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RESEARCH ARTICLE

Increased fire occurrence benefits early oak regeneration in temperate deciduous forests in part by disrupting an invasive grass-fire feedback

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Abstract

1. Feedbacks between fire and non-native grasses can lead to a grass-fire cycle that intensifies grass invasion and harms native trees. However, higher fire activity may reshape fire–grass–tree interactions by altering resource availability and reducing fire intensity. Understanding these dynamics and their effects on tree regeneration is critically important for maintaining and restoring declining oak populations in temperate deciduous forests.
2. Here, we performed a landscape-scale field experiment in oak-hickory forests of the U.S. central hardwood region to determine how grass invasion and variation in fire activity alter post-fire regeneration of oak seedlings and juveniles. We applied fire to outplanted white oak (*Quercus alba*) and black oak (*Q. velutina*) seedlings and naturally colonized juveniles in plots arrayed along a historical fire occurrence gradient that were either uninvaded or invaded by a widespread non-native grass (*Microstegium vimineum*).
3. We found that increased fire occurrence elevated light availability, with plots burnt five times receiving on average 2.5 times more light. Increased fire occurrence also reduced fire intensity, with each additional burn lowering the maximum temperature of experimental fires by 18°C. These changes contributed to post-fire oak survival rates being almost twice as high in plots burnt five times compared with those with a history of a single prior burn.
4. In contrast, *Microstegium* invasion decreased fire intensity and had no effect on post-fire oak seedling survival in plots with a history of multiple burns. *Microstegium* cover also declined as fire occurrence increased.
5. *Synthesis and applications*. These results suggest that recurring fire can mitigate the negative effects of grass invasion and create conditions more favourable for early oak regeneration in temperate deciduous forests.

KEYWORDS
fire intensity, fire–grass–tree interactions, grass-fire cycle, historical fire regime, invasive grasses, light availability, Mesophication, *Microstegium vimineum*, post-fire oak survival, prescribed fire, Resprouting

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1 | INTRODUCTION

Fire is an important driver of the structure and composition of ecosystems globally (Bond & Keeley, 2005; Bowman et al., 2009; Pausas & Keeley, 2009), including open forests, woodlands, and savannas (Hanberry et al., 2020; Ratnam et al., 2011). In open forests, fire prevents total canopy closure (Stockdale et al., 2019), enabling the persistence of many fire-tolerant species (He et al., 2019; Morrison, 2002). However, fire suppression is rising due to local policies, agriculture, and fragmentation (Arora & Melton, 2018; Fowler & Konopik, 2007). Lack of fire has allowed canopy gaps to be filled by shade-tolerant, fire-intolerant trees, leading to more mesic, less flammable understories with lower light availability (Alexander et al., 2021; Álvarez et al., 2025; Nowacki & Abrams, 2008). Oak ecosystems, in particular, have suffered across the globe as the effects of fire suppression and canopy closure inhibit oak regeneration (Altman et al., 2016; Li & Ma, 2003; Spînu et al., 2020).

Reintroducing fire and increasing fire activity can reverse these trends (Brose et al., 2013; Pile Knapp et al., 2024) and would better match historical fire regimes (Guyette et al., 2002; Ruffner & Groninger, 2006). Fire reduces the density of midstory and understory stems, especially of problematic fire-intolerant trees (Hutchinson et al., 2024; Keyser et al., 2018). The resulting increased understory light penetration and reduced competition can benefit juvenile oak trees shaded out during fire suppression (Arthur et al., 2012; Hutchinson et al., 2012). However, mechanical overstory thinning may also be necessary to achieve the light levels required for oak recruitment to the overstory (Bragg et al., 2020; Dey & Fan, 2009). Oak trees and their associated vegetation communities are ecologically important for biodiversity conservation (Grundel & Pavlovic, 2007; Narango et al., 2020; Noble & Bauer, 2022), and provide economic value through timber harvest and carbon sequestration (Huang et al., 2004). Despite widespread oak decline and the need for improved oak regeneration, forest responses to changes in fire activity remain concerningly understudied, particularly in the presence of invasive grasses (Tomat-Kelly & Flory, 2023; Varner et al., 2016).

Invasive grasses are among the most successful invasive plants globally (Pertierra et al., 2023). They can harm native ecosystems not only by outcompeting native species but also by increasing fire activity, which may positively feedback to invasion and perpetuate an invasive 'grass-fire cycle' (D'Antonio & Vitousek, 1992; Fusco et al., 2019). In non-forested arid and semiarid systems, invasive grass-fire cycles have eliminated native grasses and shrubs by disrupting the historical fire regimes under which these species have evolved (Brooks et al., 2004; D'Antonio et al., 2000). Although such cycles can also become established in temperate deciduous forests (Kerns et al., 2020), their effects on fire activity and native tree communities remain equivocal due to these environments' higher moisture and lower light availability (Tomat-Kelly & Flory, 2023). In the eastern U.S., for example, grass invasions have been found to both increase and decrease prescribed fire intensity (Flory et al., 2015; Salemme & Fraterrigo, 2021; Wagner & Fraterrigo, 2015) and result in either neutral or negative effects on tree regeneration (Flory et al., 2015; Salemme & Fraterrigo, 2021), suggesting that other factors may be influencing survival. This uncertainty complicates the use of prescribed fire for promoting oak regeneration.

Most studies evaluate invasive grass-fire feedbacks in response to single fires. However, recurring fires can more profoundly alter forest ecosystem structure and function (Cuprewich & Saunders, 2024; Knapp et al., 2015), potentially reshaping fire–grass–tree interactions (Fraterrigo & Rembelski, 2021). For example, while a single fire has little effect on understory light, recurring fires can enhance light availability (Alexander et al., 2008; Hutchinson et al., 2012; Iverson et al., 2017)–a key mechanism through which prescribed fire promotes oak regeneration in fire-suppressed forest understories (Brose et al., 2013; Rebbeck et al., 2011). On the other hand, many invasive grasses grow and reproduce better with higher light availability (Cheplick, 2010; Funk & McDaniel, 2010; Horton et al., 2010). Although single fires temporarily increase soil inorganic nitrogen (N) availability (Certini, 2005), favouring the growth of invasive grasses (Johnson et al., 2011), recurring fires tend to decrease soil N availability through volatilization, leaching, and pyrolysis (Knicker, 2007; Pellegrini et al., 2018; Soong & Cotrufo, 2015). Recurring fires can also decrease soil moisture by increasing evaporative demand (Refsland & Fraterrigo, 2018) and reducing water infiltration through the soil (Certini, 2005; MacDonald & Huffman, 2004). Together, these changes can reduce the vigour of invasive grasses (Fraterrigo & Rembelski, 2021; Rembelski & Fraterrigo, 2023), which may indirectly benefit trees by decreasing resource competition. Moreover, recurring fires tend to decrease fire intensity by reducing fuel loads (Stephens et al., 2012), which may enhance tree seedling survival (Brose & Van Lear, 1998). The benefits of recurring fires for oak regeneration may therefore outweigh the potential positive feedbacks to grass invasion. Given the ongoing and projected increases in plant invasion in forests (Iannone III et al., 2016), there is an urgent need to determine how changes in fire occurrence influence oak regeneration dynamics in grass-invaded forests.

We performed a landscape-scale field experiment along a gradient of historical fire occurrence to investigate how variation in fire occurrence affects post-fire oak seedling regeneration in grass-invaded forests. We characterized oak regeneration as post-fire survival and resprouting vigour, which constitute important, early stages in the regeneration process (Dey et al., 2009; Dey & Fan, 2009) and can be influenced by different mechanisms (Resco de Dios et al., 2020). We focused on *Microstegium vimineum* (Trin.) A. Camus, an annual C_4 grass native to Asia that is widely distributed across eastern U.S. deciduous forests. *Microstegium* can survive across a wide range of light and moisture conditions (Cheplick, 2010; Flory, 2010). Additionally, it can increase fire intensity and responds positively to fire (Wagner & Fraterrigo, 2015), which together can reduce tree regeneration in grass-invaded forests (Flory et al., 2015; Salemme & Fraterrigo, 2021). Conversely, frequent fire can reduce *Microstegium* abundance (Fraterrigo & Rembelski, 2021), making this an ideal model system for investigating relationships between fire activity, grass invasion, and tree regeneration. We asked: (1) How does variation in fire occurrence interact with grass invasion to alter resource availability and fire intensity? and (2) How do these

changes affect post-fire survival and resprouting vigour of oak seedlings and juveniles? We hypothesized that higher fire occurrence—characterized by more numerous, frequent, and recent fires—would increase light availability due to lower midstory stem density and decrease soil moisture, soil inorganic N availability, and fuel loads. In turn, we hypothesized that these changes would enhance post-fire oak regeneration by alleviating light limitation for sub-canopy oaks (Rebbeck et al., 2011), reducing resource competition from *Microstegium*, and minimizing heat-induced mortality through lower fire intensity.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in central hardwood forests within the eastern portion of the Shawnee National Forest (US Forest Service LTR occupancy permit 2023-02-15) and at Dixon Springs State Park (Illinois Department of Natural Resources permit SS24-02) in southern Illinois (37°48′ N, 88°47′ W). The climate is humid subtropical with a mean summer temperature of 25°C, mean winter temperature of 3°C, and mean annual precipitation of 1360 mm for the period from 2004 to 2025 (Western Regional Climate Center, 2025). The region is unglaciated with varying topography. The soils are silt loam Alfisols (mesic Oxyaquic Fragiudalfs) containing ca. 15% clay in the top 15 cm (NRCS et al., 2025). The dominant overstory tree species include *Quercus* spp. and *Carya* spp., with *Acer* spp., *Fraxinus* spp., *Juniperus virginiana*, *Liriodendron tulipifera*, and *Ulmus* spp. also commonly appearing in the overstory.

