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Understory Vegetation Responses to 15 Years of Repeated Fuel Reduction Treatments in the Southern Appalachian Mountains, USA

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Abstract: Decades of fire exclusion in the Southern Appalachian Mountains led to fuel accumulation and conversion from open oak-pine woodlands to closed-canopy mesic forests dominated by shade-tolerant hardwoods and shrubs that often do not support a diverse understory. Southern Appalachian forest managers and scientists recognize this and are implementing silvicultural treatments such as prescribed burning, mechanical treatments or a combination of these to restore forest structure. In this study, conducted at the Southern Appalachian Fire and Fire Surrogate Study site in Green River Game Land, North Carolina, we assessed the effects of four fuel reduction methods: burned 4x (B), mechanical treatment 2x (M), mechanical treatment 2x + burned 4x (MB), and control (C) on the changes in understory vegetation guilds from pretreatment to post-treatment years (2001–2016). The MB treatment was most effective at meeting the restoration objectives, as it resulted in increases in oak (Δ_{MB} = 23,400 stems/ha) and pine (Δ_{MB} = 900 stems/ha) stem density, importance value—calculated as the sum of relative cover and frequency—for graminoids (Δ_{MB} = 26.0), and density of oak stems >50 cm in height (Δ_{MB} = 7133 stems/ha). The B and M treatments were generally less effective, but nonetheless met a subset of the restoration objectives. The B treatment reduced ericaceous shrub cover (Δ_B = −1.2%) and increased oak stems 10–50 cm in height (Δ_B = 10,017 stems/ha), while the M treatment resulted in only modest increases of mesic hardwoods, specifically for yellow-poplar (Δ_M = 200 stems/ha) and blackgum (Δ_M = 200 stems/ha) as compared with other treatments, but significantly increased mountain laurel and rhododendron cover (Δ_M = 10.0%). Overall, these fire and fire surrogate treatments had some success in restoring understory structure, but our findings suggest a slow response in understory herbaceous vegetation.

Keywords: fire surrogates; oaks; eastern white pine; mesic hardwoods; ericaceous shrubs; graminoids; forbs

1. Introduction

A continuum of ecological communities, from savannahs to woodlands to closed canopy forests, historically existed across the southern Appalachian region, and this landscape heterogeneity was reinforced by frequent fire. In these communities, frequent fires helped create conditions that supported the regeneration of fire-maintained vegetation, including many early successional herbaceous species [1]. Over time, these species developed adaptations and physiological strategies that made them either less susceptible to fire-related mortality and/or dependent on fire for regeneration. Many species of perennial grasses and forbs, found in the Appalachians or in similar ecosystems, possess traits that suggest they benefit from—or depend upon—fire, like fire-stimulated flowering and seed production [2,3].

Frequent fire also magnifies a soil nitrogen limitation, and thus provides a competitive advantage for nitrogen-fixing plants in the understory [3].

Open woodland communities found in the southern Appalachian region were often characterized by open canopies of oak and pine, sparse hardwood, and shrub cover in the midstory, and a diverse herbaceous understory of fruiting shrubs, perennial graminoids, and forb species [4,5]. However, decades of fire exclusion have largely contributed to the loss of "open" communities, and a shift towards denser, more mesic forests [6,7]. This ecological shift, often called "mesophication", is the result of excess shade created by dense vegetation in areas that were previously open and dry, causing a cool, damp microclimatic effect in the understory [8]. These conditions support the encroachment of fire-sensitive vegetation, like eastern white pine (*Pinus strobus* L.), red maple (*Acer rubrum* L.), yellow-poplar (*Liriodendron tulipifera* L.), American beech (*Fagus grandifolia* Ehrh.), black birch (*Betula lenta* L.), blackgum (*Nyssa sylvatica* Marshall), and black cherry (*Prunus serotina* Ehrh.) [8,9]. Additionally, there has been an increase in the abundance and cover of ericaceous shrubs, like mountain laurel (*Kalmia latifolia* L.) and rhododendron (*Rhododendron* spp. L.) [10]. Additional factors contributed to these shifts in forest structure and composition, including legacy effects of late 19th and early 20th century logging practices, and the loss of American chestnut due to chestnut blight [7,11]. Collectively, these changes have resulted in increased overstory basal area, increased fuel loading, and landscape-level forest homogenization [12]. This has negatively affected the regeneration of species in the understory that are of management concern, namely oaks, yellow pines, graminoids, forbs, and fruiting shrubs [8,13]. These vegetation guilds, or groups of species, influence the future successional patterns that would result in an open woodland forest structure desired by forest managers, and thus are useful benchmarks for management and restoration monitoring.

Prescribed fire programs have expanded across the region in recent years as the ecological role of fire in the southern Appalachians has become better understood [14–16]. However, because of the region's extreme topography, variable patterns in precipitation, and rapidly expanding wildland-urban interface (WUI), it has proven to be one of the most difficult landscapes to manage with prescribed fire [17,18]. Dormant season prescribed burning (January–March) has been the most common method of prescribed fire management in the southern Appalachians since fire was reintroduced to the landscape in the late 1980s [19,20]. This is predominantly because ideal burning conditions (wind, relative humidity, fuel moisture, etc.) exist in predictable cycles during the dormant season, thus making planning easier and prescribed burning safer for managers [20]. Single dormant season burns, however, are often only marginally effective at reducing competition from mesic hardwoods in the understory and midstory [6,21]. This is because the majority of a plant's carbohydrates are stored in the roots during the dormant season, which can result in prolific resprouting in many hardwoods post-fire [16]. However, many studies have reported that oaks and other hardwoods were better maintained with repeated burns or with treatments that simulate burning, like mechanical treatments, that are often called fire surrogates [22]. Additionally, fire surrogate treatments like mechanical fuel reduction may also be necessary to meet management objectives in the WUI where prescribed burning is often difficult [13].

Studies, both in the US and internationally, report varied responses to short- long-term burning and surrogate treatments, suggesting the need for additional research. Single burning treatments are likely not sufficient to alter vegetation communities [23], however, there is some evidence that burning, combined with mechanical disturbance, can allow some focal management species to establish [24]. Repeated burning has resulted in increases in graminoid and forb cover in many places [3,25,26]. Questions still remain regarding the effectiveness of surrogates as alternatives to fire for decreasing fuels and stimulating the regeneration of focal tree species, and the effects of long-term repeated fire and fire surrogate treatments on forest composition, including herbaceous understory vegetation [6,13]. To address these knowledge gaps, the Fire and Fire Surrogate Study (FFSS) was initiated in the early 2000s [27,28]. FFSS sites address the effects of prescribed fire and alternative fuel reduction treatments, across a range of different community types, from Florida to Washington [27]. Each site involves the measurement of environmental factors, including vegetation dynamics, fuel loading and fire behavior, soils, wildlife, entomology, pathology, and economics, to quantify the ecological tradeoffs of each treatment.

A large body of literature has been produced from the southern Appalachian site, however, there are few published reports that focused on understory vegetation, more specifically long-term tree, shrub, and herbaceous species responses [13,29]. Thus, the purpose of this study is to further investigate the effects of 15 years of repeated burning (B), mechanical (M), and mechanical and burning (MB) treatments on understory vegetation guilds and/or species of management interest in the southern Appalachian Mountains. These results inform our understanding of the broad-scale implementation and efficacy of these treatments over longer periods of time, improving both FFSS-wide projects and general forest management within the Appalachian region.

Research Objectives

With the addition of one burn in 2015, and by further breaking down the understory vegetation into management-specific guilds and/or species, the purpose of this study is to determine overall changes in understory vegetation as a response to repeated B, M, MB, and C treatments from the pretreatment year (2001) to the most recent post-treatment year (2016). We used primary vegetation guilds (i.e., pines, oaks, mesic hardwoods, shrubs, graminoids, and forbs) to assess the main trends of change in the understory for all fuel reduction treatments from 2001 to 2016. We then assessed secondary guilds and/or species within each primary guild to identify the dominant vegetation responsible for driving those trends. The secondary guilds and/or species were chosen based on the managerial concerns and priorities of this region which include: red oaks, white oaks, eastern white pine, yellow pines, red maple, black birch, American beech, yellow-poplar, blackgum, black cherry, mountain laurel and *Rhododendron* spp., as well as other ericaceous shrubs, non-ericaceous shrubs, annual grasses, perennial grasses, sedges, nitrogen-fixing forbs, non-nitrogen-fixing forbs, and ferns. These secondary guilds or species were used to further explain significant ecological changes that may not have been fully explored by the trends observed from the primary vegetation guilds, or in previous studies. Few non-native species were present in the study units, and therefore they were not isolated or analyzed as a separate guild.

