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Article

Resilience of a Fire-Maintained *Pinus palustris* Woodland to Catastrophic Wind Disturbance: 10 Year Results

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Abstract: Increased interest in ecosystem recovery and resilience has been driven by concerns over global change-induced shifts in forest disturbance regimes. In frequent-fire forests, catastrophic wind disturbances modify vegetation-fuels-fire feedbacks, and these alterations may shift species composition and stand structure to alternative states relative to pre-disturbance conditions. We established permanent inventory plots in a catastrophically wind-disturbed and fire-maintained *Pinus palustris* woodland in the Alabama Fall Line Hills to examine ecosystem recovery and model the successional and developmental trajectory of the stand through age 50 years. We found that sapling height was best explained by species. Species with the greatest mean heights likely utilized different regeneration mechanisms. The simulation model projected that at age 50 years, the stand would transition to be mixedwood and dominated by *Quercus* species, *Pinus taeda*, and *P. palustris*. The projected successional pathway is likely a function of residual stems that survived the catastrophic wind disturbance and modification of vegetation-fuels-fire feedbacks. Although silvicultural interventions will be required for this system to exhibit pre-disturbance species composition and structure, we contend that the ecosystem was still resilient to the catastrophic disturbance because similar silvicultural treatments were required to create and maintain the *P. palustris* woodland prior to the disturbance event.

Keywords: mixedwoods; pine-oak (*Pinus-Quercus*); tornado; sapling; stand development; succession



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1. Introduction

All forests exist in a state of recovery from past disturbances, which influence forest development and succession [1]. Along the gradient of disturbance severity, catastrophic disturbances, events that result in the mortality of most or all overstory vegetation, are the most infrequent but the most severe [2,3]. After catastrophic disturbance, components of ecological memory, such as information and material biological legacies, persist [4]. Information and material biological legacies are the individuals, adaptations, and structures that remain post-disturbance and facilitate ecosystem recovery toward pre-disturbance conditions [5]. The retention of biological legacies provides continuity between pre- and post-disturbance forest ecosystems, and therefore drives ecological resilience [6,7]. Catastrophic wind disturbances reduce or even completely remove overhead competition and thereby increase resource availability in the regeneration layer. Microsite characteristics of the forest floor, the persistence of resting buds and seedbanks, residual seedlings, saplings, and small trees, and the arrival of new propagules influence post-disturbance tree regeneration [2]. Biological legacies are strong controls on successional and developmental pathways, which are the measures of ecological resilience of the system (i.e., ecosystem capacity to recover toward pre-disturbance conditions) [8,9].

Catastrophic disturbances modify vegetation-fuels-fire feedbacks in frequent-fire forests [10–12]. The perpetuation of fire-dependent ecosystems requires the continuous feedbacks of canopy tree-derived pyrophytic fuels (i.e., leaf litter inputs) burning with

sufficient intensity to inhibit recruitment of more fire-sensitive species [13]. Thus, frequent low-severity fires promote canopy dominance of fire-adapted tree species and create understory conditions suitable for the establishment and growth of pyrophytic ground flora [14]. Catastrophic wind disturbances modify fuel complexes and therefore alter fire effects. By killing overstory trees, catastrophic disturbances reduce or eliminate the fine surface fuels required to produce desirable fire effects [15–17]. By altering vegetation-fuels-fire feedbacks in fire-dependent ecosystems, catastrophic wind disturbances may result in shifts in forest composition, structure, and function given the complex interactions of information and material biological legacies [18]. The resilience of fire-dependent ecosystems to catastrophic wind disturbance is not well understood and this will become increasingly important as catastrophic wind events are projected to become more common in some regions (e.g., the southeastern USA) where fire-dependent ecosystems occur [19].

To examine the ecological resilience of frequent-fire forests to catastrophic wind disturbance, we established and monitored permanent inventory plots in a fire-maintained *Pinus palustris* woodland in the Alabama Fall Line Hills, USA. The study area was impacted by an EF3 tornado and we monitored recovery for the first 10 growing seasons post-disturbance. The primary goal of our study was to quantify contemporary and project future woody plant composition and structure in this fire-maintained, *P. palustris* woodland impacted by catastrophic wind disturbance to provide information on ecosystem recovery processes. Our specific objectives were to: (1) quantify woody plant composition and structure 10 years post-catastrophic wind disturbance, (2) compare and examine the influence of species and biophysical site conditions on sapling height growth, and (3) model the successional and developmental trajectory of the stand through age 50 years (year 2061). Our results provide insight on successional processes and patterns and the ecological resilience of a fire-maintained *Pinus* woodland to catastrophic wind disturbance.

2. Materials and Methods

2.1. Study Site

Our study was conducted on the Oakmulgee Ranger District of Talladega National Forest in west-central Alabama, USA. The study area occurs within the Fall Line Hills ecoregion [20] and the *Quercus-Pinus* forest region as defined by Braun [21]. The Fall Line Hills represent a physiographic transition zone between the Appalachian Highlands and the Gulf Coastal Plain [22]. Plant species richness is relatively high and forest communities contain taxa representative of both the Appalachian Highlands and Coastal Plain [23,24]. Our study site is specifically within the central *Pinus palustris* region as defined by Harper [25], where *P. palustris*-dominated woodlands occur on fire-maintained ridgetops, upper slopes, and south-to-west facing mid-slope positions. On more mesic sites, a variety of *Quercus* spp. and other hardwoods coexist and share dominance with *P. taeda* [24,26,27].

Hillslopes and ridges in the study area contain deep, moderately well-drained soils derived from the Cretaceous-aged Gordo Formation [28,29]. Maubila series soils consist of a sandy loam or loam surface layer up to 10 cm deep. These soils have clay-based substrata over 200 cm deep to bedrock [30]. The topography of the area is undulating and strongly dissected with steep slopes that commonly range from 30 to 35% [31]. Elevation in the area ranges from 90 to 160 m above mean sea level. The climate of the region is humid mesothermal, characterized by long, hot summers, short, mild winters, and no distinct dry season [32]. Mean temperature is 17.2 °C, with mean January and July temperatures of 6.6 and 26.9 °C, respectively [33]. Mean annual precipitation is 1376.21 mm [33]. The frost-free period is ca. 230 days from March to November [33].

