



## Effects of wind disturbance and salvage harvesting on macrofungal communities in a *Pinus* woodland



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### ABSTRACT

Natural disturbances alter the biophysical conditions of ecosystems, influencing patterns of structure, composition, and successional dynamics. Following high severity natural disturbance in forest ecosystems, land managers sometimes employ salvage harvesting to harvest trees killed or damaged by the disturbance agent. Despite its widespread practice, the effects of salvage harvesting on many ecosystem functions and species assemblages are still poorly understood. This study presents the first attempt to document and analyze the effects of salvage harvesting on macrofungal communities following catastrophic wind disturbance. On 27 April 2011, an EF3 tornado damaged forest stands within the Oakmulgee Ranger District of the Talladega National Forest in west-central Alabama, USA. Following the event, portions of some stands were subject to salvage harvesting. In 2016, we established three treatments, undisturbed, tornado disturbed, and salvage harvested, in stands that were dominated by *Pinus palustris* P. Miller prior to the 2011 disturbance events. Throughout the sample period, 546 occurrences of 84 macrofungal species were recorded. Tornado disturbed areas hosted the highest macrofungal species richness overall. Undisturbed areas hosted the highest species richness for ectomycorrhizal macrofungi. Salvage harvested areas had reduced species richness for both saprotrophic and ectomycorrhizal macrofungi compared to tornado disturbed plots. Non-metric multidimensional scaling ordination and permutational multivariate analysis of variance indicated that all three treatments differed in macrofungal community composition. The results indicated that salvage harvesting following catastrophic wind disturbance has the capacity to reduce macrofungal species richness and fruiting abundance. The reduction in deadwood volume and alterations to the ectomycorrhizal-associating plant community documented at salvage harvested sites is likely responsible for the observed differences in macrofungal fruiting patterns. The implications of reduced macrofungal richness in the early stages of forest development following catastrophic disturbance should be subject to long-term studies.

### 1. Introduction

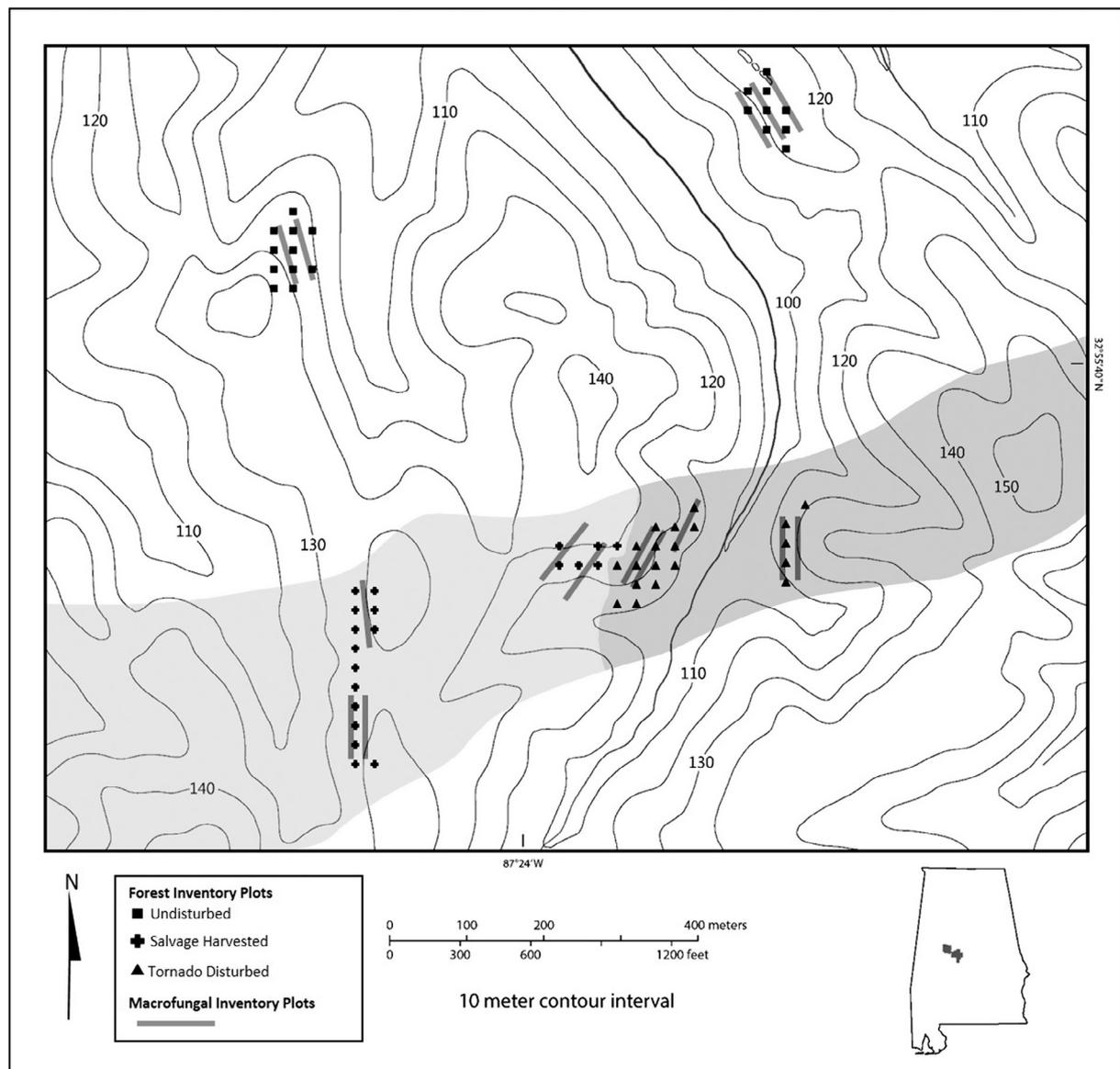
Natural disturbances are discrete events that alter the biophysical conditions of an ecosystem (Pickett and White, 1985). These events play key roles in regulating ecosystem functions, structures, and species assemblages (White and Jentsch, 2001). Because of their ability to create structural legacies and increase niche space, natural disturbances are often considered important for maintaining biodiversity (Hansen et al., 1991; Franklin et al., 2000). Following high severity natural disturbance events in forest ecosystems, land managers sometimes employ salvage harvesting to reclaim economic losses and reduce fuel loads. Although natural disturbances may be necessary for maintaining healthy ecosystems, researchers have expressed concern about the impact of salvage harvesting on ecosystem resiliency and biodiversity (Karr et al., 2004; Lindenmayer, 2006; Lindenmayer and Noss, 2006;

Waldron et al., 2013). Multiple disturbances in quick succession (i.e. compound disturbance), such as those represented by an initial disturbance and salvage harvesting, can have cumulative effects that are beyond the coping ability of native species (Paine et al., 1998, Peterson and Leach, 2008a). Salvage harvesting may also decrease habitat heterogeneity and niche space by removing structural legacies (e.g. deadwood), and altering the biophysical environment in ways not analogous to natural disturbances (e.g. soil compaction). Despite these concerns, some studies show that moderate intensity salvage harvesting does not have undesirable effects on long-term ecosystem function (Peterson and Leach, 2008a, Peterson and Leach, 2008b, Lang et al., 2009, Royo et al., 2016), thus much controversy remains concerning the use of salvage harvesting.

Understanding the impacts of disturbance events may be crucial to future forest management and conservation efforts as global climate

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**Fig. 1.** Map of the study site within the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Shaded region indicates areas disturbed by an EF3 tornado on 27 April 2011. Light grey shaded region indicates areas subsequently salvage harvested following the tornado. Squares represent undisturbed forest inventory plots, triangles represent tornado disturbed forest inventory plots, and plus signs indicate salvage harvested forest inventory plots. Grey bars indicate macrofungal inventory plots. Shaded area on the Alabama inset map indicates the Oakmulgee Ranger District.

change threatens to increase the frequency and intensity of disturbance agents such as tornados, hurricanes, and wildfires (Dale et al., 2001). Additionally, the practice of salvage harvesting following disturbance in forest ecosystems remains prevalent throughout the world, despite the dearth of information regarding its long-term ecosystem impacts (Royo et al., 2016). The majority of forest disturbance studies, including those on salvage harvesting, have focused on the alteration of woody plant composition and forest structural attributes (Peterson and Leach, 2008a; Lang et al., 2009; Waldron et al., 2013; White et al., 2014; Royo et al., 2016; Fraver et al., 2017). Few studies have considered the impacts of disturbance events on fungal communities, and a paucity of information on fungal ecology and biogeography exists for many geographic regions and ecosystem types. The differential impacts of various disturbance agents, magnitudes, and severities on fungal communities must be subject to further study to optimize conservation and management efforts concerned with protecting fungal biodiversity and associated ecosystem function.

Ectomycorrhizal (ECM) and saprotrophic fungi are two distinct fungal groups prevalent in forest ecosystems. ECM fungi derive their

carbon from living plant roots, typically those of woody species, while saprotrophic fungi derive carbon from dead organic material. Studies considering the successional patterns of ECM fungi have often found higher species richness in older forests (Visser, 1995; Fernandez-Toiran et al., 2006; Twieg et al., 2007), suggesting that many ECM fungi may not be able to persist through or establish soon after stand initiating disturbance events. These phenomena are likely caused by removal of the host plant community (e.g. mature trees) and alterations to the abiotic environment such as increased light exposure, which can raise soil temperatures and hinder ECM fungal growth (Parke et al., 1983; Bruns, 1995). Compositional shifts in ECM communities have also been reported following disturbances such as fires (Taylor and Bruns, 1999) and tornados (Craig et al., 2016), however the lack of species-specific life history data makes it difficult to assess these shifts. Harvesting operations can create impacts distinct from those of natural disturbance agents, and thus may have unique effects on ECM fungi. For example, soil compaction and mixing is often a consequence of timber harvesting that can impact soil inhabiting organisms. These disruptions in the soil environment can cause physical damage to fungal hyphae and

propagules (Brundrett, 1991), and also limit the growth of host plants (Kozłowski, 1999). Accordingly, operations that cause soil perturbation, such as clear-cut harvesting, have often been shown to negatively impact ECM fungal diversity (Hagerman et al., 2001; Jones et al., 2003; Luoma et al., 2004; Durall et al., 2006; Simard, 2009).

Saprotrophic fungi rely on dead organic material for carbon and substrate. Thus, the amount and diversity of dead organic material often correlates with saprotrophic fungal diversity (Lonsdale et al., 2008; Junninen and Komonen, 2011; Brazee et al., 2014; Dove and Keeton, 2015). Disturbances in forest ecosystems increase the amount of dead organic material in the system, and may be beneficial or necessary to maintain optimal levels of saprotrophic fungal diversity (Bässler and Müller, 2010; Brazee et al., 2014). Conversely, timber harvesting operations by definition remove dead organic material from the system, reducing the amount and diversity of substrate available to saprotrophic fungi. Accordingly, studies considering the effects of timber harvesting on saprotrophic fungi often report declines in species diversity, particularly among wood-inhabiting species (Sippola et al., 2004; Junninen et al., 2006; Müller et al., 2007).

