

# Ground flora cover, diversity, and life-history trait representation after wind disturbance, salvage logging, and prescribed fire in a *Pinus palustris* woodland

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## Abstract

**Question:** Salvage logging and prescribed fire are commonly applied in forests worldwide, yet little is known about the combined impacts of these management actions on early-successional ecosystems. We questioned how operational-scale prescribed fire would affect ground flora cover, species diversity, and life-history trait expression in *Pinus palustris* woodlands differentially impacted by an Enhanced Fujita scale 3 (EF3) tornado and salvage logging.

**Location:** Fall Line Hills, Alabama, USA (32°55'30" N, 87°24'00" W).

**Methods:** The composition and foliar cover of woody and herbaceous plants  $\leq 1$  m height were monitored before and after prescribed fire in 600 1-m<sup>2</sup> quadrats distributed throughout mature, wind-disturbed, and salvage-logged *Pinus palustris* woodlands. Plant taxa were categorized by growth habit and life form to aid interpretation of multivariate analyses used to illustrate differences in ground flora assemblages between disturbance categories.

**Results:** Prescribed fire reduced ground flora cover, but not diversity, which remained greatest in wind-disturbed sites that were not salvage-logged. Though ground flora assemblages remained disparate between disturbance categories, prescribed fire imposed some consistent selective pressures on plants with common life-history strategies. Post-fire understorey tree cover reductions coincided with increased shrub cover throughout the treatment area. Nonetheless, differences in graminoid cover were exaggerated after prescribed fire, and representation of the geophyte life form was relatively constant across space and time.

**Conclusions:** Prescribed fire did not counteract salvage-mediated reductions in ground flora diversity. Retention of downed deadwood maximized early-successional plant diversity in wind-disturbed sites. Trait-based ground flora analyses enabled a more detailed understanding of disturbance effects than aggregate metrics of foliar cover and diversity. In ecosystems with high floristic diversity, grouping plants by common life-history traits can provide a simple and effective means to monitor impacts of management actions on ecosystem recovery.

**KEYWORDS**

biological legacies, compound disturbance interaction, functional traits, ground vegetation, herbaceous layer, indicators, longleaf pine, plant diversity, Raunkiaer, resilience, succession, understory species composition

## 1 | INTRODUCTION

Plant diversity and community organization are shaped by natural and anthropogenic disturbance agents, each with unique impacts on plant succession and development (White and Jentsch, 2001). After a disturbance, the composition and spatial arrangement of residual ecosystem components are called disturbance legacies (Franklin et al., 2000; Peters et al., 2011). Disturbance legacies such as woody debris and the life-history strategies of residual species constitute the ecological memory of an ecosystem and influence recovery processes (Johnstone et al., 2016; Webster et al., 2018). Climate-driven changes in disturbance regimes globally have amplified interest in promoting forest ecosystem resilience (Turner, 2010; Seidl et al., 2016). Resilience describes the capacity of a perturbed ecosystem to maintain its intrinsic structures, feedbacks, and functions (Holling, 1973), and is measured by rates and trajectories of recovery (Angeler and Allen, 2016). Management actions taken before, during, or after unplanned perturbations can enhance or diminish ecosystem resilience.

Catastrophic wind disturbances including hurricanes and tornadoes impact many terrestrial ecosystems and are projected to become more frequent in some regions such as the southeastern United States (Webster et al., 2005; Gensini and Brooks, 2018). These large, infrequent disturbances have disproportionate impacts on ecosystem composition and structure, and require heightened attention in long-term management strategies (Dale et al., 1998; Stanturf et al., 2007). Post-disturbance salvage logging is a common management practice that removes dead and damaged trees. Salvage logging can therefore provide a partial return on otherwise lost standing timber value and potentially reduce the severity of subsequent disturbances like insect outbreaks and wildfires (Buma and Wessman, 2012; Müller et al., 2019). Despite its potential socioeconomic benefits and widespread application, the ecological consequences of salvage logging are not fully understood (Leverkus et al., 2018; Thorn et al., 2018).

In some cases, post-disturbance salvage logging can qualify as a compound disturbance interaction in which one disturbance alters ecosystem resilience to (i.e., capacity to recover from) another disturbance (Paine et al., 1998; Buma, 2015). Salvage logging can negatively impact the recovery of biological communities from birds (Georgiev et al., 2020) to bryophytes (Hernández-Hernández et al., 2017) and induce long-lasting ecosystem state shifts (Van Nieuwstadt et al., 2001; Lindenmayer et al., 2017). However, negative ecological consequences of salvage logging are not inevitable, especially with respect to woody plant recovery (Royo et al., 2016; Taylor et al., 2017). To achieve a more comprehensive understanding of post-disturbance salvage logging and compound disturbance

interactions, greater research focus is needed on the recovery of non-woody plants (Leverkus et al., 2018; Kleinman et al., 2019). Indeed, the forest disturbance ecology literature is focused primarily on metrics of tree regeneration despite understory plant communities often hosting markedly more floristic diversity than canopy strata (Roberts, 2004; Gilliam, 2007).

After stand-regenerating wind events, some plants may be more or less suited to grow in microsites sheltered by woody debris or on patches of exposed, dry soil on unearthed root mounds (Beatty, 1984; Logan et al., 2020). Salvage-logging operations that alter these structural legacies can homogenize early-successional ecosystems and the diverse biological communities they support (Swanson et al., 2011; Lindenmayer et al., 2019). Salvage logging is therefore often associated with reduced understory plant diversity and community dissimilarity (Purdon et al., 2004; Rumbaitis del Rio, 2006; Brewer et al., 2012). Nonetheless, Peterson and Leach (2008) reported no differences in understory plant diversity between unlogged and salvage-logged sites despite altered microsite conditions, and Orczewska et al. (2019) reported increased understory plant diversity in salvage-logged sites. In the latter example, however, increased plant diversity corresponded with the colonization and spread of disturbance-adapted plants that impeded recovery of late-successional species.

Trait-based assessments of understory plants can be used to determine floristic indicators of disturbance that are not always detected by metrics of foliar cover and diversity (Dale et al., 2002). Measurements of species-specific life-history traits illustrate how plants survive, colonize, and compete in disturbance-impacted areas (Donato et al., 2009; Pidgen and Mallik, 2013). For example, Knapp and Ritchie (2016) described how recently germinated shrubs were more susceptible to the mechanical impacts of salvage logging than forbs and graminoids. Non-native plant invasion is also facilitated by disturbances that liberate previously occupied growing space, and may be amplified by salvage logging through soil disturbance, propagule distribution, and mechanical damage of competing vegetation (Miller et al., 2015).

The North American Coastal Plain is a global biodiversity hotspot with over 1,800 endemic vascular plants (Noss et al., 2015). The *Pinus palustris* (longleaf pine) ecosystem once occupied ca. 37 million ha of the North American Coastal Plain, but has been reduced to less than 5% of its former extent (Frost, 2006). Remnant patches of the *Pinus palustris* ecosystem are managed with frequent, low-intensity prescribed fires that perpetuate *Pinus palustris*-dominated canopies and diverse understory plant communities (Outcalt, 2006). Specifically, prescribed fires induce shoot mortality of hardwoods that could otherwise outcompete *Pinus palustris* for canopy positions and enhance seedbed suitability and growing conditions for fire-adapted

understorey plants (Mitchell et al., 2009). Cultural and institutional support of prescribed fire is strong in the North American Coastal Plain, which provides a model for prescribed fire management in other fire-adapted forests in the North American Interior Highlands and Intermountain West (Bigelow et al., 2018). Fire science in the *Pinus palustris* ecosystem may also inform a growing international interest in prescribed fire management in regions such as southern Europe (Fernandes et al., 2013; Fuentes et al., 2018) and southwestern Australia (Burrows and McCaw, 2013).

The overarching objective of this study was to assess how operational-scale prescribed fire influenced floristic assemblages in *Pinus palustris* woodlands differentially impacted by an April 2011 Enhanced Fujita scale 3 (EF3) tornado and a subsequent salvage-logging operation. The presence and foliar cover of understorey plants were monitored before and after prescribed fire in mature, wind-disturbed, and salvage-logged sites to assess changes in plant community composition, species diversity, and life-history trait expression. A baseline study attributed greater floristic diversity in wind-disturbed sites to microsite variability associated with fallen trees, and reduced plant diversity in salvage-logged sites to habitat homogenization associated with deadwood extraction (Kleinman et al., 2017). In this study, we hypothesized that (a) floristic diversity would remain greatest after prescribed fire in wind-disturbed sites that were not logged. However, we also hypothesized that (b) prescribed fire would promote some plant community convergence by imposing consistent selective pressures on plants with common life-history strategies.

## 2 | METHODS

### 2.1 | Study area

This study was conducted in the Oakmulgee District of the Talladega National Forest in Bibb County, Alabama, USA (32°55'30" N, 87°24'00" W). The Oakmulgee District occurs in the *Quercus-Pinus* forest region of the United States (Braun, 1950) in the remnant central *Pinus palustris* hills of Alabama (Harper, 1943). In the Fall Line Hills physiographic transition zone, species from the Coastal Plain coexist with species from the adjacent Appalachian Highlands on steep, stream-carved slopes and ridges (Fenneman, 1938; Shankman and Hart, 2007). In the study area, *Pinus palustris*-dominated woodlands occur on upper slopes and south-facing lower slopes maintained with prescribed fire every 2–5 years (Beckett and Golden, 1982; Cox and Hart, 2015). Understorey plant communities are characterized by *Pteridium latiusculum* {syn: *Pteridium aquilinum*} and *Schizachyrium scoparium*, and a diversity of *Quercus* spp. and other hardwoods occur in sub-canopy strata (Teague et al., 2014; Kleinman and Hart, 2018). Hillslopes and ridges contain deep, moderately well drained soils developed from the Cretaceous-aged Gordo Formation (GSA, 2006; USDA NRCS, 2008, 2020a). The climate is humid mesothermal, with long, hot summers and year-round precipitation (Thornthwaite, 1948). Mean monthly temperature is highest in July (26.9°C) and

lowest in January (6.6°C), with a mean annual temperature of 17.2°C and mean annual precipitation of 1,376.21 mm (PRISM, 2020).

