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Prescribed fire effects on *Pinus palustris* woodland development after catastrophic wind disturbance and salvage logging

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ABSTRACT

Scientifically informed strategies to manage naturally disturbed forests are critical to support the sustained provisioning of ecosystem goods and services. In fire-adapted ecosystems, catastrophic canopy removal can disrupt surface fuel continuity and challenge the continued use of low-intensity prescribed fire. Although salvage logging is used globally after natural disturbance events, little information is available on how salvage logging interacts with subsequent use of prescribed fire. This study investigated the impacts of operational-scale prescribed fire on *Pinus palustris* (longleaf pine) stand development in areas differentially impacted by an April 2011 EF3 tornado and a subsequent salvage logging operation. Twenty 0.04-ha nested plots were systematically established in mature, wind-disturbed, and salvage-logged sites ($n = 60$) to measure seedlings, saplings, woody fuels, organic litter, and mineral soil before and after prescribed fire. Prescribed fire-induced fine fuel consumption, mineral soil exposure, and substantial sapling density reductions were observed throughout the treatment area. Prescribed fire effects were not apparently impacted by salvage logging, which did not alter the amount of fine fuels available for prescribed fire consumption. Despite overall sapling density reductions, fire-resistant *P. palustris* saplings exhibited increased densities on wind-disturbed and salvage-logged sites. *Pinus palustris* seedlings, however, exhibited marked post-fire reductions, which contrasted with a strong resprouting response observed among top-killed hardwood species. Concerning woody plant recovery, this study indicated that salvage logging was not detrimental to *P. palustris* stand development and that prescribed fire effectively enhanced recovery in unlogged and logged wind-disturbed sites.

1. Introduction

Forest disturbances alter the spatial arrangement of ecosystem components, thereby influencing successional, developmental, and functional processes (Oliver and Larson, 1996, Franklin et al., 2002). Of particular concern are forest disturbances that interact to impact the sustained provisioning of ecosystem goods and services (Turner, 2010, Thom and Seidl, 2016). Wind disturbance and fire represent major components of terrestrial disturbance regimes worldwide (MacDonald, 2003), and have substantial socioeconomic impacts on forest ecosystems in the United States (Dale et al., 2001). Salvage logging is commonly applied after natural disturbances to partially capture the economic value of wood products in damaged or dead trees, and to reduce risk and severity of subsequent disturbance events (Leverkus et al., 2018, Müller et al., 2019).

Despite its widespread social and economic importance, the ecological effects of salvage logging remain unresolved (Stanturf et al., 2007). Salvage logging, by definition, extracts deadwood that may otherwise contribute to the structural diversity of early-successional forests and serve as critical habitat in ecosystem recovery (Franklin et al., 2000, Swanson et al., 2011, Lindenmayer et al., 2019). Salvage logging can also damage residual trees, saplings, and seedlings, thereby altering post-disturbance successional trajectories (White et al., 2014, Knapp and Ritchie, 2016). As public debate continues on how to manage forests after natural disturbance events (Stokstad, 2006, Lindenmayer et al., 2017), a growing literature challenges the presumption that salvage logging always leads to negative ecological consequences (Lang et al., 2009, Fidej et al., 2016, Royo et al., 2016). For example, Peterson and Leach (2008) and Sass et al. (2018) report similar successional pathways in unlogged and logged sites despite altered microsite conditions. Salvage logging can also facilitate coexistence of species that would not otherwise persist after natural disturbances alone (Royo et al., 2016, Slyder et al., 2019).

Recent reviews of the salvage logging literature underscore that our

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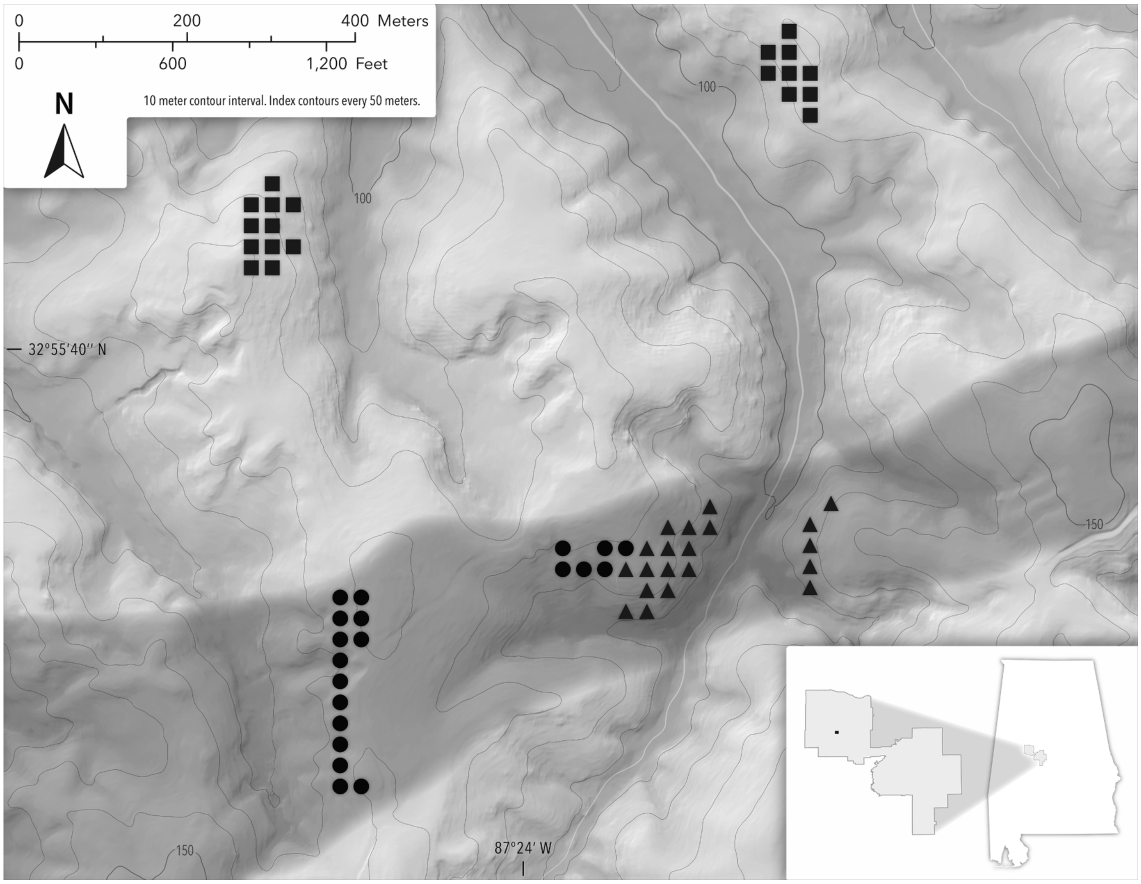

Fig. 1. Study area in the Oakmulgee District, Talladega National Forest, Alabama, USA (shaded on inset map). Tornado path is shaded, with symbols indicating plot locations in mature (squares), wind-disturbed (triangles), and salvage-logged (circles) sites.