Our hypotheses for these objectives were that treatments will significantly affect: (1) oaks, driven primarily by increases of both white oaks and red oaks in the B and MB treatments; (2) pines, driven primarily by yellow pine increases and eastern white pine decreases in the B and MB treatments; (3) mesic hardwoods, driven primarily by decreases in red maple, black birch, American beech, yellow-poplar, blackgum, and black cherry in the B, MB, and M treatments; (4) shrubs, primarily driven by decreases in mountain laurel and *Rhododendron* spp. in the B and M treatments; (5) graminoids, primarily driven by increases in perennial grasses in the B and MB treatments; and (6) forbs, primarily driven by increases in nitrogen-fixing forbs in the B and MB treatments.

2. Materials and Methods

2.1. Location

The study area is located in Polk County, North Carolina on the Green River Game Land, which is managed for wildlife, public recreation, timber, and other resources by the North Carolina Wildlife Resources Commission (Figure 1). The game land covers 5841 hectares and is classified as a mountainous region, where elevations range from about 300 m to 800 m. When the FFSS was initiated in 2001, forests were estimated to be 80 to 120 years old with no evidence of land use during those years. However, it is understood that indigenous populations likely inhabited and utilized this land prior to European settlement. Overstory forest composition in the game land consisted of various oak (*Quercus* spp.), pine (*Pinus* spp.), ericaceous shrub, mesic hardwood, and herbaceous species that changed along the elevation gradient. Shortleaf pine (*Pinus echinata* Mill.), pitch pine (*P. rigida* Mill.)

and Virginia pine (*P. virginiana* Mill.) were found on xeric ridge tops while eastern white pine was found in moist coves. Ericaceous shrubs, like mountain laurel and rhododendron, made up a dense midstory layer throughout the study area [13]. Most of the soils are of the Evard series (fine-loamy, oxidic, mesic, Typic Hapludults) in areas that can be described as moderately deep, well-drained, mountain uplands [30].

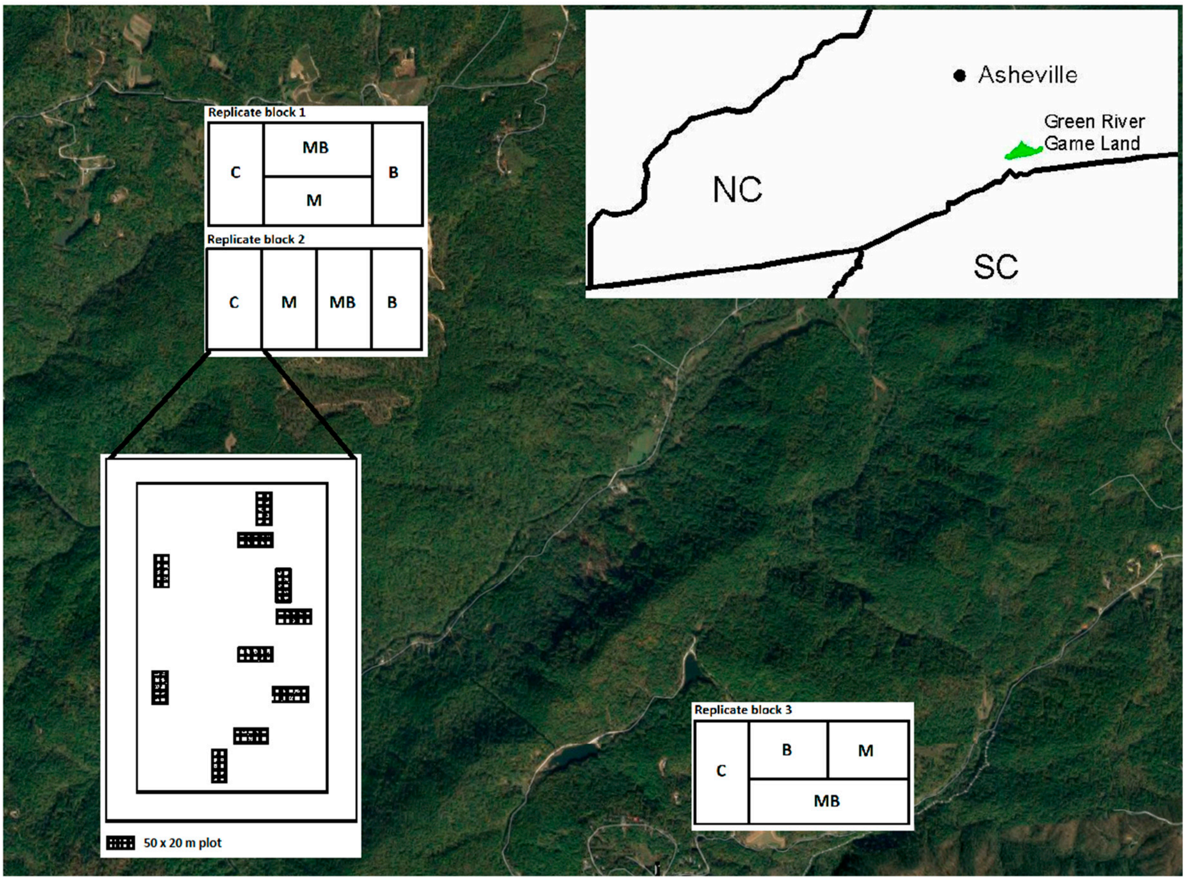

Figure 1. The treatment layout at Green River Game Land was a randomized complete block design: with 3 treatment areas, 4 treatments in each area (control = C, burned = B, mechanical removal of stems <10 cm in diameter at breast height (DBH)= M, and mechanical removal of stems <10 cm DBH + burned = MB), 10 plot origins in each area, 10 subplots in each origin, and two 1 m^2 vegetation plots per subplot. The inset is a diagram that reflects the general layout of a treatment unit, and is not to scale.

2.2. Study Design

This FFSS site is one of the few that remain active, having been treated with a total of 4 dormant-season prescribed burns and 2 mechanical treatments through 2016 [31]. Our study is based on vegetation changes following the four management treatments: dormant season prescribed burning in February or March, using either aerial ignition (spot fire) or strip head fire techniques (B) (4 total: 2003, 2006, 2012, and 2015); mechanical felling all woody stems >1.8 m tall and <10 cm in diameter, and all shrubs of any height in December–February (M) (2 total: 2001–2002, and 2012); a combination of dormant season burning and mechanical treatment (MB) (4 B: 2003, 2006, 2012, and 2015; 2 M: 2001–2002, and 2012); and no treatment to compare the results of each treatment (C) (Table 1). The study used a randomized complete block design, with all treatments replicated within 3 experimental units, totaling 12 treatment units. The treatment units cover an area of 10–12 hectares each and are surrounded by a 4-ha buffer zone, with both the treatment units and the buffer zones receiving the same treatment. Each treatment unit incorporated many combinations of elevation, aspect, and slope in the landscape, however, because landscape conditions were highly variable, these data were not separated during the analysis.

Table 1. Treatment frequency and timing for the Southern Appalachian Fire and Fire Surrogate Study site in Green River Game Land, Polk County, North Carolina. A control treatment (C), which was undisturbed during the study period, was also included.

Treatment	Number of Applications	Months	Years of Applications
Prescribed burn (B)	4	February–March	2003, 2006, 2012, 2015
Mechanical fuel reduction (M)	2	November–March	2001–2002, 2011–2012
Prescribed burn and mechanical fuel reduction (MB)	4 (B), 2 (M)	November–March	2001–2002 (M), 2003 (B), 2006 (B), 2011–2012 (M), 2012 (B), and 2015 (B)

The data used in this study were sampled in the growing season prior to any treatment application (2001), and in the second growing season following the last treatment application (2016). In 2001, 10 sampling plots (0.1 ha) were established randomly within a 50 × 50 m grid; and vegetation sampling data were collected within modified Whittaker plots divided into 10 subplots, each 10 m^2. Within each subplot, two 1 m^2 quadrats were established in the northwest and southeast corners to measure all woody and non-woody vegetation <1.4 m tall. Sampling methods and plot design for this study were established based on the FFSS protocol [32,33]. To reduce bias within the dataset, each woody stem was considered an individual count regardless of plant origin (sprout, germinant, etc.). The workable cover class data for all analyses were calculated into percentage values that represent the median of each cover class. For example, 5.5% was used for the cover class 2, etc. (Table 2).

Table 2. Data collected and used in the analyses for all recorded understory vegetation-stem density and absolute cover were used for woody species, and absolute cover was used for non-woody species. Woody stem counts were recorded into three height classes, <10 cm, 10–50 cm, and >50 cm, to quantify recruitment potential; and cover classes were recorded as follows according to the Fire and Fire Surrogate Study (FFSS) sampling protocol: 1 (<1%), 2 (1%–10%), 3 (>10%–25%), 4 (>25%–50%), 5 (>50%–75%), and 6 (>75%) [32,33].

