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Vegetation dynamics vary across topographic and fire severity gradients following prescribed burning in Great Smoky Mountains National Park

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ABSTRACT

Fire exclusion in the United States over the last century has had major impacts on forest ecosystems and landscapes. Out of a desire to reverse or mitigate the impacts of fire exclusion, some managers conduct prescribed fires meant to mimic the historic ecological role of fire and restore ecosystem properties. In the Southern Appalachians, fire exclusion in pine- and oak-dominated xeric ridge forests has allowed fire-sensitive hardwood species to establish, filling in the canopy and creating shady, moist conditions that are unfavorable for reproduction of fire-dependent pines and oaks. Managers of natural areas use prescribed fire to restore pine and oak dominance, promote pine and oak regeneration, and reduce stand densities. Here, we use multivariate analysis of monitoring data collected before and after 21 fires over 16 years in fire-suppressed xeric pine-oak forests in the Great Smoky Mountains National Park to assess how community composition and structure change after prescribed fire, to what degree changes after fire persist over time, and how the impacts of prescribed fire vary with fire severity and site environment. Fire consistently reduces stand density and shifts plots towards lower shrub cover and higher herbaceous cover. On the other hand, compositional shifts, i.e. changes in relative abundances of species, were highly variable in both magnitude and direction. Fire severity, measured as total fuel reduction and litter and duff reduction, was important for predicting the magnitude of change after fire. The magnitude of fire effects also varied with elevation, likely reflecting variation in local moisture conditions. Our results indicate that while fires do reduce stand density, they have not yet been successful in consistently restoring pine and oak dominance in the canopy. Restoring pine- and oak-dominance in xeric ridge forests in the Southern Appalachians will thus require extended management focus with flexible, adaptive, long-term planning and continued monitoring and research.

1. Introduction

Disruption of historic fire regimes, i.e. changes in the frequency, extent, timing, and intensity of fires, can have major impacts on the structure, composition, and function of forest ecosystems. The extent of burning in the United States has declined precipitously since the early 20th century, due to active fire exclusion (Tilman et al., 2000), with major consequences for North American ecosystems. Fire exclusion alters landscape structure (Baker, 1992), species composition (Parsons and DeBenedetti, 1979; Gilliam and Platt, 1999), forest structure, and carbon dynamics (North et al., 2009; Tilman et al., 2000). Out of a desire to reverse or mitigate the impacts of fire exclusion, many land managers conduct prescribed fires meant to mimic the historic ecological role of fire and restore pre-exclusion ecosystem properties. However, long-term studies of the impacts of reintroducing fire in fire-suppressed ecosystems are few, and the long-term impacts of restoring prescribed fire and how these impacts vary depending on when and where prescribed fires are conducted is not well known.

Fire exclusion in the eastern US can drive mesophication, a positive feedback in which fire-prone, open-canopy forests undergo succession towards dense, closed-canopy forests with moist microclimatic conditions and more compact, less flammable leaf litter: unfavorable conditions for fire ignition and spread (Nowacki and Abrams, 2008). Mesophication occurs more quickly at wetter sites

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where fire-sensitive mesophytic species can establish and grow more quickly than on more xeric sites. This can transform formerly fire-dependent communities to an alternate stable state in which restoration of previous forest structure and composition may be exceedingly difficult (Nowacki and Abrams, 2008). While prescribed fire may help slow or reverse the process of mesophication, doing so becomes increasingly difficult as mesophication progresses (Abrams, 2005). Thus, identifying conditions under which prescribed fire will be most effective at restoring fire-dependent communities and places where fire is most urgently needed to slow mesophication is important for making the best use of limited fire management resources and to best conserve the fire-dependent forests of the eastern US.

Mesophication occurs in the xeric pine-oak forests of the Southern Appalachians (Flatley et al., 2015). Here, fire-dependent forest communities dominated by yellow pines and oaks are found on xeric south and southwest facing slopes and ridgetops at mid-elevations (Whittaker, 1956; Jenkins, 2007). These forests were historically dominated by yellow pines (*Pinus* subgenus *pinus*) such as pitch pine (*P. rigida*), Virginia pine (*P. virginiana*), shortleaf pine (*P. echinata*), and Table Mountain pine (*P. pungens*), and by oaks, such as scarlet oak (*Quercus coccinea*), chestnut oak (*Quercus montana*), white oak (*Quercus alba*), black oak (*Quercus velutina*), and southern red oak (*Quercus falcata*). The dominant pine and oak species display adaptations to fire, such as thick bark and the ability to resprout after fire (Harmon, 1984). The seedlings of these species are also more successful after fires have altered light and seedbed conditions. Oaks have hypogeal germination, which places seedlings' root collar and dormant buds deeper in the soil than competitors with epigeal germination, and may enhance post-fire survival relative to other hardwoods (Brose and Van Lear, 1998; Brose et al., 2005). The yellow pine species require high light conditions and shallow litter and duff for germination and the oaks are moderately shade intolerant and germinate well on recently burned substrate (Zobel, 1969; Williams and Johnson, 1992; Brose et al., 2001; Brose and Waldrop, 2006; Waldrop and Brose, 1999). Table mountain pine has serotinous cones (Zobel, 1969; Barden, 1978), as does pitch pine in parts of its range (Ledig and Fryer, 1972; Givnish, 1981).

Prior to exclusion, frequent, low-intensity surface fires occurred at approximately 3–13 year intervals (Harmon, 1982; White, 1987; Aldrich et al., 2010; Feathers, 2010; Flatley et al., 2013). These fires maintained open, park-like stands with a grass and forb-dominated understory and shallow litter and duff layers (Harrod et al., 1998; Lafon et al., 2007). Occasional severe fires often followed a southern pine beetle (*Dendroctonus frontalis*) outbreak, ice storm, or other disturbance (White, 1987; Lafon and Kutac, 2003). High severity fires opened up the canopy, increased light availability, reduced the litter and duff layers, and promoted episodes of pine recruitment (Harrod et al., 2000; Wimberly and Reilly, 2007; Jenkins et al., 2011). Lightning fires can occur in the Southern Appalachians, (Harmon, 1982; Cohen et al., 2007) but the majority of historical fires that shaped pre-exclusion stands are believed to have been anthropogenic. Native Americans used low-intensity surface fire to maintain hunting and gathering grounds (Delcourt and Delcourt, 1997, 1998; Brose et al., 2001), and early European settlers used fire to improve common grazing lands and conditions for hunting and gathering, or for pest and disease prevention (Jurgelski, 2008; Aldrich et al., 2014).

