EFFECTS OF WIND DISTURBANCE AND SALVAGE HARVESTING ON ECTOMYCORRHIZAL AND SAPROTROPHIC MACROFUNGI IN A PINE WOODLAND

by

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ABSTRACT

Natural disturbances alter the biophysical conditions of ecosystems, influencing patterns of structure, composition, and successional dynamics. These disturbances often create structural legacies that promote biodiversity and ecosystem function. 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, some stands were subject to salvage harvesting. In 2016, I 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. Within each treatment, 20 0.04 ha fixed radius plots were established to collect forest inventory data. Additionally, five 10 x 100 m plots were established in each treatment and inventoried for macrofungal sporocarps between May and November 2016. Throughout the sample period, 546 occurrences of 84 macrofungal species were recorded. Tornado disturbed plots hosted the highest macrofungal species richness overall. Undisturbed plots hosted the highest species richness for ectomycorrhizal macrofungi. Salvage harvested plots 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.

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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). For example, natural disturbances can increase habitat heterogeneity and niche space through the creation of structural legacies (Franklin et al., 2000). In forest ecosystems, natural disturbances can result in structural legacies such as increased volume of deadwood, reduced live tree density, and complex vertical stratification of foliage among others. These structural legacies provide new growth substrate and alter light regimes that are important for the maintenance of certain species. Thus, natural disturbances are important for maintaining biodiversity in forest ecosystems (Hansen et al., 1991).

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 surrounding the use of salvage harvesting.

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). To date, no study has considered the effects of salvage harvesting on fungi despite their vital importance to ecosystem function. In forest ecosystems, ectomycorrhizal (ECM) fungi form symbioses with many woody plant species, enhancing nutrient and water uptake for plants in exchange for photosynthate, thereby affecting growth rates and competition between individuals (Courty et al. 2010). Networks of mycorrhizal fungi may also form plant-to-plant connections. In this way, carbon, nutrients, and water can flow between plants, resulting in major implications for establishment, competition, diversity, and successional dynamics within plant communities (van der Heijden and Horton, 2009; Simard et al., 2012). In temperate forests of the Northern Hemisphere, ecologically and commercially important genera such as *Pinus* and *Quercus* are known to associate with ECM fungi (Molina et al., 1992).

Saprotrophic fungi are also vital components of forest ecosystems because they decompose dead organic matter, and redistribute nutrients throughout the ecosystem (Boddy and Watkinson, 1995). Saproxylic species are the main decomposers of wood in many forest ecosystems as they are more adept than bacteria at decomposing recalcitrant materials such as lignin (van der Wal et al., 2013). Furthermore, these species are often considered ecosystem engineers as various wood inhabiting organisms require partially decomposed substrates (Lonsdale et al., 2008).

Many ECM and saprotrophic fungal species are classified as macrofungi (Mueller et al., 2007). Although a polyphyletic classification taxonomically, macrofungi are often considered a group when conducting ecological surveys because of similar sampling requirements and ecological functions (Mueller et al., 2004). These species are characterized by the production of large visible sporocarps that can have both ecological and social importance. The main function of the fungal sporocarp is to create and disperse sexually derived propagules of the fungus. Thus, sporocarp production is important for promoting genetic variation and dispersal of the species. Additionally, many insects, gastropods, and mammals, including humans, use macrofungal sporocarps as a food source (Fogel and Trappe, 1978; Hanski, 1989). In some regions human consumption can be financially and/or culturally important (Christensen et al., 2008; Cai et al., 2011; Tibuhwa, 2013; Schulp et al. 2014).

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. The specific objectives were to: 1) quantify differences in species composition and stand structure between undisturbed, tornado disturbed, and salvage harvested stands, 2) quantify macrofungal species composition and diversity 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.

METHODS

Study site

The study took place on the Oakmulgee Ranger District of the Talladega National Forest in Bibb County Alabama, USA. 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). Specific 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 of 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 timber sale team. 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, USFS inventory data, and ground reconnaissance. Treatment sites were selected on the likelihood of similar pre-disturbance condition, including similarities in soil type, stand age, and species composition. 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.

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). Plots were established in a systematic grid pattern along the cardinal azimuths, with 25 m spacing between plots to ensure adequate spatial coverage throughout the study sites. Within each plot, live trees ≥ 5 cm at diameter breast height (dbh, 1.37 m above ground) were measured for dbh and recorded to species. Saplings (woody stems ≥ 1 m in height and < 5 cm diameter) were tallied by species in each plot.

CWD (woody pieces ≥ 10 cm diameter and lying ≤ 45º 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 (FIA, 2005). Decay class I stems had sound wood with intact bark. Decay class II stems were mostly intact, but had partially rotten sapwood and peeling bark. Decay class III stems had sound heartwood, but rotten sapwood that was breakable by hand. Decay class IV stems had rotten heartwood that could not support its own weight, but maintained shape. Decay class V stems no longer maintained shape and were spread out on the ground. Snags (standing dead trees ≥ 10 cm dbh with crowns largely intact), snaps (standing dead trees ≥ 10 cm dbh without crown intact), and stumps (standing dead tree ≥ 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 pine or hardwood.

Fine woody debris (FWD), and litter cover were sampled by placing a 1 x 1 m subplot at the center of each plot and then moving it 3 times along the 0º, 120º, and 240º azimuths respectively for a total sampling of 10 m² per plot. Within each 1 m² transect, 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 (Barbour 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).

Macrofungal inventory

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 m² (10 x 100 m) plots were established (Arnolds, 1992; Mueller et al., 2004) and divided into 10 x 10 m subplots (Durall et al. 2006). Plots were subjectively placed with long axes running parallel to mid-slope position. Each plot was surveyed for fungal sporocarps from May 2016 through November 2016 to encompass the peak fruiting season. Hypogeous macrofungi were not considered as different sampling efforts are required to assess these species (Mueller, 2004). Plots were surveyed twice-monthly June through October and once in May and November. Species were noted for presence/absence based on sporocarp occurrence within each subplot. 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 using the following guides: Largent et al. (1977), Arora (1986), Gilbertson and Ryvarden (1986), Largent (1986), Lincoff, (1997), Bessette et al. (2000), Miller and Miller (2006), and Bessette (2007). All positive species identifications were cross-referenced with Index Fungorum (2017) for current species names.

