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ARTICLE

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Sustaining eastern oak forests: Synergistic effects of fire and topography on vegetation and fuels

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Abstract

Across much of the eastern United States, oak forests are undergoing mesophication as shade-tolerant competitors become more abundant and suppress oak regeneration. Given the historical role of anthropogenic surface fires in promoting oak dominance, prescribed fire has become important in efforts to reverse mesophication and sustain oaks. In 2000 we established the Ohio Hills Fire and Fire Surrogate (FFS) study to examine whether repeated prescribed fire (Fire), mechanical partial harvest (Mech), and their combined application (Mech + Fire) reduced the dominance of subcanopy mesophytic competitors, increased the abundance of large oak–hickory advance regeneration, created a more diverse and productive ground-layer flora, and produced fuel beds more conducive to prescribed fire, reducing the risk of high-severity wildfire. Here we report on the ~20-year effects of treatments on vegetation and fuels and examine the support for interactive effects across a topographic-moisture and energy gradient. In general, we found that Fire and Mech + Fire treatments tended to reverse mesophication while the Mech-only treatment did not. The moderate and occasionally high-intensity fires resulted in effects that were ultimately very similar between the two fire treatments but were modulated by topography with increasing fire severity on drier sites. In particular, we found support for an interaction effect between treatment and topography on forest structure and tree regeneration responses. Fire generally reduced mesophytic tree density in the midstory and sapling strata across all site conditions, while leading to substantial gains in the abundance of large oak–hickory advance regeneration on dry and intermediate landscape positions. Fire also promoted ground-layer diversity and created compositionally distinct communities across all site conditions, primarily through the increased richness of native perennial herbs. However, the fire had limited effects on fine surface fuel loading and increased the loading of large woody fuels, potentially increasing the risk of high-severity wildfire during drought conditions. We conclude that two decades of repeated fires, with and without mechanical density reduction, significantly shifted the trajectory of mesophication across most of the landscape, particularly on dry and intermediate sites, highlighting the capacity

of a periodic fire regime to sustain eastern oak forests and promote plant diversity but modulated by topography.

KEYWORDS
diversity, fire behavior, forest management, mesophication, prescribed fire, *Quercus*, regeneration, topography

INTRODUCTION

Fire suppression and land-use change have disrupted historical and largely anthropogenic fire regimes that existed for centuries in many areas of the eastern United States (Guyette et al., 2002; Lafon et al., 2017). The loss of fire is contributing to a process of growing concern referred to as mesophication, the areal expansion and increasing abundance of mesophytic and mostly fire-intolerant species that were much less prominent prior to the suppression era that began ca. 1920–1930 (Alexander et al., 2021; Nowacki & Abrams, 2008). Other factors, including shifts in precipitation and N deposition have also been suggested as contributing to mesophication (McEwan et al., 2011; Quinn Thomas et al., 2010). In response, the use of prescribed fire has become important for reducing the effects mesophication on fire-dependent communities. However, fire alone is often ineffective at achieving desired conditions in the short to medium term (Arthur et al., 2015; Hutchinson, Sutherland, & Yaussy, 2005; Waldrop et al., 2016). Instead, pairing silvicultural treatments with prescribed fire may achieve a more open structure with less abundant mesophytic trees, oak regeneration that is more abundant and larger, greater plant diversity, and improved wildlife habitat for species adapted to disturbance-mediated habitats (Brose & Van Lear, 1998; Greenberg et al., 2018; Vander Yacht et al., 2016). In addition, previous studies were largely based on a period when reintroducing fire was still a new concept and there was limited knowledge of the effects of repeated burning. Today we are better equipped to address whether returning to a periodic fire regime will achieve the desired outcomes (Arthur et al., 2021).

Oaks (*Quercus* spp.) and associated hickories (*Carya* spp.) are considered foundational species in many eastern forest landscapes, particularly in the Central Hardwood region (Fralish, 2004; Hanberry & Nowacki, 2016). Their hard mast is important for many wildlife populations. Oaks in particular also host diverse invertebrate communities, including more Lepidopteran species than any other genus in eastern North America (Tallamy & Shropshire, 2009), which, in turn promotes the abundance and diversity of higher trophic levels (McShea et al., 2007; Rodewald & Abrams, 2002; Rubbo & Kiesecker, 2004). Consequently, as disturbance regimes and environmental conditions have been altered, declining oak regeneration and dominance have been a major concern for land managers for decades (Loftis & McGee, 1993).

Eastern oaks are intermediate to intolerant of shade (Burns & Honkala, 1990). Successful oak regeneration depends on advance regeneration possessing well developed root systems that facilitate vigorous height growth after a canopy disturbance (Dey, 2014; Johnson et al., 2019). Whereas failure occurs after a canopy disturbance when small oak seedlings are outcompeted by taller regeneration of shade-tolerant or shade-intolerant species that exhibit rapid height growth (Brose et al., 2008), a process referred to as disturbance-mediated accelerated succession (Abrams & Scott, 1989). In mature unmanaged oak forests abundant shade-tolerant species in the midstory and understory create a multilayered forest structure with heavy shade in the understory that limits the survival and growth of oak seedlings (Lorimer et al., 1994).

Anthropogenic fire occurred frequently in eastern oak forests prior to the initiation of fire suppression in the early 20th century, and periodic fire is considered a key process that sustained historically open oak and oak–pine forests (Abrams, 1992; Hanberry et al., 2020). The emphasis on root growth and vigorous re-sprouting following fire and other disturbances are key ecological attributes of oaks and hickories that contribute to their resilience in a periodic fire regime (Johnson et al., 2019). There have been significant efforts in recent decades to study the effectiveness of fire as a tool to sustain oak forests. A meta-analysis of fire–oak studies in the eastern United States showed that multiple fires are more likely to increase the abundance and size of oak regeneration while suppressing undesirable species (Brose et al., 2013). However, only a few of the analyzed studies had more than two fires and durations of >10 years. Research on the reintroduction of a periodic fire regime at a management scale (i.e., stand to landscape) for longer periods (20+ years) is mostly lacking (but see Knapp et al., 2022).

The overwhelming majority of plant diversity (80%+) consists of herbaceous ground-layer species across temperate North American forests (Spicer et al., 2020). Although ground-layer diversity in oak forests is typically a secondary focus of management, its structure and

composition are critical components of habitat for higher trophic levels (Gilliam, 2007; Harper et al., 2016). Fire exclusion is increasingly recognized as a threat to the maintenance of ground-layer diversity in oak forests (Rogers et al., 2008; Royo et al., 2010; Taverna et al., 2005). The reintroduction of fire has been shown to promote ground-layer diversity as it consumes litter and duff while reducing understory tree competition and shading, creating conditions for germination and establishment from the seed bank (Hutchinson, Boerner, et al., 2005). However, low-intensity prescribed fire alone does not create canopy openings, limiting its capacity to sustain species that require higher light levels to persist and develop. The combined application of mechanical or chemical stand-density reduction and fire may better promote increases in ground-layer diversity (Royo et al., 2010), particularly in less productive oak forests and woodlands (Abella et al., 2020; Vander Yacht et al., 2020).

Fuel beds are also an important component of sustaining oak ecosystems with fire. Oak leaf litter decomposes slowly, providing a continuous fuel bed with a low bulk density that burns readily when sufficiently dry (Dickinson et al., 2016; Kreye et al., 2013; Nowacki & Abrams, 2008; Varner et al., 2021). Fire exclusion decreases flammability, because litter from mesophytic species decomposes more rapidly and has chemical properties that make their litter less likely to support combustion (Dickinson et al., 2016; Kreye et al., 2018). In a common garden experiment, overstory species composition and topographic position had independent effects on litter loading (Dickinson et al., 2016). Fuel beds dominated by oak litter had greater rates of accumulation than beds dominated by mesophytic litter and litter on dry sites decomposed more slowly than mesic sites.

Fire management activities and other disturbances increase the probability of high-severity fires during drought due to increased large woody fuel loadings, although litter fuels carry the fire (Waldrop et al., 2010, 2016). As the scale of prescribed fire increases, the probability of high-severity fires increases, particularly in mountainous terrain, where significant overstory mortality can occur on steep and dry topographic positions (Lorber et al., 2018). Although the frequency and scale of destructive wildfires in eastern oak forests are far less than in dry western ecosystems, the recent (2016) outbreak of wildfires following severe drought in the southern Appalachians (Reilly et al., 2022) suggests that fuel management strategies may become increasingly important under climate change, particularly in the expanding wildland–urban interface (Peters et al., 2013). Fire risk assessment and planning requires a better understanding of wildfire behavior and more knowledge of how silvicultural treatments, including prescribed fire, alter fuel loading and fire behavior in eastern oak forests.

Throughout most eastern oak landscapes, the effects of fire on tree regeneration, ground-layer vegetation and fuel beds are likely to be strongly modulated by topographic variability. Although the magnitude of elevation change is modest over most of this landscape, considerable topographic variability creates gradients of energy and soil moisture that drive changes in ecosystem function (e.g., decomposition and nutrient cycling) and vegetation composition over relatively short distances (tens to hundreds of meters; Boerner, 2006; Iverson et al., 1997). A cornerstone of oak silviculture is the increased probability of regeneration success for the drought-tolerant oaks (and hickories) as site moisture and productivity decrease, lessening the intensity of competition from mesophytic species (Dey, 2014; Iverson et al., 2018; Johnson et al., 2019). Conversely, at least in closed-canopied oak forests, ground-layer vegetation abundance and diversity increase with moisture and fertility (Hutchinson et al., 1999; Small & McCarthy, 2005). The influence of topography on fire effects has received relatively little attention in eastern oak fire research (but see Arthur et al., 2015, 2017; Iverson et al., 2017; Maginel et al., 2019).

In 2000, a replicate of the national Fire and Fire Surrogates (FFS) study, the Ohio Hills site, was established. The mature oak forests comprising the Ohio Hills site are representative of the effects of mesophication. Oak forests dominated the landscape, a condition that was also present prior to Euro-American colonization (ca. 1800; Dyer & Hutchinson, 2019). Industrial-era (ca. 1850–1930) anthropogenic disturbances including frequent fire and intensive timber harvesting facilitated the continued dominance of the disturbance-adapted oaks as forests redeveloped in the 20th century. Organized fire control began in 1923 and immediately reduced the area burned by wildfire (Leete, 1939). On the Ohio Hills study sites, dendrochronology research showed that the exclusion of fire coincided with the recruitment of maples (Hutchinson et al., 2008). Nearly a century of forest development without fire or major canopy disturbance has produced multilayered stands with dominance by shade-tolerant species in the midstory and sapling strata.

Key objectives of the national study were to determine the effectiveness of fire and fire surrogate (i.e., mechanical thinning) treatments, alone and in combination, to reduce fire risk and shift forests to more open-structured, resilient, and sustainable conditions (Schwilk et al., 2009). For the Ohio Hills site, a reversal of mesophication was the primary objective, which would be characterized by a suite of changes including reduced dominance of mesophytic trees beneath the canopy, an increase in the abundance

of large oak–hickory advance regeneration, fuel beds more conducive to prescribed fire, and a more diverse and productive ground-layer flora. In addition, we examined whether treatments reduced the risk of high-severity wildfire through fuel reduction. Given the correlation between oak dominance and dry landscape positions and the resulting increases in litter loading and fuel drying rates, we expected that fuel consumption and fire intensity would be greatest in those landscape positions resulting in greater reductions in tree density, and increased oak regeneration and herbaceous biomass, forming feedbacks between fuels, fire behavior, and vegetation (Mitchell et al., 2009). Here, we report on the ~20-year independent and interactive effects of fire and fire surrogate treatments and topography on these ecosystem attributes.

METHODS

Study sites

The Ohio Hills installation of the FFS study was established in 2000. Three study sites were identified: REMA (located in Vinton Furnace State Forest, Vinton County, 39°12′34″ N, 82°23′07″ W), Zaleski State Forest (Vinton County, 39°21′22″ N, 82°21′59″ W), and Tar Hollow State Forest (Ross County, 39°19′47″ N, 82°46′11″ W). The sites are located within the Southern Unglaciated Allegheny Plateau Section (Iverson et al., 2019). Topography is dissected, featuring narrow ridges and ravines with steep side slopes. The Tar Hollow site had on average greater soil moisture (see Integrated Moisture Index below), as well as higher soil fertility (greater total Nitrogen, N-cycling rates, and Ca concentration; Boerner et al., 2007). Detailed site descriptions can be found in Boerner et al. (2007) and Hutchinson et al. (2008).

Experimental design and treatments

The design was a randomized complete block, where each 80–100 ha study site (i.e., replicate block) was divided into four 20–25 ha treatment units. Treatments were mechanical partial harvest (Mech), prescribed fire (Fire), their combination (Mech + Fire), and untreated control (Cont). Treatments were initiated in the winter of 2000–2001. First, a commercial partial harvest was conducted on all Mech and Mech + Fire units, reducing basal area by an average of 30% (herbicide was not applied to cut stumps). Cutting was focused on trees in midstory and lower canopy strata 15–35 cm diameter at breast height (dbh) but larger overstory trees were removed to meet residual basal area targets when necessary. Smaller trees and saplings were not cut. Following mechanical treatments, a total of four (March–April) fires were applied to the Fire and Mech + Fire units over the course of the study. The first fires were in 2001 and were generally low to moderate intensity (flame lengths <1 m). The second fires in year 5, conducted under drier conditions, ranged from low to high intensity, and significant overstory mortality occurred in patches up to 5 ha in size on some dry south-facing slopes. The third (year 10) and fourth (year 16) fires also had some areas of high-intensity fire that led to additional mortality (see Appendix S1: Table S1 for fire weather and fuel moisture conditions in year 16). Most fires were hand-ignited but several also used helicopters for interior ignition. In general, most of the landscape was burned with strip headfires. However, the size of the strips varied considerably, from ~10 m near fire lines to ~100 m on some interior hillslopes, which, in addition to variable fire weather and fuel moisture conditions, caused variable fire intensities, including patches of high-severity fire on some upper south-facing slopes.

Data collection

Vegetation

We collected pretreatment vegetation data in 2000, hereafter year 0 and post-treatment data collection occurred periodically until year 21, but in this paper we only compared year 0 to the final post-treatment measurement. A 50-m sampling grid was distributed throughout each unit to facilitate data collection. Using the grid, in total, 10 0.1-ha (50 × 20 m) plots ($n = 120$ overall) were established within each unit. Plots were distributed to capture a range of moisture conditions, estimated by the Integrated Moisture Index (IMI; see below). In year 0, we tagged and measured dbh for all live and standing dead trees ≥10 cm dbh within each 0.1-ha plot, and we monitored mortal status and dbh during each subsequent sample. Ten 10 × 10 m subplots were nested within each plot and stems ≥1.4 m height to 9.9 cm dbh were counted by species in three of the subplots; for multistemmed clumps of resprouts, each stem >1.4 m tall was counted. Stems 50–139.9 cm tall were tallied in 20 1-m^2 microplots; here, multistemmed clumps were counted as a single stem (rootstock). In year 21, sampling of stems 50–139.9 cm height was expanded to include four additional 2-m radius (12.6 m^2) microplots due to many plots (primarily controls) having zero stems for one or more species groups. Ground-layer vegetation, the cover of vascular plants (woody and herbaceous) by species, was recorded in 12 of the microplots; here the final measurement was in year 17.