On 27 April 2011, the Oakmulgee District was impacted by an EF3 tornado with estimated maximum wind speeds of 233 km hr<sup>-1</sup> and a maximum path width of 1,609 m (National Weather Service, 2011). The tornado was one of 362 tornadoes that impacted the eastern United States during the 25–28 April 2011 Super Outbreak. After the storm, plans to salvage potentially hazardous damaged and dead wood from tornado-impacted areas were developed. From July till November 2011, wheeled feller bunchers and chainsaws were used to cut uprooted trees and logs, which were transported with wheeled skidders to a stationary knuckleboom loader. However, because the salvaged-wood market was oversupplied after the 2011 Super Outbreak, some wind-disturbed sites were not logged. This presented an opportunity to assess the individual and interacting effects of wind disturbance, salvage logging, and prescribed fire on *Pinus palustris* stand dynamics.

### 2.2 | Field methods

In March 2016, we opportunistically delineated three disturbance categories: mature, wind-disturbed, and salvage-logged (Kleinman et al., 2017; Ford et al., 2018). Mature sites were not impacted by the tornado, wind-disturbed sites were directly impacted by the tornado but not logged, and salvage-logged sites were directly impacted by the tornado and salvage-logged. The density of live woody stems  $\geq 5$  cm diameter at 1.37 m above root collar was 325 stems/ha in mature sites and 31 stems/ha in both wind-disturbed and salvage-logged sites (Kleinman et al., 2017; Ford et al., 2018). Although the conditions of this “natural experiment” (i.e., tornado and salvage logging) precluded experimental replicability, care was taken to select sites with comparable pre-disturbance conditions. We therefore used a space-for-time substitution to gain insight on the impacts of catastrophic wind disturbance and salvage logging that would not otherwise be attainable with traditional methods of experimentation (Pickett, 1989; Hargrove and Pickering, 1992; Davies and Gray, 2015). In other words, selection of sites with comparable pre-disturbance conditions enabled observed differences between sites to be attributed to the disturbance events of interest, not pre-disturbance disparities. Prior to the tornado, all sites were in stands that established in the early 1930s, were dominated by *Pinus palustris*, shared upper- and mid-slope positions with Maubila-series soils, and occurred within a 1-km<sup>2</sup> expanse of each other. Sites also occurred in the same Forest Service-delineated compartment, which ensured that sites experienced the same prescribed fire regime, including operational-scale prescribed fires in May 2010, April 2014, and April 2018. Thus, recurring fire was a background condition in all sites, but, based on the timing of our field surveys, data collected May–July 2016 were considered “before” fire data and data collected June 2018 were considered “after” fire data.

Within each of the three disturbance categories, 20 nested plots ( $n = 60$ ) were systematically established with 25-m spacing

(Figure 1). Nested plots consisted of a 400-m<sup>2</sup> fixed-radius plot and 10 nested 1-m<sup>2</sup> quadrats (10 m<sup>2</sup>). Quadrats were positioned with one at the center of each 400-m<sup>2</sup> plot and the other nine spaced evenly along the 0°, 120°, and 240° azimuths from plot center. Within each 1-m<sup>2</sup> quadrat, we recorded the composition and foliar cover of all ground flora, defined as live woody and herbaceous plants ≤1 m in height. Excluding Poaceae (grasses), ground flora were identified to the finest taxonomic resolution possible and assigned a cover class from 1–10. This cover class system was adapted from the North Carolina Vegetation Survey (NCVS), where 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).

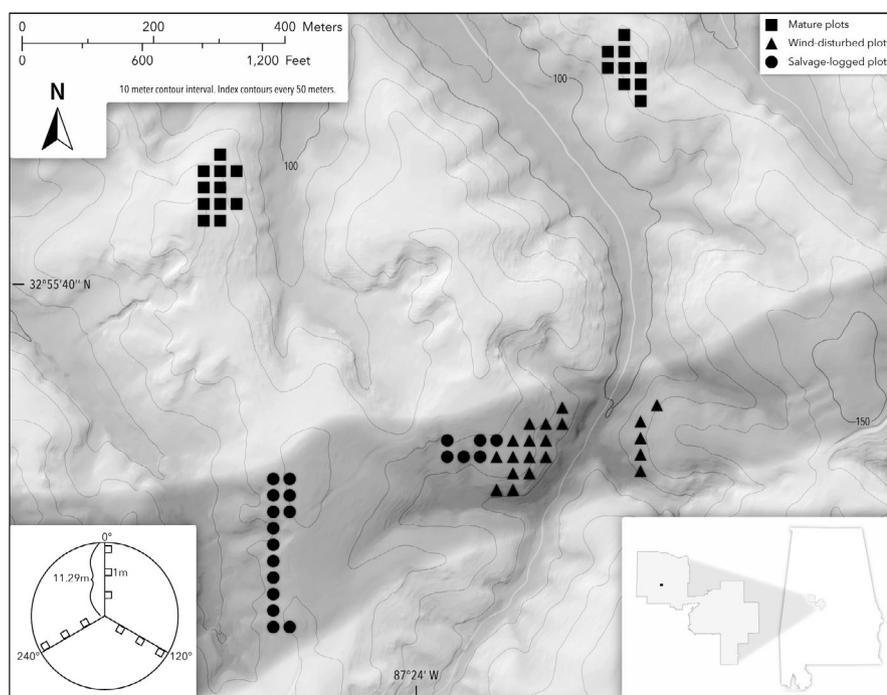
Data collected at the 400-m<sup>2</sup> plot-scale were used to interpret associations between biophysical site conditions and variation in ground flora assemblages. These data included the density of saplings (i.e., live woody stems >1 m in height and <5 cm diameter at 1.37 m above root collar) and volume of coarse woody debris (i.e., downed deadwood ≥10 cm diameter). Coarse woody debris volume was calculated with conic-paraboloid and species-specific allometric equations derived from diameter measurements taken at both ends of logs (i.e., dead stems disconnected from roots) and at 1.37 m from root plate on uprooted stems (i.e., dead stems with uplifted root networks; Ford et al., 2018; Kleinman et al., 2020). Percent slope and aspect were also measured to examine potential effects on ground flora assemblages.

### 2.3 | Analytical methods

Taxonomic concepts were standardized to Weakley (2015). Each taxon encountered was evaluated in the context of four life-history categories to achieve a detailed understanding of disturbance

effects on floristic dynamics (Appendix S1). Life-history categories included native status, duration, growth habit, and Raunkiaer (1934) life form (Table 1). Plant trait designations were guided by the USDA Fire Effects Information System and PLANTS databases (USDA Forest Service, 2020; USDA NRCS, 2020b), herbarium specimens (Keener et al., 2020), published floras (Oosting, 1942; Gibson, 1961; Palmquist et al., 2014), and, ultimately, field observations. Although many other trait-based classification schemes have been proposed (Pulsford et al., 2016), the Raunkiaer (1934) system based on locations of perennating plant parts is particularly informative in fire-prone ecosystems where the height and depth of radiant heat have major implications for plant persistence (Rowe, 1983). Post-fire resprouting ability is also important in fire-prone ecosystems (Pausas and Keeley, 2014). Information on plant resprouting ability was therefore recorded and used to interpret results, but was not assessed statistically because of limited data availability, especially for non-woody plants.

To derive plot-level ground flora cover values, quadrat-level NCVS rankings were transformed to corresponding range mid-points and averaged per plot. Plot-level cover values were grouped by constituent life-history traits to calculate the foliar cover and richness of each growth habit and life form and summed to derive total foliar cover. Plot-level cover values were reconverted to corresponding NCVS values to calculate Shannon diversity at the 10-m<sup>2</sup> scale. Plot-level metrics, which included total foliar cover, richness, and Shannon diversity and the foliar cover and richness of each growth habit and life form, were transformed as needed to achieve homoscedasticity and compared between background disturbance categories (mature, wind-disturbed, and salvage-logged) and across time (before and after prescribed fire) with 3 × 2 mixed ANOVAs. One-way ANOVAs and Tukey's honestly significant difference (HSD) tests were used to assess main effects when disturbance categories



**FIGURE 1** Plot locations in mature, wind-disturbed, and salvage-logged *Pinus palustris* woodlands in the Oakmulgee District, Talladega National Forest, Alabama, USA (shaded on bottom-right inset map). Bottom-left inset illustrates how ten 1-m<sup>2</sup> quadrats were nested within each 400-m<sup>2</sup> fixed-radius plot

**TABLE 1** Descriptions of the life-history traits used to define the 155 ground flora taxa documented in differentially disturbed *Pinus palustris* woodlands in the Fall Line Hills of Alabama, USA

Trait	State	Description
Native status	Natives	Native to Alabama, USA
	Non-natives	Not native to Alabama, USA
Duration	Annuals	Complete life cycle within one growing season
	Biennials	Complete life cycle in two growing seasons
	Perennials	Live more than two growing seasons
Growth habit	Forbs	Herbaceous plants (lack persistent aboveground woody tissue)
	Graminoids	Herbaceous plants with grass-like morphology
	Vines	Woody or herbaceous plants with climbing or trailing morphology
	Shrubs	Woody perennials <5 m height
	Trees	Woody perennials >5 m height
Life form	Geophytes	Perennating organs belowground (bulbs, rhizomes, and tubers)
	Therophytes	Perennating tissue stored in seed (annuals)
	Hemicryptophytes	Perennating buds at ground level
	Chamaephytes	Perennating buds aboveground but <0.5 m height
	Phanerophytes	Perennating buds >0.5 m height

Trait definitions follow the USDA PLANTS database (USDA NRCS, 2020b) and Raunkjær (1934).

and time did not exhibit significant interactions (levels of  $p < 0.05$  considered significant).