The USDA Forest Service manages *P. palustris* woodlands on the study site with prescribed fire on a 2–4 year rotation. The goals of the prescribed fire program are to reduce fuel loads, promote fire-adapted ground flora assemblages, top-kill woody plants that are fire-sensitive, and in mature stands, to expose bare mineral soil to promote natural regeneration of *P. palustris*. 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 Ranger

District [34]. Portions of the study area were salvaged logged from July to November 2011, as is common practice after catastrophic wind disturbance. We established a permanent plot network through the damaged area to monitor successional and structural development of the catastrophically disturbed *P. palustris* woodland [35,36]. Although care was taken in site selection, ecological studies of natural disturbance often preclude experimental replicability. To address this, we selected a site in which all plots were contained within the same watershed and USDA Forest Service compartment, and had common soil series and topographic positions.

2.2. Field Methods

After the catastrophic wind disturbance, we established a network of permanent plots to examine post-disturbance recovery for a range of response variables. Plots were established based on satellite imagery, geospatial data, and ground reconnaissance to ensure they were analogous based on biophysical and pre-disturbance conditions [35–37]. Prior to the tornado, all plots were *P. palustris*-dominated woodlands that were established in the early 1930s after regeneration harvests. All plots occurred within a 1 km² expanse of the same watershed on upper- and mid-slope positions with Maubila series soils (Aquic Hapludults). Plots were located in the same USDA Forest Service delineated compartment and experienced the same prescribed fire regime (2–4 year rotation).

The permanent plot network consisted of 60 systematically established 0.04 ha fixed-radius plots. Twenty plots were established in mature *P. palustris*-dominated woodlands that exhibited no visible tornado damage. The mature site had a basal area of 21.7 m² h⁻¹ and 90% canopy cover [35,36]. The remaining 40 plots were established in areas catastrophically disturbed by the EF3 tornado. These plots were all at least 70 m from the edge of the disturbance swath to account for forest edge effects [38]. For this study, we only used forest inventory data from the 40 permanent plots that were established in the wind-disturbed portion of the study area to examine successional development 10 years post-disturbance. All data reported here were collected during the summer of 2020, which is the tenth growing season since the catastrophic wind event. On each fixed-radius plot, we considered trees to be all live, woody stems ≥ 5 cm diameter at breast height (dbh, 1.37 m above the earth surface). We documented species and diameter for all trees. We considered saplings to be all live, woody stems ≥ 1 m height and < 5 cm dbh. We documented the species and height to the nearest 0.1 m for all saplings on each plot. When saplings occurred in clumps (i.e., as stump sprouts), the number of sprouts in the clump was documented as clump size and sapling height was measured for the tallest individual in each clump using a telescoping measuring rod.

Each 0.04 ha plot contained 10 nested 1 m² quadrats. On each plot, one quadrat was positioned at plot center and nine quadrats were evenly spaced along each the 0°, 120°, and 240° azimuths from plot center. On each quadrat, we tallied seedlings (live, woody stems < 1 m height) by species and visually estimated the percent cover of forest floor with *Pinus* litter cover. Coarse woody debris was inventoried on each plot. This value included deadwood ≥ 10 cm diameter categorized as logs (i.e., dead stems disconnected from roots) and uprooted stems (dead stems with uplifted root networks) [39]. Logs were measured for diameter at both ends and uprooted stems were measured for diameter at 1.37 m from the root plate. Percent canopy cover was estimated using a densiometer. Densiometer readings were collected at plot center and 5 m from plot center along each cardinal direction. The five values were averaged by plot and multiplied by 1.04 to determine mean plot-level canopy cover [40]. Slope gradient and aspect were also recorded for each plot.

2.3. Analytical Methods

All tree (i.e., live stems ≥ 5 cm dbh) data were standardized to the hectare level and placed into 2.5 cm diameter bins to examine the diameter distribution of the stand 10 years post-disturbance. We calculated tree density and basal area ha⁻¹ and the relative contributions for each species that occurred in the tree layer. Additionally, we quantified density and relative density by species within each 2.5 cm diameter bin. We calculated

mean height and standard deviation for all saplings by species and used ANOVA with a Tukey HSD post hoc test to evaluate differences in height by taxonomic group. Taxonomic categories were assigned based on species, abundance, and growth form. We calculated sapling stem density for all sapling species that occurred on our plots. To derive plot-level ground flora and ground cover values, quadrat-level cover values were transformed to corresponding range midpoints and averaged by plot.

To quantify the relative influence of species and environmental conditions on sapling height growth, we applied a random forest (RF) machine learning algorithm. RF is a non-parametric tool derived from classification and regression trees that is capable of accurately modeling complex interactions between variables [41,42]. The algorithm combines “trees” each generated by bootstrap samples, and retains samples for internal cross-validation (i.e., out of bag estimates, OOB). The final model output is the mean result of all trees. Model outputs include a variable importance measure, which ranks each predictor variable by mean increase in error (% IncMSE) when observed values of predictor variables are permuted through the model [41]. These values allow inference on which predictor variable has the greatest influence on the independent variable within the model. We fit one RF model to predict sapling height incorporating 200 regression trees into the model. Height was modeled for each individual sapling that occurred on our inventory plots ($n = 8191$). Predictor variables included species, clump size, plot-level canopy cover, sapling species richness, sapling density, *Pinus* litter cover, tree density, basal area, slope percent, and transformed aspect [43]. All models were cross-validated with a randomly selected training and testing subset of the data and all independent variables were analyzed for multicollinearity. RF was conducted using the package “randomForest” in R version 1.2.5001.

