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Initial conditions influence effects of prescribed burns and deer exclosure fences on tree regeneration and understory diversity in Appalachian oak-dominated forests

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ABSTRACT

Sustaining oak-dominated forests that support regionally important biodiversity in the Appalachian Mountains is a substantial challenge for land managers due to mesophication – a region-wide phenomenon in which forest composition shifts from oaks to shade tolerant, mesic species such as maples. To inform oak forest management that includes biodiversity preservation as a management objective, we established a two treatment factorial design experiment at two sites to determine the effects of prescribed fire and deer herbivory on tree regeneration and understory plant diversity in dry oak-dominated forests. Data were collected before and after treatments were applied. Prescribed burns altered species composition to favor fire-adapted species and deer exclosure fences protected woody and herbaceous species sensitive to deer browse at both sites, however the initial conditions in the forests profoundly influenced the effects of these treatments. Prescribed fires promoted oak seedlings over maple seedling where oak seedlings were well stocked. Conversely, burning favored maple seedlings to the detriment of oak seedlings in areas where chronic over-browsing resulted in a depauperate understory. Although fire reduced understory plant cover at both sites, overall understory species richness was not affected by burning. This suggests that prescribed fire did not have detrimental effects on forest understory diversity, although herbaceous species diversity was significantly reduced by burning the site with an initially depauperate understory. Fencing resulted in large increases in species richness and cover of understory plants, including more than doubling the cover of tree seedlings and the abundance of tall seedlings in fenced plots, as well as shifts in understory composition towards species sensitive to deer browse. The herbaceous layer in this study contained nearly 6 species for every one species found in the tree canopy, reaffirming the importance of the herbaceous layer in the biodiversity of Appalachian oak-dominated forests. These results provide guidance to managers of protected areas seeking to enhance oak regeneration while maintaining or promoting native plant diversity in the forest understory.

1. Introduction

Oak-dominated forests cover vast areas of dry ridgetops and mesic hillsides in the Appalachian Mountains stretching from northern Alabama into New York (Braun 1950, Dyer 2006). These forests are important regional resources because they support diverse communities of animals and plants, with >100 vertebrate species relying on acorns as crucial food sources (Brose et al. 2014) and >500 native butterfly and moth (*Lepidoptera*) species whose larvae feed on oak foliage (Tallamy and Shropshire 2009). Oak trees support more insects than maple-dominated forests, and therefore host higher abundances and greater species richness of birds (Rodewald and Abrams 2002).

However, the future of these forests is uncertain due to mesophication – a region-wide phenomenon in which forest composition shifts from oaks (*Quercus* spp.) to shade tolerant, mesic species such as maples (*Acer* spp., Nowacki and Abrams 2008, Woodall et al. 2008) caused by decades of fire suppression (Lafon et al. 2017), increasing regional precipitation (Itter et al. 2017), losses in keystone animal and

Abbreviations: AIC, Akaike information criterion; ISA, indicator species analyses; MRPP, multi-response permutation procedures.

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plant species (McEwan et al. 2011), and altered fuel flammability on the forest floor (Kreye et al. 2013). As a result, oak saplings and seedlings are typically underrepresented in oak-dominated forests (Abrams 2003, Widmann and McWilliams 2007, Brose et al. 2008, Iverson et al. 2008, Perles et al. 2014a).

The mesophication of oak forests has profound impacts not only on oak regeneration, but on the diversity of the herbaceous layer. Rogers et al. (2008) documented a 25% decline in species richness in the herbaceous layer of oak dominated forests as maples gained abundance in the forest stands, while Fralish (2004) reported that oak forests with dense maple subcanopies contain one-third the herbaceous diversity of oak forests without maples. Though often overlooked, the herbaceous layer of Appalachian oak forests contains the vast majority of forests' plant diversity and plays key roles in nutrient cycling and energy flow through the forest ecosystem (Gilliam 2007). The herbaceous layer typically receives attention only when over-abundant species (e.g. ferns) hinder tree regeneration (Horsley 1993, Lyon and Sharpe 2003). The lack of focus on the most biodiverse strata of closed-canopy oak-dominated forests limits our ability to enact forest management that both promotes oak regeneration and protects or enhances species diversity in the herbaceous layer.

Prescribed fire has been recommended as one of the most important tools for restoring oak regeneration. A synthesis of decades of oak-fire research (Brose et al. 2014) recommends silvicultural prescriptions effective at regenerating oak-dominated forests, but these prescriptions may be incompatible with the conservation mandates in some protected areas where silviculture practices are not permitted. Furthermore, the prescriptions do not specifically include the nativity and diversity of the herbaceous forest floor as a management target. In contrast to mechanical harvesting, several recent studies (Royo et al. 2010, Nuttle et al. 2013) created canopy gaps through girdling individual trees and focused on the effects of prescribed fire and canopy gaps on the diversity of the forest understory.

Herbivory by white-tailed deer (*Odocoileus virginianus*) can profoundly influence the trajectory of oak regeneration in Mid-Atlantic forests (Abrams and Johnson 2012, McGarvey et al. 2013, Blossey et al. 2019), as well as reduce understory species richness, alter species composition towards dominance of non-preferred and browse-resilient species, and speed regional biotic homogenization (Horsley et al. 2003, Cote et al. 2004, Habeck and Schultz 2015). Constructing deer exclosure fences has been a widely-used strategy to promote tree regeneration and protect understory diversity (Long et al. 2007, McGarvey et al. 2013, Bourg et al. 2017), despite the cost of installing and maintaining the fences.

To inform management of oak-dominated forests in protected areas where preservation of forest biodiversity is a guiding management objective, we established a two treatment factorial design experiment to determine the effects of prescribed fire and deer herbivory alone, and in combination, on tree regeneration and understory plants in dry oak-dominated forests. This study directly supports the understanding of how prescribed fire and deer herbivory influence regeneration and diversity in oak forests, which will allow managers of protected areas throughout the Appalachian Mountains to plan more effective treatments to meet resource objectives.