Prior to European settlement, upland forests in southern Illinois were dominated by oak and hickory species, maintained through periodic burning by Indigenous peoples (Ruffner & Groninger, 2006). In the mid-1800s, European-descended settlers used fire to clear land for agriculture and extensively logged these forests. By the mid-1900s, however, prescribed fire use declined due to agricultural abandonment and fire suppression policies, allowing forests to regenerate from existing seeds and sprouts. In recent decades, low-intensity prescribed fire has been reintroduced to restore and maintain upland forests. *Microstegium vimineum* was introduced to the region in the early 1980s and maintains an active invasion front due to dispersal limitation (Anderson et al., 2013; Tekiela & Barney, 2013). This grass invasion poses challenges to the use of fire as a management tool due to both its positive response to fire and potential to intensify fire (Flory et al., 2015; Wagner & Fraterrigo, 2015).

2.2 | Experimental design

To evaluate how variation in fire activity affects post-fire oak seedling regeneration in grass-invaded forests, we compared outplanted oak seedling responses to experimental fire in paired invaded–uninvaded forest plots arrayed along a gradient of historical fire occurrence. We characterized the fire occurrence gradient and identified potential sites by performing principal component analysis on prescribed fire data (mean fire frequency, total number of burns [hereafter, total burns], years after last fire, and length of management period [i.e. years after first fire]) maintained by land managers (Appendix S1, Figure S1). These prescribed fires occurred primarily in the spring dormant season (March–April) and occasionally in the fall–winter dormant season (November–February). From the set of potential sites, we selected 26 research sites averaging 100 ± 34 (SE) ha and spanning a broad range of historical fire occurrence (Table S1; Figure S2), all located in upland areas with hardwood-dominated canopies, relatively flat slopes (<10°), and similar aspects.

In each site, we established between one and four pairs of 5 m × 5 m plots, each pair comprising an uninvaded and *Microstegium*-invaded plot ($n = 100$ plots). Pairs were separated by at least 100 m. To control for the size, number, and species of trees in the plots, we outplanted four 1-year-old *Quercus velutina* and four *Q. alba* bare-root seedlings in each plot ($n = 800$ trees; Mason State Tree Nursery, Topeka, Illinois) in March 2023 (Appendix S1). Additionally, we selected up to eight naturally colonized oak juveniles in each plot for additional measurements (see Section 2.5). In February and March 2024, we experimentally burnt 30 plot pairs varying in historical fire occurrence (Appendix S1).

2.3 | Resource availability

To characterize resource availability, we measured light, soil inorganic N, and soil moisture availability, as well as soil temperature for its potential to inform understanding of nutrient availability and uptake (Bassirirad, 2000). To determine understory light availability, we measured photosynthetic photon flux density (PPFD) 1 m above the ground in each plot in June 2024 (Appendix S2). To determine soil inorganic N availability, we buried two nylon bags filled with 20 g of ion exchange resin beads (AmberLite MB20 Mixed Ion Exchange Resin, Sigma-Aldrich, St. Louis, MO, USA) 5 cm below the soil surface in each plot in June 2023 and retrieved them in September 2023. We analysed samples for NH_4^+-N using the salicylate method and NO_3^- plus NO_2-N using a cadmium column reduction (Lachat QuickChem 8500, Hach Company, Loveland, CO, USA), summing these values by sample and averaging by plot to represent total inorganic N availability (Appendix S2).

In February through September 2023 and 2024, we measured soil moisture (7.5 cm depth; FieldScout TDR 100, Spectrum Technologies, Inc., Aurora, IL) and soil temperature (10 cm depth; Traceable, Fisher Scientific, Waltham, MA) instantaneously several times in each plot and hourly in a subset of plots spanning the range of environmental conditions encountered using HOBO data loggers (Onset Computer Corporation, Bourne, MA, USA). To interpolate hourly soil moisture and temperature at the plot scale from the continuous records, we regressed the discrete

measurements for each plot against the continuous series that produced the highest R^2 value (mean R^2: 0.90 ± 0.01). Hourly estimates were used to calculate plot-level means for each summer (June–August) (Appendix S2).

2.4 | Fuel availability and fire intensity

Because undecomposed and partially decomposed leaf litter comprises the majority of the fuel bed in these forests, we measured the depth, mass, and moisture content of the soil O-horizon (Oi + Oe + Oa) in each plot immediately before experimental burning to characterize fuel availability. We collected two 0.14 m^2 samples of the O-horizon using a sampling frame after measuring the depth at each corner ($n = 8$). In the laboratory, we weighed samples before and after drying at 70°C for 48 h to calculate percent moisture. To quantify fire intensity (maximum fire temperature and fire residence time), four type K thermocouples with buried data loggers were deployed on the soil surface to record fire temperature every second. We placed one thermocouple in each plot quadrant halfway between two outplanted oak seedlings so that all seedlings were 0.5 m from the nearest thermocouple. For each outplanted seedling, we calculated the fire residence time as the number of seconds the fire exceeded 60°C, which is the point at which cell death can occur (Levitt, 1980).

2.5 | Plant measurements

To quantify local invasion severity, we estimated *Microstegium* cover in a 0.5 m radius circle around each outplanted oak seedling in June 2023. To assess the nutrient status of outplanted seedlings, we measured their foliar N and C content in September 2023. Using a hole punch, we collected 15 leaf punches per species per plot from the sun leaves of each living individual. Leaf punches were returned to the laboratory, dried at 60°C for 48 h, finely ground, and analysed for total N and C at the University of Illinois Urbana-Champaign (ECS 4010 CHNS-O, Costech Analytical Technologies Inc., Valencia, CA, USA).

Seedling size can strongly influence post-fire survival (Keyser et al., 2018). We therefore measured the diameter at decimetre height (10 cm; DDH) and stem height from stem base to the leading shoot tip of each outplanted seedling in February 2024 before experimental burning. We also tagged and measured up to eight naturally colonized oak juveniles (<1 m height; $n = 82$, primarily *Q. velutina*, *Q. alba*, and *Q. stellata*) in each plot for comparison with the outplanted seedlings. In September 2024, we assessed oak seedling survival and repeated size measurements for all surviving individuals to determine resprouting vigour. We defined survival as the presence of living leaves on a seedling during September measurements. Because oaks often respond to topkill by resprouting with multiple stems, resprouting vigour was defined as relative sprouted stem height or diameter for each individual, using the height or DDH of each individual's tallest, resprouted stem (Schafer & Just, 2014) in September 2024 divided by the height or DDH of its tallest stem measured before burning in February 2024.

2.6 | Statistical analysis

We used an information theoretic approach to evaluate models relating historical fire occurrence, *Microstegium* invasion, resource availability, fire intensity, and oak regeneration. This entailed fitting sets of candidate models and selecting plausible models by calculating Akaike's Information Criterion (AIC) for each model in a set. For all model sets, we included a null model containing only the random effect and covariates if present. Models with AIC values within two units of the lowest AIC value in a set (ΔAIC < 2) were considered supported (Burnham & Anderson, 2002).

To evaluate how historical fire occurrence influenced resource availability, we fit candidate linear mixed-effects models (LMMs) consisting of either total burns, fire frequency, years after fire, or management length as fixed effects, and pair as a random effect with the *nlme* package (Table S2; Pinheiro et al., 2025). Because C_4 grasses can maintain elevated soil moisture levels (Fahey et al., 2018) and *Microstegium* can increase soil inorganic N availability (Ehrenfeld et al., 2001; Lee et al., 2012), we fit additional candidate LMMs for soil moisture and inorganic N availability that contained *Microstegium* cover as a fixed effect and its additive interactions with fire occurrence variables (Table S2). To evaluate how historical fire occurrence and resource availability influenced *Microstegium* cover, we fit two sets of candidate LMMs, with one set consisting of either total burns, fire frequency, years after fire, or management length as fixed effects, and the other set consisting of either light availability or soil temperature as fixed effects, including pair as a random effect in both sets (Table S3). We fit similar candidate LMMs to evaluate how historical fire occurrence and resource availability influenced oak seedling nutrient status. We also fit candidate LMMs to evaluate relationships between fuel availability (O-horizon depth, mass, and moisture), *Microstegium* cover, soil moisture, and fire intensity (Table S4).