We used the Forest Vegetation Simulator (FVS) to project tree density and basal area by species at decadal increments to stand age 50 years (the year 2061). The FVS is a publicly available and commonly used simulation model maintained by the USDA Forest Service. The simulation model is widely used by the USDA Forest Service and other forest managers to aid in planning, management decisions, and research [44]. Our forest inventory data were formatted for use in the Southern (SN) variant of the FVS. We ran the FVS in the default setting which is deterministic mode. We provided initial stand inventory metrics including tree species and dbh for all trees ≥ 2.54 cm formatted as a tree list. The FVS allows users to modify management activities and environmental conditions to improve projection accuracy. As a management component, we added prescribed burns as a fuel treatment. We set the parameters as a prescribed fire every two years, with wind speeds of 12.8 kph at 6 m above live vegetation, dry moisture levels, 12.8 °C temperature, 90% stand area burned, and ignited before the spring flush. We modified fuel dynamics based on the photo series in Scholl and Waldrop [45] (FC-6-Pre). Finally, we modified fire behavior by adding drought events every 10 years with the duration of one year based on the observed frequency of drought in this region [33,46].

3. Results

3.1. Woody Plant Composition, Structure, and Height

Basal area of the tree layer was $0.13 \text{ m}^2 \text{ ha}^{-1}$ and total tree density was $191 \text{ stems ha}^{-1}$ (Table 1). Tree species richness was 22. Of the total basal area, 76% was from residual stems ≥ 12.5 cm dbh. The largest tree recorded on a wind-disturbed study plot was a residual *Pinus taeda* L. with a dbh of 64 cm. The largest residual *Pinus palustris* stem was 48.3 cm dbh. The five trees with the largest diameters were *Pinus* spp. (all >30 cm dbh). The majority of trees (81%) were <10 cm dbh and only 20 stems ha^{-1} were greater than 12.5 cm dbh. *Quercus* was the most abundant genus in the smallest tree size class (Figure 1). However, *Pinus* species were most common in all other diameter classes. *Pinus palustris* had the highest relative density values in the three smallest diameter size class bins (5.0–12.5 cm dbh) with 60 stems ha^{-1} (Table 1). *Pinus* represented 45% of all stems between 5 and 10 cm dbh and *Quercus* represented 49% of stems in this size class. Of *Quercus* stems in this size class, *Q. stellata* and *Q. laevis* were the most abundant.

Table 1. Density (stems ha⁻¹) and relative density (Rel. Den., % of contribution) of trees (live, woody stems ≥5 cm dbh) by diameter bins (cm) documented in a catastrophically disturbed *Pinus palustris* woodland on the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Species are ranked by total relative density.

Species	5–7.5		7.5–10		10–12.5		12.5–14.5		15–17.5		17.5–20		20–24.5		25–30		30+		Total	
	Density	Rel. Den.	Density	Rel. Den.	Density	Rel. Den.	Density	Rel. Den.	Density	Rel. Den.	Density	Rel. Den.	Density	Rel. Den.	Density	Rel. Den.	Density	Rel. Den.	Density	Rel. Den.
<i>Pinus palustris</i> Mill.	30	26	21	52	9	50	1	13	1	25	1	40	1	20	-	-	3	100	65	34
<i>Pinus taeda</i> L.	11	9	6	14	7	39	3	63	1	50	1	40	1	40	1	50	1	25	32	17
<i>Quercus stellata</i> Wangenh.	18	16	3	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21	11
<i>Quercus laevis</i> Walter	14	13	3	6	1	4	-	-	-	-	-	-	-	1	25	-	-	-	18	9
<i>Quercus coccinea</i> Munchh.	9	8	2	5	1	4	-	-	-	-	-	-	-	-	-	-	-	-	12	6
<i>Quercus marilandica</i> Munchh.	7	6	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	4
<i>Quercus nigra</i> L.	5	4	1	3	-	-	-	-	1	25	1	20	1	20	-	-	-	-	8	4
<i>Liquidambar styraciflua</i> L.	5	4	-	-	1	4	-	-	-	-	-	-	-	-	-	-	-	-	6	3
<i>Quercus alba</i> L.	4	4	-	-	-	-	-	-	-	-	-	-	-	1	25	-	-	-	5	3
<i>Quercus margaretta</i> (Ashe) Small	3	2	1	3	-	-	1	13	-	-	-	-	-	-	-	-	-	-	4	2
<i>Pinus echinata</i> Mill.	1	1	1	2	-	-	-	-	-	-	-	-	1	20	-	-	1	40	3	1
<i>Magnolia macrophylla</i> Michx.	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1
<i>Quercus velutina</i> Lam.	1	1	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1
<i>Vaccinium arboreum</i> Marshall	1	1	1	2	-	-	1	13	-	-	-	-	-	-	-	-	-	-	2	1
<i>Acer rubrum</i> L.	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0
<i>Carya glabra</i> (Mill.) Sweet	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0
<i>Cornus florida</i> L.	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0
<i>Nyssa sylvatica</i> Marshall	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0
<i>Quercus falcata</i> Michx.	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0
Total	114	100	40	100	18	100	5	100	3	100	3	100	3	100	3	100	4	165	191	100