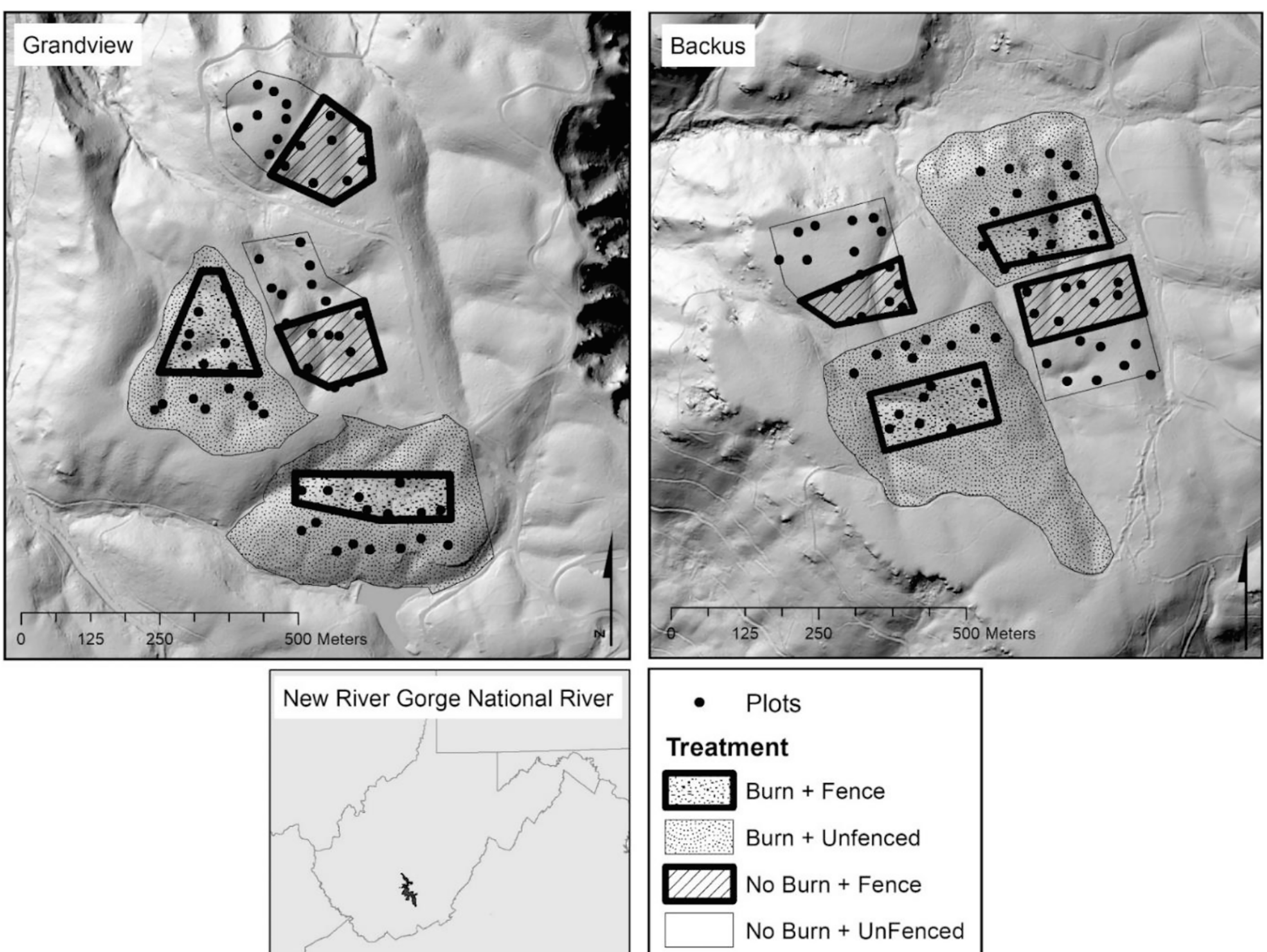

Fig. 1. Factorial study design with two treatments of prescribed fire (Burned and Unburned) and deer exclosure fence (Fenced and Unfenced) at two sites (Grandview and Backus) in New River Gorge National Park and Preserve, a unit of the National Park Service located in southern West Virginia.

2. Material and methods

This study occurs at two sites in the New River Gorge National Park and Preserve, a unit of the National Park Service located on the Allegheny Plateau in southern West Virginia (Fig. 1). Within the park, oak forests cover nearly half of the park area (Vanderhorst et al. 2007). The two sites (Backus Mountain and Grandview State Park, hereafter called Backus and Grandview) are dominated by oak-hickory forest growing on acidic, low-fertility soils, such as Nallen, Clifftop, Fenwick, Layland and Laidig series, formed in colluvium over Raleigh Sandstone of the New River Formation (Vanderhorst et al. 2007, USDA 2013, McColloch et al. 2013). Tree cores from long-term forest health monitoring plots reveal that most ridgetop oaks in those sections of the park are between 90 and 110 years old (Saladyga et al. 2020). The Backus site spans 800–845 m in elevation, while the Grandview site sits on a slightly lower ridgetop at 715–745 m. Hunting regulations are a prominent difference between the two sites. While hunting has been permitted at Backus since 1978 when the New River Gorge became part of the National Park Service, hunting has long been prohibited at Grandview, which served as a state park from 1939 to 1990 when it was transferred to the National Park Service. Under the park's new designation in 2020 as a National Park and Preserve, hunting continues to be prohibited at Grandview and permitted at Backus.

We established a factorial experiment to evaluate the effect of two treatments (prescribed burning and deer exclosure fencing) and the interaction of these treatments on tree regeneration and understory diversity. Each treatment had two levels (Burned and Unburned; Fenced and Unfenced) resulting in four treatment combinations with two replicates of each treatment at each site. Implementation of the experiment occurred as follows. Each 20-ha study site was divided into four units of roughly equal area and then prescribed burning treatments were randomly assigned to two units, leaving the remaining two units as unburned. Next, two 4-ha sample areas were identified in each burned or unburned unit, and a treatment of fenced or unfenced was randomly assigned to each area, such that each unit contained one fenced and one unfenced area (Fig. 1).

Permanent plots were used to sample vegetation within each treatment area. Because prescribed fire can be heterogeneous, we used restricted random sampling to ensure that plots were spatially distributed throughout each sample area. Each sample area was divided into eight equal polygons and those polygons were internally buffered by 8 m so that plots would not overlap spatially. One plot was then randomly located within each buffered polygon creating eight plots within each sample area.

The 128 plots were sampled using established methods adapted from the National Park Service Eastern Rivers and Mountains Inventory and Monitoring Network Vegetation Monitoring Program (Perles et al. 2014b), and the United States Forest Service Forest Inventory and Analysis Program for measuring trees and tree regeneration (USDA 2015). The plot design included several embedded sampling units (Perles et al. 2017). Tree, stand, and site measurements were collected within fixed-area, circular plots, 7.3-m in radius. Canopy closure was visually estimated and recorded as one of five cover class categories. Pole-sized trees were tallied within a 26.6-m^2 triangular quarter plot. Tree regeneration and shrub measurements were collected in one 2-m radius circular microplot, and data on understory plant composition were monitored using four 1-m^2 quadrats.

Plots were established and sampled in June 2015 before any treatments were applied. Woven-wire deer exclosure fences 2.5-m in height were constructed around the 4 areas in each site assigned to fence treatments in the winter of 2015 to 2016. Groundstory prescribed burns were conducted at the two burn units at Grandview and Backus in the springs of 2017 and 2018, respectively. Strip-head fires and backing fires were ignited with hand-help drip torches, resulting in 1.5–8 cm flame lengths, with maximum flame lengths of 15–23 cm observed in some section of Grandview. Rate of spread varied from 20 to 80 m per hour and flame depth zone ranged from 2.5 to 7.5 cm. All plots were resampled in June of 2019 using established methodologies. Throughout the study period, fences were inspected and repaired monthly to ensure fence integrity.