To visualize differences in ground flora assemblages between disturbance categories, we conducted non-metric multidimensional scaling (NMS) with PC-ORD version 7 (McCune and Mefford, 2016). Multivariate analyses were conducted separately on before- and after-fire data sets, which included the composition and NCVS cover class of all ground flora documented per plot. To moderate the influence of rare and exceptionally large plants on apparent differences in ground flora assemblages, data sets were modified to exclude taxa with single-plot occurrences and relativized by maximum by dividing plot-level cover values by the maximum values recorded per taxon (Peck, 2016). NMS scree plots were used to select the

optimal number of axes in NMS solutions, which were run 250 times with real data, applied Sørensen distance, and were cross-checked for conformity with other solutions. One-way PERMANOVAs with Sørensen distance were used to validate observed differences in ground flora assemblages. To assess relationships between biophysical site conditions and ground flora assemblages, biplot overlays were used to illustrate correlations ( $r^2$  cutoff of 0.25) between ordination axes and five environmental variables: disturbance category, transformed slope aspect (Beers et al., 1966), percent slope, sapling density, and coarse woody debris volume. To determine if floristic assemblages became more or less variable over time, values of average dispersion (i.e., scatter) between plots per disturbance category were calculated with NMS dissimilarity matrices and assessed with a  $3 \times 2$  mixed ANOVA.

Indicator species analysis was used to identify plant taxa most representative of distinct floristic assemblages based on the relative frequency and abundance of individual taxa per disturbance category (Dufrêne and Legendre, 1997). Indicator species were compared based on the life-history traits they represented. Life-history traits represented by all ground flora were then assessed with fourth-corner analysis to determine associations between each plant trait and disturbance category (Dray and Legendre, 2008). Fourth-corner analysis relates an (R) matrix of environmental characteristics (i.e., plots and associated disturbance categories) to a species trait matrix (Q) by way of a species abundance matrix (L) with five potential models. The first model was used to permute the presence or absence of each taxon independently and apply a randomization procedure to determine the significance of each plant trait and disturbance category association (Dray and Dufour, 2007; Dray and Legendre, 2008).

### 3 | RESULTS

We documented 155 plant taxa in the 600 1-m<sup>2</sup> quadrats distributed throughout mature, wind-disturbed, and salvage-logged sites. Only one quadrat, nested in a salvage-logged plot before prescribed fire, contained a non-native plant, *Veronica arvensis*. However, *Lygodium japonicum*, an aggressive non-native climbing fern, was observed in three wind-disturbed plots after prescribed fire, although not within the limits of any nested quadrats. Most plants documented were perennials (136 taxa), followed by annuals (17 taxa) and biennials (2 taxa). Over half of plants documented were forbs (79 taxa), and the next-most common growth habits were trees (38 taxa), vines (18 taxa), shrubs (14 taxa), and graminoids (4 taxa). Metrics of graminoid richness must be interpreted with caution, however, because Poaceae were not identified beyond family. The most well-represented life forms were hemicryptophytes (60 taxa) and phanerophytes (59 taxa), followed by therophytes (17 taxa), geophytes (15 taxa), and chamaephytes (4 taxa).

Prescribed fire reduced the foliar cover ( $p < 0.001$ ), but not species richness or Shannon diversity, of ground flora assemblages throughout the treatment area (Table 2). Despite overall foliar cover reductions, wind-disturbed and salvage-logged sites maintained

greater foliar cover than mature sites before and after prescribed fire ( $p < 0.001$ ). Though foliar cover was comparable on wind-disturbed and salvage-logged sites, ground flora richness and Shannon diversity remained greatest in wind-disturbed sites before ( $p = 0.033$  and  $p = 0.019$  respectively) and after ( $p = 0.002$  and  $p = 0.002$  respectively) prescribed fire.

Three-dimensional NMS solutions explained 70% and 69% (non-metric  $R^2$ -values) of variation in ground flora assemblages before and after prescribed fire, respectively (Figure 2). One-way PERMANOVAS verified observed differences in the composition and foliar cover of ground flora between disturbance categories each year ( $p < 0.001$ ). In the before-fire NMS solution, axis 1 was positively associated with coarse woody debris volume ( $r^2 = 0.25$ ) and sapling density ( $r^2 = 0.65$ ), which corresponded to the location of wind-disturbed plots in ordination space. In the after-fire NMS solution, coarse woody debris volume was positively associated with axis 3 ( $r^2 = 0.35$ ), which also corresponded to the location of wind-disturbed plots in ordination space. Sapling density, however, was positively associated with axis 2 after prescribed fire ( $r^2 = 0.29$ ), which did not correspond to any one particular disturbance category. The dispersion of plots in ordination space was impacted by the interaction of background disturbance category and time relative to prescribed fire ( $p < 0.001$ ; Figure 3). Before prescribed fire, wind-disturbed sites exhibited the greatest variability in ground flora assemblages, followed by mature sites and salvage-logged sites. After prescribed fire, mean dispersion remained lowest in salvage-logged sites, but mature sites exhibited the greatest variability in ground flora assemblages.

Indicator species analysis identified 49 taxa most representative of the ground flora assemblages observed in each disturbance category (Table 3). Before prescribed fire, two indicators were associated with mature sites, 20 were associated with wind-disturbed sites, and 11 were associated with salvage-logged sites. After prescribed fire, one indicator was associated with mature sites, 21 were associated with wind-disturbed sites, and 12 were associated with salvage-logged sites. Among the 49 indicators, the most well-represented growth habits were forbs (19 taxa) and trees (17 taxa), and the most well-represented life forms were phanerophytes (25 taxa) and hemicryptophytes (15 taxa).

Based on the growth habits and life forms represented by all ground flora, fourth-corner analysis identified a variety of

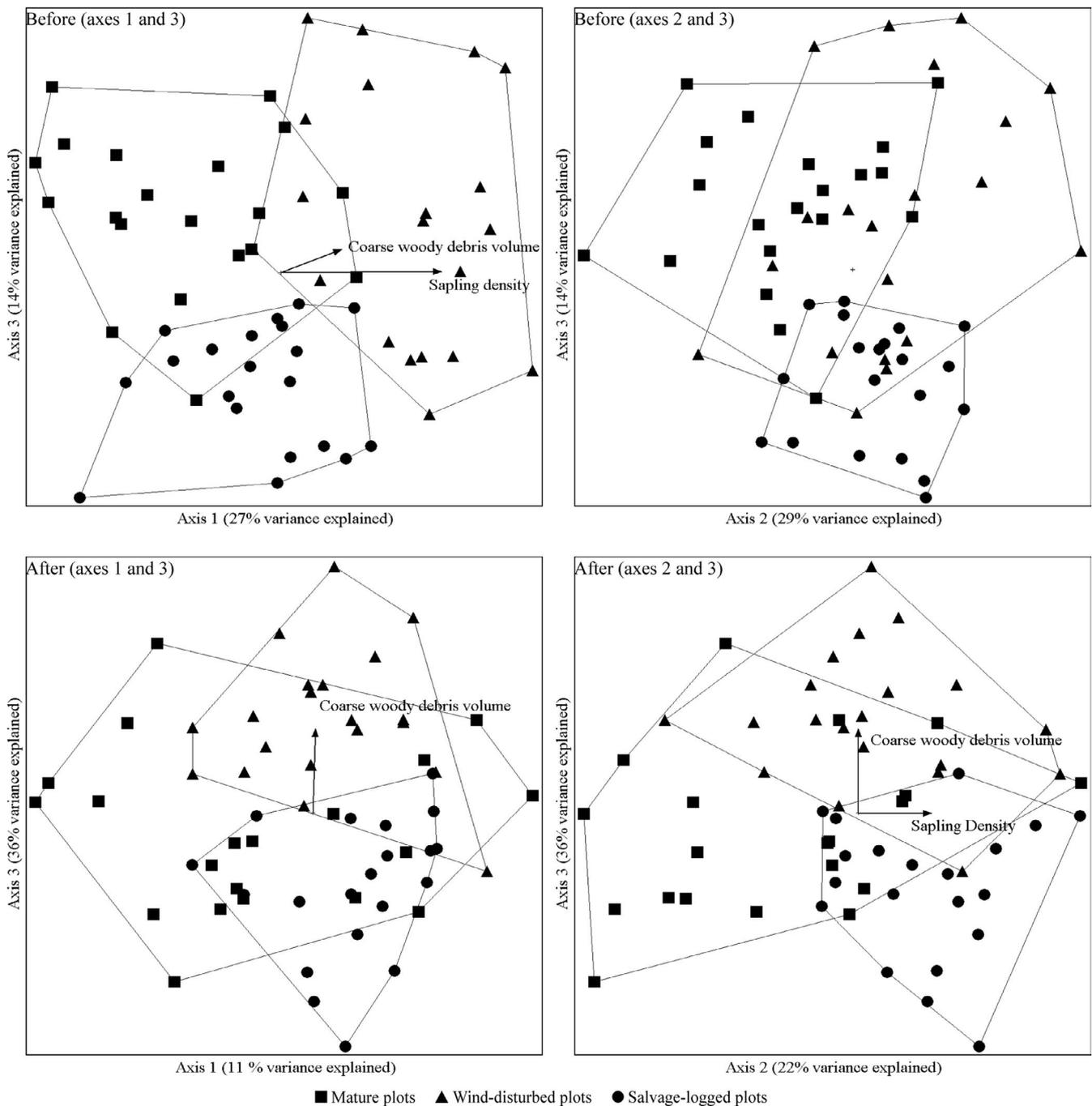
relationships between disturbance categories and life-history traits (Table 4). Mature sites were negatively associated with graminoids and shrubs, and positively associated with vines before and after prescribed fire. These results generally corresponded with individual assessments of how the foliar cover and richness of ground flora representing each life-history trait were impacted by pre-fire disturbance history, time relative to prescribed fire, and their interaction (Appendix S2, Figure 4). Mature sites exhibited the lowest graminoid cover before and after prescribed fire ( $p < 0.001$ ). Although shrub cover increased after prescribed fire throughout the treatment area ( $p < 0.001$ ), shrub cover remained lowest on mature sites. Vine cover was impacted by the interaction of disturbance category and time ( $p < 0.001$ ), and showed greater post-fire reductions on wind-disturbed and salvage-logged sites compared to mature sites. In contrast to growth habits, significant fourth-corner associations between mature sites and life forms did not persist after prescribed fire. Prior to prescribed fire, mature sites were negatively associated with therophytes and hemicryptophytes. The interaction of disturbance category and time impacted therophyte richness ( $p < 0.001$ ) and hemicryptophyte cover ( $p = 0.015$ ), which both increased slightly after prescribed fire on mature sites yet were slightly reduced on wind-disturbed and salvage-logged sites. Although fourth-corner analysis also detected a positive pre-fire relationship between mature sites and phanerophytes, wind-disturbed sites hosted greater values of phanerophyte cover and richness before ( $p = 0.001$  and  $p = 0.003$  respectively) and after ( $p = 0.006$  and  $p < 0.001$  respectively) prescribed fire.