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). 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.

Percent frequency of occurrence for all fungal species was calculated by tallying the number of plots in which a respective species occurred, and dividing by 450 (i.e., 50 subplots treatment^{-1} x 12 surveys) at the treatment level, and 120 (i.e., 10 subplots plot^{-1} x 12 surveys) at the plot level (Durall et al., 2006). These values were used to calculate diversity using the Shannon index:

$$H' = -\sum_{i=1} \left(\frac{n_i}{N}\right) \ln \left(\frac{n_i}{N}\right)$$

where *n* represents the percent frequency of occurrence of individual taxa, and *N* represents the sum of percent frequency of occurrence for all taxa (Durall et al., 2006).

To compare treatment effects on forest composition, structure, and fungal community attributes, one-way analysis of variance (ANOVA) was performed using SPSS 22.0 (IBM, Armonk, NY, USA). 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 ($p < 0.05$) 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 $\log_{10} +1$ 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 as rare species can increase the stress of NMS, despite contributing little to overall community composition (Marchant, 2002; 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 (Dufrêne and Legendre, 1997). This analysis calculates an indicator value (IV) by averaging the relative abundance of each species in each treatment by 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.

RESULTS

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 (≥ 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^{-1}) and basal area (16.21 m^2 ha^{-1}). Tornado and salvage treatments had basal areas of 1.09 m^2 ha^{-1} and 0.57 m^2 ha^{-1} respectively, and both had a tree density of 31.25 stems ha^{-1}. In total, 11 of the 17 species were ECM-associating species, belonging to the genera *Fagus*, *Pinus*, or *Quercus*. ECM species comprised 86% of stems in undisturbed, 92% in tornado, and 100% in salvage harvested treatments. ECM tree density per plot was significantly higher ($p < 0.001$) in undisturbed treatments (11.15 ± 0.92 SE stem ha^{-1}) compared to tornado (1.15 ± 0.30 SE stems ha^{-1}) and salvage (1.25 ± 0.57 SE stems ha^{-1}) treatments (Table 2).

Table 1. Density (stems ha^{-1}), relative density, dominance (m^2 ha^{-1}), 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. Asterisks indicate ectomycorrhizal species.

Species	**Density (ha^{-1})**			**Relative Density (%)**			**Dominance (m^2 ha^{-1})**			**Relative Dominance (%)**			**Importance (%)**		
	UND	**TOR**	**SALV**	**UND**	**TOR**	**SALV**	**UND**	**TOR**	**SALV**	**UND**	**TOR**	**SALV**	**UND**	**TOR**	**SALV**
Pinus palustris *	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 Michaeux *	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**

Table 2. Measures of ectomycorrhizal tree density, ectomycorrhizal sapling density, litter cover, fine woody debris cover, and canopy cover by treatment in the Oakmulgee Ranger District, Talladega National Forest, Alabama. Per plot means are ± standard error. Means in rows followed by the same letter are not significantly different at $p < 0.05$.

Parameter	**Undisturbed**	**Tornado**	**Salvage**
Ectomycorrhizal tree density ha^{-1}	279	29	31
Ectomycorrhizal tree density $plot^{-1}$	11.15 ± 0.92 (a)	1.15 ± 0.30 (b)	1.25 ± 0.57 (b)
Ectomycorrhizal sapling density ha^{-1}	333	2788	1709
Ectomycorrhizal sapling density $plot^{-1}$	13.30 ± 3.21 (a)	111.50 ± 7.42 (b)	68.35 ± 10.32 (c)
Litter cover class $plot^{-1}$	5.55 ± 0.51 (a)	4.30 ± 0.73 (b)	3.95 ± 0.94 (b)
FWD cover class $plot^{-1}$	1.05 ± 0.22 (a)	1.40 ± 0.50 (b)	1.50 ± 0.51 (b)
Canopy cover (%) $plot^{-1}$	89.82 ± 0.90 (a)	14.26 ± 2.36 (b)	5.47 ± 1.63 (c)

Sapling species richness was 46, with 20 ECM associating species belonging to the genera *Carya*, *Castanea*, *Fagus*, *Pinus*, or *Quercus* (Table 3). ECM 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 sapling in undisturbed and salvaged plots, while *Quercus coccinea* was most abundant in tornado plots. The dominant tree species, *P. palustris*, represented just 0.89%, 0.44%, and 1.69% of saplings in undisturbed, tornado, and salvage treatments respectively. ECM sapling density was significantly higher ($p < 0.001$) in tornado disturbed plots (111.50 ± 7.42 SE) compared to salvage (68.35 ± 10.32 SE) and undisturbed plots (13.30 ± 3.21 SE), and also significantly higher ($p < 0.001$) in salvaged plots compared to undisturbed plots.

Table 3. Density (stems ha^{-1}) and relative density for all live woody stems < 5 cm dbh and ≥ 1 m in height measured by treatment in the Oakmulgee Ranger District, Talladega National Forest, Alabama. Asterisks indicate ectomycorrhizal species.

Species	**Sapling stem density (stems ha^{-1})**			**Sapling stem relative density (%)**		
	UND	**TOR**	**SALV**	**UND**	**TOR**	**SALV**
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 Willdenov	-	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**

Mean forest floor litter cover per plot was higher ($p < 0.05$) in undisturbed plots (5.55 ± 0.11 SE mean cover class) compared to tornado (4.30 ± 0.16 SE mean cover class) and salvaged plots (3.95 ± 0.21 SE mean cover class). Mean FWD cover per plot was higher ($p < 0.05$) in tornado (1.40 ± 0.11 SE mean cover class) and salvaged plots (1.50 ± 0.11 SE mean cover class) compared to undisturbed plots (1.05 ± 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 ($p < 0.01$) in the undisturbed treatment (89.82% ± 0.90 SE) compared to both tornado and salvage treatments. Tornado plots had significantly higher ($p < 0.01$) canopy coverage (14.26% ± 2.36 SE) compared to salvage plots (5.47% ± 1.63 SE).