Foliar cover from the ground to 1 m height was estimated by species in the following cover (in percentage) classes: <1, 1, 2–5, 6–10, 11–25, 26–50, 51–75, and 76–100. Some taxa were recorded to the genus or family level.

Fuels

Fuels data were collected in year 16 and from 36 grid points in each unit (total $n = 432$). We sampled pre-fire and post-fire duff, litter, and 1–1000-h woody fuels along modified Brown's lines and coarse woody material (CWM) within belt transects, following Graham and McCarthy's (2006) methods. At each gridpoint, two 20 m Brown's lines were anchored 2 m from the gridpoint, and a single belt transect (80 m^2; 20 × 4 m) was centered on one of the lines. The pre-fire and post-fire samples on fire units were collected in February–March and April–May, respectively (CWM was not measured post-fire), while nonfire units were sampled in May–June. Duff and litter depth measurements were recorded at 5, 10, and 15 m along each line. We defined duff as the humic layer (Oa: organic matter of unidentifiable origin) and litter as the combined unconsolidated (Oi) and fermentation (Oe) layers, although some studies define the duff as including the Oe layer (e.g., Arthur et al., 2017). Finally, for CWM, the species, diameter at the large end (≥15 cm), diameter at the small end (≥7.6 cm), length (length >1.0 m), and decay classes I–V were recorded for each log or section of log that fell within the transect (i.e., diameters and length were of the portion of the log within the transect).

Fire behavior and fire weather

Fire behavior (consumption, residence time, reaction intensity, and fireline intensity) was estimated for Fire and Mech + Fire units across all four prescribed fires over the 20-year study period (years 1, 5, 10, and 16). To estimate fire behavior, five stainless-steel thermocouple probes (TCPs; Onset Computer Corp., Bourne Massachusetts) were placed 20 cm above the mineral soil in each 0.1-ha plot, one on each plot corner and one at the plot center. The TCPs were connected to HOBO type K thermocouple loggers (Onset Computer Corp., Bourne Massachusetts), which recorded temperature at 1 s intervals; see Bova and Dickinson (2008) for more details. Fuel consumption (in megagrams per hectare) is estimated from the time-integral temperatures and a calibration constant. Residence time was estimated from the cumulative time over which the TCP absolute rate of temperature change was >2°C s^{-1}. Reaction intensity (in kilowatts per square meter) is estimated from the ratio of consumption (in kilograms per square meter) and residence time and describes an aerial rate of fuel consumption within the flaming front. Fireline intensity was estimated but not analyzed because of the error associated with the initial heating rate of the TCPs.

For the 2016 fires, the nearest remote-access weather station (RAWS) was used to obtain maximum temperature and minimum relative humidity (RH) for each burn day. Samples of duff, litter, and 10-h woody fuel moisture were collected at all plots prior to ignition. Samples were sealed in airtight bags, weighed later on the same day to get wet weights, and dried at 50°C until moisture loss ceased. Moisture contents were calculated as a fraction of dry mass, and the time of fire arrival was determined from the peak temperature of each TCP.

Data preparation

In total, 13 vegetation variables were analyzed (Table 1). In this study we focused on ~20-year vegetation change, as the difference between pretreatment (year 0) and the most recent post-treatment measurement (i.e., years 17 or 21). For each plot, we calculated the tree basal area (in square meters per hectare) and stand density (in numbers per hectare) for stems ≥10 cm dbh. We assigned species to three groups: oak–hickory, mesophytes, and other species (Appendix S1: Table S2). We also calculated the density of midstory mesophytes (10–25 cm dbh). Species in the mesophyte group are considered the main competitors of the target oak–hickory species. Next, we calculated the densities of saplings (3–9.9 cm dbh) and large regeneration (50 cm in height–2.9 cm dbh) for each species group using the subplot and microplot measurements. For the ground-layer vegetation, we calculated the mean cover (in percentage) using cover class midpoints and richness per square meter of herbaceous and woody species per plot.

In total, 10 fuel variables were analyzed. Litter loadings were calculated from calibration equations developed from the depth and loading samples collected at the control units. Using data from all control units, the least-squares regression equation was used where loading (in kilograms per square meter) = 0.1162 × depth (in centimeters). For duff, the regression for loading was from Dickinson et al. (2016). Brown's (1974) equation was used to calculate woody loadings by time-lag class. Transect slope and particle tilt angles (a), piece diameters (d^2), and specific gravities (s) from Riccardi (2005) were used in Brown's equation. For 1000-h and larger woody fuels (≥76 mm diameter), specific gravities were assigned to rotten (0.48 g m^{-3}) and sound

TABLE 1 Mean ± 95% confidence intervals for vegetation variables pretreatment (year 0), and the last measurement period (year 21 for trees and regeneration, year 17 for ground-layer vegetation).

Variable	Control	Mechanical	Fire	Mechanical + fire
Stand structure				
Basal area, m^2 ha^{-1}	29.0 ± 1.8, 34.4 ± 2.6	28.9 ± 1.9, 26.5 ± 2.7	27.7 ± 2.6, 22.0 ± 4.4	28.7 ± 2.4, 20.4 ± 2.8
Stand density, trees ha^{-1}	367 ± 32.3, 369 ± 34.8	410 ± 36.5, 392 ± 38.9	362 ± 25.5, 170 ± 40.7	390 ± 32.7, 151 ± 34.0
Mid meso[a], trees ha^{-1}	125 ± 19.5, 160 ± 26.5	147 ± 8.4, 224 ± 33.5	143 ± 22.0, 41 ± 18.4	140 ± 26.0, 43 ± 22.7
Saplings[b]				
Mesophytes, trees ha^{-1}	456 ± 91.8, 449 ± 90.8	448 ± 62.1, 587 ± 99.7	452 ± 74.7, 213 ± 94.0	369 ± 80.1, 290 ± 127.2
Oak–hickory, trees ha^{-1}	3 ± 3.8, 1 ± 2.3	32 ± 2.7, 66 ± 44.5	27 ± 16.4, 172 ± 136.6	24 ± 13.4, 117 ± 94.8
Other spp., trees ha^{-1}	58 ± 27.3, 71 ± 47.8	55 ± 18.5, 143 ± 59.9	59 ± 32.0, 471 ± 203.8	41 ± 21.8, 282 ± 130.3
Large regeneration[c]				
Mesophytes, stems ha^{-1}	1766 ± 702, 1330 ± 440	1476 ± 714, 1839 ± 469	1042 ± 328, 3692 ± 976	1029 ± 3745, 3488 ± 892
Oak–hickory, stems ha^{-1}	110 ± 93, 465 ± 264	178 ± 127, 1206 ± 479	667 ± 338, 5980 ± 2200	201 ± 118, 5255 ± 2273
Other spp., stems ha^{-1}	340 ± 217, 374 ± 221	229 ± 139, 560 ± 174	724 ± 410, 2842 ± 768	106 ± 58, 2287 ± 636
Ground-layer				
Herbaceous species (m^{-2})	3.3 ± 0.9, 2.6 ± 0.9	2.5 ± 0.7, 2.5 ± 0.8	3.1 ± 0.9, 6.6 ± 1.2	3.7 ± 1.0, 8.0 ± 1.0
Woody species (m^{-2})	4.5 ± 0.4, 4.7 ± 0.5	4.6 ± 0.3, 4.9 ± 0.35	4.8 ± 0.4, 6.3 ± 0.5	4.5 ± 0.5, 6.7 ± 0.5
Herbaceous cover (%)	7.9 ± 4.1, 5.9 ± 3.1	4.1 ± 1.8, 4.3 ± 1.8	5.8 ± 2.3, 15.5 ± 4.1	5.7 ± 2.0, 19.3 ± 5.0
Woody cover (%)	17.8 ± 5.9, 16.0 ± 3.1	18.1 ± 3.8, 17.9 ± 2.4	20.7 ± 4.4, 51.8 ± 8.6	21.7 ± 5.5, 52.8 ± 7.5

[a]Midstory mesophytes (10–25 cm diameter at breast height [dbh]).
[b]Stems 3.0–9.9 cm diameter at breast height.
[c]Stems 50 cm height–2.9 cm diameter at breast height.

(0.63 g cm^{-3}) particles based on Riccardi's (2005) measurements. For CWM, wood volume (in cubic meters per hectare) was estimated from Smalian's formula (Wenger, 1984). Specific gravity (in grams per cubic centimeter) values for each species and decay class were taken from Hoadley (1990) and from Adams (2001) and used to calculate CWM loading (in megagrams per hectare) from wood volume (Van Wagner, 1968). Total fuel, woody fuel (sum 1–1000-h), and litter-to-10-h fuel (sum litter–10-h) were also calculated and considered for analysis. CWM loading (in megagrams per hectare) was estimated from the product of log volume per unit area and wood specific gravity. Following Brown (1974), specific gravity is a weighted average for each decay class based on proportions of each species in the 2016 sample and values from Adams (2001). For fire behavior, the average (across the four fires in years 1, 5, 10, and 16) consumption (W, in megagrams per hectare) and reaction intensity (Qi, in kilowatts per square meter) were estimated through TCP responses over the four prescribed fires (Bova & Dickinson, 2008).

The GIS-derived IMI; Iverson et al., 1997) was used to capture varying topography and soil influences on vegetation, fuels, and fire behavior. The IMI model was a 7.5-m raster with cell values scaled from 0 (generally representing dry, poor site quality) to 100 (moist, high site quality) and IMI values were extracted for each plot and gridpoint for use in the statistical analyses. The IMI can be applied in similar landscapes with dissected topography and relatively uniform bedrock geology (Peters et al., 2013).

Analytical approach

We report 20-year treatment effects and used model selection and Akaike's Information Criterion (AIC) to evaluate support for synergistic effects of FFS treatments interacting with long-term moisture regime and site productivity (i.e., IMI) to influence vegetation, fuels, and fire behavior. Our primary analytical approach included evaluating support for statistical interactions between treatment type (TRT) and the IMI. Models were fitted using linear mixed models to account for the random effects of the study site. In total five a priori models were evaluated. Models included an interaction model (TRT:IMI) to evaluate support for synergistic effects, an additive model including both TRT and IMI terms (TRT + IMI), two models including TRT and IMI only effects (TRT only and IMI only), and a null model including

random effects of study site only. The advantage of AIC in our study is that models are increasingly penalized as additional parameters are added. Thus, support for synergistic effects (i.e., interaction model) must outweigh the penalty associated with greater numbers of parameters ($k = 8$) relative to the additive TRT + IMI ($k = 5$), TRT-only ($k = 4$), and IMI only ($k = 2$) models.

Models were fitted using the "lme" function in the *nlme* package (Pinheiro et al., 2022) for the R statistical environment (https://www.r-project.org/). Plots ($n = 120$), grid points ($n = 432$), and plots among treatments receiving prescribed fire ($n = 60$) served as the statistical units of replication for vegetation, fuels, and fire behavior variables, respectively. We ranked support for the a priori models using AIC corrected for small sample sizes (AIC_c). We conducted residual analyses to inspect for linearity, normality of residuals, and homogeneity of variance. Residual analyses indicated that fuels and fire behavior variables exhibited heteroscedastic and nonnormal errors. Thus, a log (+1) transformation was applied to fuels and fire behavior variables to satisfy model assumptions. We considered all models with $\Delta AIC_c < 2$ to be equally supported.

To facilitate additional interpretation, explained variance (R^2) was estimated for each model following a revised approach by Nakagawa and Schielzeth (2013) as implemented in the r2glmm package (Jaeger, 2017). Effect sizes for TRT and IMI effects were evaluated using 95% confidence intervals. Models including TRT were structured so that the Cont treatment formed the intercept and active management effects (Mech, Fire, Mech + Fire) were evaluated against the Cont treatment. Treatments were labeled as significant when 95% confidence intervals did not overlap the Cont treatment to indicate strong differences in active management relative to the Cont.

We analyzed differences in the ground-layer community using nonmetric multidimensional scaling (nMDS) ordination and a multiresponse permutation procedure (MRPP). Data used in the ordination were prepared by compiling measurements taken during pretreatment (year 0) and for the most recent sample taken in year 17 into a single data set so that community-level associations could be evaluated before and after treatment application on a single ordination diagram and be relatable to the modeled vegetation change approach. These data included relative importance values ([mean percent relative cover + relative frequency of occurrence]/2) of herbaceous and woody plant taxa recorded in each plot. We removed rare and infrequently recorded taxa occurring in <5% of measurements before analysis. We selected Bray–Curtis dissimilarity for the compositional distance matrix for both the nMDS and MRPP analyses. A three-axes solution was selected, and a Wisconsin and square-root transformation was applied before ordination. Treatment ellipses (95%) and environmental vectors were projected onto the ordination using plot-level IMI and basal area change ($\Delta_{00–21}$ m^2 ha^{-1}) values as explanatory variables and permutation tests were used to determine the statistical significance of vector fits. The MRPP analysis was performed on the year 17 subset of data to evaluate whether there were differences in understory plant communities that emerged over the course of the study. We used a group weighting factor based on the number of plots assigned to each group $n_i/\Sigma n_i$ (where n_i is the sample size of group i). The MRPP test statistic (T) and chance-corrected within-group agreement (A) describe the separation between the groups (the more negative the value the more separation) and the within-group homogeneity compared with random expectation ($A = 1$ indicates perfect match), respectively (McCune & Grace, 2002).

Finally, to examine species-level associations with treatments, we used indicator species analysis (ISA; Dufrêne & Legendre, 1997). For the ISA, we used the mean cover values (in percentage) of species recorded in year 17 and included all taxa regardless of rarity of occurrence (McCune & Grace, 2002). The statistical significance of indicator values was determined with permutation tests. Functions provided in the *vegan* (Oksanen et al., 2022) and *labdsv* packages (Roberts, 2019) for the R statistical environment were used in the ordination, MRPP, and indicator species analyses. All permutation tests were evaluated over $n = 999$ permutations and statistical significance was set to $p = 0.05$. We report nominal p-values for the community-level and species-level results but recognize that inferences may be weakened if corrected for the number of tests performed.

RESULTS

Vegetation

There were major changes in forest structure and composition over the ~20-year study period, and treatment was the most important predictor for all vegetation change variables, being present in the top-ranked models (Tables 1 and 2, Figure 1). The top-ranked models were the TRT × IMI interaction ($n = 8$ variables) and TRT-only ($n = 5$ variables) models.