current understanding is disproportionately based on post-fire operations (Leverkus et al., 2018, Thorn et al., 2018). Compared to fire, however, wind disturbances leave distinct legacies that influence forest recovery that may be differentially impacted by salvage logging (Johnstone et al., 2016). For instance, wind disturbances deposit, but do not consume, forest floor litter and debris, and typically do not remove understory vegetation (Roberts, 2004, Gilliam et al., 2006). Moreover, although salvage logging is often justified as risk reduction, few studies have assessed the resilience of salvaged stands to subsequent disturbance events (D'Amato et al., 2011, Buma and Wessman, 2012, Taboada et al., 2018). Because wind-deposited fuel loads can amplify fire effects, post-wind disturbance salvage logging may attenuate high-intensity fires and positively impact post-fire forest recovery (Buma, 2015). Low-intensity fires, however, often require an uninterrupted fine fuel bed, and may be inhibited by surface fuel discontinuity and the potential release of less flammable plant species in wind-disturbed sites (Cannon et al., 2017). Although salvage logging can have additional impacts on plant communities and surface fuel dynamics, relatively little is known about low-intensity fire effects on sites salvage-logged after wind disturbance (Palik and Kastendick, 2009). This study investigated low-intensity prescribed fire effects on *Pinus palustris* (longleaf pine) stand development in wind-disturbed sites that were either salvage logged or not logged, as well as mature sites not impacted by catastrophic wind disturbance but subject to the same prescribed fire regime.

Prior to European settlement, *P. palustris* ecosystems occupied ca. 37 million ha across the southeastern United States and experienced frequent, low-intensity surface fires ignited by lightning strikes and Native Americans (Frost, 2006). Restricted to less than 5% of its pre-settlement extent, the endangered *P. palustris* ecosystem is now managed with prescribed fires with strong federal, state, and private support (Noss et al., 1995, Melvin, 2015). Prescribed fires facilitate a positive feedback in *P. palustris* ecosystems in which highly flammable, canopy-derived *Pinus* litter sustains frequent fires, which inhibit canopy recruitment of less fire-resistant species (Platt et al., 1988, O'Brien et al., 2008, Mitchell et al., 2009). Fire-maintained *P. palustris* stands, in turn, sustain a suite of ecosystem services, including quality habitat for federally endangered *Leuconotopicus borealis* Vieillot (red-cockaded woodpeckers), terrestrial carbon storage, and valuable, drought-tolerant timber (Kush et al., 2004, Samuelson et al., 2019). Conceptual understanding of *P. palustris* stand dynamics can be used to guide the management of other fire-adapted forests, such as neotropical *Pinus* forests of the Caribbean, *P. echinata* (shortleaf pine) forests of the North American Interior Highlands, and *P. ponderosa* (ponderosa pine) forests across the North American Intermountain West (Bigelow et al., 2018). Indeed, prescribed fire application in the southeastern United States provides a model for the management of federally endangered *Strix occidentalis* (spotted owl) habitat ranging from British Columbia to Mexico (Stephens et al., 2019).

The overarching objective of this study was to assess the impacts of operational-scale prescribed fire on *P. palustris* stand development on sites differentially impacted by an EF3 tornado and a subsequent salvage logging operation. Baseline data indicated that *P. palustris* saplings were substantially outnumbered by other species in mature, wind-disturbed, and salvage-logged sites (Kleinman et al., 2017, Ford et al., 2018). We therefore questioned whether prescribed fire would effectively enhance *P. palustris* recovery through shoot mortality of less fire-resistant species. In other words, it was unclear whether prescribed fire would reduce hardwood sapling densities on sites impacted by catastrophic canopy removal where canopy-derived *Pinus* litter may be insufficient to sustain low-intensity fire (O'Brien et al., 2008, Mitchell et al., 2009). Nonetheless, a growing literature in vegetation-fire feedbacks recognizes the importance of flammable fuels derived from other fire-adapted plants such as pyrophytic *Quercus* (oak) spp. (Kane et al., 2008, Hiers et al., 2014, Fill et al., 2015). We therefore hypothesized that wind-disturbed and salvage-logged sites, which hosted relatively high *Quercus* seedling and sapling densities and herbaceous vegetation cover (Kleinman et al., 2017), would experience prescribed fire-induced sapling density reductions. We also hypothesized that deadwood extraction on salvage-logged sites would have negligible impacts on prescribed fire effects. Specifically, we did not expect that low-intensity prescribed fire, carefully scheduled to avoid extreme weather conditions, would be altered by the presence or absence of larger (i.e. merchantable) pieces of deadwood targeted by salvage logging.

2. Methods

2.1. Study area

This study was conducted in the Oakmulgee District of the Talladega National Forest in Bibb County, Alabama (32°55′30″N, 87°24′00″W; Fig. 1). Situated in the Fall Line Hills ecoregion (level III), the Oakmulgee District occurs within the *Quercus-Pinus* forest region of the United States (Braun, 1950, Griffith et al., 2001). The Fall Line Hills physiographic transition zone spans the inland border of the Coastal Plain, where deeply eroded, marine-deposited sediments meet the steep slopes and ridges of the adjacent Appalachian Highlands (Fenneman, 1938). This environmental gradient supports plant assemblages characteristic of the Coastal Plain and Appalachian Highlands (Shankman and Hart, 2007, Kleinman and Hart, 2018). In the Oakmulgee District, *P. palustris*-dominated woodlands occur on fire-maintained upper slopes and south-facing lower slopes, and a diversity of *Quercus* spp. and other hardwoods coexist with *P. echinata* (shortleaf pine) and *P. taeda* (loblolly pine) in the overstories of unburned sites and bottomlands (Beckett and Golden, 1982).

Hillslopes and ridges in the study area contain deep, moderately-well drained soils derived from the Cretaceous-aged Gordo Formation (GSA, 2006, USDA NRCS, 2020). Maubila series soils consist of a sandy loam or loam surface layer up to 10 cm deep and clay-based substrata over 200 cm deep to bedrock (USDA NRCS, 2008). The area exhibits a humid mesothermal climate, characterized by long, hot summers and year-round precipitation (Thornthwaite, 1948). Mean temperature is 17.2 °C, with mean January and July temperatures of 6.6 °C and 26.9 °C, respectively, and mean annual precipitation is 1376.21 mm (PRISM, 2020). The frost-free period is ca. 230 days from March to November (USDA NRCS, 2008).

The USDA Forest Service manages *P. palustris* woodlands in the Oakmulgee District with prescribed fires every 2–5 years. Prescribed fires reduce fuel loads, maintain fire-adapted ground flora assemblages, top-kill fire-sensitive woody plants that would otherwise outcompete *P. palustris* for canopy dominance, and increase availability of substrate (i.e. bare soil) suitable for *P. palustris* and herbaceous plant germination. On 27 April 2011, an EF3 tornado with estimated wind speeds of 233 kph and a maximum width of 1609 m tracked through the Oakmulgee District (NWS, 2011). Within seven months, wheeled feller bunchers and chainsaws were used to salvage wind-damaged trees, which were transported with wheeled skidders to ramp sites for processing by a stationary knuckleboom loader. Salvage logging occurred near pre-existing road networks, leaving some wind-disturbed sites unlogged. Thus, the presence of areas unimpacted by the tornado, wind-disturbed but unlogged, and salvage-logged, combined with an active prescribed fire program, provided the opportunity to assess the impacts of multiple interacting disturbances on *P. palustris* woodland development.