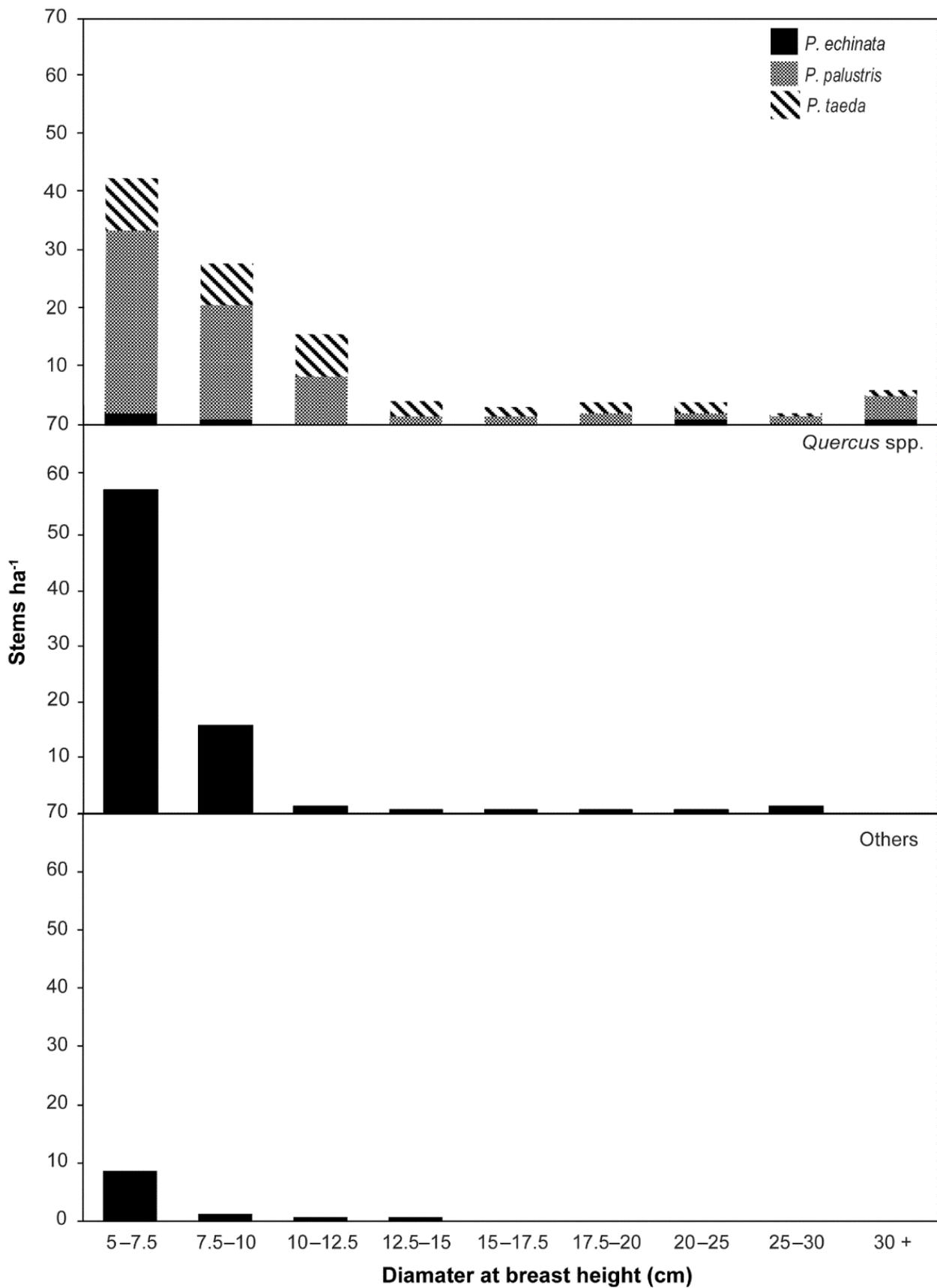


Figure 1. Density (stems ha⁻¹) of trees (live, woody stems ≥ 5 cm dbh) by dbh bins (cm) documented in a catastrophically disturbed *Pinus palustris* woodland on the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA.

Sapling density was 5119 stems ha⁻¹ (Table 2). The most abundant species in the sapling layer were *Rhus copallinum* and *Vaccinium arboreum*. Collectively, these species represented 46% of all saplings on our study plots. The most abundant arboreal species in the sapling layer were *Q. falcata*, *Liquidambar styraciflua*, and *Q. nigra*. No other species represented more than 5% of sapling layer stems. Notably, *P. palustris* and *P. taeda* had sapling densities of 74 stems ha⁻¹ and 238 stems ha⁻¹, respectively, and collectively, represented just 6% of all sapling stems. At the genus-level, *Quercus* represented 28% of all saplings with a sapling density of 1422 stems ha⁻¹. Mean sapling height was greatest for *L. styraciflua*, but height of this species was not significantly different from *P. palustris*, *Quercus* spp., *Oxydendrum arboreum*, or other *Pinus* species (Figure 2). Taxa classed with the shrub growth form (see Table 2 for a list) were significantly shorter than all other taxa, including *Rhus* spp. and *Vaccinium* spp.

Table 2. Density (stems ha⁻¹) and relative density (% of contribution), mean height, and standard deviation of mean height (SD) of saplings (live, woody stems <5 cm dbh, ≥1 m height) documented in a catastrophically disturbed *Pinus palustris* woodland on the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Species are ranked by relative density. Species with letters were placed into ^a hardwood and ^b shrub taxonomic groups used for height comparison.

Species	Density (Stems ha ⁻¹)	Relative Density (%)	Mean Height	SD
<i>Rhus copallinum</i> L.	1207.5	23.6	1.4	0.4
<i>Vaccinium arboreum</i> Marshall	1095.0	21.4	1.4	0.4
<i>Quercus falcata</i> Michx.	396.3	7.7	1.9	0.8
<i>Liquidambar styraciflua</i> L.	348.8	6.8	2.1	0.8
<i>Quercus nigra</i> L.	277.5	5.4	1.8	0.7
<i>Pinus taeda</i> L.	237.5	4.6	1.8	0.7
<i>Quercus coccinea</i> Munchh.	173.1	3.4	2.0	0.9
<i>Diospyros virginiana</i> L. ^a	161.9	3.2	1.7	0.6
<i>Quercus alba</i> L.	155.6	3.0	1.9	0.7
<i>Quercus velutina</i> Lam.	116.3	2.3	1.8	0.8
<i>Carya tomentosa</i> (Lam.) Nutt.	106.9	2.1	1.5	0.4
<i>Quercus marilandica</i> Munchh.	102.5	2.0	2.2	0.8
<i>Oxydendrum arboreum</i> (L.) DC.	85.0	1.7	1.9	0.6
<i>Quercus stellata</i> Wangenh.	79.4	1.6	1.9	0.8
<i>Pinus palustris</i> Mill.	73.8	1.4	2.0	0.9
<i>Acer rubrum</i> L.	71.3	1.4	1.6	0.5
<i>Styrax grandifolius</i> Aiton ^b	65.0	1.3	1.1	0.2
<i>Symplocos tinctoria</i> (L.) L'Hér. ^b	55.0	1.1	1.3	0.3
<i>Nyssa sylvatica</i> Marshall ^a	44.4	0.9	1.6	0.6
<i>Carya glabra</i> (Mill.) Sweet	35.0	0.7	1.6	0.5
<i>Quercus hemisphaerica</i> W. Bartram ex Willd.	33.1	0.6	1.4	0.5
<i>Quercia margaretta</i> (Ashe) Small	31.3	0.6	1.9	0.6
<i>Quercus laevis</i> Walter	28.1	0.5	2.3	0.9
<i>Quercus montana</i> Willd.	22.5	0.4	1.7	0.5
<i>Callicarpa americana</i> L.	20.0	0.4	1.2	0.2
<i>Rhus glabra</i> L.	16.9	0.3	1.4	0.2
<i>Vaccinium stamineum</i> L.	15.6	0.3	1.3	0.3
<i>Acer floridum</i> (Chapm.) Pax	13.8	0.3	1.6	0.5
<i>Sassafras albidum</i> (Nutt.) Nees ^a	13.8	0.3	1.4	0.5
<i>Quercus incana</i> W. Bartram	5.6	0.1	1.7	0.8
<i>Cornus florida</i> L. ^a	5.6	0.1	1.5	0.4
<i>Prunus umbellata</i> Elliott ^a	5.0	0.1	2.1	0.6
<i>Liriodendron tulipifera</i> L. ^a	5.0	0.1	1.7	0.5
<i>Magnolia macrophylla</i> Michx. ^a	2.5	0.0	2.7	1.0
<i>Pinus echinata</i> Mill.	1.9	0.0	2.1	0.9
<i>Vaccinium pallidum</i> Aiton	1.9	0.0	1.7	0.3
<i>Hypericum hypericoides</i> (L.) Crantz ^b	1.3	0.0	1.5	0.0
<i>Vaccinium elliotii</i> Chapm.	1.3	0.0	1.5	0.7