Basal area (BA) change was best supported by the TRT-only model, which explained 37% of the variation (Table 2). All active treatments displayed a net decrease in BA by year 21 in comparison with the Cont (nonoverlapping 95% CIs). Initially, the partial harvests in the Mech and Mech + Fire treatments reduced BA by ($\mu \pm$ SE) -8.1 ± 0.65 and -7.9 ± 0.77 m^2 ha^{-1},

TABLE 2 Summary of the top-ranked model(s) (ΔAIC_c <2) for each examined variable, including effect signs of TRT and IMI, estimated R^2 of fixed effects, degrees of freedom (df), AIC_c model weight (w_i), and *p*-value of Tukey–Freeman goodness-of-fit test.

Variable	Model	TRT (M, F, MF)	IMI	TRT:IMI (M, F, MF)	R^2	df
Overstory $\Delta_{(0–21)}$						
Tree basal area	TRT only	(−), (−), (−)			0.37	6
Stand density	Interaction	(−), (−), (−)	+	(+), (+), (+)	0.63	10
Midstory mesophytes	Interaction	−, (−), (−)	−	(+), +, +	0.60	10
Saplings $\Delta_{(0–21)}$						
Mesophytes	Interaction	+, (−), +	(−)	+, +, −	0.25	10
Oak–hickory	Interaction	+, (+), (+)	+	−, (−), −	0.15	10
Other species	Interaction	−, (+), +	−	+, (−), −	0.28	10
Large regeneration $\Delta_{(0–21)}$						
Mesophytes	Interaction	(+), (+), (+)	+	−, −, −	0.25	10
Oak–hickory	Interaction	+, (+), (+)	+	−, −, (−)	0.28	10
Other species	Interaction	+, (+), (+)	+	−, −, −	0.33	10
Ground-layer $\Delta_{(0–17)}$						
Herbaceous richness	TRT only	+, (+), (+)			0.68	6
Woody richness	TRT only	+, (+), (+)			0.33	6
Herbaceous cover	TRT only	+, (+), (+)			0.48	6
Woody cover	TRT only	+, (+), (+)			0.48	6
Fuels, $year_{(16)}$						
Duff	NULL				...	3
Litter	NULL				...	3
Woody 1-h	TRT + IMI	+, (+), (+)	(−)		0.23	7
Woody 10-h	NULL				...	3
Woody 100-h	NULL				...	3
Woody 1000-h	TRT only	+, (+), (+)			0.09	6
Coarse woody material	TRT only	+, (+), (+)			0.12	6
Litter to 10-h	TRT + IMI	−, (+), (+)	(−)		0.13	7
Total fuel	TRT only	−, (+), (+)			0.07	6
Fire behavior $\mu_{(1,5,10,16)}$						
Consumption $W_{(Mg\ ha^{-1})}$	IMI only	(+)	(−)		0.40	4
Reaction intensity $Qi_{(kW\ m^{-2})}$	IMI only	(+)	(−)		0.34	4

Note: Symbols indicate whether effects were positive (+) or negative (−) and estimates that did not overlap zero are enclosed in parentheses. Blanks indicate when treatment type (TRT) or Integrated Moisture Index (IMI) was not included in the model. W1000HR_T is the sum of rotten and sound 1000 h time-lag woody fuels, WF is total woody fuels (1–1000 h), FuelLitterTo10HR is the sum of litter and 1 and 10 h woody fuels, and TotalFuel is the sum across fuel classes excluding coarse woody material (CWM) which is the larger diameter subset of 1000 h fuels.

respectively. However, by year 21, the mean BA in the Mech treatments recovered to only -2.5 ± 0.9 of pretreatment values, while repeated fires in the Mech + Fire treatments sustained a lower BA at $-8.3 \pm 1.5\ m^2\ ha^{-1}$. Due to some areas of high-severity fire, BA on the Fire only treatment was on average reduced to $-5.7 \pm 1.6\ m^2\ ha^{-1}$ by year 21. Although TRT-only was the top-ranked model, there was generally more BA reduction on dry plots (IMI <36) than on mesic plots (IMI >50) on both the fire treatments (Figure 1a).

The fire treatments caused large and similar reductions in both overall stand density and the density of midstory (10–25 cm dbh) mesophytes. The top-ranked model for these variables was the interaction model (i.e., TRT:IMI), explaining 63% and 60% of the variation in stand and midstory mesophyte density, respectively (Table 2). Fire-caused density reductions were greater on drier plots as indicated by the positive TRT:IMI interaction effect (Figure 1b,c). For example, mean stand density was reduced by -278.8 ± 35 (Fire) and -301.5 ± 28.1

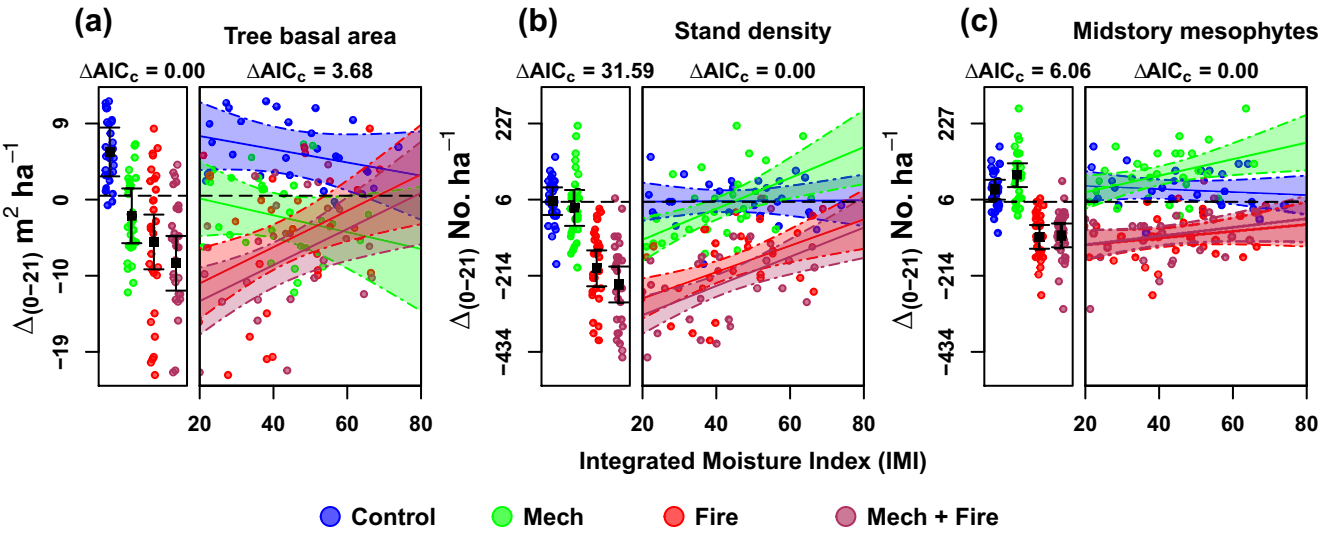

FIGURE 1 Comparison of treatment only and treatment × IMI interaction effects on changes (pretreatment year 0–21) in tree basal area (a), stand density (b), and midstory mesophyte density (c) of the study plots. Treatment and treatment × IMI model results compared for illustrative purposes. The color of each plot corresponds to treatment type (Mech refers to mechanical).

trees ha^{-1} (Mech + Fire) on dry plots versus −140 ± 27.3 (Fire) and −158 ± 30.8 trees ha^{-1} (Mech + Fire) on mesic plots. Notably, the Mech-only treatment had a release effect, resulting in the development of a more dense midstory of mesophytes by year 21. Here, the positive TRT:IMI interaction indicates greater midstory increases on mesic plots.

Prior to treatments, mesophytes were dominant (81%–87% among designated treatments) in the sapling layer. For all three species groups, the TRT:IMI interaction model was the best model of the candidates tested, with treatment effects generally largest on the fire treatments and influenced by the IMI (Table 2, Figure 2a–c). The interaction model explained 25%, 15%, and 28% of the variation in changes in mesophytes, oak–hickory, and other species densities, respectively. Oak–hickory saplings were sparse in year 0 (<30 stems ha^{-1}) across all designated treatments (Table 1). Relative to controls, oak–hickory sapling density increased on the fire treatments (nonoverlapping CIs, Table 2). However, variability was high with increases of >100 stems ha^{-1} occurring on relatively few plots (30% of Fire and 20% of Mech + Fire). Oak–hickory sapling recruitment occurred primarily on dry plots (i.e., TRT:IMI interaction; Table 2, Figure 2b). The Fire treatment also resulted in a substantial increase of saplings in the other species group, primarily on drier sites (TRT:IMI interaction; Table 2, Figure 2c); this was driven largely by sourwood (*Oxydendrum arboreum*).

For large advance regeneration (stems 50 cm tall to 2.9 cm dbh), the interaction model was top-ranked, explaining 25%, 28%, and 33% of the variation in changes in mesophytes, oak–hickory, and other species densities, respectively. Repeated fires facilitated increases in advance regeneration density across all three species groups relative to the Cont (Table 2, Figure 3d–f) but oak–hickory exhibited the largest gains (Table 1). Moreover, as indicated by support for the interaction model, these fire-mediated increases were not equal across the moisture gradient. While only 10% of burned mesic plots supported >5000 large oak–hickory stems ha^{-1} in year 21, 63% and 43% of intermediate and dry plots, respectively, exceeded 5000 stems ha^{-1}. The mean density of oak–hickory on intermediate burned plots (8052 stems ha^{-1}) exceeded that on dry plots (5644 stems ha^{-1}).

Changes in ground-layer richness (Number of species per square meter) and cover (in percentage) were best supported by the TRT-only model, explaining 33%–68% of the variation in herbaceous and woody vegetation attributes (Table 2, Figure 3). There were particularly large increases in richness and cover in the fire treatments (Fire and Mech + Fire 95% CIs did not overlap the Cont). Herbaceous richness increased by 3.5 ± 0.3 (Fire) and 4.2 ± 0.3 (Mech + Fire) species per square, while woody richness increased by 1.5 ± 0.2 (Fire) and 2.1 ± 0.3 (Mech + Fire) species. Conversely, there were no discernible differences in richness and cover changes between the Mech treatment and Cont (i.e., 95% CIs overlapping). Herbaceous cover, which was quite low pretreatment, increased on the fire treatments by 9.6 ± 1.5% (Fire) and 13.6 ± 1.6% (Mech + Fire), but remained a relatively small portion of the total cover (Table 1). Cover of woody

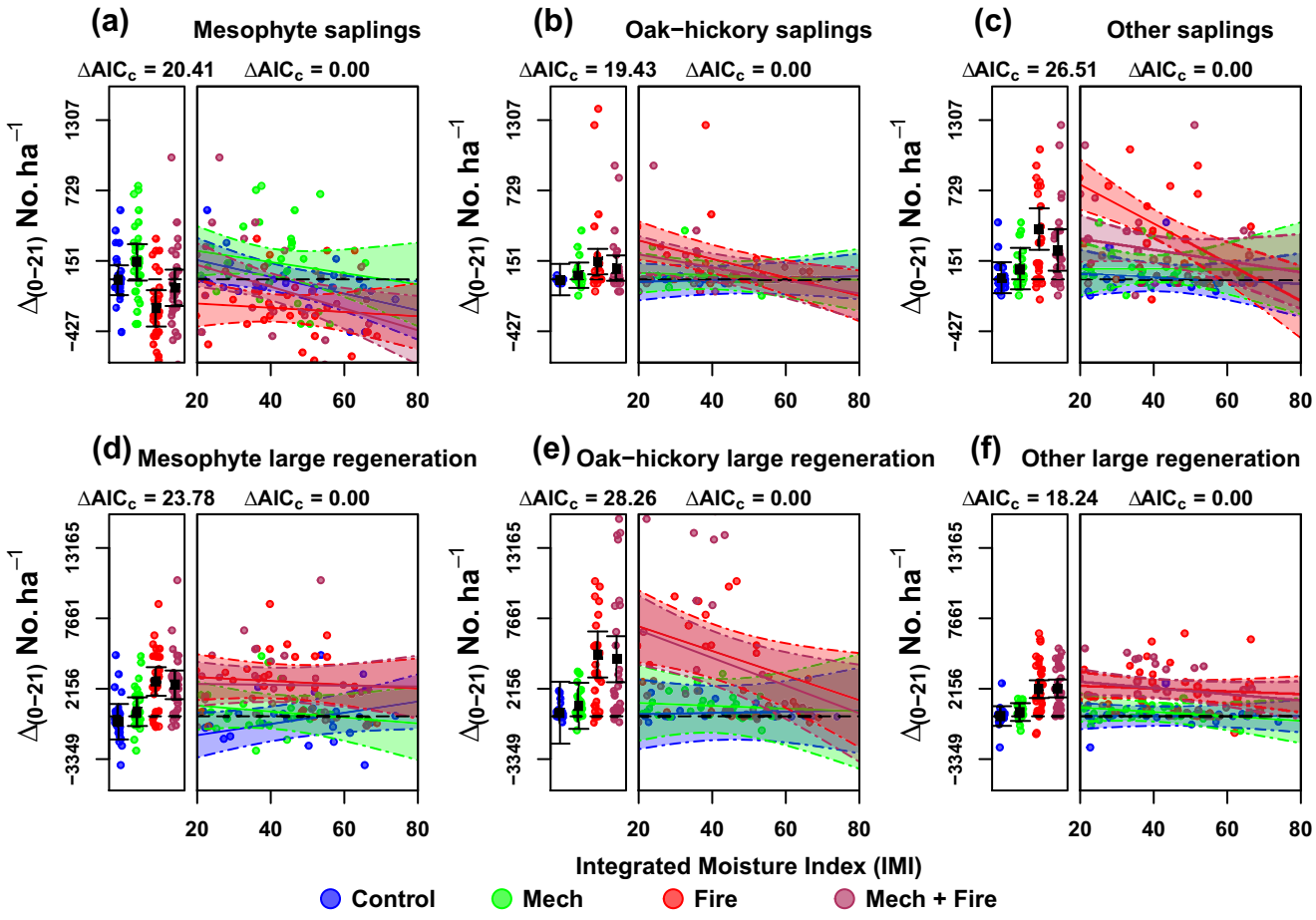

FIGURE 2 Treatment only and treatment × IMI interaction (top-ranked model for all sapling and large regeneration variables) effects on change (pretreatment year 0–21) in sapling density (a–c) and large advance regeneration density (d–f) for three species groups (mesophytes, oak–hickory, and other species) of the study plots. Treatment and treatment × IMI model results compared for illustrative purposes. The color of each plot corresponds to treatment type (Mech refers to mechanical).