Modeling to detect changes between pre- and post-treatments was conducted in the R 4.0.2 software (R Core Team 2020). We fit linear models to estimate changes in live tree basal area and density with fenced and burn treatments as effects and each site modeled separately. Tree mortality was compared among treatments within each site using Kruskal-Wallis rank sum tests, followed by Dunn's tests (Hollander and Wolfe 1973). Basal area and density for live and dead trees were compared between the two sites using two-sample t-tests, including all trees, only oak trees, and only maple trees to determine if significant differences existed in the tree canopy between the two sites.

For seedling abundance, we used the lme4 package (Bates et al. 2015) to fit generalized linear models and generalized mixed models with Poisson distributions, using fenced and burn treatments as fixed effects and treatment block as a random effect, with each site modeled separately. The best model was selected from comparison of Akaike information criteria (AIC) using the AICcmodavg package (Mazerolle 2020). Seedling density for all species, oaks, and maples were compared between the two sites using two-sample t-tests to determine if significant differences existed in tree regeneration between the two sites.

To assess average percent cover and richness of understory species, we fit linear models with fenced and burn treatments as effects for each site separately. In linear models fit for taxonomic groups (e.g. herbaceous, shrub, vine species, etc.), cover and richness data were natural log-transformed. To investigate changes in species composition on the forest floor, multi-response permutation procedures (MRPP; McCune and Grace 2002) were performed with PC-Ord 7.08 (McCune and Mefford 2018). We tested the null hypotheses that species composition did not vary: (a) between sites (Backus and Grandview) with pre-treatment and post-treatment data analyzed separately, and (b) among treatments and years within each site. Since four plots were destroyed during fence construction, plots were randomly chosen from each treatment to be included in the MRPP, which requires equal sample size. Thus, site comparisons included 20 plots for each site, and treatment-by-year comparisons included 5 plots per treatment for Backus and 7 plots per treatment for Grandview. To evaluate the differences in species composition observed between sites and among treatments and years, indicator species analyses (ISA, Dufrene and Legendre 1997) were performed in PC-Ord 7.08 (McCune and Mefford 2018).

3. Results

3.1. Forest canopy composition

Before treatments were applied, oaks comprised more than half the relative abundance in the canopy, whereas maples accounted for $<25\%$ of the canopy at both sites (Fig. 2). Canopy composition was similar between sites (t-tests, $p > 0.05$), considering basal area and density of live and dead trees, including all species and only oak species. The only significant difference between the forest canopies of the two sites was density of live maple trees. Grandview contained on average 54 fewer maple trees per hectare than Backus, though live basal area of maple trees was similar between the sites.

The tree canopy was relatively stable throughout the study, with no significant trends ($p > 0.1$) detected in live tree basal area or density, and no differences ($p > 0.1$) in tree mortality were observed among treatments at either site. Canopy closure was $> 75\%$ in nearly all (94%) plots in both sites and sampling periods. Species diversity in the forest canopy included 24 native tree species among all plots in both sites.

3.2. Tree regeneration

Despite the dominance of oaks in the canopy, no oak saplings were

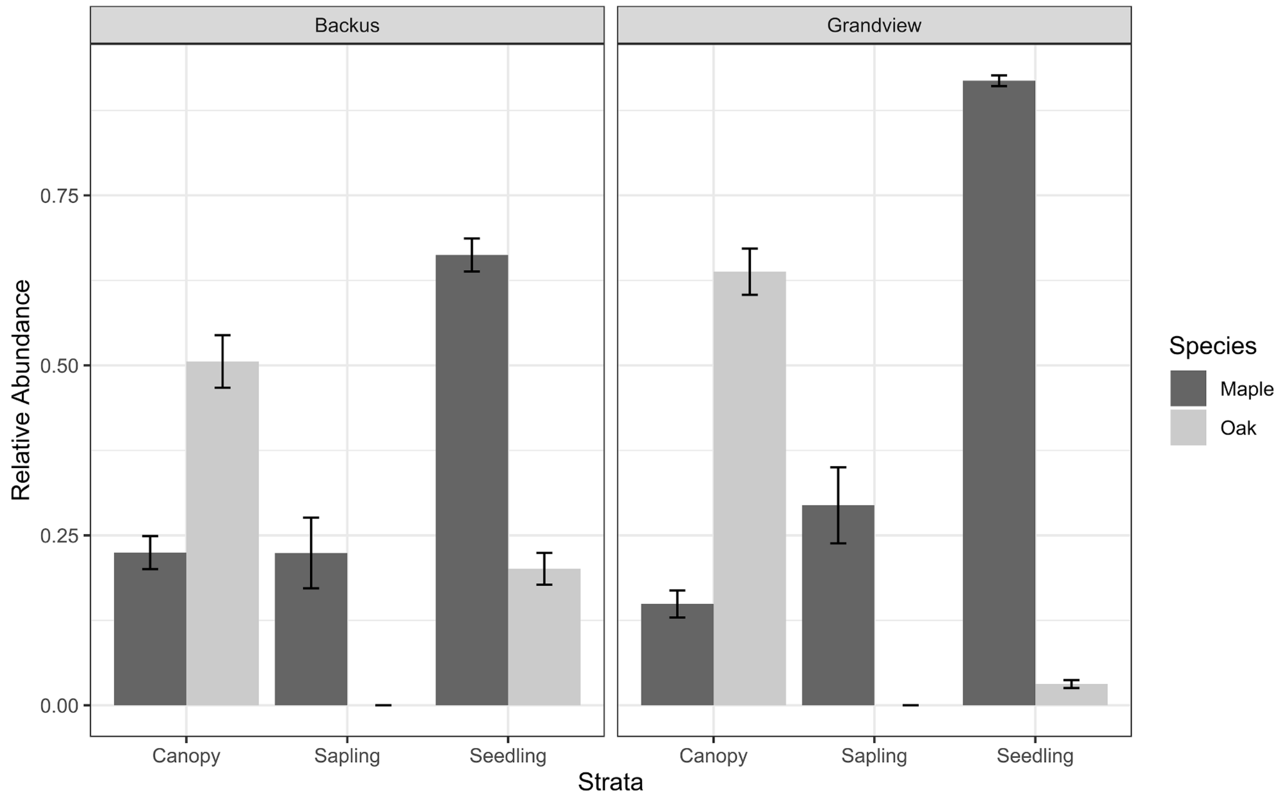

Fig. 2. Relative abundance (mean ± 1 standard error) of maple and oak species in three strata of the forest at two sites in New River Gorge National Park and Preserve. Relative basal area was calculated for the canopy stratum, and relative density was calculated for sapling and seedling strata.

observed at either site, while maples comprised <30% of saplings. Maples dominated the seedling stratum, accounting for 66.2 ± 2.4% and 91.8 ± 0.8% of seedlings at Backus and Grandview, respectively. Note that although maple trees were less abundant in Grandview, maple seedlings comprised a larger proportion of the seedling layer at Grandview than at Backus. Oaks comprised 20.1 ± 2.3% of the seedlings at