The overarching goal of this study was to analyze the effects of natural wind disturbance (tornado) and salvage harvesting on ECM and saprotrophic macrofungal communities in a montane *Pinus palustris* P. Miller woodland using sporocarp surveys. To date few studies have assessed the specific effects of tornado disturbance and/or salvage harvesting on fungal communities (Bässler et al., 2012; Cowden and Peterson, 2013; Craig et al., 2016). Our specific objectives were to: (1) quantify differences in woody plant species composition and stand structure between undisturbed, tornado disturbed, and salvage harvested stands, (2) quantify macrofungal species composition and fruiting abundance in each of the three disturbance classes, and (3) compare macrofungal communities of each disturbance class and relate them to the effects of disturbance on forest composition and structure. Based on previous studies, we hypothesized four main effects on the macrofungal community: (1) tornado disturbed areas would have decreased species richness of ECM fungi compared to undisturbed areas, (2) salvage harvested areas would have lower ECM fungal richness compared to areas left unsalvaged following the tornado, (3) saprotrophic fungal richness would be greater in tornado disturbed areas compared to undisturbed areas, and (4) salvage harvested areas would have decreased saprotrophic fungal richness compared to areas left unsalvaged following the tornado.

## 2. Methods

### 2.1. Study site

The study took place on the Oakmulgee Ranger District of the Talladega National Forest in Bibb County Alabama, USA (Fig. 1). The area was first settled by Europeans in the 1820s, extensively logged in the early 1900s, and acquired by the United States Forest Service (USFS) in 1943 (Cox and Hart, 2015). Today, the USFS manages much of the Oakmulgee Ranger District for *P. palustris* using mid-story removals in overstocked stands, regeneration harvests followed by *P. palustris* outplantings, and prescribed burns on 2–5 year intervals (USDA, 2005). The District is within the Fall Line Hills physiographic province that separates the Coastal Plain from the Appalachian Highlands (Fenneman, 1938). The topography of the region is characterized by steep narrow ridges and sandy soils (USDA, 2008). Soils of the study area are classified in the Maubila series which is typically very deep and moderately well drained (USDA, 2017). The climate is humid mesothermal with short mild winters and long hot summers (Thornthwaite, 1948). Annual mean precipitation is 140 cm with the highest mean monthly precipitation of 14.1 cm in February and the lowest mean monthly precipitation of 8.5 cm in October (PRISM, 2017). Annual mean temperature is 17 °C with monthly mean temperatures ranging from 6 °C in January to 27 °C in July (PRISM, 2017). The

typical frost free period spans from March to November (USDA, 2008).

On 27 April 2011, an EF3 tornado with winds of 233 kph struck the Oakmulgee Ranger District, damaging stands within the forest (NOAA, 2017a). The tornado tracked for 48 km with a maximum width of 1609 m (NOAA, 2017a). Sections of the tornado affected forests were subsequently salvage harvested to recover economic losses and to lessen the risk of insect and fire outbreak (Ragland, 2011). The salvage operation took place July 2011 to November 2011. All downed wood and standing damaged trees, regardless of size class and species, were subject to harvesting at the discretion of the operator. Trees were severed from stumps using a wheeled mechanical feller-buncher and chainsaws when necessary. Logs were skidded with large end elevated to the ramp site using wheeled skidders. A stationary knuckleboom loader was used to load logs for transport at the ramp site.

Three treatments: undisturbed (not disturbed by 2011 tornado), tornado disturbed, and salvage harvested (tornado disturbed and salvage harvested), were established using a combination of satellite imagery, geospatial data provided by the USDA, and ground reconnaissance. Treatment sites were selected on the likelihood of similar pre-disturbance condition, including proximity, similarities in soil type, stand age, species composition, and management history. Prior to the 2011 tornado event, all treatment areas were mature *P. palustris* forest established prior to the 1940s, and were located within 1 km of each other in the same USFS management compartment. Selected areas experienced the same prescribed burn regime, with recent burns occurring in the spring of 2010 and 2014. Thus, site selection ensured that observed differences in plant and macrofungal community composition and structure could be attributed to the 2011 disturbance events, and not differences in pre-disturbance conditions.

### 2.2. Forest inventory

Within each treatment, 20 fixed-radius 0.04 ha plots were established to assess tree composition, sapling composition, and coarse woody debris (CWD). ArcMAP version 10.2 was used to superimpose a grid with 25 m spacing over sites which met criteria for similar pre-disturbance conditions, and plot locations were determined using the grid cell coordinates. All plots were located  $\geq 25$  m within undisturbed and disturbed areas to reduce potential edge effects. Within each plot, live trees  $\geq 5$  cm at diameter breast height (dbh, 1.37 m above ground) were measured for dbh and recorded to species. Saplings (woody stems  $\geq 1$  m in height and  $< 5$  cm diameter) were tallied by species in each plot.

CWD (woody pieces  $\geq 10$  cm diameter and lying  $\leq 45^\circ$  to the ground) was measured for total length and diameter at each end. If CWD still had root plates intact, diameter 1.37 m above the root plate and total length was measured (Parker and Hart, 2014). CWD pieces with root plates intact were classified as uproots, and pieces without root plates were classified as logs. If CWD crossed the plot boundary, only the portion within the plot was considered. All pieces of CWD were classified into one of five decay classes following the guidelines of the Forest Inventory and Analysis program of the USFS, ranging from decay class I pieces that were freshly dead to decay class V pieces that were almost fully decomposed (FIA, 2005). Snags (standing dead trees  $\geq 10$  cm dbh with crowns largely intact), snaps (standing dead trees  $\geq 10$  cm dbh without crown intact), and stumps (standing dead tree  $\geq 10$  cm diameter with snapped or cut bole below 1.37 m) within each plot were tallied and assigned to decay class. Snags and snaps were measured for dbh and stumps were measured for diameter at the point of snap or cut. All CWD, snags, snaps, and stumps were classified as either *Pinus* or hardwood.

Fine woody debris (FWD), and litter cover were sampled by placing a 1 × 1 m subplot at the center of each plot and then moving it 3 times along the 0°, 120°, and 240° azimuths respectively for a total sampling of 10 m<sup>2</sup> per plot. Within each 1 m<sup>2</sup> subplot, FWD (woody pieces  $< 10$  cm diameter) and litter cover percentage was estimated using

Daubenmire cover classes (I 0–5%; II 5–25%; III 25–50%; IV 50–75%; V 75–95%; VI 95–100%). The use of broad percentage classes to estimate cover decreases differential bias when using multiple observers (Barbours et al., 1980). Litter was defined as undecomposed or partially decomposed organic material that can be readily identified and does not meet the criteria of FWD or CWD (FIA, 2005). To assess canopy cover, spherical densiometer readings were taken at the center of each plot, and at the plot edge in the four cardinal directions. Readings were averaged per plot and multiplied by 1.04 to calculate percent canopy cover (Lemmon 1957).

### 2.3. Macrofungal inventory

Macrofungi were defined as basidiomycetes and ascomycetes with large, easily observable sporocarps (Mueller et al., 2007). Macrofungal surveys were conducted in the same stands as the forest inventories, however, a different plot design was used to account for the typically sparse and irregular distribution of fungal sporocarps at the stand-scale. Within each treatment five 1000 m<sup>2</sup> (10 × 100 m) plots were established (Arnolds, 1992; Mueller et al., 2004) with long axes running parallel to mid-slope position. Plots were subdivided into 10 × 10 m subplots (Durall et al., 2006). Each plot was surveyed for fungal sporocarps from May 2016 through November 2016 to encompass the peak fruiting season. Surveys were performed twice-monthly June through October and once in May and November. Hypogeous macrofungi were not considered because different sampling efforts are required to assess these species (Mueller et al., 2004). Species were noted for presence/absence based on sporocarp occurrence within each subplot (Durall et al. 2006). If sporocarps occurred on deadwood, the substrate was classified by taxonomic group, diameter at point of sporocarp occurrence, mode of death (i.e. FWD, log, snag, snap, stump, uproot), and decay class. To avoid repeat counting, persistent sporocarps (e.g. polypores) were only recorded at their first occurrence during the survey. Sporocarps were identified to the lowest taxonomic level possible. Specimens that could not be identified to the species level in the field were collected for vouchers and separated based on common identification characteristics, including macroscopic and microscopic features (Largent et al., 1977; Arora, 1986; Gilbertson and Ryvarden, 1986; Largent, 1986; Lincoff, 1997; Bessette et al. 2000; Miller and Miller 2006; Bessette, 2007). All positive species identifications were cross-referenced with Index Fungorum (2017) for current species names.

### 2.4. Analytical methods

To characterize the forest community in each treatment, density, relative density, dominance, relative dominance, and importance (average of relative density and relative dominance) were calculated for all tree species. Density and relative density were calculated for all species within the sapling layer. CWD volume was calculated using the equation for a conic paraboloid (Fraver et al., 2007). If CWD had root plates intact, species-specific allometric equations were used to calculate volume (Woodall et al., 2011; Parker and Hart, 2014). To determine a singular plot value for FWD and litter cover, Daubenmire cover classes were converted to their midpoint value, averaged per plot, then reconverted to cover class.

To compare treatment effects, one-way analysis of variance (ANOVA) was performed using SPSS 22.0 (IBM, Armonk, NY, USA). ANOVA was performed on forest inventory variables posited to influence the fungal community (canopy cover, CWD density, CWD volume, ECM-associating tree density, ECM-associating sapling density, FWD cover, and litter cover). Additionally, ANOVA was performed to compare per plot richness of macrofungal species. In accordance with other studies, we chose to compare species richness instead of other diversity indices as sporocarp abundance is species-specific and may not accurately predict fungal community evenness (Norden et al., 2004;

Fernandez-Toiran et al., 2006; Dove and Keeton, 2015). Prior to running ANOVA, all data were visually checked for normality using histograms. Variables that did not meet statistical assumptions were either log or cube root transformed. When statistically significant differences ( $p < .05$ ) were found, a Tukey's honestly significant difference (HSD) post-hoc test was used to compare treatment means.

To further characterize and assess differences in fungal community composition across treatments, non-metric multidimensional scaling (NMS) ordination, permutational multivariate analysis of variance (PerMANOVA), and indicator species analysis (ISA) were conducted using PC-ORD v. 6.0 (McCune and Medford, 2011). NMS was used to graphically assess differences in fungal community composition across the treatments (Kruskal, 1964). Prior to running NMS, matrix data consisting of fungal species occurrences by plot were log<sub>10</sub> + 1 transformed to down-weight influence of highly abundant species (Brazee et al., 2012; Brazee et al., 2014). Additionally, species with only a single occurrence were excluded from the matrix (Brazee et al., 2012; Brazee et al., 2014). NMS ordination was run using the Sørensen (Bray-Curtis) distance measure and random starting coordinates. A two axis solution was chosen after NMS was run several times to verify consistency of results. PerMANOVA was used to further test treatment effects on fungal community composition (Anderson, 2001). Post-hoc pairwise comparisons were used after significant treatment effects were found. Permutational tests of significance were based on 4999 iterations. ISA was used to assess which fungal species were most representative of each respective treatment (Dufrene and Legendre, 1997). This analysis calculates an indicator value (IV) from the relative abundance of each species in each treatment and its constancy (number of plots in each treatment in which the species is present by total plots in the treatment). The IV ranges from 0 to 100, with 0 giving no indication of a particular treatment and 100 giving a perfect indication. To test for significance, observed IVs were tested against random values derived from 4999 permutations.