CWD density and volume were significantly higher ($p < 0.001$) in tornado plots (15.70 ± 0.85 SE pieces $plot^{-1}$; 7.16 ± 0.92 SE m^3 $plot^{-1}$) compared to undisturbed plots (2.85 ± 0.62 SE pieces $plot^{-1}$; 0.23 ± 0.10 SE m^3 $plot^{-1}$) and salvage plots (11.30 ± 0.99 SE pieces $plot^{-1}$; 0.79 ± 0.10 SE m^3 $plot^{-1}$) (Table 4). Salvage plots had significantly higher ($p < 0.001$) CWD density compared to undisturbed plots, but similar CWD volume. Pine CWD volume and density were greater than hardwood CWD volume and density in all treatments. Logs were the most common deadwood mode of death across all three treatments (Figure 1). 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 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 (Figure 2). Overall, 81% ($n = 663$) of CWD, snag/snaps, and stumps were classified as decay class II (Figure 3). 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. No deadwood pieces in the study site were classified in decay class V.

Table 4. Measures of coarse woody debris volume and density by treatment in the Oakmulgee Ranger District, Talladega National Forest, Alabama. Per plot means are ± standard error. Means in rows followed by the same letter are not significantly different at $p < 0.001$.

Parameter	Undisturbed	Tornado	Salvage
CWD density ha $^{-1}$	71	393	283
CWD density plot^{-1}	2.85 ± 0.62 (a)	15.70 ± 0.85 (b)	11.30 ± 0.99 (c)
Hardwood CWD density ha $^{-1}$	19	156	61
Hardwood CWD density plot^{-1}	0.75 ± 0.30 (a)	6.25 ± 0.70 (b)	2.45 ± 0.44 (c)
Pine CWD density ha $^{-1}$	52	237	222
Pine CWD density plot^{-1}	1.88 ± 0.46 (a)	9.45 ± 1.05 (b)	8.85 ± 0.96 (b)
CWD volume (m^3) ha $^{-1}$	5.67	179.00	19.86
CWD volume (m^3) plot^{-1}	0.23 ± 0.10 (a)	7.16 ± 0.92 (b)	0.79 ± 0.10 (a)
Hardwood CWD volume (m^3) ha $^{-1}$	0.49	31.54	4.23
Hardwood CWD volume (m^3) plot^{-1}	0.02 ± 0.01 (a)	1.26 ± 0.31 (b)	0.17 ± 0.05 (c)
Pine CWD volume (m^3) ha $^{-1}$	5.18	147.48	15.64
Pine CWD volume (m^3) plot^{-1}	0.21 ± 0.10 (a)	5.90 ± 0.93 (b)	0.63 ± 0.10 (c)

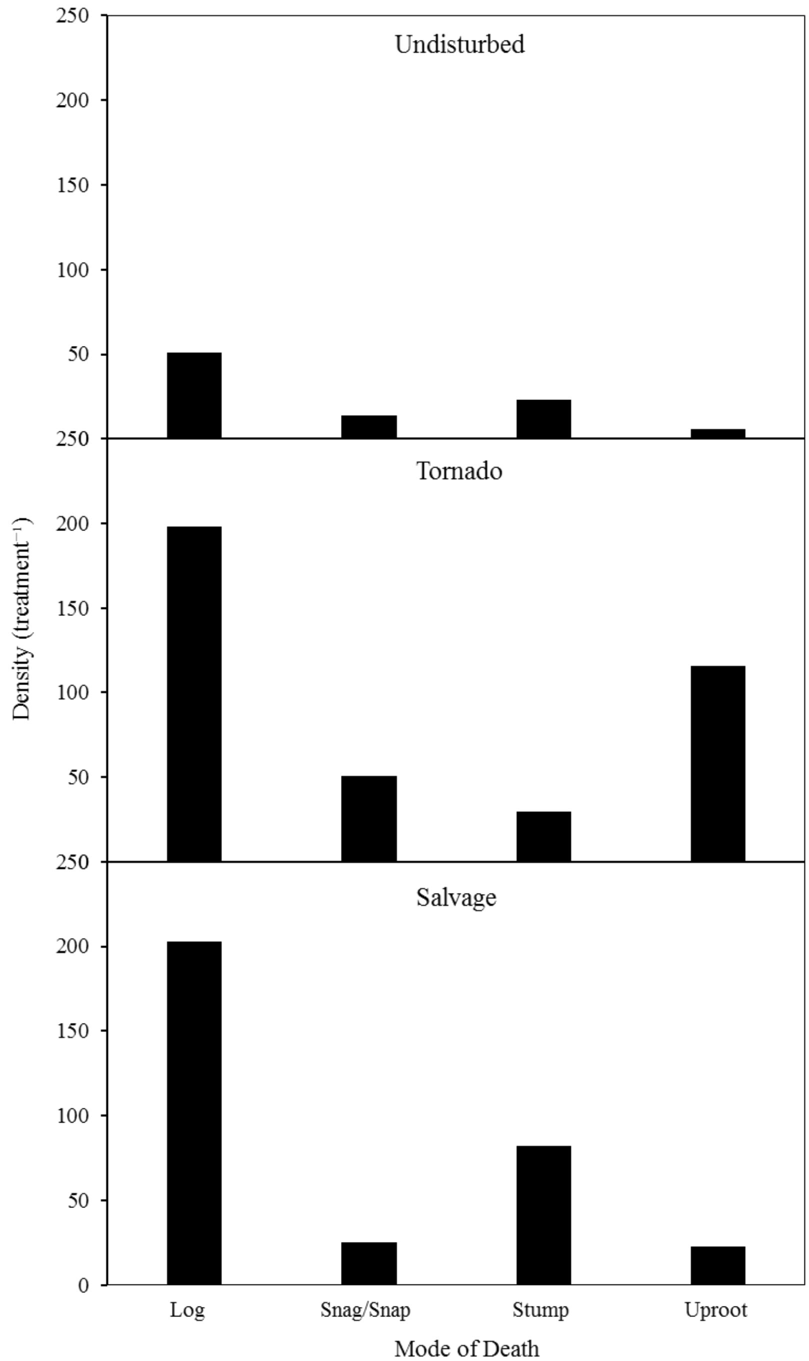

Figure 1. Density of logs (woody pieces ≥ 10 cm diameter without root plates), snag/snaps (standing dead trees ≥ 10 cm dbh with or without crown intact), stumps (standing dead trees or uproots ≥ 10 cm diameter snapped or cut below 1.37 m from root plate), and uproots (woody pieces ≥ 10 cm diameter with root plates intact) per treatment in the Oakmulgee Ranger District, Talladega National Forest, Alabama.