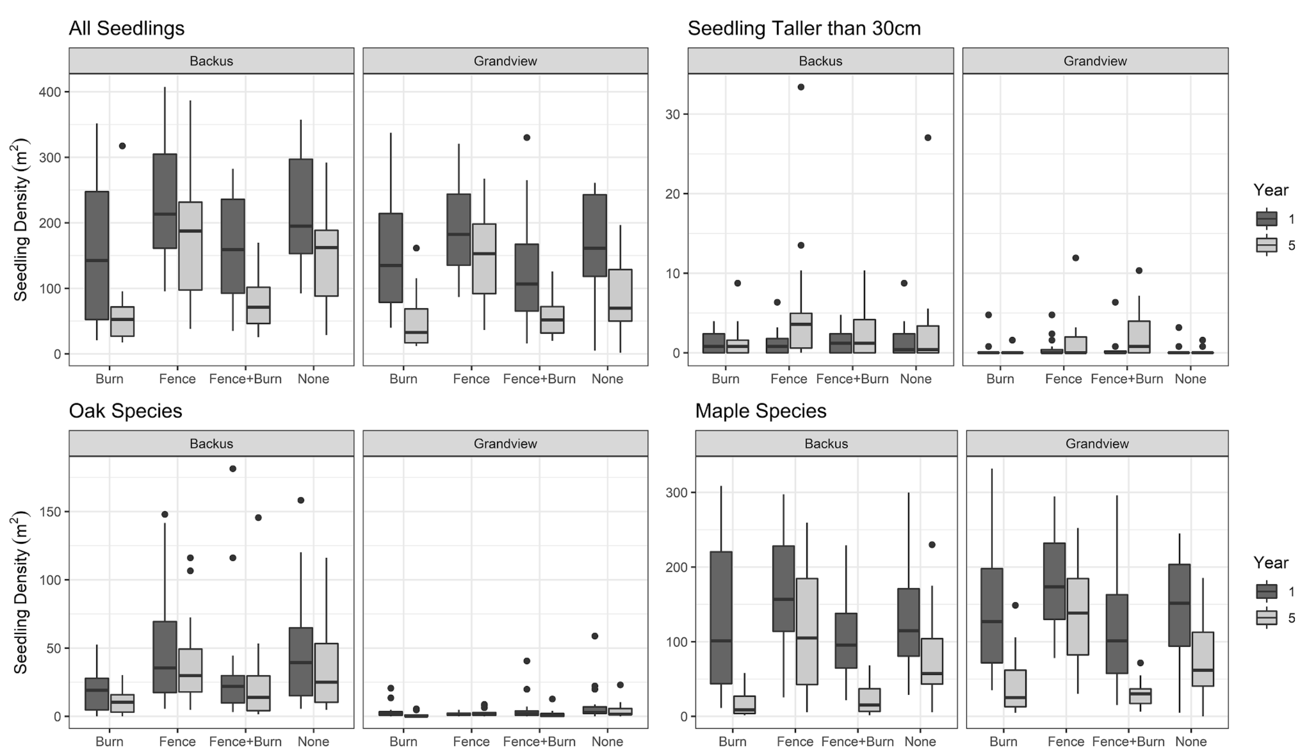

Fig. 3. Density of seedlings before treatments (Year 1) and after treatments (Year 5) in burned, fenced, burned + fenced, and no treatment plots at two sites in New River Gorge National Park and Preserve.

Backus and only 3.1 ± 0.6% of the seedlings at Grandview (Fig. 2). Although maple seedling density was not significantly different between the two sites, total seedling density and oak seedling density were significantly lower at Grandview than at Backus (Fig. 3, t-tests, $p < 0.05$). These differences persisted both pre- and post-treatments.

Total seedling density decreased between 2015 and 2019 across all treatments at both sites (Fig. 3), likely due to annual variation in seed production and survival. Prescribed burns significantly reduced seedling abundances for all species, oaks, and maples, as well as seedlings >30-cm in height (Table 1). At Backus, total seedling density was reduced by 36.4%, with a 33.0% reduction in oak seedlings and a 73.3% reduction in maple seedlings.

At Grandview, total seedling density decreased by 47.2%, while maple seedlings were significantly reduced by 53.6% and oak seedlings declined by 71.2%.

Four years after deer exclosure fences were installed, fenced plots at both sites contained significantly more total seedlings (Fig. 3, Table 1) with dramatic increases in seedlings taller than 30-cm. Fenced plots at Grandview contained nearly 6 times more tall seedlings compared to unfenced plots, while tall seedlings were 2.6 times more abundant in fenced plots at Backus. No significant increases in oak seedling density were observed in fenced plots at either site. Fenced plots at Backus contained 10% more total seedlings, primarily due to an equivalent increase in maple seedlings. At Grandview, fencing caused a 50% increase in total seedling density, with a 45% increase in maple seedlings (Fig. 3, Table 1). The interaction between fence and burn treatments was significant only for maple seedlings at Grandview, where a 31.6% reduction was observed. For all seedling variables, the initial seedling density in 2015 was a significant predictor of seedling density in 2019, however the effect sizes were small, typically < 3% (Table 1). Sapling density could not be modeled due to the small number of saplings observed over the study period.

Table 1
Log of the mean effect estimates (with standard error in paratheses) for seedling density trends in burned, fenced, burned + fenced, and no treatment plots at two sites in New River Gorge National Park and Preserve. Note that rates reported in the text were derived from the exponential of the effect estimates listed here. GLM = generalized linear model with log link; GMM = generalized mixed model with log link. Significance levels: *** $p < 0.0001$, ** $p < 0.01$, * $p < 0.05$, ns = interaction term was not significant and models without the interaction term had lower AIC compared to equivalent models including interaction.

	Burn	Fence	Burn + Fence	Pre-treatment Density	Model
Backus					
Total Seedlings	−0.453 (0.024) ***	0.100 (0.021) ***	ns	0.004 (0.000) ***	GLM (log link)
Maple Seedlings	−1.319 (0.042) ***	0.178 (0.030) ***	ns	0.006 (0.000) ***	GLM (log link)
Oak Seedlings	−0.401 (0.046) ***	0.037 (0.043)	ns	0.012 (0.000) ***	GLM (log link)
Seedlings > 30 cm Tall	−0.599 (0.431)	0.973 (0.428) *	ns	0.309 (0.023) ***	GMM (log link)
Grandview					
Total Seedlings	−0.639 (0.027) ***	0.408 (0.025) ***	ns	0.005 (0.000) ***	GLM (log link)
Maple Seedlings	−0.768 (0.044) ***	0.377 (0.033) ***	−0.381 (0.065) ***	0.006 (0.000) ***	GMM (log link)
Oak Seedlings	−1.245 (0.504) *	0.035 (0.435)	0.519 (0.668)	0.034 (0.0030) ***	GMM (log link)
Seedlings > 30 cm Tall	−0.248 (0.671)	1.775 (0.484) **	0.629 (0.710)	0.142 (0.0420) **	GMM (log link)

3.3. Understory

Compared with the 24 species documented in the canopy during the study, the forest understory was comprised of 136 species including 60 forbs, 16 graminoids, 6 ferns, 8 vines, 19 shrubs, and 27 trees. Across both sites and years, 177 taxa were observed, with 83.8% identified to species, 15.6% identified to genus, and <1% of observations identified to family or considered unknown morphospecies.