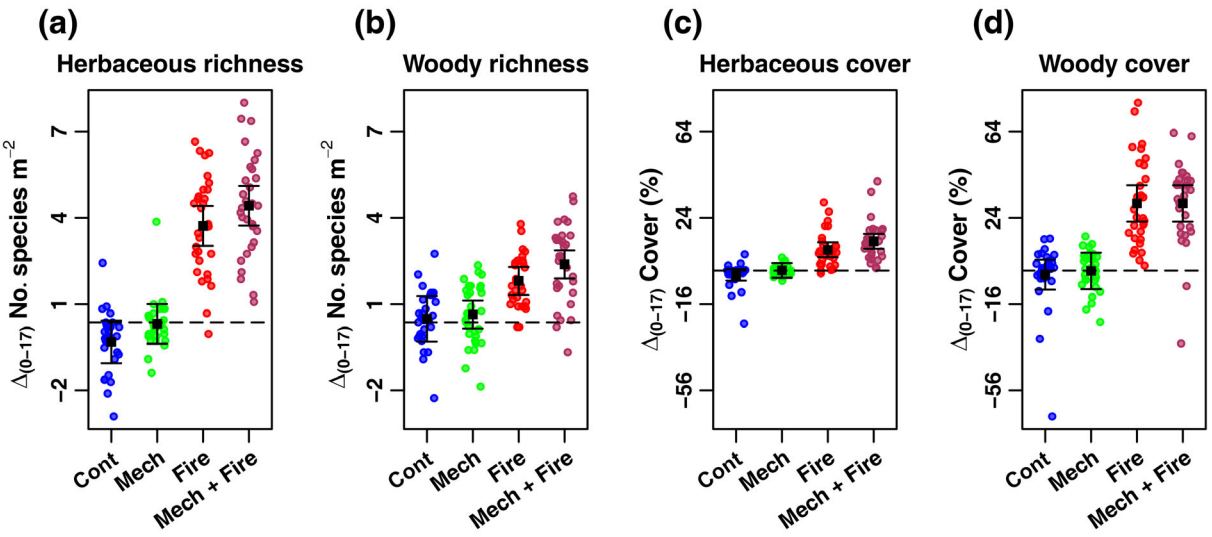

FIGURE 3 Treatment only effects (top-ranked model for understory richness and cover variables) on understory change from pretreatment (year 0) to year 17 for herbaceous richness (a), woody richness (b), herbaceous cover (c), and woody cover (d). The color of each plot corresponds to treatment type (Mech refers to mechanical).

plants increased by 31.1 ± 3.7% and 31.1 ± 3.5% in the Fire and Mech + Fire treatments, respectively (Table 1, Figure 3). The Mech-only treatment exhibited little change in ground-layer cover over time.

Among the 259 plant taxa that were recorded in years 0 and 17, a total of 128 were used for nMDS analysis (occurring in >5% of plots). The nMDS resulted in a three-axis solution with a stress metric of 13.2, transferring 66.3% of the original floristic variation to the ordination, including 44.1%, 9.4%, and 12.8% assigned to nMDS axes 1–3, respectively. We extracted the subsets of results based on the two measurement periods into separate bins to examine potential differences in community-level associations over the course of the study (Figure 4). In year 0, as expected, treatment effects were not evident. However, the year 17 ordination shows distinct groupings of burned (Fire and Mech + Fire) versus unburned (Cont and Mech) plots. Fitted vectors, IMI and BA change, to the year 17 subset indicate the first axis to be largely related to IMI (Pearson correlation of axis 1 and IMI, $r = 0.579$). Species associated with dry site conditions had low axis 1 scores, while species with fidelity to mesic sites had high axis 1 scores. The second axis revealed a gradient largely associated with treatment type, with Fire and Mech + Fire plots having low axis 2 scores relative to Cont and Mech, with axis 2 scores correlated with BA change, an indication of fire intensity ($r = 0.561$). Axis 3 also showed a fire treatment gradient and was correlated with BA change ($r = -0.352$).

The MRPP results confirmed significant differences in composition among treatments ($T = -0.294$, $p = 0.001$,

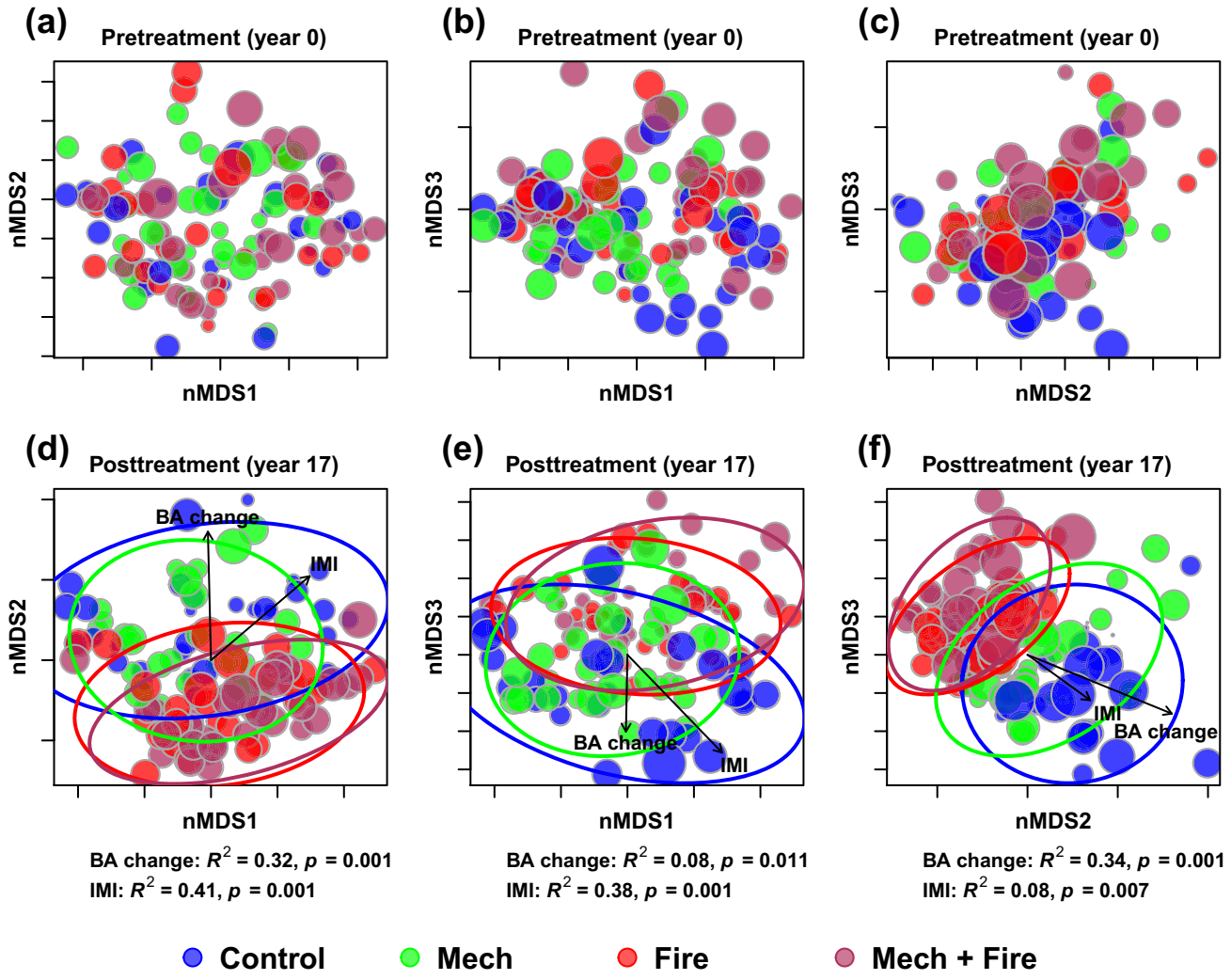

FIGURE 4 Distribution of plots based on understory herbaceous and woody plant composition at pretreatment (year 0) (a–c) and the last measurement (year 17) (d–f) in three-dimensional nMDS ordination space. Samples from both time periods were ordinated together to allow visualization of potential treatment effects on community change. The color of each plot corresponds to treatment type (Mech refers to mechanical) and close plots indicate similar community compositions and remote plots indicate dissimilar community compositions. Vectors of IMI and basal area change (from year 0 to 17) are fitted to the plots in year 17 to facilitate interpretation of community patterns (R^2 indicate the degree of fit to the associated axes and p-values based on 999 permutations).

$n = 999$ permutations; Table 3). Multiple pairwise comparisons indicated that Fire and Mech + Fire were compositionally similar to one another and were distinct from the Cont and Mech treatments, which were similar to one another. Because of the compositional similarity between the Fire and Mech + Fire treatments, we assigned a single "Fire" treatment in the ISA. Sixty taxa were significant indicators of fire treatment while only five species were indicators of unburned treatments (Table 4). Among the fire indicators, 72% were herbaceous, and a majority (60%) belonged to four taxonomic groups: composites (Asteraceae), legumes (Fabaceae), grasses (Poaceae), and oaks (*Quercus*).

Fuels, fire behavior, and fire weather

Total fuel loading (in megagrams per hectare) increased on mechanical and fire treatments relative to controls (Figure 5, Table 5) and there was also support for the interactive model as total fuels increased most on drier sites (Table 2). The increases in large-diameter woody fuel loadings (1000 h and CWM) were the largest effects observed (Table 5, Figure 5). Duff loadings were slightly lower on burned treatment units than on control units (Figure 5). In contrast, fine woody material (the 1 h time-lag class, <0.6 cm diameter) and larger diameter woody material (the 1000 h time-lag class, ≥7.6 cm diameter) increased on burned treatment units (Table 5). For 1 h woody fuels, there was an additional increase on drier sites (Table 2). The sum of litter and 1 and 10 h woody fuels, the fine fuels that primarily support surface fire flame front propagation, showed an additive increase on both fire treatments (Table 5) and on drier sites within those treatments. There were no differences seen in litter and 10 and 100 h woody fuel loadings across treatments or any effect of IMI gradients.

For the 2016 fires, fire weather and associated fuel moisture varied modestly among burns (Appendix S1: Table S1). Litter moisture varied from 22% to 52% prior to burns. Duff moisture ranged from 92% to 139% and 10 h time-lag woody fuels ranged from 18% to 38% prior to burns. Maximum temperatures ranged from 22.4 to 25.2°C on burn days while minimum RH ranged from 13% to 22%.

Fire behavior estimated from TCP was primarily affected by IMI (Table 2, Figure 6). Based on the TCP response, consumption in the flame front averaged 6.9 Mg ha^{-1}. This compares favorably with a direct measurement of 8.2 Mg ha^{-1} for combined litter and 1 and 10 h time-lag woody fuels based on pre-fire and post-fire measurements (Table 5). Direct measurements showed the greatest absolute consumption was of litter followed by duff and 1000 h time-lag woody fuels (Table 5). Proportionally, the most complete consumption was seen in litter (66%) followed by 1 h woody (45%) and duff (43%; Table 5). Proportional consumption for 100 and 1000 h woody fuels was the lowest among the fuel classes (Table 5). Flame residence time averaged 19 s (±1.9 s 95% CI). Average consumption (6.9 Mg ha^{-1} ± 1.2 95% CI) and reaction intensity (1897 kW m^{-2} ± 137 CI) were used to characterize fire behavior as an average over all burn years. Missing data due to equipment failure (primarily in year 1 burns) were not included in the average.

DISCUSSION

Mesophication of eastern oak forests is characterized by increasing densities of shade-tolerant and fire-sensitive species, heavily shaded understories lacking large oak

TABLE 3 Summary statistics for the multiresponse permutation procedure (MRPP) analysis, examining differences in ground-layer species composition at year 2017 and among the different treatment categories.

Treatments	Observed δ	Expected δ	*T*	*A*	*P*
Treatment effect	0.649	0.687	−0.294	0.056	0.001
Multiple comparisons					
Cont versus Mech	0.656	0.661	−0.043	0.008	0.066
Cont versus Fire	0.657	0.697	−0.299	0.057	0.001
Cont versus Mech + Fire	0.663	0.710	−0.338	0.067	0.001
Mech versus Fire	0.635	0.661	−0.230	0.040	0.001
Mech versus Mech + Fire	0.641	0.674	−0.266	0.050	0.001
Fire versus Mech + Fire	0.642	0.643	−0.010	0.002	0.227

Note: Observed and expected δ are the weighted mean within-group and overall mean distances, respectively, *T* is the test statistic, *A* is the chance-corrected within-group agreement, and *P* is the proportion of permutations where the expected δ was smaller than the observed δ (based on Bray–Curtis dissimilarity and 999 permutations). The MRPP analysis was conducted across all treatment categories and for multiple pairwise combinations. Average within-group distance (Bray–Curtis): Control = 0.678; Mechanical = 0.634; Fire = 0.635; Mech + Fire = 0.648.

TABLE 4 Statistically significant ground-layer indicator taxa in year 17.