For wind-disturbed sites, fourth-corner analysis identified negative relationships with vines and positive relationships with shrubs before and after prescribed fire. Prior to prescribed fire, vine cover was substantially lower on wind-disturbed sites compared to salvage-logged sites, and after prescribed fire, wind-disturbed sites contained the lowest vine cover. Shrub cover was greatest on wind-disturbed sites before ( $p = 0.001$ ) and after ( $p = 0.044$ ) prescribed fire, and compared to mature sites, shrub richness was also greater in wind-disturbed sites before ( $p = 0.004$ ) and after ( $p = 0.001$ ) prescribed fire. Although a positive fourth-corner association between mature sites and trees was only detected with post-fire data, tree richness was greatest in wind-disturbed sites before ( $p = 0.023$ ) and after ( $p = 0.009$ ) prescribed fire. Pre-fire tree cover was also greatest on wind-disturbed sites ( $p = 0.049$ ), but

Metric	Time	Mature	Wind	Salvage
Foliar cover (%)	2016 A	40.0 ± 4.5 a	73.7 ± 3.8 b	70.3 ± 3.7 b
	2018 B	24.8 ± 3.1 a	46.2 ± 2.8 b	45.8 ± 2.5 b
Richness	2016 A	25.1 ± 1.3 a	33.7 ± 1.3 b	29.1 ± 1.2 a
	2018 A	24.5 ± 1.7 a	33.9 ± 1.6 b	26.3 ± 1.2 a
Shannon diversity	2016 A	3.0 ± 0.1 a	3.3 ± 0.0 b	3.1 ± 0.0 a
	2018 A	3.0 ± 0.1 a	3.3 ± 0.0 b	3.0 ± 0.1 a

**TABLE 2** Mean ± standard error (SE) foliar cover (%), richness (taxa per 10 m<sup>2</sup>), and Shannon diversity of ground flora in mature, wind-disturbed, and salvage-logged *Pinus palustris* woodlands in the Fall Line Hills of Alabama, USA

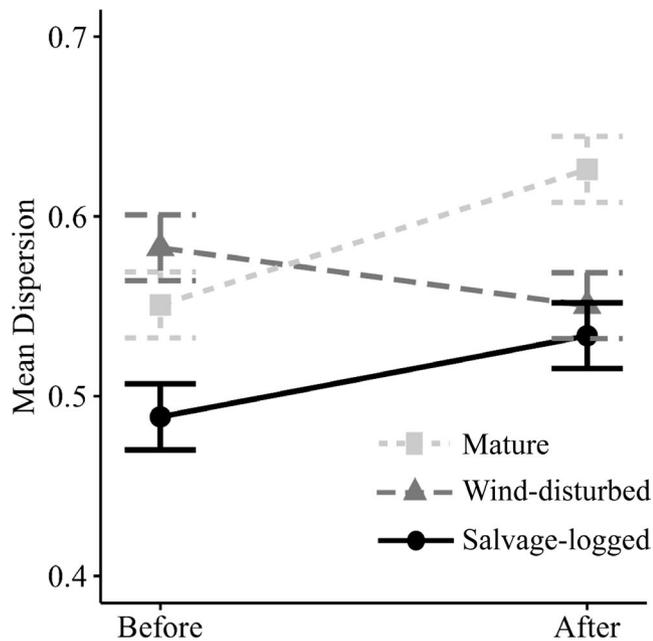
Note:: Different capital letters indicate significant differences between years ( $p < 0.05$ ) and lower-case letters indicate significant differences between pre-fire conditions ( $p < 0.05$ ) within years based on Tukey's pairwise comparisons.



**FIGURE 2** Three-dimensional NMS solutions before (top two panels) and after (bottom two panels) prescribed fire based on the composition and foliar cover of ground flora documented in mature, wind-disturbed, and salvage-logged plots. Convex hulls (loops) include plots in the same disturbance category and biplot overlays (arrows) indicate associations between environmental variables and ordination axes

after treatment area-wide tree cover reductions ( $p < 0.001$ ), the foliar cover of trees did not significantly differ between disturbance categories. The only fourth-corner association detected between wind-disturbed sites and life forms was a negative post-fire chamaephyte relationship. Though foliar cover and richness of chamaephytes averaged less than 1% and one taxon per 10 m<sup>2</sup>, respectively, on plots throughout the treatment area, post-fire chamaephyte richness was greater on salvage-logged sites compared to wind-disturbed sites ( $p = 0.028$ ).

Salvage-logged sites showed positive fourth-corner associations with graminoids and negative associations with trees before and after prescribed fire. The foliar cover of graminoids was consistently greatest on salvage-logged sites, although only significantly greater than wind-disturbed sites after prescribed fire ( $p = 0.037$ ). In contrast, salvage-logged sites contained significantly lower tree cover than wind-disturbed sites before prescribed fire ( $p = 0.015$ ), but not after. Tree richness, however, remained lower on salvage-logged sites compared to wind-disturbed sites before ( $p = 0.023$ ) and



**FIGURE 3** Disturbance category and time had a significant interaction ( $p < 0.001$ ) on the average dissimilarity (i.e., dispersion) of ground flora assemblages documented in mature, wind-disturbed, and salvage-logged plots before (2016) and after (2018) prescribed fire

after ( $p = 0.009$ ) prescribed fire. Although fourth-corner analysis detected a positive post-fire relationship between salvage-logged sites and forbs, forb cover and richness did not significantly differ between wind-disturbed and salvage-logged sites. In terms of life forms, salvage-logged sites exhibited a positive fourth-corner relationship with hemicryptophytes and a negative relationship with phanerophytes before and after prescribed fire. Hemicryptophyte cover was consistently greatest on salvage-logged sites, and, compared to wind-disturbed sites, phanerophyte cover was lower on salvage-logged sites before and after prescribed fire. Salvage-logged sites also exhibited a positive pre-fire fourth-corner relationship with therophytes and a positive post-fire fourth-corner relationship with chamaephytes.

## 4 | DISCUSSION

Prescribed fire reduced the foliar cover of ground flora assemblages throughout the treatment area. Floristic diversity, however, was relatively unchanged. Similar results were reported by Fuentes et al. (2018), who documented significantly reduced cover, but not diversity, of understorey plants after prescribed fire in a *Pinus halepensis* forest of Northeastern Spain. In support of our first hypothesis, wind-disturbed sites hosted the greatest ground flora richness and Shannon diversity before and after prescribed fire, which was attributed to a complexity of microsites and microclimatic conditions associated with coarse woody debris. Indeed, ground flora assemblages in wind-disturbed sites were correlated with coarse wood debris volume before and after prescribed fire. Ground flora assemblages

on wind-disturbed sites were also correlated with sapling density before, but not after, prescribed fire. These results corresponded with a companion study that documented only slight post-fire coarse woody debris volume reductions, yet substantial prescribed fire-mediated sapling density reductions in the same study area (Kleinman et al., 2020). Whereas prescribed fire offset differences in sapling densities between wind-disturbed and salvage-logged sites, ground flora assemblages remained disparate. In other words, prescribed fire did not remedy salvage-mediated differences in understorey plant recovery.

Legacies of deadwood extraction persisted on salvage-logged sites. In addition to reduced ground flora diversity, salvage-logged sites exhibited the lowest mean dispersion of ground flora assemblages. Metrics of mean dispersion indicated how variable, not necessarily how diverse, ground flora assemblages were within disturbance categories. Specifically, mean dispersion values indicated how dissimilar ground flora assemblages were between plots in each disturbance category. The relatively low dispersion observed in salvage-logged sites indicated that deadwood extraction homogenized ground flora assemblages. Early stages of plant succession are most often limited by moisture and nutrient availability (Muller, 2014). Whereas downed deadwood contributed to a complex mosaic of sheltered, moist microsites and decomposition-derived soil organic matter in wind-disturbed sites, mechanical extraction of deadwood resulted in more uniform growing conditions in salvage-logged sites. Moreover, direct impacts of salvage-logging machinery, log skidding, and additional soil disturbance likely contributed to the loss of some ground flora that were observed in wind-disturbed sites but absent from salvage-logged sites (Brewer et al., 2012).

Interestingly, post-fire dispersion of ground flora assemblages was greatest in mature sites. This demonstrated that, after prescribed fire, mature sites hosted ground flora assemblages that were most dissimilar from one plot to the next. Working within 1 km of the study area, Goode et al. (2020) also documented greater ground flora variability in the interior forest compared to the tornado swath and forest edge. Variability between ground flora assemblages in mature sites was attributed primarily to gap-scale disturbances such as lightning strikes and single-tree blowdown events (Palik and Pederson, 1996). Though mature sites typically hosted a continuous *Pinus palustris*-dominated canopy and uninterrupted *Pinus* litter-composed fuel bed, it was not uncommon to encounter a canopy gap (Kleinman et al., 2017). The density of snapped, uprooted, and standing dead stems (snags) >5 cm diameter at 1.37 m height was 25 stems/ha in mature sites (2016 data). We contend that canopy gaps supported early-successional ground flora within a matrix of mature woodlands, and thereby contributed to greater intra-stand variability than sites that experienced catastrophic canopy removal. Moreover, fire-induced fuel consumption on mature sites facilitated establishment and growth of therophytes and hemicryptophytes. Therophytes typically complete their short life cycles on recently exposed ground (Raunkiaer, 1934), and hemicryptophyte shoot penetration of the litter layer may be enhanced with litter mass reductions (Facelli and Pickett, 1991).