Species richness and cover of understory plants was significantly higher at Backus, compared to Grandview (Fig. 3, t-tests, $p < 0.001$), and understory plant species composition was significantly different between sites in both years (MRPP, $p < 0.0001$). Comparing the two sites in year 1 before treatments were applied, indicator species analysis revealed 34 species were more abundant in the understory at Backus, notably seedlings of oak (*Quercus alba, Q. rubra, Q. prinus, Q. velutina*) and other canopy trees (*Oxydendron arboreum, Sassafras albidum, Fraxinus americana, Prunus serotina, Carya* spp.), as well as common shrubs (*Ilex montana, Hamamelis virginiana, Viburnum acerifolium*), graminoids and herbs (ISA, p values < 0.05). Six species characterized Grandview pre-treatment, including seedlings of American beech (*Fagus grandifolia*) and eastern white pine (*Pinus strobus*, ISA, p values < 0.05).

Within the Backus site, species composition did not differ significantly among treatments in year 1 (MRPP, $p = 0.15$), though significant differences in species composition among treatments were observed post-treatment (MRPP, $p = 0.002$). Indicator species analysis comparing all treatment-by-year combinations showed that tulip poplar (*Liriodendron tulipifera*) seedlings were more abundant in burned plots, and deerberry (*Vaccinium stamineum*) and sassafras (*Sassafras albidum*) were more abundant in plots that were both burned and fenced (ISA, p values < 0.05). Unburned fenced plots were characterized by white oak (*Quercus alba*) seedlings, maple-leaved viburnum (*Viburnum acerifolium*), and eight other herbaceous species, including three species sensitive to deer browse (*Uvularia perfoliata, Prosartes lanuginosa, Medeola virginiana*, ISA, p values < 0.05).

At Grandview, understory plant composition differed among treatments both pre-treatment (MRPP, $p = 0.008$) and post-treatment (MRPP, $p < 0.0001$). However, indicator species analysis comparing all treatment-by-year combinations identified characteristic species only in post-treatment plots. Woody species that resprout strongly after fire (*Liriodendron tulipifera, Sassafras albidum, Nyssa sylvatica, Vaccinium pallidum*) were more abundant in plots that were fenced and burned (ISA, p values < 0.05), though two species not typically resilient to fire (*Magnolia fraseri, Gaultheria procumbens*) were also more abundant in these plots. Fenced, unburned plots contained significantly higher abundance of woody species that do not tolerate fire (*Acer rubrum, Carya* spp., *Viburnum acerifolium, Smilax rotundifolia*), herbaceous species (*Anemone quinquefolia, Stellaria pubera, Polygonatum pubesescens, Dioscorea* spp.) and Christmas fern (*Polystichum acrostichoides*). Red oak seedlings (*Quercus rubra*) were significantly more abundant in control plots post-treatment (ISA, p values < 0.05), due to a masting event.

The cover of plants on the forest floor increased between 2015 and 2019 in plots that were not fenced or burned (Fig. 4), likely due to annual variation in precipitation and temperature. Cover of all understory plants increased in fenced plots by 60% at Backus and 70% at Grandview. Looking at taxonomic groups, significant increases in cover between 89% and 180% were observed for herbaceous, tree, shrub, and vine species at both sites in fenced plots. In particular, tree seedling cover was over two times greater in fenced plots in Grandview compared to the other treatments (Table 2). Burning resulted in a 63% and 64% decrease in understory cover at Backus and Grandview, respectively (Table 2). At Backus, cover of herbaceous, tree, and shrub species all decreased in burned plots by approximately 48%, while vine cover decreased by 72%. At Grandview, significant cover decreases were observed in burned plots only for tree seedlings (−68%). For nearly all

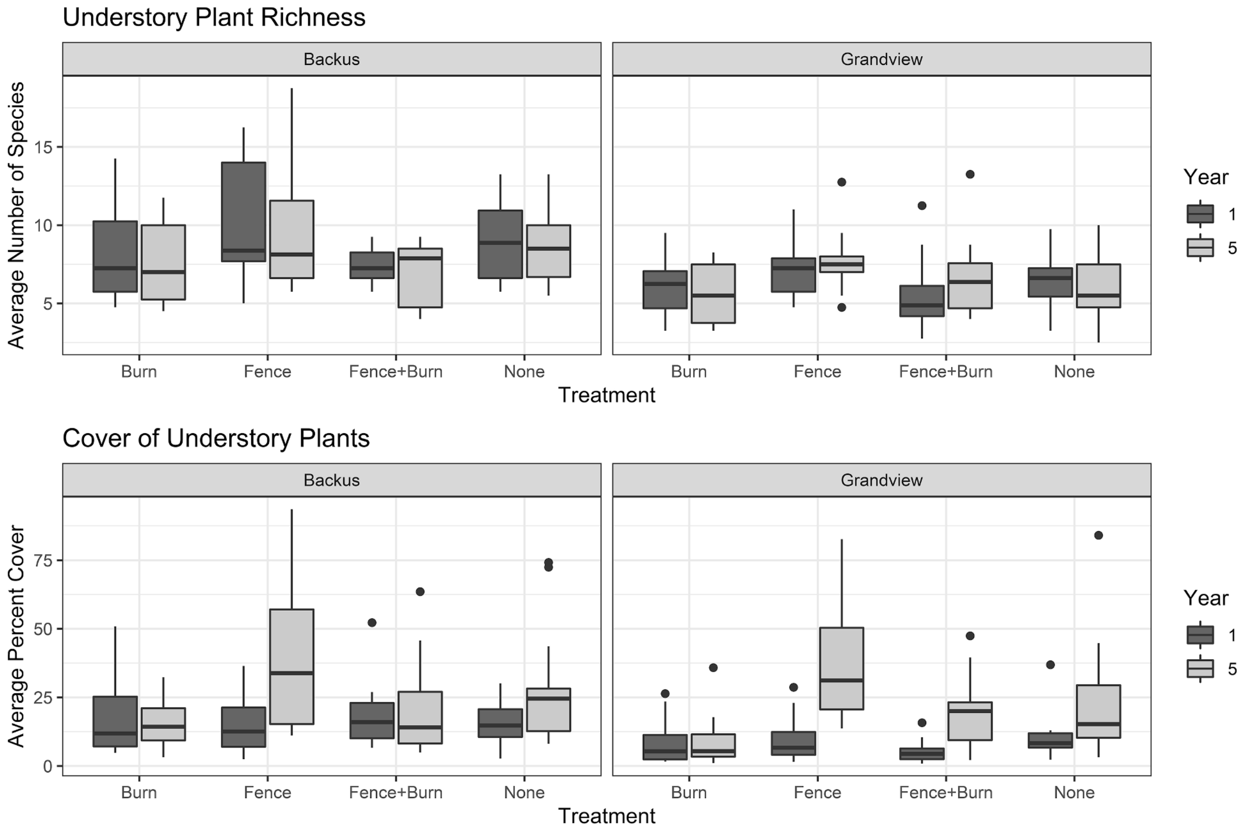

Fig. 4. Species richness and percent cover of understory plants before treatments (Year 1) and after treatments (Year 5) in burned, fenced, burned + fenced, and no treatment plots at two sites in New River Gorge National Park and Preserve.

