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Response by vertical strata to catastrophic wind in restored *Pinus palustris* stands[1]

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Abstract. *Pinus palustris* Mill. (longleaf pine) ecosystems support a diversity of rare plants and animals, but have been substantially degraded by historical human impacts. A suite of natural disturbances influence development and succession in *P. palustris* ecosystems, ranging from frequent, low-intensity events such as surface fires to infrequent, catastrophic events such as hurricanes. Like hurricanes, tornadoes may produce catastrophic winds that create canopy openings necessary for regeneration of *P. palustris* and other shade-intolerant species. Despite their pervasiveness in some *P. palustris* ecosystems, we know relatively little about the impacts of tornadoes. Our study, conducted July–August 2015 in fire-restored *P. palustris* stands of the Alabama Fall Line Hills, applied a nested sampling design to compare dead trees, live trees, saplings, seedlings, and herbaceous plants in plots either undisturbed or directly impacted by an Enhanced Fujita scale 3 tornado on April 27, 2011. Most wind-killed trees were uprooted or snapped, and consisted primarily of large *P. palustris* stems. *Pinus palustris* persisted, however, with increased relative densities in the tree, sapling, and seedling strata of wind-disturbed neighborhoods. The relative densities of *Quercus* L. (oak) trees and saplings also increased. Combined with an herbaceous stratum composition typical of other restored *P. palustris* stands, desirable woody species recovery indicated that the stands surveyed here were resilient to the 2011 tornado. Contrary to expectations, the tornado reduced woody stem diversity and herbaceous cover. These results may serve as a benchmark for tracking species-specific changes in *P. palustris* communities and guide management decisions, including those designed to promote native forest diversity.

Key words: Alabama, Fall Line Hills, *Pinus palustris* longleaf pine, tornado, wind disturbance

Natural disturbances alter the structure and composition of all forests, thereby directing forest development and succession (Oliver and Larson 1996, Frelich 2002). Disturbances vary in type, frequency, and severity (White and Pickett 1985), and are often classified along a gradient from frequent, gap-scale disturbances to infrequent, catastrophic events (Cowden *et al*. 2014, Hart 2016). Second to fire, wind is the most widespread natural disturbance in terrestrial ecosystems (MacDonald 2003), and is arguably the most pervasive natural disturbance in forests of eastern North America (Peterson, Cannon, and Godfrey 2016). Wind directly alters forest structure by stripping leaves, breaking branches, and snapping and uprooting trees (Gardiner, Berry, and Moulia 2016), thereby increasing light transmittance, detrital input, and exposure of bare mineral soil (Mitchell 2013). Plant community composition and recovery after disturbance are in part determined by the abilities of species to regenerate and compete in these altered abiotic conditions.

Tornadoes reach the greatest intensity of all types of wind disturbance (Everham and Brokaw 1996), and are ranked on the Enhanced Fujita (EF) scale by increasing wind speeds from EF0 to EF5 (WSEC 2006). Globally, the USA experiences the highest frequency of tornadoes, averaging 1,253 tornadoes per year of which 3% are documented as high-intensity events (EF3 and higher; NCDC 2016). Thus, relatively few tornadoes reach high-intensity classification. Whereas hurricanes and other catastrophic tropical cyclones (*i.e.*, storms and depressions) often have patchy impacts across a broad spatial extent (Kupfer *et al*. 2008), high-intensity tornadoes are characteristically narrow, killing most or all trees in localized tracks.

Once extensive across the southeastern USA, *Pinus palustris* (longleaf pine) ecosystems have been largely removed or degraded by agricultural land clearing and grazing, industrial-scale logging, and fire suppression (Frost 1993, 2006), ranking them among the most endangered ecosystems in the USA (Noss, LaRoe, and Scott 1995). Resto-

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ration efforts based on natural disturbance regimes are often used to increase native biodiversity and enhance ecosystem resilience to perturbations (Long 2009). This restoration approach is especially common in *P. palustris* ecosystems where prescribed fire regimes promote desirable species assemblages and structural characteristics that were historically sustained by frequent, low-intensity surface fires (Van Lear *et al.* 2005). Frequent surface fires maintain a relatively open midstory and suppress woody plants that would otherwise outcompete *P. palustris* for canopy recruitment (Platt, Evans, and Rathbun 1988). Beyond increasing the abundance of *P. palustris* seedlings relative to other species with canopy potential, frequent surface fires increase the species richness of "resident" herbaceous stratum plants ($\leq$ 1 m height) to levels unparalleled by other temperate forests in North America (Gilliam, Platt, and Peet 2006, Gilliam 2007). This diverse herbaceous stratum coupled with an open midstory and *P. palustris*–dominated canopy supports a variety of rare animals, including the endangered *Leuconotopicus borealis* Vieillot (red-cockaded woodpecker), which preferentially nests in mature *P. palustris* trees and often motivates *P. palustris* restoration efforts (Engstrom 1993).

In addition to surface fires, continued canopy recruitment of *P. palustris* may require creation of canopy openings (gaps), which vary in spatial extent and frequency based on their causal disturbance agent (Palik, Mitchell, and Hiers 2002). Lightning is often reported as the most frequent cause of canopy mortality in *P. palustris* ecosystems followed by wind disturbance, which has potential to create larger canopy gaps than lightning (Platt, Evans, and Rathbun 1988; Palik and Pederson 1996; Outcalt 2008). Our understanding of wind disturbance in *P. palustris* ecosystems is focused primarily on hurricanes (Gilliam, Platt, and Peet 2006). However, we hypothesize that tornadoes are responsible for more canopy disturbances in montane (noncoastal) *P. palustris* systems where thunderstorms (Holle, Cummins, and Brooks 2016) and hurricanes (HRD 2016) are less common.

Although the impacts of tornadoes are well recognized in some forest ecosystems, few studies have directly assessed their impacts in *P. palustris* systems. Outcalt (2008) attributed 13% of overstory mortality in a 10-yr study in central Florida to wind disturbance primarily caused by a single tornado. Liu *et al.* (1997) described an intermediate-severity tornado that accelerated succession of a mixed-*Pinus* savanna in southeastern Texas toward hardwood dominance. To our knowledge, the effects of tornado-generated catastrophic wind disturbance have not been reported in *P. palustris* ecosystems, especially with respect to nonwoody plants.

The overarching goal of our study was to assess how catastrophic wind disturbance affects fire-restored *P. palustris* woodlands. Specifically, our objectives were to characterize and describe differences in the structure and composition of (a) dead trees, (b) live trees, (c) saplings, (d) seedlings, and (e) herbaceous plants in neighborhoods of fire-restored *P. palustris* stands that were either unaffected or directly impacted by an EF3 tornado. Results provide increased understanding of forest stratum responses to catastrophic wind disturbance in fire-restored stands, and in turn enhance our understanding of *P. palustris* stand dynamics in the context of two interacting disturbances. Documentation of species assemblages and responses to catastrophic wind disturbance may serve as a benchmark for tracking changes in *P. palustris* community composition and guide management decisions, including those designed to promote native forest diversity.