**TABLE 3** Indicator values (average relative frequency and abundance) with corresponding *p*-values (\*, <0.05; \*\*, <0.01; \*\*\*, <0.001) of plant taxa most representative of mature, wind-disturbed, and salvage-logged sites before (2016) and after (2018) prescribed fire in *Pinus palustris* woodlands in the Fall Line Hills of Alabama, USA

Indicator species	Before	After	Growth habit	Raunkiaer life form
Mature				
<i>Acer rubrum</i>	35.4*		Tree	Phanerophyte
<i>Cornus florida</i>	30.7*		Tree	Phanerophyte
<i>Solidago odora</i>		40.1*	Forb	Hemicryptophyte
Wind-disturbed				
<i>Scleria triglomerata</i>		32.5*	Graminoid	Geophyte
<i>Conyza canadensis</i>	58.2***		Forb	Therophyte
<i>Erechtites hieraciifolius</i>		39.2**	Forb	Therophyte
<i>Eupatorium capillifolium</i>	25**		Forb	Hemicryptophyte
<i>Eupatorium rotundifolium</i>		32.4**	Forb	Hemicryptophyte
<i>Lactuca canadensis</i>	67.3***	56.2***	Forb	Hemicryptophyte
<i>Lespedeza violacea</i>		22.5*	Forb	Hemicryptophyte
<i>Osmundastrum cinnamomeum</i>	20*	20*	Forb	Hemicryptophyte
<i>Phytolacca americana</i>	20*		Forb	Geophyte
<i>Pityopsis graminifolia</i>		45.7***	Forb	Hemicryptophyte
<i>Scutellaria elliptica</i>	20*		Forb	Hemicryptophyte
<i>Solidago</i> spp.		33.3**	Forb	Hemicryptophyte
<i>Symphotrichum</i>	41.6**		Forb	Hemicryptophyte
<i>Parthenocissus quinquefolia</i>	20*	25**	Vine	Phanerophyte
<i>Smilax smallii</i>	20*		Vine	Phanerophyte
<i>Rhus copallinum</i>	45.1**	43.6**	Shrub	Phanerophyte
<i>Rhus glabra</i>		30**	Shrub	Phanerophyte
<i>Rubus</i> spp.		31*	Shrub	Hemicryptophyte
<i>Styrax grandifolius</i>	39.6***	50.9***	Shrub	Phanerophyte
<i>Vaccinium stamineum</i>	51.1***		Shrub	Phanerophyte
<i>Carya glabra</i>	36.8**		Tree	Phanerophyte
<i>Carya tomentosa</i>		35*	Tree	Phanerophyte
<i>Liquidambar styraciflua</i>	30.5*	37.2**	Tree	Phanerophyte
<i>Liriodendron tulipifera</i>	20*		Tree	Phanerophyte
<i>Nyssa sylvatica</i>	40*	33.1*	Tree	Phanerophyte
<i>Prunus umbellata</i>		22.5*	Tree	Phanerophyte
<i>Quercus alba</i>	53.1***	51.3***	Tree	Phanerophyte
<i>Quercus coccinea</i>	39.7**		Tree	Phanerophyte
<i>Quercus falcata</i>		41.4*	Tree	Phanerophyte
<i>Quercus velutina</i>	38.4**	46.4***	Tree	Phanerophyte
<i>Symplocos tinctoria</i>	30**	40***	Tree	Phanerophyte
Salvage-logged				
Poaceae	43.9**	46.8***	Graminoid	Hemicryptophyte
<i>Agalinis purpurea</i>	61***	45***	Forb	Therophyte
<i>Coreopsis major</i>	43.4**	44.7**	Forb	Hemicryptophyte
<i>Diodella teres</i>	25.7*	35**	Forb	Therophyte
<i>Hypericum gentianoides</i>	24.5*		Forb	Therophyte
<i>Tephrosia virginiana</i>	55.3***	52.1***	Forb	Hemicryptophyte

(Continues)

TABLE 3 (Continued)

Indicator species	Before	After	Growth habit	Raunkiaer life form
<i>Tragia smallii</i>		40.3*	Forb	Hemicryptophyte
<i>Gelsemium sempervirens</i>	46***	47.5***	Vine	Phanerophyte
<i>Smilax glauca</i>		40.7*	Vine	Phanerophyte
<i>Stylisma humistrata</i>	22.5*		Vine	Geophyte
<i>Gaylussacia dumosa</i>	34.4*	36*	Shrub	Chamaephyte
<i>Pinus</i> spp.		32.8*	Tree	Phanerophyte
<i>Quercus falcata</i>	41.8*		Tree	Phanerophyte
<i>Quercus laevis</i>		20.8*	Tree	Phanerophyte
<i>Quercus nigra</i>	46.6**	34*	Tree	Phanerophyte

Although ground flora assemblages remained dissimilar between disturbance categories, prescribed fire imposed consistent plant trait selection throughout the treatment area, which supported our second hypothesis. Prior to prescribed fire, wind-disturbed sites hosted the greatest foliar cover of ground flora classified as trees (i.e., woody plants with the potential to grow over 5 m height), which was likely a legacy of canopy tree removal and competitive release. Reduced understorey tree cover on salvage-logged sites may have been a legacy of stem damage from salvage-logging machinery. Despite these pre-fire differences, prescribed fire reduced understorey tree cover throughout the treatment area and thereby negated differences in understorey tree cover between disturbance categories. Nonetheless, post-fire

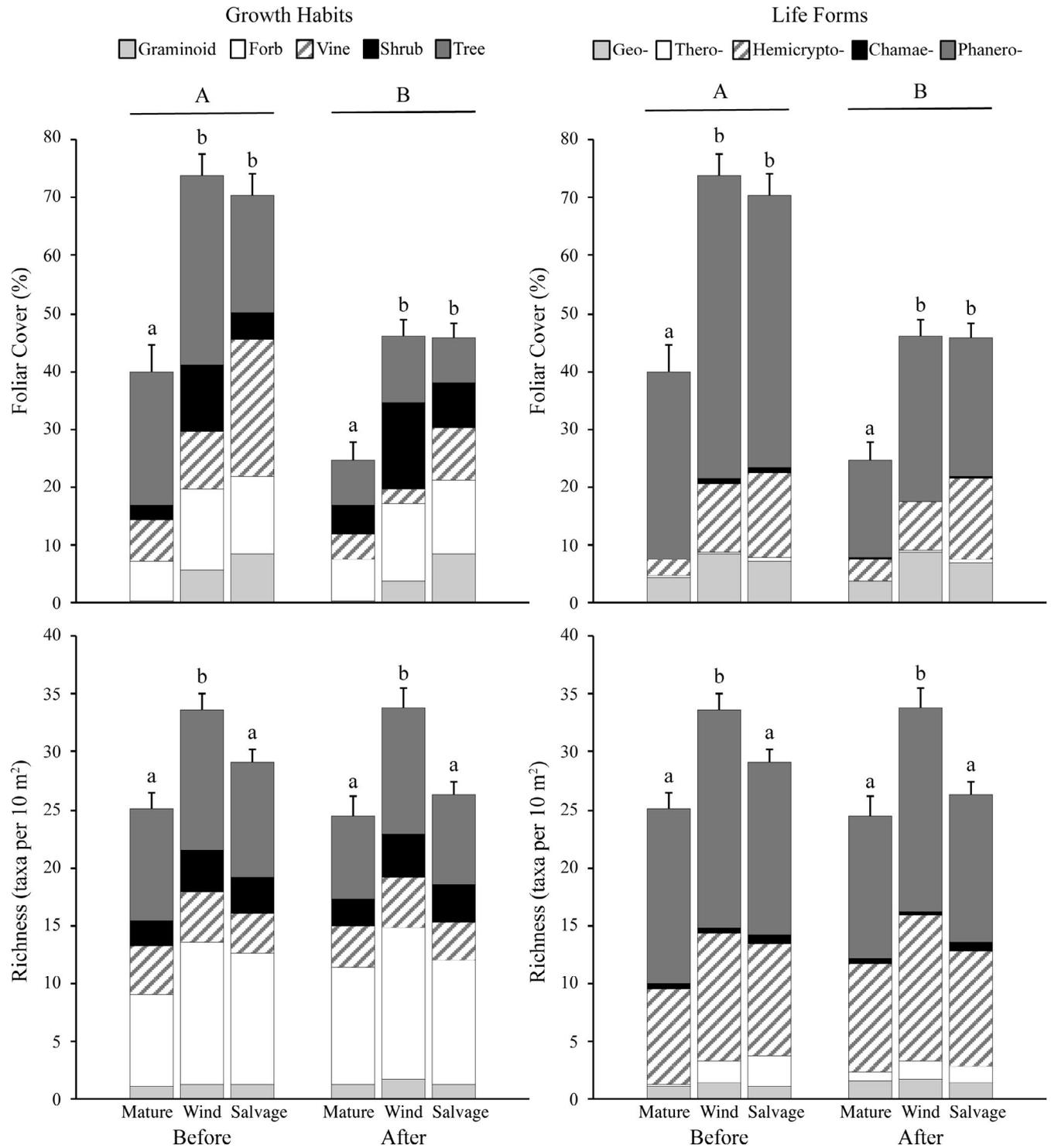
tree richness remained greatest in wind-disturbed sites. Persistent differences in understorey tree richness were attributed to the post-fire resprouting abilities of trees in the study area. Whereas woody plant biomass can take two or more years to recover to pre-fire conditions, the ability to resprout enables woody plant persistence in fire-adapted ecosystems (Peterson et al., 2007). For the trees in this study for which physiological information was available, only *Symplocos tinctoria* was listed as not having the ability to resprout (USDA Forest Service, 2020; USDA NRCS, 2020b). However, we contend that *Symplocos tinctoria*, which was an indicator of wind-disturbed sites before and after prescribed fire, can indeed produce new shoots from surviving rootstocks after above-ground mortality (Appendix S3).