## 3. Results

### 3.1. Forest composition and structure

Overall tree species richness was 17. *Pinus palustris* was the most dominant species in all three treatments accounting for 73% of basal area and 46% of all stems ( $\geq 5$  cm dbh) throughout the study site (Table 1). *Pinus palustris* and *Pinus taeda* were the only species in the tree layer common to all three treatments. Undisturbed treatments had the highest tree density (325.00 stems ha<sup>-1</sup>) and basal area (16.21 m<sup>2</sup> ha<sup>-1</sup>). Tornado and salvage treatments had basal areas of 1.09 m<sup>2</sup> ha<sup>-1</sup> and 0.57 m<sup>2</sup> ha<sup>-1</sup> respectively, and both had a tree density of 31 stems ha<sup>-1</sup>. In total, 11 of the 17 species were ECM-associating species, belonging to the genera *Fagus*, *Pinus*, or *Quercus*. These species comprised 86% of stems in undisturbed, 92% in tornado, and 100% in salvage harvested treatments.

Sapling species richness was 46, with 20 ECM-associating species belonging to the genera *Carya*, *Castanea*, *Fagus*, *Pinus*, or *Quercus*. ECM-associating species accounted for 9.90%, 36.38%, and 38.61% of saplings in undisturbed, tornado, and salvage treatments respectively. *Quercus falcata* was the most abundant ECM-associating sapling in undisturbed and salvaged plots and *Quercus coccinea* was most abundant in tornado plots. The dominant tree species, *P. palustris*, represented only 0.89%, 0.44%, and 1.69% of saplings in undisturbed, tornado, and salvage treatments respectively.

Logs were the most common deadwood mode of death across all three treatments (Fig. 2). Uproots were the second most common mode of death in tornado plots, and stumps were the second most common mode of death in undisturbed and salvage plots. In the salvage harvested treatment, 79% ( $n = 65$ ) of the stumps were recently cut by blade. Of these cut stumps, 36 were uprooted and 29 were rooted. The diameter distribution of CWD, snags/snaps, and stumps was similar

**Table 1**

Density (stems ha<sup>-1</sup>), relative density, dominance (m<sup>2</sup> ha<sup>-1</sup>), relative dominance, and importance (average of relative density and relative dominance) for all live woody stems ≥ 5 cm dbh measured by treatment in the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Asterisks indicate ectomycorrhizal-associating species.

Species	Density (ha <sup>-1</sup> )			Relative density (%)			Dominance (m <sup>2</sup> ha <sup>-1</sup> )			Relative dominance (%)			Importance (%)		
	UND	TOR	SALV	UND	TOR	SALV	UND	TOR	SALV	UND	TOR	SALV	UND	TOR	SALV
<i>Pinus palustris</i> *	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
<i>Pinus taeda</i> 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
<i>Quercus marilandica</i> Muenchhausen *	21.25	1.25	–	6.54	4.00	–	0.59	0.06	–	2.72	5.71	–	4.63	4.85	–
<i>Quercus falcata</i> Michaux *	15.00	–	–	4.62	–	–	0.87	–	–	4.01	–	–	4.31	–	–
<i>Cornus florida</i> Linnaeus	20.00	–	–	6.15	–	–	0.23	–	–	1.06	–	–	3.61	–	–
<i>Nyssa sylvatica</i> Marshall	15.00	–	–	4.62	–	–	0.35	–	–	1.63	–	–	3.12	–	–
<i>Quercus stellata</i> Wangenheim *	12.50	6.25	–	3.85	20.00	–	0.22	0.13	–	1.01	11.57	–	2.43	15.78	–
<i>Pinus echinata</i> P. Miller *	6.25	2.50	–	1.92	8.00	–	0.53	0.18	–	2.44	16.39	–	2.18	12.19	–
<i>Oxydendrum arboreum</i> (Linnaeus) A.P. de Candolle	7.50	–	–	2.31	–	–	0.22	–	–	1.00	–	–	1.66	–	–
<i>Quercus alba</i> Linnaeus *	5.00	2.50	–	1.54	8.00	–	0.08	0.12	–	0.37	11.09	–	0.95	9.55	–
<i>Quercus velutina</i> Lamarck *	1.25	–	–	0.38	–	–	0.12	–	–	0.56	–	–	0.47	–	–
<i>Liriodendron tulipifera</i> Linnaeus	1.25	–	–	0.38	–	–	0.11	–	–	0.52	–	–	0.45	–	–
<i>Diospyros virginiana</i> Linnaeus	1.25	–	–	0.38	–	–	0.02	–	–	0.11	–	–	0.25	–	–
<i>Liquidambar styraciflua</i> Linnaeus	1.25	2.50	–	0.38	8.00	–	0.01	0.03	–	0.04	2.82	–	0.21	5.41	–
<i>Fagus grandifolia</i> Ehrhart *	1.25	–	–	0.38	–	–	0.01	–	–	0.03	–	–	0.21	–	–
<i>Quercus coccinea</i> Muenchhausen *	–	–	1.25	–	–	4.00	–	–	0.07	–	–	12.62	–	–	8.31
<i>Quercus montana</i> Willdenow *	–	1.25	–	–	4.00	–	–	0.01	–	–	0.47	–	–	2.23	–
<b>Total</b>	<b>325.00</b>	<b>31.25</b>	<b>31.25</b>	<b>100.00</b>	<b>100.00</b>	<b>100.00</b>	<b>21.69</b>	<b>1.09</b>	<b>0.57</b>	<b>100.00</b>	<b>100.00</b>	<b>100.00</b>	<b>100.00</b>	<b>100.00</b>	<b>100.00</b>

across all treatments with the highest densities occurring in 10–15 and 15–20 cm size classes, then decreasing with increasing size until a small spike in the > 40 cm size class (Fig. 3). Overall, 81% ( $n = 663$ ) of CWD, snag/snaps, and stumps were classified as decay class II. Decay class distribution was similar in all three treatments with the majority of deadwood pieces in decay class II, followed by classes III, IV, and I respectively (Fig. 4). No deadwood pieces in the study site were classified in decay class V.

### 3.2. Comparison of treatment effects on forest inventory variables

We statistically compared plot level means of 11 forest inventory variables posited to most directly influence the macrofungal community (Table 2). ECM-associating tree density per plot was significantly higher ( $p < .001$ ) in undisturbed treatments ( $11.15 \pm 0.92$  SE stem ha<sup>-1</sup>) compared to tornado ( $1.15 \pm 0.30$  SE stems ha<sup>-1</sup>) and salvage ( $1.25 \pm 0.57$  SE stems ha<sup>-1</sup>) treatments. ECM-associating sapling density was significantly higher ( $p < .001$ ) in tornado disturbed plots ( $111.50 \pm 7.42$  SE) compared to salvage ( $68.35 \pm 10.32$  SE) and undisturbed plots ( $13.30 \pm 3.21$  SE), and also significantly higher ( $p < .001$ ) in salvaged plots compared to undisturbed plots. CWD density and volume were significantly higher ( $p < .001$ ) in tornado plots ( $15.70 \pm 0.85$  SE pieces plot<sup>-1</sup>;  $7.16 \pm 0.92$  SE m<sup>3</sup> plot<sup>-1</sup>) compared to undisturbed plots ( $2.85 \pm 0.62$  SE pieces plot<sup>-1</sup>;  $0.23 \pm 0.10$  SE m<sup>3</sup> plot<sup>-1</sup>) and salvage plots ( $11.30 \pm 0.99$  SE pieces plot<sup>-1</sup>;  $0.79 \pm 0.10$  SE m<sup>3</sup> plot<sup>-1</sup>). Salvage plots had significantly higher ( $p < .001$ ) CWD density compared to undisturbed plots, but similar CWD volume. *Pinus* CWD volume and density were greater than hardwood CWD volume and density in all treatments. Mean forest floor litter cover per plot was higher ( $p < .05$ ) in undisturbed plots ( $5.55 \pm 0.11$  SE mean cover class) compared to tornado ( $4.30 \pm 0.16$  SE mean cover class) and salvaged plots ( $3.95 \pm 0.21$  SE mean cover class). Mean FWD cover per plot was higher ( $p < .05$ ) in tornado ( $1.40 \pm 0.11$  SE mean cover class) and salvaged plots ( $1.50 \pm 0.11$  SE mean cover class) compared to undisturbed plots ( $1.05 \pm 0.05$  SE mean cover class), however, mean plot cover class values for all treatments corresponded to 0–5% cover. Mean canopy cover per plot was significantly higher ( $p < .01$ ) in the undisturbed treatment ( $89.82\% \pm 0.90$  SE) compared to both tornado and salvage treatments. Tornado plots had significantly higher ( $p < .01$ ) canopy coverage

( $14.26\% \pm 2.36$  SE) compared to salvage plots ( $5.47\% \pm 1.63$  SE).

### 3.3. Macrofungal community

In total, 546 occurrences of 84 macrofungal species were recorded throughout the study site (Table 3). Per plot richness was significantly higher ( $p < .03$ ) in tornado disturbed plots ( $25.60 \pm 2.34$  SE) compared to undisturbed ( $14.00 \pm 1.94$  SE) and salvage plots ( $14.00 \pm 1.72$  SE) (Table 2). Of the 84 species, 33 were classified as ECM fungi. The most prevalent families represented in the ECM community were Amanitaceae ( $n = 9$  species), Boletaceae ( $n = 9$  species), and Russulaceae ( $n = 6$  species). ECM fungal richness was highest in the undisturbed treatment ( $n = 23$ ) followed by tornado ( $n = 16$ ) and salvage ( $n = 12$ ) treatments respectively. Per plot ECM fungal richness was significantly higher ( $p < .02$ ) in undisturbed plots ( $9.00 \pm 1.02$  SE) compared to salvage harvested plots ( $4.20 \pm 0.77$  SE). Of the 33 ECM species documented in the study site, 14 were unique to the undisturbed treatment, four to the tornado treatment, and three to the salvage treatment. Overall, six ECM species were common to all three treatments. Of these six ECM species, two were most abundant in undisturbed areas, three in tornado disturbed areas, and one in salvage harvested areas. Salvage harvested areas had the lowest abundance for three of these species. Only three ECM species co-occupied undisturbed and tornado sites only, with similar abundances for these species in each treatment. Additionally, three ECM species co-occupied tornado and salvage harvested sites only, with greater abundance in tornado areas for two of the species, and identical abundance in both areas for the third.