Methods. Study Area. We conducted our research in the Oakmulgee Ranger District of the Talladega National Forest in Hale County of western Alabama. The Oakmulgee Ranger District occurs in the Fall Line Hills physiographic province (Fenneman 1938). The Fall Line Hills ecoregion (level III) in Alabama represents a transition zone between the Coastal Plain and Appalachian Highlands (Griffith *et al.* 2001, Shankman and Hart 2007, Cox and Hart 2015). Sedimentary, Cretaceous-age Tuscaloosa and Coker formations compose the geologic surface, consisting primarily of sand, gravel, and clay, and supporting steep slopes and ridges with deep, well-drained, and moderately permeable soils (Reed 1905; Szabo, Osborne, and Neatherly 1998; USDA NRCS 2006, 2016).

The region has a humid mesothermal climate characterized by long, hot summers and short, mild winters (Thornthwaite 1948). Annual temperature of the study area averages 17 °C (PRISM Climate Group 2016). July has the highest mean monthly temperature of 27 °C and January has the lowest mean monthly temperature of 7 °C (PRISM Climate Group 2016). Annual precipitation of the region averages 1,376 mm (PRISM Climate Group 2016). February has the highest mean monthly precipitation of 138 mm and October has the lowest mean monthly precipitation of 88 mm (PRISM Climate Group 2016). The frost-free period typically spans March to November (USDA NRCS 2006).

Braun (1950) classified the regional vegetation as *Quercus-Pinus*. Specifically, the Fall Line Hills ecoregion is recognized for its *P. palustris*–dominated plant communities (Harper 1943, Griffith *et al.* 2001). The US National Vegetation Classification (USNVC) "*Pinus palustris/Schizachyrium scoparium–Pteridium aquilinum* Woodland" vegetation association best describes our study area dominated by *P. palustris*, *Schizachyrium scoparium* (Michx.) Nash, and *Pteridium aquilinum* (L.) Kuhn var. *pseudocaudatum* (Clute) A. Heller, with a range of *Quercus* and other mesic hardwood species in the midstory, and a high diversity of Asteraceae and Fabaceae in the herbaceous stratum (Beckett and Golden 1982, Teague *et al.* 2014).

Direct human impacts on forest ecosystems in the Oakmulgee Ranger District peaked in the early 1900s when Kaul Lumber Company preferentially harvested *P. palustris* in combination with an annual fire return interval (Reed 1905, Cox and Hart 2015). *Pinus palustris* dominance was further reduced during a period of fire suppression beginning in 1922 (Harper 1943). Federal acquisition of the land occurred in 1943 and since that time staff on the Oakmulgee Ranger District has prioritized *P. palustris* restoration (USDA Forest Service 2005). Restoration efforts including midstory removals in overstocked *P. palustris* stands, regeneration harvests followed by site preparation and *P. palustris* outplanting, and establishment of a 2–5-yr prescribed fire rotation are widespread and ongoing throughout the forest. Since first surveyed in 1820, *P. palustris* has remained the most abundant tree species in our study area; however, human impacts have driven the replacement of large, primary-growth trees by a higher density of comparatively smaller trees (Cox and Hart 2015).

On April 27, 2011, a strong, long-tracked wedge tornado classified as EF3 tracked across the Oakmulgee Ranger District. This tornado was one of the 362 confirmed tornadoes during the 2011 Super Outbreak event from April 25, 2011 to April 28, 2011. The tornado had estimated maximum wind speeds of 233 km h^{-1}, a maximum path width of 1.6 km, and a length of 116 km (NWS 2011). Some fire-restored *P. palustris* stands were affected, providing an opportunity to investigate their response to catastrophic wind disturbance.

FIELD METHODS. A combination of aerial photography, geospatial metadata provided by the US Department of Agriculture (USDA) Forest Service, and ground reconnaissance was used to select two comparable fire-restored *P. palustris*–dominated stands with sections (neighborhoods) both unaffected and directly impacted by the tornado. The selected stands had a combined area of 45 ha of which approximately 15 ha were wind-disturbed. Within the selected stands, we categorized neighborhoods as undisturbed if they were not visibly affected by the tornado and wind-disturbed if they were directly impacted by the tornado. The Forest Service groups stands into compartments and conducts prescribed fires at the compartment scale. Therefore, we selected stands located in the same compartment to ensure they had been burned on the same contemporary fire regime. At the time of sampling, July–August 2015, the compartment had been most recently burned in February 2006 as increased hazardous fuel loads from wind-induced mortality prevented prescribed burning after the tornado. Stands were also selected based on criteria that they established in the 1930s, had the same soil types (USDA NRCS 2016), and shared upper-slope positions (TNM 2016). In addition to a visual authentication of the site conditions in the field, we used increment borers to verify the age of subjectively selected canopy trees in undisturbed neighborhoods and on the periphery of wind-disturbed neighborhoods.

We used ArcMap version 10.2 to superimpose a grid with 50-m spacing over the selected stands and establish plot locations at centroids of the grid cells. After excluding plots within 50 m of neighborhood boundaries to reduce the influence of edge effects, we selected 21 undisturbed plots and 18 wind-disturbed plots. At each plot location, we measured ecological variables at sampling unit sizes appropriate to characterize the variables of interest, where variables with finer-scale spatial heterogeneity were measured in smaller sampling units. Our nested sampling design consisted of a 400-m^2 (0.04-ha) fixed-radius plot, a 40-m^2 fixed-radius plot nested 5 m west of the center of the

400-m^2 plot, and 10 1 × 1–m quadrats (10 m^2) arranged with the center quadrat sharing plot center with the 400-m^2 plot and the other nine quadrats divided equally among the 0°, 120°, and 240° azimuths from plot center.

Canopy cover and the composition and structure of dead and live stems $\geq$ 5 cm diameter 1.37 m above root collar (diameter at breast height, dbh) were measured in the 400-m^2 fixed-radius plots. Canopy cover was measured as a proxy for canopy light interception, and was determined using spherical convex densitometer readings taken at five locations throughout each 400-m^2 plot: one at plot center, and one in each cardinal direction 5 m from plot center.

We measured and defined dead trees as dead woody stems $\geq$ 5 cm diameter at 1.37 m above the root collar and rooted in a 400-m^2 plot. Pieces of deadwood that occupied plot space but were not rooted in a plot were not included in our survey, nor were other pieces of deadwood $<$ 5 cm diameter. This definition of dead trees was selected to facilitate direct comparison to live trees (*i.e.*, live woody stems $\geq$ 5 cm dbh) rooted in each 400-m^2 plot. Dead trees were tallied to quantify density, identified to the lowest taxonomic level possible to assess taxon-specific mortality trends, and assigned a mode of death to describe the structural legacies of disturbance. Dead tree modes of death included uprooted (stem with uplifted root network), snapped (standing dead stem broken below crown), and snag (standing dead stem with crown intact, White *et al.* 2015).