2.2. Experimental design and field methods

In March 2016, at the start of the sixth growing season post-wind disturbance, satellite imagery, geospatial data, and ground reconnaissance were used to select sites with analogous pre-disturbance conditions (Kleinman et al., 2017, Ford et al., 2018). Sites with the greatest possible similarity in pre-disturbance biophysical conditions were selected so observed differences in site conditions could be attributed to the disturbance events of interest, not pre-disturbance variability. Although less robust than experimental inference, such space-for-time substitutions are necessary to advance understanding of "natural experiments" (e.g. tornadoes) in which experimental replicability is not always practical (Pickett, 1989, Hargrove and Pickering, 1992, Davies and Gray, 2015). Selected sites were *P. palustris*-dominated woodlands that originated in the early 1930s after industrial-scale logging and federal acquisition of the land. Sites occur within a 1 km^2 expanse of the same watershed on upper- and mid-slope positions with Maubila series soils. Sites are located in the same Forest Service-delineated compartment, which ensures they experience the same prescribed fire regime. The most recent prescribed fires in the compartment occurred May 2010 before the tornado, April 2014 before field sampling, and April 2018 before and after field data collection. As such, data collected May–July of 2016 and 2017 are referred to as "before fire" or "pre-fire" data, and data collected June 2018 are referred to as "after fire" or "post-fire" data. We note, however, that pre- and post-fire data must be interpreted with caution because, based on the timing of study initiation, impacts of the April 2014 prescribed fire cannot be distilled from April 2018 prescribed fire effects.

We delineated three pre-fire disturbance categories in the selected sites (Kleinman et al., 2017, Ford et al., 2018). Mature sites exhibited no visible tornado damage, and had a basal area of 21.7 m^2h^{-1} and 90% canopy cover. Wind-disturbed sites included areas directly impacted by the tornado that were left unlogged, and had a residual basal area of 1.1 m^2h^{-1} and 14% canopy cover. Salvage-logged sites were impacted by the tornado and exhibited obvious signs of salvage logging, including mechanically cut stems, and had a residual basal area of 0.6 m^2h^{-1} and 5% canopy cover. The relatively sharp transition zone (ca. 70 m) between sites unimpacted by the April 2011 EF3 tornado and sites that experienced catastrophic canopy removal was avoided to reduce potential variability in disturbance severity along the forest edge (Goode et al., 2020). Twenty nested plots were systematically established with 25-m spacing in each disturbance category ($n = 60$). Nested plots consisted of a 400-m^2 plot and ten nested 1 × 1 m quadrats (10 m^2). Center quadrats were positioned at the center of each 400-m^2 plot, and the other nine quadrats were spaced evenly along the 0°, 120°, and 240° azimuths from plot center.

The largest sampling units (400-m^2 plots) were used to survey saplings (live woody stems > 1 m in height and < 5 cm at 1.37 m above root collar) and downed coarse woody debris (CWD) in 2016 and 2018. Coarse woody debris included deadwood ≥ 10 cm diameter categorized as logs (i.e. dead stems disconnected from roots) and uprooted stems (dead stems with uplifted root networks; USDA, 2016). Logs were measured for diameter at both ends and uprooted stems were measured for diameter at 1.37 m from root plate. Coarse woody debris was also measured for length and assigned a decay class from I to V according to increasing degree of decay (USDA, 2016).

In 2016 and 2018, saplings were identified and tallied in each 400-m^2 plot, and seedlings, defined as live woody stems ≤ 1 m in height of seed or sprout origin, were identified and tallied in nested 1-m^2 quadrats. Nested quadrats were also used to estimate the percent cover of ground surface categories in 2017 and 2018. Ground surface categories included CWD, fine woody debris (FWD, woody material < 10 cm diameter), bare mineral soil, and organic litter (dead, nonwoody material), which was further distinguished as *Pinus* litter, Poaceae (grass) litter, or other litter (i.e. broadleaves and duff). Ground surface categories were assigned a cover class from 0 to 10 adapted from the North

Carolina Vegetation Survey (NCVS), where 0 = absent, 1 = trace, 2 = 0–1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95%, and 10 = 95–100% (Peet et al., 1998).

2.3. Analytical methods

Mixed (split-plot) ANOVAs were used to assess differences in response variables between background disturbance categories (mature, wind-disturbed, and salvage-logged) and across time (before and after prescribed fire). When disturbance categories and time failed to exhibit significant interactions, main effects were assessed with one-way ANOVAs and Tukey HSD tests (levels of $P < 0.05$ considered significant). Changes in aboveground biomass were used to assess prescribed fire severity and infer qualities of prescribed fire intensity (i.e. physical energy released; Keeley, 2009). Specifically, the volume of CWD and the percent cover of ground surface categories were compared between disturbance categories before and after prescribed fire. To assess impacts of prescribed fire on woody plant reproduction in areas differentially impacted by wind disturbance and salvage logging, sapling and seedling density, richness, and Shannon diversity were compared before and after prescribed fire. All response variables were standardized to the hectare level and transformed as necessary for statistical analyses to meet assumptions of homoscedasticity.

To calculate CWD volume (m^3ha^{-1}), a conic paraboloid equation was used for logs (Fraver et al., 2007), and species-specific allometric equations were used for uprooted stems (Woodall et al., 2011, Parker and Hart, 2014, Ford et al., 2018). Based on decay dynamics of species in the study area, CWD in decay classes II and III were likely deposited by the wind event and were therefore referred to as wind-deposited CWD (Russell et al., 2014, Ulyshen et al., 2018). Proportions of wind-deposited CWD in decay classes II and III were compared between 2016 and 2018 to assess impacts of decay on CWD volume reductions. To calculate plot-level ground surface cover values, quadrat-level NCVS rankings were converted to corresponding range midpoints, averaged per plot, and reconverted to NCVS cover classes (Peet et al., 1998). Seedling densities were summed across quadrats to determine plot-level densities, and, together with sapling densities, were compared by species to assess disturbance impacts on woody plant competition and vertical stratification.

3. Results

3.1. Fire severity

The volume of CWD was significantly impacted by the interaction of pre-fire disturbance history and time relative to prescribed fire ($P < 0.001$). Before prescribed fire, CWD volume was 5.7 m^3ha^{-1} on mature sites, 179.0 m^3ha^{-1} on wind-disturbed sites, and 19.9 m^3ha^{-1} on salvage-logged sites. After prescribed fire, CWD volume was reduced by only 3% on mature sites, but dropped 22% and 29% on wind-disturbed and salvage-logged sites, respectively (Fig. 2). On mature sites, CWD in decay classes II and III accounted for 70% (i.e. 4.0 m^3ha^{-1}) of the CWD volume documented on these sites in 2016, and may be considered background mortality. On wind-disturbed and salvage-logged sites, CWD in decay classes II and III (i.e. wind-deposited CWD) accounted for 99.8% and 98.9% of the CWD volume documented on these sites in 2016 and 2018, respectively. Over the duration of the study, the proportion of wind-deposited CWD categorized as decay class II decreased and the proportion categorized as decay class III increased (Fig. 3). In 2016, decay class II stems composed 93% of the volume of wind-deposited CWD on wind-disturbed and salvage-logged sites, but only 59% in 2018. This reduction was counterbalanced by decay class III stems, which composed 7% of the volume of wind-deposited CWD on wind-disturbed and salvage-logged sites in 2016 and 41% in 2018.