Table 2. Cont.

Species	Density (Stems ha ⁻¹)	Relative Density (%)	Mean Height	SD
<i>Acer saccharum</i> Marshall	1.3	0.0	1.3	0.4
<i>Magnolia virginiana</i> L. ^a	0.6	0.0	2.5	0.0
<i>Ilex vomitoria</i> Aiton	0.6	0.0	2.0	0.0
<i>Asimina parviflora</i> Michx. Dunal ^b	0.6	0.0	1.6	0.0
<i>Aesculus pavia</i> L. ^b	0.6	0.0	1.5	0.0
<i>Quercus rubra</i> L.	0.6	0.0	1.3	0.0
<i>Aralia spinosa</i> L. ^b	0.6	0.0	1.2	0.0
<i>Castanea Pumila</i> (L.) Mill. ^a	0.6	0.0	1.2	0.0
<i>Ilex opaca</i> Aiton ^a	0.6	0.0	1.2	0.0
<i>Hamamelis virginiana</i> L. ^b	0.6	0.0	1.1	0.0
TOTAL	5119.4	100.0	–	–

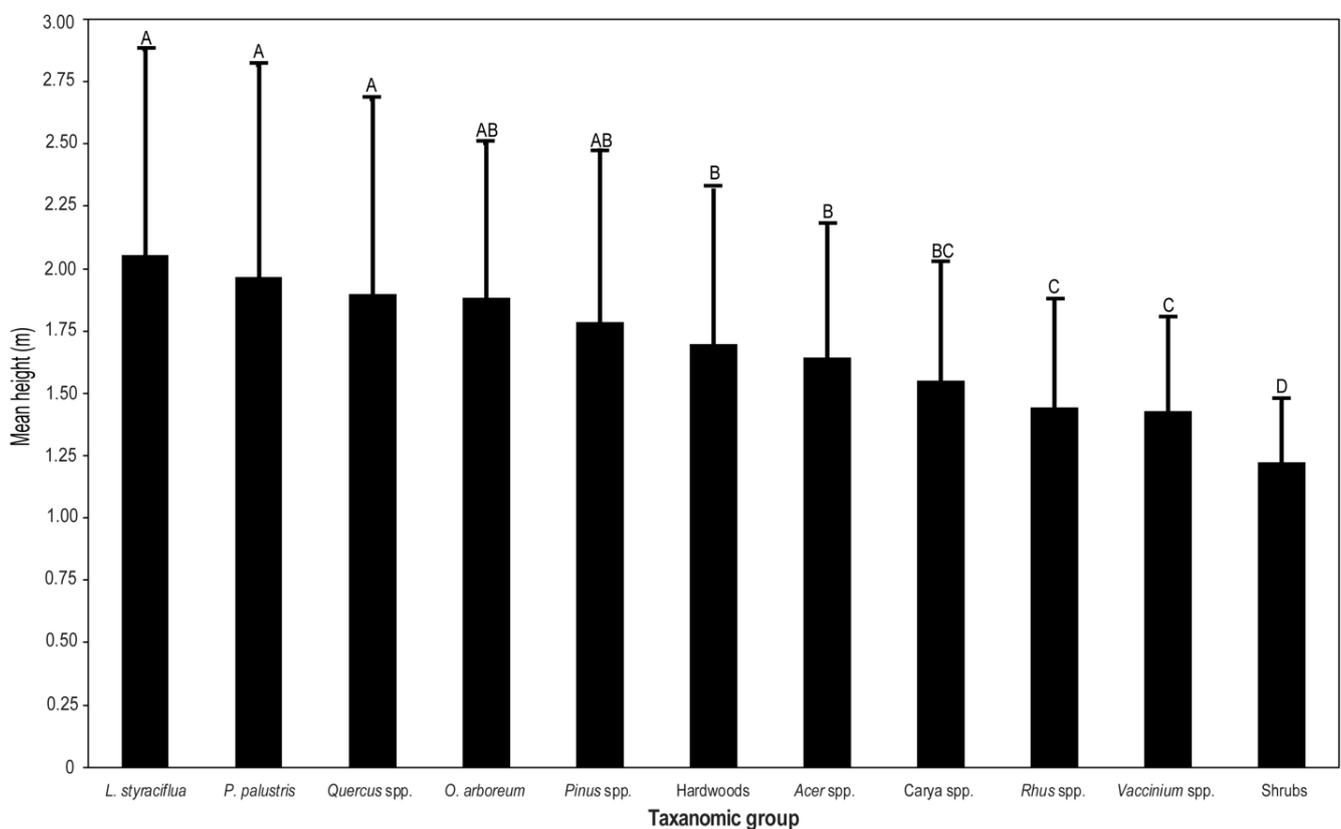


Figure 2. Mean height (m) of saplings (live, woody stems <5 cm dbh, ≥ 1 m height) by taxonomic group in a catastrophically disturbed *Pinus palustris* woodland on the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. Species are ranked by total relative density. Different letters indicate significant differences at $p < 0.05$.