To distinguish dead trees that had been dead for different periods, we assigned them a decay classification from I to IV according to increasing degree of decay (adapted from Fraver, Wagner, and Day 2002, White *et al.* 2015). Decay class I stems had sound wood and intact bark. Decay class II stems had partially rotten wood with bark that could be easily removed. Decay class III stems had substantially rotten wood that could be broken apart by hand or boot. Decay class IV stems were completely rotten and material was compacted. Based on time since disturbance ($<$ 5 yr) and decay dynamics of *P. palustris* (Means 2006) and other common species in our study area (Russell *et al.* 2014), dead trees in decay class II were considered "wind-killed trees" if they were documented in wind-disturbed neighborhoods. Decay class II stems in undisturbed neighborhoods were called "background mortality," and combined with decay class I stems were expected to represent approximately 2% of live tree density (Palik and Pederson 1996).

Live trees (live woody stems $\geq$ 5 cm dbh) were tallied to quantify density, measured for dbh to determine basal area and diameter distribution, identified to catalogue species composition, and assigned a crown class to describe vertical stratification. Crown classes included canopy, intermediate, and overtopped, and were based on crown height and light interception compared to the adjacent canopy (Oliver and Larson 1996).

We documented saplings (live woody stems $>$ 1.2 m height and $<$ 5 cm diameter) and seedlings (live woody stems $\leq$ 1.2 m height) in the nested 40-m^2 fixed-radius plots. Saplings and seedlings were tallied to quantify density and identified to catalogue composition. *Vaccinium* was not identified beyond genus in the sapling or seedling strata. With the exception of *P. palustris*, *Pinus* species were not identified beyond genus in the seedling stratum.

Herbaceous plants (vascular plants lacking persistent, aboveground woody growth) were inventoried in the 10 1 × 1–m quadrats (10 m^2 per plot). To describe herbaceous plant composition, we identified herbaceous plants to the lowest taxonomic level possible given available reproductive structures. To quantify the relative abundance of different life forms in each disturbance category, we assigned herbaceous plants to one of four life forms (adapted from Miller and Miller 2005, Platt *et al.* 2006), and visually estimated their percentage of cover using panels sized to cover 1% and 5% of each 1-m^2 quadrat as guides. Life forms consisted of ferns, forbs, graminoids (Cyperaceae, Juncaceae, and Poaceae), and vines. Coverage by life form was estimated by 1% increments up to 5% and then 5% increments up to 100% in each quadrat.

ANALYTICAL METHODS. Dead trees classified as wind-killed trees and background mortality were standardized to the hectare level and grouped by 5-cm diameter size classes and modes of death to assess what trees (size classes) were more likely to be killed by the storm and by what means (modes of death). Densiometer readings were multiplied by 1.04 to calculate canopy cover percentages (Lemmon 1957). Canopy cover percentages were averaged per plot and compared between disturbance categories with a two-sample *t* test.

To evaluate disturbance severity, average basal area (m^2 ha^{-1}) was compared between disturbance categories with a two-sample *t* test. Trees were grouped by species and compared with structural descriptors to assess the distribution of different species in each disturbance category. Descriptors included density (trees ha^{-1}), relative density (percentage of total trees), dominance (m^2 ha^{-1}), relative dominance (percentage of total basal area), and importance (average of relative density and relative dominance). To compare the diameter distribution of trees in undisturbed and wind-disturbed neighborhoods, trees were grouped by 5-cm dbh size classes and standardized to the hectare level. Crown class frequencies were standardized to the hectare level to assess the vertical stratification of undisturbed and wind-disturbed neighborhoods.

Trees were assigned to taxonomic groups to identify structural trends among species with similar life history traits and management considerations. *Pinus palustris* composed the Longleaf Pine Group, *Pinus taeda* and *Pinus echinata* composed the Loblolly-Shortleaf Pine Group, *Quercus* species and *Carya* species composed the Oak-Hickory Group, and the remaining species composed the Others Group.

Saplings and seedlings were grouped by taxa and compared between disturbance categories using density and relative density. To evaluate the successional trajectory of undisturbed and wind-disturbed neighborhoods, we omitted saplings and seedlings without canopy potential (*Aesculus pavia*, *Asimina parviflora*, *Callicarpa americana*, *Cornus florida*, *Rhus copallina*, *Symplocos tinctoria*, and *Vaccinium*), and assigned remaining taxa one of the same taxonomic groups as the trees. Based on observations in neighboring stands, seedlings in the Loblolly-Shortleaf Pine Group may have included a minor component of *Pinus virginiana* Mill. Sapling and seedling counts in each taxonomic group per plot were standardized to the hectare level and power-transformed to meet assumptions of homoscedasticity. We used a two-way factorial analysis of variance (ANOVA) to compare sapling and seedling counts among and between taxonomic groups and disturbance categories.

To assess woody stem biodiversity, density-based measures of richness, Shannon diversity, and evenness were calculated for trees, saplings, and seedlings in each plot, and compared between disturbance categories with two-sample *t* tests. Herbaceous plants were ranked by frequency to describe the most common taxa in the study area. Percentage-of-cover estimations of herbaceous life forms were averaged per plot and log-transformed to meet assumptions of homoscedasticity. We used a two-way factorial ANOVA to compare herbaceous cover among and between life forms and disturbance categories.

Results. DEAD TREES. *Pinus* species composed 97% of dead trees in the study area, of which at least 88% were *P. palustris* (some dead *Pinus* stems were not distinguishable beyond genus because of advanced decay). The majority (71%) of dead trees surveyed were in decay class II, of which 94% were documented in wind-disturbed neighborhoods (wind-killed trees) and 6% were in undisturbed neighborhoods (background mortality). Accordingly, dead tree density peaked at decay class II in wind-disturbed neighborhoods where 4%, 80%, 13%, and 3% of dead stems were categorized as decay classes I, II, III, and IV, respectively. No such trend was observed in undisturbed neighborhoods where 42%, 27%, and 31% of dead stems were categorized as decay classes I, II, and III, respectively. The disturbance categories had comparatively different diameter distribution shapes of decay class II stems (Fig. 1). Wind-killed trees increased in larger size classes up to 30–35 cm diameter and then decreased up to 50–55 cm diameter, whereas density of decay class II stems in undisturbed neighborhoods (background mortality) decreased in larger size classes up to 40–45 cm diameter. In total, wind-killed trees comprised 85% of uprooted stems and 65% of snapped stems in the study area, of which 45% were uprooted and 53% were snapped.

LIVE TREES. Canopy cover was greater on undisturbed plots ($P < 0.001$), averaging 40% ± 3% SE compared to 12% ± 2% SE on wind-disturbed plots. Tree density in undisturbed neighborhoods was 998 trees ha^{-1} and in wind-disturbed neighborhoods was 111 trees ha^{-1} (Table 1). Undisturbed neighborhoods had significantly greater basal area than wind-disturbed neighborhoods ($P < 0.001$), averaging 19.4 ± 1.4 m^2 ha^{-1} SE in undisturbed plots and 4.1 ± 1.0 m^2 ha^{-1} SE in wind-disturbed plots.