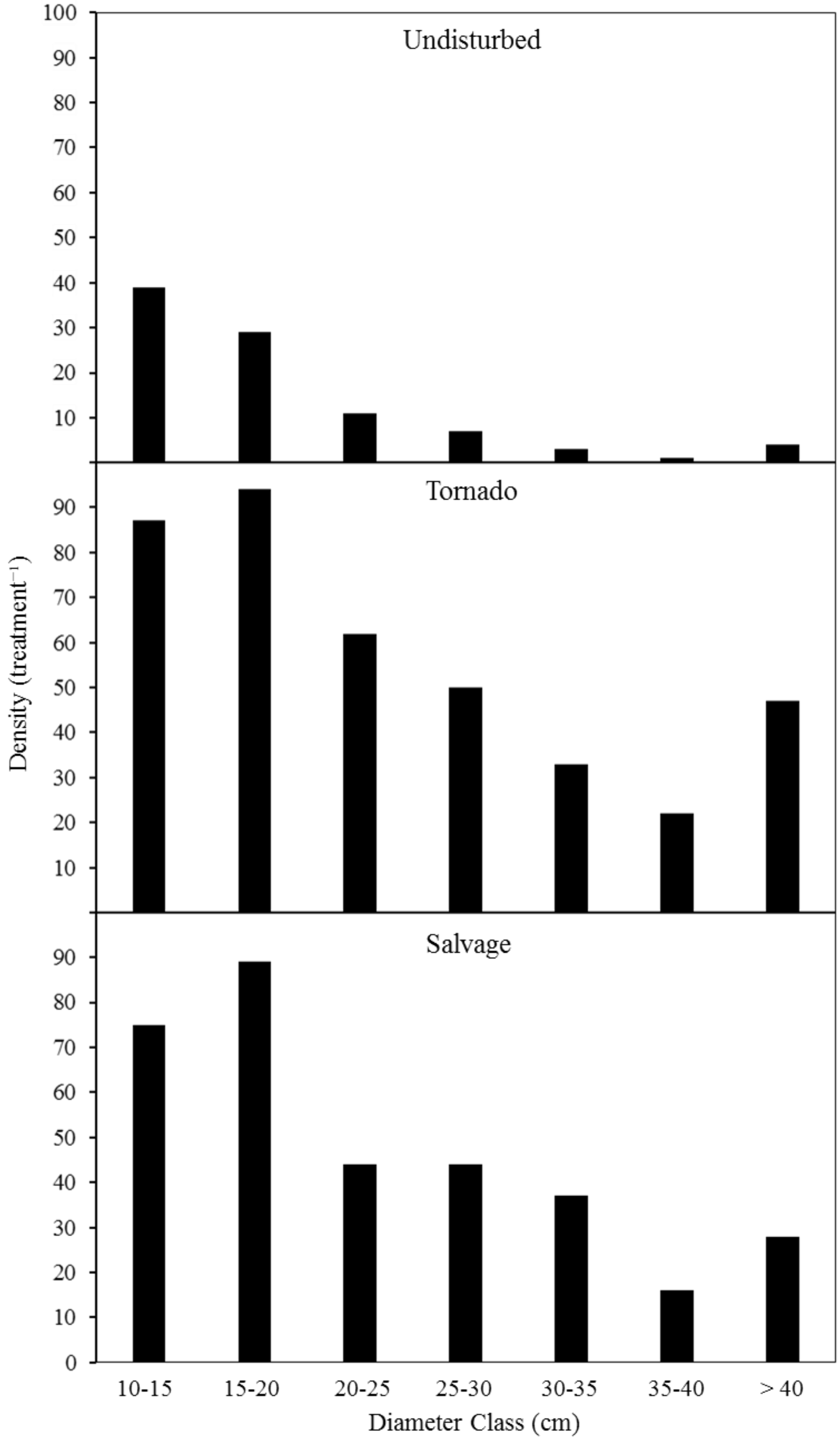

Figure 2. Diameter class distribution of woody pieces ≥ 10 cm diameter by treatment in the Oakmulgee Ranger District, Talladega National Forest, Alabama.