3.2. Biotic and Abiotic Influence on Sapling Height

The RF model explained 42% of the variance in sapling height with a root mean square error (RMSE) of 0.534. The sapling height model included all 12 predictor variables as no variables had negative percent increase in mean square error (%IncMSE) values. Species had the greatest influence on sapling height and had a %IncMSE value of 72.4 (Figure 3). The next most influential predictor was clump size (21.9 %IncMSE). No other predictor had a %IncMSE greater than 15.0. Clump size was positively related to sapling height. Sapling richness was positively related to sapling height growth. Basal area of trees plot⁻¹ was negatively related to height growth. No linear relationship existed between sapling height growth and CWD volume or *Pinus* litter cover. The model confirmed the importance of

species on height growth, notably the significantly greater height of *L. styraciflua*, *P. taeda*, and *P. palustris* and the shorter height of shrub species.

3.3. Stand Successional Trajectory

The FVS projected basal area of $21.9 \text{ m}^2 \text{ ha}^{-1}$ and tree density of $494 \text{ stems ha}^{-1}$ in the year 2061 (stand age 50). Basal area steadily increased in increments of $4\text{--}6 \text{ m}^2 \text{ ha}^{-1}$ every 10 years (Figure 4). Tree density increased between 2021 and 2031, followed by an incremental decrease in stems ha^{-1} between 2031 and 2061 of ca. 18 stems ha^{-1} . When species were placed into taxonomic groups, *Pinus* spp. had the greatest projected basal area ($10.5 \text{ m}^2 \text{ ha}^{-1}$) in 2061, which accounted for nearly half of the basal area (48%). *Quercus* spp. had a projected basal area of $8.78 \text{ m}^2 \text{ ha}^{-1}$ (40%) in 2061 and all other individuals had a combined basal area of $2.62 \text{ m}^2 \text{ ha}^{-1}$. *Quercus* spp. were projected to be the most abundant species (ca. 50%), followed by *Pinus* spp. and other species (ca. 25% each). Species level projections indicated that *P. taeda* will be the most dominant species in 2061 ($5.12 \text{ m}^2 \text{ ha}^{-1}$), followed by *P. palustris* ($4.67 \text{ m}^2 \text{ ha}^{-1}$) and *Q. falcata* ($3.12 \text{ m}^2 \text{ ha}^{-1}$). No other species was projected to have a basal area $>1.5 \text{ m}^2 \text{ ha}^{-1}$ in 2061. Notably, *P. palustris* relative density and dominance were projected at stand age 50 years to be 14% and 21%, respectively.

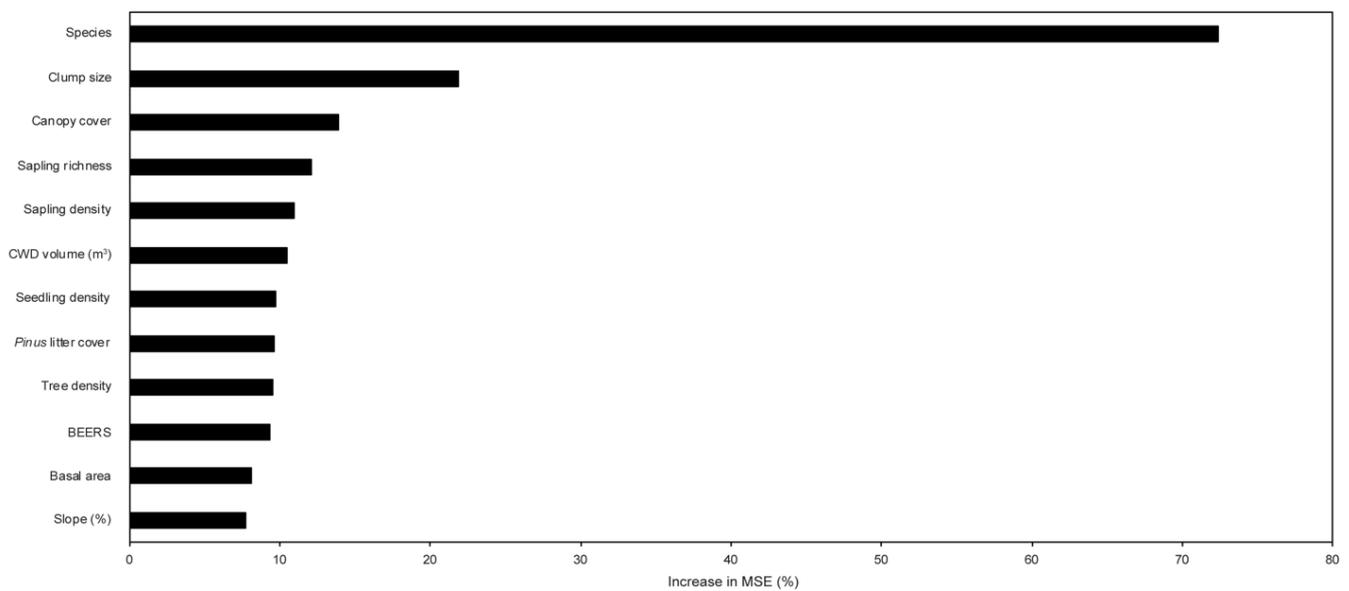


Figure 3. Importance ranking for the influence of species and biophysical site conditions on sapling height. CWD is coarse woody debris. BEERS is transformed aspect. The percent increase in mean square error (MSE) is the increase in model error when the predictor variable was randomly permuted.

