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Research Article

Influence of Altered Fire Return Intervals on Plant Diversity in the East Texas Pineywoods

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ABSTRACT

The re-establishment of historic fire return intervals is vital to restoring forest health, species diversity, natural succession pathways and reduction of some invasive species. Studies in southern pine understory plant communities have revealed increased plant diversity and richness in response to fire, particularly in longleaf pine dominated sites. We aimed to further investigate the effect of fire frequency, stand characteristics and site management on understory plant community compositions in East Texas. Using 20 years of burn history data, fire return intervals were classified as either high or low; plots were also analyzed by site and cover type. Fuel load, litter depth, basal area, and canopy cover were recorded. Understory species occurrence was recorded to genus level and separated into grass, forb, and woody growth form groups. Our results indicated that grass and forb richness increased in response to greater fire frequencies. This effect was observed across multiple sites, with high fire frequency groups containing nearly twice as many grass species and over three times as many forb species. Increased basal area and litter depth were negatively correlated with forb, grass, and total richness. Increased understory plant richness was found on frequently burned upland pine communities, so management objectives that include increasing understory diversity in this region should include short interval prescribed fire rotations.

Keywords: Plant diversity; Richness; Prescribed Fire; Pineywoods; Ordination

INTRODUCTION

For millennia, ecosystems in North America have been impacted by fire, influencing the evolution of many species, human use of fire has also evolved over time [1,2]. Fire regimes result from the cumulative interaction of fire, vegetation, climate, humans, topography and in combination with other disturbances, are both spatially and temporally intertwined [3,4]. As a disturbance, fire is one of the most influential natural forces exerted on plant communities. In disturbance regimes, and specifically in wildland fire regimes, the presence of keystone plant species determines species composition [5,6].

Fire exclusion policies of the early 1900s in the United States altered pre-existing forest composition, resulting in excessive understory fuel loading, accumulation of hazardous ladder fuels and reduced quality of wildlife habitat [7]. Fuel conditions such as type, loading, structure, and continuity, as well as climatic variables, influence the intensity of fire events, which will also influence fuel variables following fire events [8]. The level of mortality and the frequency of fire may change due to anthropogenic fire exclusion or natural shifts in climatic factors; if the change in mortality is significant or continuous, the plant community composition will shift toward species that favor the new conditions [9,10]. The consequence of increased plant community richness and diversity following fire is pervasive, as the localized accumulation of biological heterogeneity reinforces prolonged ecosystem resistance amid dynamic disturbance regimes [11].

The pine-bluestem (*Pinus-Andropogon*) plant association historically dominated most of the southeastern United States, and formed a complex network of patches across the landscape which sustained frequent, low-intensity surface fires [12]. In the Southeastern United States, longleaf pine (Pinus palustris) savannahs were considered the most diverse herbaceous ecosystems in North America, due to the understory of grasses and forbs resulting from a combination of frequent high density lightning strikes and Native Americans. At the regional level, fire regime effects are complex results of long-term climatic shifts interwoven with human activities and natural disturbance regimes [13-15].

The significant reduction in longleaf pine savannahs has caused pronounced changes in plant community compositions across the south, with reduced understory diversity through increased

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light-intercepting midstories. Competition with midstory and overstory species reduces the effectiveness of longleaf pine natural regeneration, and without fire, nutrient recycling is slower and decreases in native graminoid diversity result from the buildup of woody debris and litter on the forest floor [16-18].

The majority of the Pineywoods ecoregion of Texas was comprised of longleaf pine and mixed longleaf-loblolly (*P. taeda*)-shortleaf (*P. echinata*)-hardwood forests. These pine species shed needles which form a fuel bed promoting fire spread and intensity; while reducing encroachment of woody species [19]. The historical fire return interval of the longleaf pine communities in east Texas has been estimated to be between 1 to 3 years, and for mixed pine-hardwood communities between 4 to 6 years [20]. Understory hardwoods and grasses found in longleaf pine and mixed-pine hardwood communities are typically dominated by species with underground rhizomes and extensive storage organs that enable them to persist after loss of aboveground biomass [21,22].

Longleaf pine-bluestem communities support a heterogeneous understory, with nearly 200 grass species identified as part of this type forbs also account for a sizable portion of the ground cover. Woody understory plants, including shrubs and vines, are frequently found in this type; however, their abundance is related to degree of disturbance [23]. Shortleaf pine has the widest distribution of any pine in the southeastern United States, and it tolerates a wide variety of soil and site conditions. Seedlings between 2-3 months of age develop a distinctive j-shaped crook near the surface, where axillary buds are formed which will initiate growth if the upper stem is damaged or killed. Due to the high fire frequency across its native range, this adaptation was likely naturally selected as a resistance to fire, and sprouting ability diminishes once diameter growth exceeds 15-20 cm in diameter [24]. Common associated species in shortleaf pine communities resemble that of longleaf pine and is linked to fire [25]. The highly adaptable loblolly pine is the dominant overstory species on nearly 11.8 million hectares from eastern Texas to the Atlantic coast in Virginia and is considered fire resistant. However, it is less fire adapted than longleaf and shortleaf pines and can be killed by moderately intense surface fires when young [26,27]. Frequent summer fires will maintain the more mature loblolly pine-grassland plant community. Crown damage generally results in greater mortality than that caused by basal damage. However, older trees tend to exhibit a greater resistance to scorch than younger trees [28]. Herbaceous cover includes bluestem, panicum (Panicum spp.), various sedges, and fennels; frequent fires in the southern pine-bluestem community increased species diversity and richness [26,29,30]. Extended fire return intervals have altered the understory composition of these ecosystems. The reduction of shade tolerant grasses is a priority on many sites in East Texas, as understory species abundance was reduced by increases in overstory cover [31].

Federal agencies such as the United States Department of the Interior, Department of Agriculture, Fish and Wildlife Service, and the Bureau of Land Management implement fire management policies which promote prescribed burning for a variety of objectives, and also adhere to the US National Fire Plan, which is a long-term fuels reduction program created with the goal of restoring the historical structure, diversity, and dynamics of forest and rangeland ecosystems [32]. Prescribed fire by private landowners, Non-Government Organizations (NGOs), and timber companies have used prescribed fire for many of the same management objectives [33].

Historically, the southeastern United States experienced recurring fires during the mid to late growing season [20]. Current application of prescribed fires is during the dormant to early growing seasons when fire behavior and intensities are more easily predicted and the risk of fire escape is more easily mitigated; this shift to dormant season burns limits control of encroaching hardwood species and over time these individuals grow large enough that the use of fire is not sufficient to cause mortality [24,33].

The goal of this research was to assess the effect which fire frequency has on understory plant community composition in East Texas. The specific objectives were to: Compare different burn regime frequencies (high/low) and their effects on understory plant community composition; analyze cover type stand characteristics and how their properties affect understory species richness and evaluate changes in species richness based on the differences in stand characteristics.

MATERIALS AND METHODS

Site description

The Angelina and Sabine National Forests comprise over 121,000 hectares. Longleaf pine is the dominant cover type on the southern portion of the Angelina, while shortleaf and loblolly pine dominate the rest. The Sabine currently has a mixed cover type of shortleaf, loblolly and to a lesser extent, longleaf pine (Figure 1). Soils on the Angelina/Sabine range from sandy well drained uplands to poorly drained clayey bottomlands. Prescribed fires are implemented to aid the recovery of the endangered red-cockaded woodpecker and fuels reduction. The 5,395-hectare upland island wilderness within the Angelina National Forest was set aside in 1984, and is comprised of cover types from pitcher plant (*Nepenthes gracilis*) bogs to longleaf pine forests. The soils consist of well drained sandy uplands to poorly drained clayey bottomlands. The Davy Crockett National Forest covers more than 64,750 hectares, with a predominant overstory a loblolly-shortleaf mix. Hardwood species make up a substantial component of the forest, particularly near the Neches River. Soils range from deep, well drained, rapidly permeable soils on uplands to poorly drained anaerobic clays [34].

The Nature Conservancy's Roy E. Larson Sandyland Sanctuary (Sandyland) protects 2,288 hectares of longleaf pine savannah, to achieve this goal, prescribed fire is applied at intervals as narrow as two years [35]. An extremely biodiverse area, the preserve is connected to United States National Park Service's Big Thicket National Preserve.

The privately owned Winston 8 Ranch is composed of 1,374 hectares of longleaf and loblolly pine forests, pastures and wetlands (Sand County Foundation, 2020). Hardwood species on site included planted wildlife mast species and a variety of native species. These areas provide habitat for white-tailed deer (*Odocoileus virginianus*), bobwhite quail (*Colinus virginianus*), and eastern wild turkey (*Meleagris gallopavo*). Soils are generally very deep sandy and well drained with moderate to slow permeability.

Field data collection

To determine understory vegetative species composition prior to and following prescribed burning with different fire frequencies, cover types and sites, 57 circular plots were measured across six sites in East Texas (Table 1). Plot locations were randomly selected using the ArcGIS random point tool. Plots were 0.083 ha, with a radius of 16.3 m., with three transects radiating from plot center in 120° intervals (Figure 2). Along each transect, woody species composition, herbaceous cover, downed woody debris, and litter depth was measured. Tree (≥ 5.08 cm diameter) heights were recorded and spatially referenced based on distance from plot center. Understory composition was tallied by genus or species within three, 0.3 × 0.6 m. rectangular subplots located to the right of each transect. Each subplot was marked to aid in post-fire/recapture data collection. Using a modified version of the Brown method downed woody debris was inventoried along each transect [36].

