), and may be viewed as surrogates for pre-disturbance conditions in the study area as well as a reference condition for what wind- and compound-disturbed areas may recover toward.

Wind-disturbed plots had the greatest sapling density, richness, and diversity, although sapling diversity was not significantly different between wind- and compound-disturbed plots. Increased sapling diversity caused by catastrophic wind was also documented by Dobrowolska (2015) and Peterson and Pickett (1995). However, Kleinman and Hart (2017) documented reduced sapling diversity in proximal stands effected by the same tornado, which was attributed to an unusually long fire-free interval on that site before and after the storm. Thus, increased sapling diversity in this study may be attributed in part to the interacting effects of wind disturbance and recurring prescribed fire. Most sapling species that occurred on undisturbed plots were also documented on wind- and compound-disturbed plots. These findings supported Roberts et al. (2016), who discussed the persistence of forest-interior species and addition of ruderal species following canopy removal. This study exemplified an initial floristics model of succession, where species typical of mature stands were present from stand initiation in patches regenerated by catastrophic disturbance (Oliver and Larson, 1996).

Pine species, which composed most canopy trees in undisturbed (mature) plots in the study area, were present in the sapling stratum, but were markedly outnumbered by other species in all disturbance categories. To recover toward pre-disturbance conditions of longleaf pine dominance (and thereby exhibit ecosystem resiliency) longleaf pine saplings must increase in relative density. Prescribed fires could continue to be used to temporarily suppress other species, however, many woody competitors of longleaf pine actually increase in density when they resprout after fire (Olson and Platt, 1995). Additionally, surface fires may be less effective than desired in wind- and compound-disturbed patches with reduced cover of pine needles, which are a major component of the pyrogenic fuel load needed to carry surface fires in longleaf pine ecosystems (Platt et al., 1988).

The ubiquitous abundance of sparkleberry, winged sumac, red maple, and oak saplings was attributed in part to the ability of these species to sprout vigorously after fire (Gilbert et al., 2003; Olson and Platt, 1995; Waldrop et al., 1992). Winged sumac had disproportionately high densities on wind-disturbed plots, which may have had a strong impact on other plants in these areas. For instance, Blum and Rice (1969) documented increased proportions of tannic acid in soil and duff beneath winged sumac, which had inhibitory effects on nitrogen fixation by legumes (Fabaceae). Petranka and McPherson (1979) also demonstrated allelopathy in winged sumac, and described substantially diminished light availability under clonal winged sumac growth forms. Although red maple is sometimes characterized as a fire-susceptible species that benefits from long-fire free periods in longleaf pine ecosystems (Varner et al., 2005), red maple is also known to sprout vigorously after fire (Gilbert et al., 2003). Because red maple is a characteristically shade-tolerant species in these systems, it was expected to reach its greatest densities under closed canopies on undisturbed plots. Relatively high and unexpected densities of red maple saplings on wind- and compound-disturbed plots were attributed to pre-disturbance establishment. Oak species are characteristically shade-intolerant, and respond well to disturbance and increased light availability (Dey, 2002). Thus, increased oak sapling densities on wind- and compound-disturbed plots were attributed to increased light availability facilitated by canopy removal.

4.3. Ground flora

Ground flora represented species documented May–July 2016 on plots in fire-restored longleaf pine woodlands that experienced different levels of disturbance severity. A supplementary floristic inventory (unpublished results) documented 52 additional species in the study area. Therefore, lack of plot-level species documentation in a disturbance category did not necessarily imply absence. However, it was clear that each disturbance category had unique species that contributed to increased beta and gamma diversity. These results supported Royo et al. (2016) who discussed species that benefited from salvage harvesting, which promoted species coexistence and diversity at the landscape scale.