We evaluated how historical fire occurrence, invasion, resource availability, and fire intensity influenced post-fire oak survival using a three-step process. First, we fit a set of candidate generalized linear mixed-effects models (GLMMs) with a binomial distribution (*lme4* package; Bates et al., 2015) consisting of either fire occurrence variables, *Microstegium* cover, or their interactions as fixed effects, with pair as a random effect and initial oak seedling height and species as covariates (Table S5). Because preliminary analyses suggested historical fire occurrence influenced resource availability and fire intensity, we next fit a set of candidate GLMMs consisting of resource availability variables, maximum fire temperature, *Microstegium* cover, or their interactions as fixed effects (i.e. proximate drivers), with plot as a random effect

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and initial oak seedling height and species as covariates (Table S5). We repeated these steps to evaluate how historical fire occurrence, invasion, resource availability, and fire intensity influenced resprouting vigour, using LMMs with the fixed and random effects noted above and initial oak seedling height or diameter (as appropriate to account for allometric scaling) and species as covariates (Table S5). Post-fire oak survival and resprouting vigour analyses were performed separately for outplanted seedlings and naturally colonized juveniles. Finally, to evaluate the effect of individual predictors in the survival and resprouting models, we conducted unconditional model averaging with the *AICcmodavg* package (Burnham & Anderson, 2002; Mazerolle, 2023).

To quantify the relative magnitudes of direct and indirect effects of historical fire activity and invasion on post-fire oak seedling survival and resprouting vigour, we fit two structural equation models (SEM) using the *piecewiseSEM* package (Lefcheck, 2016), with survival and resprouting vigour as the response variables (Appendix S3). Resprouting vigour of outplanted seedlings was modelled using resprouting height because we did not find significant relationships between resprouting diameter and resource availability. Our initial models were based on the hypothesized relationships whereby fire occurrence increases light availability and decreases soil moisture, soil inorganic N, and O-horizon depth, which directly and indirectly influence *Microstegium* cover and ultimately improve oak seedling regeneration. We specified plot and pair as random effects, depending on predictor variables, to account for any non-independence of the residuals. Our previous analyses informed variable selection, and we removed nonsense independence claims during model tuning. We calculated goodness-of-fit using Fisher's *C* statistic in which a $p > 0.05$ indicates the SEM fits the data. We log-transformed response variables as needed to meet normality and homogeneity of variance assumptions and centred and scaled continuous predictor variables to enable comparison of effect sizes. Analyses were considered significant at $p < 0.05$ and marginally significant at $0.05 \leq p < 0.10$. All analyses were conducted using R v. 4.4.1 statistical software (R Core Team, 2024).

3 | RESULTS

3.1 | Fire occurrence, invasion, and resource availability

Of the resource variables measured, only light availability was significantly related to historical fire occurrence (Table S6). Light availability increased with total burns (Tables S2 and S6; Figure 1), averaging 7.8 ± 1.9 (SE) % in plots burnt once and 19.5 ± 2.2% in plots burnt five or more times. Soil moisture increased significantly with *Microstegium* cover (Figure S3) and marginally with total burns (Tables S2 and S6). Soil inorganic N availability also increased significantly with *Microstegium* cover (Figure S4). Although models including the additive interactions of *Microstegium* cover and historical fire occurrence variables were supported, none of the fire variables had a significant effect on soil inorganic N availability (Tables S2 and S6). Similarly, none of the historical fire variables had a significant effect on soil temperature, even though models including these terms were supported (Tables S2 and S6).

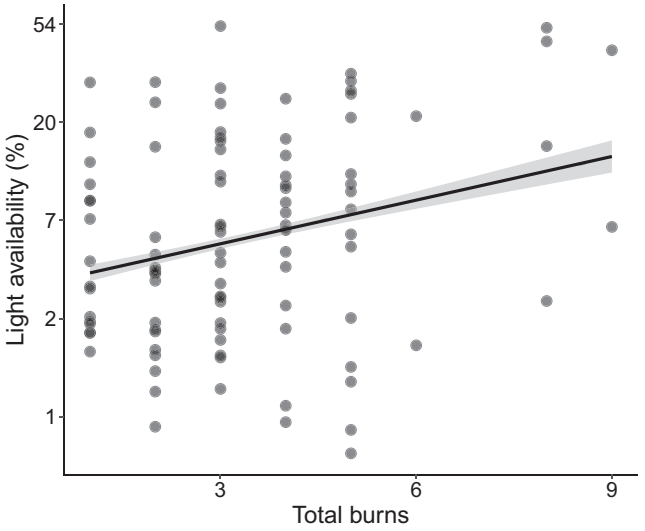


FIGURE 1 Relationship between total burns and light availability (%). Light availability was log-transformed to meet normality and homogeneity of variance assumptions and graphed on a logarithmic scale. Points are observed values. Shaded region surrounding the regression line is 95% confidence interval.

Examining the predictors of variation in *Microstegium* cover, we did not find support for a relationship with historical fire occurrence. Models including historical fire variables ranked lower than the null model, and none of the historical fire variables had a significant effect on *Microstegium* cover (Tables S3 and S7). However, there was a significant, positive relationship between *Microstegium* cover and light availability.

3.2 | Fuel availability and fire intensity

Experimental fires had an average maximum temperature of 204 ± 13 (SE)°C (range: 44–484°C; Table S8) and an average residence time (seconds above 60°C) of 408 ± 29 s (range: 0–1008 s; Table S8). Both maximum fire temperature and fire residence time were positively related to O-horizon depth (Tables S4 and S9; Figure S5), with maximum fire temperature increasing by 41°C and residence time increasing by 65 s for every additional cm of O-horizon depth. In contrast, there was no significant relationship between maximum fire temperature and *Microstegium* cover (estimate: −0.28 ± 0.13) or soil moisture (estimate: −0.31 ± 0.15), and a marginal negative relationship between fire residence time and *Microstegium* cover (Table S9). Although *Microstegium* cover was not significantly related to fuel moisture (estimate: 0.11 ± 0.15) or O-horizon depth (estimate: 0.12 ± 0.12), it was positively related to soil moisture (Tables S4 and S9).

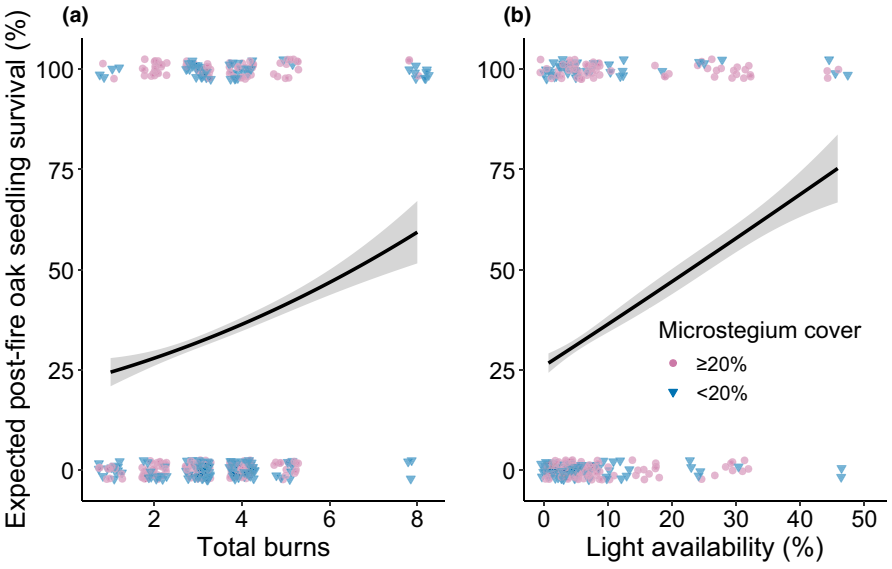


FIGURE 2 Relationships between expected post-fire oak seedling survival and (a) total burns, and (b) light availability. *Microstegium* cover was modelled continuously but is shown as a categorical variable to improve visualization. Points are observed outcomes and are jittered vertically and horizontally. Shaded regions surrounding the logistic regression lines are 95% confidence intervals.

3.3 | Post-fire oak seedling survival, resprouting vigour and leaf nutrient status

Overall, 653 of the 800 (82%) outplanted oak seedlings survived the initial growing season, and neither historical fire occurrence nor invasion affected first-year survival. Twenty of these surviving seedlings could not be found in February 2024 when pre-fire measurements took place and were excluded from further analysis. Of the 363 outplanted oak seedlings treated with fire, 130 (36%) seedlings survived, with 110 of the surviving seedlings (85%) suffering topkill and resprouting. Over the same period, 200 of 270 (74%) unburnt oak seedlings survived. Historical fire occurrence was positively related to post-fire survival of outplanted seedlings, with total burns being the best predictor. Post-fire survival was 81% higher in plots with five prior burns compared with plots with one burn prior to experimental fire (Table S5; Figures 2a and 3). Although the model consisting of the additive effects of total burns and *Microstegium* cover was also supported, it ranked lower than the null model, and there was no statistical evidence of an effect of *Microstegium* cover on post-fire survival (estimate: 0.08, 95% CI: −0.22–0.37; Table S5; Figure 3). However, there was a non-significant trend for declining survival with increasing *Microstegium* cover in plots with only one historical burn (Figure S6). Across all models, initial oak seedling height was positively associated with survival, while oak species had no effect (Figure 3).