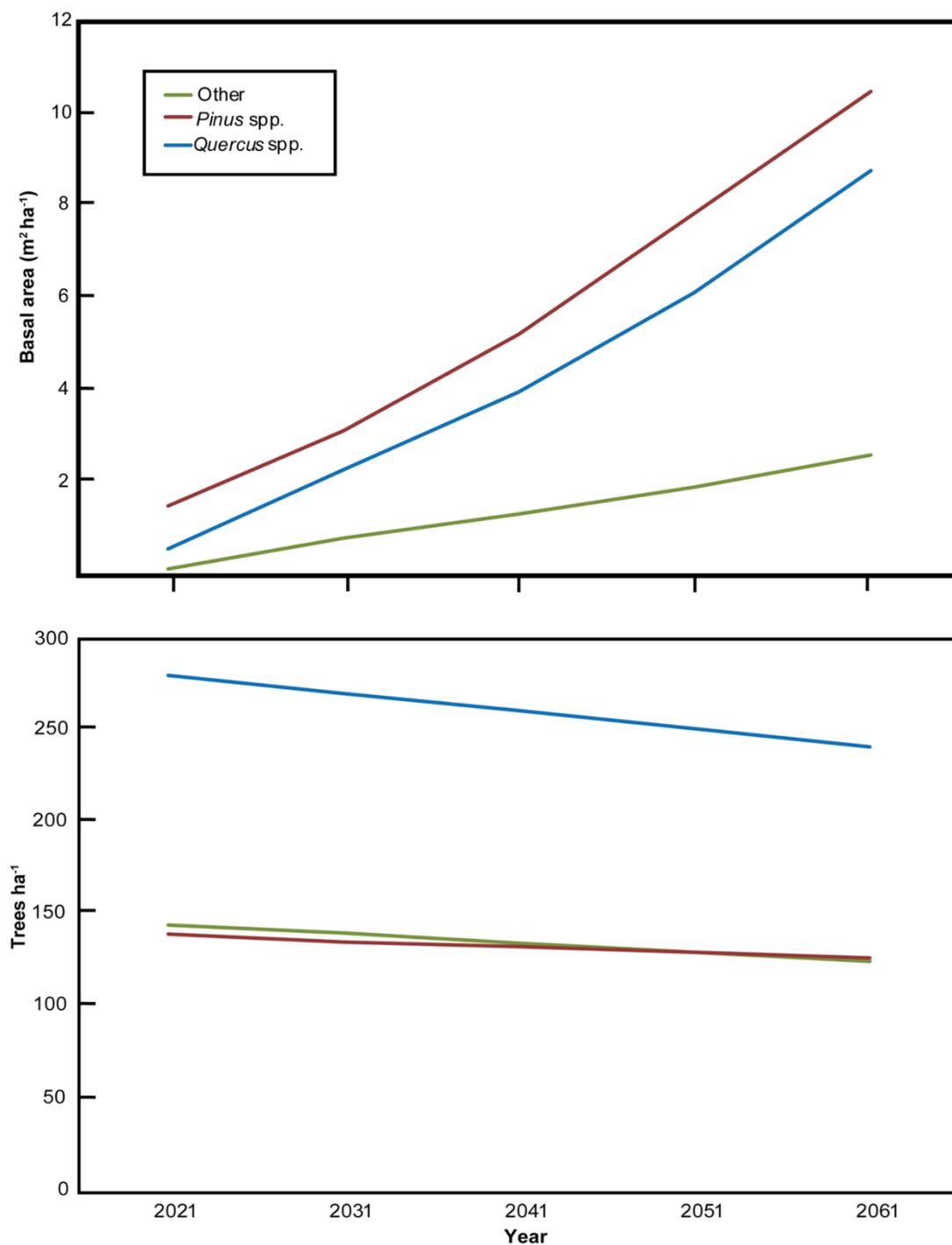


Figure 4. Forest Vegetation Simulator (FVS) model projection of tree basal area (m² ha⁻¹) and density (stems ha⁻¹) of *Pinus* spp. (red), *Quercus* spp. (blue) and other spp. (green) from 2021 to 2061 (stand age 50 years) in a catastrophically disturbed *Pinus palustris* woodland on the Oakmulgee Ranger District, Talladega National Forest, Alabama, USA.

4. Discussion

4.1. Current Stand Conditions

The basal area at stand age 10 was relatively high. We estimate that residual stems that survived the wind disturbance comprised ca. 24% of the total basal area on the wind-disturbed plots. Although we cannot be certain which stems established before the disturbance, we hypothesize most, and perhaps all, stems ≥ 12.5 cm dbh were residuals

or living biological legacies. Although few large residual stems (e.g., stems >30 cm dbh) occurred on our wind-disturbed plots, those that did exist were all either *Pinus* and xeric *Quercus* spp. Of the trees in smaller diameter classes (i.e., <12.5 cm dbh), we speculate *P. taeda* established from a mixture of pre-existing seedlings that survived the canopy disturbance and seed deposited just before or immediately after the disturbance. Sexually mature *P. taeda* stems occurred in mature stands along the edges of the tornado swath [38]. *Pinus palustris* in the small tree diameter size classes were likely advance reproduction in the form of sapling and seedling stems at the time of canopy disturbance. *Pinus palustris* is well known for having a grass stage when biomass production is largely confined to the root network. This stage typically lasts from 4 to 5 years but can range from 2 to 20 years [47,48]. *Quercus* stems in the smaller tree size classes likely occurred as advance reproduction in the regeneration layer prior to canopy disturbance. In fire-maintained *P. palustris* woodlands, it is common for there to be an abundance of *Quercus* stems in the seedling and sapling layers [49]. These stems are typically top-killed by the frequent low-intensity surface fires that maintain *P. palustris* dominance and woodland conditions in these systems. Therefore, 10 years post-disturbance, we suspect that most of the stand basal area consisted of stems that existed prior to the catastrophic wind disturbance as either larger residual stems or as advance reproduction. This highlights the importance of living biological legacies on post-disturbance stand recovery.