Saprotrophic species richness was 51, with the highest richness documented in the tornado treatment ( $n = 45$ ) followed by salvage ( $n = 21$ ) and undisturbed ( $n = 15$ ) respectively. Per plot saprotrophic species richness was significantly higher ( $p < .001$ ) in the tornado treatment ( $18.40 \pm 2.63$  SE) compared to undisturbed ( $5.00 \pm 1.13$  SE) and salvage harvested treatments ( $9.80 \pm 1.15$  SE). In total, 25 saprotrophic species were unique to the tornado treatment, with undisturbed and salvage treatments hosting three unique species each. Overall, 10 saprotrophic species were common to all three treatments with tornado areas hosting the highest abundance for five of these species. Additionally, eight saprotrophic species were common to tornado and salvage harvested sites only. Of these species, five were most

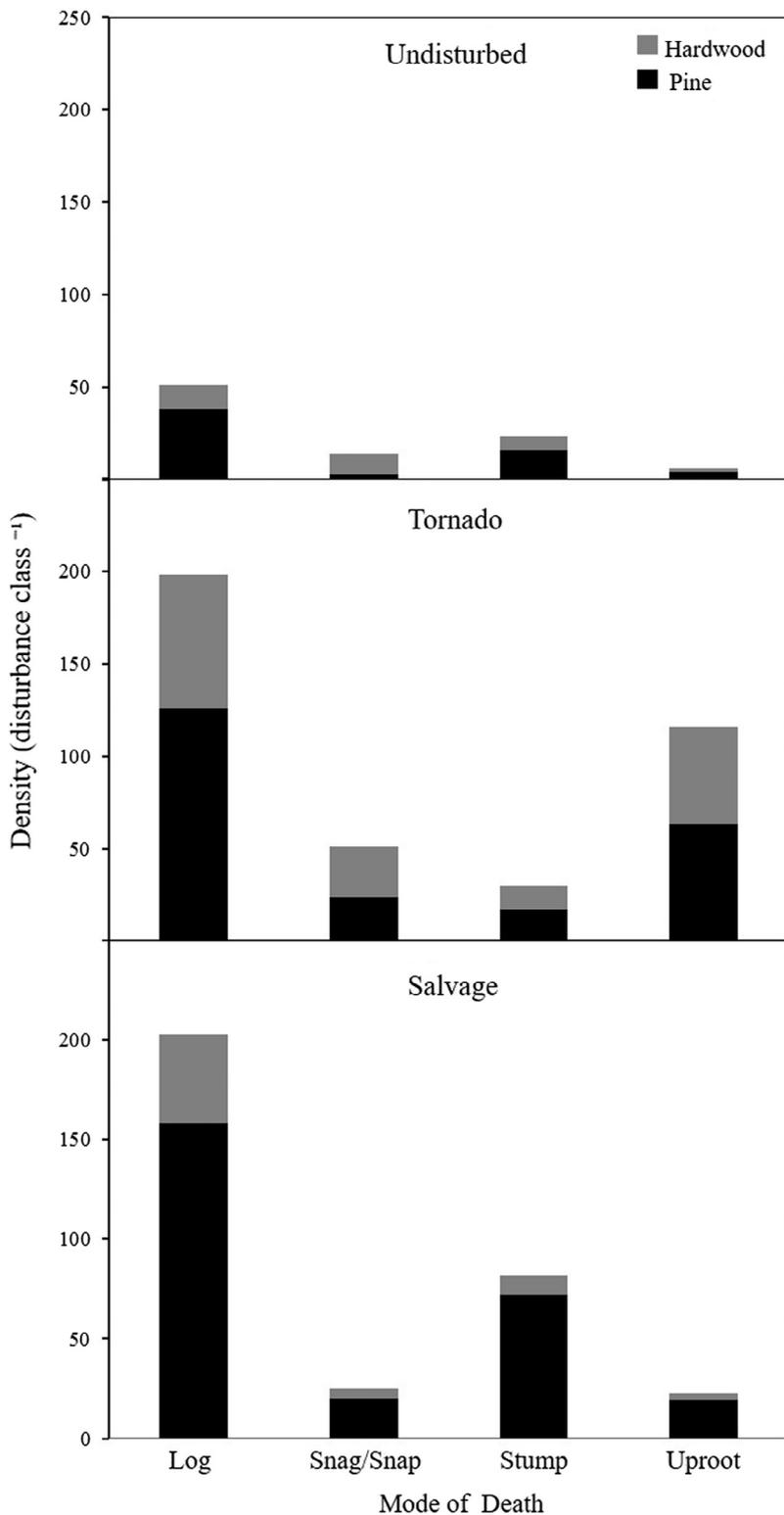


Fig. 2. Mode of death distribution for all woody pieces  $\geq 10$  cm diameter by treatment in the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Modes of death include: logs (woody pieces  $\geq 10$  cm diameter without root plates), snag/snaps (standing dead trees  $\geq 10$  cm dbh with or without crown intact), stumps (standing dead trees or uproots  $\geq 10$  cm diameter snapped or cut below 1.37 m from root plate), and uproots (woody pieces  $\geq 10$  cm diameter with root plates intact).

abundant in tornado areas, one was most abundant in salvage harvested areas, and two had equal abundance in both areas. Only two saprotrophic species were common to undisturbed and tornado sites only, and they had equal abundance in both treatments.

Of the 51 saprotrophic species, 33 were saproxylic, and the remaining 18 occurred on litter or soil. Throughout the study site, 276 saproxylic fruiting occurrences were documented, with 39 in undisturbed areas, 166 in tornado disturbed areas, and 71 in salvage harvested areas. Overall, 220 occurrences were recorded on hardwood

substrate and 56 on *Pinus*. Two species, *Cerrena unicolor* and *Dacryopinax spathularia*, were recorded on both hardwood and *Pinus* substrates. FWD hosted 119 saproxylic fruiting occurrences, and larger deadwood hosted 157 occurrences. Of these, a considerable majority occurred on logs ( $n = 109$ ) followed by uproots ( $n = 23$ ), snags/snaps ( $n = 17$ ), and stumps ( $n = 8$ ) (Fig. 5). The number of saproxylic fruiting occurrences generally decreased with increasing deadwood diameter in all three treatments (Fig. 6). In total, 97% ( $n = 267$ ) of saproxylic fruiting occurrences were documented on decay class II

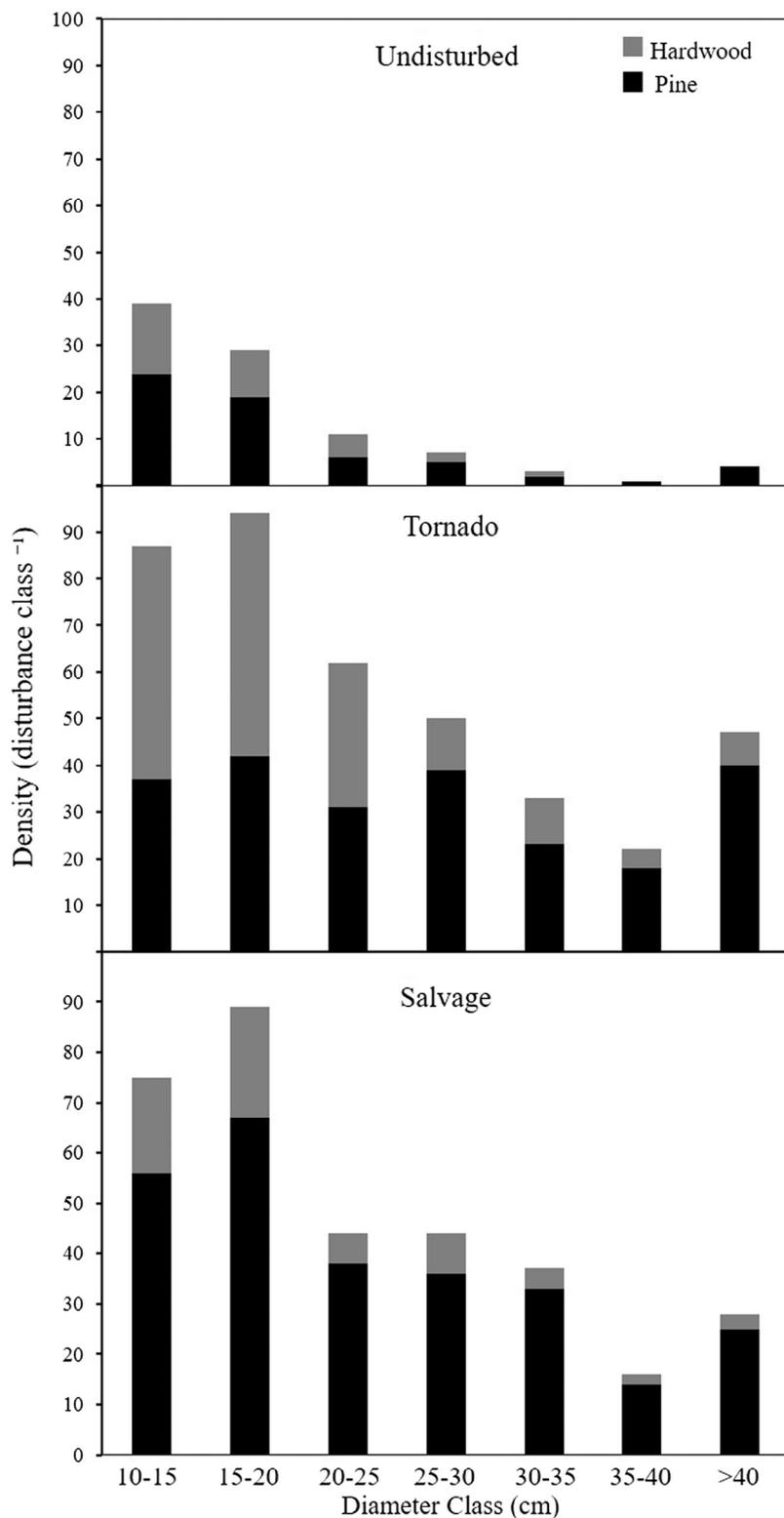


Fig. 3. Diameter class distribution for all woody pieces  $\geq 10$  cm diameter by treatment in the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA.

substrates (Fig. 7).