Experimental design sampling

Plots were classified into low (<5 burns in past 20 years) and high (≥ 5 burns in past 20 years) fire frequency groups. Cover types (longleaf pine, shortleaf pine, loblolly pine, mixed pine-hardwood) were assigned based on basal area calculations with species comprising >80% of plot basal areas representing the cover type. Normality testing using a Shapiro-Wilk test revealed a non-normal data distribution for five variables (species richness, litter depth, fuel loading, overstory canopy cover, and hardwood basal area). These were transformed using logarithmic and square root functions. Welch t-test was conducted to compare the differences between high and low fire frequency groups. Analysis of Variance and Tukey's post-hoc analysis was used to examine the differences among the four cover types and six sites (Davy Crockett, Angelina, and Sabine National Forests, Sandyland Sanctuary, Winston 8 Ranch and Upland Island Wilderness). Non-metric multi-dimensional scaling was used to display the relationships between species presence/absence and the three groups (fire frequency, cover type, site). Correlations were calculated using Pearsons's method. All tests were conducted with a confidence level of 0.90 and performed using R version 4.3.0 [37].

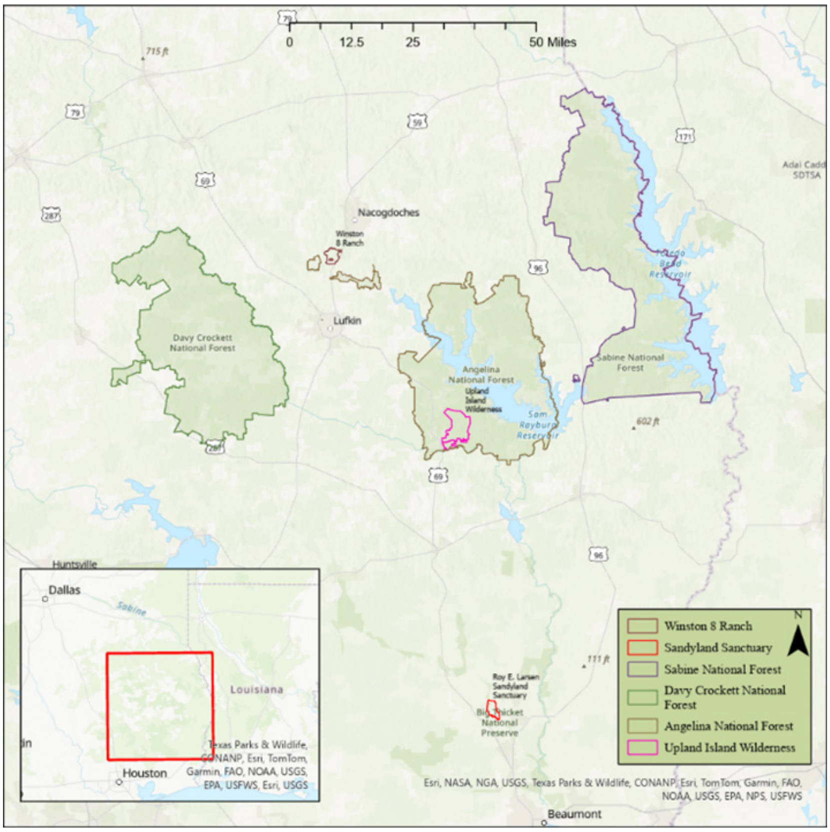

Figure 1: East Texas study areas include Angelina, Sabine, Davy Crockett National Forests, Upland Island Wilderness, The Nature Conservancy's Sandyland Sanctuary Winston 8 Ranch.

Table 1: Total number of plots in each site, cover type (Plots with >80% species basal area), fire frequency (high>5, low<5) burns in 20 years.

Site	N	Cover Type	N	Fire Frequency	N
Angelina N.F.	11	Longleaf Pine	12	High	34
Davy Crockett N.F	15	Shortleaf Pine	17	Low	23
Sabine N.F.	4	Loblolly Pine	17		
Sandyland Sanctuary	10	Mixed Pine-Hardwood	11		
Upland Island Wilderness	10				
Winston 8	7				
Total					57

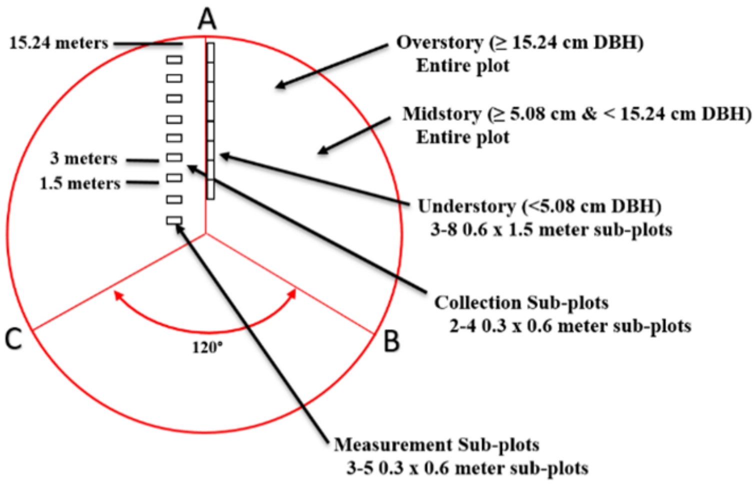

Figure 2: Circular plot design, adapted from Wall et al.

RESULTS

Fuel loading

Excluding Winston 8 Ranch, fuel loads were quantified at 50 plots (Table 2). There was no significant difference in the fuel loading of the high/low fire frequency groups (Table 3), but loblolly pine had significantly greater fuel loads than longleaf pine and the mixed pine-hardwood cover types (Tables 4 and 5).

Litter depth

Litter depth significantly differed between the high/low frequency and cover type groups (Tables 2 and 4), with shortleaf pine, loblolly pine, and mixed pine hardwood cover types having greater litter depths than longleaf pine. Upland Island Wilderness, Angelina, and Davy Crockett National Forests were significantly greater than the Sandyland Sanctuary (Table 5). Litter depth was negatively correlated to grass, forb, total richness and with the number of burns (Table 6).

Overstory basal area

Hardwood basal areas ranged from 0 to 21.14 m^2/ha, with an average of 6.18 m^2/ha (Table 2). There was a significant difference between the hardwood basal area of high/low frequency and cover type groups (Tables 3 and 4). Mixed pine-hardwood cover types had significantly greater hardwood basal areas than the longleaf pine and loblolly pine, and Upland Island Wilderness was significantly greater than Sandyland Sanctuary (Table 5). Total, grass and forb richness and the number of burns during a 20-year period had a negative correlation with hardwood basal area (Table 6). High fire frequency sites had significantly lower softwood basal areas than low fire frequency sites), and shortleaf pine cover types lower softwood basal area than mixed-pine hardwood, but greater than longleaf pine. There was also a significant difference in softwood basal area, as Upland Island Wilderness had greater softwood basal areas than all other sites and Sandyland Sanctuary was significantly lower than all of the others (Tables 2-5). Total, grass and forb richness and the number of burns during a 20-year period again had a negative correlation with hardwood basal area (Table 6). Total basal was significantly different between the high/low frequency groups. Negative correlations with total basal area were found for total, grass and forb richness, as well as with number of burns during a 20-year period.

Canopy cover

Shortleaf pine cover type had a lower canopy cover than mixed-pine hardwood, but greater than longleaf pine and was there also a significant difference between the high/low frequency groups, with high fire frequency sites lower than low fire frequency sites and there were significant differences in mean canopy cover by site (Tables 2-5). Total and forb richness had a negative correlation with canopy cover, as did the number of burns during a 20-year period (Table 6).

Understory richness

There was a significant difference between the grass richness of high/low frequency groups as the high fire frequency sites had a greater number of grasses and forbs (Tables 2-4). Shortleaf pine and pine-hardwood cover types contained significantly fewer forbs than longleaf pine and loblolly pine. And a significant difference in forb richness greater at Sandyland Sanctuary than Upland Island (Table 5). Forb richness was found to be positively correlated with the number of burns during a 20-year period (Table 6). There were significant differences in mean woody richness between sites, as Winston 8 Ranch had fewer woody growth forms than Sabine and Davy Crocket National Forests. Woody richness was not found to be correlated with number of burns in a 20-year period (Table 5). There was a significant difference between the total richness of high/low frequency groups, high fire frequency sites had greater richness than low fire frequency sites (Tables 2 and 3). Total richness was found to be positively correlated with the number of burns during a 20-year period (Table 6).

Species observations

129 species were observed across all plots (Table 7). The most observed species in the woody growth form category was American beautyberry (*Callicarpa americana*), and the most observed grass species was inland sea oats (*Chasmanthium latifolium*) with longleaf uniloa (*Chasmanthium sessifolium*) a close second. The most observed forb species was butterfly pea (*Clitoria mariana*). The most common species observed on high and low frequency sites was similar to total richness for all plots, but the most common forb observed in the low fire frequency group was elephants' foot (*Elephantopus tomentosus*) (Table 8). The most common woody, grass and forbs in the shortleaf pine and mixed pine-hardwood cover types were American beautyberry, inland sea oats, and elephant's

foot. Loblolly pine cover types most common growth forms were blackberry (*Rubus* L spp.), panicgrass (*Panicum* spp.), and blue wild indigo (*Baptisia australis*); longleaf pine cover types most observed woody, forb, and grass were yaupon (*Ilex vomitoria.*), ragweed (Ambrosia artemisiifolia), and little bluestem (*Schizachyrium scoparium*) (Table 9).