Family	Species	Life form	TRT	IV	*p*	*f*
Asteraceae	*Ageratina altissima*	Fb	F	42.8	0.001	34
Asteraceae	*Asteraceae* spp.	Fb	F	46.4	0.001	35
Asteraceae	*Eupatorium sessilifolium*	Fb	F	37.8	0.001	25
Asteraceae	*Eurybia macrophylla*	Fb	F	27.3	0.003	27
Asteraceae	*Helianthus divaricatus*	Fb	F	21.7	0.002	13
Asteraceae	*Helianthus microcephalus*	Fb	F	30.0	0.001	18
Asteraceae	*Prenanthese* spp.	Fb	F	27.9	0.003	25
Asteraceae	*Solidago bicolor*	Fb	F	25.8	0.002	17
Asteraceae	*Solidago caesia*	Fb	F	67.6	0.001	65
Asteraceae	*Solidago erecta*	Fb	F	21.7	0.008	13
Asteraceae	*Solidago* spp.	Fb	F	19.3	0.012	13
Asteraceae	*Solidago ulmifolia*	Fb	F	21.7	0.005	13
Asteraceae	*Symphyotrichum divaricatum*	Fb	F	51.4	0.001	56
Asteraceae	*Symphyotrichum undulatum*	Fb	F	26.3	0.001	17
Boraginaceae	*Hackelia virginiana*	Fb	F	17.3	0.015	15
Euphorbiaceae	*Acalypha virginica*	Fb	F	21.7	0.004	13
Fabaceae	*Amphicarpaea bracteata*	Fb	F	55.8	0.001	48
Fabaceae	*Chamaecrista nictitans*	Fb	F	26.7	0.003	16
Fabaceae	*Desmodium glutinosum*	Fb	F	24.6	0.009	19
Fabaceae	*Desmodium nudiflorum*	Fb	F	46.8	0.001	77
Fabaceae	*Desmodium paniculatum*	Fb	F	16.7	0.011	10
Fabaceae	*Lespedeza* spp.	Fb	F	22.7	0.002	15
Lamiaceae	*Collinsonia canadensis*	Fb	F	25.4	0.003	21
Oxalidaceae	*Oxalis* spp.	Fb	F	28.3	0.001	17
Primulaceae	*Lysimachia quadriflora*	Fb	F	62.4	0.001	62
Ranunculaceae	*Actaea racemosa*	Fb	F	19.7	0.043	29
Rosaceae	*Potentilla canadensis/simplex*	Fb	F	48.0	0.001	55
Rubiaceae	*Galium triflorum*	Fb	F	40.8	0.003	55
Scrophulariaceae	*Aureolaria laevigata*	Fb	F	31.4	0.001	23
Violaceae	*Viola* spp.	Fb	F	53.0	0.001	84
Adiantaceae	*Adiantum pedatum*	Fn	F	16.5	0.037	16
Cyperaceae	*Carex* spp.	Gr	F	64.6	0.001	105
Poaceae	*Brachyelytrum erectum*	Gr	F	27.4	0.028	45
Poaceae	*Danthonia spicata*	Gr	F	23.0	0.009	20
Poaceae	*Diarrhena americana*	Gr	F	17.7	0.042	18
Poaceae	*Dichanthelium boscii*	Gr	F	62.5	0.001	56
Poaceae	*Dichanthelium commutatum*	Gr	F	46.2	0.001	33
Poaceae	*Dichanthelium latifolium*	Gr	F	32.1	0.003	22
Poaceae	*Microstegium vimineum*	Gr	F	19.8	0.023	14
Poaceae	*Poaceae* spp.	Gr	F	13.0	0.046	12
Anacardiaceae	*Rhus copallinum/glabra*	Sh	F	59.8	0.001	39
Ericaceae	*Vaccinium palidum*	Sh	F	35.2	0.031	67

(Continues)

TABLE 4 (Continued)

Family	Species	Life form	TRT	IV	*p*	*f*
Hydrangeaceae	*Hydrangea arborescens*	Sh	F	29.8	0.013	38
Rosaceae	*Rubus* spp.	Sh	F	78.7	0.001	100
Aceraceae	*Acer rubrum*	Tr	F	48.5	0.029	119
Cornaceae	*Nyssa sylvatica*	Tr	F	57.2	0.001	84
Ericaceae	*Oxydendrum arboreum*	Tr	F	35.0	0.007	55
Fabaceae	*Robinia pseudoacacia*	Tr	F	16.6	0.016	11
Fagaceae	*Quercus alba*	Tr	F	53.6	0.004	83
Fagaceae	*Quercus coccinea*	Tr	F	35.7	0.023	55
Fagaceae	*Quercus montana*	Tr	F	55.5	0.001	85
Fagaceae	*Quercus rubra*	Tr	F	48.4	0.001	47
Fagaceae	*Quercus velutina*	Tr	F	46.6	0.004	78
Juglandaceae	*Carya tomentosa*	Tr	F	57.9	0.001	57
Lauraceae	*Sassafras albidum*	Tr	F	71.8	0.001	93
Magnoliaceae	*Liriodendron tulipifera*	Tr	F	72.9	0.001	76
Salicaceae	*Populus grandidentata*	Tr	F	13.3	0.046	10
Vitaceae	*Vitis* spp.	Wv	F	75.7	0.001	76
Liliaceae	*Smilacina racemosa*	Fb	M	23.8	0.038	40
Rosaceae	*Amelanchier arborea*	Tr	M	24.4	0.035	33
Liliaceae	*Trillium grandiflorum*	Fb	C	17.7	0.012	13
Aspleniaceae	*Thelypteris noveboracensis*	Fn	C	29.9	0.001	21
Fagaceae	*Fagus grandifolia*	Tr	C	37.9	0.001	39

Note: Includes corresponding indicator value (IV), *p*-value, and frequency of occurrence (*f*, number of plots present in; of 120 total) for the different treatment categories (C = control, M = mechanical, and F = fire and mechanical + fire). Life form abbreviations are Fb = forb, Fn = fern, Gr = graminoid, Sh = shrub, Tr = tree, Wv = woody vine. Nomenclature is from the USDA Plants Database (https://plants.usda.gov/home).
Abbreviation: TRT, treatment type.

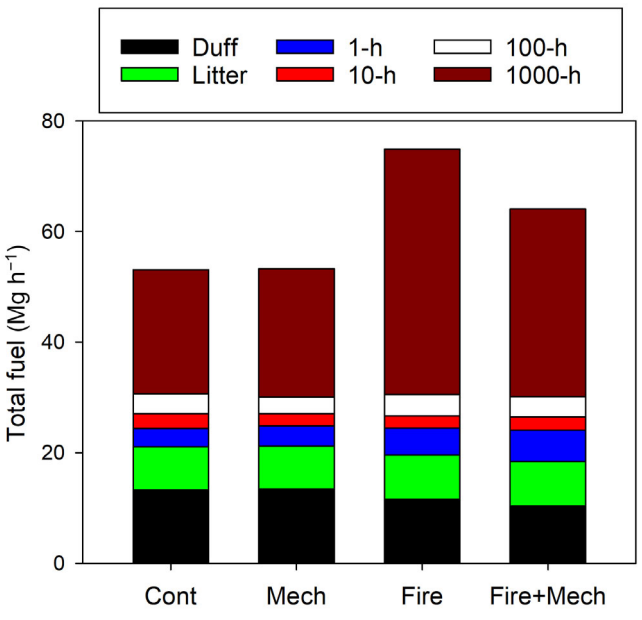

FIGURE 5 Fuel loadings by category in 2016, 7 years after the third fire on the Fire only and Mech + Fire treatments.

advance regeneration, and a ground-layer flora largely lacking disturbance-adapted species that require moderate light. Two decades of repeated fires (Fire and Mech + Fire treatments) generally shifted these attributes away from mesophication. In contrast, the Mech-only treatment exerted little to no long-term changes. Repeated prescribed fires alone, applied at the stand scale typically have limited effects on stand structure and fuels in the short to medium term (Arthur et al., 2015; Hutchinson, Yaussy, et al., 2012; Waldrop et al., 2016). However, the moderate and occasionally high-intensity prescribed fires on our study sites generated vegetation and fuel responses that were ultimately quite similar between the two fire treatments, despite the initial stand-density reduction on the Mech + Fire treatment. After two decades, four fires substantially reduced and sustained lower densities of mesophytes in the midstory and sapling layers and thus limited the probability that future canopy gaps will be filled by mesophytes. In a separate study we found that a series of 3–5 low to moderate

TABLE 5 Pre-fire fuel loadings at grid points for all treatments and consumption in 2016 in burned units (fire and mechanical + fire treatments).

Fuel class	Cont	Mech	Fire	Mech + Fire	Consumption (Mg ha^{-1})	Proportional consumption
DUFF	13.3 ± 1.7	13.5 ± 2.2	11.6 ± 1.5	10.4 ± 1.0	4.7 ± 1.0	0.43
LITTER	7.8 ± 0.4	7.7 ± 0.4	8.0 ± 0.3	7.9 ± 0.3	5.4 ± 0.3	0.68
Woody–1 h	3.3 ± 0.3	3.7 ± 0.3	4.9 ± 0.4	5.7 ± 0.5	2.4 ± 0.3	0.45
Woody–10 h	2.7 ± 0.3	2.2 ± 0.2	2.2 ± 0.3	2.4 ± 0.3	0.4 ± 0.2	0.16
Woody–100 h	3.6 ± 0.6	3.0 ± 0.6	3.9 ± 0.7	3.7 ± 0.6	0.2 ± 0.4	0.06
Woody–1000 h	22.3 ± 4.9	23.2 ± 5.4	44.4 ± 7.3	33.8 ± 6.8	3.9 ± 2.5	0.10
CWM	7.6 ± 2.9	10.3 ± 3.2	23.6 ± 5.9	16.8 ± 3.8	NA	NA
Litter to 10 h	13.8 ± 0.6	13.5 ± 0.6	15.2 ± 0.8	16.1 ± 0.8	14.6 ± 0.4	0.52
Total fuel	53.0 ± 5.3	53.2 ± 6.4	75.0 + 7.6	64.0 ± 7.3	16.9 ± 3.1	0.24

Note: Proportional consumption is calculated based on the ratio of consumption and pre-fire loading, both averaged across sites. Means and confidence interval (95%) were calculated for data from all sites.
Abbreviation: CWM, coarse woody material.

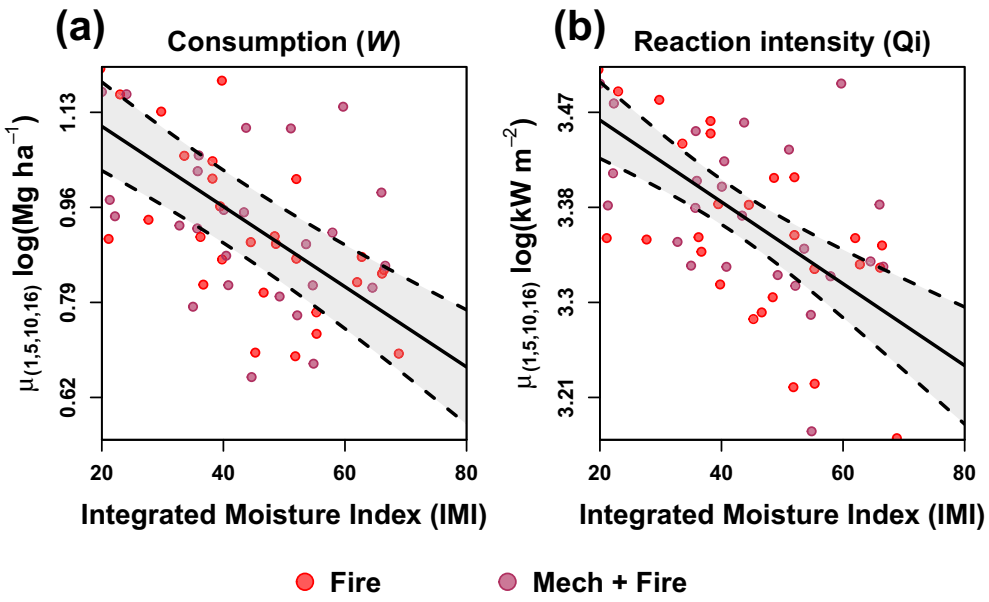

FIGURE 6 (a, b) Relationship between the Integrated Moisture Index and two fire behavior variables based on thermocouple probe (TCP) response to fires. Probe response was calibrated (Bova & Dickinson, 2008) to provide fuel consumption (*W*) and reaction intensity (Qi). Estimates from TCP response reflect flaming combustion and flame front propagation and discount residual smoldering.

intensity prescribed fires, by greatly reducing midstory and sapling densities, resulted in subsequent natural canopy gaps not being filled by maples in contrast with gaps in unburned stands which were (Hutchinson, Long, et al., 2012).

In addition, by incorporating model selection, we demonstrate the importance of topographic-moisture gradients in modulating treatment effects, particularly among stand density and tree regeneration responses. This concept, while expected, has not been rigorously tested across all treatments for a suite of vegetation and fuel responses, in previous Ohio Hills FFS studies (Albrect & McCarthy, 2006; Iverson et al., 2017; Waldrop et al., 2008). Our use of an interaction model allowed us to explicitly test this hypothesis and evaluate its support against treatment-only and topography-only models. We found support for the interaction model in the majority of vegetation responses. From an oak management perspective, this modeling framework provides direct support for targeted restoration efforts (Iverson et al., 2017). Here, we found

that intermediate and dry sites within both fire treatments experienced increases in large oak–hickory regeneration over the ~20-year study period, and that this response was best explained by the inherent interaction between treatment type and topographic-moisture gradients beyond that of treatment only. While treatment-only effects were best supported for ground-layer vegetation responses, caution is warranted in interpreting whether topography and its interaction with treatment affected ground-layer response. Note that changes in ground-layer species composition were significantly associated with topographic moisture and basal area reduction (an indicator of fire intensity). It may be that the lack of interaction effects on ground-layer responses modeled in this study was masked by an oversimplification of compositional data into the univariate descriptors of richness and cover (Rotenberry, 1985).

On the controls in our study, stand composition gradually shifted as mortality (16%) of overstory trees (>25 cm dbh) was primarily oaks (79%) and ingrowth to the midstory was predominantly mesophytic species (87%). The Mech-only treatment had a similar pattern of mortality (20% mortality with 91% being oaks) and ingrowth (82% mesophytes). Oak mortality typically occurred at the single-tree gap scale. Red maple, the most abundant midstory tree on these sites, is shade tolerant and able to persist as saplings and poles beneath the oak canopy for many decades (Hutchinson et al., 2008) but then grow rapidly when canopy gaps are formed (Tift & Fajvan, 1999). For both unburned treatments, future canopy gaps appear poised to be filled by the shade-tolerant species that dominate the midstory, leading to the gradual replacement of the oak-dominated canopy.

Although the Mech-only treatment primarily removed trees in the midstory and lower canopy, the basal area was reduced by 30%, which served as a moderate-intensity release cut. Without fire or additional treatments (e.g., herbicide), the Mech exhibited, to some degree, the process of disturbance-mediated accelerated succession to mesophytic dominance that has been described in other oak-dominated forests, following logging or natural canopy disturbance (Abrams & Nowacki, 1992; Abrams & Scott, 1989; Holzmueller et al., 2012). However, because an oak-dominated overstory remains on the Mech-only treatment, the conversion to a different forest type has not yet occurred and could potentially be impeded with intensive management to reduce the midstory dominance of mesophytes.

Periodic fires are considered to have been the primary factor sustaining eastern oak forests prior to the fire suppression era, by promoting oak regeneration and limiting the establishment and persistence of fire-sensitive species (Abrams, 1992; Arthur et al., 2021). When our study began, oak–hickory seedlings were relatively abundant (median 17,000 seedlings ha^{-1}) but only a small percentage were large (>50 cm tall) and oak saplings were essentially absent, a condition that has been well-documented in unmanaged stands throughout the eastern United States (Aldrich et al., 2005; Nowacki & Abrams, 1992; Vander Yacht et al., 2019). Both fire treatments considerably increased the abundance of large oak–hickory advance regeneration, relative to the significant but smaller gains by nonoaks. Although oak advance regeneration is often resilient after fire (Brose & Van Lear, 1998; Fan et al., 2012), small oak seedlings lacking well developed roots are susceptible to fire-caused mortality (Brose & Van Lear, 2004). The significant gains in large oak regeneration at our sites suggest that oak seedling mortality was limited, but without tracking individual seedlings we cannot estimate mortality rates. It is possible that fire may also have facilitated greater establishment of new oak seedlings during mast years through litter and duff reduction and greater light availability, as shown in other studies (Barnes & Van Lear, 1998; Greenler et al., 2020; Royse et al., 2010).