The diameter distributions of undisturbed and wind-disturbed neighborhoods were skewed toward smaller trees, with approximately half of

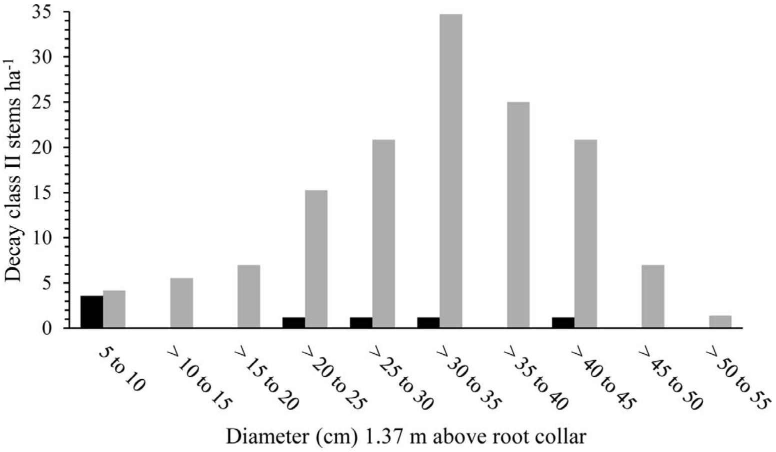

Fig. 1. Density (stems ha^{-1}) of decay class II stems in undisturbed (black bars) and wind-disturbed (gray bars) neighborhoods of *Pinus palustris* stands in the Oakmulgee Ranger District of the Talladega National Forest, Alabama.

trees in both disturbance categories grouped in the 5–10-cm dbh size class. Tree density decreased with increasing diameter in both disturbance categories, but undisturbed neighborhoods had trees in larger size classes. Undisturbed neighborhoods had trees in all size classes up to 60–65 cm dbh, with the largest tree recorded as 62 cm dbh, whereas wind-disturbed neighborhoods had no trees beyond 45–50 cm dbh, with the largest tree recorded as 47 cm dbh.

Intermediate trees dominated the vertical stratification of both disturbance categories, composing 78% of trees in undisturbed neighborhoods and 70% of trees in wind-disturbed neighborhoods. Wind-disturbed neighborhoods had fewer trees per hectare in every crown class. Canopy trees comprised 142 trees ha^{-1} in undisturbed neighborhoods and 31 trees ha^{-1} in wind-disturbed neighborhoods. Intermediate trees comprised 781 trees ha^{-1} in undisturbed neighborhoods and 78 trees ha^{-1} in wind-disturbed neighborhoods. Overtopped trees comprised 75 trees ha^{-1} in undisturbed neighborhoods and 3 trees ha^{-1} in wind-disturbed neighborhoods.

We documented 14 tree species in total. Undisturbed plots had greater tree richness, Shannon diversity, and evenness than wind-disturbed plots (Table 2); however, only differences in richness were statistically significant ($P < 0.05$). The Longleaf Pine Group was the most important (based on density and dominance) tree taxonomic group in the study area, with a relative density of 62% in undisturbed neighborhoods and 65% in wind-disturbed neighborhoods. The Loblolly-Shortleaf Pine Group had the second greatest relative density in undisturbed neighborhoods (30%), and the lowest relative density in wind-disturbed neighborhoods (6%). The Oak-Hickory Group had the lowest relative density in undisturbed neighborhoods (1%), but had a greater relative density in wind-disturbed neighborhoods (10%). Notably, *Quercus marilandica* and *Quercus falcata* both ranked fifth in relative density by individual species in undisturbed neighborhoods (1%), but had the fourth and fifth greatest relative densities in wind-disturbed neighborhoods (4% and 3%, respectively). The Others Group had a relative density of 6% in undisturbed neighborhoods and 19% in wind-disturbed neighborhoods. By individual species, *Liquidambar styraciflua* showed the greatest increase in relative density in the Others Group, ranking third in relative density in undisturbed neighborhoods (5%) and second in wind-disturbed neighborhoods (13%).

Saplings. We identified 28 sapling taxa in the study area, with 2,083 saplings ha^{-1} in undisturbed neighborhoods and 2,320 saplings ha^{-1} in wind-disturbed neighborhoods (Table 3). We found no statistical differences ($P < 0.05$) in average sapling richness, Shannon diversity, or evenness between undisturbed and wind-disturbed plots. Ranked by relative density, the five most abundant sapling taxa in undisturbed neighborhoods were *Vaccinium* (36%), *P. echinata* (13%), *Oxydendrum arboreum* (13%), *Callicarpa americana* (9%), and *L. styraciflua* (7%). The five most abundant sapling taxa

Table 1. Density (stems ha^{-1}), relative density, dominance (basal area, m^2 ha^{-1}), relative dominance, and relative importance (mean of relative density and relative dominance) of trees (live stems $\geq$ 5 cm diameter at breast height) documented in undisturbed and wind-disturbed (wind) neighborhoods of *Pinus palustris* stands in the Oakmulgee Ranger District of the Talladega National Forest, Alabama. Species are ranked by importance in undisturbed neighborhoods.

	Density (stems ha^{-1})		Relative density (%)		Dominance (m^2 ha^{-1})		Relative dominance (%)		Importance (%)	
Species	Undisturbed	Wind	Undisturbed	Wind	Undisturbed	Wind	Undisturbed	Wind	Undisturbed	Wind
Pinus palustris Mill.	621.4	72.2	62.3	65.0	13.8	3.3	70.9	90.4	66.6	77.6
Pinus echinata Mill.	300.0	6.9	30.1	6.2	5.1	0.0	26.3	0.9	28.2	3.6
Liquidambar styraciflua L.	46.4	13.9	4.7	12.5	0.2	0.1	0.9	1.6	2.8	7.1
Quercus marilandica Münchh.	6.0	4.2	0.6	3.7	0.1	0.0	0.5	0.3	0.6	2.0
Oxydendrum arboreum (L.) DC.	7.1	2.8	0.7	2.5	0.0	0.0	0.1	0.4	0.4	1.5
Quercus falcata Michx.	6.0	2.8	0.6	2.5	0.0	0.0	0.1	1.3	0.3	1.9
Liriodendron tulipifera L.	4.8	—	0.5	—	0.0	—	0.1	—	0.3	—
Quercus rubra L.	1.2	—	0.1	—	0.1	—	0.4	—	0.2	—
Pinus taeda L.	1.2	—	0.1	—	0.1	—	0.4	—	0.2	—
Nyssa sylvatica Marshall	1.2	2.8	0.1	2.5	0.0	0.1	0.2	2.5	0.2	2.5
Prunus serotina Ehrh.	2.4	—	0.2	—	0.0		0.1	—	0.2	—
Quercus stellata Wangenh.	—	2.8	—	2.5	—	0.0	—	0.9	—	1.7
Carya tomentosa (Lam.) Nutt.	—	1.4	—	1.3	—	0.1	—	1.6	—	1.4
Ilex opaca Aiton	—	1.4	—	1.3	—	—	—	0.1	—	0.7
Total	997.6	111.1	100.0	100.0	19.4	3.6	100.0	100.0	100.0	100.0

Table 2. Density-based measures of richness, Shannon diversity, and evenness in undisturbed and wind-disturbed (wind) plots in *Pinus palustris* stands in the Oakmulgee Ranger District of the Talladega National Forest, Alabama. Tree values represent 400-m^2 plot averages and standard errors. Sapling and seedling values represent 40-m^2 plot averages and standard errors. Values with different letters indicate differences between disturbance categories at $P < 0.05$.