The final two-axis NMS solution (final stress = 12.89, cumulative  $r^2 = 87.1\%$ ) showed that treatments were well segregated based on macrofungal community composition (Fig. 8). Axis 1 accounted for 63.9% of the variation in the dataset, and was positively correlated to undisturbed plots and negatively to tornado and salvage plots. Tornado and salvage plots were separated on axis 2, which accounted for 23.2% of variation in the dataset. PerMANOVA results indicated that all three treatments were significantly different ( $p < .02$ ) in macrofungal

community composition. ISA revealed 12 indicator species overall ( $p < .05$ ), nine for tornado, two for undisturbed, and one for salvage (Table 4). Indicator species for the tornado treatment included seven saprotrophic species (*C. unicolor*, *Daedaleopsis confragosa*, *D. spathularia*, *Lentinus crinitus*, *Marasmius* sp., *Trichaptum bifforme*, and *Trametes elegans*) and two ECM species (*Pisolithus arhizus* and *Retiboletus ornatipes*). The indicator species for the undisturbed treatment were both ECM species belonging to the genus *Cantharellus* (*Cantharellus cibarius*, and *Cantharellus cinnabarinus*). *Gymnopus dryophilous*, a saprotroph, was the

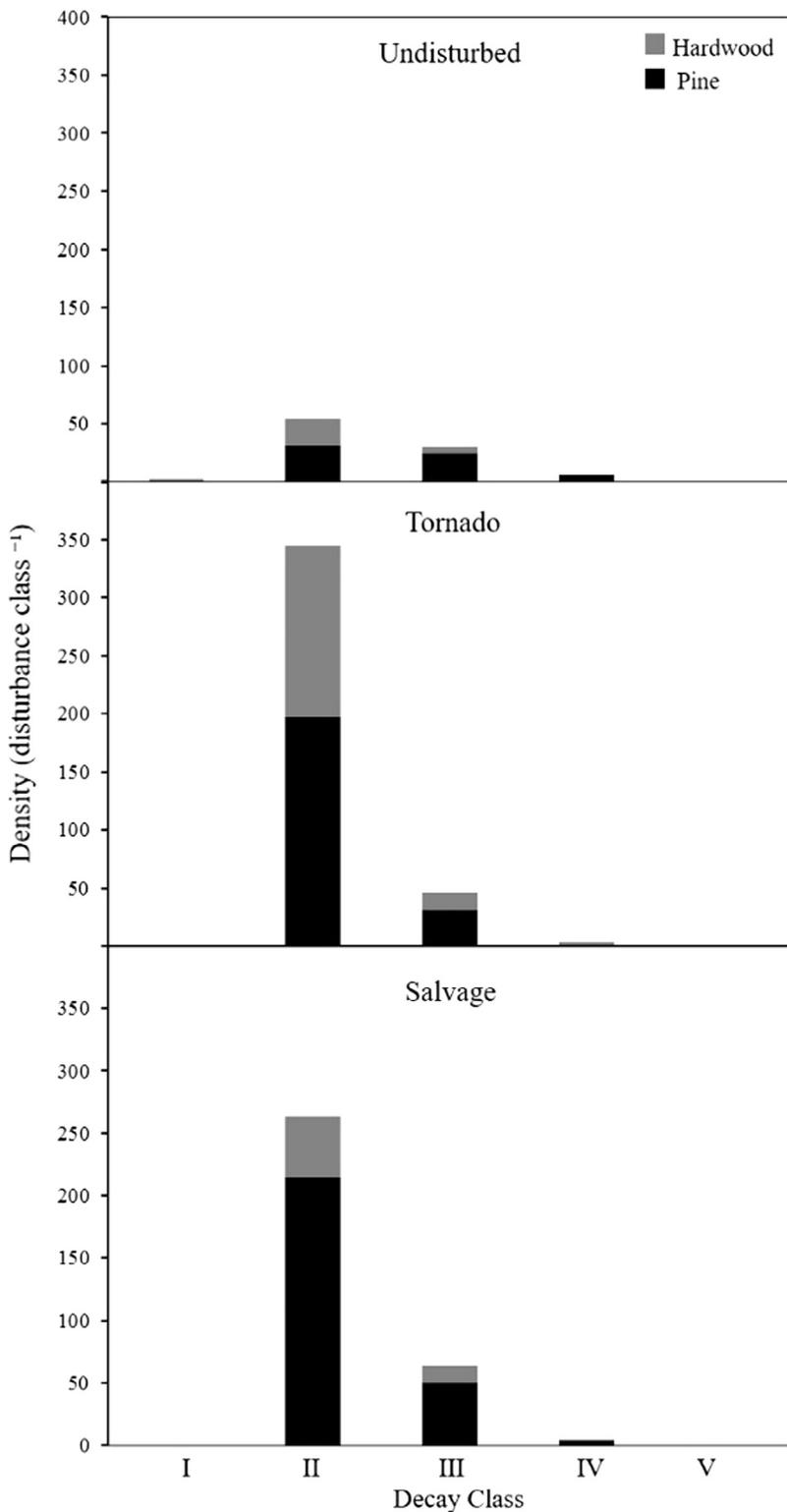


Fig. 4. Decay class distribution for all woody pieces  $\geq 10$  cm diameter by treatment in the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Decay classes follow the guidelines of the USFS FIA (2005).

only indicator species for the salvage treatment.

#### 4. Discussion

##### 4.1. Disturbance impacts on structural legacies

The tornado and salvage harvesting disturbances documented in this study had considerable impacts on forest composition and structure. Nearly all live tree basal area was removed by the tornado event,

signifying a catastrophic disturbance. Structural legacies including increased canopy openness and increased density and volume of deadwood were documented in tornado disturbed areas. The high levels of canopy openness resulted in significantly higher density of ECM saplings, particularly in the genus *Quercus*, while sapling density of *P. palustris* slightly decreased. Without active management, it is likely that forest composition will shift from *P. palustris* dominance to *Quercus* dominance. The stand was burned in 2014 to promote *P. palustris* regeneration, through competition reduction. However, fuels in the

**Table 2**

Statistical comparisons of forest inventory and macrofungal community variables in the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. All variables were tested for significant difference ( $p < .05$ ) in plot level means across disturbance classes using one-way ANOVA.  $F$ -value and degrees of freedom ( $DF$ ) are given for each variable. Per plot means are  $\pm$  standard error. Means in rows followed by the same letter are not significantly different at  $p < .05$ .

Parameter	Undisturbed	Tornado	Salvage	$F$	$DF$
Ectomycorrhizal tree density plot1	11.15 $\pm$ 0.92 (a)	1.15 $\pm$ 0.30 (b)	1.25 $\pm$ 0.57 (b)	49.03	59
Ectomycorrhizal sapling density plot1	13.30 $\pm$ 3.21 (a)	111.50 $\pm$ 7.42 (b)	68.35 $\pm$ 10.32 (c)	61.95	59
CWD density plot1	2.85 $\pm$ 0.62 (a)	15.70 $\pm$ 0.85 (b)	11.30 $\pm$ 0.99 (c)	58.51	59
Hardwood CWD density plot1	0.75 $\pm$ 0.30 (a)	6.25 $\pm$ 0.70 (b)	2.45 $\pm$ 0.44 (c)	28.43	59
Pine CWD density plot1	1.88 $\pm$ 0.46 (a)	9.45 $\pm$ 1.05 (b)	8.85 $\pm$ 0.96 (b)	27.67	59
CWD volume (m <sup>3</sup> ) plot1	0.23 $\pm$ 0.10 (a)	7.16 $\pm$ 0.92 (b)	0.79 $\pm$ 0.10 (a)	51.36	59
Hardwood CWD volume (m <sup>3</sup> ) plot1	0.02 $\pm$ 0.01 (a)	1.26 $\pm$ 0.31 (b)	0.17 $\pm$ 0.05 (c)	49.00	59
Pine CWD volume (m <sup>3</sup> ) plot1	0.21 $\pm$ 0.10 (a)	5.90 $\pm$ 0.93 (b)	0.63 $\pm$ 0.10 (c)	85.99	59
FWD cover class plot1	1.05 $\pm$ 0.22 (a)	1.40 $\pm$ 0.50 (b)	1.50 $\pm$ 0.51 (b)	5.92	59
Litter cover class plot1	5.55 $\pm$ 0.51 (a)	4.30 $\pm$ 0.73 (b)	3.95 $\pm$ 0.94 (b)	25.13	59
Canopy cover (%) plot1	89.82 $\pm$ 0.90 (a)	14.26 $\pm$ 2.36 (b)	5.47 $\pm$ 1.63 (c)	715.48	59
Macrofungal richness plot1	14.00 $\pm$ 1.94 (a)	25.60 $\pm$ 2.34 (b)	14.00 $\pm$ 1.72 (a)	7.65	14
Ectomycorrhizal fungal richness plot1	9.00 $\pm$ 1.02 (a)	7.20 $\pm$ 1.21 (ab)	4.20 $\pm$ 0.77 (b)	5.37	14
Saprotrophic fungal richness plot1	5.00 $\pm$ 1.13 (a)	18.40 $\pm$ 2.63 (b)	9.80 $\pm$ 1.15 (a)	14.60	14

disturbed areas were likely less contiguous because of reduced litter cover. Nearly all live canopy trees were killed in tornado disturbed areas. Thus, litter input will likely remain low and limit the effectiveness of prescribe burning efforts until fuel accumulation becomes more substantial.

The vast majority of deadwood in the disturbed treatments were in decay class II, indicating that stems killed by the tornado event have not yet entered advanced stages of decay. Deadwood density and volume were increased by the tornado event, and decreased by salvage harvesting. Interestingly, deadwood volume was reduced more extensively than deadwood density. This indicated that the salvage harvesting operation removed entire deadwood pieces and harvested only portions of other pieces. The presence of both uprooted and rooted cut stumps indicated that salvage harvesting removed uprooted stems, snags/snaps, and damaged live trees. The operation decreased deadwood in most size classes except for FWD. Fraver et al. (2017) documented a similar pattern, indicating the tendency for salvage harvesting operations to leave smaller deadwood and slash on site.

#### 4.2. Disturbance effects on the macrofungal community

Our study aimed to test four main hypotheses on the effects of tornado disturbance and salvage harvesting on saprotrophic and ECM macrofungi. We hypothesized that tornado disturbance would decrease ECM fungal richness, and salvage harvesting would subsequently decrease it further. Although we did document this trend, it was not supported statistically, perhaps because of low sample size and/or short sampling period. Our hypotheses that tornado disturbance would increase saprotrophic fungal richness and salvage harvesting would decrease saprotrophic fungal richness were supported with statistically significant results. Additionally, NMS results showed that overall macrofungal community composition was significantly altered by tornado disturbance and subsequent salvage harvesting. Our sample size was too low to statistically test for compositional difference between treatments for saprotrophic and ECM fungal communities individually. Future studies will likely need to focus on individual groups and/or species for longer time periods to attain sufficient sample size, and to record the species-specific ecological trends necessary to further analyze and discuss compositional shifts in fungal communities following disturbance.