TABLE 4 Positive (+) and negative (-) associations with corresponding *p*-values (\*, <0.05; \*\*, <0.01; \*\*\*, <0.001) between life-history traits and background disturbance categories before (2016) and after (2018) prescribed fire in *Pinus palustris* woodlands in the Fall Line Hills of Alabama, USA

Trait	State	Time	Mature	Wind	Salvage
Growth habit	Graminoid	Before	(-)**		(+)**
		After	(-)**		(+)**
	Forb	Before			(+)*
		After			
	Vine	Before	(+)*	(-)**	
		After	(+)*	(-)**	
	Shrub	Before	(-)*	(+)**	
		After	(-)**	(+)*	
	Tree	Before			(-)**
		After			(+)**
Life form	Geophyte	Before			
		After			
	Therophyte	Before	(-)**		(+)**
		After			
	Hemicryptophyte	Before	(-)*		(+)**
		After			(+)**
	Chamaephyte	Before			
		After		(-)**	(+)**
	Phanerophyte	Before	(+)**		(-)**
		After			(-)**

Prescribed fire-induced understorey tree cover reductions coincided with increased shrub cover throughout the treatment area. We suspect that shrubs captured some of the growing space previously occupied by top-killed understorey trees. Like trees, the large majority of shrubs in the study area can resprout, with two listed exceptions of *Rhododendron canescens* and *Styrax grandifolius* (USDA

Forest Service, 2020; USDA NRCS, 2020b). Nonetheless, *Styrax grandifolius* was an indicator of wind-disturbed sites before and after prescribed fire, and can in fact regenerate from underground rhizomes after fire (Hill, 2007; Appendix S3). Barefoot et al. (2019) also reported *Styrax grandifolius* as an indicator of mechanically thinned mixed *Pinus*-hardwood stands subject to a three-year prescribed fire



**FIGURE 4** Foliar cover (%) and richness (taxa per 10 m<sup>2</sup>) of ground flora representing each growth habit and life form documented in mature, wind-disturbed, and salvage-logged plots before (2016) and after (2018) prescribed fire. 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

rotation. *Rhus copallinum* was the other indicator shrub of wind-disturbed sites before and after prescribed fire. *Rhus copallinum* can rapidly resprout in sites impacted by wind and fire disturbances (Cannon et al., 2019), and composed the greatest post-fire densities of seedlings (live woody stems <1 m height) and saplings in wind-disturbed sites (Kleinman et al., 2020). On salvage-logged sites, the subshrub *Gaylussacia dumosa* was a significant indicator before and after prescribed fire. The underground rhizomes of *Gaylussacia dumosa* are resistant to fire and are stimulated to resprout after above-ground foliar consumption (Coladonato, 1992). *Gaylussacia dumosa* was also the only indicator species representative of the chamaephyte growth habit, and its common occurrence corresponded with greater levels of post-fire chamaephyte richness on salvage-logged sites.

Like understory trees, prescribed fire reduced the foliar cover of phanerophytes throughout the treatment area. This reduction counteracted a pre-fire disparity between salvage-logged and mature sites in the foliar cover of phanerophytes. Whereas trees and vines were distinguished by growth habit, the phanerophyte life form included all trees and some vines. *Gelsemium sempervirens* was a particularly widespread woody vine, and was a significant indicator of salvage-logged sites before and after prescribed fire. Emery and Hart (2020) used laboratory burns to assess the flammability of fuels collected in the study area, and classified *Gelsemium sempervirens* vines and leaves in a moderate-high flammability group. We contend that the substantial vine cover reductions observed in salvage-logged sites largely represented *Gelsemium sempervirens* consumption.

Though prescribed fire counteracted some differences in woody plant cover, differences in graminoid cover were exaggerated. Graminoid cover was consistently lowest on mature sites with intact canopies and consequently lower understory light availability. However, whereas pre-fire graminoid cover was comparable on wind-disturbed and salvage-logged sites, post-fire graminoid cover was greatest on salvage-logged sites. These results corresponded with others who attributed increased cover of light-demanding graminoids to the reduction of shade (Peterson et al., 2007; Policelli et al., 2019). The removal of standing and leaning deadwood maximized understory light availability in salvage-logged sites (Kleinman et al., 2017). Nonetheless, whereas the Poaceae (grass) family was a significant indicator of salvage-logged sites, the sedge *Scleria triglomerata* was a significant indicator of wind-disturbed sites. These results were attributed to the photosynthetic pathways of the constituent indicators. Peterson et al. (2007) described how  $C_4$  grasses and sedges exhibited the greatest responses to increased light availability, whereas  $C_3$  grasses and sedges were associated with partial shading. Though Poaceae were not identified beyond family in this study, the most common graminoids in the study area were  $C_4$  bunchgrasses (e.g. *Schizachyrium scoparium*; Becket and Golden, 1982; Teague et al., 2014). In contrast, *Scleria triglomerata*, which utilizes a  $C_3$  photosynthetic pathway (Bruhl and Wilson, 2007), was perhaps better adapted to grow in the partial shade near downed woody debris in wind-disturbed sites (Pearcy and Ehleringer, 1984).

Among all growth habits and life forms assessed, geophytes were least impacted by disturbance category and time relative to prescribed fire. We suspect that the relatively consistent representation of geophytes across space and time reflected a long-term legacy of recurrent low-intensity fire in the study area. Although below-ground perennating tissues are primarily recognized as a drought-survival adaptation (Raunkjær, 1934), the geophytic life-history strategy also confers resilience in fire-adapted ecosystems where underground growth buds are protected from surface fires (Ruiters et al., 1993; Dale et al., 2002). Moreover, compared to life forms with surface-level and above-ground growth buds, geophytes may have been better protected from the mechanical impacts of salvage logging in the understory.

## 5 | CONCLUSIONS

With changing disturbance regimes in forest ecosystems worldwide, it is increasingly important to consider how management actions impact ecosystem resilience (Turner, 2010; Seidl et al., 2016). Though many response variables can be used to assess ecosystem recovery rates and trajectories, forest resilience is most often assessed by metrics of tree regeneration. Ground flora assemblages, however, can indicate disturbance effects with greater sensitivity than woody plant-based metrics, in part because of the greater diversity of life-history traits they represent (Roberts, 2004; Gilliam, 2007). For example, here we report that, although prescribed fire offset differences in sapling densities between unlogged and logged wind-disturbed sites (Kleinman et al., 2020), ground flora assemblages remained disparate. It is therefore critical to consider the “resilience of what” in assessments of post-disturbance management actions on ecosystem recovery (Carpenter et al., 2001; Kleinman et al., 2019).

Within the ground flora stratum, a variety of response variable-specific outcomes were observed. Salvage logging reduced ground flora diversity, but did not alter foliar cover. Prescribed fire reduced foliar cover, but did not alter ground flora diversity. Because salvage-logged sites continued to support homogenized ground flora assemblages with reduced floristic diversity, we recommend leaving some wind-disturbed zones unlogged to serve as ground flora refugia if ground flora resilience is a management objective. Indeed, a key silvicultural strategy to combat global change is to increase representation of a broad range of functional traits to enhance ecosystem adaptation potential.

Beyond aggregate metrics of foliar cover and diversity, this study demonstrated the efficacy of trait-based plant community analyses to achieve a detailed understanding of natural and anthropogenic disturbance effects on floristic dynamics. Prescribed fire reduced understory tree cover throughout the treatment area, which corresponded with increased shrub cover, and exaggerated the disproportionate cover of graminoids on salvage-logged sites. Prescribed fire also facilitated establishment and growth therophytes and hemicryptophytes in mature sites, and increased chamaephyte representation in salvage-logged sites. The geophyte

life form, however, was apparently unaffected by catastrophic wind disturbance, salvage logging, and prescribed fire. In species-rich ecosystems like the *Pinus palustris* ecosystem, grouping ground flora by common growth habits and life forms can provide a simple and effective method to monitor post-disturbance ecosystem recovery (Dale et al., 2002).

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## AUTHOR CONTRIBUTIONS

JSK and JLH conceived and designed the study; JSK and JDG collected and analyzed the data; JSK wrote the first draft of the manuscript and JDG and JLH contributed critically to the drafts.

## DATA AVAILABILITY STATEMENT

The data used and analyzed in this study are archived on an internal server of The University of Alabama and are available from the corresponding author upon reasonable request.