The proximate drivers of variation in post-fire survival of outplanted oaks included light availability and maximum fire temperature (Table S5; Figure 3). Survival was 85% higher in plots with 25% light availability compared with plots with 5% light availability (Figures 2b and 3) and 27% lower for fires that reached 250°C compared with fires that reached 150°C (Table S5; Figure 3). Although the model consisting of light availability, maximum fire temperature, and *Microstegium* cover was also supported (Table S5), the effect of *Microstegium* cover was not significant (estimate: −0.1, 95% CI: −0.4–0.2; Table S5; Figure 3). Across all models, initial oak seedling height was positively associated with survival, while oak species had no effect (Figure 3).

Similar to post-fire survival, the resprouting vigour of outplanted seedlings was positively related to historical fire occurrence. Both relative resprout height and diameter increased with total burns (Table S5; Figures 3 and 4a; Figure S7), increasing 35% and 47% more in plots that had five prior burns compared with plots that had one prior burn. Resprout height was also positively related to *Microstegium* cover (Table S5; Figure 3). Across all models, initial seedling size was negatively related to resprout size, while oak species had no effect (Table S5; Figure 3).

Evaluating the proximate drivers of variation in resprouting vigour, we found that relative resprout height was best predicted by soil moisture (Table S5; Figures 3 and 4b), with a 21% greater increase in resprout height in plots with 25% soil water content compared with plots with 15% soil water content. Resprouting vigour was also positively related to light availability, with slightly stronger effects on resprouting height than diameter (Table S5; Figure 3). Across all models, initial seedling size was negatively related to resprout size, while oak species had no effect (Table S3).

Of the naturally colonized oak juveniles, 76 out of 82 (93%) survived burning. None of the fire or resource variables significantly predicted post-fire survival of naturally colonized oak juveniles (Table S10; Figure S8). However, the average height and diameter of natural juveniles that perished were 25.8 ± 5.2 cm and 3.2 ± 0.7 cm, versus 40.5 ± 2.2 cm and 4.1 ± 0.2 cm for those that survived.

Similar to outplanted seedlings, resprouting vigour of naturally colonized oaks was positively related to historical fire occurrence. Relative resprout height increased with increasing total burns and decreasing years after fire (Table S10; Figure S8). Although resprout diameter was best predicted by the null model, models including total burns and years after fire were also supported (Table S10), with relative resprout diameter increasing with total burns and decreasing with years after fire (Figure S8). *Microstegium* cover did not affect

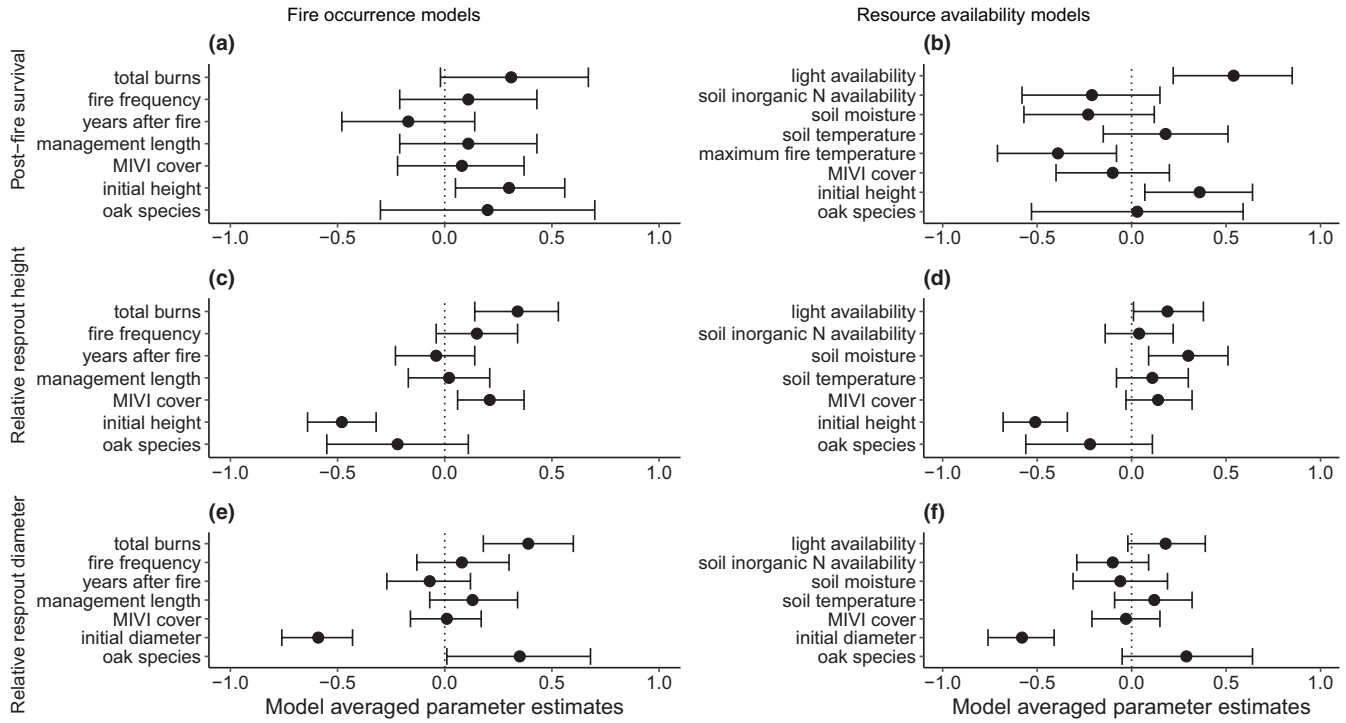
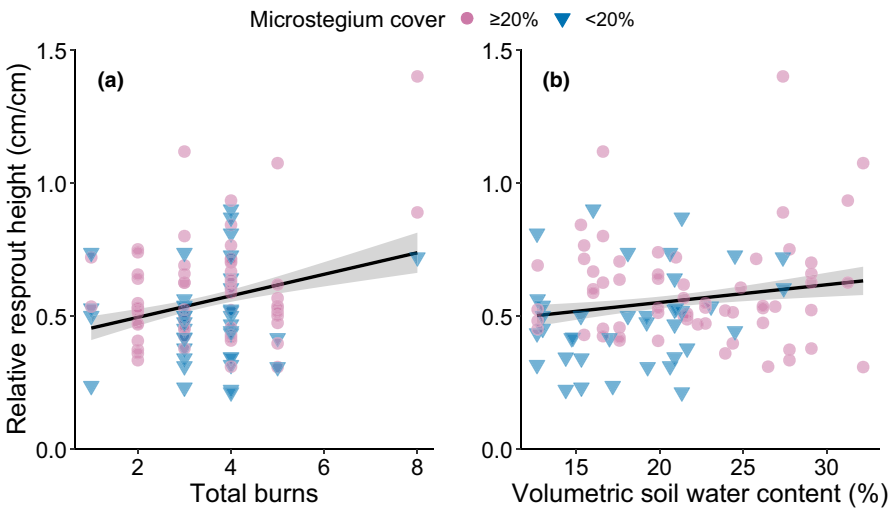


FIGURE 3 Model averaged parameter estimates predicting (a, b) post-fire survival, (c, d) relative resprout height, and (e, f) relative resprout diameter of (a, c, e) outplanted oak seedlings using fire occurrence models and (b, d, f) resource availability models. *Microstegium* cover was included in both sets of models, and fire intensity was included in the post-fire survival models. In all models, plot was included as a random effect. Error bars represent the 95% confidence interval. Intervals that do not contain 0 indicate a parameter that significantly predicts a given oak seedling outcome.

FIGURE 4 Relationships between post-fire relative resprout height of outplanted oak seedlings and (a) total burns, and (b) soil moisture. Relative resprout height was defined for each individual seedling as its tallest resprouted stem in the September after the fire divided by its tallest pre-fire stem. *Microstegium* cover was modelled continuously but is shown as a categorical variable to improve visualization. Points are observed outcomes. Shaded regions surrounding the regression lines are 95% confidence intervals.



resprouting vigour, nor did it interact with historical fire occurrence. There was also no effect of oak species. However, initial size was negatively related to resprout size (Table S10; Figure S8).