We expected that treatment effects on large oak–hickory advance regeneration would increase from mesic to dry site conditions. However, while mesic plots had the fewest large oak–hickory stems on fire treatments by year 21, densities on intermediate burned plots exceeded that on dry plots, contradicting the paradigm that oak regeneration success increases linearly as site productivity decreases in moderately productive stands (Johnson et al., 2019). We believe this outcome was driven primarily by the fact that intermediate plots generally had greater densities of small (<50 cm tall) oak–hickory seedlings than dry plots prior to treatments. However, it is also possible that the higher intensity fires on dry plots caused greater mortality of oak–hickory seedlings while stimulating the development of nonoak saplings, resulting in greater competition for the oaks and hickories. Finally, tall sumac shrubs (*Rhus glabra* and *R. copallinum*, not included in the tree groups) were also abundant on many dry intensely burned plots.

Fire caused a reduction of mesophytic saplings, which were dominant prior to treatments, a common finding in fire–oak research (Brose et al., 2013). However, even after four fires, mesophytic species were still a component of the sapling layer, as well as the large advanced regeneration layer. Among the mesophytes, the shade-intolerant yellow-poplar was the most abundant species in the sapling strata on fire treatments in year 21, and despite its affinity for mesic sites, its densities were generally highest on dry burned sites that were more open. Overall, however, the composition of the large advance regeneration was shifted toward increased oak–hickory dominance on dry and intermediate sites, a majority of the landscape. Iverson et al. (2019) showed that 70% of

the forested landscape in the Ohio Hills (17 counties) is classified as Dry Oak Forest and Dry-mesic Mixed-Oak Hardwood Forest, analogous to the dry and intermediate IMI classes in our study.

Repeated fires also promoted greater ground-layer diversity primarily by increasing the small-scale richness of perennial herbaceous plants and community analyses showed that fire created compositionally distinct communities. It has been proposed that prescribed fire may be detrimental to ground-layer diversity in eastern deciduous forests, particularly on mesic sites (Matlack, 2013). However, we found that mean herbaceous richness increased with burning across the topographic-moisture gradient; from 1.8 to 3.9 (dry), 2.6 to 4.4 (intermediate), and 4.9 to 6.3 (mesic) species per square meter. In addition, ISA showed that only a few species were indicators of unburned treatments, suggesting that few species were negatively impacted by fire. Leaf litter and duff are a mechanical barrier to germination from seed (Facelli & Pickett, 1991), and limit light penetration to the mineral soil, which is required for the germination of many herbaceous species in eastern forests (Baskin & Baskin, 1988). Each fire consumed forest floor biomass, creating windows of opportunity for germination. In addition, most of the fire indicators were present before treatments but occurred at very low frequencies, so it is also likely that the sustained increase in understory light on the fire treatments stimulated reproduction, leading to greater establishment. Although seed bank longevity is unknown for the great majority of individual ground flora species in our region, many of the herbaceous taxa that were fire indicators are in genera known to have the capacity to form at least short-term persistent seed banks (e.g., *Helianthus*, *Solidago*, *Symphyotrichum*, *Eupatorium*, *Desmodium*, *Lespedeza*, *Dichanthelium*; Olmstead, unpublished database). Our results highlight the importance of the seed bank as a reservoir for diversity in long-undisturbed oak forests. Woody taxa known to form persistent seed banks were also significant indicators of fire (e.g., sumacs, brambles [*Rubus* spp.], yellow-poplar, grapevine [*Vitis* spp.]). Conversely, it is also likely that after decades of closed-canopy conditions in these moderately productive forest sites, there has been significant seed bank attrition for species that require moderate light levels to reproduce. More robust seed bank responses to restoration treatments after decades of fire exclusion have been shown in less productive eastern oak ecosystems (Abella et al., 2020; Vander Yacht et al., 2017).

One management goal in our study was to create a more robust (i.e., greater cover) herbaceous ground-layer flora. Despite the large gains in herbaceous richness with fire, cover increases, while significant, were limited as woody plants dominated the ground-layer structure. Greater herbaceous productivity may have been achieved on our sites with more frequent burning, which has been shown on less productive sites (Maginel et al., 2019; Peterson et al., 2007; Vander Yacht et al., 2017).

While the main objective of the FFS treatments in western sites was to test methods for reducing fuels and wildfire hazards, the treatments on eastern hardwood sites, where droughts are typically infrequent and of short duration, were focused on reversing mesophication. In terms of wildfire hazard, the Ohio Hills fire treatments had limited effects on fine surface fuels by year 16, 6 years after the third fire. This is supported by the findings of Stambaugh et al. (2007), who found that 75% of pre-burn litter loading is achieved 4 years after fire in oak forests (see also Waldrop et al., 2010). The increases in larger woody fuels, resulting from areas of high-intensity fire, probably will have minimal effects on fire behavior and effects during typically prescribed fire conditions given their limited consumption (10%; Table 5). However, their consumption may be a consideration for wildfire risk during drought conditions as they become available because of low moisture content. Duff and large-diameter woody material are the largest pools of dead and down biomass on these sites and in other mixed-oak forests (Loucks et al., 2008) and duff is the largest source of consumed biomass in wildfires on some eastern oak sites (Carpenter et al., 2021). In the southern Appalachians significant tree mortality of fire-tolerant ectomycorrhizal (EM) species (primarily oaks) occurred after the 2016 wildfire outbreak on sites where flame lengths and rate of spread were low. Carpenter et al. (2021) showed that dominance by EM species had resulted in greater duff accumulation during decades of fire exclusion, and that consumption of fine roots in the duff drove tree mortality. On our sites, litter accounted for the most consumed biomass in the year 16 fire, followed by duff and 1000 h downed woody material, both of which had high biomass but low percent consumption. Duff loadings prior to the 2016 fires were less but not significantly so on fire treatments 6 years after the previous fire, suggesting that more frequent fires may be required to reduce wildfire-related risks of high duff loading. In our study region (Central Appalachian Plateau), duff accumulation tends to be less, likely due in part to the lack of dense ericaceous shrub cover that is found in the Appalachian Mountains.

We had expected positive feedback on fuels, fire behavior, and fire effects (Mitchell et al., 2009) that would result in increases in fuel loading and consumption and fire intensity on drier sites. We did find that fuel consumption and reaction intensity increased on drier sites. The increases likely reflect, in part, the moderate increase in fine fuels on those sites. Similar increases in fuel loading

on drier sites have been reported in oak forests, for example, higher duff (Loucks et al., 2008), and litter (Waldrop et al., 2010) loading. More importantly, increases in fuel consumption and reaction intensity on drier sites probably reflect greater insolation, windier conditions on southerly aspects that face the prevailing winds, and reduced fuel moisture (Dickinson et al., 2016). Although increases in fine fuels on fire treatments and on drier sites were modest, the decrease in mesophytic litter input may have resulted in greater reaction intensities through reduced fuel bed bulk densities and a chemical composition more conducive to combustion (Dickinson et al., 2016; Varner et al., 2021). There was little evidence of feedbacks between fire and IMI for ground-layer woody or herbaceous cover. We conclude that positive feedback among fuels, fire behavior, and fire effects was not strong overall.

Management implications

Silviculturists, wildlife biologists, ecologists, and fire practitioners require more information on how fire and mechanical treatments affect a range of ecosystem attributes over the long term. We found that, in general, both the Fire and Mech + Fire treatments reduced stand density and basal area, created canopy openings on dry sites, and increased oak–hickory regeneration and ground-layer diversity, but did not lead to fuel reduction. Our finding that the Fire only treatment had similar outcomes to the Fire + Mech treatment, suggests that the long-term application of periodic fire alone (with moderate intensity), can deter the process of mesophication across the majority of the upland landscape. This bodes well for oak management in areas where timber harvesting is constrained and moderate-intensity fire, which has a greater impact on the midstory and includes some overstory mortality, can be accomplished and is within the overall management objectives.

Topographic variability was an important driver of fire effects on stand structure. However, we found that intermediate sites, which generally burned at moderate intensity, developed abundant large oak–hickory regeneration, suggesting that high-intensity fire is not required to promote oak–hickory and may be counterproductive to some degree by creating greater levels of competition from less-desired species. More conservative ignition strategies and avoiding burning during drier conditions would have limited the extent of higher severity fire in our study. In addition, the patches of high-severity fire produced large standing dead trees (snags), which made burning more challenging as the study progressed. Despite felling snags near fire lines, interior snags often caught fire, occasionally sending embers outside of the burn units, causing spot fires.

Fire effects on fauna are a key management consideration but have not been examined extensively on the Ohio FFS sites. Documented direct fire effects (i.e., injury and mortality) on wildlife are rare in eastern oak forests (Harper et al., 2016). Individuals of a range of species have risk avoidance strategies and fire management tactics can be used to reduce risks (Dickinson et al., 2010; Harris et al., 2020; Jorge et al., 2021; Layne et al., 2021). Indirect effects of prescribed fire through habitat alteration are influenced largely by the fire regime (frequency, intensity). Unless fire intensity is high enough to kill a portion of the overstory and stimulate understory vegetation, burning in closed-canopy forests has provided little benefit for most wildlife species in the region unless accompanied by partial harvest (Harper et al., 2016). Patches of overstory mortality created and sustained by the Fire + Mech treatment at the Green River FFS site in the southern Appalachians (Waldrop et al., 2016) were shown to increase the abundance of bird species that require early successional habitat while sustaining the abundance and diversity of late-successional species (Greenberg et al., 2018). The extent of overstory mortality at Green River was similar to that in our Ohio Hills fire treatments on drier sites. Fire-caused tree mortality has benefits for wildlife because it creates snags and coarse woody debris (Harper et al., 2016). Prescribed fire may also provide food sources for vertebrates over the short and long term. In the short term, northern bat (*Myotis septentrionalis*) diets after burns became enriched in dipterans, many of which were specialists on newly dead wood (Lacki et al., 2009). In the longer term, oaks provide a range of benefits to wildlife including mast production, litter quality, and the high diversity of Lepidopteran species that oaks support (McShea et al., 2007; Rodewald & Abrams, 2002; Rubbo & Kiesecker, 2004; Tallamy & Shropshire, 2009). Because the topography of eastern oak forests is often complex, applying fire on landscape positions best suited for burning and oak management may be an effective approach to increasing regional landscape heterogeneity and biological diversity (Harper et al., 2016; Moorman et al., 2011).

From a timber management standpoint, there was significant value loss where high-intensity fire occurred. In addition to mortality, fire-caused bole damage on surviving trees was significant in these areas. While repeated low-intensity fires have been shown to cause relatively minor levels of oak timber value loss (Marschall et al., 2014) repeated fires on drier landscape positions, where fire intensity is often greater, have resulted in more substantial value loss, particularly among the less fire-tolerant red oak group (Mann et al., 2020).

In addition to enhancing oak–hickory regeneration, the fire-driven increase in ground-layer diversity provides

an additional benefit of periodic burning in oak forests. Even after decades of fire exclusion there was a germination response from the seed bank. Conversely, a historical flora that included one of our sites (Hall, 1958) indicates that some species associated with open oak forest and woodland conditions and described as common are now sparse or extirpated. Many of these species were not observed in our study, suggesting limited seed bank persistence. We also found that 2 decades of periodic fire did not create an herb-dominated ground-layer structure. In the 4–6 years between fires, woody sprouts grew rapidly and became dominant. Where a robust herbaceous layer is a primary management objective, more frequent fire or seeding will be necessary, at least in moderately productive oak forests.

The Mech-only treatment was similar to a silvicultural low thinning, applied to increase the growth rates of overstory trees (Johnson et al., 2019). This is a practice applied in some oak forests when timber production is the primary management objective, although typically in younger stands (<60 years; Johnson et al., 2019). However, we found that a mesophyte-dominated midstory had developed two decades after silvicultural thinning as applied in this study, with densities exceeding pretreatment levels, particularly on mesic sites. This suggests that silvicultural thinning may make it more difficult to sustain oaks in the future by accelerating succession. The application of herbicide to cut stumps would have decreased the degree of midstory redevelopment. However, ingrowth from the sapling layer, which was heavily dominated by shade-tolerant species, was a major contributor to midstory redevelopment. Treating smaller stems with herbicide is often cost-prohibitive, as is noncommercial low thinning in younger stands. While the intensive application of herbicide likely would have resulted in better oak regeneration outcomes, the ground-layer response may have been limited without the fire-caused forest floor disturbance.

Differences in fire effects were also evident among our three study sites. The sites were selected and analyzed as replicate blocks and all were dominated by oaks in the overstory and were mostly similar in stand age and structure when the study began. However, while two of the sites (REMA, Zaleski) were largely similar with respect to soil fertility, the Tar Hollow site was more productive (not fully captured by the topography-based IMI) and fire effects were less pronounced, particularly for oak–hickory regeneration. While using landscape-scale topographic gradients to focus prescribed fire and other oak management strategies is a promising strategy (Iverson et al., 2018), the local site differences in our study highlight the need for careful "on the ground" site selection. This is particularly true given the limited number of burn windows and operational capacity to conduct prescribed fire throughout much of the eastern oak region. However, we acknowledge that on federal lands, prescribed fire is often conducted at the landscape-scale (burn units >250 ha) and site-specific considerations may be impractical.

The partial reversal of mesophication documented in this study is encouraging but the structure and composition of oak-dominated forests in the eastern United States are highly variable due to differences in climate, site quality, and land use, including the intensity of deer browsing. Although our study included a range of site conditions quantified by the IMI, it still represents only local variation within the Ohio Hills region. We documented significant gains in the abundance of large oak–hickory advance regeneration, but it is important to note that when the study began, small oak–hickory seedlings were relatively abundant, which is often not the case on more productive sites or where deer browsing intensity is greater. In addition, the relative gains in oak–hickory regeneration compared with that of mesophytic species that we document in this study have not consistently been shown in other relatively long-term prescribed fire studies in the central and southern Appalachians, where red maple sprouts continued to dominate the regeneration strata, despite increases in the abundance of large oak stems (Keyser et al., 2017; Schweitzer et al., 2016). These varied results suggest regional differences in the sprouting capacity of red maple and other oak competitors after repeated burning, but more research is needed to document whether this is true, and if so, to understand the causal mechanisms.

CONCLUSIONS

We found that repeated fires, with and without mechanical stand-density reduction, shifted oak forests in the Ohio Hills to a desired condition of reduced midstory dominance of mesophytes, greater abundance of large oak–hickory advance regeneration relative to competitors, and greater ground-layer species diversity. We also found that topographic-moisture conditions mediated the effects of fire as dry and intermediate sites exhibited larger shifts away from mesophication and toward sustaining future oak dominance. While mechanical treatments alone can be effective in limiting the primary management objective of reduced fire risk in dry western forests (see Hood et al., 2024; Stephens et al., 2023), we found that thinning without fire served to reinforce rather than limit the process of mesophication in eastern oak forests, shifting stands further away from the primary objective of sustaining oak dominance.