Vegetation Type	Vegetation Guild	Variable	Data collected	Measurement	Units
Woody	Oaks	Stem density	Individual count	1 count per stem	Avg stems/ha
	Pines	Stem height	Category	<10, 10 – 50, or >50 cm	Avg stems/ha
	Mesic Hardwoods	Absolute cover	Cover class[1]	1, 2, 3, 4, 5, 6	Avg %
Non-woody	Shrubs Graminoids Forbs	Absolute cover	Cover class[1]	1, 2, 3, 4, 5, 6	Avg %

[1] Cover Classes recorded as: 1 (<1%), 2 (1%–10%), 3 (>10%–25%), 4 (>25%–50%), 5 (>50%–75%), and 6 (>75%).

We acknowledge that the asynchronous nature of the experimental treatments potentially confounded our results, because the time since last treatment varied (2 growing seasons for B treatment, 4 for M). This, however, was an unavoidable reality of applying landscape-level treatments, since it would have been logistically and financially challenging to conduct 2 or more mechanical treatments during the study period.

2.3. Analysis

All analyses were conducted on delta (Δ) values, which were calculated by taking the difference of abundance data measures (2016–2001) within each 10 m^2 plot in each treatment unit. For the initial analyses, each recorded species was grouped into one of six primary vegetation guilds (pines, oaks, mesic hardwoods, shrubs, graminoids, or forbs) to assess the main understory vegetation responses to repeated treatments (C, B, M, and MB) over time. Importance values (IV) were calculated for primary guilds, based on the data available for woody and non-woody species, by the sum of abundance measurements (woody species: density, cover, and frequency; non-woody species: cover and frequency) divided by the number of abundance measurements used (3 woody species and 2 non-woody species). These values were calculated as (relative density of woody stems + relative cover % + relative frequency %) ÷ 3 and (relative cover % of non-woody species + relative frequency %) ÷ 2. Analysis of variance (ANOVA) was conducted to determine the change in overall stem density, absolute cover %, IV, and stem density of each height class for tree species (oaks, pines, and mesic hardwoods), as well as ANOVA was performed on absolute cover % and IV for shrubs, graminoids, and forbs.

For the secondary analyses, we separated all species into one of 13 secondary vegetation guilds: yellow pines, eastern white pine, red oaks, white oaks, mountain laurel and rhododendron, other ericaceous shrubs, non-ericaceous shrubs, annual grasses, perennial grasses, sedges, nitrogen-fixing forbs, non-nitrogen-fixing forbs, and ferns. Additional ANOVAs were conducted on data from each of these secondary vegetation guilds to identify specific groups of influential species driving the major understory changes from 2001 to 2016. These secondary vegetation guilds were identified based on the regional management objectives, with particular interest in species that were of managerial concern like mountain laurel and *Rhododendron* spp., mesic hardwood species (red maple, black birch, American beech, yellow-poplar, blackgum, and black cherry), and eastern white pine (species defined as in Nowacki and Abrams [8]).

A cube root transformation was applied to all data used in the ANOVAs to meet assumptions of normality. All models consisted of the Δ abundance measurement as the response variable, treatment as the fixed variable, and replicate block as the random variable. We calculated degrees of freedom for each ANOVA using the Satterthwaite approximation and least squared means (LSM) comparisons from each model. When LSM comparisons indicated a significant treatment effect at α <0.05, we used Tukey's Honestly Significant Difference (THSD) for post-hoc pairwise treatment comparisons. We conducted all analyses using the lmerTest package in the program *R* [30,34].

3. Results

Results will be presented below based on the six primary guilds of interest: oaks, pines, mesic hardwoods, shrubs, graminoids, and forbs.

3.1. Oaks

The MB and B treatments significantly increased the total stem density, absolute cover %, density of stems 10–50 cm in height, and density of stems >50 cm in height of the primary oak guild ($F_{3114} = 7.3$, $p < 0.01$). Oaks observed in this guild included: scarlet oak (*Q. coccinea* Münchh.), white oak (*Q. alba* L.), post oak (*Q. stellata* Wangenh.), Northern red oak (*Q. rubra* L.), Southern red oak (*Q. falcata* Michx.), and water oak (*Q. nigra* L.). The total density of oak stems increased significantly following the MB (Δ = 23,400 ± SD 13,185 stems/ha) and B (Δ = 21,700 ± 14,694 stems/ha) treatments, and these increases were significantly different from those observed in C plots and after M treatments (Figure 2a, Table 3). Absolute cover % of oaks significantly increased after MB (Δ = 6.7% ± 5.2%) treatments which was statistically different from significant increases observed in the B (Δ = 3.3% ± 5.2%) treatments ($p < 0.01$, Figure 2b). The change in importance values of oaks was not significant from 2001 to 2016 relative to other vegetation guilds (Figure 2c). Changes in the density of oak stems <10 cm were not significant following treatments, oak stems 10–50 cm significantly increased after B (Δ = 10,017 ± 10,870 stems/ha) and MB (Δ = 7933 ± 10,903 stems/ha) treatments ($p < 0.01$), and stems >50 cm significantly increased after MB (Δ = 7133 ± 8271 stems/ha) treatments ($p < 0.01$, Figure 3).

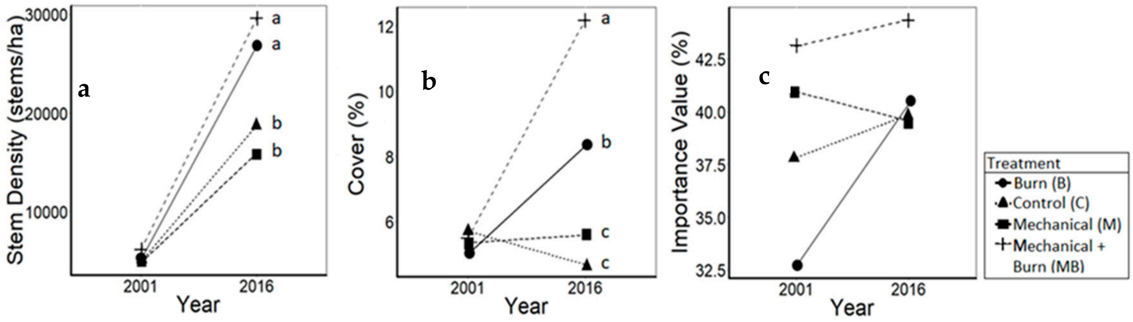

Figure 2. Oak (**a**) stem density (stems/ha), (**b**) absolute cover (%), and (**c**) importance value results showing the 4 treatment effects (control = C, burned = B, mechanical removal of stems <10 cm DBH = M, and mechanical removal of stems <10 cm DBH + burned = MB) from 3 analysis of variance (ANOVA). Post-hoc comparison (Tukey's Honest Significant Difference Test. THSD) letters show differences between treatment effects from 2001 to 2016.

Table 3. Change in abundancy for the secondary vegetation guilds after 15 years (2001–2016) of repeated treatments (control = C, burned = B, mechanical removal of stems <10 cm in diameter at breast height (DBH) = M, and mechanical removal of stems <10 cm DBH + burned = MB). Means, standard deviations, and *p*-values for each ANOVA are indicated in parentheses next to each guild. Lowercase letters identify the statistically different treatment effect at $p < 0.05$.