The most common species by growth form on the Angelina National Forest were sweetgum (*Liquidambar styraciflua*), little bluestem, and wild bean (*Strophostyles* sp.). Davy Crockett National Forest had the same common species as shortleaf pine and mixed pine-hardwood groups.

In the Sabine National Forest, the most common woody was blackberry, the most common grass was inland sea oats, and the most common forb was St. Andrews cross (*Hypericum hypericoides*). Sandylands' most common woody was longleaf pine with little bluestem and ragweed. Winston 8 had the most common growth form as panicgrass, followed by woody blackberry and blue wild indigo (Table 10).

Ordination

Non-Metric Multi-Dimensional Scaling (NMDS) was conducted to visualize the distribution of understory species across the fire frequency groups. To confirm that the modeling did an adequate job of representing community structure, a subsample NMDS was conducted with 15 sites which resulted in a more acceptable average stress of 0.144. Ordination displayed distinct groupings of fire frequency sites with low fire frequency sites aligned with the presence of the *Chasmanthium* (Figure 3). Longleaf pine cover types were strongly correlated with multiple woody, forb, and grass genera while mixed pine hardwood cover types were associated with the presence of *Chasmanthium* (Figure 4). Ordination also showed associations between the Davy Crockett National Forest and Upland Island Wilderness with the *Chasmanthium* genus. Sandyland Sanctuary and the Pinus genus showed associations which are likely due to the large amount of understory pine regeneration. The Angelina National Forest showed the most amount of dissimilarity between sites, while Sandyland Sanctuary was distinctly grouped separately (Figure 5).

Table 2: Summary statistics (n, min, max, mean, standard error, standard deviation, mean confidence interval) for fuel loading, litter depth, basal area, canopy cover and species richness.

N	Min	Max	Mean	Standard error	Standard deviation	Mean confidence interval (0.95)
Apr	Apr	Apr	Apr	Apr	Apr	Apr
	Fuel loading				**Tonnes ha^{+}**	
50	2.3	82.24	19.81	2.61	18.49	5.25
	Litter depth				**cm**	
50	0.81	8.28	3.39	0.24	1.7	0.48
	Hardwood basal area				**m^2 ha^{-1}**	
41	0	21.14	6.18	0.89	5.68	1.79
	Softwood basal area				**m^2 ha^{-1}**	
41	5.73	53.52	24.9	1.86	11.93	3.77
	Total basal area				**m^2 ha^{-1}**	
41	5.73	57.62	30.9	2.3	14.76	4.66
	Canopy cover				**%**	
57	13.5	97.92	55.6	3.17	23.97	6.36
	Grass richness					
57	0	5	2.49	0.17	1.34	0.35
	Forb richness					
57	0	8	2.18	0.24	1.81	0.48
	Woody richness					
57	2	9	4.88	0.23	1.73	0.46
	Total richness					
57	4	21	8.98	0.45	3.37	0.89

Table 3: Two sample t-test analysis of high and low fire frequency groups.

Variable	High frequency	Low frequency	Pr(>F)
Fuel loading	7.501	7.189	0.829
Litter depth	1.156	1.522	0.023
Hardwood basal area	17.435	37.86	0.008
Softwood basal area	81.973	139.435	0.0001
Total basal area	97.398	177.293	0.0001
Canopy cover	46.77	71.324	0.002
Grass richness	2.364	1.579	0.026
Forb richness	3	0.947	0.0001
Woody richness	5.182	5.105	0.89
Total richness	12.364	7.789	0.0001

Table 4: Analysis of Variance output measuring the difference in variable values between 4 cover type groups and 6 sites.

Variable	Cover type	site
	Pr(>F)	Pr(>F)
Fuel loading	0.016	0.052
Litter depth	0.0001	0.0001
Hardwood basal area	0.002	0.018
Softwood basal area	0.0001	0.0001
Total basal area	0.0001	0.0001
Canopy cover	0.0001	0.0001
Grass richness	0.069	0.083
Forb richness	0.0001	0.011
Woody richness	0.686	0.025
Total richness	0.089	0.045

Table 5: Variable means measured in this study and analyzed using ANOVA.

	Cover Type				Site					
	Longleaf	Loblolly	Shortleaf	Mixed	Angelina	Crockett	Sabine	Sandyland	Winston	Upland island
Fuel Loading (MT ha^{-1})	16.30b	24.07a	25.46a	11.04b	23.20a	27.06a	26.38	11.25b		10.92b
Litter (cm)	2.08b	4.27a	3.51a	3.83a	4.90a	3.02bc	3.40abc	1,71c		3.81ab
Canopy Cover (%)	27.18c	58.20b	57.60b	79.28a	49.90b	58.53b	74.72ab	26.28c	53.08b	80.69a
HW BA (m^2 ha^{-1})	2.29b	4.43b	6.63ab	10.68a	0.65b	1.21b	1.35ab	0.37b		1.61a
SW BA (m^2 ha^{-1})	11.98c	22.27b	26.30a	37.52b	4.35b	4.09b	2.00bc	1.96c		6.20a
Total BA (m^2 ha^{-1})	13.26c	26.70b	32.92b	48.20a	4.93b	5.33b	4.70b	2.18c		7.83a
Grass richness	2.33a	2.29a	1.59a	1.45a	1.1ab	2ab	2.4ab	3.3a	4.0ab	0.9b
Forb richness	3.17a	3.06a	1.47b	0.82b	0.9bc	2.1bc	2.9abc	3.2a	4.0ab	1.1c
Woody richness	4.50a	4.94a	5.36a	4.76a	6.0ab	4.1b	6.9a	4.0ab	3.7b	5.4ab
Total richness	10.00a	10.29a	7.92b	7.64b	10.09a	8.40a	10.25a	9.70a	10.30a	9.29a

Note: Longleaf, Loblolly, Shortleaf=pine species, Mixed=Mixed Pine-Hardwood; Angelina, Crockett, Sabine=National Forests, Sandyland=TNC Sandyland; Winston=Winston 8 Ranch; Upland Island=Upland Island Wilderness; HW=Hardwood; SW=Softwood. Different letters within a row within Cover Type or Site represent statistically significant differences ($p<0.10$).

Table 6: Pearson's correlations between variables assessed in this study.

Variable 1	Variable 2	R	p
Litter depth (cm)	Total richness	-0.43	0.0055
	Grass richness	-0.44	0.0045
	Forb richness	-0.5	0.0001
	Total burns in 20 years	-0.29	0.067
Hardwood basal area (m^2 ha^{-1})	Total richness	-0.38	0.018
	Grass richness	-0.35	0.033
	Forb richness	-0.35	0.032
	Total burns in 20 years	-0.51	0.0062
Softwood basal area (m^2 ha^{-1})	Total richness	-0.44	0.0042
	Grass richness	-0.44	0.0037
	Forb richness	-0.58	0.0001
	Total burns in 20 years	-0.59	0.0001
Total basal area (m^2 ha^{-1})	Total richness	-0.48	0.0014
	Grass richness	-0.49	0.0013
	Forb richness	-0.62	0.0001
	Total burns in 20 years	-0.69	0.0001
Canopy cover (%)	Total richness	-0.24	0.072
	Forb richness	-0.41	0.0019
	Total burns in 20 years	-0.34	0.0099
Total burns in 20 years	Total richness	0.23	0.086
	Grass richness	0.32	0.017
	Woody richness	0.45	0.0004
	Forb richness	0.45	0.0001

Table 7: Species contributing to total richness by life form (woody, forb, grass) measured across all sites.

Woody	R	Forb	R	Grass	R
Callicarpa americana L.	40	*Clitoria mariana* L.	13	*Chasmanthium latifolium* Michx.	32
Ilex vomitoria Sol.	32	*Clitoria ternatea* L.	12	*Chasmanthium sessiliflorum* Michx.	30
Pinus echinata Mill.	32	*Elephantophus tomentosus* L.	12	*Panicum* sp. L.	21
Quercus alba L.	31	*Ambrosia artemisiifolia* L.	10	*Schizachyrium scoparium* Michx.	18
Pinus taeda L.	25	*Ambrosia psilostachya* DC	8	*Dicanthelium oligosanthes* Schult.	12
Smilax sp. L.	22	*Elephantopus carolinianus* Raeusch	8	*Sporobolus* sp. L.	9
Rubus sp. L.	18	*Baptisia australis* L.	6	*Andropogon gyrans* Ashe	8