AUTHOR CONTRIBUTIONS

Todd Hutchinson, Bryce Adams, and Matthew Dickinson wrote the manuscript. Bryce Adams performed the statistical analyses. Alejandro Royo and Melissa Thomas-Van Gundy provided significant editorial comments and suggestions. Maryjane Heckel assembled the fuels dataset, performed the loading calculations, and provided editorial feedback on the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Hutchinson & Dickinson, 2024) are available in the USDA Forest Service Research Data Archive at https://doi.org/10.2737/RDS-2023-0059.

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REFERENCES

Abella, S. R., K. S. Menard, T. A. Schetter, L. A. Sprow, and J. F. Jaeger. 2020. "Rapid and Transient Changes during 20 Years of Restoration Management in Savanna-Woodland-Prairie Habitats Threatened by Woody Plant Encroachment." *Plant Ecology* 221: 1201–17.

Abrams, M. D. 1992. "Fire and the Development of Oak Forests." *Bioscience* 42: 346–353.

Abrams, M. D., and G. J. Nowacki. 1992. "Historical Variation in Fire, Oak Recruitment, and Post-Logging Accelerated Succession in Central Pennsylvania." *Bulletin of the Torrey Botanical Club* 119(1): 19–28.

Abrams, M. D., and M. L. Scott. 1989. "Disturbance-Mediated Accelerated Succession in Two Michigan Forest Types." *Forest Science* 35(1): 42–49.

Adams, M. B. 2001. "Specific Gravity of Coarse Woody Debris for Some Central Appalachian Hardwood Forest Species." USDA Forest Service, Research Paper NE-716.

Albrect, M. A., and B. C. McCarthy. 2006. "Effects of Fire and Thinning on Tree Recruitment in Central Hardwood Forests." *Forest Ecology and Management* 226: 88–103.

Aldrich, P. R., G. R. Parker, J. Romero-Severson, and C. H. Michler. 2005. "Confirmation of Oak Recruitment Failure in Indiana Old-Growth Forest: 75 Years of Data." *Forest Science* 5: 406–416.

Alexander, H. D., C. Siegert, J. S. Brewer, J. Kreye, M. A. Lashley, J. K. McDaniel, A. K. Paulson, H. J. Renninger, and J. M. Varner. 2021. "Mesophication of Oak Landscapes: Evidence, Knowledge Gaps, and Future Research." *Bioscience* 71(5): 531–542.

Arthur, M. A., B. A. Blankenship, A. Schörgendorfer, and H. D. Alexander. 2017. "Alterations to the Fuel Bed after Single and Repeated Prescribed Fires in an Appalachian Hardwood Forest." *Forest Ecology and Management* 403: 126–136.

Arthur, M. A., B. A. Blankenship, A. Schörgendorfer, D. L. Loftis, and H. D. Alexander. 2015. "Changes in Stand Structure and Tree Vigor with Repeated Prescribed Fire in an Appalachian Hardwood Forest." *Forest Ecology and Management* 340: 46–61.

Arthur, M. A., J. M. Varner, C. W. Lafon, H. D. Alexander, D. C. Dey, C. A. Harper, S. P. Horn, T. F. Hutchinson, T. L. Keyser, and M. A. Lashley. 2021. "Fire Ecology and Management in Eastern Broadleaf and Appalachian Forests." In *Fire Ecology and Management: Past, Present, and Future of US Forested Ecosystems*, edited by C. H. Greenberg and B. Collins, 105–147. Cham: Springer.

Barnes, T., and D. Van Lear. 1998. "Prescribed Fire Effects on Advanced Regeneration in Mixed Hardwood Stands." *Southern Journal of Applied Forestry* 22: 138–142.

Baskin, C. C., and J. M. Baskin. 1988. "Germination Ecophysiology of Herbaceous Plant Species in a Temperate Region." *American Journal of Botany* 75: 286–305.

Boerner, R. E. J. 2006. "Unraveling the Gordian Knot: Interactions among Vegetation, Topography, and Soil Properties in the Central and Southern Appalachians." *The Journal of the Torrey Botanical Society* 133: 321–361.

Boerner, R. E. J., J. A. Brinkman, and D. A. Yaussy. 2007. "Ecosystem Restoration Treatments Affect Soil Physical and Chemical Properties in Appalachian Mixed Oak Forests." In *Proceedings, 15th Central Hardwood Forest Conference*, edited by D. S. Buckley and W. K. Clatterbuck, 107–115. Asheville, NC: USDA Forest Service, Southern Research Station, SRS-GTR-101 [CD-ROM].

Bova, A. S., and M. B. Dickinson. 2008. "Beyond "Fire Temperatures": Calibrating Thermocouple Probes and Modeling their Response to Surface Fires in Hardwood Fuels." *Canadian Journal of Forest Research* 38: 1008–20.

Brose, P. H., D. C. Dey, R. J. Phillips, and T. A. Waldrop. 2013. "A Meta-Analysis of the Fire-Oak Hypothesis: Does Prescribed Burning Promote Oak Reproduction in Eastern North America?" *Forest Science* 59: 322–334.

Brose, P. H., K. W. Gottschalk, S. B. Horsley, P. D. Knopp, J. N. Kochenderfer, B. J. McGuinness, G. W. Miller, T. E. Ristau, S. H. Stoleson, and S. L. Stout. 2008. "Prescribing Regeneration Treatments for Mixed-Oak Forests in the Mid-Atlantic Region." USDA Forest Service General Technical Reports NRS-33. 100 p.

Brose, P. H., and D. H. Van Lear. 1998. "Responses of Hardwood Advance Regeneration to Seasonal Prescribed Fires in Oak-Dominated Shelterwood Stands." *Canadian Journal of Forest Research* 28: 331–39.

Brose, P. H., and D. H. Van Lear. 2004. "Survival of Hardwood Regeneration during Prescribed Fires: The Importance of Root

Development and Root Collar Location." In *Upland Oak Ecology Symposium: History, Current Conditions, and Sustainability*, edited by M. A. Spetich, 123–27. Asheville, NC: USDA Forest Service, Southern Research Station, GTR-SRS-73.

Brown, J. K. 1974. "Handbook for Inventorying Downed Woody Material." USDA Forest Service General Technical Reports INT-16.

Burns, R. M., and B. H. Honkala. 1990. "Silvics of North America." In *Agricultural Handbook 654*, Vol. 2. Hardwoods: USDA Forest Service.

Carpenter, D. O., M. K. Taylor, M. A. Callaham, J. K. Hiers, E. L. Loudermilk, J. J. O'Brien, and N. Wurzburger. 2021. "Benefit or Liability? The Ectomycorrhizal Association May Undermine Tree Adaptations to Fire after Long-Term Fire Exclusion." *Ecosystems* 24: 1059–74.

Dey, D. C. 2014. "Sustaining Oak Forests in Eastern North America: Regeneration and Recruitment, the Pillars of Sustainability." *Forest Science* 60: 926–942.

Dickinson, M. B., T. F. Hutchinson, M. Dietenberger, F. Matt, and M. P. Peters. 2016. "Litter Species Composition and Topographic Effects on Fuels and Modeled Fire Behavior in an Oak-Hickory Forest in the Eastern USA." *PLoS One* 11: e0159997.

Dickinson, M. B., J. C. Norris, A. S. Bova, R. L. Kremens, V. Young, and M. J. Lacki. 2010. "Effects of Wildland Fire Smoke on a Tree-Roosting Bat: Integrating a Plume Model, Field Measurements, and Mammalian Dose–Response Relationships." *Canadian Journal of Forest Research* 40: 2187–2203.

Dufrêne, M., and P. Legendre. 1997. "Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach." *Ecological Monographs* 67: 345–366.

Dyer, J. M., and T. F. Hutchinson. 2019. "Topography and Soils-Based Mapping Reveals Fine-Scale Compositional Shifts over Two Centuries within a Central Appalachian Landscape." *Forest Ecology and Management* 433: 33–42.

Facelli, J. M., and S. T. Pickett. 1991. "Plant Litter: Its Dynamics and Effects on Plant Community Structure." *The Botanical Review* 57: 1–32.

Fan, Z., Z. Ma, D. C. Dey, and S. D. Roberts. 2012. "Response of Advance Reproduction of Oaks and Associated Species to Repeated Prescribed Fires in Upland Oak-Hickory Forests, Missouri." *Forest Ecology and Management* 266: 160–69.

Fralish, J. S. 2004. "The Keystone Role of Oak and Hickory in the Central Hardwood Forest." In *Upland Oak Ecology Symposium: History, Current Conditions, and Sustainability*, edited by M. A. Spetich, 78–87. Asheville, NC: USDA Forest Service, Southern Research Station, GTR-SRS-73.

Gilliam, F. S. 2007. "The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems." *Bioscience* 57: 845–858.

Graham, J. B., and B. C. McCarthy. 2006. "Forest Floor Fuel Dynamics in Mixed-Oak Forests of South-Eastern Ohio." *International Journal of Wildland Fire* 15: 479–488.

Greenberg, C. H., J. Tomcho, A. Livings-Tomcho, J. D. Lanham, T. A. Waldrop, D. Simon, and D. Hagan. 2018. "Long-Term Avian Response to Fire Severity, Repeated Burning, and Mechanical Fuel Reduction in Upland Hardwood Forest." *Forest Ecology and Management* 424: 367–377.

Greenler, S. M., R. K. Swihart, and M. R. Saunders. 2020. "Prescribed Fire Promotes Acorn Survival and Seedling Emergence from Simulated Caches." *Forest Ecology and Management* 464: 118063.

Guyette, R. P., R.-M. Muzika, and D. C. Dey. 2002. "Dynamics of an Anthropogenic Fire Regime." *Ecosystems* 5: 472–486.

Hall, G. W. 1958. "The Vascular Flora of the Vinton Furnace Experimental Forest." *Ohio Journal of Science* 58: 357–365.

Hanberry, B. B., D. C. Bragg, and H. D. Alexander. 2020. "Open Forest Ecosystems: An Excluded State." *Forest Ecology and Management* 472: 118256.

Hanberry, B. B., and G. J. Nowacki. 2016. "Oaks Were the Historical Foundation Genus of the East-Central United States." *Quaternary Science Reviews* 145: 94–103.

Harper, C. A., W. M. Ford, M. A. Lashley, C. E. Moorman, and M. C. Stambaugh. 2016. "Fire Effects on Wildlife in the Central Hardwoods and Appalachian Regions, USA." *Fire Ecology* 12(2): 127–159.

Harris, K. A., J. D. Clark, R. D. Elmore, and C. A. Harper. 2020. "Direct and Indirect Effects of Fire on Eastern Box Turtles." *The Journal of Wildlife Management* 84: 1384–95.

Hoadley, R. B. 1990. *Identifying Wood: Accurate Results with Simple Tools*. Newtown, CT: Taunton Press.

Hood, S. M., J. S. Crotteau, and C. C. Cleveland. 2024. "Long-Term Efficacy of Fuel Reduction and Restoration Treatments in Northern Rockies Dry Forests." *Ecological Applications* 34(2): 1–22. https://doi.org/10.1002/eap.2940.

Holzmueller, E. J., D. J. Gibson, and P. F. Suchecki. 2012. "Accelerated Succession Following an Intense Wind Strom in an Oak-Dominated Forest." *Forest Ecology and Management* 279: 141–46.

Hutchinson, T. F., R. E. Boerner, L. R. Iverson, S. Sutherland, and E. K. Sutherland. 1999. "Landscape Patterns of Understory Composition and Richness across a Moisture and Nitrogen Mineralization Gradient in Ohio (USA) *Quercus* Forests." *Plant Ecology* 144: 177–189.

Hutchinson, T. F., R. E. Boerner, S. Sutherland, E. K. Sutherland, M. Ortt, and L. R. Iverson. 2005. "Prescribed Fire Effects on the Herbaceous Layer of Mixed-Oak Forests." *Canadian Journal of Forest Research* 35: 877–890.

Hutchinson, T. F., and M. B. Dickinson. 2024. *Ohio Hills Fire and Fire Surrogate Study: Vegetation, Fuels, and Fire Behavior*. Fort Collins: Forest Service Research Data Archive. https://doi.org/10.2737/RDS-2023-0059.

Hutchinson, T. F., R. P. Long, R. D. Ford, and E. K. Sutherland. 2008. "Fire History and the Establishment of Oaks and Maples in Second-Growth Forests." *Canadian Journal of Forest Research* 38: 1184–98.

Hutchinson, T. F., R. P. Long, J. Rebbeck, E. K. Sutherland, and D. A. Yaussy. 2012. "Repeated Prescribed Fires Alter Gap-Phase Regeneration in Mixed-Oak Forests." *Canadian Journal of Forest Research* 42: 303–314.

Hutchinson, T. F., E. K. Sutherland, and D. A. Yaussy. 2005. "Effects of Repeated Prescribed Fires on the Structure, Composition, and Regeneration of Mixed-Oak Forests in Ohio." *Forest Ecology and Management* 218: 210–228.

Hutchinson, T. F., D. A. Yaussy, R. P. Long, J. Rebbeck, and E. K. Sutherland. 2012. "Long-Term (13-Year) Effects of Repeated Prescribed Fires on Stand Structure and Tree Regeneration in Mixed-Oak Forests." *Forest Ecology and Management* 286: 87–100.

Iverson, L. R., J. L. Bartig, G. J. Nowacki, M. P. Peters, J. M. Dyer, T. F. Hutchinson, S. N. Matthews, and B. T. Adams. 2019. "USDA Forest Service section, Subsection, and Landtype

Descriptions for Southeastern Ohio." Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station, Research MapNRS-10. 6 p. [Printed map included] https://doi.org/10.2737/NRS-RMAP-10

Iverson, L. R., M. E. Dale, C. T. Scott, and A. Prasad. 1997. "A GIS-Derived Integrated Moisture Index to Predict Forest Composition and Productivity of Ohio Forests (USA)." *Landscape Ecology* 12: 331–348.

Iverson, L. R., T. F. Hutchinson, M. P. Peters, and D. A. Yaussy. 2017. "Long-Term Response of Oak-Hickory Regeneration to Partial Harvest and Repeated Fires: Influence of Light and Moisture." *Ecosphere* 8(1): e01642.

Iverson, L. R., M. P. Peters, J. L. Bartig, J. Rebbeck, T. F. Hutchinson, S. N. Matthews, and S. Stout. 2018. "Spatial Modeling and Inventories for Prioritizing Investment into Oak-Hickory Restoration." *Forest Ecology and Management* 424: 355–366.