Stratum	Biodiversity index	Mean ± SE	
		Undisturbed	Wind
Tree	Richness	3.05 ± 0.37 a	1.94 ± 0.35 b
	Shannon diversity	0.51 ± 0.08 a	0.47 ± 0.12 a
	Evenness	0.68 ± 0.27 a	0.47 ± 0.10 a
Sapling	Richness	2.95 ± 0.31 a	2.61 ± 0.44 a
	Shannon diversity	0.79 ± 0.11 a	0.61 ± 0.12 a
	Evenness	0.65 ± 0.08 a	0.59 ± 0.10 a
Seedling	Richness	7.29 ± 0.53 a	6.17 ± 0.41 a
	Shannon diversity	1.37 ± 0.09 a	1.07 ± 0.11 b
	Evenness	0.71 ± 0.04 a	0.60 ± 0.05 a

in wind-disturbed neighborhoods were *Vaccinium* (59%), *P. palustris* (14%), *Q. falcata* (7%), *Nyssa sylvatica* (5%), and *Rhus copallinum* (3%).

Disturbance category and taxonomic group had a significant interaction effect on canopy-potential sapling density ($P < 0.05$). Taxonomic groups with *Pinus* saplings exhibited opposite responses to the storm (Fig. 2). The Longleaf Pine Group averaged 48 saplings ha^{-1} in undisturbed neighborhoods and 320 saplings ha^{-1} in wind-undisturbed neighborhoods. The Loblolly-Shortleaf Pine Group averaged 274 saplings ha^{-1} in undisturbed neighborhoods and 42 saplings ha^{-1} in wind-disturbed neighborhoods. The Oak-Hickory Group averaged 274 saplings ha^{-1} in undisturbed neighborhoods and 292 saplings ha^{-1} in wind-disturbed neighborhoods, and the Others Group averaged 450 saplings ha^{-1} in undisturbed neighborhoods and 222 saplings ha^{-1} in wind-disturbed neighborhoods.

SEEDLINGS. We identified 30 seedling taxa in the study area, with 20,287 seedlings ha^{-1} in undisturbed neighborhoods and 25,722 seedlings ha^{-1} in wind-disturbed neighborhoods (Table 4). Undisturbed plots had greater average seedling richness, Shannon diversity, and evenness than wind-disturbed plots (Table 2), however, only differences in Shannon diversity were statistically significant ($P < 0.05$). Ranked by relative density, the five most abundant seedling taxa in both disturbance categories were *Vaccinium*, *P. palustris*, *Q. falcata*, *Pinus* species (excluding *P. palustris*), and *R. copallinum*. Whereas the two most abundant seedling taxa, *Vaccinium* and *P. palustris*, showed increased relative densities in wind-disturbed neighborhoods, *Q. falcata*, *Pinus* species, and *R. copallinum* showed reduced relative densities in wind-disturbed neighborhoods. *Vaccinium* com-

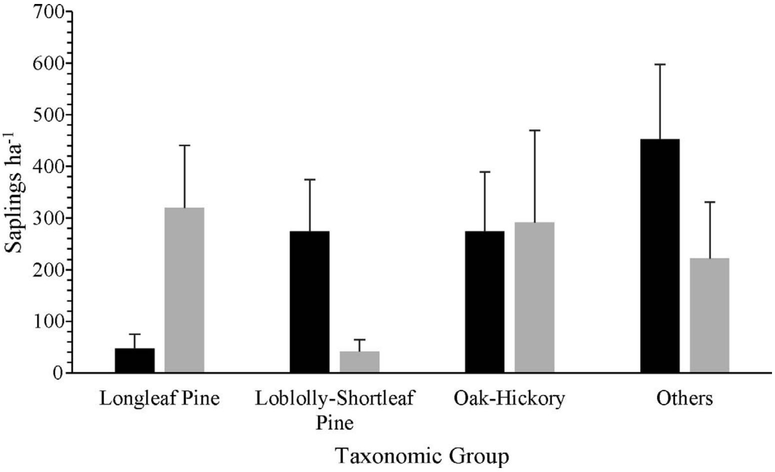

FIG. 2. Average density (stems ha^{-1}) with standard errors of saplings (live woody stems > 1.2 m height and < 5 cm diameter) with canopy potential categorized by taxonomic group in undisturbed (black bars) and wind-disturbed (gray bars) neighborhoods of *Pinus palustris* stands in the Oakmulgee Ranger District of the Talladega National Forest, Alabama. Disturbance category and taxonomic group had a significant interaction effect on canopy-potential sapling density ($P < 0.05$).

Table 3. Density (stems ha^{-1}) and relative density of saplings (live woody stems > 1.2 m height and < 5 cm diameter at breast height) documented in undisturbed and wind-disturbed (wind) neighborhoods of *Pinus palustris* stands in the Oakmulgee Ranger District of the Talladega National Forest, Alabama.

	Density (stems ha^{-1})		Relative density (%)	
Species	Undisturbed	Wind	Undisturbed	Wind
Acer rubrum L.	—	13.9	—	0.6
Aesculus pavia L.	23.8	—	1.1	—
Callicarpa americana L.	178.6	13.9	8.6	0.6
Carya glabra (Mill.) Sweet	—	27.8	—	1.2
Diospyros virginiana L.	23.8	—	1.1	—
Ilex opaca	23.8	—	1.1	—
Liquidambar styraciflua	154.8	27.8	7.4	1.2
Liriodendron tulipifera	11.9	13.9	0.6	0.6
Nyssa sylvatica	—	125.0	—	5.4
Oxydendrum arboreum	261.9	13.9	12.6	0.6
Pinus echinata	273.8	27.8	13.2	1.2
Pinus palustris	47.6	319.4	2.3	13.8
Pinus taeda	—	13.9	—	0.6
Prunus serotina	—	13.9	—	0.6
Quercus coccinea Münchh.	—	27.8	—	1.2
Quercus falcata	71.4	152.8	3.4	6.6
Quercus hemisphaerica W. Bartram ex Wild.	71.4	13.9	3.4	0.6
Quercus marilandica	131.0	27.8	6.3	1.2
Quercus stellata	—	41.7	—	1.8
Rhus copallinum L.	23.8	69.4	1.1	3.0
Sassafras albidum (Nutt.) Nees	—	13.9	—	0.6
Symplocos tinctoria (L.) L'Hér.	35.7	—	1.7	—
Vaccinium L.	750.0	1,361.1	36.0	58.7
Total	2,083.3	2,319.6	100.0	100.0

posed over half of all seedlings in both undisturbed (53%) and wind-disturbed (67%) neighborhoods. *Pinus palustris* had a relative density of 11% in undisturbed neighborhoods and 21% in wind-disturbed neighborhoods. Of 11 *Quercus* species identified, *Q. falcata* was the most abundant, with a relative density of 10% in undisturbed neighborhoods and 3% in wind-disturbed neighborhoods. *Pinus* species (excluding *P. palustris*) had a relative density of 6% in undisturbed neighborhoods and 2% in wind-disturbed neighborhoods, and *R. copallinum* had a relative density of 3% in undisturbed neighborhoods and 2% in wind-disturbed neighborhoods.