Fire exclusion and changes in human fire-use patterns since the early 20th century have greatly changed structure and composition in xeric pine-oak forests (Harmon, 1982; Harrod et al., 1998). In the absence of frequent fire, fire-sensitive species such as red maple (*Acer rubrum*), blackgum (*Nyssa sylvatica*), yellow poplar (*Liriodendron Tulipifera*), and white pine (*Pinus strobus*) can grow large enough to resist fire (Harmon, 1984). These trees fill in the canopy and create shady, moist conditions that are conducive to their own reproduction and unfavorable for regeneration of fire-dependent species (Harrod and White, 1999). Fire exclusion has led to declines in the abundance of yellow pines and oaks and loss of landscape diversity across the Southern Appalachians (Harrod et al., 1998, 2000; Brose and Waldrop, 2006). Deep litter and duff layers have accumulated, and conditions have become shady and moist so that the occasional unintentional fire is not intense enough or large enough to reduce the litter and duff, kill back fire sensitive species, and promote pine or oak regeneration (Vose et al., 1995; Harrod et al., 1998). As a result, management agencies such as the National Park Service and US Forest Service have begun to use prescribed fire to restore pre-exclusion conditions.

These efforts have had mixed success. Elliott et al. (1999) found that while *Pinus rigida* seedlings were abundant after a prescribed fire in Nantahala National Forest, North Carolina, most died within two years after fire and ultimately, *P. rigida* seedling density was less two years after prescribed fire than before. This may have been due to competition for light from shrubs like mountain laurel (*Kalmia latifolia*), which resprouted vigorously after fire. Welch et al. (2000) found *P. rigida* and *Pinus pungens* seedlings present after low intensity prescribed fire. However, shrubs and hardwoods were not exposed to lethal temperatures, and resprouted to such an extent that understory density after fire was twice that before fire within a year after prescribed fire. Jenkins et al. (2011) found that below a certain threshold of fire severity, yellow pine seedlings were not observed following prescribed fire in the Great Smoky Mountains National Park (GSMNP). These studies demonstrate that to successfully promote pine regeneration, prescribed fire must open the canopy, reduce litter and duff, and expose competitors to lethal temperatures. They also suggest that effects of prescribed fire observed in the short term may diminish over time. Because data for longer than two years after a prescribed fire are often unavailable, evaluating the effectiveness of prescribed fire at achieving management goals in the long-term is difficult.

Prescribed fire or a particular prescribed fire regime can have different effects depending on the environment, climate, or history of a given location. In wetter sites where mesophication is hypothesized to proceed more quickly (Abrams, 2005; Nowacki and Abrams, 2008), low- to medium-severity prescribed fire may not cause mortality of fire-sensitive species if they have grown large enough to resist fire. The effects of low- to medium-severity fire may be greater at drier sites if fire-sensitive species are still present in the smaller size classes. The most xeric sites with rocky, thin soil may not require prescribed fire at all to maintain populations of *P. rigida* or *P. pungens* (Williams, 1998; Barden, 2000), though these sites are relatively uncommon in GSMNP. Many studies of prescribed fire in the Southern Appalachians examine the effects of only one fire and do not compare impacts across a gradient of environmental, topographical, and fire conditions. Better understanding where to focus prescribed fire efforts requires examining the effects of multiple fires across an environmental gradient.

In this study, we use long-term fire effects monitoring data from GSMNP spanning 16 years and 21 fires to address the following questions:

(1) How does introducing prescribed fire to a long-unburned forest affect adult tree community structure and composition?
(2) Do these changes persist over time?
(3) Do the magnitude of change and the degree to which changes are maintained over time vary with site environment conditions and/or fire severity?

2. Methods

2.1. Study area

GSMNP is located in the southern Appalachian Mountains, along the border between North Carolina and Tennessee. Elevation ranges from 267 m to 2025 m. Mean annual temperature in nearby Gatlinburg, TN is 13 °C and mean annual precipitation averages 1430 mm (Jenkins et al., 2011). Precipitation varies throughout the park and increases with elevation (Shanks, 1954).

Xeric ridge forests cover about 16% of total park area (33,000 ha), largely on ridgetops and exposed south- to west-facing slopes, and are dominated by *Pinus* and *Quercus* species (Jenkins, 2007). The yellow pine species *P. rigida*, *P. pungens*, *Pinus echinata*, and *Pinus virginiana* dominate the driest of these forests, while less dry sites are dominated by *P. strobus*, *Quercus coccinea*, and *Q. montana*. Prior to fire exclusion, these forests experienced regular fire, with a return interval of approximately 3–13 years (Harmon, 1982). Other common tree species are *A. rubrum*, *N. sylvatica*, *Tsuga canadensis*, and *Oxydendrum arboreum*. These forests have a well-developed shrub layer, with common species including *K. latifolia*, *Vaccinium* species, and *Gaylussacia* species. Prior to fire exclusion, these communities may have had a greater abundance and diversity of herbaceous species, but these are largely absent today (Harrod et al., 2000).

Fire exclusion since the founding of the park in 1931 has resulted in changes to forest structure and composition and decreased regeneration of fire-dependent pine and oak species (Harmon, 1984; Harrod et al., 1998, 2000). Since 1996, GSMNP management has been conducting prescribed burns with the main objectives of reducing stand densities and promoting regeneration of fire dependent species, especially yellow pines (Jenkins et al., 2011). Since the start of the program, 21 prescribed fires were conducted in the park ranging in size from 18 to 939 ha (Fig. 1). Fires have been conducted throughout the park, with the majority in the western portion of the park. Burn date has varied from late winter (March) to early fall (September), but the majority of burns were conducted in early spring (April). To monitor vegetation communities' responses to prescribed burning and to provide feedback for adaptive management, the National Park Service (NPS) established a fire effects monitoring program in 1997. The program implements a standardized set of protocols to assess fuel and vegetation conditions prior to burning and at set intervals post-burn, and to monitor conditions during fires (USDI National Park Service, 2003).

2.2. Data collection

Vegetation and fuels data were collected according to the protocols in the National Park Service's fire monitoring handbook (USDI National Park Service, 2003). Plots were sampled within one year prior to the first burn, and again one, two, five, and ten years after fire. Sampling events are denoted throughout this paper as "pre", "fire1year1", "fire1year2", etc., with "fire1" or "fire2" indicating that the sampling date was after the first or second fire, respectively, and year1, 2, 5, or 10 indicating how many years after the fire sampling occurred. The monitoring cycle begins again after every burn. A total of 39 0.1 ha plots were included in this study: 19 that were burned once and 20 that were burned twice. Eleven of these plots were sampled up to five years after the second fire (fire2year5), the longest time interval included in this study. Due to differences in the timing of prescribed burns as well as logistical considerations, not all plots have been sampled on all possible sampling events.