In the sapling layer, shrubs (i.e., *Vaccinium* spp. and *Rhus* spp.) were disproportionately abundant. These shrub taxa are commonly found in the understory and midstory of mature *P. palustris* woodlands and lack potential to achieve canopy dominance [35]. Of the saplings with canopy potential, *Quercus* spp. were the most abundant (28%). The modified vegetation-fuels-fire feedback likely resulted in reduced mortality of *Quercus* spp. and other hardwoods that would otherwise be top-killed by low-intensity prescribed fire [17]. This was evident in the lack of height difference between *Quercus* spp. and fire-adapted *P. palustris*. We hypothesize that the *Quercus* stems exhibited relatively high growth rates because they were sprouts from well-developed root networks that existed prior to catastrophic wind disturbance [50]. With modified fuel complexes that inhibit desirable fire effects, hardwoods can quickly grow in height from established root systems [51,52]. Early seral taxa exhibited high growth rates as well, notably, *L. styraciflua* and *P. taeda*. *Pinus palustris* saplings were not significantly taller than *P. taeda*, which was unexpected because we hypothesized that most *P. taeda* would have been killed by prescribed fire. *Pinus palustris* height growth is initially slow compared to *P. taeda* as *P. palustris* can remain in the grass stage (i.e., the seedling stage) for extended periods [47,48]. We suspect that the majority of *P. palustris* were present in the grass stage prior to catastrophic disturbance and recruited into the sapling stage after canopy removal. Relatively little is known about *P. palustris* sapling growth, especially compared to other regional *Pinus* species [49]. When *P. palustris* emerges from the grass stage to the sapling or “rocket” stage, height growth is comparable to other *Pinus* species with which it commonly co-occurs [53]. In the RF height model, species was the most important predictor variable. Regardless of other biophysical site conditions, stem height was best explained by species-specific patterns. We documented an abundance of sapling species with variable growth forms and life-history strategies.

4.2. Projected Stand Conditions

Based on the FVS model, the stand was projected to be classed as *Quercus-Pinus* at stand age 50 years. This species composition fits the description of mixedwood stands [54]. Prior to the catastrophic wind disturbance, this was a *P. palustris*-dominated woodland. In portions of the stand that were not impacted by the catastrophic disturbance, basal area was 21.69 m² ha⁻¹ and the relative dominance of *P. palustris* was 75% [35]. In fire-maintained *P. palustris* woodlands near this study site, basal areas of 21.29 m² ha⁻¹ with *P. palustris* representing 97% of basal area [46] and 20.87 m² ha⁻¹ with *P. palustris* representing 94% of basal area [55] have been documented. The FVS model projects basal area at stand age 50 to be 21.90 m² ha⁻¹, which approximates the pre-disturbance condition and was similar to

the basal area of other fire-maintained *P. palustris* woodlands on the Oakmulgee Ranger District. Thus, at stand age 50 years, the basal area was projected to be within an acceptable range for fire-maintained *P. palustris* woodlands in the Alabama Fall Line Hills. However, the canopy species composition was not projected to remain *P. palustris* dominant. The FVS model projects this will be a mixedwood stand under the current disturbance regime without other active management. The FVS model projects *P. palustris* relative dominance to be just 21% at stand age 50 years. Stand composition at that time is projected to have a strong component of *Quercus* species (40% relative dominance) and *P. taeda* (26% relative dominance). However, we acknowledge that plot-level data were aggregated and analyzed in our study. Based on our plot data and field observations, we hypothesize that some neighborhoods will be *P. palustris* dominant, some will be *P. taeda* dominant, and some will support relatively equal mixtures of *Pinus* and *Quercus* taxa. We attribute the patchy nature of neighborhood composition within the broader stand to biological legacies, patchy fire behavior that resulted from the loss of *Pinus* litter production from canopy trees, and inherent microsite variability [50].

The FVS model did not project, and our field data do not indicate that prescribed fires will be sufficient by themselves to inhibit recruitment of *P. taeda* or *Quercus* species. We suspect that by stand age 10 years, some stems from these taxa have reached sufficient size to survive low-intensity prescribed fires [56,57]. However, we documented a high density of *P. taeda* and *Quercus* spp. in the sapling layer that are still likely susceptible to prescribed fire induced plant or shoot mortality. Although *P. palustris* is not projected to dominate this stand under the current disturbance regime, stochastic events (e.g., severe droughts) may result in mortality of co-occurring tree species. Regardless, silvicultural treatments will be required to supplement the prescribed fire program to promote *P. palustris* dominance on this site as existed prior to catastrophic wind disturbance. If the FVS projection was correct, *P. taeda* and *Quercus* stems will need to be chemically or mechanically removed from neighborhoods within the stand that lack *P. palustris* dominance. These silvicultural treatments are commonly required to create and maintain *P. palustris* woodlands in the Alabama Fall Line Hills.

5. Conclusions

A decade after catastrophic wind disturbance, the fire-maintained *P. palustris* woodland studied here was not projected by the simulation model to return to pre-disturbance conditions. Prior to the wind disturbance event, the stand was dominated by *P. palustris*. The simulation model projected that at age 50 years, the stand would be dominated by mixed *Quercus* spp., *P. taeda*, and *P. palustris* (i.e., mixedwood). The projected successional pathway is likely a function of residual stems that survived the catastrophic wind disturbance and modification of vegetation-fuels-fire feedbacks (i.e., biological legacies). Some woody stems have likely crossed size thresholds so that they are not susceptible to mortality from frequent prescribed fire. Although the stand was projected to be compositionally dissimilar from the pre-disturbance condition under the current disturbance regime (i.e., prescribed fire on a 2–4 year rotation), we contend that the fire-maintained *P. palustris* woodland may in fact be considered resilient to the catastrophic wind event. With additional silvicultural treatments, such as thinning of undesirable species, composition and stand structure could be moved toward pre-disturbance conditions. Silvicultural interventions were required in this and all other *P. palustris* woodlands in the Alabama Fall Line Hills that are compositionally, structurally, and functionally desirable by managers. So, although this stand will almost certainly require silvicultural intervention to return to pre-disturbance conditions, that should not be surprising given that those interventions are always required in this region to create and maintain *P. palustris* woodlands. In other words, routine silvicultural entries may be considered part of the initial system properties in which this ecosystem is recovering towards [58]. As forest ecosystem resilience transitions from theory to practice, we should acknowledge the role of silviculture and the treatments that were required prior to disturbance to create desired stand conditions. If a similar series

of treatments post-disturbance will result in pre-disturbance composition, structure, and function, then the ecosystem should be considered resilient.

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