Jaeger, B. 2017. "r2glmm: Computes R Squared for Mixed (Multilevel) Models." R Package Version 0.1.2. https://cran.r-project.org/package=r2glmm.

Johnson, P. S., S. R. Shifley, R. Rogers, D. C. Dey, and J. M. Kabrick. 2019. *The Ecology and Silviculture of Oaks*. Wallingford, UK: CABI.

Jorge, M. H., W. M. Ford, S. E. Sweeten, S. R. Freeze, M. C. True, M. J. St Germain, H. Taylor, K. M. Gorman, E. P. Garrison, and M. J. Cherry. 2021. "Winter Roost Selection of Lasiurine Tree Bats in a Pyric Landscape." *PLoS One* 16: e0245695.

Keyser, T. L., M. A. Arthur, and D. L. Loftis. 2017. "Repeated Burning Alters the Structure and Composition of Hardwood Regeneration in Oak-Dominated Forests of Eastern Kentucky, USA." *Forest Ecology and Management* 393: 1–11.

Knapp, B. O., C. J. Maginel, B. Graham, J. M. Kabrick, and D. C. Dey. 2022. "Escaping the Fire Trap: Does Frequent, Landscape-Scale Burning Inhibit Tree Recruitment in a Temperate Broadleaf Ecosystem?" *Forest Ecology and Management* 513: 120191.

Kreye, J. K., J. M. Varner, G. W. Hamby, and J. M. Kane. 2018. "Mesophytic Litter Dampens Flammability in Fire-Excluded Pyrophytic Oak–Hickory Woodlands." *Ecosphere* 9(1): e02078.

Kreye, J. K., J. M. Varner, J. K. Hiers, and J. Mola. 2013. "Toward a Mechanism for Eastern North American Forest Mesophication: Differential Litter Drying across 17 Species." *Ecological Applications* 23: 1976–86.

Lacki, M. J., D. R. Cox, L. E. Dodd, and M. B. Dickinson. 2009. "Response of Northern Bats (*Myotis septentrionalis*) to Prescribed Fires in Eastern Kentucky Forests." *Journal of Mammalogy* 90: 1165–75.

Lafon, C. W., A. T. Naito, H. D. Grissino-Mayer, S. P. Horn, and T. A. Waldrop. 2017. "Fire history of the Appalachian Region: A Review and Synthesis." USDA Forest Service, General Technical Reports SRS-219. 97 p.

Layne, J. T., D. Green, A. Scesny, and L. W. Robbins. 2021. "Eastern Red Bat Responses to Fire during Winter Torpor." *Forests* 12(10): 1347.

Leete, B. E. 1939. *Forest Fires in Ohio: 1923 to 1935*. Wooster: Ohio Agricultural Experiment Station. Bulletin 598.

Loftis, D. L., and C. E. McGee. 1993. "Oak Regeneration: Serious Problems, Practical Recommendations." In *Symposium Proceedings* 319. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station GTR SE-84.

Lorber, J., M. Thomas-Van Gundy, and S. Croy. 2018. "Characterizing Effects of Prescribed Fire on Forest Canopy Cover in the George Washington and Jefferson National Forests." USDA Forest Service, Research Paper NRS-30, 31 p.

Lorimer, C. G., J. W. Chapman, and W. D. Lambert. 1994. "Tall Understorey Vegetation as a Factor in the Poor Development of Oak Seedlings beneath Mature Stands." *Journal of Ecology* 82: 227–237.

Loucks, E., M. A. Arthur, J. E. Lyons, and D. L. Loftis. 2008. "Characterization of Fuel before and after a Single Prescribed Fire in an Appalachian Hardwood Forest." *Southern Journal of Applied Forestry* 32: 80–88.

Maginel, C., B. Knapp, J. M. Kabrick, and R.-M. Muzika. 2019. "Landscape and Site Level Responses of Woody Structure and Ground Flora to Repeated Prescribed Fire in the Missouri Ozarks." *Canadian Journal of Forest Research* 48(8): 1004–14.

Mann, D. P., J. K. Wiedenbeck, D. C. Dey, and M. R. Saunders. 2020. "Evaluating Economic Impacts of Prescribed Fire in the Central Hardwood Region." *Journal of Forestry* 118: 275–288.

Marschall, J. M., R. P. Guyette, M. C. Stambaugh, and A. P. Stevenson. 2014. "Fire Damage Effects on Red Oak Timber Product Value." *Forest Ecology and Management* 320: 182–89.

Matlack, G. R. 2013. "Reassessment of the Use of Fire as a Management Tool in Deciduous Forests of Eastern North America." *Conservation Biology* 27: 916–926.

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

McEwan, R. W., J. M. Dyer, and N. Pederson. 2011. "Multiple Interacting Ecosystem Drivers: Toward an Encompassing Hypothesis of Oak Forest Dynamics across Eastern North America." *Ecography* 34: 244–256.

McShea, W. J., W. M. Healy, P. Devers, T. Fearer, F. H. Koch, D. Stauffer, and J. Waldon. 2007. "Forestry Matters: Decline of Oaks Will Impact Wildlife in Hardwood Forests." *The Journal of Wildlife Management* 71: 1717–28.

Mitchell, R. J., J. K. Hiers, J. O'Brien, and G. Starr. 2009. "Ecological Forestry in the Southeast: Understanding the Ecology of Fuels." *Journal of Forestry* 107: 391–97.

Moorman, C. E., K. R. Russell, and C. H. Greenberg. 2011. "Reptile and Amphibian Response to Hardwood Forest Management and Early Successional Habitats." In *Sustaining Young Forest Communities: Ecology and Management of Early Successional Habitats in the Central Hardwood Region, USA*. Managing Forest Ecosystems, Vol. 2011, edited by C. H. Greenberg, B. S. Collins, and F. R. Thompson III, 191–208. Dordrecht, Heidelberg, London, New York: Springer Science and Business Media.

Nakagawa, S., and H. Schielzeth. 2013. "A General and Simple Method for Obtaining R2 from Generalized Linear Mixed-Effects Models." *Methods in Ecology and Evolution* 4: 133–142.

Nowacki, G. J., and M. D. Abrams. 1992. "Community, Edaphic, and Historical Analysis of Mixed Oak Forests of the Ridge and Valley Province in Central Pennsylvania." *Canadian Journal of Forest Research* 22: 790–800.

Nowacki, G. J., and M. D. Abrams. 2008. "The Demise of Fire and "Mesophication" of Forests in the Eastern United States." *Bioscience* 58: 123–138.

Oksanen, J., G. L. Simpson, F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, et al. 2022. "vegan: Community

Ecology Package." R Package Version 2.6-2. https://cran.r-project.org/package=vegan.

Peters, M. P., L. R. Iverson, S. N. Matthews, and A. M. Prasad. 2013. "Wildfire Hazard Mapping: Exploring Site Conditions in Eastern US Wildland–Urban Interfaces." *International Journal of Wildland Fire* 22: 567–578.

Peterson, D. W., P. B. Reich, and K. J. Wrage. 2007. "Plant Functional Group Responses to Fire Frequency and Tree Canopy Cover Gradients in Oak Savannas and Woodlands." *Journal of Vegetation Science* 18: 3–12.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2022. "nlme: Linear and Nonlinear Mixed Effects Models." R Package Version 3.1-155. https://cran.r-project.org/package=nlme.

Quinn Thomas, R., C. D. Canham, K. C. Weathers, and C. L. Goodale. 2010. "Increased Tree Carbon Storage in Response to Nitrogen Deposition in the US." *Nature Geoscience* 3(1): 13–17.

Reilly, M. J., S. P. Norman, J. J. O'Brien, and E. L. Loudermilk. 2022. "Drivers and Ecological Impacts of a Wildfire Outbreak in the Southern Appalachian Mountains after Decades of Fire Exclusion." *Forest Ecology and Management* 524: 120500.

Riccardi, C. L. 2005. *The Effect of Prescribed Fire on Fuel Loads, Seed Germination, and Acorn Weevils (Coleoptera: Curculionidae) in Mixed-Oak Forests of Central Appalachia*. PhD dissertation. Athens: Ohio University.

Roberts, D. W. 2019. "labdsv: Ordination and Multivariate Analysis for Ecology." R Package Version 2.0-1. https://cran.r-project.org/package=labdsv.

Rodewald, A. D., and M. D. Abrams. 2002. "Floristics and Avian Community Structure: Implications for Regional Changes in Eastern Forest Composition." *Forest Science* 48: 267–272.

Rogers, D. A., T. P. Rooney, D. Olson, and D. M. Waller. 2008. "Shifts in Southern Wisconsin Forest Canopy and Understory Richness, Composition, and Heterogeneity." *Ecology* 89: 2482–92.

Rotenberry, J. T. 1985. "The Role of Habitat in Avian Community Composition: Physiognomy or Floristics?" *Oecologia* 67: 213–17.

Royo, A. A., R. Collins, M. B. Adams, C. Kirschbaum, and W. P. Carson. 2010. "Pervasive Interactions between Ungulate Browsers and Disturbance Regimes Promote Temperate Forest Herbaceous Diversity." *Ecology* 91: 93–105.

Royse, J., M. A. Arthur, A. Schörgendorfer, and D. L. Loftis. 2010. "Establishment and Growth of Oak (*Quercus alba*, *Quercus prinus*) Seedlings in Burned and Fire-Excluded Upland Forests on the Cumberland Plateau." *Forest Ecology and Management* 260: 502–510.

Rubbo, M. J., and J. M. Kiesecker. 2004. "Leaf Litter Composition and Community Structure: Translating Regional Species Changes into Local Dynamics." *Ecology* 85: 2519–25.

Schweitzer, C. J., D. C. Dey, and Y. Wang. 2016. "Hardwood-Pine Mixedwoods Stand Dynamics Following Thinning and Prescribed Burning." *Fire Ecology* 12: 85–104.

Schwilk, D. W., J. E. Keeley, E. E. Knapp, J. McIver, J. D. Bailey, C. J. Fettig, C. E. Fiedler, R. J. Harrod, J. J. Moghaddas, and K. W. Outcalt. 2009. "The National Fire and Fire Surrogate Study: Effects of Fuel Reduction Methods on Forest Vegetation Structure and Fuels." *Ecological Applications* 19: 285–304.

Small, C. J., and B. C. McCarthy. 2005. "Relationship of Understory Diversity to Soil Nitrogen, Topographic Variation, and Stand Age in an Eastern Oak Forest, USA." *Forest Ecology and Management* 217: 229–243.

Spicer, M. E., H. Mellor, and W. P. Carson. 2020. "Seeing beyond the Trees: A Comparison of Tropical and Temperate Plant Growth Forms and their Vertical Distribution." *Ecology* 101: e02974.

Stambaugh, M. C., R. P. Guyette, and D. C. Dey. 2007. "Forest Fuels and Landscape-Level Fire Risk Assessment of the Ozark Highlands, Missouri." In *Proceedings,15th Central Hardwood Forest Conference*, edited by D. S. Buckley and W. K. Clatterbuck, 258–266. Asheville, NC: USDA Forest Service, Southern Research Station, e-General Technical Report SRS-101. 770 p. [CD-ROM].

Stephens, S. L., D. E. Foster, J. J. Battles, A. A. Bernal, B. M. Collins, R. Hedges, J. J. Moghaddas, A. T. Roughton, and R. A. York. 2023. "Forest Restoration and Fuels Reduction Work: Different Pathways for Achieving Success in the Sierra Nevada." *Ecological Applications*: e2932. https://doi.org/10.1002/eap.2932.

Tallamy, D. W., and K. J. Shropshire. 2009. "Ranking Lepidopteran Use of Native Versus Introduced Plants." *Conservation Biology* 23: 941–47.

Taverna, K., R. K. Peet, and L. C. Phillips. 2005. "Long-Term Change in Ground-Layer Vegetation of Deciduous Forests of the North Carolina Piedmont, USA." *Journal of Ecology* 93: 202–213.

Tift, B. D., and M. A. Fajvan. 1999. "Red Maple Dynamics in Appalachian Hardwood Stands in West Virginia." *Canadian Journal of Forest Research* 29: 157–165.

Van Wagner, C. 1968. "The Line Intersect Method in Forest Fuel Sampling." *Forest Science* 14: 20–26.

Vander Yacht, A. L., S. A. Barrioz, P. D. Keyser, C. A. Harper, D. S. Buckley, D. A. Buehler, and R. D. Applegate. 2017. "Vegetation Response to Canopy Disturbance and Season of Burn during Oak Woodland and Savanna Restoration in Tennessee." *Forest Ecology and Management* 390: 187–202.

Vander Yacht, A. L., P. D. Keyser, S. A. Barrioz, C. Kwit, M. C. Stambaugh, W. K. Clatterbuck, and R. Jacobs. 2020. "Litter to Glitter: Promoting Herbaceous Groundcover and Diversity in Mid-southern USA Oak Forests Using Canopy Disturbance and Fire." *Fire Ecology* 16(1): 1–19.

Vander Yacht, A. L., P. D. Keyser, S. A. Barrioz, C. Kwit, M. C. Stambaugh, W. K. Clatterbuck, and D. M. Simon. 2019. "Reversing Mesophication Effects on Understory Woody Vegetation in Mid-Southern Oak Forests." *Forest Science* 65(3): 289–303.

Vander Yacht, A. L., P. D. Keyser, D. A. Buehler, C. A. Harper, D. S. Buckley, and R. D. Applegate. 2016. "Avian Occupancy Response to Oak Woodland and Savanna Restoration." *The Journal of Wildlife Management* 80(6): 1091–1105.

Varner, J. M., J. M. Kane, J. K. Kreye, and T. M. Shearman. 2021. "Litter Flammability of 50 Southeastern North American Tree Species: Evidence for Mesophication Gradients across Multiple Ecosystems." *Frontiers in Forests and Global Change* 4: 727042.

Waldrop, T. A., D. L. Hagan, and D. M. Simon. 2016. "Repeated Application of Fuel Reduction Treatments in the Southern Appalachian Mountains, USA: Implications for Achieving Management Goals." *Fire Ecology* 12(2): 28–47.

Waldrop, T. A., R. A. Phillips, and D. A. Simon. 2010. "Fuels and Predicted Fire Behavior in the Southern Appalachian Mountains after Fire and Fire Surrogate Treatments." *Forest Science* 56: 32–45.

Waldrop, T. A., D. A. Yaussy, R. J. Phillips, T. F. Hutchinson, L. Brudnak, and R. E. J. Boerner. 2008. "Fuel Reduction Treatments Affect Stand Structure of Hardwood Forests in Western North Carolina and Southern Ohio, USA." *Forest Ecology and Management* 255: 3117–29.

Wenger, K. F. 1984. *Forestry Handbook*. New York: John Wiley & Sons.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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