#### 4.3. Disturbance effects on ECM fungal community

Changes in ECM fungal communities following disturbance events largely result from three phenomena: changes in ECM fungal inoculum, shifts in the ECM plant host community, and perturbation to the soil

environment (Jones et al., 2003; Cowden and Peterson, 2013). These factors were likely affected by tornado and salvage harvesting disturbances, resulting in the observed alterations to the ECM fungal community. The tornado induced mortality of mature ECM-associating trees likely reduced ECM fungal inoculum in the form of hyphae attached to live roots, causing the slight decrease in ECM species richness documented in tornado disturbed areas. Of the 16 species documented in tornado disturbed areas, nine were found in undisturbed areas. Many of these ECM species were likely able to survive the death of mature host trees by colonizing regenerating ECM-associating trees (i.e. saplings), either through propagules that survived in the soil or propagule dispersal from the surrounding environment. The compositional shift of ECM-associating vegetation, largely from mature *Pinus* to regenerating *Quercus*, also likely has implications for the compositional patterns documented in the ECM fungal community. Host specificity of ECM fungi varies among species, and can be impacted by several biotic and abiotic factors (Molina et al., 1992; Bruns et al., 2002a). Thus, documentation of species or genera specific ECM associations in the region should be a point of future research to better understand how vegetation shifts following disturbance impact ECM fungal communities, and how shifts in the ECM fungal community influence patterns of development in the vegetation community.

Salvage harvested areas hosted the lowest ECM fungal species richness and lower levels of abundance for many of the species co-occupying other treatments. This result lends support to our second hypothesis that salvage harvesting would further reduce ECM species richness, although the result was not statistically significant. The reduction of ECM fungal richness and abundance in salvage harvested areas was likely caused by a combination of ECM-associating tree mortality and soil perturbations. Although soil characteristics were not quantified in this study, inferences can be made on how ECM communities were impacted by changes to the soil environment. Canopy cover was significantly reduced in tornado and salvage disturbed areas. This significant canopy removal increased soil exposure to full sunlight, likely increasing soil temperatures, and decreasing soil moisture. These effects were potentially greater in the salvage harvested treatment, as higher sapling density in the tornado treatment allowed less direct sunlight to reach soils in these areas. The formation of ECM relationships can be hindered by high soil temperatures (Parke et al., 1983), and thus negatively impact overall ECM species richness and abundance until closed canopy conditions return. Additionally, topsoil removal and signs of soil compaction were more prevalent in salvage harvested areas. Soil perturbations such as these are commonly associated with salvage harvesting operations (Lindenmayer and Noss, 2006). These types of soil disturbances can limit ECM-associating plant growth (Kozłowski, 1999), and limit ECM fungal establishment directly by

Table 3

Macrofungal species and subplot level occurrences per treatment documented in the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Asterisks indicate ectomycorrhizal species.

Species	Und	Tor	Salv
<i>Agaricus pocillator</i> Murrill	0	1	0
<i>Amanita brunnescens</i> G.F. Atk. *	0	1	1
<i>Amanita ceciliae</i> (Berk. & Broome) Bas *	1	0	0
<i>Amanita citrina</i> Pers. *	0	15	6
<i>Amanita cokeri</i> E.-J. Gilbert & Kühner *	1	1	0
<i>Amanita longipes</i> Bas *	0	1	0
<i>Amanita rubescens</i> Pers. *	2	0	0
<i>Amanita spreta</i> (Peck) Sacc. *	2	4	1
<i>Amanita virosa</i> Bertill. *	0	0	1
<i>Amanita volvata</i> (Peck) Lloyd *	1	0	0
<i>Arachnion album</i> Schwein.	0	1	0
<i>Arrhenia epichysium</i> (Pers.)	0	1	0
<i>Aureoboletus auriporus</i> (Peck) Pouzar *	1	0	0
<i>Auricularia auricula</i> (Bull.) Quéf.	0	1	0
<i>Bovista acuminata</i> (Bosc) Kreisel	0	1	0
<i>Callistosporium luteo-olivaceum</i> (Berk. & M.A. Curtis)	0	2	0
<i>Cantharellus cibarius</i> Fr. *	7	0	0
<i>Cantharellus cinnabarinus</i> (Schwein.) Schwein. *	7	0	0
<i>Cerrena unicolor</i> (Bull.) Murrill	0	19	10
<i>Chalciporus pseudorubrinellus</i> (A.H. Sm. & Thiers) *	1	0	0
<i>Coprinopsis cinerea</i> (Schaeff.)	0	3	0
<i>Cortinarius</i> sp. *	1	0	0
<i>Cortinarius</i> sp. 2 *	1	0	0
<i>Crepidotus mollis</i> (Schaeff.) Staudé	1	1	0
<i>Dacryopinax spathularia</i> (Schwein.) G.W. Martin	1	17	4
<i>Daedaleopsis confragosa</i> (Bolton) J. Schröt.	0	6	1
<i>Daldinia concentrica</i> (Bolton) Ces. & De Not.	0	1	0
<i>Entoloma vernum</i> S. Lundell	0	0	5
<i>Fomes fasciatus</i> (Sw.) Cooke	0	3	4
<i>Ganoderma curtisii</i> (Berk.) Murrill	1	4	2
<i>Ganoderma lucidum</i> (Curtis) P. Karst.	1	0	0
<i>Geastrum floriforme</i> Vittad.	0	3	1
<i>Gloeophyllum sepiarium</i> (Wulfen) P. Karst.	0	1	1
<i>Gymnopilus penetrans</i> (Fr.) Murrill	0	1	0
<i>Gymnopilus dryophilus</i> (Bull.) Murrill	1	3	21
<i>Gymnopilus foetidus</i> (Sowerby) P.M. Kirk	0	3	0
<i>Gymnopilus perforans</i> (Hoffm.) Antonín & Noordel.	1	0	0
<i>Hemileccinum subglabripes</i> (Peck) Halling *	1	0	0
<i>Hohenbuehelia petaloides</i> (Bull.) Schulzer	0	3	0
<i>Hymenopeziza megalospora</i> (Clem.) R.H. Petersen	0	1	0
<i>Inocybe</i> sp.	0	0	1
<i>Laccaria laccata</i> (Scop.) Cooke *	2	2	0
<i>Lactarius camphoratus</i> (Bull.) Fr. *	13	4	2
<i>Lactarius deceptivus</i> Peck *	2	0	0
<i>Lactarius</i> sp. *	1	0	0
<i>Leccinellum albellum</i> (Peck) Bresinsky & Manfr. Binder *	1	0	0
<i>Leccinum roseoscabrum</i> Singer & R. Williams *	1	1	3
<i>Lentinus arcularius</i> (Batsch) Zmitr.	0	2	0
<i>Lentinus crinitus</i> (L.) Fr.	0	5	0
<i>Leucocoprinus cepitipes</i> (Sowerby) Pat.	0	5	0
<i>Leucocoprinus fragilissimus</i> (Ravenel ex Berk. & M.A. Curtis) Pat.	0	1	1
<i>Lycoperdon marginatum</i> Vittad.	0	1	0
<i>Marasmius pulcherripes</i> Peck	0	2	0
<i>Marasmius</i> sp.	0	40	20
<i>Mycena leptcephala</i> (Pers.) Gillet	2	0	0
<i>Mycena</i> sp.	0	0	3
<i>Mycena</i> sp. 2	0	1	0
<i>Mycena</i> sp. 3	0	1	0
<i>Panus rudis</i> Fr.	0	1	0
<i>Phellinus gilvus</i> (Schwein.) Pat.	2	2	0
<i>Pholiota polychroa</i> (Berk.) A.H. Sm. & H.J. Brodie	1	1	0
<i>Pisolithus arhizus</i> (Scop.) Rauschert *	0	12	1
<i>Pleurotus dryinus</i> (Pers.) P. Kumm.	0	0	1
<i>Pluteus cervinus</i> (Schaeff.) P. Kumm.	0	3	2
<i>Pluteus leoninus</i> (Schaeff.) P. Kumm.	0	1	0
<i>Psathyrella umbonata</i> (Peck) A.H. Sm.	0	1	0
<i>Pulveroboletus ravenelii</i> (Berk. & M.A. Curtis) Murrill *	6	8	4
<i>Retiboletus ornatipes</i> Manfr. Binder & Bresinsky *	3	11	4
<i>Russula perlactea</i> Murrill *	0	1	0
<i>Russula silvicola</i> Shaffer *	1	2	0
<i>Russula</i> sp. *	0	2	0
<i>Schizophyllum commune</i> Fr.	3	8	7

Table 3 (continued)

Species	Und	Tor	Salv
<i>Stereum ostrea</i> (Blume & T. Nees) Fr.	4	19	9
<i>Strobilomyces strobilaceus</i> (Scop.) Berk. *	0	1	0
<i>Suillus decipiens</i> (Peck) Kuntze *	3	0	0
<i>Thelephora</i> sp. *	0	0	1
<i>Trametes elegans</i> (Spreng.) Fr.	0	15	0
<i>Trametes versicolor</i> (L.) Lloyd	2	5	5
<i>Trichaptum abietinum</i> (Dicks.) Ryvarden	8	10	13
<i>Trichaptum bifforme</i> (Fr.) Ryvarden	8	14	1
<i>Tricholomopsis decora</i> (Fr.) Singer	0	1	0
<i>Tricholomopsis formosa</i> (Murrill) Singer	1	1	2
<i>Tylopilus rhoadsiae</i> (Murrill) Murrill *	15	3	8
<i>Xylaria hypoxylon</i> (L.) Grev.	2	2	1

damaging or removing fungal propagules (i.e. hyphae, sclerotia, and spores) that survived the effects of tornado disturbance (Brundrett, 1991).

Several ECM genera that are often considered early successional such as *Inocybe*, *Pisolithus*, *Laccaria*, and *Thelephora* (Miller, 1987; Visser, 1995; Nara, 2006) were documented in disturbed areas. Two members of the genus *Cantharellus* were indicator species of undisturbed areas, indicating that these species have a propensity for mature forest and are not able to withstand the effects of catastrophic wind disturbance. ECM species in the genus *Amanita* are often considered late-successional (Bruns et al., 2002b; Dove and Keeton, 2015; Craig et al., 2016), however, of the nine *Amanita* species documented in this study, eight occurred in disturbed areas. These findings highlight the need for greater understanding of species-specific life history traits in specific biophysical settings, and the need to carefully consider the use of broad ecological generalizations based on family or genera level classification. Without extensive knowledge of species-specific life history traits, it remains difficult to assess the factors causing compositional shifts in these systems following disturbance.

#### 4.4. Disturbance effects on saprotrophic fungal community

Our hypotheses that tornado disturbance would increase saprotrophic species richness, and subsequent salvage harvesting would decrease saprotrophic species richness were strongly supported by the results. The volume and density of substrate for saprotrophic fungi were altered by both tornado and salvage harvesting disturbances, resulting in the distinct compositional patterns across the three treatments. Most saprotrophic species were saproxylic. Therefore, the increase in woody substrates following the tornado, and subsequent decrease in woody substrates through salvage harvesting, likely had the most direct effect on saprotrophic species richness and abundance. One exception was documented in the fruiting patterns of saproxylic species on FWD. Tornado and salvage harvested plots contained similar amounts of FWD, yet fruiting occurrences on FWD were more prevalent in the tornado treatment. This may be related to the significant reduction in sapling density of the salvage harvested treatment compared to the tornado treatment. Soils in the tornado treatment were less exposed to direct sunlight because of higher sapling density. Thus, FWD resting on soils in the tornado treatment may have experienced more humid microclimates and less extreme temperature fluctuation, creating more stable habitat conditions, and promoting macrofungal activity. These microclimatic effects would be more apparent in macrofungal fruiting patterns on FWD, as smaller deadwood pieces dry more quickly than larger deadwood pieces.