During each sampling event, trees larger than 15 cm dbh were measured and identified to species in the entire 0.1 ha plot. Trees between 2.5 and 15 cm dbh were measured and identified in a 250 m^2 subplot. Measurements in the subplot were multiplied by four for all analyses to match the full plot scale. Herb, shrub, subshrub, and vine cover were measured along two 50 m transects in each plot. Along each transect, a pole was dropped every 30 cm and the height and species of every individual intersecting the pole were recorded. Cover was calculated by totaling the number of points at which a species is recorded by the total number of points sampled, and cover by lifeform (herb, shrub, subshrub, vine) was

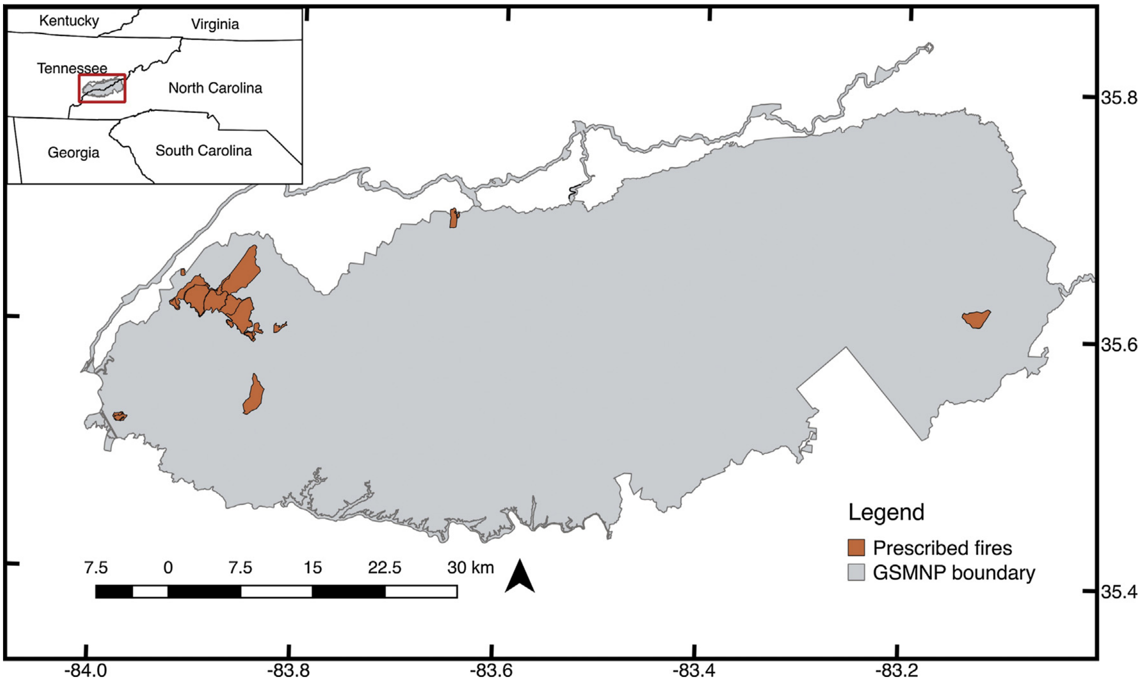

Fig. 1. Prescribed fires in the Great Smoky Mountains National Park. Prescribed burns have been conducted throughout the park, but efforts have been focused on the western portion of the park.

calculated by summing percent cover of all herb and shrub species in a plot. Seedlings were tallied by species in a 50 m^2 subplot. Seedling data are not included in our analyses; they are reported in Jenkins et al. (2011).

Dead and downed woody fuels, litter, and duff were sampled using methods described by Brown (1974) along four randomly oriented 15.2 m transects in each plot. Fuel loadings were calculated based on Brown (1974) and Brown et al. (1982) with values for specific gravity of downed woody material and bulk density of litter and duff from Jenkins et al. (2011). Total fuel reduction after fire and average reduction of litter and duff were included in analyses as measures of fire severity. Depth of litter and duff are hypothesized to be important factors in determining success of pine and oak regeneration, and were also included in analyses.

Topography is linked to moisture conditions and thus the distribution of fire and plant species across the GSMNP (Whittaker, 1956; Harmon et al., 1983; Flatley et al., 2011). Therefore, we included measures of topographic position (elevation, slope, aspect, topographic convergence index) as environmental variables (Table 1). A digital elevation model (DEM) for GSMNP was derived from the United States Geological Service nationwide 10-m DEM (Gesch et al., 2002; Gesch, 2007). Slope and aspect were derived from the DEM in ArcGIS (ESRI, 2011). Aspect is used as a proxy for insolation at a site. Southwest facing slopes receive the most radiation, while northeast facing slopes experience the least. To reflect this, aspect was transformed using the equation

$$A_T = -\cos(45 - A) \tag{1}$$

where A_T is the transformed aspect and A is the aspect measured in degrees, so that a maximum value of 1 represents southwest facing slopes and a minimum value of -1 represents a northeast facing slope (Pierce et al., 2005). Topographic convergence index (TCI), the ratio of uphill contributing area to slope, was used as a proxy for soil moisture (Beven and Kirkby, 1979). TCI was calculated from the USGS DEM using the terraflow package in GRASS (Arge et al., 2003).

2.3. Analysis

Management objectives in GSMNP are largely focused on restoring pine and oak dominance in the canopy. Therefore, we focused on examining and explaining changes in density and species composition of trees larger than 2.5 cm DBH. Prior to analyses, all trees in genus *Carya* were grouped together because the majority were missing species identifications. We also removed rare species, i.e. species found in less than five percent of samples, in order to reduce noise and enhance our ability to detect relationships between community composition and environment and burn characteristics (McCune and Grace, 2002).

For all analyses, we used stem abundance data and conducted analyses with both total abundance and relative abundance data. Analysis of total abundance data captures changes in the number of stems in a plot in addition to changes in species composition, whereas analysis of relative abundance data reduces the emphasis on change in total number of individuals and instead reflects only changes in relative quantities of different species (McCune and Grace, 2002). Because many plots underwent major changes in tree density after fire, analyses of unstandardized abundance data predominantly reflected changes in structure and not necessarily in relative abundance of different species. Therefore, we repeated the analyses with both sets of data to assess trends in composition as well as structure after fire.

To assess changes in stand structure and community composition, we used non-metric multidimensional scaling ordination (NMS, Kruskal, 1964) as implemented in the vegan package in R (Oksanen et al., 2011; R Development Core Team, 2010). NMS makes no assumptions about the shape of species occurrence distributions or about the relationship between species occurrences and environmental gradients. Individual observations are arranged in a low-dimensional space so that the distances between points in ordination space correspond to dissimilarities between samples. Environment variables are overlaid as biplot vectors after ordination, where the direction of a vector represents the correlation between that variable and each ordination axis, and the length represents the strength of the correlation.

Pairwise dissimilarities between plots were calculated using the Bray–Curtis (Sorenson's) dissimilarity index. All plots that were sampled before and at least once following fire were included in the ordination and all sampling events for these plots were included as separate entries in the data. A step-down procedure was used to determine the proper dimensionality for each NMS solution. Varimax rotation was used to rotate each solution so that NMS axis 1 explained the most variance. To test for separation of burned and unburned plots, we assessed whether the variation within burned vs. unburned groups of plots was less than the variation between groups. To do this we conducted Mantel tests on the distance matrix between points in ordination space and a pairwise design matrix (Legendre and Legendre, 1998), which contrasts pairs of samples that are in the same group with those that are in a different.