Based on ground cover estimates taken on nested quadrats, the percent surface cover of CWD was also reduced, albeit almost imperceptibly, after prescribed fire ($P = 0.048$, Table 1, Fig. 4). From 2017 to 2018, average CWD cover changed from 0.4% ± 0.2% (standard error, SE) to 0.3% ± 0.2% (SE) on mature plots, 10.0% ± 1.5% (SE) to 7.8% ± 1.2% (SE) on wind-disturbed plots, and 3.6% ± 0.9% (SE) to 2.4% ± 0.8 (SE) on salvage-logged plots. Excluding the surface cover of CWD, which was lower on salvage-logged plots compared to wind-disturbed plots ($P = 0.006$), surface cover categories did not significantly differ between wind-disturbed and salvage-logged plots before prescribed fire. Mature plots, however, were characterized by less exposed mineral soil and Poaceae litter cover ($P < 0.001$ and $P = 0.005$, respectively), and more *Pinus* litter cover ($P < 0.001$), than wind-disturbed and salvage-logged plots. After prescribed fire, all disturbance categories exhibited increased bare mineral soil exposure and reduced *Pinus* and Poaceae litter cover ($P < 0.001$).

3.2. Woody plant regeneration

The interaction of pre-fire disturbance history and time relative to prescribed fire significantly impacted the density of saplings ($P < 0.001$) and seedlings ($P = 0.008$; Table 2, Fig. 2). After prescribed fire, reduced sapling densities were observed on mature, wind-disturbed, and salvage-logged sites (Table 3), which coincided with increases in seedling densities (Table 4). Changes were most pronounced on wind-disturbed sites where prescribed fire reduced sapling density by 6,156 stems ha^{-1}, compared to reductions of 2,709 stems ha^{-1} and 2,746 stems ha^{-1} on mature and salvage-logged sites, respectively. Despite overall sapling density reductions, the density of *P. palustris* saplings increased after prescribed fire on wind-disturbed and salvage-logged sites. Before prescribed fire, *P. palustris* saplings were outnumbered by 21 other species on wind-disturbed sites and 13 other species on salvage-logged sites. After prescribed fire, however, *P. palustris* saplings were outnumbered by only seven and three other species on wind-disturbed and salvage-logged sites, respectively. In contrast to *P. palustris*, these other species (i.e. *Liquidambar styraciflua*, *Quercus coccinea*, *Q. falcata*, *Q. nigra*, *Q. stellata*, *Rhus copallinum*, and *Vaccinium arboreum*), all exhibited marked post-fire sapling density reductions compared to pre-fire measurements. After prescribed fire, mature, wind-disturbed, and salvage-logged sites also exhibited reduced sapling species richness ($P < 0.001$) and Shannon diversity ($P = 0.015$) values (Table 5). Nonetheless, sapling species richness and Shannon diversity remained lowest in mature sites before and after prescribed fire ($P < 0.001$). Compared to salvage-logged sites, wind-disturbed sites hosted greater pre-fire values of sapling species richness ($P = 0.015$) and Shannon diversity ($P = 0.013$), however, prescribed fire negated these differences.

Contrary to the sapling stratum, *P. palustris* seedling densities were reduced after prescribed fire by 42% and 46% in wind-disturbed and salvage logged sites, respectively. Mature sites exhibited an even greater *P. palustris* seedling density reduction of 90%. This relative seedling density reduction was exceeded only by other *Pinus* spp. (i.e. combined *P. echinata* and *P. taeda* seedling densities), which were reduced by 98% in mature sites, and 56% and 70% in wind-disturbed and salvage-logged sites, respectively. Other species with noteworthy seedling density reductions included *Cornus florida*, *Q. laevis*, and *Q. stellata*, which exhibited reduced post-fire seedling densities in all three disturbance categories. Whereas *P. palustris* composed the majority of seedlings counted on mature plots prior to prescribed fire, six other seedling species outnumbered *P. palustris* on mature plots after prescribed fire. Four of these species (i.e. *Gaylussacia dumosa*, *Q. alba*, *Q. falcata*, and *Rhus copallinum*), exhibited more than doubled seedling densities after prescribed fire in all disturbance categories. Although total seedling densities increased after prescribed fire, seedling richness and Shannon diversity values were reduced in every disturbance category ($P < 0.001$, Table 5). Nonetheless, seedling richness remained greatest on wind-disturbed plots before ($P = 0.027$) and after prescribed fire ($P = 0.037$).

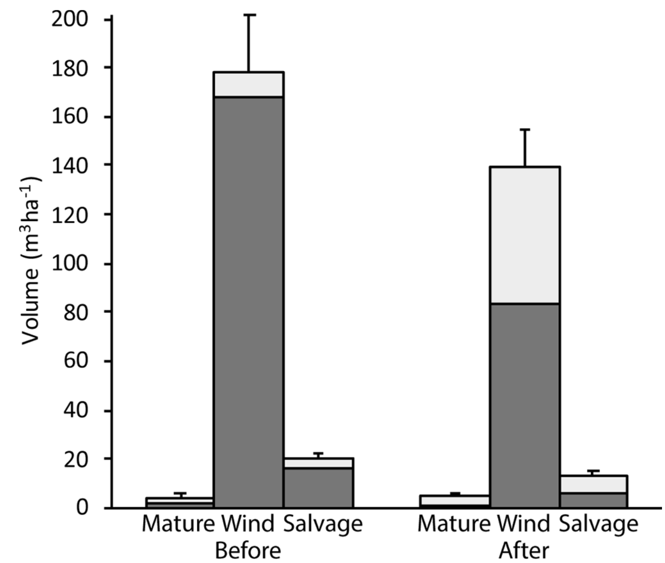

Fig. 2. Disturbance category and time relative to prescribed fire had significant interactions on the average volume of coarse woody debris (CWD, P < 0.001), sapling density (P < 0.001), and seedling density (P = 0.008) documented in mature (light gray squares, short-dashed lines), wind-disturbed (dark gray triangles, long-dashed lines), and salvage-logged (black circles, solid lines) plots before (2016) and after (2018) prescribed fire.

4. Discussion

Global recognition of more frequent and severe forest disturbance events has motivated mounting interest in strategies to manage naturally disturbed forests (Seidl et al., 2017, Sommerfeld et al., 2018). Of all catastrophic wind disturbances that impact forest ecosystems, tornadoes reach the greatest wind speeds and mortality rates (Everham and Brokaw, 1996), and are becoming increasingly frequent in the southeastern United States (Gensini and Brooks, 2018). Forest managers and policy makers must therefore be increasingly prepared to consider the potential ecological consequences of post-wind disturbance salvage logging. Results and recommendations of this study may be used to develop strategies to manage other forests subject to catastrophic canopy removal, especially fire-adapted forests managed with low-intensity prescribed fires.