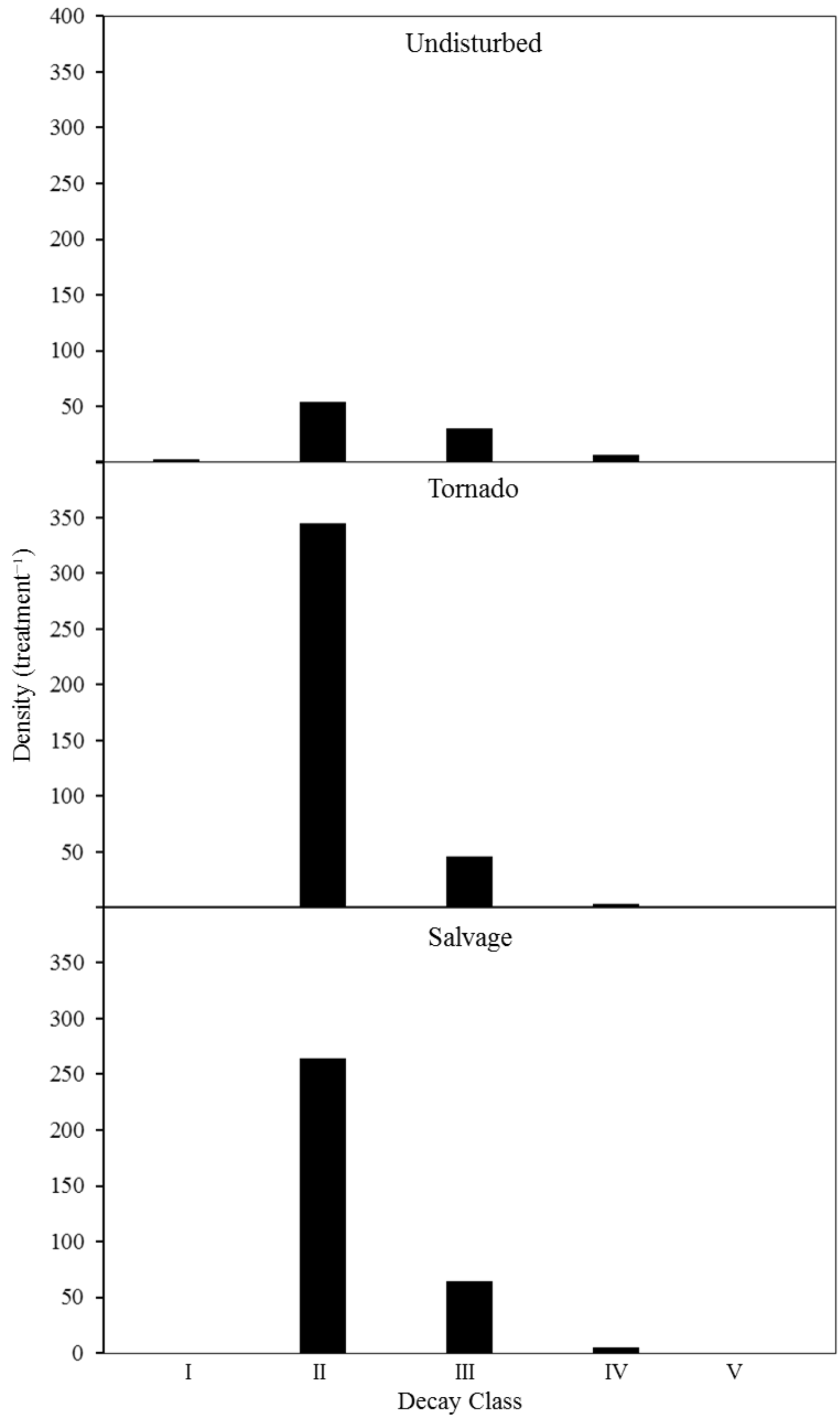

Figure 3. Density of woody pieces ≥ 10 cm diameter by decay class per treatment in the Oakmulgee Ranger District, Talladega National Forest, Alabama. Decay classes follow the guidelines of the USFS FIA (2005).

Macrofungal community

In total, 546 occurrences of 84 macrofungal species were recorded throughout the study site (Table 5). Per plot richness and diversity were both significantly higher ($p < 0.03$) in tornado disturbed plots compared to undisturbed and salvage plots, which were similar in both measures (Table 6). 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 ($p < 0.02$) in undisturbed plots (9.00 ± 1.02 SE) compared to salvage harvested plots (4.20 ± 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.

Table 5. Macrofungal species and subplot level occurrences per treatment documented in the Oakmulgee Ranger District, Talladega National Forest, Alabama. Asterisks indicate ectomycorrhizal species.

Species	**Und**	**Tor**	**Salv**
Agaricus pocillator Murrill	0	1	0
Amanita brunnescens G.F. Atk. *	0	1	1
Amanita ceciliae (Berk. & Broome) Bas *	1	0	0
Amanita citrina Pers. *	0	15	6
Amanita cokeri E.-J. Gilbert & Kühner *	1	1	0
Amanita longipes Bas *	0	1	0
Amanita rubescens Pers. *	2	0	0
Amanita spreta (Peck) Sacc. *	2	4	1
Amanita virosa Bertill. *	0	0	1
Amanita volvata (Peck) Lloyd *	1	0	0
Arachnion album Schwein.	0	1	0
Arrhenia epichysium (Pers.)	0	1	0
Aureoboletus auriporus (Peck) Pouzar *	1	0	0
Auricularia auricula (Bull.) Quél.	0	1	0
Bovista acuminata (Bosc) Kreisel	0	1	0
Callistosporium luteo-olivaceum (Berk. & M.A. Curtis)	0	2	0
Cantharellus cibarius Fr. *	7	0	0
Cantharellus cinnabarinus (Schwein.) Schwein. *	7	0	0
Cerrena unicolor (Bull.) Murrill	0	19	10
Chalciporus pseudorubinellus (A.H. Sm. & Thiers) *	1	0	0
Coprinopsis cinerea (Schaeff.)	0	3	0
Cortinarius sp. *	1	0	0
Cortinarius sp. 2 *	1	0	0
Crepidotus mollis (Schaeff.) Staude	1	1	0
Dacryopinax spathularia (Schwein.) G.W. Martin	1	17	4
Daedaleopsis confragosa (Bolton) J. Schröt.	0	6	1
Daldinia concentrica (Bolton) Ces. & De Not.	0	1	0
Entoloma vernum S. Lundell	0	0	5
Fomes fasciatus (Sw.) Cooke	0	3	4
Ganoderma curtisii (Berk.) Murrill	1	4	2
Ganoderma lucidum (Curtis) P. Karst.	1	0	0
Geastrum floriforme Vittad.	0	3	1
Gloeophyllum sepiarium (Wulfen) P. Karst.	0	1	1
Gymnopilus penetrans (Fr.) Murrill	0	1	0
Gymnopus dryophilus (Bull.) Murrill	1	3	21
Gymnopus foetidus (Sowerby) P.M. Kirk	0	3	0
Gymnopus perforans (Hoffm.) Antonín & Noordel.	1	0	0
Hemileccinum subglabripes (Peck) Halling *	1	0	0
Hohenbuehelia petaloides (Bull.) Schulzer	0	3	0