Individual environment variables (Table 1) were overlaid as biplot vectors on the ordination. Only correlation vectors that were significant ($P < 0.05$) were plotted. Species scores were calculated as average ordination scores weighted by species abundances. Correlations between the ordination axes and environment variables and species abundances were calculated using the ecodist package in R (Goslee and Urban, 2007). To analyze plots' changes over time, change vectors connecting a plot at one sampling event to itself at a later sampling event were visually compared.

The dataset has a longitudinal gradient, with plots spanning the width of the park (Fig. 1). Because the mountains to the east are higher than those to the west, elevation is highly correlated with longitude ($r = 0.87$, $p < 0.0001$). We expected that the effect of longitude would be largely mediated through elevation. To test whether there was an effect of longitude beyond the effect of elevation, we used linear regression to predict ordination scores on NMS axis 1 (the axis with which elevation and longitude were most strongly correlated) from elevation, and then from both

Table 1
Environmental variables used in analyses.

Variable (abbreviation)	Description	Mean (range)
Elevation	Plot elevation (m)	599.0 (331.3–1046.6)
Slope	Plot slope angle (°)	20.5 (6.2–39.2)
Aspect	Transformed aspect (−1 to 1)	−0.03 (−1, 1)
TCI	Topographic convergence index	4.3 (3.2–7.5)
Total fuel reduction	Pre-fire fuel loadings – post-fire fuel loadings (tons/ha)	12.4 (−7.1–27.0)
Litter and duff reduction	Pre-fire litter and duff depth – post-fire litter and duff depth (cm)	4.3 (0.1–8.1)
Litter and duff depth	Depth of litter and duff (cm)	7.7 (1.0–21.1)

elevation and longitude. An *F*-test of the two models demonstrated that longitude does not contribute significantly beyond elevation ($p = 0.08$). Therefore, we excluded longitude from analyses.

To analyze how the magnitude of change within plots varies with environment and with fire severity, and whether these changes are maintained over time, we calculated Spearman's rank correlation between the environment variables of interest (Table 1) and each plot's dissimilarity to itself before fire and 1, 2, and 5 years after the first fire, and 1 and 5 years after the second fire. A plot's dissimilarity to itself is correlated with the length of the change vectors plotted in ordination space, but is preferable for use in statistical analyses because the ordination does not perfectly represent the dissimilarities between plots in two-dimensional space.

3. Results

3.1. Ordination of unstandardized abundance data

The step-down procedure suggested a two-dimensional solution, and the final stress in two dimensions was 0.22. The ordination axes had a cumulative R^2 of 0.71 with NMS axis 1 explaining most of the variation (Table 2). Burned and unburned plots overlap in ordination space, but the unburned plots are more closely grouped in ordination space and overlap with only some of the burned plots (Fig. 2a). The results of the Mantel test comparing within- and between-group variance of burned vs. unburned plots were not significant, indicating that differences between the two groups (burned vs. unburned) were not significantly different from differences within groups, despite the visual pattern of separation in ordination space (Mantel $r = 0.02$, $P = 0.25$).

Table 2
Results from 2-dimensional NMS ordination of unstandardized abundance data. Only significant correlations ($P < 0.05$) are reported.

	Axis 1	Axis 2
% Variance explained	0.42	0.29
Cumulative variance explained	0.42	0.71
Species correlations with ordination axes		
Acer rubrum	0.62	−0.13
Amelanchier arborea	0.22	0
Betula lenta	0.36	0
Carya spp.	0.29	0
Cornus florida	0	0.13
Ilex opaca	0.16	−0.17
Liriodendron tulipifera	0.35	0
Nyssa sylvatica	0	−0.40
Oxydendrum arboretum	0.45	−0.24
Pinus echinata	−0.15	0
Pinus rigida	−0.36	−0.47
Pinus strobus	0.29	−0.40
Pinus virginiana	−0.32	−0.54
Quercus alba	0.33	0
Quercus coccinea	0.34	−0.17
Quercus falcata	0	−0.23
Quercus montana	0.28	0.28
Quercus velutina	0.23	0
Sassafras albidum	0	0
Tsuga canadensis	0.53	0
Environment variables correlations with ordination axes		
Elevation	0.63	
Slope		
Aspect		0.24
TCI		
Total fuel reduction	−0.4	
Litter and duff reduction	−0.22	0.20
Depth of litter and duff	0.43	−0.44
Shrub cover	0.20	−0.35
Herbaceous cover	−0.49	0.27
Total plot density (stems/ha)	0.21	−0.47

Species scores plotted in ordination space were biased towards the area occupied by the unburned plots (Fig. 2b), which suggests that all species are present at higher abundances in unburned plots than burned plots, and decline in abundance after fire. The yellow pines' (*P. rigida*, *P. echinata*, and *P. virginiana*) species scores are located closest to the area in ordination space where burned plots dominate, suggesting that these species' abundances change the least after fire, i.e. that these species experience the lowest post-fire mortality.

Neither slope nor TCI were significantly correlated with an NMS axis, but all other environmental variables were correlated with axis 1 and/or 2 (Table 2). NMS axis 1 is most strongly correlated with elevation, and most negatively correlated with herbaceous cover and total fuel reduction. NMS axis 2 is correlated with the fire severity measures (fuel reduction), variables that are affected by fire (shrub and herb cover, total tree density), and with aspect (Table 2, Fig. 2c and d).

Change vectors drawn for individual plots from before fire to one year after fire showed a trend towards lower density, lower shrub cover, and higher herb cover immediately after fire (Fig. 3a). Plot dissimilarity with itself over this time period varies from 0.03 to 0.86, with a mean of 0.33. In most plots, the majority of change takes place within the first year after fire: subsequent change vectors, drawn from samples one year after fire to two years after fire, and from two years after fire to five years after fire, are shorter on average, and do not show any major trend in any direction (Fig. 3b and c). Change vectors drawn from before fire to five years after the second fire show an overall trend towards lower density, lower shrub cover, and higher herbaceous cover (Fig. 3d), suggesting that changes in density after the first fire are maintained over time. Plots' dissimilarities to themselves over that interval range from 0.15 to 0.85, with a mean of 0.5.

Changes that occur immediately after fire largely persist over time. If changes to plot structure and composition caused by fire began to revert to prior conditions in the years following fire, change vectors for years two and five would trend in the opposite direction than the change vectors immediately following fire. Instead, change vectors plotted from fire1year1 to fire1year5 (Fig. 3b) are short on average and no single direction predominates, indicating that changes in later years are much smaller in magnitude than those immediately following fire, and are not necessarily in the opposite direction of the immediate changes. A second fire tends to shift plots in the same direction in ordination space as the first fire, though the average magnitude of change is smaller than the first fire (Fig. 3c).