Secondary Vegetation Guild or Species	Treatment	Stems/ha in 2001	Stems/ha in 2016	Change in Stems (avg/ha)	
White oaks ($F_{3114} = 2.8$, $p = 0.04$)	C	2500.0	14,550.0	12,050.0 (± 16,518.0)	ab
	B	1633.3	14,983.3	13,350.0 (± 11,827.9)	b
	M	1750.0	8333.3	6583.3 (± 8381.1)	a
	MB	2466.7	15,083.3	12,616.7 (± 12,792.6)	ab
Red oaks ($F_{3,116} = 12.5$, $p < 0.01$)	C	2400.0	4183.3	1835.0 (± 2100.0)	a
	B	3466.7	11,816.7	8359.0 (± 7050.0)	bc
	M	3033.3	7600.0	4565.0 (± 3450.0)	b
	MB	3783.3	14,566.7	10,785.0 (± 6450.0)	c
Yellow pines ($F_{3114} = 10.3$, $p < 0.01$)	C	0.0	16.7	16.7 (± 91.3)	a
	B	50.0	766.7	716.7 (± 1243.5)	b
	M	16.7	66.7	50.0 (± 201.3)	a
	MB	0.0	900.0	900.0 (± 2127.0)	b
Eastern white pines ($F_{3116} = 2.0$, $p = 0.12$)	C	0.0	33.3	33.3 (± 126.9)	
	B	116.7	50.0	−66.7 (± 340.7)	
	M	66.7	150.0	83.3 (± 437.1)	
	MB	50.0	0.0	−50.0 (± 152.6)	
Red maple (*Acer rubrum*) ($F_{3114} = 18.1$, $p < 0.01$)	C	9866.7	10,016.7	150.0 (± 8273.5)	a
	B	13,766.7	34,416.7	20,650.0 (± 25,490.4)	c
	M	4550.0	10,850.0	6300.0 (± 9201.4)	b
	MB	8616.7	9633.3	1016.7 (± 7082.6)	a
Yellow-poplar (*Liriodendron tulipifera*) ($F_{3114} = 9.5$, $p < 0.01$)	C	650.0	583.3	−83.3 (± 558.4)	a
	B	1050.0	5033.3	1566.7 (± 2718.8)	b
	M	333.3	433.3	200.0 (± 783.5)	a
	MB	400.0	2550.0	2100.0 (± 3521.9)	b
Blackgum (*Nyssa sylvatica*) ($F_{3116} = 10.0$, $p < 0.01$)	C	233.3	750.0	448.5 (± 720.2)	a
	B	1183.3	4666.7	1472.1 (± 1984.8)	a
	M	466.7	750.0	288.8 (± 805.2)	a
	MB	350.0	3633.3	3505.5 (± 3531.8)	b
Black birch (*Betula lenta*) ($F_{3116} = 0.5$, $p = 0.66$)	C	0.0	33.3	33.3 (± 126.9)	
	B	0.0	150.0	133.3 (± 730.3)	
	M	0.0	0.0	0.0 (± 0.0)	
	MB	0.0	16.7	16.7 (± 91.3)	

Table 3. *Cont.*

Secondary Vegetation Guild or Species	Treatment	Stems/ha in 2001	Stems/ha in 2016	Change in Stems (avg/ha)	
American beech (*Fagus grandifolia*) ($F_{3114.9} = 1.0$, $p = 0.40$)	C	0.0	0.0	0.0 (± 0.0)	
	B	16.7	50.0	0.0 (± 0.0)	
	M	16.7	16.7	0.0 (± 0.0)	
	MB	0.0	33.3	33.3 (± 182.6)	
Black cherry (*Prunus serotina*) ($F_{3116} = 1.1$, $p = 0.34$)	C	266.7	250.0	−17.2 (± 608.6)	
	B	433.3	850.0	230.3 (± 817.2)	
	M	200.0	83.3	−86.4 (± 373.3)	
	MB	166.7	266.7	63.6 (± 468.6)	
Secondary Vegetation Guild or Species	**Treatment**	**Absolute Cover (%)**	**Absolute Cover %**	**Change in Absolute Cover (avg %)**	
Mountain laurel (*Kalmia latifolia*) & *Rhododendron* spp. ($F_{3114} = 7.3$, $p < 0.01$)	C	16.0	18.3	2.3 (± 12.0)	a
	B	15.0	11.8	−3.1 (± 9.7)	a
	M	15.8	25.8	10.0 (± 12.5)	b
	MB	15.0	15.4	0.4 (± 12.0)	a
Other ericaceous shrubs ($F_{3114} = 1.6$, $p = 0.19$)	C	11.9	8.6	−3.3 (± 7.9)	
	B	10.1	10.1	0.0 (± 7.1)	
	M	11.7	12.3	0.6 (± 6.4)	
	MB	14.1	15.1	1.0 (± 8.5)	
Non-ericaceous shrubs ($F_{3114} = 3.1$, $p = 0.03$)	C	5.6	4.4	−1.2 (± 8.2)	a
	B	5.9	9.1	3.2 (± 8.3)	ab
	M	2.8	6.2	3.4 (± 12.8)	ab
	MB	7.6	13.0	5.4 (± 12.1)	b
Annual grasses ($F_{3114} = 0.5$, $p = 0.69$)	C	0.0	0.0	0.0 (± 0.1)	
	B	0.0	0.0	0.0 (± 0.0)	
	M	0.0	0.6	0.6 (± 3.3)	
	MB	0.0	0.2	0.2 (± 1.0)	
Perennial grasses ($F_{3114} = 31.6$, $p < 0.01$)	C	1.7	3.2	1.5 (± 7.4)	a
	B	0.7	2.4	1.7 (± 2.5)	b
	M	0.7	0.7	0.0 (± 1.9)	a
	MB	0.9	3.6	2.7 (± 2.7)	c
Sedges ($F_{3116} = 15.4$, $p < 0.01$)	C	0.4	0.2	−0.2 (± 1.0)	a
	B	0.6	1.9	1.3 (± 2.5)	b
	M	0.7	1.0	0.3 (± 1.7)	a
	MB	0.5	3.0	2.5 (± 3.8)	b
Nitrogen-fixing forbs ($F_{3114} = 6.0$, $p < 0.01$)	C	0.8	1.0	0.1 (± 2.5)	a
	B	0.0	0.7	0.7 (± 1.7)	a
	M	0.0	1.4	1.4 (± 3.6)	a
	MB	0.0	1.5	1.5 (± 2.4)	b
Non-nitrogen-fixing forbs ($F_{3116} = 9.1$, $p < 0.01$)	C	3.9	3.4	−0.6 (± 2.8)	a
	B	3.1	4.3	1.2 (± 3.1)	bc
	M	3.6	3.7	0.2 (± 3.7)	ab
	MB	4.3	5.7	1.3 (± 4.2)	c
Ferns ($F_{3114} = 1.9$, $p = 0.12$)	C	4.0	0.8	−3.2 (± 8.7)	
	B	1.6	1.7	0.1 (± 4.1)	
	M	1.0	1.7	0.5 (± 3.2)	
	MB	2.2	3.4	1.4 (± 6.7)	

Stem density of red and white oaks within the secondary oak guild was significantly increased by MB and B treatments, with more increases in white oak density then red oak following those treatments in 2016. Significant increases in white oak stem density following B (Δ = 13,350 ± 11,828 stems/ha) were statistically different from those observed after M (Δ = 6583 ± 8381 stems/ha) treatments. However, increases in MB treatments and in C plots were statistically similar to both B and M treatments

($p = 0.04$, Table 3). Significant increases of red oak stem density in MB (Δ = 10,783 ± 6423 stems/ha) were statistically similar to those after B (Δ = 8350 ± 7023 stems/ha), and different from the increases observed after M (Δ = 4567 ± 4567 stems/ha) treatments; but these increases were statistically different from those in C plots ($p < 0.01$, Table 3).

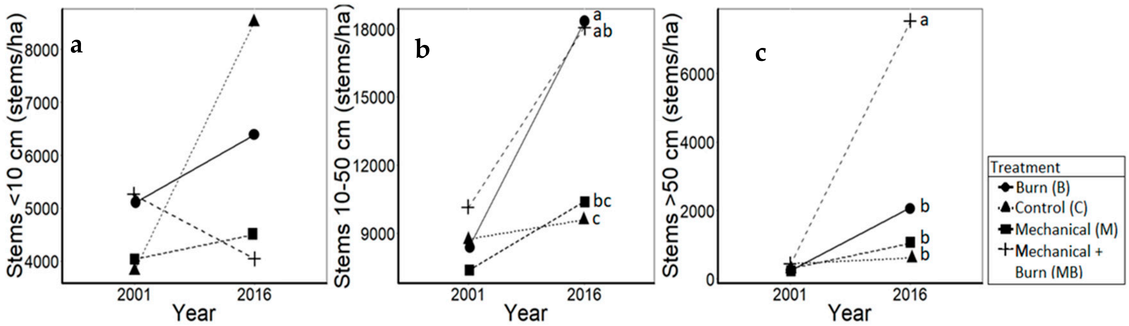

Figure 3. Oak stems (**a**) <10 cm, (**b**) 10–50 cm, and (**c**) >50 cm results showing the 4 treatment effects (control = C, burned = B, mechanical removal of stems <10 cm DBH = M, and mechanical removal of stems <10 cm DBH + burned = MB) from 3 analysis of variance (ANOVA). Post-hoc comparison (Tukey's Honest Significant Difference Test, THSD) letters show differences between treatment effects from 2001 to 2016.