The proximate drivers of resprouting vigour for naturally colonized oak juveniles were similar to those of outplanted seedlings. Resprout height was best predicted by light availability (Table S10), with higher light availability increasing relative resprout height (Figure S8). Resprout diameter was best predicted by soil temperature, followed by light availability (Table S10), with warmer soil and higher light availability increasing resprout diameter (Figure S8). *Microstegium* cover did not affect resprouting vigour, nor did it interact with fire occurrence. There was also no effect of oak species. However, initial size was negatively related to relative resprout size (Table S10; Figure S8).

3.4 | Seedling nutrient status

The nutrient status of outplanted seedlings did not vary with historical fire occurrence or *Microstegium* cover ($p > 0.1$ for all

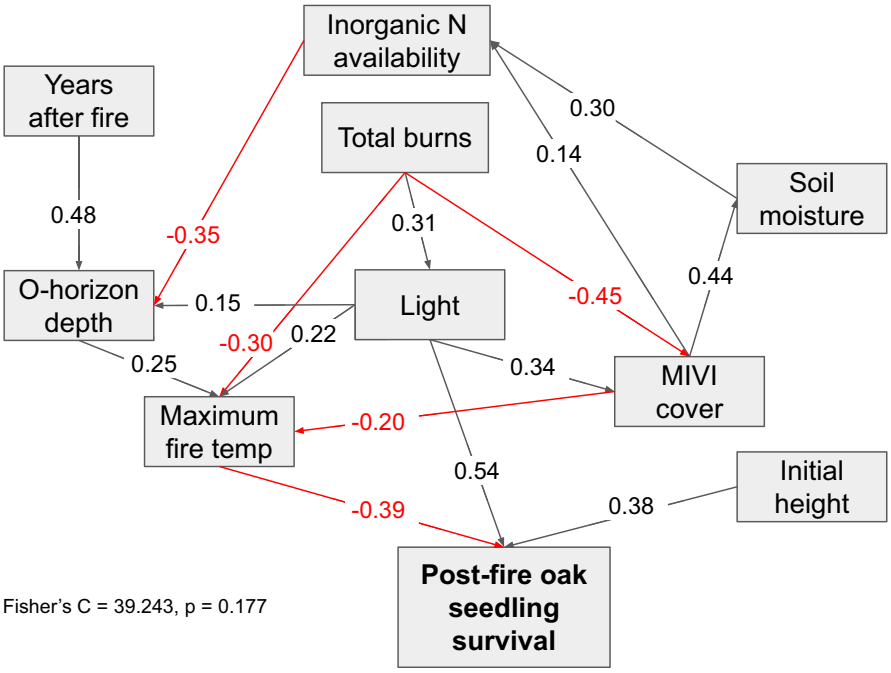


FIGURE 5 Structural equation model showing the ultimate and proximate drivers of post-fire oak seedling survival. Arrows represent significant relationships ($p < 0.05$), with black arrows representing positive relationships and red arrows representing negative relationships. The values next to each arrow represent the standardized effect size of the given predictor variable on the response variable. MIVI refers to *Microstegium vimineum*. The Fisher's *C* and *p*-value in the bottom left correspond to the entire model, with a *p*-value of >0.05 indicating a well-fit model.

models). However, leaf N (%; $p = 0.02$) increased and leaf C:N ratio ($p = 0.07$) decreased with soil NH_4^+-N.

3.5 | Structural equation modelling

The SEM for post-fire oak seedling survival adequately fit our data (Fisher's $C = 39.2$, df = 32, $p = 0.18$) and revealed that higher fire occurrence promoted survival via the indirect pathways of light availability and maximum fire temperature (marginal $R^2 = 0.15$, conditional $R^2 = 0.21$, Figure 5). The main drivers of these changes were total burns and years after fire. As total burns increased, light availability increased ($p = 0.04$) and maximum fire temperature decreased ($p = 0.002$). There was also a weak positive indirect effect of total burns on maximum fire temperature, mediated by the positive effect of light availability on O-horizon depth ($p < 0.001$). Years after fire indirectly increased maximum fire temperature through its positive effect on O-horizon depth ($p = 0.01$). Standardized effect sizes indicated that the strongest predictor of survival was the positive effect of light availability ($p < 0.001$), followed by the negative effect of maximum fire temperature ($p = 0.01$), and the positive effect of initial height ($p = 0.006$). Additionally, there was a marginal negative interaction between initial height and light availability on survival ($p = 0.06$; Figure S9), such that light had a diminishing effect as seedling height increased.

There was no direct effect of *Microstegium* cover on post-fire oak seedling survival (Figure 5). However, by decreasing maximum fire temperature ($p = 0.02$), *Microstegium* cover exerted a weak positive indirect effect on survival. Total burns had a negative direct effect on *Microstegium* cover ($p = 0.05$), despite the weak positive indirect effect on cover through light availability ($p < 0.001$). As expected, there were positive relationships between soil moisture and *Microstegium* cover ($p < 0.001$), soil moisture and soil inorganic N ($p < 0.001$), and *Microstegium* cover and soil inorganic N ($p < 0.001$). However, neither soil moisture nor soil inorganic N availability was affected by fire occurrence, nor did they influence post-fire oak seedling survival, except for a weak indirect effect of soil inorganic N availability on O-horizon depth ($p < 0.001$), with higher inorganic N decreasing depth.

The SEM for resprouting vigour adequately fit our data (Fisher's $C = 14.4$, df = 14, $p = 0.42$) and revealed that higher fire occurrence promoted resprout height via the indirect pathway of light availability (marginal $R^2 = 0.34$, conditional $R^2 = 0.36$, Figure 6), with higher total burns increasing light availability ($p = 0.05$). Standardized effect sizes indicated that the strongest predictor of resprouting vigour was the negative effect of initial height ($p < 0.001$), followed by the positive effects of soil moisture ($p = 0.006$) and light availability ($p = 0.005$).

We did not find a significant effect of *Microstegium* cover on resprouting vigour (Figure 6). Similar to survival, total burns had a negative direct effect on *Microstegium* cover ($p = 0.008$), despite the weak positive indirect effect on cover through light availability ($p < 0.001$). Higher soil moisture increased *Microstegium* cover ($p < 0.001$) but was not influenced by fire occurrence. Soil inorganic N availability increased with soil moisture ($p < 0.001$) and *Microstegium* cover ($p = 0.02$) and decreased with total burns ($p = 0.04$).

4 | DISCUSSION

We experimentally burnt plots established across a fire occurrence gradient containing outplanted oak seedlings and naturally colonized oak juveniles to investigate how an invasive grass alters the effect of fire on early oak regeneration, namely post-fire survival

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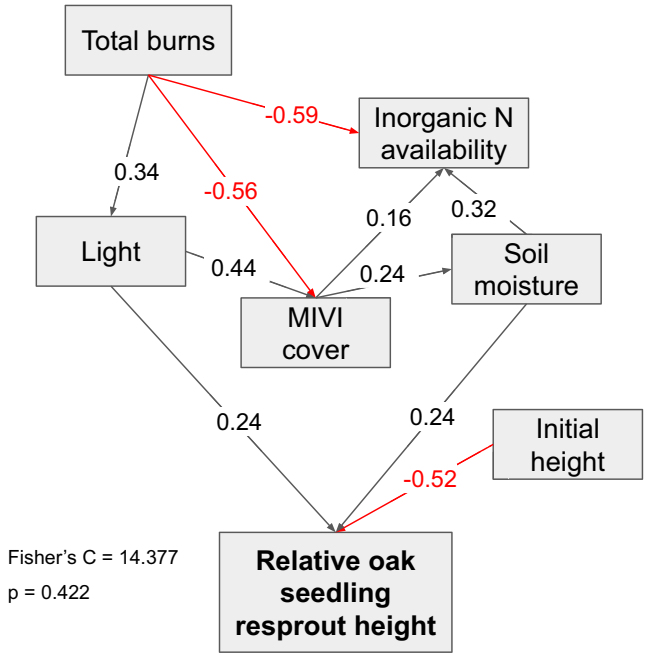


FIGURE 6 Structural equation model showing the ultimate and proximate drivers of post-fire relative oak seedling resprout height. Arrows represent significant relationships ($p < 0.05$), with black arrows representing positive relationships and red arrows representing negative relationships. The values next to each arrow represent the standardized effect size of the given predictor variable on the response variable. MIVI refers to *Microstegium vimineum*. The Fisher's *C* and *p*-value on the bottom left correspond to the entire model, with a *p*-value of >0.05 indicating a well-fit model.

and resprouting vigour. Previous studies have found that invasive grasses can harm native plants and ecosystems by creating positive feedbacks with fire activity (Brooks et al., 2004; D'Antonio & Vitousek, 1992), with several finding damage to tree seedlings due to interactions between grass and fire (Flory et al., 2015; Salemme & Fraterrigo, 2021). This interaction potentially conflicts with prescribed fire management goals, such as improving oak regeneration. However, when considering 26 years of prescribed fire occurrence, we found that historical fire occurrence is positively related to post-fire oak seedling regeneration, with the benefits from higher fire occurrence overriding the effects of grass invasion (Figure 2a; Figure S6). Our results demonstrate that early oak regeneration increases because recurring fire enhances light availability and reduces fuel loads, leading to lower intensity fires that reduce mortality and conditions that promote resprouting following topkill (Figures 5 and 6). Resprouted oak juveniles that naturally colonized also showed a positive response to recurring fire and light availability (Figure S8). Collectively, these results suggest that in temperate deciduous forests, grass invasion does not counteract the ability of recurring prescribed fire to promote early oak regeneration.