Hymenopellis megalospora (Clem.) R.H. Petersen	0	1	0
Inocybe sp. *	0	0	1
Laccaria laccata (Scop.) Cooke *	2	2	0
Lactarius camphoratus (Bull.) Fr. *	13	4	2
Lactarius deceptivus Peck *	2	0	0
Lactarius sp. *	1	0	0
Leccinellum albellum (Peck) Bresinsky & Manfr. Binder *	1	0	0
Leccinum roseoscabrum Singer & R. Williams *	1	1	3
Lentinus arcularius (Batsch) Zmitr.	0	2	0
Lentinus crinitus (L.) Fr.	0	5	0
Leucocoprinus cepistipes (Sowerby) Pat.	0	5	0
Leucocoprinus fragilissimus (Ravenel ex Berk. & M.A. Curtis) Pat.	0	1	1
Lycoperdon marginatum Vittad.	0	1	0
Marasmius pulcherripes Peck	0	2	0
Marasmius sp.	0	40	20
Mycena leptocephala (Pers.) Gillet	2	0	0
Mycena sp.	0	0	3
Mycena sp. 2	0	1	0
Mycena sp. 3	0	1	0
Panus rudis Fr.	0	1	0
Phellinus gilvus (Schwein.) Pat.	2	2	0
Pholiota polychroa (Berk.) A.H. Sm. & H.J. Brodie	0	1	0
Pisolithus arhizus (Scop.) Rauschert *	0	12	1
Pleurotus dryinus (Pers.) P. Kumm.	0	0	1
Pluteus cervinus (Schaeff.) P. Kumm.	0	3	2
Pluteus leoninus (Schaeff.) P. Kumm.	0	1	0
Psathyrella umbonata (Peck) A.H. Sm.	0	1	0
Pulveroboletus ravenelii (Berk. & M.A. Curtis) Murrill *	6	8	4
Retiboletus ornatipes Manfr. Binder & Bresinsky *	3	11	4
Russula perlactea Murrill *	0	1	0
Russula silvicola Shaffer *	1	2	0
Russula sp. *	0	2	0
Schizophyllum commune Fr.	3	8	7
Stereum ostrea (Blume & T. Nees) Fr.	4	19	9
Strobilomyces strobilaceus (Scop.) Berk. *	0	1	0
Suillus decipiens (Peck) Kuntze *	3	0	0
Thelephora sp. *	0	0	1
Trametes elegans (Spreng.) Fr.	0	15	0
Trametes versicolor (L.) Lloyd	2	5	5
Trichaptum abietinum (Dicks.) Ryvarden	8	10	13
Trichaptum biforme (Fr.) Ryvarden	8	14	1
Tricholomopsis decora (Fr.) Singer	0	1	0
Tricholomopsis formosa (Murrill) Singer	1	1	2
Tylopilus rhoadsiae (Murrill) Murrill *	15	3	8
Xylaria hypoxylon (L.) Grev.	2	2	1

Table 6. Measures of diversity and richness for macrofungal groups by treatment in the Oakmulgee Ranger District, Talladega National Forest, Alabama. Per plot means are ± standard error. Means in rows followed by the same letter are not significantly different at $p < 0.05$.

Parameter	**Undisturbed**	**Tornado**	**Salvage**
Diversity (H')	3.18	3.47	3.01
Diversity (H') $plot^{-1}$	2.41 ± 0.13 (a)	2.97 ± 0.07 (b)	2.41 ± 0.13 (a)
Richness	38	61	33
Richness $plot^{-1}$	14.00 ± 1.94 (a)	25.60 ± 2.34 (b)	14.00 ± 1.72 (a)
ECM Richness	23	16	12
ECM Richness $plot^{-1}$	9.00 ± 1.02 (a)	7.20 ± 1.21 (ab)	4.20 ± 0.77 (b)
Saprotrophic Richness	15	45	21
Saprotrophic Richness $plot^{-1}$	5.00 ± 1.13 (a)	18.40 ± 2.63 (b)	9.80 ± 1.15 (a)

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 ($p < 0.001$) in the tornado treatment compared to undisturbed and salvage harvested treatments. 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 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 pine (Figure 4). Two species, *Cerrena unicolor* and *Dacryopinax spathularia*, were recorded on both hardwood and pine substrates. FWD accounted for 119 saproxylic fruiting occurrences, with larger deadwood accounting for the remaining 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). The number of saproxylic fruiting occurrences generally decreased with increasing deadwood diameter in all three treatments. In total, 97% (n = 267) of saproxylic fruiting occurrences were documented on decay class II substrates.