Consistent with Rumbaitis del Rio (2006), species diversity of ground flora was greatest on wind-disturbed plots and reduced on compound-disturbed plots. A substantial amount of the unique flora on wind-disturbed plots appeared to be growing on moist ground beneath uprooted stems and logs (personal observation). For example, globe beakrush (*Rhynchospora globularis* (Chapman) Small) and netted chainfern (*Lorinseria areolata* (Linnaeus) C. Presl) require moist habitat, and were growing on damp substrate seemingly facilitated by buildup around coarse woody debris that was unique to unharvested wind-disturbed plots. Buma (2015) characterized compound disturbances by habitat homogenization. Habitat homogenization was most noticeable on compound-disturbed plots by a reduction in coarse woody debris. Variability in light availability was also reduced on compound-disturbed plots, which had fewer areas shaded by leaning dead stems and thickets of saplings. Species diversity is often associated with ecological resilience (Peterson et al., 1998) and community production (Dybzinski et al., 2008; Premer et al., 2016). Thus, reduced ground flora diversity on compound-disturbed plots may lead to alternate recovery trajectories whereby pre-disturbance ground flora community conditions are not achieved (Kreyling et al., 2008).

Light, nutrients, and moisture are often identified as the primary resources required by plants. The NMS solution supported Muller (2014) who reported that nutrients and moisture are often more limiting than light in early stages of succession, and that light often becomes more limiting in later stages of succession. Ground flora on undisturbed plots was most positively associated with percent canopy cover, basal area, and tree density, and most negatively associated with sapling density. Thus, factors related to light availability had the greatest influence on distinguishing undisturbed plots with closed canopies from disturbed plots with open canopies. Differences in ground flora between wind- and compound-disturbed plots may be attributed primarily to differences in moisture and nutrient availability associated with differences in the volume of coarse woody debris and density of dead hardwood stems. However, variation in light availability associated with sapling density and leaning dead stems likely also influenced differences in ground flora between wind- and compound-disturbed plots. Consistent with site selection criteria for similar pre-disturbance biophysical site conditions, transformed slope aspect and percent slope were not associated with differences in ground flora assemblages in the NMS solution.

The life history of indicator species exemplified differences in species assemblages attributed to variation in the biophysical conditions across disturbance categories. Both indicators of undisturbed plots were woody generalists with known shade tolerance (Harrington and Bluhm, 2000). Red maple is often associated with mature forests, as is flowering dogwood, which grows almost exclusively under the shade of other trees (Burns and Honkala, 1990). The only herbaceous generalist in wind-disturbed plots, *Symphyotrichum* spp., was ubiquitous throughout the study area, and represented multiple species because of difficulty distinguishing some *Symphyotrichum* species in the field. However, *Symphyotrichum* species that were identifiable to species (e.g. *S. patens* (Aiton) G.L. Nesom) were individually assessed (i.e. not included with the broader *Symphyotrichum* spp. group in multivariate analyses). Herbaceous specialists on wind-disturbed plots, including tall lettuce, common horseweed, and dog fennel, are commonly associated with disturbed areas (Weakley, 2015). Cinnamon fern was a noteworthy herbaceous specialist, capable of forming dense colonies. Interestingly, the only woody specialists in the study area were associated with wind-disturbed plots, including deerberry, snowbell, and horse sugar. Weakley (2015) ascribed the herbaceous specialists of compound-disturbed plots to dry, open habitats. The majority of indicator species on compound-disturbed plots were generalists that were ubiquitous throughout the study area (e.g. goat's rue, yellow jessamine, grass, water oak, and southern red oak), supporting the claim that salvage harvesting promoted habitat homogenization. Indicator species of all disturbance categories were native to Alabama (Keener et al., 2017), which is interesting given that exotic invasive plants are often associated with disturbed areas.

4.4. Differential fire effects

Spatial proximity of the sites and occurrence in the same compartment (burn unit) moderated variation in the pre-disturbance prescribed fire regime, which can influence pine mortality during and after wind disturbance (Platt et al., 2002). Of greater concern was the April 2014 prescribed fire, which was conducted three growing seasons after the wind disturbance and salvage harvesting operation. At this time, the sites likely had different fuel loads, which likely resulted in differential fire effects. Indeed, an impetus for salvage harvesting in the study area was to reduce accumulation of fuels, which would be potentially damaging to residual vegetation if consumed by fire. For example, Buma and Wessman (2011) documented effects of catastrophic fire following wind disturbance and salvage harvesting in a subalpine forest of northern Colorado, and attributed decreased coniferous regeneration in unharvested wind-disturbed patches to more intense fires.