Although *Microstegium vimineum* has been shown to reduce post-fire tree seedling survival in forests experiencing lower fire occurrence or where fire occurrence is unknown (Flory et al., 2015; Salemme & Fraterrigo, 2021), we found limited support for this effect (Figure S6). Moreover, there was no effect of *Microstegium* on post-fire survival as fire occurrence increased. Increasing fire occurrence also reduced *Microstegium* vigour (Figure 5), suggesting that recurring burns may disrupt positive feedbacks between *Microstegium* and fire either by altering N availability (Fraterrigo & Rembelski, 2021) or by reducing seed viability and seedling emergence (Emery et al., 2013; Wagner & Fraterrigo, 2015). Although single fires can only affect the current seedbank, the cumulative effects of recurring fires on an annual grass could reduce population abundance over time.

Beyond reducing grass invasion, our results also support the hypothesis that recurring fires increase oak regeneration by increasing light availability (Hutchinson et al., 2012; Iverson et al., 2017). Although prescribed fire intensity in temperate forests may be too low to reduce overstory canopy cover in many cases (Dey & Fan, 2009; Hutchinson et al., 2005), and overstory recruitment can require mechanical overstory thinning (Bragg et al., 2020), these fires can reduce midstory stem density, thereby increasing understory light availability (Brose et al., 2013; Hutchinson et al., 2024). Light availability determines the extent to which oak seedlings can photosynthesize, develop root systems, and store non-structural carbohydrates below-ground (Brose, 2008; Dillaway et al., 2007; Resco de Dios et al., 2020), which are crucial factors controlling post-fire resprouting (Bond & Midgley, 2001; Bowen & Pate, 1993; Dey & Fan, 2009). In our study, taller outplanted seedlings and naturally colonized juveniles both had higher post-fire survival rates. These individuals would have been better able to compete for light (Figure S9) and may have also had larger root systems (Jacobs et al., 2005; Knapp et al., 2006), which would promote resprouting.

Following fire, resprouts that quickly reach a size class that can tolerate fire will have a better chance of escaping mortality from subsequent fires (Grady & Hoffmann, 2012). Yet, post-fire survival and resprouting vigour do not necessarily correlate and can result from differing mechanisms (Resco de Dios et al., 2020). In our study, resprouting vigour increased with light availability, likely for the same reasons as post-fire survival. However, the relative resprouting height of seedlings also increased with soil moisture (Figures 3, 4 and 6). Soil moisture has previously been shown to increase the growth of resprouting oak and other tree seedlings (Grady & Hoffmann, 2012; Refsland & Fraterrigo, 2018; Resco de Dios et al., 2020). Contrary to expectations, we found a weak positive relationship between soil moisture and total burns when accounting for *Microstegium* cover (Table S6). Past fires may not have been intense enough or recent enough to reduce soil moisture (MacDonald & Huffman, 2004). Furthermore, although unmeasured, we observed higher understory vegetation cover in plots with higher fire occurrence, a pattern also observed in other forests (Burton et al., 2011; Knapp et al., 2015). Dense understory vegetation can promote a moister soil microclimate (Pickering et al., 2021), with moisture in the top 20 cm of soil decreasing when vegetation is removed (Barzegaran et al., 2022; Wang et al., 2011; Zhang et al., 2020). Thus, it is possible that soil moisture increased with total burns due to increased understory plant cover, resulting in stronger resprouting vigour.

We also found that higher fire occurrence increased post-fire oak regeneration by reducing fire intensity through reductions to fuel loads (Stephens et al., 2012). Our results showed fewer historical burns leading to increased maximum fire temperature (Figure 5). Fire intensity is also influenced by years after fire, as several years must pass before litter reaches pre-fire levels (Stambaugh et al., 2006). We found that O-horizon depth increased with years after fire (Figure 5), which led to an increase in maximum fire temperature and residence time (Figure S5), as deeper litter increases fire intensity (Ganteaume et al., 2011). Higher fire intensity can reduce post-fire tree seedling survival by increasing tree tissue damage (Brose & Van Lear, 1998; Ward, 2015). Indeed, maximum fire temperature was the second most important variable after light availability for determining post-fire oak seedling survival, with hotter fires resulting in higher mortality (Figure 5).

Fire intensity is often increased by invasive grasses, including *Microstegium*, through increased fuel loads or continuity (Brooks et al., 2004; D'Antonio & Vitousek, 1992; Flory et al., 2015; Wagner & Fraterrigo, 2015). These effects are intensified when burning under dry conditions, especially following a wet year in which invasive grasses can grow more vigorously (Balch et al., 2013), potentially leading to increased tree seedling mortality (Ward, 2015). However, invasive grasses have also been found to decrease fire intensity by reducing fuel loads and increasing fuel moisture (McGranahan et al., 2013); have no effect on fire intensity (Poulos & Roy, 2015); and decrease fire severity, especially in wetter years (Pilliod et al., 2017). These differences underscore the importance of interannual weather variability for shaping the invasive grass-fire intensity relationship (Salemme & Fraterrigo, 2021), and align with recent evidence indicating that weather conditions exert greater influence than fuel conditions on fire behaviour in oak forests (Wepryk et al., 2025). Moreover, in our study, we found a negative relationship between *Microstegium* cover and fire intensity (Tables S4 and S9; Figure 5), and a positive relationship between *Microstegium* and soil moisture (Tables S4 and S9; Figure S3), but no relationship between *Microstegium* cover and fuel loads or fuel moisture (Table S4). This suggests that *Microstegium* cover dampened fire intensity mainly by selecting for wetter environments and potentially by promoting wetter conditions. As a C_4 grass, *Microstegium* would be expected to reduce overall water loss from the soil during the growing season because C_4 plants have lower evapotranspiration rates than C_3 plants (Feldhake & Boyer, 1986), which might have led to higher soil moisture during the dormant season. However, additional research is needed to evaluate these potential microclimate effects across seasons and their influence on fire intensity. Had our experimental burns occurred during the growing season, a practice many land managers support (Knapp et al., 2009), it would likely have been difficult for the fire to carry across the living *Microstegium* biomass (Flory & Lewis, 2009). Despite lower fire intensity, oak seedlings are more vulnerable to mortality during the growing season (Keyser et al., 2019), making the potential effect of burn season on the fire–grass–tree relationship somewhat ambiguous. Collectively, these findings suggest that the effects of *Microstegium* on fire intensity in temperate forests will strongly depend on site conditions and the timing and weather surrounding burns.

The interaction between fire, non-native grass invasion, and native tree regeneration is a globally important issue (Kerns et al., 2020; Nowacki & Abrams, 2008). Fire plays a key role in maintaining open forests and can favour non-native grasses (D'Antonio & Vitousek, 1992; Hanberry et al., 2020), suppressing tree recruitment and reducing regeneration. Understanding the effects of prescribed fire on these relationships and the response of oak regeneration is crucial for optimal forest management, especially in systems where the same challenges co-occur. We found that increased fire occurrence improves post-fire oak seedling survival and resprouting vigour by increasing understory light availability and decreasing fire intensity through O-horizon reductions. Prior studies in forests experiencing low or unknown fire occurrence have found a negative effect of *Microstegium* on post-fire oak survival (Flory et al., 2015; Salemme & Fraterrigo, 2021), but our results suggest that with recurring fires, *Microstegium* does not inhibit post-fire oak regeneration. Furthermore, we found that recurring fires led to lower *Microstegium* cover. This implies that in temperate forests invaded by *Microstegium*, recurring fires may disrupt the grass-fire feedback loop, mitigating harm to native plants by limiting fire intensity and increasing resource availability. Overall, our results show that recurring fires improve early oak regeneration, even in the presence of an invasive grass.

AUTHOR CONTRIBUTIONS

Jennifer M. Fraterrigo conceived the ideas and designed the study. Dan Marshalla collected and analysed the data. Dan Marshalla and Jennifer M. Fraterrigo co-wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available from the Illinois Data Bank at https://doi.org/10.13012/B2IDB-8802487_V1 (Marshalla & Fraterrigo, 2025).