Liquidambar styraciflua L.	16	*Eupatorium capillifolium* Lam	6	*Dicanthelium* sp. Gould	4
Vitis aestivalis Michx.	16	*Eupatorium serotinum* Michx.	5	*Andropogon virginicus* L.	3
Vitis rotundifolia Michx.	15	*Polypremum procumbens* L.	5	*Andropogon ternarius* Michx.Michx.	1
Vaccinium arboretum Marsh. Marsh..	12	*Strophostyles* sp. L.	5	*Bothriochola laguroides* DC	1
Pinus palustris Mill.	10	*Viola sororia* Willd.	5	*Bromus catharticus* Vahl	1
Quercus incana Bart.	10	*Croton capitatus* Michx.	4	*Muhlenbergia capillaris* Lam.	1
Carya ovata Mill.	9	*Hypericum hypericoides* Crantz.	4	*Paspalum* sp. L.	1
Quercus marilandica Muenchh.	7	*Oxalis stricta* L.	4		
Myrica cerifera L.	6	*Solidago* sp. L.	4		
Parthenocissus quinquefolia L.	6	*Viola* sp. L.	4		
Quercus falcata Michx.	6	*Aster* sp. L.	3		
Sassafras albidum Nutt.	6	*Crotalaria rotundifolia* Gmel.	3		
Acer rubrum L.	5	*Galactia regularis* Browne	3		
Carya texana Buck.	5	*Liatris aspera* Michx.	3		
Gelsemium sempervirens J. St-Hil.	5	*Pityopsis gramnifolia* Nutt.	3		
Quercus stellata Wangenh.	5	*Solidago altissima* L.	3		
Ligustrum sinese Lour.	4	*Cirsium horridulum* Michx.	2		
Quercus margarettae Ashe.	4	*Crotalaria sagittalis* L.	2		
Quercus nigra L.	4	*Erythrina herbacea* L.	2		
Ulmus alata Michx.	4	*Helianthus agustifolius* L.	2		
Ampelopsis arborea L.	3	*Solanum carolinense* L.	2		
Bignonia capreolata L.	3	*Centrosema virginianum* L.	1		
Ditrysinia fruticosa Bart.	3	*Cirsium* sp. Mill.	1		
Rhus copallinum L.	3	*Cnidoscolus texanus* Small	1		
Toxicodendron radicans L.	3	*Dalea* sp. L.	1		
Ulmus sp. L.	3	*Desmodium* sp. Desv.	1		
Vaccinium elliottii Chapm.	3	*Diodia* sp. L.	1		
Crataegus marshallii Eggl.	2	*Galactia* sp. Browne.	1		
Persea borbonia L.	2	*Galium* sp. L.	1		
Quercus sp. L.	2	*Grindelia squarrosa* Pursh.	1		
Cercis Canadensis L.	1	*Hackelia virginiana* L.	1		

Diospyros virginiana L.	1	*Helianthus* sp. L.	1
Lonicera japonica Thunb.	1	*Heterotheca subaxillaris* Lam.	1
Michella repens L.	1	*Hexasepalum teres* Walter.	1
Nyssa sylvatica Marsh.	1	*Ipomea* sp. L.	1
Ostrya virginiana Mill.	1	*Jasminum mesnyi* Hance.	1
Quercus macrocarpa Michx.	1	*Liatris elegans* Walter.	1
Ulmus crassifolia Nutt.	1	*Liatris* sp. Schreb.	1
		Ionactis linariifolia Greene.	1
		Mentha sp. L.	1
		Mimosa microphylla Dryand.	1
		Pilea sp. Gray.	1
		Passiflora incarnata L.	1
		Phytoacca decandra L.	1
		Potentillia indica Andr.	1
		Primula sp. L.	1
		Pseudognaphalium obtusifolium L.	1
		Rhynchosia latifolia Michx.	1
		Ruellia pedunculatia Torr.	1
		Scutellaria integrifolia L.	1
		Sida sp. L.	1
		Solanum dimiatum Raf.	1
		Stylosanthes biflora L.	1
		Symphyotrichum sp. Nees.	1
		Tragia urticifolia Michx.	1
		Vernonia texana Gray.	1
		Vicia sp. L.	1
		Perilla frutescens L.	1
		Taraxacum sp. Wigg.	1

Note: R=number of plots.

Table 8: Species contributing to total richness by life form (W=woody, F=forb, G=grass, FE=fern, Su=succulent) measured across high and low fire frequencies.

High frequency			Low frequency		
GF	**Species**	**R**	**GF**	**Species**	**R**
W	*Callicarpa americana* L.	19	W	*Callicarpa americana* L.	21
W	*Ilex vomitoria* Sol.	19	G	*Chasmanthium latifolium* Michx.	18
W	*Quercus alba* L.	19	G	*Chasmanthium sessiliflorum* Michx.	18
W	*Pinus echinata* Mill.	17	W	*Pinus echinata* Mill.	15

G	*Chasmanthium latifolium* Michx.	14	W	*Ilex vomitoria* Sol.	13
G	*Panicum* sp. L.	14	W	*Quercus alba* L.	12
W	*Pinus taeda* L.	14	W	*Pinus taeda* L.	11
G	*Schizachyrium scoparium* Michx.	14	W	*Smilax* sp. L.	9
W	*Smilax* sp. L.	13	W	*Vitis aestivalis* Michx.	8
G	*Chasmanthium sessiliflorum* Michx.	12	W	*Vitis rotundifolia* Michx.	8
F	*Clitoria mariana* L.	12	G	*Panicum* sp. L.	7
W	*Liquidambar styraciflua* L.	12	F	*Elephantophus tomentosus* L.	6
W	*Rubus* sp. L.	12	W	*Rubus* sp. L.	6
F	*Clitoria ternatea* L.	11	F	*Elephantopus carolinianus* Raeusch	5
W	*Pinus palustris* Mill.	9	G	*Dicanthelium oligosanthes* Schult.	4
W	*Quercus incana* Bart.	9	W	*Liquidambar styraciflua* L.	4
W	*Vaccinium arboretum* Marsh.	9	G	*Schizachyrium scoparium* Michx.	4
G	*Dicanthelium oligosanthes* Schult.	8	W	*Acer rubrum* L.	3
G	*Sporobolus* sp. L.	8	F	*Ambrosia artemisiifolia* L.	3
W	*Vitis aestivalis* Michx.	8	W	*Ditrysinia fruticosa* Bart.	3
F	*Ambrosia artemisiifolia* L.	7	F	*Eupatorium capillifolium* Lam	3
G	*Andropogon gyrans* Ashe	7	F	*Eupatorium serotinum* Michx.	3
S	*Carex* sp. L.	7	W	*Parthenocissus quinquefolia* L.	3
W	*Carya ovata* Mill.	7	W	*Quercus falcata* Michx.	3
W	*Vitis rotundifolia* Michx.	7	W	*Quercus stellata* Wangenh.	3
F	*Ambrosia psilostachya* DC	6	W	*Vaccinium arboretum* Marsh.	3
F	*Baptisia australis* L.	6	F	*Ambrosia psilostachya* DC	2
F	*Elephantophus tomentosus* L.	6	S	*Carex* sp. L.	2
W	*Quercus marilandica* Muenchh.	6	W	*Carya ovata* Mill.	2
W	*Carya texana* Buck.	5	G	*Dicanthelium* sp. Gould	2
F	*Polypremum procumbens* L.	5	F	*Erythrina herbacea* L.	2
W	*Sassafras albidum* Nutt.	5	W	*Gelsemium sempervirens* St-Hil.	2
F	*Strophostyles* sp. L.	5	W	*Myrica cerifera* L.	2
F	*Viola sororia* Willd.	5	W	*Quercus nigra* L. L.	2
F	*Croton capitatus* Michx.	4	W	*Ulmus alata* Michx.	2
F	*Hypericum hypericoides* Crantz.	4	W	*Vaccinium elliottii* Chapm.	2
W	*Myrica cerifera* L.	4	W	*Ampelopsis arborea* L.	1

FE	*Pteridium aquilinum* Kuhn.	4	G	*Andropogon gyrans* Ashe	1
F	*Solidago* sp. L.	4	G	*Andropogon virginicus* L.	1
F	*Viola* sp. L.	4	W	*Bignonia capreolata* L.	1
F	*Aster* sp. L.	3	F	*Centrosema virginianum* L.	1
F	*Elephantopus carolinianus* Raeusch	3	W	*Cercis Canadensis* L.	1
F	*Eupatorium capillifolium* Lam	3	F	*Clitoria mariana* L.	1
W	*Gelsemium sempervirens* J. St-Hil.	3	F	*Clitoria ternatea* L.	1
F	*Liatris aspera* Michx.	3	W	*Crataegus marshallii* Eggl.	1
W	*Ligustrum sinese* Lour.	3	F	*Crotalaria rotundifolia* Gmel.	1
FE	*Lygodium japonicum* Thunb.	3	F	*Crotalaria sagittalis* L.	1
F	*Oxalis stricta* L.	3	F	*Diodia* sp. L.	1
W	*Parthenocissus quinquefolia* L.	3	F	*Galactia regularis* P.Browne	1
F	*Pityopsis gramnifolia* Nutt.	3	F	*Galactia* sp. Browne.	1
W	*Quercus falcata* Michx.	3	F	*Galium* sp. L.	1
W	*Quercus margarettae* Ashe.	3	F	*Hackelia virginiana* L.	1
F	*Solidago altissima* L.	3	F	*Ipomea* sp. L.	1
W	*Toxicodendron radicans* L.	3	W	*Ligustrum sinese* Lour.	1
W	*Acer rubrum* L.	2	W	*Nyssa sylvatica* Marsh.	1
W	*Ampelopsis arborea* L.	2	W	*Ostrya virginiana* Mill.	1
G	*Andropogon virginicus* L.	2	F	*Oxalis stricta* L.	1
W	*Bignonia capreolata* L.	2	W	*Persea borbonia* L.	1
F	*Cirsium horridulum* Michx.	2	W	*Pinus palustris* Mill.	1
F	*Crotalaria rotundifolia JF* Gmel.	2	F	*Potentillia indica* Andr.	1
G	*Dicanthelium* sp. Gould	2	W	*Quercus incana* Bart.	1
F	*Eupatorium serotinum* Michx.	2	W	*Quercus macrocarpa* Michx.	1
F	*Galactia regularis* P.Browne	2	W	*Quercus margarettae* Ashe.	1
F	*Helianthus agustifolius* L.	2	W	*Quercus marilandica* Muench.	1
W	*Quercus nigra* L.	2	W	*Rhus copallinum* L.	1
W	*Quercus* sp. L.	2	F	*Rhynchosia latifolia* Michx.	1
W	*Quercus stellata* Wangenh.	2	W	*Sassafras albidum* Nutt.	1
W	*Rhus copallinum* L.	2	G	*Sporobolus* sp. L.	1
F	*Solanum carolinense* L.	2	W	*Ulmus crassifolia* Nutt.	1
W	*Ulmus alata* Michx.	2	W	*Ulmus* sp. L.	1
W	*Ulmus* sp. L.	2			
G	*Andropogon ternarius* Michx.	1			