Based on before- and after-prescribed fire data collected in areas differentially impacted by catastrophic wind disturbance and salvage logging, salvage logging did not alter the amount of fine fuels available for prescribed fire consumption. With the exception of CWD, the percent cover of surface fuel categories did not significantly differ between wind-disturbed and salvage-logged sites before prescribed fire. To echo Fraver et al. (2017), these results can be attributed to the retention of slash on salvaged sites where merchantable deadwood extraction, not fuels reduction, was the primary management objective. Considering that larger fuels (i.e. CWD) have a negligible impact on fire ignition and rate of spread compared to fine fuels with a higher surface-area-to-volume ratio (Rothermel, 1972), we contend that prescribed fire intensity was largely unaffected by deadwood extraction on salvage-logged sites. Nonetheless, these results must be interpreted with caution because an earlier (April 2014) prescribed fire, conducted before this study was initiated, likely altered fine fuels in the study area and may have been differentially impacted by salvage logging.

Although slight post-fire reductions in the percent cover and volume of CWD were observed, these reductions could be attributed to decay processes other than prescribed fire consumption (Cornwell et al., 2009). Between the 2016 and 2018 deadwood surveys, approximately one-third of the CWD volume documented on wind-disturbed and salvage-logged sites transitioned from decay class II to decay class III. Compared to decay class II stems, decay class III stems have sapwood that can be broken apart by hand (USDA, 2016). This decay class transition was not surprising considering that, during 2016 baseline data collection, Ford et al. (2018) documented 97% of saproxylic (i.e.

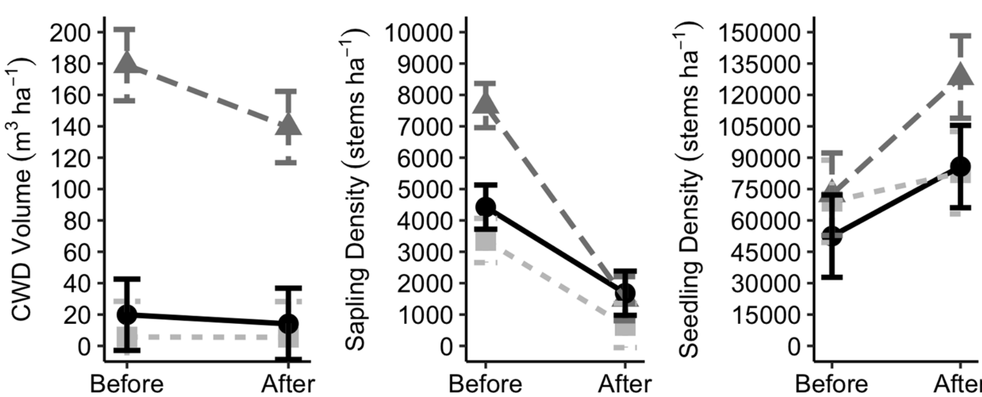

Fig. 3. Volume (m^{3}ha^{-1}) of coarse woody debris (CWD) categorized as decay class II (dark gray bars) and decay class III (light gray bars) in mature, wind-disturbed, and salvage-logged plots before (2016) and after (2018) prescribed fire.

Table 1
Summary of mixed ANOVAs used to assess the impacts of pre-fire conditions (mature, wind-disturbed, and salvage-logged), time relative to prescribed fire (before and after), and their interaction on ground surface cover categories. Statistically significant values (P < 0.05) are indicated with bold text.

Surface Cover (%)	Pre-Fire Condition (C)			Time (T)			C × T		
	F-values	*P*-values	df	*F*-values	*P*-values	df	*F*-values	*P*-values	df
Coarse Woody Debris	88.72	**< 0.001**	2	4.085	**0.048**	1	0.634	0.534	2
Fine Woody Debris	6.595	**0.003**	2	0.096	0.758	1	1.269	0.289	2
Bare Mineral Soil	89.92	**< 0.001**	2	74.22	**< 0.001**	1	0.764	0.47	2
Pinus Litter	185.1	**< 0.001**	2	29.816	**< 0.001**	1	1.452	0.243	2
Poaceae Litter	27.43	**< 0.001**	2	59.376	**< 0.001**	1	2.305	0.109	2
Other Litter	7.634	**0.001**	2	30.911	**< 0.001**	1	6.818	**0.002**	2

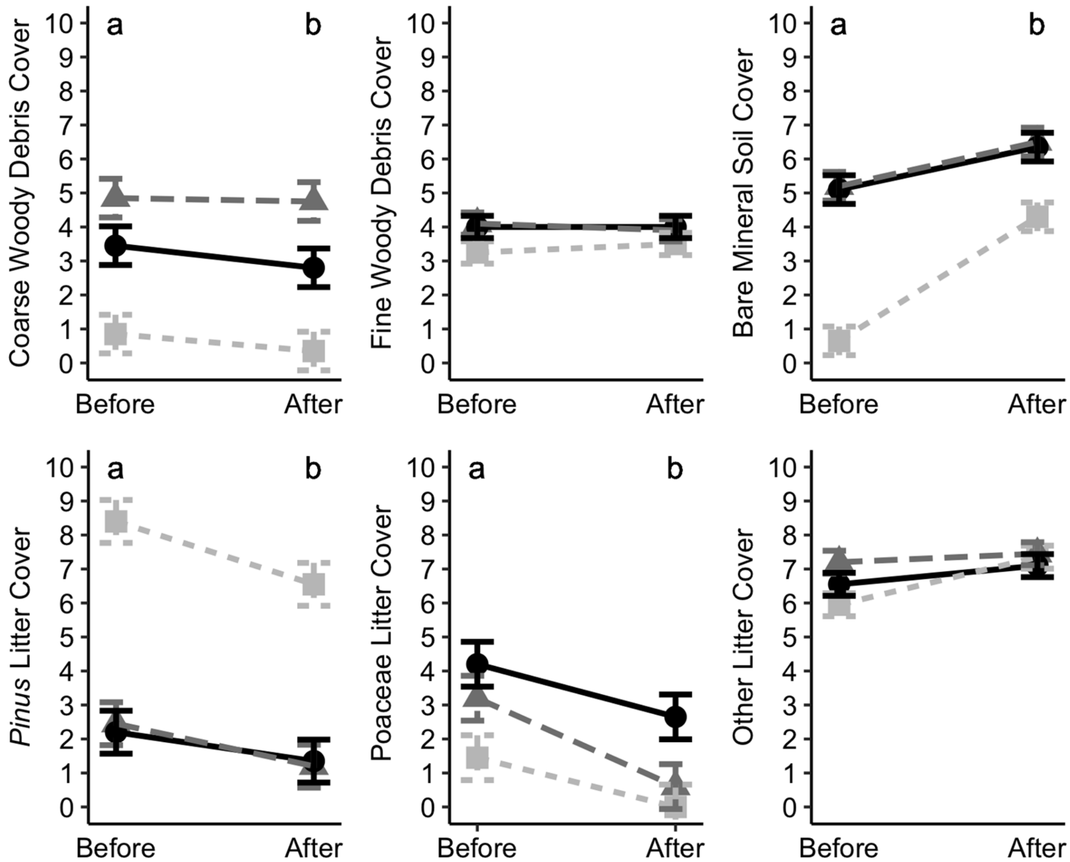

Fig. 4. Average cover of ground surface categories documented in mature (light gray squares, short-dashed lines), wind-disturbed (dark gray triangles, long-dashed lines), and salvage-logged (black circles, solid lines) plots before (2017) and after (2018) prescribed fire. Cover classes are adapted from Peet et al. (1998), where 0 = absent, 1 = trace, 2 = 0–1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95%, and 10 = 95–100%. Lower-case letters indicate significant before-and-after differences in the percent cover of coarse woody debris ($P = 0.048$), bare mineral soil ($P < 0.001$), *Pinus* litter ($P < 0.001$), and Poaceae litter ($P < 0.001$).