3.2. Ordination of relative abundance data

The step-down procedure conducted with relative abundance data again suggested a two-dimensional solution. The final stress was 0.22, and the combined R^2 of the axes was 0.73 (Table 3). There did not appear to be any clustering in the distribution of burned and unburned plots in ordination space (Fig. 4a), and the Mantel test comparing within- and between-group variance indicated between group dissimilarities were not significantly different from within group dissimilarities (mantel $r = -0.06$, $p = 0.97$).

Species scores were distributed more widely throughout ordination space than in the previous ordination (Fig. 4b). NMS axis 1 was strongly correlated with elevation and with depth of litter and duff, and negatively correlated with herbaceous cover and total fuel reduction (Table 3; Fig. 4c). NMS axis 2 was negatively correlated with TCI and herbaceous cover, and most positively correlated with depth of litter and duff and with shrub cover. Herbaceous and shrub cover were again negatively correlated with each other, and herbaceous cover and fire severity (total fuel reduction) are positively correlated and increasing towards the left in Fig. 4.

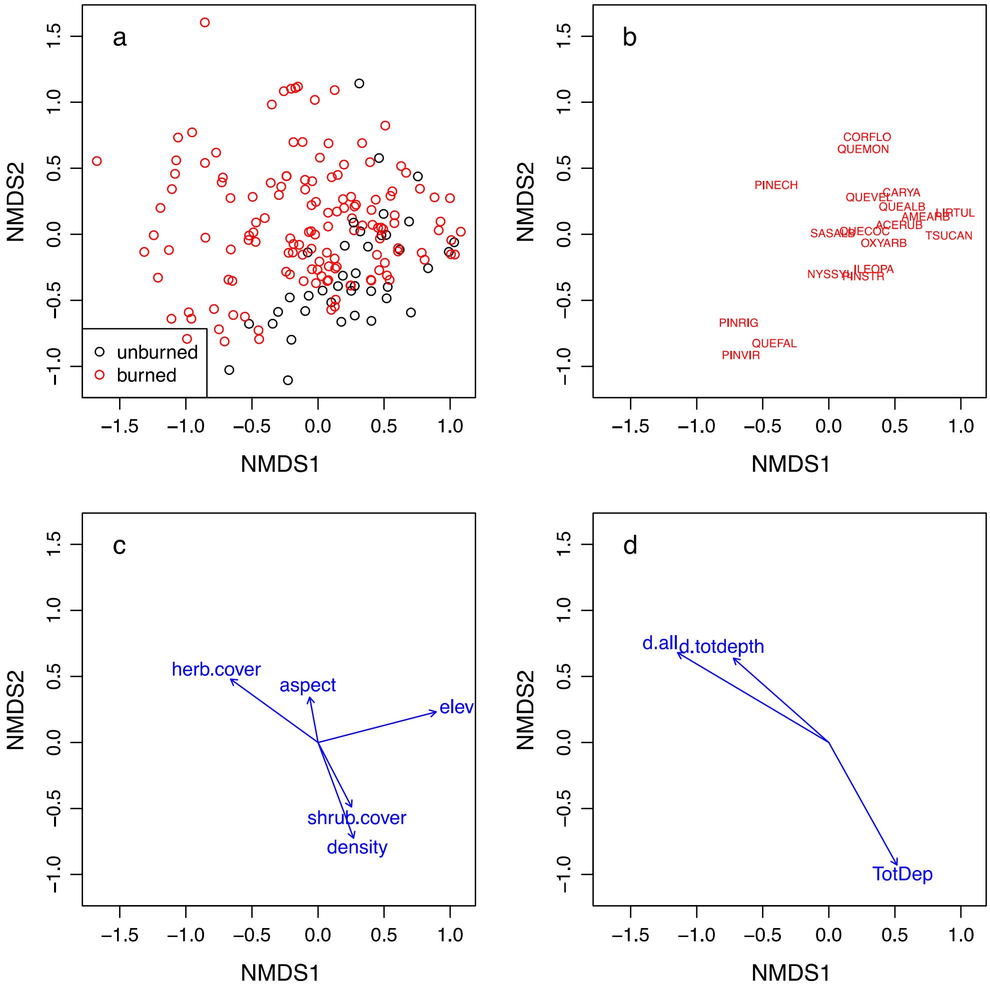

Fig. 2. Results from NMS ordination of abundance data. (a) Samples. (b) Species scores. (c) Environment vectors. Only significant vectors ($p > 0.05$) are displayed. (d) Vectors for burn characteristics. d.all = total fuel reduction, d.totdepth = litter and duff reduction, TotDep = depth of litter and duff at time of sampling.

The yellow pines are located towards the left side of the graph, suggesting that they have higher relative abundance at lower elevations and at sites that have high herbaceous cover and have experienced more severe fires. The more mesophytic species such as *A. rubrum*, *T. canadensis*, and *P. strobus* have their maxima towards the upper right side of the figure, at higher elevations and in areas with higher shrub cover, deeper litter and duff, and less severe fires. Change vectors plotted over all time periods did not show any clear temporal trends with regards to composition in either the short- or long-term. Fig. 4d shows change vectors plotted from before fire to fire2year5; the lack of directional trend pictured is representative of the trends observed over all time intervals (not shown).

3.3. Relationship between environment and magnitude of structural/compositional change

Correlations between environment and fire variables and a plot's dissimilarity to itself calculated from unstandardized abundance data showed elevation to be consistently important over time. Variables associated with fire severity were significantly positively correlated with a plot's dissimilarity to itself in the shorter term, and less important in the long-term, whereas variables associated with topography (slope and aspect) were not correlated with the magnitude of change in the short term, but were correlated with the longer-term magnitude of change (Table 4). Because a different subset of plots were included in correlation analyses from year to year due to differences in sampling between the plots, a different range of each of the variables tested was represented in each round of analysis. For example, the range of elevation in the analyses for fire1year1 is 331–1047 m, while the range for fire1year5 is only 331–635 m, which may explain the switch in the sign of the relationship for pre-fire to fire1year5 dissimilarity.

Correlation analyses conducted with dissimilarity values calculated from relative abundance data did not show the same patterns. Elevation was not consistently significant, though it was generally negatively correlated with the magnitude of change after fire. Aspect and TCI were never significant, and slope was significant only in the interval from pre-fire to fire1year5. Variables relating to fire severity are significantly correlated with the magnitude of compositional change from pre-fire to two years after the first fire, and depth of litter and duff is important for the first two years after a prescribed fire.