cover variables, value in 2015 was a significant predictor of the value in 2019, however the effect sizes were small, 11 to 18% (Table 2). One notable exception was tree seedling cover in Grandview, for which pre-treatment cover was not a significant predictor, indicating that fencing and burning treatments at Grandview were more important to tree seedling cover than the initial conditions.

Overall diversity of plant species in the forest understory was stable between 2015 and 2019 at Backus regardless of treatment. A 44% increase in species richness in Grandview fenced plots was the only significant change in understory diversity at that site (Fig. 4, Table 2). Tree seedlings and herbaceous species were the only taxonomic groups with non-zero and non-modal data distributions for which species richness models could be fit. At Backus, a 16% reduction in tree seedling species richness in burned plots was the only significant change observed. Burned plots in Grandview contained 20% fewer herbaceous species, while fenced plots in Grandview saw a 26–27% increase in herbaceous and tree seedling richness, respectively (Table 2). For all species richness variables, value in 2015 was a significant predictor of the value in 2019.

4. Discussion

Prescribed burns altered species composition to favor fire-adapted species and deer exclosure fences protected woody and herbaceous species sensitive to deer browse at both sites, however the initial conditions in the forests profoundly influenced the effects of these treatments. Despite containing similar forest canopies, the understories of the two sites were significantly different pre-treatment, with diverse tree seedling and shrub layers characterizing the forests at Backus, and species typically avoided by deer characterizing the Grandview understory. The depauperate understory at Grandview is typical of forests experiencing decades-long legacy of over-abundant deer (Abrams and Johnson 2012). Given the initial depauperate understory at Grandview, fencing resulted in large increases in species richness and cover of understory plants, including more than doubling the cover of tree seedlings in fenced plots. The large increase in species diversity in Grandview fenced plots is encouraging given previous studies suggesting the legacy of over-browse can reduce forest diversity for decades following deer exclusion (Royo et al. 2010, Habeck and Schultz 2015). Even in Backus' more diverse understory, fencing increased understory plant cover, and the composition of fenced plots became characterized by species in the Liliacaea that are preferred deer browse (Perles et al. 2014b).

While fences promoted increases in seedling abundance for all species and maples at both sites, the increases were more substantial at Grandview due to the significantly lower initial stocking level relative to Backus. However, dramatic increases in tall seedlings were observed at both sites in fenced plots, confirming that reduced browse pressure is crucial for seedlings to mature into saplings, which were largely absent from the current forests. Oak seedling density did not increase in fenced plots, due to insufficient light in the closed canopy forest, the high initial oak stocking at Backus, or a combination of these two factors.

Prescribed fires drastically reduced total seedling abundance, however, the relative effect of the fires on oaks versus maples varied between the two sites. Initial pre-treatment oak seedling density was over 38,000 oak seedlings per hectare at Backus and only 5,300 oak seedlings per hectare at Grandview. The severe decline (71%) in oak seedlings in burned plots at Grandview was likely due to the initial poor level of oak seedling stocking. We hypothesize that the lack of oak regeneration in Grandview is caused by decades of browse by over-abundant deer who shelter in the refugia where hunting is prohibited. Oak seedlings that have been repeatedly browsed lack the reserve resources in their root systems to resprout after fire (Johnson et al. 2009). At higher seedling stocking levels in Backus, the prescribed fire disproportionally reduced

Table 2
Mean effect estimates (with standard error in paratheses) from linear models for trends in cover and richness of understory species in burned, fenced, and no treatment plots at two sites in New River Gorge National Park and Preserve. The interaction of burn + fence was not significant for any of the variables and is not reported. Note that rates reported in the text were derived from the exponential of the effect estimates listed here for variables that were log transformed. Significance levels: *** $p < 0.0001$, ** $p < 0.01$, * $p < 0.05$.

		Burn	Fence	Pre-treatment Value
	Percent Cover			
Backus	All Species	−16.543 (3.971) **	13.621 (3.95) **	1.144 (0.186) ***
	Herbaceous Species (log transformed)	−0.634 (0.236) **	0.840 (0.236) **	0.696 (0.081) ***
	Shrub Species (log transformed)	−0.654 (0.286) *	0.816 (0.278) **	0.900 (0.086) ***
	Tree Species (log transformed)	−0.655 (0.147) ***	0.623 (0.149) ***	0.577 (0.093) ***
	Vine Species (log transformed)	−1.280 (0.329) **	0.828 (0.33) *	0.663 (0.093) ***
Grandview	All Species	−11.636 (3.262) **	15.965 (3.247) ***	1.521 (0.229) ***
	Herbaceous Species (log transformed)	−0.601 (0.344)	0.898 (0.336) **	0.827 (0.139) ***
	Shrub Species (log transformed)	−0.365 (0.319)	0.718 (0.295) **	1.01 (0.088) ***
	Tree Species (log transformed)	−1.133 (0.324) **	1.130 (0.326) **	0.088 (0.131)
	Vine Species (log transformed)	−0.300 (0.242)	1.030 (0.24) ***	0.492 (0.098) ***
	Species Richness			
Backus	All Species	−0.726 (0.987)	−0.047 (0.96)	0.851 (0.077) ***
	Herbaceous Species (log transformed)	−0.025 (0.08)	−0.015 (0.079)	0.817 (0.062) ***
	Tree Species (log transformed)	−0.173 (0.049) **	−0.041 (0.048)	0.437 (0.114) **
Grandview	All Species	−1.456 (0.932)	3.466 (0.905) **	0.671 (0.101) ***
	Herbaceous Species (log transformed)	−0.221 (0.085) **	0.232 (0.084) **	0.681 (0.062) ***
	Tree Species (log transformed)	−0.050 (0.077)	0.241 (0.072) ***	0.478 (0.121) **

maple seedlings, compared to a much smaller reduction in oak seedlings. At Backus, tree seedling species diversity decreased in burned plots as fire intolerant species were adversely affected by the prescribed burn, while tree seedling diversity was unaffected by burning in the less-diverse understory at Grandview.