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## REFERENCES

- Angeler, D.G. and Allen, C.R. (2016) Quantifying resilience. *Journal of Applied Ecology*, 53, 617–624.
- Barefoot, C.R., Willson, K.G., Hart, J.L., Schweitzer, C.J. and Dey, D.C. (2019) Effects of thinning and prescribed fire frequency on ground flora in mixed *Pinus*-hardwood stands. *Forest Ecology and Management*, 432, 729–740.
- Beatty, S.W. (1984) Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology*, 65, 1406–1419.
- Beckett, S. and Golden, M.S. (1982) Forest vegetation and vascular flora of Reed Brake Research Natural Area, Alabama. *Castanea*, 47, 368–392.
- Beers, T.W., Dress, P.E. and Wensel, L.C. (1966) Aspect transformation in site productivity research. *Journal of Forestry*, 64, 691–692.
- Bigelow, S.W., Stambaugh, M.C., O'Brien, J.J., Larson, A.J. and Battaglia, M.A. (2018) Longleaf pine restoration in context comparisons of frequent fire forests. In: Kirkman, L.K. and Jack, S.B. (Eds.) *Ecological restoration and management of longleaf pine forests*. Boca Raton, FL: CRC Press, Taylor & Francis Group, pp. 311–338.
- Braun, E.L. (1950) *Eastern Deciduous Forests of North America*. Caldwell, NJ: The Blackburn Press, p. 596.
- Brewer, J.S., Bertz, C.A., Cannon, J.B., Chesser, J.D. and Maynard, E.E. (2012) Do natural disturbances or the forestry practices that follow them convert forests to early-successional communities? *Ecological Applications*, 22, 442–458.
- Bruhl, J.J. and Wilson, K.L. (2007) Towards a comprehensive survey of C<sub>3</sub> and C<sub>4</sub> photosynthetic pathways in Cyperaceae. *Aliso*, 23, 99–148.
- Buma, B. (2015) Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere*, 6, 70.
- Buma, B. and Wessman, C.A. (2012) Differential species responses to compounded perturbations and implications for landscape heterogeneity and resilience. *Forest Ecology and Management*, 266, 25–33.
- Burrows, N. and McCaw, L. (2013) Prescribed burning in southwestern Australian forests. *Frontiers in Ecology and the Environment*, 11, e25–e34.
- Cannon, J.B., Henderson, S.K., Bailey, M.H. and Peterson, C.J. (2019) Interactions between wind and fire disturbance in forests: competing amplifying and buffering effects. *Forest Ecology and Management*, 436, 117–128.
- Carpenter, S., Walker, B., Anderies, J.M. and Abel, N. (2001) From metaphor to measurement: resilience of what to what? *Ecosystems*, 4, 765–781.
- Coladonato, M. (1992) *Gaylussacia dumosa*. In: *Fire Effects Information System*, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available at <https://www.fs.fed.us/database/feis/plants/shrub/gaydum/all.html> [Accessed 16 June 2020]
- Cox, L.E. and Hart, J.L. (2015) Two centuries of forest compositional and structural changes in the Alabama Fall Line Hills. *American Midland Naturalist*, 174, 218–237.
- Dale, V.H., Beyeler, S.C. and Jackson, B. (2002) Understory vegetation indicators of anthropogenic disturbance in longleaf pine forests at Fort Benning, Georgia, USA. *Ecological Indicators*, 1, 155–170.
- Dale, V.H., Lugo, A.E., MacMahon, J.A. and Pickett, S.T.A. (1998) Ecosystem management in the context of large, infrequent disturbances. *Ecosystems*, 1, 546–557.
- Davies, G.M. and Gray, A. (2015) Don't let spurious accusations of pseudoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). *Ecology and Evolution*, 5, 5295–5304.
- Donato, D.C., Fontaine, J.B., Robinson, W.D., Kauffman, J.B. and Law, B.E. (2009) Vegetation response to a short interval between high-severity wildfires in a mixed-evergreen forest. *Journal of Ecology*, 97, 142–154.
- Dray, S. and Dufour, A.B. (2007) The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, 22, 1–20.
- Dray, S. and Legendre, P. (2008) Testing the species traits-environment relationships: the fourth-corner problem revisited. *Ecology*, 89, 3400–3412.
- Dufrène, M. and Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67, 345–366.
- Emery, R.K. and Hart, J.L. (2020) Flammability characteristics of surface fuels in a longleaf pine (*Pinus palustris* Mill.) woodland. *Fire*, 3, 39.
- Facelli, J.M. and Pickett, S.T.A. (1991) Plant litter: its dynamics and effects on plant community structure. *The Botanical Review*, 57, 1–32.
- Fenneman, N.M. (1938) *Physiography of Eastern United States*. New York, NY: McGraw-Hill, p. 714.
- Fernandes, P.M., Davies, G.M., Ascolia, D., Fernández, C., Moreira, F., Rigolot, E. et al. (2013) Prescribed burning in southern Europe: developing fire management in a dynamic landscape. *Frontiers in Ecology and the Environment*, 11, e4–e14.
- Ford, S.A., Kleinman, J.S. and Hart, J.L. (2018) Effects of wind disturbance and salvage harvesting on macrofungal communities in a *Pinus* woodland. *Forest Ecology and Management*, 407, 31–46.
- Franklin, J.F., Lindenmayer, D., MacMahon, J.A., McKee, A., Magnuson, J., Perry, D.A. et al. (2000) Threads of continuity. *Conservation in Practice*, 1, 8–17.
- Frost, C.C. (2006) History and future of the longleaf pine ecosystem. In: Jose, S., Jokela, E.J. and Miller, D.L. (Eds.) *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration*. New York, NY: Springer, pp. 9–42.
- Fuentes, L., Duguay, B. and Nadal-Sala, D. (2018) Short-term effects of spring prescribed burning on the understory vegetation of a *Pinus halepensis* forest in Northeastern Spain. *Science of the Total Environment*, 610–611, 720–731.

- Gensini, V.A. and Brooks, H.E. (2018) Spatial trends in United States tornado frequency. *Climate and Atmospheric Science*, 1, 38.
- Georgiev, K.B., Chao, A., Castro, J., Chen, Y., Choi, C., Fontaine, J.B. et al. (2020) Salvage logging changes the taxonomic, phylogenetic and functional successional trajectories of forest bird communities. *Journal of Applied Ecology*, 57, 1103–1112.
- Gibson, D. (1961) Life-forms of Kentucky flowering plants. *The American Midland Naturalist*, 66, 1–60.
- Gilliam, F.S. (2007) The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience*, 57, 845–858.
- Goode, J.D., Kleinman, J.S., Hart, J.L. and Bhuta, A.R.R. (2020) Edge influence on composition and structure of a *Pinus palustris* woodland following catastrophic wind disturbance. *Canadian Journal of Forest Research*, 50, 332–341.
- GSA (Geological Survey of Alabama) (2006) Geologic map of Alabama, digital version 1.0: Alabama Geological Survey Special Map 220A [adapted from Szabo, M.W., Osborne, W.E., Copeland, C.W. Jr and Neathery, T.L. (1988) Geologic map of Alabama (1:250, 000): Alabama Geological Survey Special Map 220].
- Hargrove, W.W. and Pickering, J. (1992) Pseudoreplication: a *sine qua non* for regional ecology. *Landscape Ecology*, 6, 251–258.
- Harper, R.M. (1943) *Forests of Alabama*. Geological Survey of Alabama, Monograph 10. Wetumpka, AL: Wetumpka Printing Company, p. 230.
- Hernández-Hernández, R., Castro, J., Aguilar, M.D., Fernandez-Lopez, A.B. and Gonzalez-Mancebo, J.M. (2017) Post-fire salvage logging imposes a new disturbance that retards succession: the case of bryophyte communities in a Macaronesian laurel forest. *Forests*, 8, 252.
- Hill, S.R. (2007) Conservation assessment for the Bigleaf snowbell (*Styrax grandifolius* Ait.). *INHS Technical Report*, 65, 1–35.
- Holling, C.S. (1973) Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4, 1–23.
- Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E. et al. (2016) Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, 14, 369–378.
- Keener, B.R., Diamond, A.R., Davenport, L.J., Davison, P.G., Ginzburg, S.L., Hansen, C.J. et al. (2020) *Alabama Plant Atlas*. Available at: <http://floraofalabama.org/> [Accessed 10 August 2020].
- Kleinman, J.S., Ford, S.A. and Hart, J.L. (2017) Catastrophic wind and salvage harvesting effects on woodland plants. *Forest Ecology and Management*, 403, 112–125.
- Kleinman, J.S., Goode, J.D., Fries, A.C. and Hart, J.L. (2019) Ecological consequences of compound disturbances in forest ecosystems: a systematic review. *Ecosphere*, 10, e02962.
- Kleinman, J.S. and Hart, J.L. (2018) Vascular flora of longleaf pine woodlands after wind disturbance and salvage harvesting in the Alabama Fall Line Hills. *Castanea*, 83, 183–195.
- Kleinman, J.S., Goode, J.D., Hart, J.L. and Dey, D.C. (2020) Prescribed fire effects on *Pinus palustris* woodland development after catastrophic wind disturbance and salvage logging. *Forest Ecology and Management*, 468, 118173.
- Knapp, E.E. and Ritchie, M.W. (2016) Response of understory vegetation to salvage logging following a high-severity wildfire. *Ecosphere*, 7, e01550.
- Leverkus, A.B., Rey Benayas, J.M., Castro, J., Boucher, D., Brewer, S., Collins, B.M. et al. (2018) Salvage logging effects on regulating and supporting ecosystem services—A systematic map. *Canadian Journal of Forest Research*, 48, 983–1000.
- Lindenmayer, D., Thorn, S. and Banks, S. (2017) Please do not disturb ecosystems further. *Nature Ecology and Evolution*, 1, 0031.
- Lindenmayer, D.B., Westgate, M.J., Scheele, B.C., Foster, C.N. and Blair, D.P. (2019) Key perspectives on early successional forests subject to stand-replacing disturbances. *Forest Ecology and Management*, 454, 117656.
- Logan, A.T., Goode, J.D., Keellings, D.J. and Hart, J.L. (2020) Microsite influence on woody plant regeneration in a *Pinus palustris* woodland following catastrophic disturbance. *Forests*, 11, 588.
- McCune, B. and Mefford, M.J. (2016) *PC-ORD. Multivariate analysis of Ecological Data, Version 7.0 for Windows*. Corvallis, OR: Wild Blueberry Media.
- Miller, J.H., Manning, S.T. and Enloe, S.F. (2015) *A Management Guide for Invasive Plants in Southern Forests*. Asheville, NC: USDA Forest Service SRS-GTR-131, pp. 120.
- Mitchell, R.J., Hiers, J.K., O'Brien, J. and Starr, G. (2009) Ecological forestry in the Southeast: understanding the ecology of fuels. *Journal of Forestry*, 107, 391–397.
- Muller, R.N. (2014) Nutrient relations of the herbaceous layer in deciduous forest ecosystems. In: Gilliam, F.S. (Ed.) *The Herbaceous Layer in Forests of Eastern North America*, 2nd edition. New York, NY: Oxford University Press, pp. 13–34.
- Müller, J., Noss, R., Thorn, S., Bässler, C., Leverkus, A.B. and Lindenmayer, D. (2019) Increasing disturbance demands new policies to conserve intact forest. *Conservation Letters*, 12, e12449.
- Noss, R.F., Platt, W.J., Sorrie, B.A., Weakley, A.S., Means, D.B., Costanza, J. et al. (2015) How global biodiversity hotspots may go unrecognized: lessons from the North American Coastal Plain. *Diversity and Distributions*, 21, 236–244.
- National Weather Service (2011) *Sawyer-ville-Eoline (Greene, Hale and Bibb Counties) EF-3 Tornado April 27, 2011*. Available at: [https://www.weather.gov/bmx/event\\_04272011sawyer-ville](https://www.weather.gov/bmx/event_04272011sawyer-ville) [Accessed 7 August 2020]
- Oosting, H.J. (1942) An ecological analysis of the plant communities of Piedmont, North Carolina. *The American Midland Naturalist*, 28, 1–126.
- Orczewska, A., Czortek, P. and Jaroszewicz, B. (2019) The impact of salvage logging on herb layer species composition and plant community recovery in Białowieża Forest. *Biodiversity and Conservation*, 28, 3407–3428.
- Outcalt, K.W. (2006) Prescribed burning for understory restoration. In: Jose, S., Jokela, E.J. and Miller, D.L. (Eds.) *The Longleaf Pine Ecosystem: Ecology, Silviculture and Restoration*. Springer Science: New York, NY, pp. 326–329.
- Paine, R.T., Tegner, M.J. and Johnson, E.A. (1998) Compounded perturbations yield ecological surprises. *Ecosystems*, 1, 535–545.
- Palik, B.J. and Pederson, N. (1996) Overstory mortality and canopy disturbances in longleaf pine ecosystems. *Canadian Journal of Forest Research*, 26, 2035–2047.
- Palmquist, K.A., Peet, R.K. and Weakley, A.S. (2014) Changes in plant species richness following reduced fire frequency and drought in one of the most species-rich savannas in North America. *Journal of Vegetation Science*, 25, 1426–1437.
- Pausas, J.G. and Keeley, J.E. (2014) Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist*, 204, 55–65.
- Pearcy, R.W. and Ehleringer, J. (1984) Comparative ecophysiology of C<sub>3</sub> and C<sub>4</sub> plants. *Plant, Cell and Environment*, 7, 1–13.
- Peck, J.E. (2016) *Multivariate Analysis for Ecologists: Step-by-Step using PC-ORD*. Glendon Beach, OR: MjM Software Design, p. 192.
- Peet, R.K., Wentworth, T.R. and White, P.S. (1998) A flexible, multipurpose method for recording vegetation composition and structure. *Castanea*, 63, 262–274.
- Peters, D.P.C., Lugo, A.E., Chapin, F.S., Pickett, S.T.A., Duniway, M., Rocha, A.V. et al. (2011) Cross-system comparisons elucidate disturbance complexities and generalities. *Ecosphere*, 2, 81.
- Peterson, D.W., Reich, P.B. and Wrage, K.J. (2007) Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands. *Journal of Vegetation Science*, 18, 3–12.
- Peterson, C.J. and Leach, A.D. (2008) Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. *Forestry*, 81, 361–376.