4. Discussion

Prescribed fires in GSMNP aim to maintain or restore pine and oak dominance, promote pine and oak regeneration, and reduce stand densities (Jenkins et al., 2011). Our results suggest that prescribed fire generally does reduce stand densities after fire, but effects on composition and relative dominance of pine and oak species are less consistent and vary with burn and site characteristics.

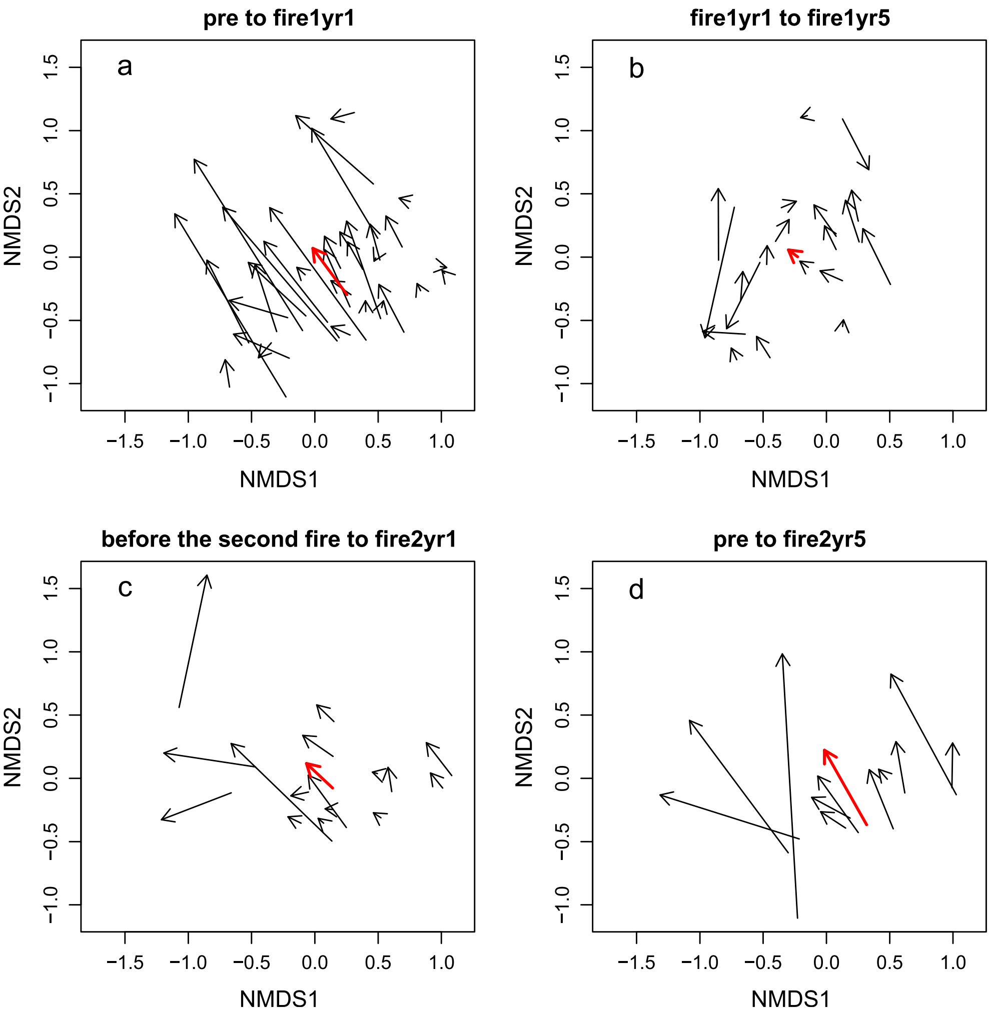

Fig. 3. Change vectors. Red arrows represent the average vector. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The effectiveness of prescribed fire in achieving management goals will thus depend on pre-burn forest composition and structure, environmental characteristics of the burn site, burn severity, and the number and timing of burns.

4.1. Impacts of prescribed fires on forest community structure and composition

Reducing stand density is important for creating high light conditions that promote pine and oak regeneration (Elliott et al., 1999; Welch et al., 2000; Jenkins et al., 2011) and is a desired outcome of prescribed fire in the Great Smoky Mountains. Results from the ordination of unstandardized abundance data indicate that stand density declines immediately after both the first and second fires, and that these reductions are maintained over the duration of the study (Fig. 3). Plots also shift towards higher herbaceous cover and lower shrub cover. Low shrub cover after fire is associated with increased pine seedling abundance after fire (Jenkins et al., 2011), and historically, some fire dependent stands in GSMNP had an understory dominated by herbaceous species (Harrod et al., 2000). Thus, in general prescribed fire does seem to be shifting these stands towards historic conditions by reducing stand density and shrub layer competition with pine and oak seedlings and promoting herbaceous species dominance.

However, the differences between the ordinations of unstandardized and relative abundance data demonstrate that while plots generally shift towards lower stem density after fire, the data show no clear pattern with regards to changes in species composition after fire. Variation in the magnitude of compositional change after fire can be explained by variation in mortality and stem density change: dissimilarity measures for each individual plot between pre-fire to fire1year1 calculated from unstandardized and relative abundance data are correlated ($r = 0.85$, $p < 0.0001$). Fires that kill a larger number of individuals thus cause larger changes in relative abundance, indicating that in these more severe fires, post-fire mortality is not uniformly distributed across species.

The direction of compositional change after fire is highly variable across plots. Relative dominance of pine and oak does increase in some plots, while composition in other plots changes very little or in unexpected directions. Our finding is consistent with another recent study of multiple fires in nearby Linville Gorge, North Carolina, which found only minor changes in tree species composition despite changes in structure (Hagan et al., 2015). Our results show no clear trend towards post-fire dominance by any one particular species or group of species across plots. This may be due to differences across plots in susceptibility to fire-induced mortality among fire-sensitive and fire-adapted species. Post-fire mortality is influenced by fire severity, species traits, and the size of individual trees (Pausas et al., 2004; Brando et al., 2012). Though pines are generally considered to be more fire resistant than maples, large individuals of *A. rubrum* (red maple) or other hardwoods can survive fire, especially low- to medium-intensity fire (Harmon, 1984). In some

Table 3
Results from 2-dimensional NMS ordination of relative abundance data. Only significant correlations ($P < 0.05$) are displayed.