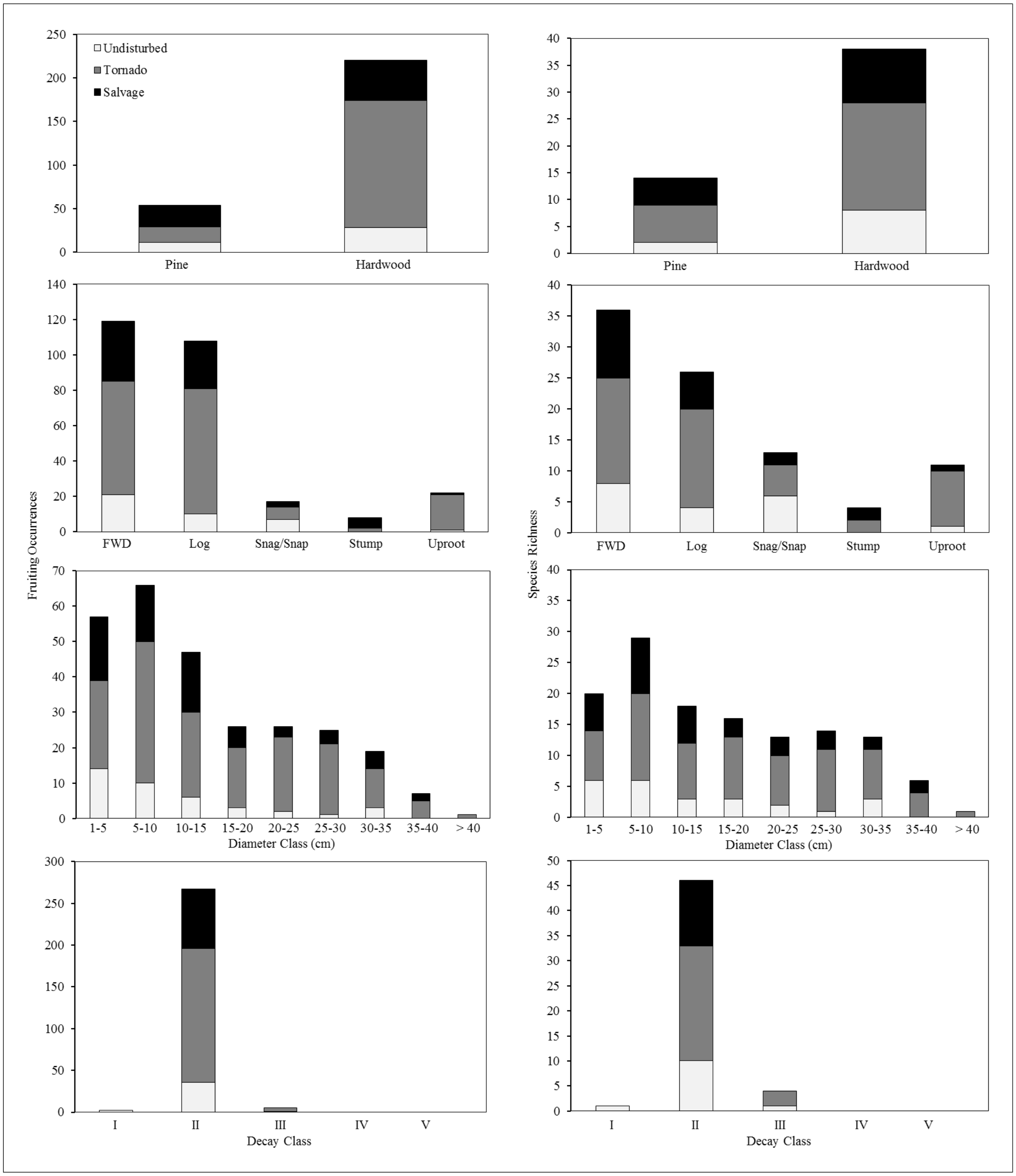

Figure 4. Saproxylic macrofungal fruiting occurrences and species richness documented on woody substrates in the Oakmulgee Ranger District, Talladega National Forest, Alabama. Substrates are classified by taxonomic group, mode of death, diameter class, and decay class. Modes of death include FWD (woody 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). Decay classes follow the guidelines of the USFS FIA (2005).

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 (Figure 5). 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 ($p < 0.02$) in macrofungal community composition. ISA revealed 12 indicator species overall ($p < 0.05$), nine for tornado, two for undisturbed, and one for salvage (Table 7). Indicator species for the tornado treatment included seven saprotrophic species (*C. unicolor, Daedaleopsis confragosa*, *D. spathularia*, *Lentinus crinitus*, *Marasmius sp.*, *Trichaptum biforme*, *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 only indicator species for the salvage treatment.

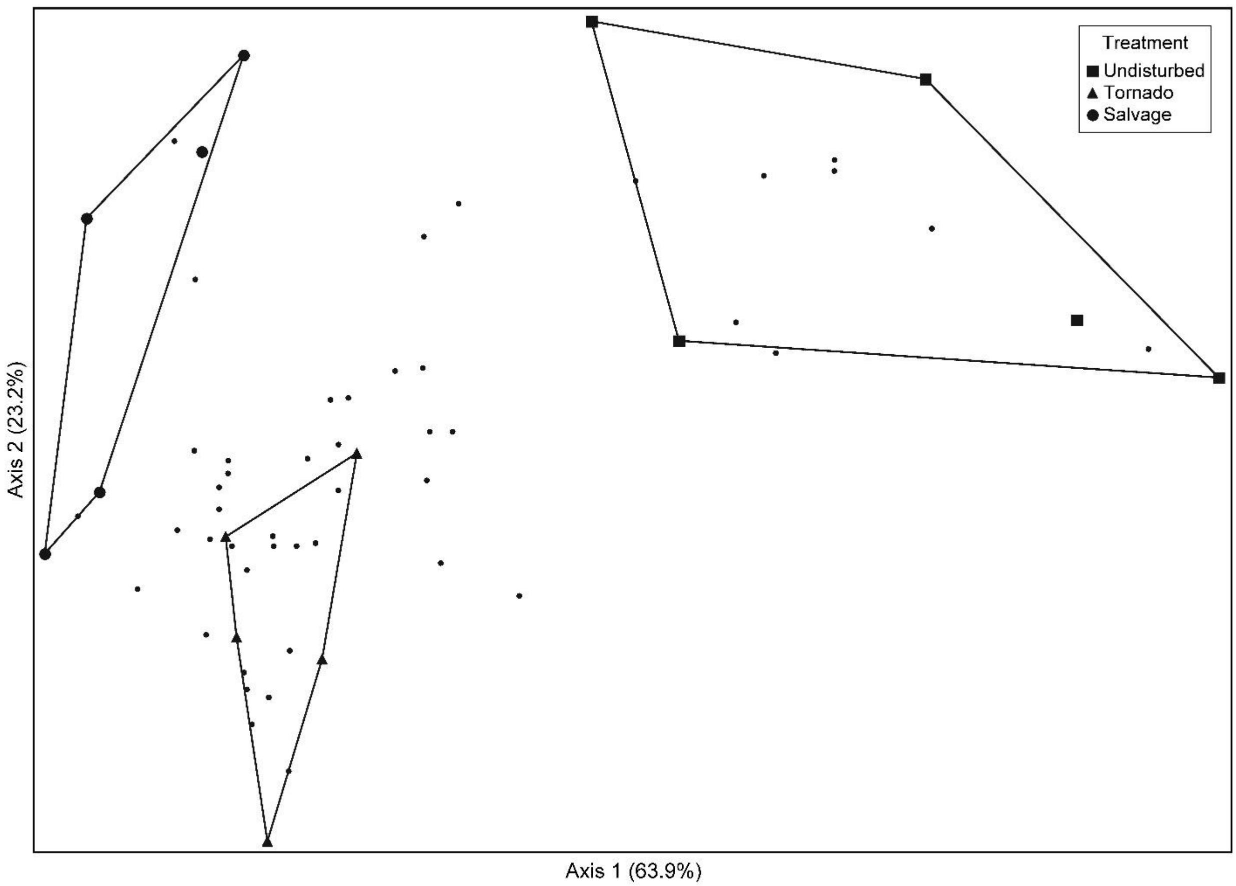

Figure 5. Non-metric multidimensional scaling ordination summarizing variation in macrofungal community at the plot level (stress = 12.89; cumulative r^2 = 87.1%) in the Oakmulgee Ranger District, Talladega National Forest, Alabama. Sørensen (Bray-Curtis) distance measure was used to measure dissimilarity in composition between plots. Convex hulls connect plots of the same treatment. Small circles represent macrofungal species.