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REFERENCES

Alexander, H. D., Arthur, M. A., Loftis, D. L., & Green, S. R. (2008). Survival and growth of upland oak and co-occurring competitor seedlings following single and repeated prescribed fires. *Forest Ecology and Management*, *256*(5), 1021–1030. https://doi.org/10.1016/j.foreco.2008.06.004

Alexander, H. D., Siegert, C., Brewer, J. S., Kreye, J., Lashley, M. A., McDaniel, J. K., Paulson, A. K., Renninger, H. J., & Varner, J. M. (2021). Mesophication of oak landscapes: Evidence, knowledge gaps, and future research. *BioScience*, *71*(5), 531–542. https://doi.org/10.1093/biosci/biaa169

Altman, J., Fibich, P., Leps, J., Uemura, S., Hara, T., & Dolezal, J. (2016). Linking spatiotemporal disturbance history with tree regeneration and diversity in an old-growth forest in northern Japan. *Perspectives in Plant Ecology, Evolution and Systematics*, *21*, 1–13. https://doi.org/10.1016/j.ppees.2016.04.003

Álvarez, J., Dalling, J. W., Edgington, J. M., & Fraterrigo, J. M. (2025). Homogenization of a temperate old-growth forest remnant in central Illinois following the introduction of Dutch elm disease (*Ophiostoma novo-ulmi*) and emerald ash borer (*Agrilus planipennis*). *Forest Ecology and Management*, *585*, 122707. https://doi.org/10.1016/j.foreco.2025.122707

Anderson, D. P., Turner, M. G., Pearson, S. M., Albright, T. P., Peet, R. K., & Wieben, A. (2013). Predicting Microstegium vimineum invasion in natural plant communities of the southern Blue Ridge Mountains, USA. *Biological Invasions*, *15*(6), 1217–1230. https://doi.org/10.1007/s10530-012-0361-3

Arora, V. K., & Melton, J. R. (2018). Reduction in global area burned and wildfire emissions since 1930s enhances carbon uptake by land. *Nature Communications*, *9*(1), 1326. https://doi.org/10.1038/s41467-018-03838-0

Arthur, M. A., Alexander, H. D., Dey, D. C., Schweitzer, C. J., & Loftis, D. L. (2012). Refining the oak-fire hypothesis for management of oak-dominated forests of the eastern United States. *Journal of Forestry*, *110*, 257–266. https://doi.org/10.5849/jof.11-080

Balch, J. K., Bradley, B. A., D'Antonio, C. M., & Gómez-Dans, J. (2013). Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global Change Biology*, *19*(1), 173–183. https://doi.org/10.1111/gcb.12046

Barzegaran, F., Erfanzadah, R., & Saber Amoli, S. (2022). The effect of woody plants on the understory soil parameters is different between grazed and ungrazed areas. *Community Ecology*, *23*(2), 187–196. https://doi.org/10.1007/s42974-022-00090-x

Bassirirad, H. (2000). Kinetics of nutrient uptake by roots: Responses to global change. *New Phytologist*, *147*(1), 155–169. https://doi.org/10.1046/j.1469-8137.2000.00682.x

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bond, W. J., & Keeley, J. E. (2005). Fire as a global 'herbivore': The ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, *20*(7), 387–394. https://doi.org/10.1016/j.tree.2005.04.025

Bond, W. J., & Midgley, J. J. (2001). Ecology of sprouting in woody plants: The persistence niche. *Trends in Ecology & Evolution*, *16*(1), 45–51. https://doi.org/10.1016/S0169-5347(00)02033-4

Bowen, B. J., & Pate, J. S. (1993). The significance of root starch in post-fire shoot recovery of the resprouter *Stirlingia latifolia* R. Br. (Proteaceae). *Annals of Botany*, *72*(1), 7–16. https://doi.org/10.1006/anbo.1993.1075

Bowman, D. M. J. S., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., D'Antonio, C. M., DeFries, R. S., Doyle, J. C., Harrison, S. P., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C. A., Marston, J. B., Moritz, M. A., Prentice, I. C., Roos, C. I., Scott, A. C., … Pyne, S. J. (2009). Fire in the Earth system. *Science*, *324*(5926), 481–484. https://doi.org/10.1126/science.1163886

Bragg, D. C., Hanberry, B. B., Hutchinson, T. F., Jack, S. B., & Kabrick, J. M. (2020). Silvicultural options for open forest management in eastern North America. *Forest Ecology and Management*, *474*, 118383. https://doi.org/10.1016/j.foreco.2020.118383

Brooks, M. L., D'Antonio, C. M., Richardson, D. M., Grace, J. B., Keeley, J. E., DiTomaso, J. M., Hobbs, R. J., Pellant, M., & Pyke, D. (2004). Effects of invasive alien plants on fire regimes. *BioScience*, *54*(7), 677–688. https://doi.org/10.1641/0006-3568(2004)054[0677:EOIAPO]2.0.CO;2

Brose, P. H. (2008). Root development of acorn-origin oak seedlings in shelterwood stands on the Appalachian Plateau of northern Pennsylvania: 4-year results. *Forest Ecology and Management*, *255*(8), 3374–3381. https://doi.org/10.1016/j.foreco.2008.02.021

Brose, P. H., Dey, D. C., Phillips, R. J., & Waldrop, T. A. (2013). A meta-analysis of the fire-oak hypothesis: Does prescribed burning promote oak reproduction in eastern North America? *Forest Science*, *59*(3), 322–334. https://doi.org/10.5849/forsci.12-039

Brose, P. H., & Van Lear, D. H. (1998). Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. *Canadian Journal of Forest Research*, *28*(3), 331–339. https://doi.org/10.1139/x97-218

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). Springer. https://doi.org/10.1007/b97636

Burton, J. A., Hallgren, S. W., Fuhlendorf, S. D., & Leslie, D. M. (2011). Understory response to varying fire frequencies after 20 years of prescribed burning in an upland oak forest. *Plant Ecology*, *212*(9), 1513–1525. https://doi.org/10.1007/s11258-011-9926-y

Certini, G. (2005). Effects of fire on properties of forest soils: A review. *Oecologia*, *143*(1), 1–10. https://doi.org/10.1007/s00442-004-1788-8

Cheplick, G. P. (2010). Limits to local spatial spread in a highly invasive annual grass (*Microstegium vimineum*). *Biological Invasions*, *12*(6), 1759–1771. https://doi.org/10.1007/s10530-009-9587-0

Cuprewich, S. A., & Saunders, M. R. (2024). Evaluating the impact of prescribed surface fire on seedlings in the Central Hardwood Region, USA. *Forestry*, *97*(1), 94–106. https://doi.org/10.1093/forestry/cpac064

D'Antonio, C. M., Tunison, J. T., & Loh, R. K. (2000). Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. *Austral Ecology*, *25*(5), 507–522. https://doi.org/10.1046/j.1442-9993.2000.01079.x

D'Antonio, C. M., & Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, *23*, 63–87. https://doi.org/10.1146/annurev.es.23.110192.000431

Dey, D. C., & Fan, Z. (2009). A review of fire and oak regeneration and overstory recruitment. In T. F. Hutchinson (Ed.), *Proceedings of the 3rd Fire in Eastern Oak Forests Conference; 2008 May 20–22; Carbondale, IL. Gen. Tech. Rep. NRS-P-46* (pp. 2–20). U.S. Department of Agriculture, Forest Service, Northern Research Station. https://research.fs.usda.gov/treesearch/17288

Dey, D. C., Spetich, M. A., Weigel, D. R., Johnson, P. S., Graney, D. L., & Kabrick, J. M. (2009). A suggested approach for design of oak (*Quercus* L.) regeneration research considering regional differences. *New Forests*, *37*(2), 123–135. https://doi.org/10.1007/s11056-008-9113-8

Dillaway, D. N., Stringer, J. W., & Rieske, L. K. (2007). Light availability influences root carbohydrates, and potentially vigor, in white oak advance regeneration. *Forest Ecology and Management*, *250*(3), 227–233. https://doi.org/10.1016/j.foreco.2007.05.019

Ehrenfeld, J. G., Kourtev, P., & Huang, W. (2001). Changes in soil functions following invasions of exotic understory plants in deciduous

forests. *Ecological Applications*, *11*(5), 1287–1300. https://doi.org/10.1890/1051-0761(2001)011[1287:CISFFI]2.0.CO;2

Emery, S. M., Luke Flory, S., Clay, K., Robb, J. R., & Winters, B. (2013). Demographic responses of the invasive annual grass *Microstegium vimineum* to prescribed fires and herbicide. *Forest Ecology and Management*, *308*, 207–213. https://doi.org/10.1016/j.foreco.2013.08.002

Fahey, C., Angelini, C., & Flory, S. L. (2018). Grass invasion and drought interact to alter the diversity and structure of native plant communities. *Ecology*, *99*(12), 2692–2702. https://doi.org/10.1002/ecy.2536

Feldhake, C. M., & Boyer, D. G. (1986). Effect of soil temperature on evapotranspiration by C3 and C4 grasses. *Agricultural and Forest Meteorology*, *37*(4), 309–318. https://doi.org/10.1016/0168-1923(86)90068-7

Flory, S. L. (2010). Management of Microstegium vimineum invasions and recovery of resident plant communities. *Restoration Ecology*, *18*(1), 103–112. https://doi.org/10.1111/j.1526-100X.2008.00425.x

Flory, S. L., Clay, K., Emery, S. M., Robb, J. R., & Winters, B. (2015). Fire and non-native grass invasion interact to suppress tree regeneration in temperate deciduous forests. *Journal of Applied Ecology*, *52*(4), 992–1000. https://doi.org/10.1111/1365-2664.12437

Flory, S. L., & Lewis, J. (2009). Nonchemical methods for managing Japanese stiltgrass (*Microstegium vimineum*). *Invasive Plant Science and Management*, *2*(4), 301–308. https://doi.org/10.1614/IPSM-09-026.1

Fowler, C., & Konopik, E. (2007). The history of fire in the southern United States. *Human Ecology Review*, *14*(2), 165–176.