Although not directly quantified, the April 2014 prescribed fire was characterized as low-intensity (personal communication), and only charred coarse woody debris in the study area (personal observation). This fire was likely more continuous in undisturbed areas with less exposed mineral soil and a greater proportion of canopy-derived pine needle litter. Nonetheless, we posit that despite variation in post-disturbance prescribed fire effects, our results are more relevant to other systems than had prescribed fire been withheld after the disturbance events. Fire exclusion is considered an unnatural disturbance in longleaf pine ecosystems, which are both adapted to and dependent on fire (Moser and Wade, 2005). Thus, continuity of a pre-existing fire regime, albeit having differential effects, was less of an additional perturbation than had the sites not experienced post-disturbance fire.

5. Management implications

Despite the global applications of post-wind disturbance salvage harvesting on reclaiming financial investments and mitigating risks associated with wind-damaged trees, its ecological consequences remain unresolved. Compound disturbances, including post-wind disturbance salvage harvesting, may be criticized for delaying recovery toward pre-disturbance conditions or resulting in alternate ecosystem states. Based on the composition of woody plants documented in this study, both wind- and compound-disturbed plots had potential to return to pre-disturbance conditions and thereby exhibit ecosystem resiliency. Interestingly, the sapling density of longleaf pine, the most desirable species in the system investigated, increased with collective disturbance severity. Thus, salvage harvesting may be conducted as needed if maintaining advanced regeneration of longleaf pine is a primary management objective. However, longleaf pine saplings were markedly outnumbered by other species in all disturbance categories.

Although prescribed fire is often utilized to reduce woody competition in longleaf pine ecosystems, this may prove difficult to execute in wind- and compound-disturbed areas lacking canopy cover. Indeed, the even and abundant pine needle fuels required to sustain the frequent surface fires that drive longleaf pine ecosystem dynamics are predicated by the presence of a continuous pine-dominated canopy to provide these fuels (Mitchell et al., 2006). It is possible that a fire conducted in dry summer conditions would successfully control hardwoods during the leaf-on period, but safety concerns and restrictions would make such an intense fire operationally difficult to accomplish. Nonetheless, burning salvaged areas with a reduction in coarse woody debris would be less intense than burning unharvested wind-disturbed plots in similar climatic conditions (Buma and Wessman, 2011). Alternatively, a “brown then burn” strategy may be utilized, whereby woody plants are treated with herbicide in preparation for a fire in less extreme conditions (Brockway et al., 2006). Regardless of the approach prescribed for hardwood control, we advise caution interpreting this study, which documented an early stage of recovery. Longleaf pine seedlings, which may remain in the “grass stage” for over 10 years, exhibited adequate stocking in all disturbance categories. Thus, a sufficient density of longleaf pine seedlings may recruit to the sapling and tree strata under the current management regime.

Ground flora diversity was reduced from wind- to compound-disturbed plots, which was attributed to salvage harvest-mediated habitat homogenization. Although plant assemblages on compound-disturbed plots were characterized by generalists, invasive species were not documented. Additionally, compound-disturbed plots had higher plant diversity than undisturbed plots, including some species that were not documented on unharvested wind-disturbed sites. Thus, the presence of both wind-disturbed patches left unharvested and compound-disturbed patches may support greater stand-scale (collective) biodiversity than either disturbance category individually. If maintenance of biodiversity is a primary management objective, then it may be beneficial to leave patches unharvested within salvaged stands. This study documented the individual and collective impacts of catastrophic wind disturbance and salvage harvesting on biophysical conditions in longleaf pine woodlands after five growing seasons. Documented response by trees, saplings, and ground flora may provide insight used to make decisions on salvage harvesting and maintenance of biodiversity in other forests.

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