G	*Bothriochola laguroides* DC	1
G	*Bromus catharticus* Vahl	1
F	*Cirsium* sp. Mill.	1
F	*Cnidoscolus texanus* Small	1
W	*Crataegus marshallii* Eggl.	1
F	*Crotalaria sagittalis* L.	1
F	*Dalea* sp. L.	1
F	*Desmodium* sp. Desv.	1
W	*Diospyros virginiana* L.	1
F	*Grindelia squarrosa* Pursh.	1
F	*Helianthus* sp. L.	1
F	*Heterotheca subaxillaris* Lam.	1
F	*Hexasepalum teres* Walter.	1
F	*Jasminum mesnyi* Hance.	1
F	*Liatris elegans* Walter.	1
F	*Liatris* sp. Schreb.	1
F	*Lonactis* linarifolia	1
W	*Lonicera japonica* Thunb.	1
F	*Mentha* sp. L.	1
W	*Michella repens* L.	1
F	*Mimosa microphylla* Dryand.	1
G	*Muhlenbergia capillaris* Lam.	1
F	*Palea* sp. L.	1
G	*Paspalum* sp. L.	1
F	*Passiflora incarnata* L.	1
W	*Persea borbonia* L.	1
F	*Phytoacca decandra* L.	1
F	*Primula* sp. L.	1
F	*Pseudognaphalium obtusifolium* L.	1
F	*Ruellia pedunculatia* Torr.	1
F	*Scutellaria integrifolia* L.	1
F	*Sida* sp. L.	1
F	*Solanum dimiatum* Raf.	1
F	*Stylosanthes biflora* L.	1
F	*Symphyotrichum* sp. Nees.	1
F	*Tragia urticifolia* Michx.	1
W	*Vaccinium elliottii* Chapm.	1
F	*Vernonia texana* Gray.	1
F	*Vicia* sp. L.	1
SU	*Yucca filamentosa* L.	1

Note: GF=Growth Form; R=number of plots.

Table 9: Species contributing to total richness by life form (W=woody, F=forb, G=grass, FE=fern, Su=succulent) measured across shortleaf pine, loblolly pine, longleaf pine, mixed pine-hardwood cover type.

GF	Species	R	GF	Species	R
	Shortleaf pine			**Loblolly pine**	
W	*Callicarpa americana* L.	16	W	*Rubus* sp. L.	13
G	*Chasmanthium latifolium* Michx.	15	W	*Callicarpa americana* L.	12
G	*Chasmanthium sessiliflorum* Michx.	15	G	*Panicum* sp. L.	12
W	*Quercus alba* L.	10	W	*Smilax* sp. L.	9
W	*Liquidambar styraciflua* L.	8	S	*Carex* sp. L.	7
W	*Pinus echinata* Mill.	8	G	*Chasmanthium latifolium* Michx.	7
W	*Vitis aestivalis* Michx.	7	W	*Ilex vomitoria* Sol.	7
W	*Ilex vomitoria* Sol.	6	W	*Quercus alba* L.	7
G	*Schizachyrium scoparium* Michx.	6	W	*Vitis aestivalis* Michx.	6
W	*Smilax* sp. L.	6	W	*Vitis rotundifolia* Michx.	6
W	*Vitis rotundifolia* Michx.	6	F	*Baptisia australis* L..	5
F	*Elephantophus tomentosus* L.	5	G	*Chasmanthium sessiliflorum* Michx.	5
W	*Pinus taeda* L.	5	W	*Pinus echinata* Mill.	5
W	*Ligustrum sinese* Lour.	4	W	*Pinus taeda* L.	5
W	*Ulmus alata* Michx.	4	G	*Schizachyrium scoparium* Michx.	5
G	*Dicanthelium oligosanthes* Schult.	3	W	*Vaccinium arboretum* Marsh.	5
G	*Dicanthelium* sp. Gould	3	F	*Viola sororia* Willd.	5
F	*Eupatorium capillifolium* Lam	3	F	*Clitoria mariana* L.	4
F	*Eupatorium serotinum* Michx.	3	W	*Liquidambar styraciflua* L.	4
F	*Galactia regularis* P.Browne	3	F	*Soldago* sp.	4
W	*Parthenocissus quinquefolia* L.	3	G	*Sporobolus* sp. L.	4
W	*Quercus falcata* Michx.	3	F	*Strophostyles* sp. L.	4
W	*Rubus* sp. L.	3	F	*Viola* sp. L.	4
W	*Ampelopsis arborea* L.	2	F	*Aster* sp. L.	3
W	*Bignonia capreolata* L.	2	F	*Clitoria ternatea* L.	3
W	*Carya ovata* Mill.	2	F	*Croton capitatus* Michx.	3
F	*Clitoria mariana* L.	2	G	*Dicanthelium oligosanthes* Schult.	3
F	*Clitoria ternatea* L.	2	W	*Gelsemium sempervirens* St-Hil.	3
F	*Elephantopus carolinianus* Raeusch	2	W	*Sassafras albidum* Nutt.	3
F	*Erythrina herbacea* L.	2	F	*Solidago altissima* L.	3
FE	*Lygodium japonicum* Thunb.	2	W	*Acer rubrum* L.	2
W	*Myrica cerifera* L.	2	G	*Andropogon gyrans* Ashe	2
F	*Oxalis stricta* L.	2	F	*Elephantophus tomentosus* L.	2

W	*Quercus* sp. L.	2	F	*Eupatorium capillifolium* Lam	2
W	*Quercus stellata* Wangenh.	2	F	*Eupatorium serotinum* Michx.	2
W	*Ulmus* sp. L.	2	F	*Helianthus agustifolius* L.	2
F	*Ambrosia artemisiifolia* L.	1	F	*Hypericum hypericoides* Crantz.	2
G	*Andropogon gyrans* Ashe	1	F	*Liatris aspera* Michx.	2
W	*Carya texana* Buck.	1	W	*Myrica cerifera* L.	2
W	*Cercis Canadensis* L.	1	F	*Oxalis stricta* L.	2
W	*Diospyros virginiana* L.	1	FE	*Pteridium aquilinum*	2
F	*Galactia* sp. Browne.	1	W	*Quercus falcata* Michx.	2
F	*Galium* sp. L.	1	W	*Quercus marilandica* Muenchh.	2
W	*Gelsemium sempervirens* J. St-Hil.	1	W	*Quercus nigra* L.	2
F	*Jasminum mesnyi* Hance.	1	W	*Quercus stellata* Wangenh.	2
W	*Lonicera japonica* Thunb.	1	W	*Rhus copallinum* L.	2
W	*Michella repens* L.	1	F	*Solanum carolinense* L.	2
W	*Nyssa sylvatica* Marsh.	1	W	*Toxicodendron radicans* L.	2
G	*Panicum* sp. L.	1	F	*Ambrosia artemisiifolia* L.	1
F	*Passiflora incarnata* L.	1	W	*Ampelopsis arborea* L.	1
W	*Quercus marilandica* Muenchh.	1	G	*Andropogon virginicus* L.	1
W	*Quercus nigra* L.	1	W	*Bignonia capreolata* L.	1
W	*Rhus copallinum* L.	1	G	*Bromus catharticus* Vahl	1
F	*Rhynchosia latifolia* Michx.	1	F	*Cirsium horridulum* Michx.	1
W	*Sassafras albidum* Nutt.	1	W	*Crataegus marshallii* Eggl.	1
F	*Strophostyles* sp. L.	1	F	*Crotalaria rotundifolia* Gmel.	1
W	*Toxicodendron radicans* L.	1	F	*Crotalaria sagittalis* L.	1
W	*Ulmus crassifolia* Nutt.	1	F	*Desmodium* sp. Desv.	1
			G	*Dicanthelium* sp. Gould	1
			F	*Elephantopus carolinianus* Raeusch	1
			F	*Helianthus* sp. L.	1
			F	*Hexasepalum teres* Walter.	1
			F	*Liatris* sp. Schreb.	1
			F	*Lonactis linarifolia*	1
			F	*Mentha* sp. L.	1
			W	*Parthenocissus quinquefolia* L.	1
			G	*Paspalum* sp. L.	1