Table 2
Summary of mixed ANOVAs used to assess the impacts of pre-fire conditions (mature, wind-disturbed, and salvage-logged), time relative to prescribed fire (before and after), and their interaction on sapling (woody stems > 1 m height and < 5 cm diameter) and seedling (woody stems < 1 m height) density (stems ha^{-1}), richness (*S*), and Shannon diversity (*H'*). Statistically significant values ($P < 0.05$) are indicated with bold text.

Regeneration Layer	Metric	Pre-Fire Condition (C)			Time (T)			C × T		
		F-values	*P*-values	df	*F*-values	*P*-values	df	*F*-values	*P*-values	df
Sapling	Density	23.02	**< 0.001**	2	301.3	**< 0.001**	1	13.74	**< 0.001**	2
	Richness	51.38	**< 0.001**	2	106.3	**< 0.001**	1	1.053	0.356	2
	Shannon Diversity	47.53	**< 0.001**	2	6.274	**0.015**	1	0.775	0.466	2
Seedling	Density	3.215	**0.048**	2	31.38	**< 0.001**	1	5.27	**0.008**	2
	Richness	6.101	**0.004**	2	34.82	**< 0.001**	1	0.02	0.98	2
	Shannon Diversity	3.417	**0.04**	2	40.851	**< 0.001**	1	0.517	0.599	2

wood-decomposing) fungi occurrences on decay class II stems. Ulyshen et al. (2018) also described how wood-decomposing microbes, favored by hot and humid conditions, likely accelerated wood decay rates in frequently burned *P. palustris* stands. Though prescribed fires that consume large volumes of CWD have been reported in other forest types (Randall-Parker and Miller, 2002, Knapp et al., 2005), results of this study align more closely with Hanula et al. (2012), who documented frequent low-intensity prescribed fires with negligible impacts on CWD volumes in a *P. palustris* flatwood ecosystem.

Contrary to CWD, sapling densities were substantially reduced after prescribed fire, indicating that prescribed fire top-killed woody plants throughout the treatment area. A ubiquitous increase in exposed mineral soil combined with *Pinus* and Poaceae litter reductions further corroborated the efficacy of prescribed fire in all disturbance categories. However, whereas canopy-derived *Pinus* litter likely sustained prescribed fire in mature sites (Platt et al., 1988, Mitchell et al., 2009), the pre-fire surface cover of *Pinus* litter averaged less than 2% on wind-disturbed and salvage-logged sites. Yet, wind-disturbed and salvage-logged sites exhibited fire-mediated sapling mortality, indicating that other fuels must have sustained the prescribed fire. These results supported recent advancements in our conceptual understanding of frequently burned *P. palustris* stands in which fire-adapted plants besides *P. palustris* produce pyrogenic fuels (Fill et al., 2015). In fact, wind-disturbed and salvage-logged sites contained relatively high seedling and sapling densities of all *Quercus* species identified by Kane et al. (2008) as “fire facilitators” (i.e. *Q. falcata*, *Q. laevis*, *Q. margarettae*, and *Q. stellata*). Nonetheless, *Q. nigra*, which has low litter flammability, also exhibited relatively high densities, demonstrating the complexity

Table 3
Density (stems ha^{-1}) of saplings (woody stems > 1 m height and < 5 cm diameter) documented in mature, wind-disturbed, and salvage-logged plots before (2016) and after (2018) prescribed fire.

Species	Saplings ha^{-1}					
	Mature		Wind		Salvage	
	2016	2018	2016	2018	2016	2018
Acer floridanum (Chapm.) Pax	–	–	49	–	–	–
Acer rubrum L.	649	10	249	5	181	23
Acer saccharum Marshall	–	–	1	–	–	–
Aesculus pavia L.	–	–	1	–	–	–
Asimina parviflora (Michx.) Dunal	–	–	5	–	–	–
Callicarpa americana L.	60	–	26	–	8	–
Carya glabra (Mill.) Sweet	4	–	166	34	9	1
Carya tomentosa (Lam.) Nutt.	19	3	130	24	31	6
Castanea dentata (Marshall) Borkh.	–	1	–	–	–	–
Castanea pumila (L.) Mill.	5	–	–	–	4	3
Cornus florida L.	54	–	8	5	43	4
Diospyros virginiana L.	158	79	324	31	109	26
Fagus grandifolia Ehrh.	1	–	–	–	–	–
Hamamelis virginiana L.	–	–	58	5	1	–
Ilex opaca Aiton	–	–	–	–	1	–
Liquidambar styraciflua L.	114	19	541	76	254	68
Liriodendron tulipifera L.	–	–	1	–	11	1
Magnolia macrophylla Michx.	–	–	10	–	5	1
Magnolia virginiana L.	–	–	–	–	5	5
Nyssa sylvatica Marshall	3	20	10	53	65	24
Oxydendrum arboreum (L.) DC.	144	181	570	50	103	74
Pinus echinata Mill.	–	–	4	–	–	3
Pinus palustris Mill.	30	11	34	56	75	123
Pinus taeda L.	14	5	21	29	35	93
Prunus serotina Ehrh.	–	–	3	–	1	–
Prunus umbellata Elliott	–	–	–	3	–	–
Quercus alba L.	34	4	389	45	51	8
Quercus coccinea Münchh.	48	15	544	140	88	49
Quercus falcata Michx.	60	10	443	141	430	208
Quercus hemisphaerica Bartram ex Willd.	–	1	19	6	18	4
Quercus incana Bartram	4	–	9	–	24	3
Quercus laevis Walter	6	–	16	1	61	21
Quercus margarettae W.W. Ashe ex Small	9	–	48	8	94	24
Quercus marilandica Münchh. var. *marilandica*	43	8	38	23	235	104
Quercus montana Willd.	–	–	50	6	1	3
Quercus nigra L.	8	–	469	71	379	91
Quercus rubra L.	3	5	4	11	4	1
Quercus stellata Wangenh.	29	10	115	69	96	46
Quercus velutina Lam.	19	10	291	43	75	28
Rhus copallinum L.	380	114	1366	363	500	238
Rhus glabra L.	–	–	25	31	3	–
Sassafras albidum (Nutt.) Nees	3	–	24	3	45	6
Styrax grandifolius Aiton	–	30	146	25	3	6
Symplocos tinctoria (L.) L'Hér.	–	–	216	–	10	–
Vaccinium arboreum Marshall	1448	116	1203	138	1325	375
Vaccinium elliottii Chapm.	14	–	1	–	23	–
Vaccinium pallidum Aiton	–	–	9	–	–	–
Vaccinium stamineum L.	4	–	29	13	23	14
TOTAL	3360	651	7661	1505	4425	1679

of fuel bed composition and flammability (Hiers et al., 2014). Based on fuels collected on the same plots described herein, Emery and Hart (in review) found that wind-disturbed and salvage-logged sites also contained other highly flammable fuels derived from species such as *Gelsemium sempervirens* (L.) St.-Hil. and *Vaccinium stamineum*.