A significant main effect of taxonomic group ($P < 0.001$) and a significant interaction effect between disturbance category and taxonomic group ($P < 0.05$) on canopy-potential seedling density were apparent. With the exception of the Longleaf Pine Group, all canopy-potential taxonomic groups had lower average seedling densities in wind-disturbed plots (Fig. 3). Longleaf Pine averaged 2,238 seedlings ha^{-1} in undisturbed neighborhoods and 5,403 seedlings ha^{-1} in wind-disturbed neighborhoods. The Loblolly-Shortleaf Pine Group averaged 1,119 seedlings ha^{-1} in undisturbed neighborhoods and 556 seedlings ha^{-1} in wind-disturbed neighborhoods. The Oak-Hickory Group averaged 3,369 seedlings ha^{-1} in undisturbed neighborhoods and 1,250 seedlings ha^{-1} in wind-disturbed neighborhoods. The Others Group averaged 1,238 seedlings ha^{-1} in undisturbed neighborhoods and 569 seedlings ha^{-1} in wind-disturbed neighborhoods.

HERBACEOUS PLANTS. Ranked by frequency, Poaceae was the most common herbaceous plant taxon, occurring in 100% of undisturbed and wind-disturbed plots. *Gelsemium sempervirens* (L.) W.T. Aiton ranked second, occurring in 100% of undisturbed and 89% of wind-disturbed plots. Second to *G. sempervirens* in the vine life form group and fourth most common overall, *Smilax glauca* Walter occurred in 76% of undisturbed plots and 83% of wind-disturbed plots. *Pteridium aquilinum* ranked third in overall frequency, occurring in 76% of undisturbed plots and 83% of wind-disturbed plots. Fifth overall, *Coreopsis major* Walter was the most common forb, occurring in 86% of undisturbed plots and 61% of wind-disturbed plots, followed by *Sericocarpus*

Table 4. Density (stems ha^{-1}) and relative density of seedlings (live woody stems $\leq$ 1.2 m height) documented in undisturbed and wind-disturbed (wind) neighborhoods of longleaf pine stands in the Oakmulgee Ranger District of the Talladega National Forest, Alabama.

	Density (stems ha^{-1})		Relative density (%)	
Species	Undisturbed	Wind	Undisturbed	Wind
Acer rubrum	202.4	55.6	1.0	0.2
Aesculus pavia	83.3	—	0.4	—
Asimina parviflora (Michx.) Dunal	178.6	—	0.9	—
Callicarpa Americana	523.8	27.8	2.6	0.1
Carya glabra	107.1	—	0.5	—
Carya tomentosa	154.8	55.6	0.8	0.2
Cornus florida L.	11.9	27.8	0.1	0.1
Diospyros virginiana	214.3	69.4	1.1	0.3
Liquidambar styraciflua	381.0	41.7	1.9	0.2
Liriodendron tulipifera	11.9	—	0.1	—
Nyssa sylvatica	83.3	333.3	0.4	1.3
Oxydendrum arboreum	273.8	—	1.3	—
Pinus spp. L.	1,119.9	555.6	5.5	2.2
Pinus palustris	2,238.1	5,402.8	11.0	21.0
Prunus serotine	71.4	—	0.4	—
Quercus alba L.	23.8	—	0.1	—
Quercus coccinea	47.6	41.7	0.2	0.2
Quercus falcate	2,095.2	708.3	10.3	2.8
Quercus hemisphaerica	107.1	97.2	0.5	0.4
Quercus incana W. Bartram	—	41.7	—	0.2
Quercus marilandica	714.3	152.8	3.5	0.6
Quercus montana Willd.	11.9	—	0.1	—
Quercus nigra L.	11.9	55.6	0.1	0.2
Quercus rubra	35.7	13.9	0.2	0.1
Quercus stellate	—	83.3	—	0.3
Quercus velutina Lam.	59.5	—	0.3	—
Rhus copallinum	642.9	500.0	3.2	1.9
Sassafras albidum	—	69.4	—	0.3
Symplocos tinctoria	154.8	263.9	0.8	1.0
Vaccinium	10,726.2	17,125.0	52.9	66.5
Total	20,286.5	25,722.4	100.0	100.0

tortifolius (Michx.) Nees (71% and 61%, respectively), *Symphyotrichum* Nees (86% and 39%, respectively), *Solidago odora* Aiton (76% and 44%, respectively), *Tephrosia virginiana* (L.) Pers. (67% and 56%, respectively), *Pityopsis graminifolia* (Michx.) Nutt. (57% and 33%, respectively), *Eupatorium rotundifolium* L. (71% and 11%, respectively), *Trilisa odoratissima* (J.F. Gmel.) Cass. (24% and 50%, respectively), and *Vernonia angustifolia* Michx. (33% and 33%, respectively).

Herbaceous cover averaged 42% ± 4% SE on undisturbed plots and 31% ± 2% SE on wind-disturbed plots, and these values were significantly different ($P < 0.05$). Life form also had a significant main effect on herbaceous cover ($P < 0.001$). Ferns were the only life form with increased cover on wind-disturbed plots, averaging 10% cover on undisturbed plots and exceeding other life forms with 14% cover on wind-disturbed plots (Fig. 4). Forbs had the least cover in both disturbance categories, averaging 6% cover on undisturbed plots and 3% cover on wind-disturbed plots. Graminoids averaged 9% cover on undisturbed plots and 7% cover on wind-disturbed plots. Vines had the greatest cover on undisturbed plots, averaging 17% cover on undisturbed plots and 8% cover on wind-disturbed plots.