			F	*Phytoacca decandra* L.	1
			F	*Pityopsis gramnifolia* Nutt.	1
			F	*Primula* sp. L.	1
			F	*Ruellia pedunculatia* Torr.	1
			F	*Scutellaria integrifolia* L.	1
			F	*Sida* sp. L.	1
			F	*Solanum dimiatum* Raf.	1
			F	*Stylosanthes biflora* L.	1
			F	*Symphyotrichum* sp. Nees.	1
			F	*Tragia urticifolia* Michx.	1
			F	*Vernonia texana* Gray.	1
			F	*Vicia* sp. L.	1
	Longleaf pine			**Mixed pine-hardwood**	
W	*Ilex vomitoria* Sol.	10	W	*Callicarpa americana* L.	9
W	*Pinus echinata* Mill.	10	G	*Chasmanthium latifolium* Michx.	8
W	*Pinus palustris*	10	G	*Chasmanthium sessiliflorum* Michx.	8
W	*Quercus alba* L.	10	W	*Ilex vomitoria* Sol.	8
W	*Quercus incana* Bart.	10	W	*Pinus echinata* Mill.	8
F	*Ambrosia artemisiifolia* L.	7	W	*Pinus taeda* L.	7
F	*Ambrosia psilostachya* DC	7	W	*Smilax* sp. L.	5
F	*Clitoria mariana* L.	7	F	*Elephantophus tomentosus* L.	4
F	*Clitoria ternatea* L.	7	F	*Elephantopus carolinianus* Raeusch	4
W	*Pinus taeda* L.	7	G	*Panicum* sp. L.	4
G	*Schizachyrium scoparium* Michx.	7	W	*Ditrysinia fruticosa* Bart.	3
W	*Carya ovata* Mill.	6	W	*Quercus alba* L.	3
G	*Andropogon gyrans* Ashe	5	W	*Vaccinium arboretum* Marsh.	3
G	*Dicanthelium oligosanthes* Schult.	5	W	*Vitis aestivalis* Michx.	3
F	*Polypremum procumbens* L.	5	W	*Vitis rotundifolia* Michx.	3
G	*Sporobolus* sp. L.	5	W	*Acer rubrum* L.	2
W	*Carya texana* Buck.	4	W	*Parthenocissus quinquefolia* L.	2
W	*Quercus margarettae* Ashe.	4	W	*Vaccinium elliottii* Chapm.	2
W	*Quercus marilandica* Muenchh.	4	F	*Ambrosia artemisiifolia* L.	1
W	*Vaccinium arboretum* Marsh.	4	F	*Ambrosia psilostachya* DC	1
W	*Liquidambar styraciflua* L.	3	S	*Carex* sp. L.	1
G	*Panicum* sp. L.	3	W	*Carya ovata* Mill.	1

G	*Andropogon virginicus* L.	2	F	*Centrosema virginianum* L.	1
W	*Callicarpa americana* L.	2	W	*Crataegus marshallii* Eggl.	1
F	*Crotalaria rotundifolia* JF Gmel.	2	G	*Dicanthelium oligosanthes* Schult.	1
F	*Hypericum hypericoides* Crantz.	2	F	*Diodia* sp. L.	1
W	*Persea borbonia* L.	2	W	*Gelsemium sempervirens* J. St-Hil.	1
F	*Pityopsis gramnifolia* Nutt.	2	F	*Hackelia virginiana* L.	1
FE	*Pteridium aquilinum*	2	F	*Ipomea* sp. L.	1
W	*Sassafras albidum* Nutt.	2	W	*Liquidambar styraciflua* L.	1
G	*Andropogon ternarius* Michx.	1	W	*Myrica cerifera* L.	1
F	*Baptisia australis* L.	1	F	*Potentillia indica* Andr.	1
G	*Bothriochola laguroides* DC	1	W	*Quercus nigra* L.	1
S	*Carex* sp. L.	1	W	*Quercus stellata* Wangenh.	1
G	*Chasmanthium latifolium* Michx.	1	W	*Rubus* sp. L.	1
G	*Chasmanthium sessiliflorum* Michx.	1	W	*Ulmus* sp. L.	1
F	*Cirsium horridulum* Michx.	1			
F	*Cirsium* sp. Mill.	1			
F	*Cnidoscolus texanus* Small	1			
F	*Crotalaria sagittalis* L.	1			
F	*Croton capitatus* Michx.	1			
F	*Dalea* sp. L.	1			
F	*Elephantophus tomentosus* L.	1			
F	*Elephantopus carolinianus* Raeusch	1			
F	*Eupatorium capillifolium* Lam	1			
F	*Grindelia squarrosa* Pursh.	1			
F	*Heterotheca subaxillaris* Lam.	1			
F	*Liatris aspera* Michx.	1			
F	*Liatris elegans* Walter.	1			
FE	*Lygodium japonicum* Thunb.	1			
F	*Mimosa microphylla* Dryand.	1			
G	*Muhlenbergia capillaris* Lam.	1			
W	*Myrica cerifera* L.	1			
F	*Palea* sp.	1			
F	*Pseudognaphalium obtusifolium* L.	1			
W	*Quercus falcata* Michx.	1			
W	*Rubus* sp. L.	1			
W	*Smilax* sp. L.	1			
W	*Vaccinium elliottii* Chapm.	1			
SU	*Yucca filamentosa* L.	1			

Note: GF=Growth Form; R=richness

Table 10: Species contributing to total richness by life form (W=woody, F=forb, G=grass, FE=fern, Su=succulent) measured across site type (Angelina National Forest, Davy Crockett National Forest, Sabine National Forest, Sandyland Sanctuary, land Island Wilderness, Winston 8 Ranch).

GF	Species	R	GF	Species	R
	Angelina NF			**Davy crockett NF**	
W	*Liquidambar styraciflua* L.	8	W	*Callicarpa americana* L.	14
W	*Callicarpa americana* L.	7	G	*Chasmanthium latifolium* Michx.	14
W	*Smilax* sp. L.	7	G	*Chasmanthium sessiliflorum* Michx.	14
W	*Ilex vomitoria* Sol.	6	W	*Quercus alba* L.	9
W	*Quercus alba* L.	5	W	*Pinus echinata* Mill.	8
G	*Schizachyrium scoparium* Michx.	5	W	*Vitis aestivalis* Michx.	7
FE	*Pteridium aquilinum*	4	W	*Liquidambar styraciflua* L.	6
G	*Chasmanthium latifolium* Michx.	3	W	*Vitis rotundifolia* Michx.	6
G	*Chasmanthium sessiliflorum* Michx.	3	F	*Elephantophus tomentosus* L.	5
W	*Gelsemium sempervirens* J. St-Hil.	3	W	*Pinus taeda* L.	5
W	*Myrica cerifera* L.	3	W	*Ilex vomitoria* Sol.	4
G	*Panicum* sp. L.	3	W	*Ligustrum sinese* Lour.	4
W	*Rubus* sp. L.	3	G	*Schizachyrium scoparium* Michx.	4
W	*Sassafras albidum* Nutt.	3	W	*Smilax* sp. L.	4
F	*Strophostyles* sp. L.	3	W	*Ulmus alata* Michx.	4
W	*Vitis aestivalis* Michx.	3	G	*Dicanthelium oligosanthes* Schult.	3
W	*Vitis rotundifolia* Michx.	3	G	*Dicanthelium* sp. Gould	3
G	*Andropogon gyrans* Ashe	2	F	*Eupatorium capillifolium* Lam	3
S	*Carex* sp. L.	2	F	*Eupatorium serotinum* Michx.	3
G	*Dicanthelium oligosanthes* Schult.	2	F	*Galactia regularis* P.Browne	3
F	*Elephantophus tomentosus* L.	2	W	*Ampelopsis arborea* L.	2
F	*Liatris aspera* Michx.	2	W	*Bignonia capreolata* L.	2
F	*Lygodium japonicum* Thunb.	2	W	*Carya ovata* Mill.	2
W	*Quercus falcata* Michx.	2	F	*Clitoria mariana* L.	2
W	*Quercus stellata* Wangenh.	2	F	*Clitoria ternatea* L.	2
W	*Rhus copallinum* L.	2	F	*Elephantopus carolinianus* Raeusch	2
W	*Acer rubrum* L.	1	F	*Erythrina herbacea* L.	2
F	*Baptisia australis* L..	1	F	*Oxalis stricta* L.	2
W	*Bignonia capreolata* L.	1	W	*Parthenocissus quinquefolia* L.	2
G	*Bromus catharticus* Vahl	1	W	*Quercus falcata* Michx.	2
F	*Clitoria mariana* L.	1	W	*Quercus* sp. L.	2
F	*Clitoria ternatea* L.	1	W	*Quercus stellata* Wangenh.	2
W	*Crataegus marshallii* Eggl.	1	W	*Rubus* sp. L.	2
F	*Crotalaria rotundifolia* JF Gmel.	1	W	*Ulmus* sp. L.	2
F	*Crotalaria sagittalis* L.	1	F	*Ambrosia artemisiifolia* L.	1
F	*Croton capitatus* Michx.	1	G	*Andropogon gyrans* Ashe	1
F	*Desmodium* sp. Desv.	1	W	*Carya texana* Buck.	1