3.2. *Pines*

While both the MB and B treatments significantly increased total stem density and density of stems <10 cm in height of the primary pine guild, most increases observed after MB were statistically similar to M treatments and C plots ($F_{3114} = 4.5$, $p < 0.01$). The significant increases of total stem density following MB (Δ = 850 ± 2146 stems/ha) were similar to those after B (Δ = 650 ± 1153 stems/ha) and M (Δ = 134 ± 472 stems/ha) treatments, and C (Δ = 54 ± 153 stems/ha) plots, but increases after B were statistically different from M and C (Figure 4a, Table 3). Absolute cover of pines decreased after all treatments except MB (Δ = 1.1% ± 3.9%), but these changes were only significantly different from B (Δ = −1.2% ± 2.2%) treatments ($p = 0.05$, Figure 4b). The change in importance values of pines was not significant from 2001 to 2016 relative to other vegetation guilds (Figure 4c). Density of pine stems <10 cm in height significantly increased following B (Δ = 567 ± 1081 stems/ha) treatments ($p < 0.01$), stems 10–50 cm only significantly increased following MB (Δ = 500 ± 1752 stems/ha) treatments ($p = 0.02$), and changes observed in stems >50 cm were not significant (Figure 5).

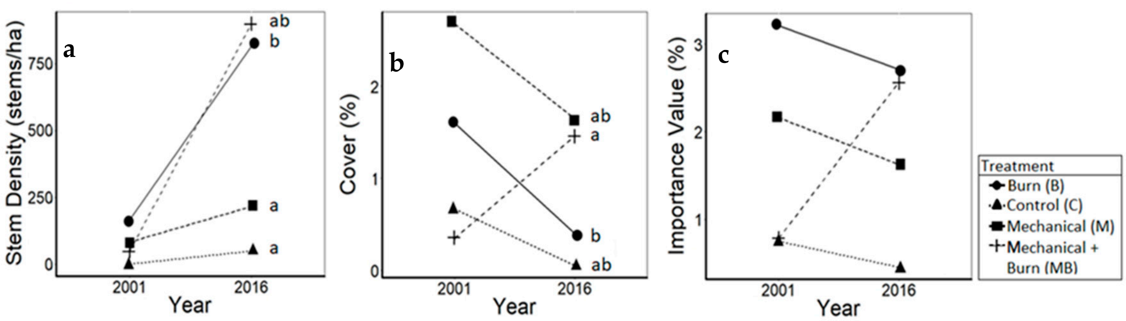

Figure 4. Pine primary guild (**a**) stem density (stems/ha), (**b**) absolute cover (%), and (**c**) importance value results showing the 4 treatment effects (control = C, burned = B, mechanical removal of stems <10 cm in diameter at breast height (DBH) = M, and mechanical removal of stems <10 cm DBH + burned = MB) from 3 analysis of variance (ANOVA). Post-hoc comparison (Tukey's Honest Significant Difference Test, THSD) letters show differences between treatment effects from 2001 to 2016.

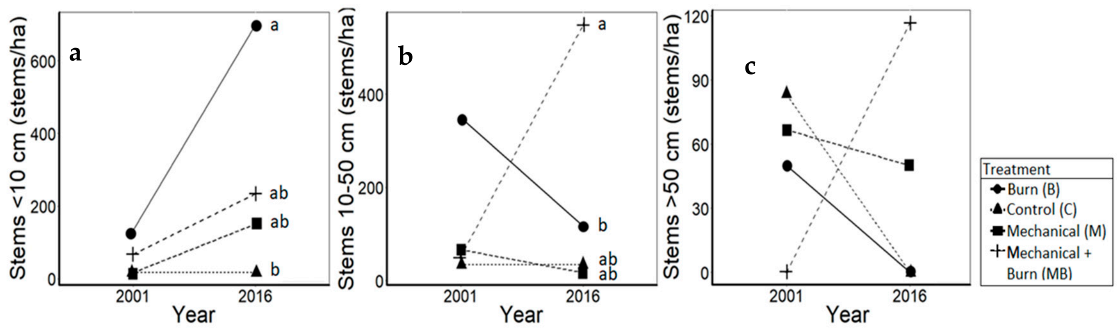

Figure 5. Pine primary guild stem density results for stems (**a**) <10 cm, (**b**) 10–50 cm, and (**c**) >50 cm in height showing the 4 treatment effects (control = C, burned = B, mechanical removal of stems <10 cm in diameter at breast height (DBH) = M, and mechanical removal of stems <10 cm DBH + burned = MB) from 3 analysis of variance (ANOVA). Post-hoc comparison (Tukey's Honest Significant Difference Test; THSD) letters show differences between treatment effects from 2001 to 2016.

Stem density within the secondary pine guild was impacted predominantly by MB and B treatments, with significant increases of yellow pine and non-significant decreases of eastern white pine in both treatments. Density of the yellow pine species, identified as pitch pine, loblolly pine, and Virginia pine) increased significantly following MB (Δ = 900 ± 2127 stems/ha) and B (Δ = 717 ± 1244 stems/ha) treatments, and were statistically different from the increases in M (Δ = 50.0 ± 201.3 stems/ha) treatments and C (Δ = 16.7 ± 91.3 stems/ha) plots ($p < 0.01$, Table 3).Though decreases were observed for eastern white pine, the changes in stem density were not significant (Table 3).

3.3. Mesic Hardwoods

The trends observed in the primary mesic hardwood guild were variable, with significant increases in abundance measures following all treatments except the C plots, the most substantial increases following B, and many statistically similar responses shared by B, M, and MB ($F_{3114} = 16.7$, $p < 0.01$). Total stem density of mesic hardwoods significantly increased following B (Δ = 24,067 ± 26,447 stems/ha) treatments, but these were statistically different from increases observed after M (Δ = 6717 ± 9974 stems/ha) and MB (Δ = 6700 ± 8923 stems/ha) treatments (Figure 6a, Table 3). Significant increases in absolute cover following MB (Δ = 6.0% ± 4.5%), B (Δ = 3.5% ± 3.8%), and M (Δ = 2.8% ± 2.6%) treatments were all statistically similar ($p < 0.01$, Figure 6b). The change in importance values for mesic hardwoods was significant relative to other vegetation guilds following M (Δ = 7.6 ± 11.0) treatments, but those were only statistically different from C ($p < 0.01$, Figure 6c). Density of stems <10 cm in height significantly increased after B (Δ = 18,383 ± 27,964 stems/ha) treatments alone ($p < 0.01$). Significant increases of stems 10–50 cm observed after MB (Δ = 3283 ± 2772 stems/ha), B (Δ = 2733 ± 3503 stems/ha), and M (Δ = 2200 ± 3305 stems/ha) treatments were statistically similar ($p < 0.01$). Significant increases of stems >50 cm were observed after MB (Δ = 5350 ± 3831 stems/ha), which was statistically different from those following B (Δ = 2950 ± 3304 stems/ha) and M (Δ = 1233 ± 1394 stems/ha) treatments ($p < 0.01$, Figure 7).

Stem density increases within the secondary mesic hardwood guild were only significant for red maple after B and M treatments, yellow-poplar after MB and B treatments, and blackgum after MB treatments. The treatments did not have a significant effect on black birch, American beech, and black cherry response from 2001 to 2016. Red maple density significantly increased after B (Δ = 38,983 ± 25,490 stems/ha) and M (Δ = 5600 ± 901 stems/ha) treatments, but these increases were statistically different from each other, MB treatments and C plots ($p < 0.01$, Table 3). Yellow-poplar stem density significantly increased after MB (Δ = 2100 ± 3522 stems/ha) and B (Δ = 1567 ± 2719 stems/ha) treatments, and they were statistically different from responses following M treatments and C plots ($p < 0.01$, Table 3). Blackgum stem density significantly increased following

MB (Δ = 3517 ± 3532 stems/ha) treatments, and these were statistically different from B, C, and M ($p < 0.01$, Table 3).

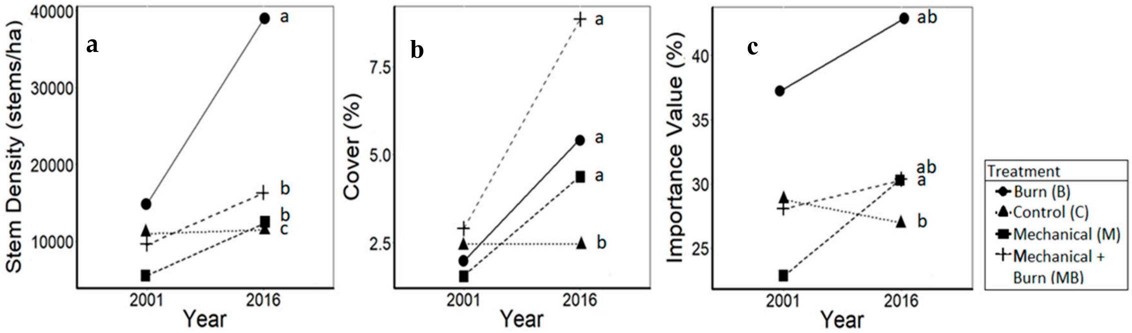

Figure 6. Mesic hardwood primary guild (**a**) stem density (stems/ha), (**b**) absolute cover (%), and (**c**) importance value results showing the 4 treatment effects (control = C, burned = B, mechanical removal of stems <10 cm in diameter at breast height (DBH) = M, and mechanical removal of stems <10 cm DBH + burned = MB) from 3 analysis of variance (ANOVA). Post-hoc comparison (Tukey's Honest Significant Difference Test, THSD) letters show differences between treatment effects from 2001 to 2016.