	Axis 1	Axis 2
% Variance explained	0.45	0.28
Cumulative variance explained	0.45	0.73
Species correlations with ordination axes		
Acer rubrum	0.61	0.41
Amelanchier arborea	0.25	0
Betula lenta	0.35	0
Carya spp.	0.19	−0.30
Cornus florida	0	−0.34
Ilex opaca	0.16	0.16
Liriodendron tulipifera	0.34	0
Nyssa sylvatica	−0.23	−0.35
Oxydendrum arboretum	0.39	0
Pinus echinata	−0.32	−0.44
Pinus rigida	−0.60	0.43
Pinus strobus	0.19	0.22
Pinus virginiana	−0.76	0
Quercus alba	0.26	−0.30
Quercus coccinea	0.21	0.20
Quercus falcata	−0.13	0
Quercus montana	0	−0.72
Quercus velutina	0.18	−0.26
Sassafras albidum	0	−0.21
Tsuga canadensis	0.57	0
Environment variables correlations with ordination axes		
Elevation	0.67	0
Slope		
Aspect		
TCI	0	−0.25
Total fuel reduction	−0.32	
Litter and duff reduction		
Depth of litter and duff	0.29	−0.37
Shrub cover	0.14	0.31
Herbaceous cover	−0.37	−0.17
Total plot density (stems/ha)	0	0.15

plots, individuals of fire-sensitive hardwood species are present in larger size classes and can survive low-severity fire, and so fire does not reduce their relative dominance though it does cause some mortality in smaller size classes (Fig. S1). In plots where fire-sensitive species are confined to smaller size classes and larger size classes are dominated by pines and oaks, fire causes disproportionate mortality in these species and helps restore pine/oak dominance (Fig. S2). The lack of a consistent direction of post-fire compositional shifts likely reflects differences across plots in pre-fire structure and composition and in burn characteristics.

This suggests that while prescribed fire in GSMNP has reduced stand densities and shifted composition of adult trees, the goal of restoring pine/oak dominance in the canopy remains elusive. Achieving this goal in the future may depend on whether or not seedlings of yellow pine and oak species establish and recruit into adult size classes after prescribed fire. Analysis of seedling data from the same dataset found that abundance of pine seedlings after prescribed fire varies greatly across plots, and depends on fire severity (Jenkins et al., 2011). In some plots, pine seedlings were entirely absent after low-severity prescribed fire. Other studies have also found that prescribed fires, particularly more severe fires, do promote seedling establishment of yellow pines and oaks (Elliott et al., 1999; Welch et al., 2000; Harrod et al., 2000). Because there are a number of environmental and demographic filters that can prevent seedlings from recruiting into larger size classes, further monitoring of these plots is necessary to determine whether prescribed fire can promote pine and oak regeneration into the canopy. Fires may be necessary at regular intervals to maintain favorable conditions for young individuals.

Changes that take place after prescribed fire are maintained over the duration of the study. Changes in density and composition observed over time are likely mostly from mortality, and not recruitment of new individuals into adult size classes, because relatively few seedlings grow large enough to be included in sampling within the five year monitoring period. The species composition and stem density of new recruits are key to understanding long-term structural and compositional changes after fire, and continued monitoring of recruitment of seedlings and saplings into larger size classes is necessary.

4.2. Relationship between environment, fire severity, and impacts of prescribed fire

The impacts of fire exclusion in the Southern Appalachians vary from site to site depending on the local environment and pre-exclusion conditions (Flatley et al., 2015). Likewise, prescribed fire effects depend on the local environment, pre-fire conditions, and burn characteristics. As expected, we found a strong effect of fire severity, which was correlated with the magnitude of compositional and structural change after fire. This is consistent with other studies in the Southern Appalachians, which have found that fire severity is an important predictor of fire effects and post-fire regeneration of pines (Groeschl et al., 1992; Harrod et al., 1998; Elliott et al., 1999; Wimberly and Reilly, 2007; Jenkins et al., 2011; Pallai, 2015). Fire severity is related to site moisture at the time of burning (Wimberly and Reilly, 2007; Jenkins et al., 2011). Weather and climate conditions leading up to a burn are important and measures of drought such as the Keetch-Byram Drought Index can predict fire severity (Jenkins et al., 2011). Thus, the expected severity of prescribed fire given weather conditions at a particular time should be factored into decisions about when and where to burn.

Topography, including elevation, slope, aspect, and TCI, underlies landscape heterogeneity in moisture conditions and influences patterns of fire severity and fire effects in the Southern Appalachians and in other mountainous regions (Collins et al., 2006; Flatley et al., 2011, 2015; Hagan et al., 2015; Kane et al., 2015; Lyderson and North, 2012; Miller and Urban, 1999; Urban et al., 2000). Accordingly, we found a strong effect of elevation in our analyses, likely due to the relationship between elevation and moisture in GSMNP. Elevation is strongly correlated with precipitation (Shanks, 1954), and the highest elevation plots in this dataset are located in the eastern part of the park which is generally more mesic. These differences in moisture lead to differences in fire severity, as wetter sites are less prone to high-severity fire.

Elevation and moisture differences may also relate to differences in the rate and type of changes that occurred during the fire exclusion period, affecting pre-fire conditions and shaping the magnitude and direction of fire effects. Our results support Nowacki and Abrams' (2008) assertion that mesophication occurs more quickly and is more steadfast on mesic sites, because they tend to have more favorable growing conditions. In the GSMNP, this would mean that during the fire exclusion period, the more mesic sites that once supported fire dependent vegetation would have grown denser and shadier than the drier, lower elevation sites in the western part of the park, and would have individuals of fire-sensitive species large enough to resist fire. Therefore, prescribed burns would be less effective at restoring pine/oak dominance. Our results support this hypothesis. Elevation is correlated with pre-fire depth of litter and duff ($r = 0.25$, $p = 0.008$) and a plot's elevation and the average pre-fire DBH of non-pine/oak species are marginally significantly correlated ($r = 0.30$, $p = 0.06$). Plots at higher elevations experience less severe fires (Tables 2 and 3) and change less after fire (Tables 4 and 5). Encroachment of hardwoods and other fire sensitive species will be easier to reverse on sites where individuals of these species are still small and susceptible to fire, but prescribed fire or other management interventions