Discussion. Dead Trees. Relatively few decay class II stems were documented in undisturbed neighborhoods (background mortality), and those documented in wind-disturbed neighborhoods (wind-killed trees) exhibited mortality patterns closely aligned with similar studies and expectations based on the predisturbance conditions of the study area. The disproportionate ratio of conifers, especially *P. palustris*, to hardwoods in our study warrants caution in making general conclusions on taxon-specific mortality trends. Wind-induced mortality is positively related to tree size (Foster

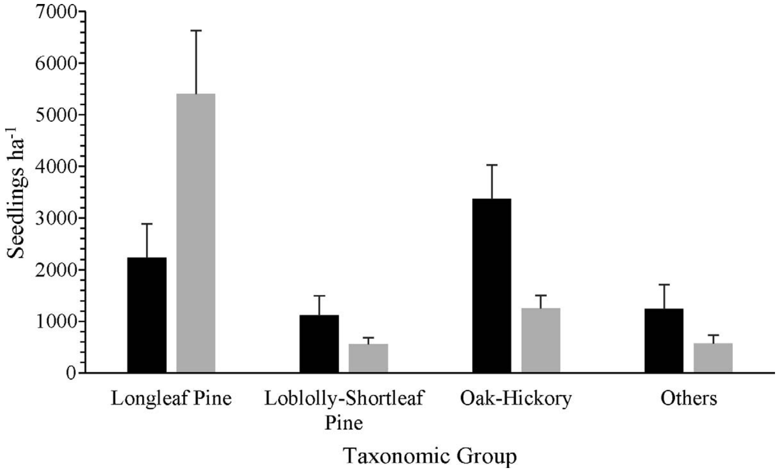

FIG. 3. Average density (stems ha^{-1}) with standard errors of seedlings (live woody stems $\leq$ 1.2 m height) with canopy potential categorized by taxonomic group in undisturbed (black bars) and wind-disturbed (gray bars) neighborhoods of *Pinus palustris* stands in the Oakmulgee Ranger District of the Talladega National Forest, Alabama. Taxonomic group had a significant main effect on canopy-potential seedling density ($P <$ 0.001), and disturbance category and taxonomic group had a significant interaction effect on canopy-potential seedling density ($P <$ 0.05).

and Boose 1992, Peterson 2007, Xi *et al.* 2008, White *et al.* 2015). Thus, *P. palustris* trees, which comprised the majority of canopy trees, were more susceptible to the wind disturbance. We documented increased chances of wind induced mortality with larger trees up to 30–35 cm diameter above root collar, at which few larger trees were documented dead or alive. Most wind-killed trees were uprooted or snapped, and these modes of death occurred at approximately equal proportions. Similar chances of root failure below ground and stem failure above ground may have reflected a resource allocation tradeoff between tree root and stem growth before the storm (Quine and Gardiner 2007). Additionally, some snapped *P. palustris* stems may be attributed to pre-existing *L. borealis* cavity-trees, which are more likely to snap at the cavity than uproot (Bainbridge *et al.* 2011).

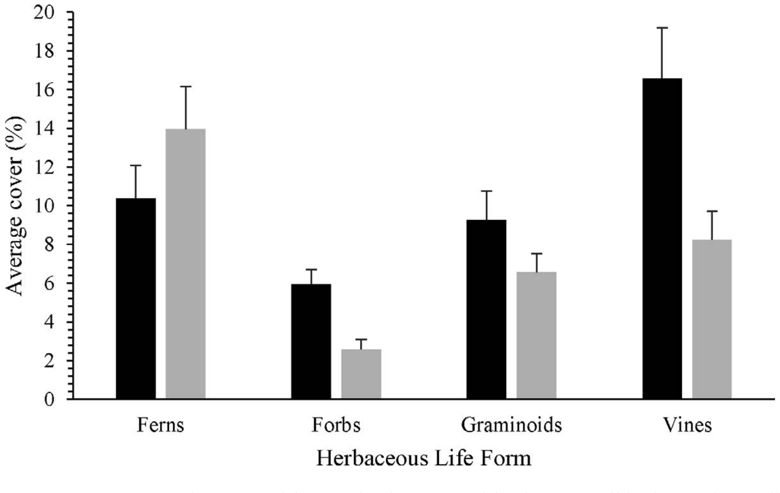

FIG. 4. Average percentage of cover with standard errors of herbaceous life forms in undisturbed (black bars) and wind-disturbed (gray bars) neighborhoods of *Pinus palustris* stands in the Oakmulgee Ranger District of the Talladega National Forest, Alabama. Life form had a significant main effect on herbaceous cover ($P <$ 0.001), and disturbance category had a significant main effect on herbaceous cover ($P <$ 0.05).

Overall, large *P. palustris* trees appeared most affected by the wind event, and contributed to the majority of uprooted and snapped stems documented in the study area.

LIVE TREES. Undisturbed and wind-disturbed neighborhoods showed marked differences in tree density and basal area, which was expected based on the catastrophic magnitude of the tornado. Reduced measures of tree biodiversity in wind-disturbed plots supported Peterson (2000) who discussed common reductions in canopy diversity when density-based measures of abundance were compared. Based on diameter distribution and vertical stratification, trees in wind-disturbed neighborhoods were likely advanced regeneration at the time of the wind event, and recruited to the tree stratum after the storm. The advanced regeneration that recruited was likely fire-tolerant, because the stands were in fire-maintained conditions before the storm.

Typically, after wind disturbance, recruitment of advanced reproduction to the tree stratum occurs in response to increased light transmittance through a wind-disturbed canopy (Oliver and Larson 1996, Gilliam, Platt, and Peek 2006). We observed this in our study, but we also documented many small-diameter trees with an intermediate crown class in undisturbed neighborhoods, of which most were *P. palustris* and *P. echinata*. This indicated that advanced *P. palustris* and *P. echinata* regeneration recruited to the tree stratum in undisturbed neighborhoods despite undisturbed neighborhoods having significantly greater canopy cover than wind-disturbed neighborhoods. Because staff on the national forest conduct prescribed fires at the compartment scale, and wind-disturbed neighborhoods within the compartment had hazardous fuel loads from wind-induced mortality, neither undisturbed nor wind-disturbed neighborhoods were burned after the storm. We posit that this lack of fire precipitated the pulse of *P. palustris* and *P. echinata* recruitment to the tree stratum in undisturbed neighborhoods. Thus, the wind event had an indirect effect beyond its localized track of catastrophic disturbance by excluding prescribed fire, which potentially allowed a new cohort of *Pinus* species to recruit in sections of the stands both undisturbed and directly impacted by the tornado.

Although the Longleaf Pine Group was the most important (based on density and dominance) tree taxonomic group in both disturbance categories, the Oak-Hickory Group and Others Group showed greater increases in relative density from undisturbed to wind-disturbed neighborhoods. Based on more noticeable differences in relative tree densities, we speculate that advanced regeneration in the Oak-Hickory Group and Others Group benefitted more from increased light transmittance in wind-disturbed plots. *Quercus* species in particular are described as shade-intolerant, relying on increased light for canopy recruitment, and so is *L. styraciflua*, the species in the Others Group that showed the greatest increase in relative density from undisturbed to wind-disturbed neighborhoods (Dey 2002).

The Loblolly-Shortleaf Pine Group was the only tree taxonomic group to have reduced relative density in wind-disturbed neighborhoods. Primarily composed of fire-resistant and shade-intolerant *P. echinata*, this group was likely not eliminated by predisturbance prescribed fire or unresponsive to increased light transmittance brought about by the wind event. Rather, *P. echinata* was probably outcompeted because of its slow growth rate in comparison to *P. palustris* and its other hardwood competitors (Kabrick *et al.* 2015).