As recommended by Hutchinson et al. (2012), the initial conditions on the ground are critical for prescribed fire to successfully promote oak regeneration. Subsequent prescribed fires at these sites may benefit oak regeneration, especially within the fences where oak seedlings are protected from browse. A *meta*-analysis of prescribed fire effects on oak regeneration found that one-third of studies using a single prescribed fire had negative effects on oak regeneration (Brose et al. 2013), whereas multiple prescribed fires promoted oak regeneration in over half of the studies.

The low intensity prescribed fires used in this study did not cause canopy tree mortality and thus did not increase the amount of light to the forest floor, which is a key factor in promoting oak regeneration (Hutchinson et al. 2012). Once advanced oak regeneration is established, using higher intensity fires or girdling selected trees to create canopy gaps will allow oak saplings to mature into the canopy if they are protected from excessive browse (Collins and Carson 2003, Nuttle et al. 2013). The successive application of prescribed fire, combined with naturally-formed or human-induced canopy gaps under low browse pressure, can improve oak regeneration and tree seedling diversity (Hutchinson et al. 2005a, 2005b; Nuttle et al. 2013; Thomas-Van Gundy et al. 2018).

Although fire reduced understory plant cover at both sites, overall understory species richness was not affected by the prescribed fire, suggesting that prescribed fire did not have detrimental effects on forest understory diversity. Prescribed fires conducted in the dormant season influence woody species more than herbaceous species that are not fully emerged during the burn (Bowles et al. 2007). Similar results were reported by Hutchinson et al. (2005a) and are encouraging for the use of prescribed fire in protected areas whose mission include biodiversity preservation within forest ecosystems. In fact, prescribed burns that create canopy gaps have been shown to increase herbaceous diversity through increased heterogeneity of light and edaphic conditions on the forest floor (Bowles et al. 2007). However, in Grandview's depauperate understory, herbaceous species diversity was reduced in burned plots, further cautioning against applying prescribed fire to degraded forest stands. The herbaceous layer in this study contained nearly 6 species for every one species found in the tree canopy (similar to diversity levels reported by Gilliam 2007), underscoring the importance of the herbaceous layer in plant diversity of oak-dominated forests.

5. Conclusions

These results provide guidance to managers of protected areas seeking to enhance oak regeneration in oak-dominated forests while maintaining or promoting native plant diversity in the forest understory. The initial conditions of the forest understory must be considered before applying prescribed fire, however, dormant-season burns can be a valuable tool to promote oak regeneration and herbaceous diversity. Under current levels of deer browse, fences are effective and necessary to protect oak regeneration and sensitive herbaceous species. As this study continues, the effects of subsequent prescribed burns and continued protective effects of deer exclosure fences will further inform the management of dry oak forests in the Appalachians.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author's contributions

ADR and LDG coordinated and implemented the collection of field data. SJP assisted with field data collection, lead the data analysis, and drafted the manuscript. XMN provided statistical expertise and guidance on the analytical approaches and interpretation of the model results. All authors read and approved of the final manuscript.

References

Abrams, M.D., 2003. Where has all the white oak gone? Bioscience 53, 927–939.

Abrams, M.D., Johnson, S.E., 2012. Long-term impacts of deer exclosures on mixed-oak forest composition at the Valley Forge National Historical Park, Pennsylvania, USA. J. Torrety Botanical Soc. 139 (2), 167–180.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Braun, E.L., 1950. Deciduous Forests of Eastern North America. Philadelphia, PA: Blakiston.

Bowles, M.L., Jacobs, K.A., Mengler, J.L., 2007. Long-term changes in an oak forest's woody understory and herb layer with repeated burning. J. Torrey Bot. Soc. 134 (2), 223–237.

Blossey, B., Curtis, P., Boulanger, J., Dávalos, A., 2019. Red oak seedlings as indicators of deer browse pressure: gauging the outcome of different white-tailed deer management approaches. Ecol. Evol. 9 (23), 13085–13103. https://doi.org/10.1002/ece3.v9.2310.1002/ece3.5729.

Bourg, N.A., McShea, W.J., Herrmann, V., Stewart, C.M., 2017. Interactive effects of deer exclusion and exotic plant removal on deciduous forest understory communities. plx046 AoB Plants 9. https://doi.org/10.1093/aobpla/plx046.

Brose, P.H., Gottschalk, K.W., Horsley, S.B., Knopp, P.D., Kochenderfer, J.N., McGuinness, B.J., Miller, G.W., Ristau, T.E., Stoleson, S.H., Stout, S.L., 2008. Prescribing regeneration treatments for mixed-oak forests in the Mid-Atlantic region. Gen. Tech. Rep. NRS-33. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 100 pp.

Brose, P.H., Dey, D.C., Phillips, R.J., Waldrop, T.A., 2013. A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak reproduction in eastern North America? Forest Sci. 59 (3), 322–334.

Brose, P.H., Dey, D.C., Waldrop, T.A., 2014. The fire–oak literature of eastern North America: synthesis and guidelines. Gen. Tech. Rep. NRS-135. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 98 p.

Cote, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. Syst. 35, 113–147.

Collins, R.J., Carson, W.P., 2003. The fire and oak hypothesis: incorporating the influence of deer browsing and canopy gaps. In: Van Sambeek, J.W., Dawson, J.O., Ponder, F., Jr., Loewenstein, E.F., Fralish, J.S., (Eds.), Proceedings, 13th Central Hardwood Forest conference; 2002 April 1-3; Urbana, IL. Gen. Tech. Rep. NC-234. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Research Station, pp. 44–63. 565 p.

Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366. https://doi.org/10.2307/2963459.

Dyer, J.M., 2006. Revisiting the deciduous forests of eastern North America. Bioscience 56 (4), 341–352.

Fralish, J.S., 2004. The keystone role of oak and hickory in the central hardwood forest. In: Spetich, M.A. (Ed.), Upland oak ecology symposium: history, current conditions, and sustainability. Gen. Tech. Rep. SRS–73. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station, 2004, 311 p.

Gilliam, F.S., 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience 57 (10), 845–858.

Habeck, C.W., Schultz, A.K., 2015. Community-level impacts of white-tailed deer on understorey plants in North American forests: a meta-analysis. AoB PLANTS 7: plv119. https://doi.org/10.1093/aobpla/plv119.

Hollander, M., Wolfe, D.A., 1973. Nonparametric Statistical Methods. John Wiley & Sons, New York, pp. 115–120.

Horsley, S.B., 1993. Mechanisms of interference between hayscented fern and black cherry. Can. J. For. Res. 23 (10), 2059–2069.

Horsley, S.B., Stout, S.L., deCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecol. Appl. 13 (1), 98–118.

Hutchinson, T.F., Sutherland, E.K., Yaussy, D.A., 2005a. Effects of repeated prescribed fires on the structure, composition, and regeneration of mixed-oak forests in Ohio. For. Ecol. Manage. 218, 210–228.

Hutchinson, T.F., Boerner, R.EJ., Sutherland, S., Sutherland, E.K., Ortt, M., Iverson, L.R., 2005b. Prescribed fire effects on the herbaceous layer of mixed-oak forests. Can. J. For. Res. 35 (4), 877–890.