Patterns of saproxylic species richness and fruiting occurrences on larger woody pieces closely resembled patterns of substrate density classified by decay class, diameter class, and mode of death throughout the study site. Decay class II, smaller diameter classes, and log mode of death characterized most of the available substrate, and had the highest number of saproxylic fruiting occurrences. Contrary to this pattern,

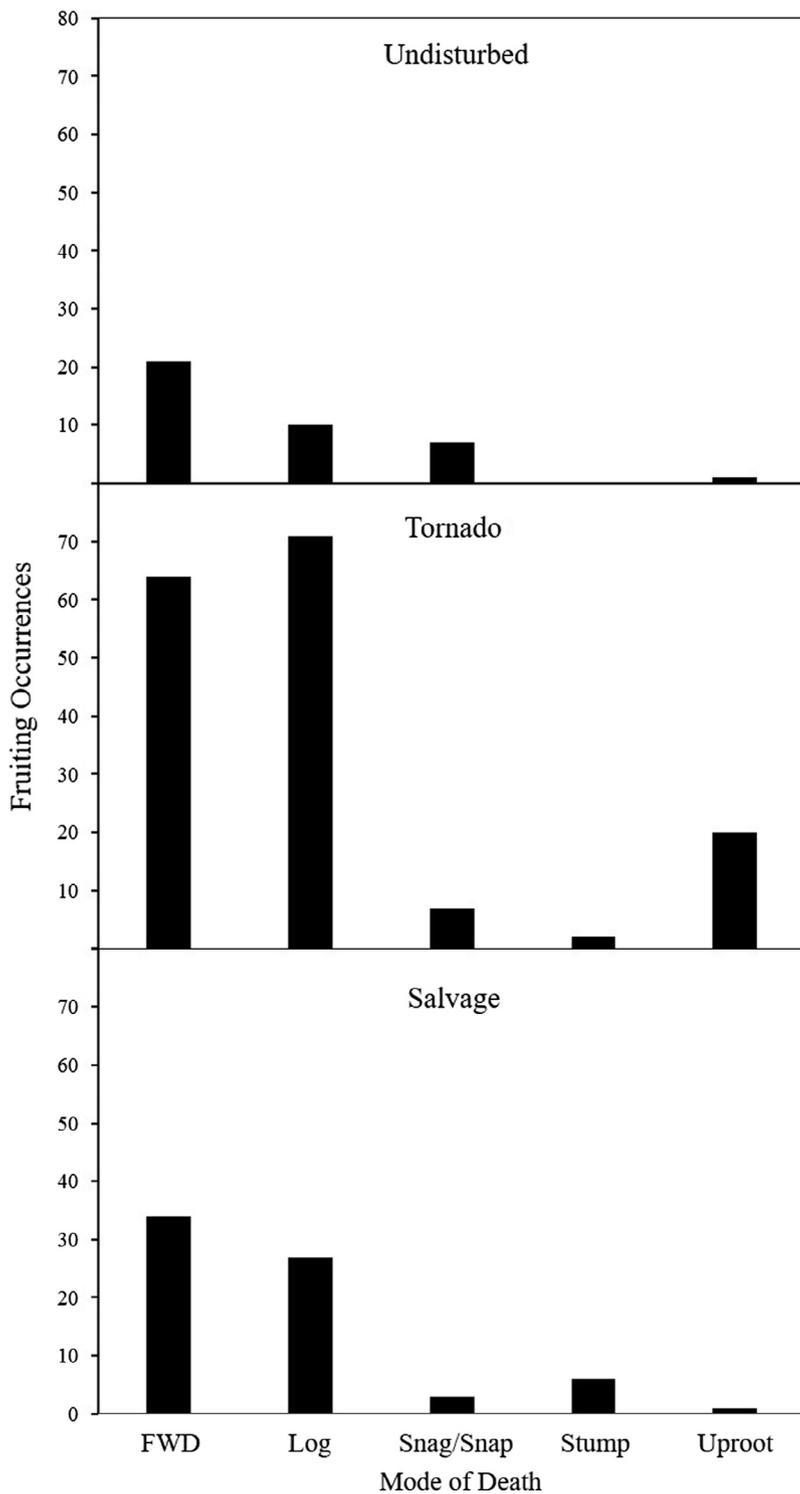


Fig. 5. Mode of death distribution for substrates documented with saproxylic macrofungal fruiting occurrences in the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Modes of death include FWD (woody pieces < 10 cm diameter), logs (woody pieces ≥ 10 cm diameter without root plates), snag/snaps (standing dead trees ≥ 10 cm dbh with or without crown intact), stumps (standing dead trees or uproots ≥ 10 cm diameter snapped or cut below 1.37 m from root plate), and uproots (woody pieces ≥ 10 cm diameter with root plates intact).

hardwood substrates hosted substantially more species and fruiting occurrences than *Pinus* substrates, despite higher levels of *Pinus* deadwood density and volume in all three treatments. *Pinus* wood typically decays slower than hardwood in comparable settings (Weedon et al., 2009), and hosts less fungal biomass in the initial stages of decay (Noll et al., 2016). As *Pinus* deadwood enters more advanced stages of decay, saprotrophic species richness and abundance will likely increase in the study site, particularly in tornado-disturbed areas which hosted significantly higher volume of *Pinus*-composed deadwood. Future studies may follow the deadwood dynamics of the system, as the onset of advanced decay will likely exacerbate differences in deadwood structural

legacies and saproxylic fungal communities between treatments.

### 5. Conclusion

Although macrofungal studies utilizing single year fruiting body surveys likely underestimate true diversity and abundance, the results provide broad patterns of treatment effects on macrofungal communities from which to draw management recommendations (Oria-de-Rueda et al., 2010; Dove and Keeton, 2015; Dejene et al., 2017). Another limitation of our study is the lack of pre-disturbance data. We utilized a space for time substitution under the assumption that all areas

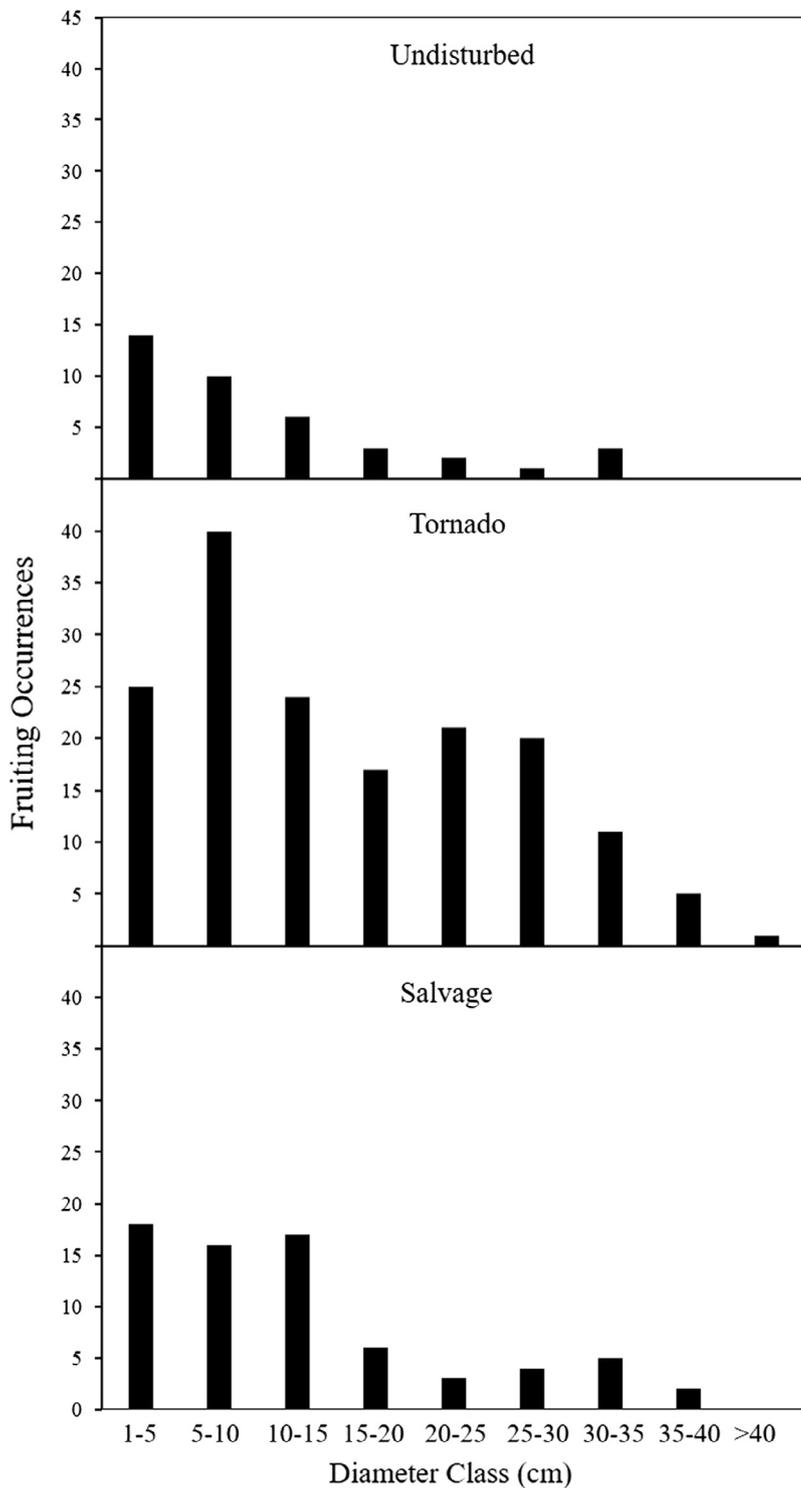


Fig. 6. Diameter class distribution of substrates documented with saproxylic macrofungal fruiting occurrences in the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA.

were similar in forest composition and structure prior to the 2011 tornado. A combination of ground reconnaissance, historical satellite data, and USDA data was used to ensure that differences between pre-disturbance conditions of each treatment were as limited as possible. Thus, we are confident that the patterns documented in our study resulted from the disturbances and not variation in pre-disturbance conditions. In addition to providing broad ecological patterns and management recommendations, the results also provide a preliminary species inventory from a region and ecosystem type with a paucity of macrofungal community information.