G	*Dicanthelium* sp. Gould	1	W	*Cercis Canadensis* L.	1
F	*Elephantopus carolinianus* Raeusch	1	W	*Diospyros virginiana* L.	1
F	*Eupatorium capillifolium* Lam	1	F	*Galactia* sp. Browne.	1
F	*Eupatorium serotinum* Michx.	1	F	*Galium* sp. L.	1
F	*Helianthus agustifolius* L. L. L.	1	F	*Jasminum mesnyi* Hance.	1
F	*Helianthus* sp. L.	1	FE	*Lygodium japonicum* Thunb.	1
F	*Hexasepalum teres* Walter.	1	W	*Michella repens* L.	1
F	*Liatris* sp. Schreb.	1	W	*Myrica cerifera* L.	1
F	*Lonactis linarifolia*	1	W	*Nyssa sylvatica* Marsh.	1
W	*Lonicera japonica* Thunb.	1	G	*Panicum* sp. L.	1
W	*Ostrya virginiana* Mill.	1	F	*Passiflora incarnata* L.	1
W	*Parthenocissus quinquefolia* L.	1	W	*Quercus marilandica* Muenchh.	1
G	*Paspalum* sp. L.	1	W	*Quercus nigra* L.	1
W	*Pinus echinata* Mill.	1	W	*Rhus copallinum* L.	1
W	*Pinus taeda* L.	1	F	*Rhynchosia latifolia* Michx.	1
F	*Pityopsis gramnifolia* Nutt.	1	W	*Sassafras albidum* Nutt.	1
F	*Primula* sp. L.	1	F	*Strophostyles* sp. L.	1
W	*Quercus macrocarpa* Michx.	1	W	*Toxicodendron radicans* L.	1
F	*Ruellia pedunculatia* Torr.	1	W	*Ulmus crassifolia* Nutt.	1
F	*Scutellaria integrifolia* L.	1			
F	*Stylosanthes biflora* L.	1			
W	*Toxicodendron radicans* L.	1			
F	*Tragia urticifolia* Michx.	1			
W	*Vaccinium arboretum* Marsh.	1			
F	*Vernonia texana* Gray.	1			
F	*Viola sororia* Willd.	1			
	Sabine NF			**Sandyland sanctuary**	
W	*Rubus* sp. L.	4	W	*Pinus echinata* Mill.	10
W	*Callicarpa americana* L.	3	W	*Pinus palustris*	10
S	*Carex* sp. L.	3	W	*Quercus alba* L.	10
G	*Chasmanthium latifolium* Michx.	3	W	*Quercus incana* Bart.	10
G	*Chasmanthium sessiliflorum* Michx.	3	W	*Ilex vomitoria* Sol.	9
W	*Ilex vomitoria* Sol.	3	F	*Ambrosia artemisiifolia* L.	7
G	*Panicum* sp. L.	3	F	*Ambrosia psilostachya* DC	7
W	*Quercus alba* L.	3	F	*Clitoria mariana* L.	7
W	*Smilax* sp. L.	3	F	*Clitoria ternatea* L.	7
W	*Vaccinium arboretum* Marsh.	3	W	*Pinus taeda* L.	7
W	*Vitis aestivalis* Michx.	3	G	*Schizachyrium scoparium* Michx.	7
W	*Vitis rotundifolia* Michx.	3	W	*Carya ovata* Mill.	6
W	*Acer rubrum* L.	2	G	*Dicanthelium oligosanthes* Schult.	5

F	*Hypericum hypericoides* Crantz.	2	F	*Polypremum procumbens* L.	5
W	*Pinus echinata* Mill.	2	G	*Sporobolus* sp. L.	5
W	*Pinus taeda* L.	2	G	*Andropogon gyrans* Ashe	4
W	*Quercus marilandica* Muenchh.	2	W	*Carya texana* Buck.	4
W	*Quercus nigra* L.	2	W	*Quercus margarettae* Ashe.	4
F	*Soldago* sp.	2	W	*Quercus marilandica* Muenchh.	4
F	*Ambrosia artemisiifolia* L.	1	W	*Vaccinium arboretum* Marsh.	4
F	*Clitoria mariana* L.	1	G	*Panicum* sp. L.	3
G	*Dicanthelium oligosanthes* Schult.	1	G	*Andropogon virginicus* L.	2
F	*Elephantophus tomentosus* L.	1	F	*Crotalaria rotundifolia* Gmel.	2
F	*Elephantopus carolinianus* Raeusch	1	F	*Hypericum hypericoides* Crantz.	2
F	*Eupatorium capillifolium* Lam	1	W	*Persea borbonia* L.	2
F	*Eupatorium serotinum* Michx.	1	F	*Pityopsis gramnifolia* Nutt.	2
W	*Gelsemium sempervirens* J. St-Hil.	1	G	*Andropogon ternarius* Michx. Var. ternarius	1
F	*Helianthus agustifolius* L. L. L.	1	F	*Baptisia australis* L..	1
W	*Myrica cerifera* L.	1	G	*Bothriochola laguroides* DC	1
W	*Parthenocissus quinquefolia* L.	1	W	*Callicarpa americana* L.	1
F	*Phytoacca decandra* L.	1	S	*Carex* sp. L.	1
G	*Schizachyrium scoparium* Michx.	1	G	*Chasmanthium latifolium* Michx.	1
F	*Solanum carolinense* L.	1	G	*Chasmanthium sessiliflorum* Michx.	1
F	*Solanum dimiatum* Raf.	1	F	*Cirsium horridulum* Michx.	1
F	*Solidago altissima* L.	1	F	*Cirsium* sp. Mill.	1
F	*Strophostyles* sp. L.	1	F	*Cnidoscolus texanus* Small	1
F	*Symphyotrichum* sp. Nees.	1	F	*Crotalaria sagittalis* L.	1
W	*Toxicodendron radicans* L.	1	F	*Croton capitatus* Michx.	1
F	*Vicia* sp. L.	1	F	*Dalea* sp. L.	1
F	*Viola sororia* Willd.	1	F	*Eupatorium capillifolium* Lam	1
F	*Viola* sp. L.	1	F	*Grindelia squarrosa* Pursh.	1
			F	*Heterotheca subaxillaris* Lam.	1
			F	*Liatris aspera* Michx.	1
			F	*Liatris elegans* Walter.	1
			W	*Liquidambar styraciflua* L.	1
			F	*Mimosa microphylla* Dryand.	1
			G	*Muhlenbergia capillaris* Lam.	1
			F	*Palea* sp.	1
			F	*Pseudognaphalium obtusifolium* L.	1
			W	*Quercus falcata* Michx.	1
			W	*Rubus* sp. L.	1
			W	*Smilax* sp. L.	1
			W	*Vaccinium elliottii* Chapm.	1

			SU	*Yucca filamentosa* L.	1
	Upland island wilderness			**Winston 8 ranch**	
W	*Callicarpa americana* L.	9	G	*Panicum* sp. L.	7
G	*Chasmanthium latifolium* Michx.	8	W	*Rubus* sp. L.	7
G	*Chasmanthium sessiliflorum* Michx.	8	W	*Callicarpa americana* L.	6
W	*Ilex vomitoria* Sol.	8	F	*Baptisia australis* L..	4
W	*Pinus echinata* Mill.	8	G	*Sporobolus* sp. L.	4
W	*Pinus taeda* L.	7	F	*Aster* sp. L.	3
W	*Smilax* sp. L.	5	G	*Chasmanthium latifolium* Michx.	3
F	*Elephantophus tomentosus* L.	4	W	*Pinus echinata* Mill.	3
F	*Elephantopus carolinianus* Raeusch	4	W	*Pinus taeda* L.	3
G	*Panicum* sp. L.	4	F	*Viola sororia* Willd.	3
W	*Ditrysinia fruticosa* Bart.	3	F	*Viola* sp. L.	3
W	*Quercus alba* L.	3	S	*Carex* sp. L.	2
W	*Vaccinium arboretum* Marsh.	3	F	*Clitoria mariana* L.	2
W	*Vitis aestivalis* Michx.	3	F	*Clitoria ternatea* L.	2
W	*Vitis rotundifolia* Michx.	3	F	*Croton capitatus* Michx.	2
W	*Acer rubrum* L.	2	W	*Ilex vomitoria* Sol.	2
W	*Parthenocissus quinquefolia* L.	2	F	*Oxalis stricta* L.	2
W	*Vaccinium elliottii* Chapm.	2	W	*Sassafras albidum* Nutt.	2
F	*Ambrosia artemisiifolia* L.	1	W	*Smilax* sp. L.	2
F	*Ambrosia psilostachya* DC	1	F	*Soldago* sp.	2
S	*Carex* sp. L.	1	F	*Solidago altissima* L.	2
W	*Carya ovata* Mill.	1	W	*Ampelopsis arborea* L.	1
F	*Centrosema virginianum* L.	1	G	*Andropogon gyrans* Ashe	1
W	*Crataegus marshallii* Eggl.	1	G	*Andropogon virginicus* L.	1
G	*Dicanthelium oligosanthes* Schult.	1	G	*Chasmanthium sessiliflorum* Michx.	1
F	*Diodia* sp. L.	1	F	*Cirsium horridulum* Michx.	1
W	*Gelsemium sempervirens* J. St-Hil.	1	F	*Mentha* sp. L.	1
F	*Hackelia virginiana* L.	1	W	*Quercus alba* L.	1
F	*Ipomea* sp. L.	1	W	*Quercus falcata* Michx.	1
W	*Liquidambar styraciflua* L.	1	G	*Schizachyrium scoparium* Michx.	1
W	*Myrica cerifera* L.	1	F	*Sida* sp. L.	1
F	*Potentillia indica* Andr.	1	F	*Solanum carolinense* L.	1
W	*Quercus nigra* L. L.	1	W	*Vaccinium arboretum* Marsh.	1
W	*Quercus stellata* Wangenh.	1			
W	*Rubus* sp. L.	1			
W	*Ulmus* sp. L.	1			

Note: NF=National Forest; GF=Growth Form; R=richness.

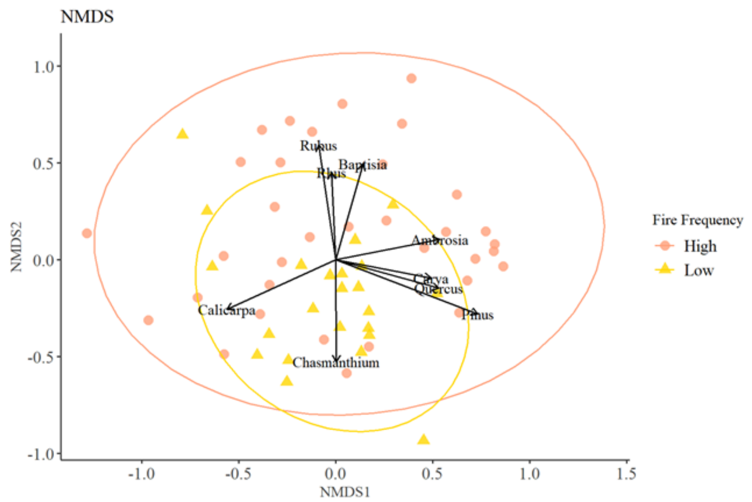

Figure 3: Non-metric multidimensional scaling constructed using fire frequency as groups overlaid with significant species scores ($p \leq 0.001$).