Despite overall sapling density reductions, *P. palustris* exhibited increased post-fire sapling densities on wind-disturbed and salvage-logged sites. Thus, prescribed fire enhanced *P. palustris* recovery on these sites through shoot mortality of less fire-resistant species. Indeed, *P. palustris* saplings are particularly fire-resistant, in part because of thick bark and tufts of long needles to protect aboveground meristematic tissues (Brockway et al., 2006). Fire-induced competition reduction and corresponding increases in resource availability may have also stimulated *P. palustris* seedling recruitment to the sapling stratum (Grelen, 1978, Ramsey et al., 2003). However, although prescribed fire increased *P. palustris* sapling densities and reduced hardwood sapling densities, *P. palustris* saplings remained outnumbered by other species on wind-disturbed and salvage-logged sites. Nonetheless, we expect that continued application of prescribed fire will continue to relegate hardwood species to smaller size classes (Bond and Midgley, 2001, Grady and Hoffman, 2012), and thereby facilitate the stratification of *P. palustris* saplings above less fire-resistant woody plants (Bigelow and Whelan, 2019). Indeed, many studies show that a regime of repeated prescribed fires is needed produce desired compositional and structural changes (Boyer, 1990, Waldrop and Lloyd, 1991, and others cited in Knapp et al., 2009). Observationally, *P. palustris* sapling appeared taller than most other saplings, and we therefore recommend that future studies quantify sapling heights to demonstrate how *P. palustris* saplings, despite being outnumbered, stratify above less fire-resistant competitors with repeated application of prescribed fire. Counter to wind-disturbed and salvage-logged sites, mature sites hosted fewer *P. palustris* saplings after prescribed fire. However, we observed no fire-killed *P. palustris* saplings on mature plots, which would have been discernable based on burnt terminal buds. As such, sapling density reductions on mature sites were attributed to *P. palustris* sapling growth to the tree size class (i.e. ≥ 5 cm diameter), not prescribed fire-mediated mortality.

In fire-prone ecosystems globally, plants can persist with two non-exclusive post-fire regeneration strategies: seeding and resprouting (Marais et al., 2014, Pausas and Keeley, 2014). *Pinus palustris* exemplifies the seeding strategy, whereby fire-resistant juveniles recruit to canopy positions and produce seed-bearing cones. Resprouting occurs when top-killed individuals produce new shoots from surviving tissues at or below ground level. Study area-wide reductions in sapling densities and corresponding increases in seedling densities exemplified a post-fire resprouting response. For instance, on wind-disturbed sites, *Vaccinium arboreum* and *Rhus copallinum* were each reduced by over 1000 sapling stems ha^{-1} after prescribed fire, but gained over 10,000 and 20,000 seedling stems ha^{-1}, respectively. Although *V. arboreum* is better-known for a third post-fire strategy (i.e. colonization), in which animal- or water-dispersed seeds are transported from unburned sites (Tirmenstein, 1991), Olson and Platt (1995) also described post-fire *V. arboreum* (and *R. copallinum*) resprouting. Our observations also corresponded with Cannon et al. (2019), who reported rapid clonal establishment of *R. copallinum* on wind-and-fire impacted sites, and Hiers et al. (2014), who described the resprouting ability of most *Quercus* species documented in this study. Results of this study can also be conceptualized through resistance- and resilience-based disturbance-response syndromes (Batista and Platt, 2003): *P. palustris* saplings survived prescribed fire and exhibited modest post-fire recruitment (resistant syndrome), whereas most hardwood species experienced shoot mortality, yet exhibited prolific post-fire clonal recovery (resilient syndrome).

Though some *P. palustris* seedlings can also resprout after prescribed fire (Knapp et al., 2018), we observed marked post-fire *P. palustris* seedling reductions, especially on mature sites. Grace and Platt (1995) and Jack et al. (2010) described how prescribed fire-induced *P. palustris* mortality rates were greatest among smaller seedling size classes and in areas with greater surface *Pinus* litter loads, which facilitated prescribed fires of greater intensities. We therefore suspect that mature sites, which contained the greatest surface *Pinus* litter cover and the highest pre-fire *P. palustris* seedling densities, experienced the greatest prescribed fire intensities and, consequently, the greatest *P. palustris* seedling mortality rates. *Pinus palustris* seedlings and saplings are also especially vulnerable to fire-induced mortality during shoot elongation (i.e. the "candling stage") in the early growing season. Although

Table 4
Density (stems ha^{-1}) of seedings (woody stems < 1 m height) documented in mature, wind-disturbed, and salvage-logged plots before (2016) and after (2018) prescribed fire.

Species	Seedlings ha^{-1}					
	Mature		Wind		Salvage	
	2016	2018	2016	2018	2016	2018
Acer floridanum (Chapm.) Pax	–	–	200	650	–	–
Acer rubrum L.	1950	4200	400	650	400	350
Aesculus pavia L.	–	–	–	150	–	–
Asimina parviflora (Michx.) Dunal	500	750	350	800	200	600
Callicarpa americana L.	200	–	200	250	200	200
Carya glabra (Mill.) Sweet	200	300	850	300	–	50
Carya tomentosa (Lam.) Nutt.	800	850	1150	1700	1100	550
Cornus florida L.	2600	950	150	–	1050	350
Diospyros virginiana L.	500	850	700	2100	250	1450
Gaylussacia dumosa (Andrews) Torr. & A.Gray	4500	13,350	100	800	8700	22,250
Hamamelis virginiana L.	–	–	–	350	–	–
Hydrangea quercifolia Bartram	50	–	–	–	–	–
Juniperus virginiana L.	–	–	–	–	50	–
Liquidambar styraciflua L.	–	–	2000	4100	350	1050
Liriodendron tulipifera L.	–	100	250	100	–	50
Nestronia umbellula Raf.	150	–	–	–	–	–
Nyssa sylvatica Marshall	3300	700	4300	4650	2100	2500
Oxydendrum arboreum (L.) DC.	850	600	650	1600	200	1000
Pinus L.	6250	100	2150	950	8000	2400
Pinus palustris Mill.	18,100	1900	4050	2350	6500	3500
Prunus serotina Ehrh.	–	–	50	150	–	–
Prunus umbellata Elliott	–	–	250	450	200	250
Quercus alba L.	1250	5550	1500	5250	–	200
Quercus coccinea Münchh.	450	500	600	300	250	100
Quercus falcata Michx.	1250	4400	2700	9800	2450	6450
Quercus hemisphaerica Bartram ex Willd.	450	500	50	200	50	–
Quercus incana Bartram	–	600	–	–	200	–
Quercus laevis Walter	200	–	150	50	400	250
Quercus margarettae W.W. Ashe ex Small	950	1300	900	600	950	950
Quercus marilandica Münchh. var. *marilandica*	200	550	300	600	650	950
Quercus montana Willd.	–	–	400	1600	–	–
Quercus nigra L.	450	650	1350	2250	1750	2150
Quercus rubra L.	850	800	150	500	–	–
Quercus stellata Wangenh.	2800	850	600	250	100	50
Quercus velutina Lam.	550	–	900	1000	250	150
Rhododendron canescens (Michx.) Sweet	–	–	950	1000	–	–
Rhus copallinum L.	2300	12,700	8900	32,400	4500	16,150
Rhus glabra L.	–	–	100	250	–	–
Sassafras albidum (Nutt.) Nees	600	600	550	550	350	2300
Styrax grandifolius Aiton	–	–	7950	11,650	550	700
Symplocos tinctoria (L.) L'Hér.	–	–	4600	5750	600	850
Vaccinium arboreum Marshall	15,950	26,700	18,800	30,700	9950	17,700
Vaccinium elliottii Chapm.	950	1450	400	–	–	–
Vaccinium pallidum Aiton	–	–	250	100	–	–
Vaccinium stamineum L.	–	1000	2650	1650	200	250
TOTAL	69,150	82,800	72,550	128,550	52,500	85,750