Hutchinson, T.F., Yaussy, D.A., Long, R.P., Rebbeck, J., Sutherland, E.K., 2012. Long-term (13-year) effects of repeated prescribed fires on stand structure and tree regeneration in mixed-oak forests. For. Ecol. Manage. 286, 87–100.

Itter, M.S., Finley, A.O., D'Amato, A.W., Foster, J.R., Bradford, J.B., 2017. Variable effects of climate on forest growth in relation to climate extremes, disturbance, and forest dynamics. Ecol. Appl. 27 (4), 1082–1095.

Iverson, L.R., Hutchinson, T.F., Prasad, A.M., Peters, M.P., 2008. Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern U.S.: 7-year results. For. Ecol. Manage. 255, 3035–3050.

Johnson, P.S., Shifley, S.R., Rogers, R., 2009. The Ecology and Silviculture of Oaks, second ed. CABI International, New York, NY.

Kreye, J.K., Varner, J.M., Hiers, J.K., Mola, J., 2013. Toward a mechanism for eastern North American forest mesophication: differential litter drying across 17 species. Ecol. Appl.. 23 (8), 1976–1986.

Lafon, C.W., Naito, A.T., Grissino-Mayer, H.D., Horn, S.P., Waldrop, T.A., 2017. Fire history of the Appalachian region: a review and synthesis. Gen. Tech. Rep. SRS-219. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 97 p.

Long, Z.T., Pendergast, T.H., Carson, W.P., 2007. The impact of deer on relationships between tree growth and mortality in an old-growth beech-maple forest. Forest Ecol. Manage. 252 (1-3), 230–238.

Lyon, J., Sharpe, W.E., 2003. Impacts of hay-scented fern on nutrition of northern red oak seedlings. J. Plant Nutr. 26 (3), 487–502.

Mazerolle, M.J., 2020. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3-1. https://cran.r-project.org/ package=AICcmodavg.

McColloch, G.H., Hunt, P.J., McColloch, J.S., Peck, R.L., Blake, B.M. Jr., Matchen, D.L., Gooding, S.E., 2013. Bedrock Geology of the New River Gorge National River, West Virginia, West Virginia Geological and Economic Survey, Geologic Quadrangle Maps of West Virginia, Open File Map OF-1301, 4 map sheets, 1:24,000 scale. (GRI Source Map ID 75738).

McCune, B., Mefford, M.J., 2018. PC-ORD. Multivariate Analysis of Ecological Data. Version 7.08.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.

McEwan, R.W., Dyer, J.M., Pederson, N., 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. Ecography 34 (2), 244–256.

McGarvey, J.C., Bourg, N.A., Thompson, J.R., McShea, W.J., Shen, X., 2013. Effects of twenty years or deer exclusion on woody vegetation at three life-history stages in a mid-Atlantic temperate deciduous forest. Northeastern Naturalist 20 (3), 451–468.

Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and "mesophication" of forests in the eastern United States. Bioscience 58 (2), 123–138.

Nuttle, T., Royo, A.A., Adams, M.B., Carson, W.P., 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. Ecol. Monogr. 83 (1), 3–17.

Perles, S.J., Manning, D.R., Callahan, K.K., Marshall, M.R., 2014a. Forest health monitoring in the Eastern Rivers and Mountains Network: 2009–2012 summary report. Natural Resource Report NPS/ERMN/NRR—2014/803. National Park Service, Fort Collins, Colorado.

Perles, S.J., Finley, J., Manning, D.R., Marshall, M.R., 2014b. Vegetation and soil monitoring protocol for the Eastern Rivers and Mountains Network, Version 3. Natural Resource Report NPS/ERMN/NRR—2014/758. National Park Service. Fort Collins, Colorado.

Perles, S., Forder, M., Paull, S., Fry, J., 2017. The oak regeneration study in New River Gorge National River: monitoring the effects of prescribed burning and deer exclusion on tree regeneration and groundlayer diversity in xeric oak-dominated forests. Natural Resource Report NPS/ERMN/NRR—2017/1374. National Park Service, Fort Collins, Colorado.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rodewald, A.D., Abrams, M.D., 2002. Floristics and avian community structure: implications for regional changes in eastern forest composition. Forest Sci. 48, 267–272.

Rogers, D.A., Rooney, T.P., Olson, D., Waller, D.M., 2008. Shifts in southern wisconsin forest canopy and understory richness, composition, and heterogeneity. Ecology 89 (9), 2482–2492.

Royo, A.A., Stout, S.L., deCalesta, D.S., Pierson, T.G., 2010. Restoring forest herb communities through landscape-level deer her reductions: is recover limited by legacy effects? Biol. Conserv. 143, 2425–2434.

Saladyga, T., Maxwell, R.S., Perles, S.J., 2020. Landscape-scale tree growth dynamics at three southern West Virginia National Parks: Bluestone National Scenic River. Gauley River National Recreation Area, and New River Gorge National River. Natural Resource Report NPS/ERMN/NRR—2020/2123. National Park Service, Fort Collins, Colorado.

Tallamy, D.W., Shropshire, K.J., 2009. Ranking lepidopteran use of native versus introduced plants. Conserv. Biol. 23 (4), 941–947.

Thomas-Van Gundy, M.A., Schuler, T.M., Adams, M.B., 2018. Early impacts of fire and canopy gaps on seedling and sapling layers: evidence for reversing mesophication? In: Kirschman, Julia E., (Ed.), comp. 2018. Proceedings of the 19th biennial southern silvicultural research conference. e-Gen. Tech. Rep. SRS-234. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station, pp. 372–382.

United States Department of Agriculture, Natural Resources Conservation Service, and United States Department of the Interior, National Park Service. 2013. Soil survey of New River Gorge National River, West Virginia. Accessible online at: http://soils.usda.gov/survey/printed_surveys/.

United States Department of Agriculture, Forest Service. 2015. Forest Inventory and Analysis National Core Field Guide. Version 7.0. United States Forest Service.

Vanderhorst, J.P., Jeuck, J., Gawler, S.C., 2007. Vegetation Classification and Mapping of New River Gorge National River, West Virginia. Technical Report NPS/NER/NRTR—2007/092. National Park Service. Philadelphia, PA.

Widmann, R.H., McWilliams, W.H., 2007. Changes in the oak resource in the Mid-Atlantic States (DE, MD, NJ, PA, and WV) using Forest Inventory and Analysis data. In: Proceedings of the Society of American Foresters 2006 National Convention; 2006 October 25–29; Pittsburgh, PA. Bethesda, MD: Society of American Foresters, pp. 221–233.

Woodall, C.W., Morin, R.S., Steinman, J.R., Perry, C.H., 2008. Status of oak seedlings and saplings in the northern United States: implications for sustainability of oak forests. In: Jacobs, D.F., Michler, C.H. (Eds.), Proceedings of the 16th central hardwoods forest conference. Gen. Tech. Rep NRS-P-24. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station, pp. 535–542.