The tornado event documented in this study exemplified

catastrophic disturbance, as nearly all live tree basal area was removed from impacted areas. The results indicate that catastrophic wind events have the capacity to increase richness and abundance of saprotrophic fungi without drastically reducing ECM fungal richness and fruiting abundance in these systems. This indicates that natural disturbance is important for maintaining macrofungal diversity (Bruns, 1995; Bässler and Müller, 2010; Craig, et al., 2016). Other studies that considered the effects of emulated natural canopy disturbance on macrofungal communities have reached similar conclusions (Brazee et al., 2012; Dove and Keeton, 2015), although the treatments documented in these studies featured much smaller levels of canopy removal. The level of

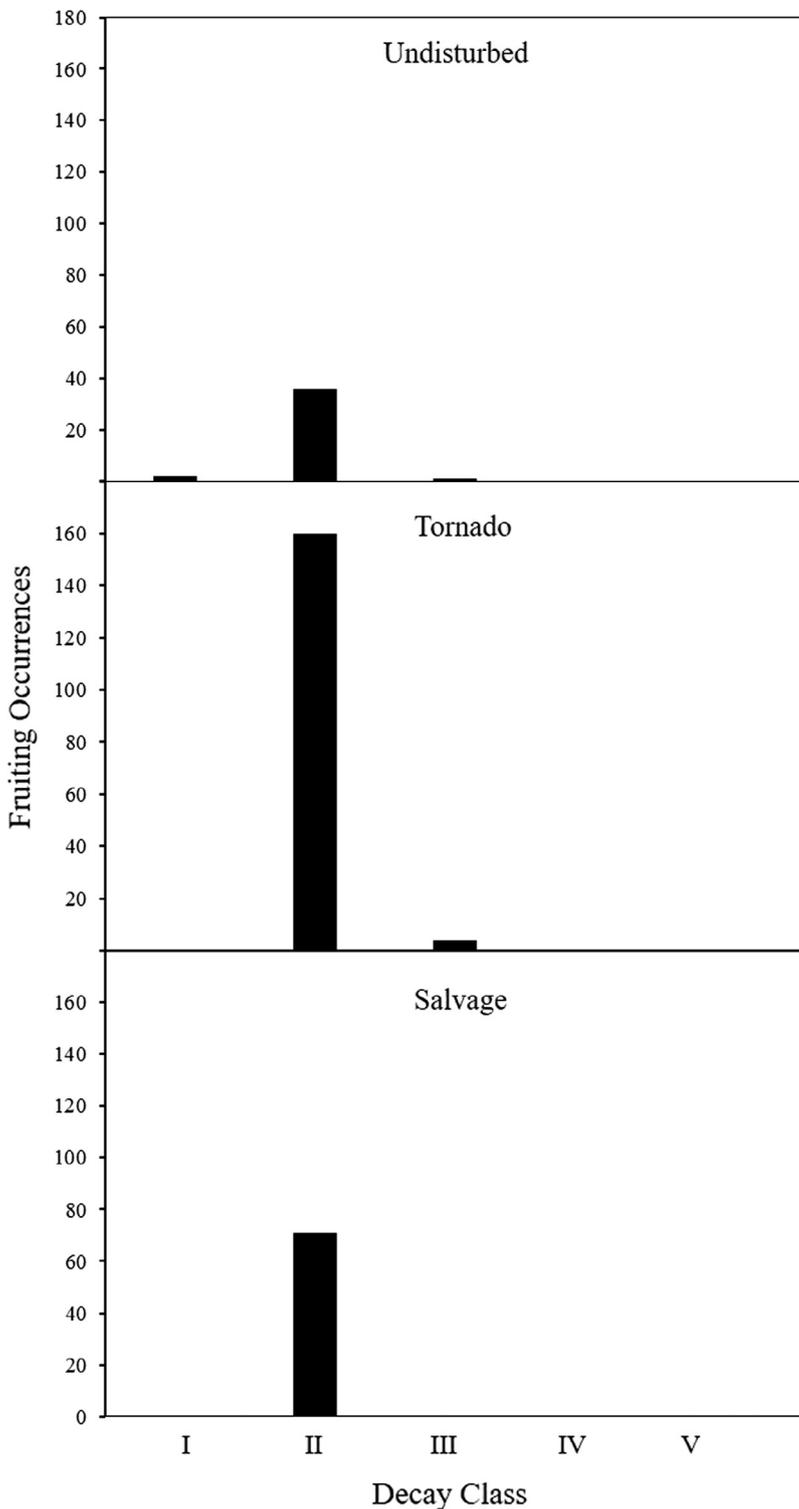
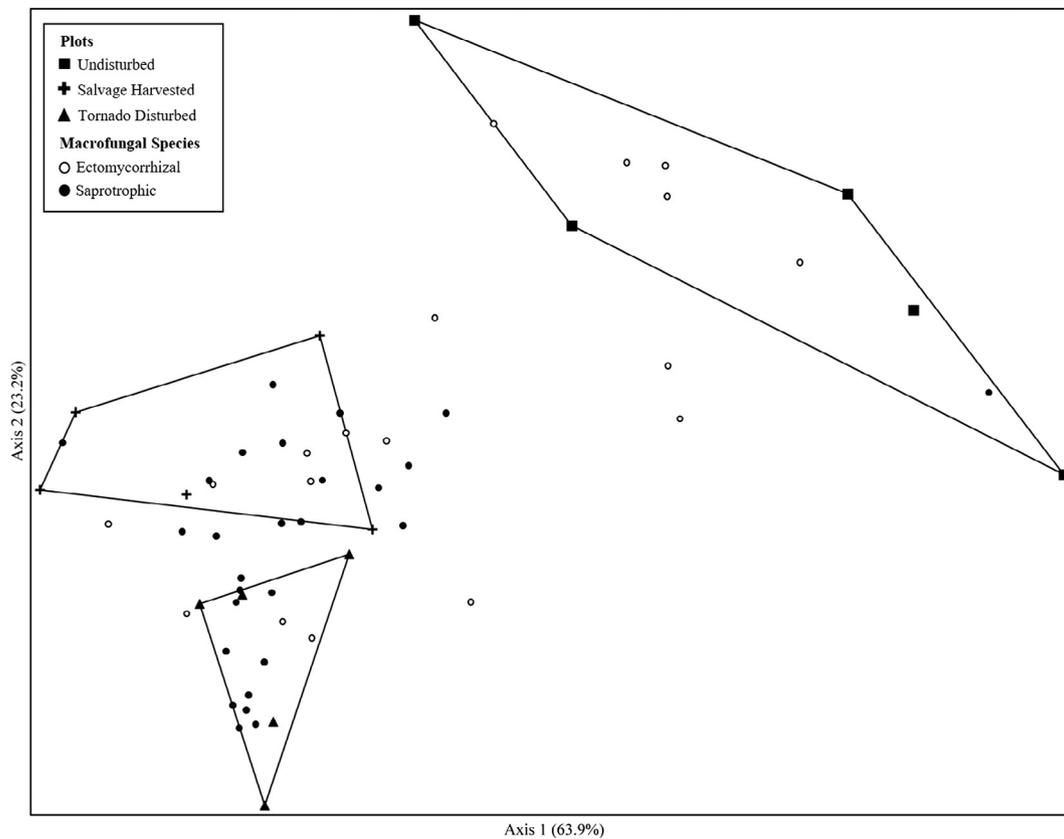


Fig. 7. Decay class distribution of substrates documented with saproxylic macrofungal fruiting occurrences in the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Decay classes follow the guidelines of the USFS FIA (2005).

canopy removal documented in this study resembles clearcut harvesting, which has often been implicated in decreasing ECM fungal richness and abundance (Hagerman et al., 2001; Jones et al., 2003; Luoma et al., 2004; Durall et al., 2006; Simard, 2009). Thus, the effects of clearcut harvesting systems on macrofungal communities may not be analogous to those of natural catastrophic disturbance, likely because clearcut harvesting can cause soil perturbations and does not leave extensive amounts of deadwood on site. Assessing the differences between natural disturbance and emulated disturbance should be a point of future research, to ensure that macrofungal communities and their

associated ecosystem functions are not considerably altered by management practices designed to emulate natural ecological processes.

The results of this study indicate that salvage harvesting following catastrophic disturbance reduces both saprotrophic and ECM fungal richness and fruiting abundance. Because of the short-term nature of our study, care must be taken when interpreting these results. Future studies will be needed to assess the continued development of fungal communities across the treatments, and whether or not the differences documented in this study are only short lived. Accordingly, short-term studies on salvage harvesting have been shown to overestimate



**Fig. 8.** Non-metric multidimensional scaling ordination summarizing variation in macrofungal community at the plot level (stress = 12.89; cumulative  $r^2 = 87.1\%$ ) in the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Sørensen (Bray-Curtis) distance measure was used to measure dissimilarity in composition between plots. Squares represent undisturbed plots, triangles represent tornado disturbed plots, and plus signs represent salvage harvested plots. Convex hulls connect plots of the same treatment. Hollow circles represent ectomycorrhizal fungal species. Black circles represent saprotrophic fungal species.

**Table 4**

Results of indicator species analysis, showing indicator values for all significant indicators ( $p < .05$ ) by treatment in the Oakmulgee Ranger District of the Talladega National Forest, Alabama, USA. Indicator values range from 0 to 100 with 0 giving no indication of a treatment and 100 giving perfect indication. Asterisks indicate ectomycorrhizal species.

Species	Indicator value			p
	Undisturbed	Tornado	Salvage	
<i>C. cibarius</i> *	100	–	–	0.001
<i>C. cinnabarinus</i> *	80	–	–	0.010
<i>C. unicolor</i>	–	61	–	0.014
<i>D. confragosa</i>	–	67	–	0.037
<i>D. spathularia</i>	–	69	–	0.005
<i>G. dryophilous</i>	–	–	75	0.008
<i>L. crinitus</i>	–	80	–	0.009
<i>Marasmius</i> sp.	–	57	–	0.003
<i>P. arhizus</i> *	–	70	–	0.013
<i>R. ornaticipes</i> *	–	51	–	0.011
<i>T. biforme</i>	–	100	–	0.016
<i>T. elegans</i>	–	80	–	0.012

negative impacts on ecosystem health (Royo et al., 2016). However, if distinct fungal communities do persist throughout the development of these stands, they may affect long-term ecosystem composition and functioning. For example, the reduction of ECM and saprotrophic fungal abundance and diversity will likely have major implications for nutrient distribution throughout the system, potentially shifting the competitive outcomes and successional trajectories of plant communities.

For managers wishing to maintain macrofungal diversity and associated ecosystem functions in early developmental stages, it may be beneficial to limit access or restrict salvage harvesting operations from

some portions of the disturbed areas. Unsalvaged patches would be protected from direct soil perturbation and removal of structural legacies such as deadwood would be limited, thereby maintaining more optimal habitat conditions for macrofungal communities. Areas that are salvage harvested should attempt to limit soil perturbation and retain as much woody debris as possible, given the specific management objectives. This includes leaving slash and other unmarketable woody materials throughout the site, using harvesting equipment fitted with high flotation rubber tires or tracks, and conducting operations when soils are dry or frozen in applicable climates.

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