Table 5
Average richness and Shannon diversity of saplings (woody plants > 1 m height and < 5 cm dbh) and seedlings (woody plants < 1 m height) documented in mature, wind-disturbed, and salvage-logged plots. Sapling values reflect 400-m^2 plot averages and seedling values reflect 10-m^2 plot averages. Different capital letters denote significant differences between years ($P < 0.05$), and lower-case letters denote significant differences between pre-fire conditions ($P < 0.05$) within years based on Tukey's pairwise comparisons.

Regeneration Layer	Metric	Time		Pre-Fire Condition					
				Mature		Wind		Salvage	
Sapling	Richness	2016	A	9.6 ± 1.0	a	19.6 ± 0.7	b	16.3 ± 0.7	c
		2018	B	5.0 ± 0.6	a	14.0 ± 0.8	b	12.3 ± 0.9	b
	Shannon Diversity	2016	A	1.2 ± 0.1	a	2.3 ± 0.1	b	2.1 ± 0.1	c
		2018	B	1.1 ± 0.1	a	2.2 ± 0.1	b	2.0 ± 0.1	b
Seedling	Richness	2016	A	9.3 ± 0.6	a	11.9 ± 0.7	b	9.3 ± 0.5	a
		2018	B	7.4 ± 0.8	a	10.0 ± 0.7	b	7.5 ± 0.6	a
	Shannon Diversity	2016	A	1.7 ± 0.1		1.9 ± 0.1		1.8 ± 0.1	
		2018	B	1.3 ± 0.1		1.7 ± 0.1		1.5 ± 0.1	

prescribed fires are purposefully conducted when wind speeds are sufficient to maintain flame heights below lethal levels for candling *P. palustris* saplings, the timing of prescribed fire in the early growing season could have also amplified mortality of candling *P. palustris* seedlings.

5. Management implications

We recognize that assessments of whether and how disturbances impact forest resilience can depend on which response variables are assessed (Kleinman et al., 2019). Indeed, we did not measure carbon stocks (Buma et al., 2014), insects (Cobb et al., 2007), soil properties (Kishchuk et al., 2015), or a multitude of other ecosystem components that may be negatively impacted by salvage logging (Lindenmayer et al., 2017). However, with respect to woody plant recovery, this study supported other studies that suggested that negative ecological consequences of salvage logging are not necessarily a certainty (Peterson and Leach, 2008, Lang et al., 2009, Fidej et al., 2016, Royo et al., 2016, Sass et al., 2018, Slyder et al., 2019). In 2016, salvage-logged sites hosted the greatest *P. palustris* sapling densities, indicating that salvage logging did not alter short-term recovery toward pre-disturbance canopy conditions (Kleinman et al., 2017, Ford et al., 2018). However, *P. palustris* saplings were substantially outnumbered by other species at this time, and it was unclear whether prescribed fire would effectively induce shoot mortality of woody competitors in areas lacking a continuous canopy-derived *Pinus* litter fuel bed. It was also unclear how deadwood extraction would impact prescribed fire effects on salvage-logged sites. Here we report that, despite a paucity of *Pinus* litter on wind-disturbed and salvage-logged sites, prescribed fire enhanced *P. palustris* recovery by top-killing less fire-resistant species.

The response variables we measured to assess prescribed fire effects (i.e. fine fuel consumption, mineral soil exposure, and sapling density reductions) were not apparently impacted by deadwood extraction on salvage-logged sites. The efficacy of prescribed fire in wind-disturbed and salvage-logged sites was attributed primarily to pyrogenic fine fuels derived from broadleaved plants such as fire-facilitating *Quercus* species (Kane et al., 2008, Hiers et al., 2014, Fill et al., 2015). We therefore highlight the importance of alternative pyrogenic fuel sources to maintain prescribed fires, especially after stand-regenerating events, and recommend retention of fine fuels on salvage-logged sites to facilitate continued use of prescribed fire. We also suspect that prescribed fire, conducted in April, was particularly effective at top-killing hardwood saplings shortly after they had invested energy into aboveground growth (Glitzenstein et al., 1995, Drewa et al., 2006). As such, we support the continued use of early growing-season fires to promote *P. palustris* recovery, yet acknowledge inconclusive evidence regarding timing of prescribed fire within the growing season (Reilly et al., 2017).

Although prescribed fire improved post-disturbance stand development toward *P. palustris* dominance, *P. palustris* saplings remained ubiquitously outnumbered by other hardwood species. Whereas some of these species (i.e. *Rhus copallinum* and *Vaccinium arboreum*) do not typically transcend understory positions, *Quercus* spp. (especially *Q. coccinea* and *Q. falcata*) were particularly abundant, and may achieve canopy positions without more intensive management to supplement prescribed fire such as mechanical removal and/or selective herbicide application. Nonetheless, contrary to *P. palustris*, these species all exhibited marked post-fire sapling density reductions, and repeated use of prescribed fire may effectively control these species over time. In addition to repeated use of prescribed fire, a shorter prescribed fire-return interval might also enhance *P. palustris* recovery. For example, in mature sites, transition from a four- to two-year prescribed fire-return interval would help maintain lower *Pinus* litter fuel loads, which would in turn support less intense fires and consequently lower *P. palustris* seedling mortality rates (Jack et al., 2010). A shorter prescribed fire-return interval would also increase the likelihood of exposed bare mineral soil, which is required for successful *P. palustris* seed germination (Brockway et al., 2006), corresponding with *P. palustris* cone production, which occurs at rather sporadic intervals (Chen et al., 2018).

CRediT authorship contribution statement

Jonathan S. Kleinman: Conceptualization, Methodology, Writing - original draft. **Jonathan D. Goode:** Conceptualization, Methodology, Writing - review & editing. **Justin L. Hart:** Conceptualization, Methodology, Writing - review & editing. **Daniel C. Dey:** Conceptualization, Methodology, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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