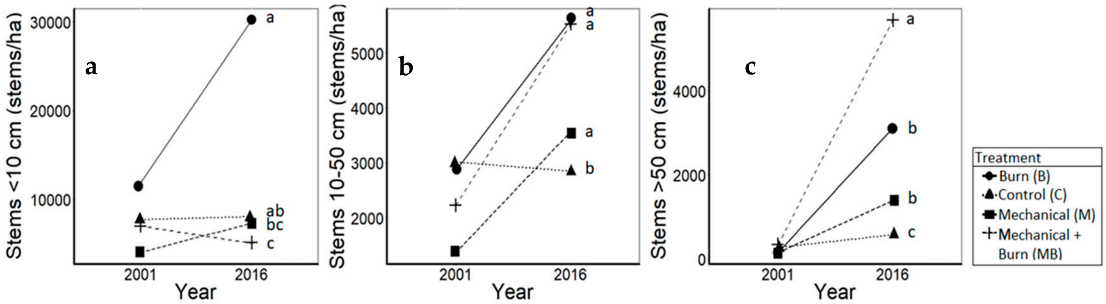

Figure 7. Mesic hardwood primary guild stem density results for stems (**a**) <10 cm, (**b**) 10–50 cm, and (**c**) >50 cm in height showing the 4 treatment effects (control = C, burned = B, mechanical removal of stems <10 cm in diameter at breast height (DBH) = M, and mechanical removal of stems <10 cm DBH + burned = MB) from 3 analysis of variance (ANOVA). Post-hoc comparison (Tukey's Honest Significant Difference Test, THSD) letters show differences between treatment effects from 2001 to 2016.

3.4. Shrubs

Overall, the M treatments significantly increased absolute cover and importance value of the primary shrub guild ($F_{3,114} = 3.8$, $p = 0.01$). Cover increased significantly following M (Δ = 4.5% ± 7.1%) treatments, and this was statistically different from the decreases observed after C, B, and MB ($p = 0.01$, Figure 8a, Table 3). The change of importance values for shrubs was significant following M (Δ = 4.7 ± 14.4) treatments relative to other vegetation guilds, which was only statistically different from MB treatments ($p < 0.01$, Figure 8b).

Within the secondary shrub guild, only M and MB produced significant changes in absolute cover of mountain laurel/*Rhododendron* spp. and non-ericaceous shrubs, while changes in absolute cover of other ericaceous shrubs were non-significant from 2001 to 2016. Absolute cover of mountain laurel/*Rhododendron* spp. significantly increased following M alone (Δ = 10.0% ± 12.5%), and were statistically different from C plots, and MB and B treatments ($p < 0.01$, Table 3). Absolute cover of non-ericaceous shrubs significantly increased following MB (Δ = 5.4% ± 1.6%) treatments and were statistically different from decreases observed in C (Δ = − 1.2% ± 1.5%) plots ($p = 0.03$, Table 3).

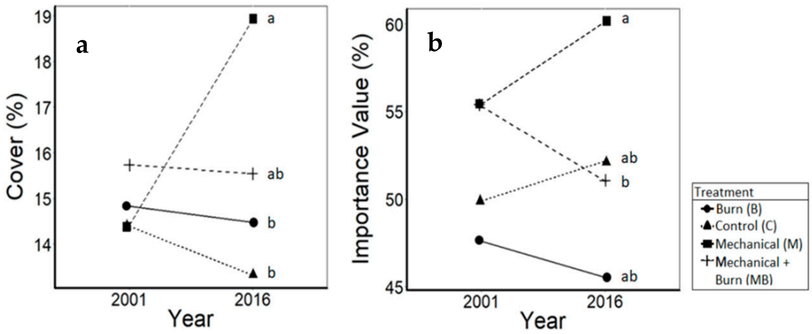

Figure 8. Shrub primary guild (**a**) absolute cover (%) and (**b**) importance value results showing the 4 treatment effects (control = C, burned = B, mechanical removal of stems <10 cm in diameter at breast height (DBH) = M, and mechanical removal of stems <10 cm DBH + burned = MB) from 3 analysis of variance (ANOVA). Post-hoc comparison (Tukey's Honest Significant Difference Test, THSD) letters show differences between treatment effects from 2001 to 2016.

3.5. Graminoids

The MB treatment resulted in significant increases of absolute cover and importance value of the primary graminoid guild ($F_{3,114} = 9.5$, $p < 0.01$). Significant increases of cover following MB ($\Delta = 2.8\% \pm 2.5\%$) treatments were statistically different from M ($\Delta = 0.0\% \pm 2.0\%$) treatments where there was no change from 2001 to 2016 ($p < 0.01$, Figure 9a, Table 3). The change in importance values was significant following MB ($\Delta = 26.0 \pm 14.7$) and B ($\Delta = 11.5 \pm 12.1$) treatments relative to other vegetation guilds, but these changes were statistically different from each other, M and C ($p < 0.01$, Figure 9b).

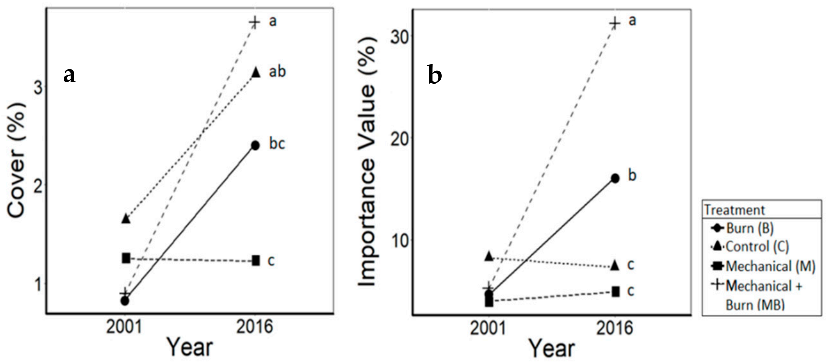

Figure 9. Graminoid primary guild (**a**) absolute cover (%) and (**b**) importance value results showing the 4 treatment effects (control = C, burned = B, mechanical removal of stems <10 cm in diameter at breast height (DBH) = M, and mechanical removal of stems <10 cm DBH + burned = MB) from 3 analysis of variance (ANOVA). Post-hoc comparison (Tukey's Honest Significant Difference Test, THSD) letters show differences between treatment effects from 2001 to 2016.

Within the secondary graminoid guild, only MB produced significant increases in absolute cover of perennial grasses and sedges, while changes in cover of annual grasses were not significant from 2001 to 2016. The significant increases in absolute cover of perennial grasses following MB ($\Delta = 2.7\% \pm 2.7\%$) were statistically different from M treatments where there was no change from 2001 to 2016($p < 0.01$, Table 3); and significant increases in absolute cover of sedges following MB ($\Delta = 2.5\% \pm 3.8\%$) differed statistically from the minimal declines observed in C plots ($p < 0.01$, Table 3).

3.6. Forbs

Overall, none of the treatments significantly affected the primary forb guild. There was little to no change following MB ($\Delta = 1.2\% \pm 4.2\%$), M ($\Delta = 0.1\% \pm 3.6\%$), and B ($\Delta = 0.0\% \pm 6.6\%$) treatments, or in C (Δ = −0.8% ± 3.7%) plots ($F_{3,116}$ = 1.9, Figure 10a; Table 3). Similarly, the change of importance values for forbs from 2001 to 2016 was not significant, and declined in all treatments relative to other vegetation guilds (Figure 10b).