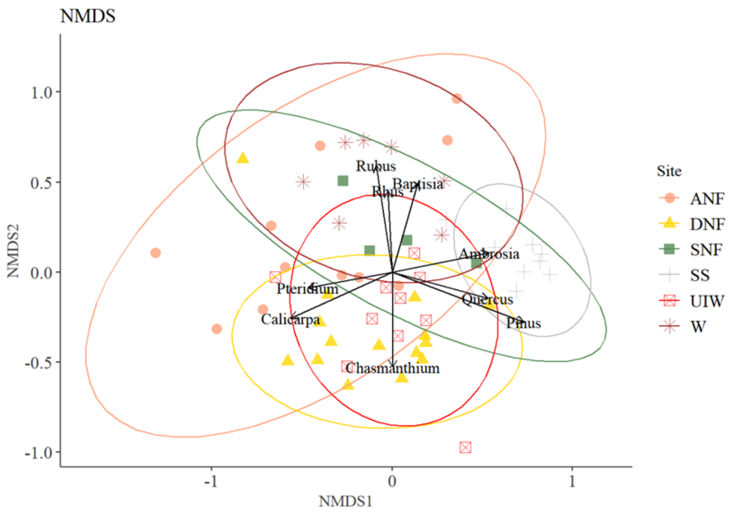

Figure 4: Non-metric multidimensional scaling constructed using cover type as groups overlaid with significant species scores ($p \leq 0.001$).

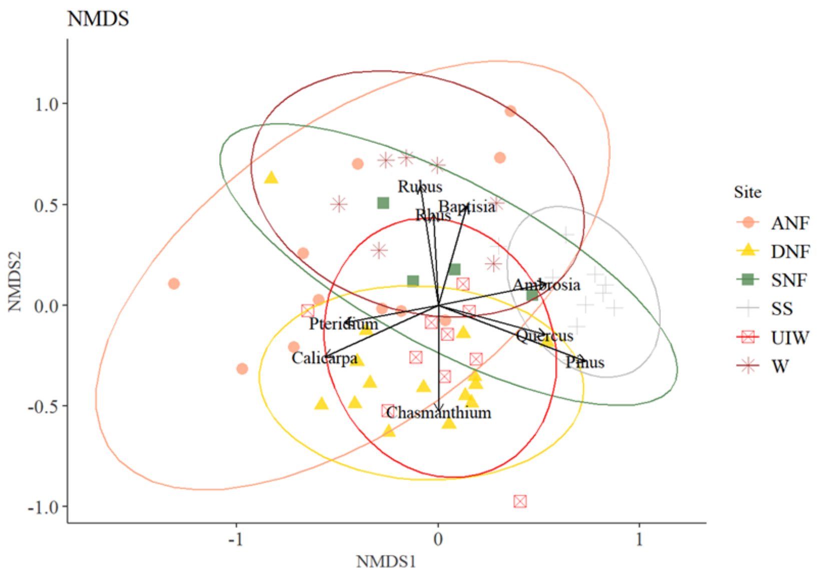

Figure 5: Non-metric multidimensional scaling constructed using sites as groups overlaid with significant species scores ($p \leq 0.001$).

DISCUSSION

High fire frequency sites had lower litter depths, basal areas and canopy cover, supporting previous research on the effects of prescribed fire frequencies on stand characteristics of pine stands [38]. The most common understory species were similar on both low and high fire frequency sites. However, high fire frequency groups contained nearly twice as many grass genera and over three times as many forb genera. Others have found similar effects of increased fire frequency on pine associated understory plant compositions [11,30,39,40].

Woody plant richness was not found to be different between the high and low frequency groups, most likely due to the repeated spouting of woody plants following dormant season fires [19,22]. Due to repeated top kill but not total removal of woody genera, quantifying species richness alone may not be effective to determine the effect of fire on woody plant understory communities [41].

Stand characteristics of cover types in east Texas vary on both spatial and temporal scales [42]. Loblolly pine had greater fuel loads and the second highest total basal area of the cover types. This relationship between basal area and fuel load has been previously reported [43]. Litter depths were greatest on loblolly, shortleaf and mixed pine hardwood types. The high continuity and flammability of longleaf pine litter provides a more homogeneous substrate for fires which reduces unburnt patches of understory and spatially less litter [44].

Total overstory basal areas were greatest on mixed pine hardwood cover types, followed by loblolly and shortleaf pines. The cause for this is multi-factorial; longleaf pine cover types were located on more well drained sites and included bluejack (*Quercus incana* Bartram) and blackjack (*Q. marilandica* Muenchh.) oaks and various hickories. Hardwoods on these sites are commonly smaller in diameter than hardwoods (sweetgum, southern red oak (*Q. falcata* michx.), etc.) found on more productive sites. The repeated effect of increased fire intensities appears to suppress shrubs and saplings, leading to lower recruitment and associated increases in basal area [21,43].

Hardwood basal areas were greater on mixed pine hardwood types than longleaf pine or loblolly pine, while similar to shortleaf pine. This similarity between shortleaf pine and mixed pine-hardwood stands may be due to the progression over time of shortleaf cover types into larger diameter stands with a hardwood component [16]. Softwood basal areas were greatest on the mixed pine hardwood cover type compared to all others, while longleaf pine types were lower than both loblolly and shortleaf pine. The lack of fire for decades on the Upland Island Wilderness have prevented fires from causing stem mortality and have contributed to the high basal areas [17]. Overall canopy cover was greatest on mixed pine hardwood sites, with longleaf pine cover types containing the lowest canopy cover. Fire and resulting gap formations play a role in the regeneration of longleaf pine, and the increased flammability of longleaf pine likely contributes to gap formation and the creation of savannah like plant communities [4,21].

There was no difference in grass richness between cover types, but forb richness was greatest on longleaf and loblolly types, possible driven by managers using growing season burns more frequently in these types [44]. Total and woody richness was not found to be different between cover types, and burning at intervals greater than 2 years may promote woody species establishment in pine understory communities [45].

Hardwood basal areas were not found to be different between the three National Forest sites, while Upland Island Wilderness had a greater hardwood basal area than Sandyland Sanctuary. Softwood and total basal areas were much greater on Upland Island Wilderness and much lower on Sandyland Sanctuary compared to the National Forest sites. Intensive management at Sandyland with the goal of lowering basal areas have previously been shown to benefit longleaf pine regeneration in uneven aged stands [46]. Upland Island Wilderness had been without intensive management for many years, so the introduction of growing season fires may help lower basal areas.

Canopy cover at Upland Island Wilderness were greater than Sandyland, Winston 8 and the Angelina and Davy Crockett National Forests, but not different than on the Sabine. These results are due to the different management strategies used to achieve management goals. The lower canopy cover allows increased light penetration and greater recruitment of longleaf pine seedlings, while the higher canopy cover observed at Upland Island Wilderness is a consequence of fire exclusion and has suppressive effects on forb production [4].

Fuel load, litter depth, basal area, and canopy cover contribute to changes in understory plant communities. Greater litter depths are associated with lower richness, likely because of the suppressive effect increased litter depths have on the establishment of new grasses and forbs in pine understories [47]. Litter depths decreased linearly in response to increased burning over a 20-year period, aligning with previous studies. Previous studies have also shown that increases in basal area and canopy cover led to lower species richness through increased competition for sunlight and space [31,48].

Increases in canopy cover were found to be correlated with lower forb richness, while differences in grass richness remained insignificant, possibly due to the establishment of understory grasses which thrive in shaded environments. The relationship between the number of burns in a 20-year period and the richness of forbs and grasses was found to be linear due to the direct and indirect effects of repeated fires on litter depth, basal area and canopy cover [38,48,49].

We found that the *Chasmanthium* species skewed strongly towards low fire frequency sites while high fire frequency sites had greater species diversity. There was a strong relationship between longleaf pine and multiple plant genera including *Schizachyrium*, while *Chasmanthium* aligned with both mixed pine-hardwood and shortleaf pine and Rubus skewed towards loblolly pine plots. Sites were not as dissimilar as expected, the exception being Sandyland Sanctuary, likely in part due to the geographic separation and unique management structure of Sandyland Sanctuary in comparison to the other sites. The *Chasmanthium* genera associated with Upland Island Wilderness and the Davy Crockett National Forest, while Sandyland Sanctuary had greater association with the Ambrosia, Carya, Quercus and Pinus genera: Winston 8, Angelina and Sabine National Forests were all associated with Rubus, Baptisia, and Rhus genera.

CONCLUSION

Overall, the plant diversity in East Texas increased through the implementation of high frequency prescribed fire, shifting stand characteristics regardless of cover type or site to favor the development of diverse understories. The fire dependent nature of these communities demands frequent fires to reduce the vigor and establishment of shade tolerant hardwood species and their stress on overstory pines as well as interception of light to the understory. The intentional reduction of fire frequency in these communities has been the greatest disturbance over the past 100 years. The re-establishment of historical fire frequencies alone may not be enough to shift these communities back to desired or historical compositions. However, the how land managers accomplish this and at what point satisfactory restoration is reached remains to be determined.

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AUTHOR CONTRIBUTION

All authors contributed towards project conceptualization and design, and have approved the final manuscript. WS wrote the initial draft and performed the majority of analysis. WS and BO were the primary authors of the manuscript, and KRK and JG provided substantial edits to the manuscript.

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CONFLICT OF INTEREST

The authors declare they have no conflict of interest.

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