SAPLINGS AND SEEDLINGS. In total, we documented over double the amount of species in the sapling and seedling strata compared to the tree stratum. Such disparities are especially common in conifer forests dominated by few tree species (Gilliam 2007). Among sapling and seedling strata, reduced biodiversity in wind-disturbed plots contradicted studies that reported greater woody stem diversity in areas disturbed by catastrophic wind (Peterson and Pickett 1995, Dobrowolska 2015). However, Denslow (1985) predicted lower species diversity when areas that are regularly subjected to low-intensity disturbances experience an infrequent, high-intensity event. Our results supported this model, as the study area was maintained by frequent surface fires, but experienced an infrequent, high-intensity wind storm. Although we did not compare our stands to those that were burned after the storm, we speculate that poststorm prescribed fire exclusion may provide an additional explanation for the uncharacteristically low woody diversity in wind-disturbed neighborhoods. In fire-adapted ecosystems, some species require burned substrate for germination, and so lack of fire may have precluded their success. Interruption of a recurring disturbance such as surface fire in *P. palustris* ecosystems may be viewed as an additional perturbation in multiple disturbance severity models such the one proposed by Roberts (2004), and our study provides impetus for further assessing fire exclusion as an impediment in forest recovery.

The five most abundant sapling taxa differed between disturbance categories, but the five most abundant seedling taxa remained the same. Interestingly, the five most abundant sapling taxa in wind-disturbed neighborhoods matched the five most abundant seedling taxa, with the exception of fourth most abundant sapling taxon, *N. sylvatica*, replacing *Pinus* species (excluding *P. palustris*). Because the most abundant seedling taxa were more competitive in wind-disturbed neighborhoods, we suggest that the wind event perpetuated the most abundant seedling taxa into the sapling stratum.

The wind event also facilitated increased relative densities of the most abundant taxa within strata. In particular, *Vaccinium* and *P. palustris* had increased relative densities in wind-disturbed neighborhoods, whereas most other seedling and sapling taxa had lower relative densities in wind-disturbed neighborhoods. The relative density of *Vaccinium* far exceeded those of other taxa in both sapling and seedling strata in both disturbance categories, and so revealed less on disturbance-mediated forest dynamics. However, changes in the relative density of *P. palustris* appeared wind-induced, especially in the sapling stratum where *P. palustris* was a minor component in undisturbed neighborhoods but had the second greatest relative density in wind-disturbed neighborhoods. As in the tree stratum, decreased relative densities of *P. echinata* saplings and seedlings mirrored increased relative densities of *P. palustris* saplings and seedlings. These differences in *Pinus* densities may be attributed to the superior ability of *P. palustris* to grow in dry conditions such as those enhanced by wind-induced canopy openings (Sayer, Brissette, and Barnett 2005).

The relative densities of individual sapling and seedling taxa with canopy potential dictated changes in their corresponding taxonomic groups. Longleaf pine saplings and seedlings and Oak-Hickory saplings were the only groups with increased relative densities in wind-disturbed neighborhoods. Thus, the tornado seems to have facilitated continued dominance of desirable species in our study area by increasing the competitive ability of *P. palustris* and creating conditions where *Quercus* seedlings could outcompete other hardwoods for growth into the sapling stratum.

Herbaceous Plants. Herbaceous plants must compete with woody plants for growing space (Gilliam 2007), and so herbaceous cover may have been reduced on wind-disturbed plots because of increased sapling and seedling density. However, these results deviated from other studies that described increased herbaceous cover when canopy cover was reduced (Harrington and Edwards 1999, Platt *et al*. 2006). The effects of fire on reducing woody competition and increasing herbaceous cover in *P. palustris* ecosystems have been reported in other studies (*e.g*., Brockway and Lewis 1997, Stokes *et al*. 2010). Likewise, herbaceous cover is known to diminish with long fire-free periods (Walker and Silletti 2006). Like woody diversity, we speculate that herbaceous cover may have been reduced in wind-disturbed neighborhoods because fire was withheld after the disturbance thereby barring creation of suitable regeneration substrate in the fire-adapted herbaceous community. However, we must be cautious with this supposition as we did not survey stands that continued to be burned after the tornado for comparison.

Our study corroborated others that described increased *Pteridium aquilinum*, a persistent and widespread fern, in disturbed areas (Skutch 1929, Roberts and Gilliam 1995). Along with Poaceae, the taxonomic family of *S. scoparium*, *Pteridium aquilinum* is recognized as a chief component of the herbaceous stratum in our study area (Beckett and Golden 1982, Teague *et al*. 2014). It follows that Poaceae was the most frequent herbaceous taxon, and its corresponding life form, graminoids, had the most consistent cover. We attributed low forb cover in both disturbance categories to the small stature of most forbs and not a lack of their presence. Compositionally, the most common forb taxa supported the USNVC description of high Asteraceae diversity, and closely corresponded with the flora reported in proximal stands (Beckett and Golden 1982, Teague *et al*. 2014). It was interesting that vines had more cover than other life forms on wind-disturbed plots. *Gelsemium sempervirens* and *Smilax glauca* were particularly abundant. It was unexpected, however, that vines had reduced cover on wind-disturbed plots, as other vines documented on the site such as *Muscadinia rotundifolia* (Michx.) Small var.

rotundifolia and *Rubus* L. typically grow well in open forests (Miller and Miller 2005). As with overall herbaceous cover, we must be discerning in interpreting changes in the cover of herbaceous life forms because the herbaceous stratum, especially in *P. palustris* ecosystems, is both adapted and sensitive to fire, and these stands endured an unusually long fire-free period.

Conclusions. We documented the impact of a 2011 EF3 tornado that tracked through the Alabama Fall Line Hills and resulted in a path of catastrophic disturbance in fire-restored *P. palustris* stands. We noted increased chances of wind-induced mortality in larger trees, and approximately equal proportions of uprooted and snapped stems. Despite constituting the majority of dead stems, *P. palustris* persisted with increased relative densities in the tree, sapling, and seedling strata of wind-disturbed neighborhoods. The relative densities of *Quercus* trees and saplings were also greater in wind-disturbed neighborhoods. Thus, the wind event reinforced a positive feedback by facilitating the continued dominance of *P. palustris* and a relatively strong component of *Quercus* species. This desirable woody species recovery coupled with an herbaceous stratum composition comparable to other restored stands in the Talladega National Forest led us to conclude that the *P. palustris* stands studied here were resilient to catastrophic wind disturbance. Contrary to our expectations based on other studies, woody stem diversity and herbaceous cover were reduced in wind-disturbed neighborhoods. Although we did not directly compare the wind-disturbed and fire-excluded stands to wind-disturbed stands that continued to be burned after the storm, we suspect that poststorm prescribed fire exclusion was in part responsible for this discrepancy. Nonetheless, our study provides unique insight to a suite of investigations on the role of wind disturbance in *P. palustris* stand dynamics as the effects of high-intensity tornadoes in these systems have not been well documented, especially with respect to herbaceous plants. We hope that the species-specific responses reported serve as a benchmark for understanding and tracking changes in *P. palustris* communities, and may guide management decisions including those designed to restore and promote native diversity in similar ecosystems.

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