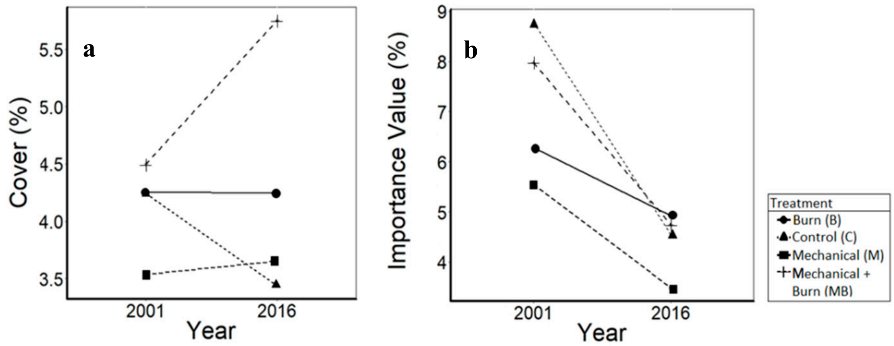

Figure 10. Forb primary guild (**a**) absolute cover (%) and (**b**) importance value results showing the 4 treatment effects (control = C, burned = B, mechanical removal of stems <10 cm in diameter at breast height (DBH) = M, and mechanical removal of stems <10 cm DBH + burned = MB) from 3 analysis of variance (ANOVA). Post-hoc comparison (Tukey's Honest Significant Difference Test, THSD) letters show differences between treatment effects from 2001 to 2016.

Within the secondary forb guild, only MB produced significant increases in absolute cover of nitrogen-fixing forbs, while changes in cover of non-nitrogen-fixing forbs and ferns were not significant from 2001 to 2016. The significant increases in absolute cover of nitrogen-fixing forbs following MB (Δ = 2.5% ± 2.4%) treatments was statistically different from B and M treatments, and in C plots ($p < 0.01$, Table 3).

4. Discussion

The desired management goals for the Southern Appalachian region include reducing mesic ericaceous shrub and hardwood cover to create more light availability for desired open woodland forest composition, which includes oaks and yellow pines with a lush herbaceous understory of fruiting ericaceous shrubs, graminoids, and forbs. To achieve this, we investigated the response of understory woody and non-woody vegetation after four repeated treatment applications from 2001–2016. By measuring stem density, absolute cover %, importance value, and density of three stem height classes for woody species, we were able to draw conclusions about the potential changes to future forest structure and competition in the understory. By measuring absolute cover % and importance value for non-woody vegetation, we were able to observe potential patterns and fluctuations in the herbaceous flora over time. We expected the treatment with the most reductions in basal area and litter cover (MB) to closest resemble an open woodland vegetative community. We also expected to see a more gradual open woodland community develop following prescribed burning treatments (B), which had been reintroduced to the landscape for restoration purposes. The repeated mechanical treatment was expected to potentially reduce the amount of larger ericaceous shrub and mesic hardwood stems, however, it produced more sprouting and cover as compared with the other treatments. A potential limitation to our study, as mentioned in previous sections, is that our analyses did not include time-since-treatment measurements, and therefore we were unable to report the variation between treatments over time. However, our findings after M treatments (last treated in 2012 versus 2015 for the other treatments) suggest that time since last treatment is relatively insignificant. For example, regardless of the length of time since the last treatment, none of the stem heights for woody species after 15 years of M were taller than those in the other treatments. Additionally, fire behavior is influenced by topography, and therefore varied across the study site [13]. However, the blocks and replicate units were set up to account for all prevailing topographical conditions, so topographical effects should not have influenced our results.

4.1. Oaks

Dramatic increases in overall understory oak stem density following MB and B treatments is consistent with other studies that found significant positive oak seedling response to prescribed burning and mechanical treatments [6,14,35]. This is likely the result of greater basal area reductions, which increased light availability to the forest floor, stimulating sprout and stem growth. Data presented in Waldrop et al. [13] confirms this by reporting significant declines in overstory basal area in MB ($\Delta = -0.9$ m^2 ha^{-1}) and B ($\Delta = -1.3$ m^2 ha^{-1}), versus increases observed in M ($\Delta = +3.0$ m^2 ha^{-1}) and C ($\Delta = +3.9$ m^2 ha^{-1}) treatments. Additionally, other multi-year studies have reported improved seedbed conditions and temporarily decreased competition from hardwood species following prescribed burning treatments [35,36]. This was also observed in our prescribed burn plots, thus suggesting that repeated prescribed burning is improving understory conditions that provide a competitive advantage for oak seedlings or resprouts. In IV of oaks the changes were non-significant, however, the largest increase was observed after B, which was slightly greater than the increases in IV of mesic hardwoods. This suggests that repeated burning is enhancing the competitive ability of oaks over other understory species. Increases of oak stems 10–50 cm and >50 cm observed in B and MB indicates high recruitment potential into the midstory and overstory, which also supports the increase in IV. According to a model produced by Steiner et al. [37], even a small advance regeneration less than 30 cm in height, as was observed in our results, can make significant contributions to future forest stand structure. Though changes in oak stems <10 cm were non-significant, our results suggest that: (1) there is an abundance of oak regeneration occurring regardless of disturbance type, as observed in C; (2) B consistently increases oak regeneration and advances oak seedlings into taller height classes; and (3) MB increases stem recruitment into taller height classes, which was evident from the reduction of small stems in 2016. The significant increases in absolute cover of oaks following MB and B as compared with the decreases in cover after C, also suggests that these treatments enhanced leaf growth as a physiological response to increased light levels, which subsequently increases net photosynthesis [38]. With regards to developing an open woodland community, the most effective treatment should both enhance oak regeneration and provide recruitment opportunity into larger size classes. Therefore, MB is likely the most effective treatment for oak succession over time.

Prior to treatments in 2001, the proportion of dominant understory red oak species (scarlet oak and Northern red oak) and white oak species (white oak and chestnut oak) was relatively equal in density among all study sites. Both red and white oak guilds showed significant increases following repeated B and MB treatments in 2016. However, there were more observed increases of white oak density across all treatments as compared with red oak, as compliant with other studies conducted in upland oak forests [39,40]. While the source of substantial white oak increases in C is unknown, we believe that several masting events may have caused this trend. In addition, the disproportion of red oak to white oak density in 2016 is likely due to several differences in phenology that may be distinctively affected by our treatments. Red oak acorns typically mature in two growing seasons, overwinter on the forest floor, and require 20–30% moisture loss to successfully germinate the following spring; while white oak acorns typically mature in one growing season, require 30–50% moisture loss, and germinate in the fall immediately after abscission [41,42]. This gives white oak species somewhat of an advantage, as viable seeds likely had time to germinate prior to dormant season burning in March, increasing the probability of survival [43,44]. In addition, successful white oak regeneration combined with previously reported structural changes following MB and B (i.e., thinner litter and duff layers, decreased overstory basal area, etc.) suggests drier understory conditions following these treatments. Exposure of red oak to these conditions may have led to acorn mortality or inhibited shoot growth in MB and B, as these species tend to insufficiently resist drought and heat during early stages of life [42,44,45]. The smaller increases of both red and white oaks observed in M suggest that competition from resprouting shrubs may have impeded oak regeneration in those treatment units. M treatments did not alter forest structure in a manner consistent with MB or B. While single prescribed burns often result in the insufficient top-killing of shrubs, subsequent fires applied in this study likely eliminated many resprouts in the B and MB treatments.

4.2. Pines

An increase in pine stem density was stimulated by greater reductions in basal area in MB and B. This was likely attributed to the increases observed in yellow pine (*P. virginiana, P. taeda,* and *P. rigida*) stem density after B and MB treatments, which closely follows results from related studies also conducted in the southern Appalachians [13,46]. These studies suggest that prescribed burning created favorable microsite conditions for yellow pines that include: decreased litter and duff cover to allow germination in mineral soil and reduced midstory stem density for increased light availability to the forest floor [13,46]. Increases of absolute pine cover in MB and decreases in all other treatments suggests that pines benefit greatly from disturbances that result in less basal area and more openings in the canopy. Similarly, the large reductions of absolute cover in B are likely the result of substantial white pine reductions, which was also observed in other studies that utilized repeated prescribed burning to control mesic species competition [47,48]. Though importance values were not significantly changed from 2001 to 2016, the only increase was observed following MB treatments, where pine abundance was greater than or comparable to oaks, mesic hardwoods, shrubs, and forbs. This increase of pine IV in MB was likely attributed to the substantial increases of pine stems 10–50 cm and >50 cm in height, coupled with moderate increases in stems <10 cm. This advance of stems into taller height classes provides evidence that, despite the smaller densities of this guild as compared with other species, pines will continue growing in height and contribute to future forest stand structure in our study area [37].