Table 7. Results of indicator species analysis, showing indicator values for all significant indicators ($p < 0.05$) by treatment in the Oakmulgee Ranger District of the Talladega National Forest, Alabama. Indicator values range from 0 - 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**	
C. cibarius *	100	-	-	0.001
C. cinnabarinus *	80	-	-	0.010
C. unicolor	-	61	-	0.014
D. confragosa	-	67	-	0.037
D. spathularia	-	69	-	0.005
G. dryophilous	-	-	75	0.008
L. crinitus	-	80	-	0.009
Marasmius sp.	-	57	-	0.003
P. arhizus *	-	70	-	0.013
R. ornatipes *	-	51	-	0.011
T. biforme	-	100	-	0.016
T. elegans	-	80	-	0.012

DISCUSSION

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. These events shift forest ecosystems into the stand initiation stage of development (Oliver and Larson, 1996), which typically features dominance by fast growing shade-intolerant ruderal species. Catastrophic disturbance events are relatively infrequent, occurring at a return interval of several hundred to several thousand years in forests of the eastern United States (Seymour and White, 2002). The rate of high intensity tornados (EF3 - EF5) in the United States was 37.5 per year from 1991 to 2010 (NOAA 2017b). However, the onset of global climate change may increase the frequency and intensity of disturbance agents such as tornados, hurricanes, and wildfires (Dale et al., 2001), thus, understanding the impacts of these events may be crucial to future forest management and conservation efforts. Additionally, the practice of salvage harvesting following catastrophic disturbance remains prevalent throughout the world, despite the dearth of information regarding its long-term ecosystem impacts (Royo et al., 2016). The outcomes of salvage harvesting operations are likely influenced by the conditions of the initial disturbance, specific salvage harvesting guidelines, biophysical setting, and the species assemblage of interest (Peterson and Leach, 2008a; Royo et al., 2016; Fraver et al., 2017), thus, more context specific research is necessary before generalizations regarding the practice of salvage harvesting can be made.

Disturbance impacts on structural legacies

The tornado event documented in this study created structural legacies including increased canopy openness and increased density and volume of deadwood. 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 prescribe burned in 2014 to promote *P. palustris* regeneration, through competition reduction. However, fuels in the 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, however, deadwood volume was decreased 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 with the exception of FWD. Fraver et al. (2017) documented a similar pattern, indicating the tendency for salvage harvesting operations to leave smaller deadwood and slash on site.

Disturbance effects on the 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). 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. 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 likely a typical impact of salvage harvesting operations (Lindenmayer and Noss, 2006). These types of soil disturbance can limit ECM-associating plant growth (Kozlowski, 1999), and limit ECM fungal establishment directly by 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. Interestingly, four of the six ECM species documented in all three treatments belong to the Boletaceae. This indicates the ability of these species to withstand disturbance using a generalist ecological strategy that allows them to persist in distinct biophysical environments. 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.

Disturbance effects on the saprotrophic fungal community

The volume and density of substrate for saprotrophic fungi were altered by both tornado and salvage harvesting disturbances, resulting in distinct compositional patterns across the three treatments. The majority of 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 apparent soil perturbation and significant reduction in sapling density of the salvage harvested treatment compared to the tornado treatment. Because of compaction, soils in the salvage harvested treatment likely had less water holding capacity than soils of the tornado treatment. Additionally, 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, hardwood substrates hosted substantially more species and fruiting occurrences than pine substrates, despite higher levels of pine deadwood density and volume in all three treatments. Pine wood typically decays slower than hardwood in comparable settings (Weedon et al., 2008), and hosts less fungal biomass in the initial stages of decay (Noll et al., 2016). As pine 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 pine-composed deadwood. Large volume deadwood also decays relatively slowly, and typically maintains more stable temperature and moisture conditions, thereby promoting fungal activity over longer periods of time (Bader et al., 1995; Brazee et al., 2014). Thus, large volume deadwood will also likely increase in importance with advancing decay. 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.

Management implications

Although macrofungal studies utilizing single year fruiting body surveys likely underestimate true diversity and abundance, the results provide broad patterns of disturbance effects on macrofungal communities from which to draw management recommendations (Oria-de-Rueda, et al., 2010; Dove and Keeton, 2015). Without the associated disturbances, we would expect macrofungal fruiting patterns to be similar throughout the study site, because all areas were similar in forest composition, structure, and edaphic characteristics prior to the 2011 disturbance events. Additionally, the proximity of the study sites ensured that plots experienced similar temperature and precipitation levels throughout the sample period. Therefore, the differences in macrofungal species composition and fruiting patterns documented in this study more than likely resulted from the disturbance effects. 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 very little 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; Bassler and Mueller, 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 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. Short-term studies on salvage harvesting may overestimate negative impacts on ecosystem health (Royo et al., 2016), however, the alterations to early successional fungal communities will likely have effects on long-term ecosystem development patterns. 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. The true extent to which future ecosystems are altered by comparatively lower fungal diversity in early stages of development must be subject to long-term studies. For managers wishing to maintain macrofungal diversity and associated ecosystem functions in early developmental stages, it may be beneficial to limit access of salvage harvesting operations following disturbance. This will protect areas from soil perturbation and limit the removal of structural legacies such as deadwood, thereby, maintaining more optimal habitat conditions for macrofungal communities. Areas that are salvage harvested should 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 on 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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