- Pickett, S.T.A. (1989) Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (Ed.) *Long-term Studies in Ecology: Approaches and Alternatives*. New York, NY: Springer-Verlag, pp. 110–135.
- Pidgen, K. and Mallik, A.U. (2013) Ecology of compounding disturbances: the effects of prescribed burning after clearcutting. *Ecosystems*, 16, 170–181.
- Policelli, N., Picca, P. and Gómez Villafaña, I.E. (2019) Is prescribed fire a suitable management tool to reduce shrub encroachment in palm savannas? *Restoration Ecology*, 27, 109–119.
- PRISM Climate Group (2020) *Data Explorer: Time Series Values for Individual Locations*. Available at: <http://www.prism.oregonstate.edu/explorer/> [Accessed 10 February 2020]
- Pulsford, S.A., Lindenmayer, D.B. and Driscoll, D.A. (2016) A succession of theories: purging redundancy from disturbance theory. *Biological Reviews*, 91, 148–167.
- Purdon, M., Brais, S. and Bergeron, Y. (2004) Initial response of understorey vegetation to fire severity and salvage-logging in the southern boreal forest of Québec. *Applied Vegetation Science*, 7, 49–60.
- Raunkiaer, C. (1934) *The Life Forms of Plants and Statistical Plant Geography*. Oxford: Clarendon Press.
- Roberts, M.R. (2004) Response of the herbaceous layer to natural disturbance in North American forests. *Canadian Journal of Botany*, 82, 1273–1283.
- Rowe, J.S. (1983) Concepts of fire effects on plant individuals and species. In: Wein, R.W. and MacLean, D.A. (Eds.) *The Role of Fire in Northern Circumpolar Ecosystems*. New York, NY: John Wiley & Sons, pp. 135–154.
- Royo, A.A., Peterson, C.J., Stanovick, J.S. and Carson, W.P. (2016) Evaluating the ecological impacts of salvage logging: can natural and anthropogenic disturbances promote coexistence? *Ecology*, 97, 1566–1582.
- Ruiters, C., McKenzie, B. and Raitt, L.M. (1993) Life-history studies of the perennial geophyte *Haemanthus pubescens* L. subspecies *pubescens* (Amaryllidaceae) in lowland coastal fynbos, South Africa. *International Journal of Plant Sciences*, 154, 441–449.
- Rumbaitis del Rio, C.M. (2006) Changes in understory composition following catastrophic windthrow and salvage logging in a sub-alpine forest ecosystem. *Canadian Journal of Forest Research*, 36, 2943–2954.
- Seidl, R., Spies, T.A., Peterson, D.L., Stephens, S.L. and Hick, J.A. (2016) Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. *Journal of Applied Ecology*, 53, 120–129.
- Shankman, D. and Hart, J.L. (2007) The Fall Line: a physiographic-forest vegetation boundary. *Geographical Review*, 97, 502–519.
- Stanturf, J.A., Goodrick, S.L. and Outcalt, K.W. (2007) Disturbance and coastal forests: a strategic approach to forest management in hurricane impact zones. *Forest Ecology and Management*, 250, 119–135.
- Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L. et al. (2011) The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, 9, 117–125.
- Taylor, A.R., MacLean, D.A., McPhee, D., Dracup, E. and Keys, K. (2017) Salvaging has minimal impacts on vegetation regeneration 10 years after severe windthrow. *Forest Ecology and Management*, 406, 19–27.
- Teague, J., Palmquist, K.A., Peet, R.K. and Carr, S. (2014) *Pinus palustris/Schizachyrium scoparium - Pteridium aquilinum Woodland* [Version Date: November 7, 2014]. United States National Vegetation Classification. Washington, DC: Federal Geographic Data Committee.
- Thorn, S., Bässler, C., Brandl, R., Burton, P.J., Cahall, R., Campbell, J.L. et al. (2018) Impacts of salvage logging on biodiversity: a meta-analysis. *Journal of Applied Ecology*, 55, 279–289.
- Thornthwaite, C.W. (1948) An approach toward rational classification of climate. *Geographical Review*, 38, 55–94.
- Turner, M.G. (2010) Disturbance and landscape dynamics in a changing world. *Ecology*, 91, 2833–2849.
- USDA Forest Service (2020) *Fire Effects Information System (FEIS)*. Available at: <https://www.feis-crs.org/feis/> [Accessed 10 August 2020]
- USDA NRCS (2008) *Soil Survey of Bibb County, Alabama*. Available at: [http://soils.usda.gov/survey/printed\\_surveys/](http://soils.usda.gov/survey/printed_surveys/) [Accessed 10 August 2020]
- USDA NRCS (2020a) *Web Soil Survey*. Available at: <http://websoilsurvey.sc.egov.usda.gov/> [Accessed 10 August 2020]
- USDA NRCS (2020b) *The PLANTS Database*. Available at: <http://plants.usda.gov> [Accessed 10 August 2020]
- Van Nieuwstadt, M.G.L., Sheil, D. and Kartawinata, K. (2001) The ecological consequences of logging in the burned forests of East Kalimantan, Indonesia. *Conservation Biology*, 15, 1183–1186.
- Weakley, A.S. (2015) *Flora of the Southern and Mid-Atlantic States*. Chapel Hill, NC: University of North Carolina, North Carolina Botanical Garden. Available at: [http://www.herbarium.unc.edu/FloraArchives/WeakleyFlora\\_2015-05-29.pdf](http://www.herbarium.unc.edu/FloraArchives/WeakleyFlora_2015-05-29.pdf) [Accessed 21 May 2015].
- Webster, P.J., Holland, G.J., Curry, J.A. and Chang, H.-R. (2005) Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science*, 309, 1844–1846.
- Webster, C.R., Dickinson, Y.L., Burton, J.I., Frelich, L.E., Jenkins, M.A., Kern, C.C. et al. (2018) Promoting and maintaining diversity in contemporary hardwood forests: confronting contemporary drivers of change and the loss of ecological memory. *Forest Ecology and Management*, 421, 98–108.
- White, P.S. and Jentsch, A. (2001) The search for generality in studies of disturbance and ecosystem dynamics. *Progress in Botany*, 62, 399–449.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**Appendix S1** Plant trait designations of the ground flora taxa documented in differentially disturbed *Pinus palustris* woodlands in the Fall Line Hills of Alabama, USA

**Appendix S2** Summary of mixed ANOVAs used to assess impacts of pre-fire conditions, time, and their interaction on the foliar cover and richness of ground flora in each growth habit and life form

**Appendix S3** Photographs of live *Symplocos tinctoria* shoots and live *Styrax grandifolius* shoots growing from the same rootstocks as fire-killed shoots

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