Little to no change in white pine regeneration in B and MB suggest potential for eastern white pine control using FFSS treatments. Though many pine species are inhibited by fire when young, results from Elliott et al. [49] show that eastern white pines were especially inhibited by fire during the germination process. Eastern white pine seeds are typically dispersed during early fall months and overwinter in the leaf litter until spring when warmer conditions are present for germination [48–50]. This predisposes seed and germinants on the forest floor to a higher probability of mortality during a dormant season prescribed burns, as observed following the March burns conducted in our study [51,52]. In addition, unlike some yellow pine species found in the southern Appalachians (pitch pine and shortleaf pine), eastern white pine lacks the ability to resprout following top-kill by fire [53,54]. Because significant increases of yellow pine stem density occurred after MB and B, this suggests that additional mechanical reduction of competitive hardwood species may also be necessary for successful yellow pine regeneration [55–57]. While Jenkins et al. [53] reported greater increases in yellow pine seedling density in M as compared with B, we observed the opposite, which again likely highlights the role of competition from resprouting shrubs in our study area.

4.3. Mesic Hardwoods

Mesic hardwood stem density was stimulated by repeated prescribed burns, while absolute cover was stimulated by MB, B, and M treatments. Most mesic hardwood stem density increases observed following B resulted from the increases of stems <10 cm and 10–50 cm, and the increases in cover following MB resulted from increases of stems 10–50 cm and >50 cm. Additionally, the growth of mesic hardwoods is proven competitive as increases of IV were observed in M, B, and MB as compared with other understory vegetation guilds. However, oaks showed a sharper increase in IV as compared with mesic hardwoods in B, suggesting that oak growth may surpass competition by other hardwoods with repeated prescribed burning. The increase of IV observed following M, in addition to the significant increases of stems 10–50 cm, also suggests that repeated mechanical treatments is creating taller stems as a result of sprout growth from a lack of top-kill. Within this guild, our results indicate that red maple, yellow-poplar, and blackgum were the drivers of these increases, which is supported by other studies reporting that these are the most dominant species observed in late-successional southern Appalachian forests [8,13,58].

The significant increase of mesic hardwood stem density in B was driven predominantly by increases of red maple. In addition, increases of red maple were likely the result of increases of mesic hardwood stems <10 cm and 10–50 cm observed in B treatments. A study conducted by Iverson et al. [59] reported that small red maple seedlings were initially stimulated by fire, but after the third burn, small seedlings densities were reduced by 81%. This could support the trend observed in our results, where fewer tall stems were observed in B. Nonetheless, our results contradict much existing research that report decreases in red maple stem density following one or two prescribed burn treatments [35,60,61]. This may be because most red maple regeneration occurred from basal resprouts, resprout clumps insulated inner stems from fire damage, fires were not hot enough, or frequent dormant season burning may be creating more favorable microsite conditions for red maple by decreasing the litter and duff layers and allowing root growth into mineral soil [38,62,63]. Red maple responded least-favorably to C and MB, suggesting slowed growth from competition of other understory hardwoods in C, as represented by the changes of IV, or mortality after repeated mechanical reductions and/or increased fire severity in MB which may facilitate adequate control of this species. Yellow-poplar and blackgum were much less abundant before any of the treatments but increased following MB treatments. These trends likely influenced the increases of mesic hardwood cover, and the increases of stems 10–50 cm and >50 cm following MB treatments. Our results coincide with results by Phillips et al. [58] and Iverson et al. [59], who reported scarcity of yellow-poplar prior to treatments due to their light-demanding nature and the lack of a large canopy-opening disturbance. They also reported that burning stimulated growth of these species, but insufficient light availability reduced seedling abundance over time [58,59]. In addition, these smaller mesic hardwood saplings are likely the most susceptible to fire-related mortality, as their bark is not fully-developed and the flames are in closer proximity to their leaves and buds than that of taller individuals [64].

4.4. Shrubs

We observed increases in absolute shrub cover following repeated M treatments and little to no change in the other treatments. This trend is predominantly explained by a lack of top-kill and consequential resprouting of mountain laurel and *Rhododendron* spp. observed after M treatments, whereas subsequent burns eliminated resprout potential in B and MB [13,32,65]. Additionally, significant increases of IV following M suggests that these species are more competitive in these treatment areas relative to other understory species. Some short-term studies report decreases in shrubs and hardwood saplings after thinning, but these results are not consistent with ours and were likely temporary [58]. Our findings are consistent with longer-term studies that report decreases in ericaceous shrub cover following one or two burn treatments [32,35,60]. This suggests that ericaceous species, like mountain laurel and *Rhododendron* spp., can be effectively controlled in the understory after repeated burning or burning and mechanical treatments. This was also reflected in the reductions of IV observed following MB and B treatments as compared with other understory species.

Other ericaceous shrubs, which were predominantly comprised of Blue Ridge blueberry (*Vaccinium pallidum* Aiton), maleberry (*Lyonia ligustrina* (L.) DC.), doghobble (*Leucothoe fontanesiana* (Steud.) Sleumer and *Eubotrys recurvus* (Buckley) Britton), and black huckleberry (*Gaylussacia baccata* (Wangenh.) K. Koch), were generally unaffected by disturbance, except for non-significant increases in MB. This general lack of change is likely the result of increases in competitive understory species. Non-ericaceous shrubs were not highly abundant in our plots prior to the treatments, but seemed to respond positively to B, M, and MB over time. This suggests that fire and fire surrogate treatments may create opportunities for non-ericaceous shrubs, such as chinquapin (*Castanea pumila* (L.) Mill.) and possumhaw (*Viburnum nudum* L.), that otherwise would have been outcompeted by mountain laurel and *Rhododendron* spp.

4.5. Graminoids

Other studies conducted in this region have reported moderate but non-significant increases in graminoid cover following disturbance [60,66]. However, a study by Phillips and Waldrop [32] reported significant increases in graminoid cover following MB and B treatments, particularly for perennial grasses (e.g., *Panicum* spp.) and sedges (*Andropogon* sp. and *Carex* spp.). In our results, increases of absolute cover and IV were mostly found in MB treatments, suggesting that additive effects of M and B on basal area reduction provides sufficient light availability for graminoid regeneration [13,64]. However, there was low abundance of graminoids throughout all treatments, which may be the result of dispersal limitations. That is, seeds may be absent in the seedbank, seed production may be low, or source populations may be scarce/distant regardless of disturbance [67]. It is likely that the conditions required for graminoid germination may not be optimal in B, M, and C units. This was observed in a study by Shiffman and Johnson [68], which reported seed accumulation in the humus layer in a southern Appalachian oak forest, instead of the mineral soil, which resulted in seeds decaying from excess moisture. Additionally, studies in similar areas reported that prescribed fires often do not completely consume the humus layer, and therefore may not stimulate the germination of relict graminoid seeds in the mineral soil seedbank [69,70].

4.6. Forbs

While our findings showed that total forb cover and IV did not significantly change from 2001 to 2016, we observed significant increases of nitrogen-fixing forb cover over time. Other studies reported that the most significant increases occurred following more intensive treatments [32,47,60,64,71]. Reductions in overstory basal area, like those reported by Waldrop et al. (2016), create more available space and sunlight, which in turn promotes the growth of forbs, especially light-demanding nitrogen-fixers. However, both our findings and those of Waldrop et al. [13] suggest that the rapid regeneration of competitive woody species quickly decreases light availability on the forest floor in the years following treatment. These results were reflective of the substantial decreases in IV following all treatments, especially in MB and M. Therefore, sustained light availability and control of competitive understory species, brought on by larger structural changes and/or continued disturbance, will be required for most forb species to become persistent in the understory community [47,60]. Our trends coincide with results from a study by Barefoot et al. [64], which reported greater forb, graminoid, and legume cover following thinning and three prescribed burns. However, they also found a substantial increase in non-nitrogen-fixing forbs over time, which was not evident from our data [64].

5. Conclusions

This study provides insight into the effects of 15 years of repeated fire and fire surrogate treatments on understory vegetation, as needed to support the management goals of the southern Appalachian region. With the exception of the control (C), each of the treatments satisfy a subset of the understory management objectives by reducing some competition from mesic hardwoods (M and MB) and ericaceous shrub cover (B and MB), and increasing oaks, pines, graminoids, and forbs in the understory (B and MB). The most immediate structural change occurred in MB, which will likely result in the most favorable outcomes for oak, yellow pine, and herbaceous species regeneration. While MB produced effects most consistent with our restoration goals, similar results may eventually be achievable with repeated B treatments, thus highlighting the importance of continuing long-term studies such as this. Our results also suggest that MB and B treatments are producing slight microclimatic changes in the understory, facilitating the growth of more poor-xeric site species such as scarlet oak, white oak, chestnut oak, yellow pines, and nitrogen-fixing forbs. Continuing research of longer-term repeated treatment effects on stem height classes will also provide more evidence for future forest structure and effectiveness of mesic hardwood species control. We also propose adding additional dimensions, such as including more frequent burns, potentially during different seasons, and conducting seedbank inventories, particularly for graminoids.

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