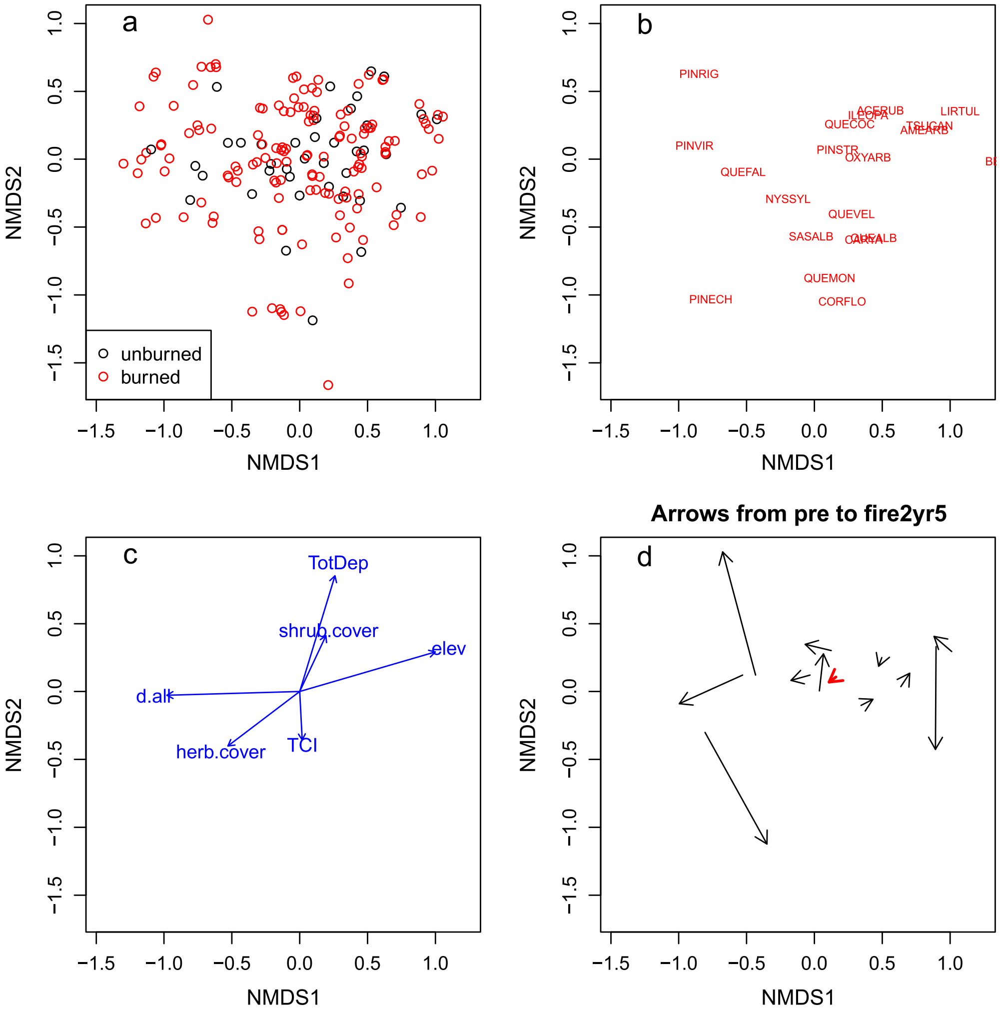

Fig. 4. Results from ordinations with relative abundance data. (a) Plots color-coded by burned vs. unburned. (b) Species scores. (c) Environment vectors. Only significant vectors ($p > 0.05$) are displayed. (d) Change vectors drawn from before fire to 5 years after the second fire. The red vector is the average vector. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4

Spearman's correlation between environment variables and plots' dissimilarity to itself calculated from unstandardized abundance data for given monitoring statuses. Only significant results are displayed.

Environment/fire variable	Pre to f1y1 ($n = 33$)	Pre to f1y2 ($n = 34$)	Pre to f1y5 ($n = 20$)	Pre to f2y1 ($n = 16$)	Pre to f2y5 ($n = 11$)
Elevation	-0.39^{*}	-0.45^{**}	$0.39^{\cdot}$	-0.69^{**}	$-0.61^{\cdot}$
Aspect		$0.31^{\cdot}$	$0.42^{\cdot}$		
Slope			-0.51^{*}		
TCI					
Total fuel reduction	$0.34^{\cdot}$	0.43^{*}			
Litter and duff reduction		0.42^{*}			
Depth of litter and duff	-0.65^{*}	-0.79^{***}			$-0.62^{\cdot}$

Significance codes:
$^{\cdot}$ $P < 0.1$.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

Table 5

Spearman's correlation between environment variables and plots' dissimilarity to itself calculated from relativized density data for given monitoring statuses. Only significant results are displayed.

Environment/fire variable	Pre to f1y1 ($n = 33$)	Pre to f1y2 ($n = 34$)	Pre to f1y5 ($n = 20$)	Pre to f2y1 ($n = 16$)	Pre to f2y5 ($n = 11$)
Elevation		$-0.31^{\cdot}$		-0.73^{**}	$-0.54^{\cdot}$
Aspect					
Slope			-0.48^{*}		
TCI					
Total fuel reduction		0.40^{*}			
Litter and duff reduction		0.42^{*}			
Depth of litter and duff	-0.60^{*}	-0.75^{***}			

Significance codes:
$^{\cdot}$ $P < 0.1$.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

targeting fire-sensitive species may be more urgently needed on the more mesic higher elevation sites in order to achieve restoration goals.

4.3. Conclusions

Fire exclusion has affected the structure, function, and composition of xeric pine-oak forests in GSMNP. The recent reintroduction of prescribed fire in the park has aimed to reduce stand densities and promote pine and oak regeneration. We used multivariate techniques to assess changes in forest stand structure and composition following reintroduction of prescribed fire in fire-suppressed stands. Our results indicate that while fires do cause mortality that reduces stand density, this mortality has not consistently restored pine and oak dominance in the canopy. However, other studies have found that prescribed fire does promote establishment of yellow pine seedlings (Jenkins et al., 2011; Elliott et al., 1999; Welch et al., 2000). Further monitoring of prescribed fires and their impacts will be necessary to determine whether increased seedling establishment leads to the maintenance and restoration of dominance in the canopy.

Lightning fire is rare in GSMNP, the pre-human importance of lightning fire is unknown, and historic fire regimes were dominated by anthropogenic fire (Harmon, 1982; Cohen et al., 2007). Lightning fires, even if let burn, are unlikely to account for the abundance of xeric-pine oak forests across the Southern Appalachian landscape. Therefore, maintaining xeric pine-oak forests at their pre-suppression abundance would require an enduring commitment to prescribed fire. This study includes some plots that have experienced two prescribed fires, but does not explicitly consider characteristics of the fire regime other than fire severity, such as fire frequency, fire season, or fire size. These variables can be important in driving the response to prescribed fire in terms of fuel consumption, tree dynamics, stand diversity and other post-fire effects (Glitzenstein et al., 1995; Sparks et al., 1998; Peterson and Reich, 2001; Andersen et al., 2005; Knapp et al., 2005). Future research in the Southern Appalachians should investigate the role of the fire regime in determining effects of prescribed fire.

Prescribed fire alone may not be the most effective strategy to restore and maintain pine and oak dominance in xeric ridge forests in the Southern Appalachians. For example, a combination of fuel treatments and prescribed fires has shown promise for restoring open woodland structure at another Southern Appalachian site (Waldrop et al., 2013, 2014). In addition, restoration at some sites where mesophication has progressed furthest may no longer be feasible, perhaps precluding maintaining xeric pine-oak forests at their historically broad geographic range (Grissino-Mayer, 2016). Managers should take this into account, prioritizing restoration at sites where historical fidelity is still possible, and focusing on maintaining biodiversity in novel ecosystems. Understanding how to maintain and restore pine- and oak- dominated xeric ridge forests in the Southern Appalachians is a long-term project and will require flexible, adaptive management planning accompanied by continued monitoring and research.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.01.027.

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