Fraterrigo, J. M., & Rembelski, M. K. (2021). Frequent fire reduces the magnitude of positive interactions between an invasive grass and soil microbes in temperate forests. *Ecosystems*, *24*(7), 1738–1755. https://doi.org/10.1007/s10021-021-00615-x

Funk, J. L., & McDaniel, S. (2010). Altering light availability to restore invaded forest: The predictive role of plant traits. *Restoration Ecology*, *18*(6), 865–872. https://doi.org/10.1111/j.1526-100X.2008.00515.x

Fusco, E. J., Finn, J. T., Balch, J. K., Nagy, R. C., & Bradley, B. A. (2019). Invasive grasses increase fire occurrence and frequency across US ecoregions. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(47), 23594–23599. https://doi.org/10.1073/pnas.1908253116

Ganteaume, A., Marielle, J., Corinne, L.-M., Thomas, C., & Laurent, B. (2011). Effects of vegetation type and fire regime on flammability of undisturbed litter in southeastern France. *Forest Ecology and Management*, *261*(12), 2223–2231. https://doi.org/10.1016/j.foreco.2010.09.046

Grady, J. M., & Hoffmann, W. A. (2012). Caught in a fire trap: Recurring fire creates stable size equilibria in woody resprouters. *Ecology*, *93*(9), 2052–2060. https://doi.org/10.1890/12-0354.1

Grundel, R., & Pavlovic, N. B. (2007). Distinctiveness, use, and value of midwestern oak savannas and woodlands as avian habitats. *Auk*, *124*(3), 969–985. https://doi.org/10.1093/auk/124.3.969

Guyette, R. P., Muzika, R. M., & Dey, D. C. (2002). Dynamics of an anthropogenic fire regime. *Ecosystems*, *5*(5), 472–486.

Hanberry, B. B., Bragg, D. C., & Alexander, H. D. (2020). Open forest ecosystems: An excluded state. *Forest Ecology and Management*, *472*, 118256. https://doi.org/10.1016/j.foreco.2020.118256

He, T., Lamont, B. B., & Pausas, J. G. (2019). Fire as a key driver of Earth's biodiversity. *Biological Reviews*, *94*(6), 1983–2010. https://doi.org/10.1111/brv.12544

Horton, J. L., Fortner, R., & Goklany, M. (2010). Photosynthetic characteristics of the C4 invasive exotic grass *Miscanthus sinensis* Andersson growing along gradients of light intensity in the southeastern United States. *Castanea*, *75*(1), 52–66. https://doi.org/10.2179/08-040.1

Huang, C.-H., Bates, R., Kronrad, G. D., & Cheng, S. (2004). Economic analyses of sequestering carbon in loblolly pine, cherrybark oak, and northern red oak in the United States. *Environmental Management*, *33*(1), S187–S199. https://doi.org/10.1007/s00267-003-9129-y

Hutchinson, T. F., Adams, B. T., Dickinson, M. B., Heckel, M., Royo, A. A., & Thomas-Van Gundy, M. A. (2024). Sustaining eastern oak forests: Synergistic effects of fire and topography on vegetation and fuels. *Ecological Applications*, *34*(3), e2948. https://doi.org/10.1002/eap.2948

Hutchinson, T. F., Long, R. P., Rebbeck, J., Sutherland, E. K., & Yaussy, D. A. (2012). Repeated prescribed fires alter gap-phase regeneration in mixed-oak forests. *Canadian Journal of Forest Research*, *42*(2), 303–314. https://doi.org/10.1139/X11-184

Hutchinson, T. F., Sutherland, E. K., & Yaussy, D. A. (2005). Effects of repeated prescribed fires on the structure, composition, and regeneration of mixed-oak forests in Ohio. *Forest Ecology and Management*, *218*(1), 210–228. https://doi.org/10.1016/j.foreco.2005.07.011

Iannone, B. V., III, Potter, K. M., Guo, Q., Liebhold, A. M., Pijanowski, B. C., Oswalt, C. M., & Fei, S. (2016). Biological invasion hotspots: A trait-based perspective reveals new sub-continental patterns. *Ecography*, *39*(10), 961–969. https://doi.org/10.1111/ecog.01973

Iverson, L. R., Hutchinson, T. F., Peters, M. P., & Yaussy, D. A. (2017). Long-term response of oak-hickory regeneration to partial harvest and repeated fires: Influence of light and moisture. *Ecosphere*, *8*(1), e01642. https://doi.org/10.1002/ecs2.1642

Jacobs, D. F., Salifu, K. F., & Seifert, J. R. (2005). Relative contribution of initial root and shoot morphology in predicting field performance of hardwood seedlings. *New Forests*, *30*(2), 235–251. https://doi.org/10.1007/s11056-005-5419-y

Johnson, B. G., Johnson, D. W., Chambers, J. C., & Blank, R. R. (2011). Fire effects on the mobilization and uptake of nitrogen by cheatgrass (*Bromus tectorum* L.). *Plant and Soil*, *341*(1), 437–445. https://doi.org/10.1007/s11104-010-0656-z

Kerns, B. K., Tortorelli, C., Day, M. A., Nietupski, T., Barros, A. M. G., Kim, J. B., & Krawchuk, M. A. (2020). Invasive grasses: A new perfect storm for forested ecosystems? *Forest Ecology and Management*, *463*, 117985. https://doi.org/10.1016/j.foreco.2020.117985

Keyser, T. L., Greenberg, C. H., & Henry McNab, W. (2019). Season of burn effects on vegetation structure and composition in oak-dominated Appalachian hardwood forests. *Forest Ecology and Management*, *433*, 441–452. https://doi.org/10.1016/j.foreco.2018.11.027

Keyser, T. L., McDaniel, V. L., Klein, R. N., Drees, D. G., Burton, J. A., & Forder, M. M. (2018). Short-term stem mortality of 10 deciduous broadleaved species following prescribed burning in upland forests of the southern US. *International Journal of Wildland Fire*, *27*, 42–51. https://doi.org/10.1071/WF17058

Knapp, B. O., Stephan, K., & Hubbart, J. A. (2015). Structure and composition of an oak-hickory forest after over 60 years of repeated prescribed burning in Missouri, U.S.A. *Forest Ecology and Management*, *344*, 95–109. https://doi.org/10.1016/j.foreco.2015.02.009

Knapp, B. O., Wang, G. G., Van Lear, D. H., & Walker, J. L. (2006). Predicting root biomass of burned and unburned white oak advance reproduction from diameter and height. *Southern Journal of Applied Forestry*, *30*(1), 40–45. https://doi.org/10.1093/sjaf/30.1.40

Knapp, E. E., Estes, B. L., & Skinner, C. N. (2009). *Ecological effects of prescribed fire season: A literature review and synthesis for managers*. Gen. Tech. Rep. PSW-GTR-224. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. https://doi.org/10.2737/PSW-GTR-224

Knicker, H. (2007). How does fire affect the nature and stability of soil organic nitrogen and carbon? A review. *Biogeochemistry*, *85*(1), 91–118. https://doi.org/10.1007/s10533-007-9104-4

Lee, M. R., Flory, S. L., & Phillips, R. P. (2012). Positive feedbacks to growth of an invasive grass through alteration of nitrogen cycling. *Oecologia*, *170*(2), 457–465. https://doi.org/10.1007/s00442-012-2309-9

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in *r* for ecology, evolution, and systematics. *Methods in*

Ecology and Evolution, *7*(5), 573–579. https://doi.org/10.1111/2041-210X.12512

Levitt, J. (1980). High-temperature or heat stress. In *Chilling, Freezing, and High Temperature Stresses*, 2nd ed., (pp. 347–393). Academic Press. https://doi.org/10.1016/B978-0-12-445501-6.50016-6

Li, Q., & Ma, K. (2003). Factors affecting establishment of *Quercus liaotungensis* Koidz. under mature mixed oak forest overstory and in shrubland. *Forest Ecology and Management*, *176*(1), 133–146. https://doi.org/10.1016/S0378-1127(02)00274-8

MacDonald, L. H., & Huffman, E. L. (2004). Post-fire soil water repellency. *Soil Science Society of America Journal*, *68*(5), 1729–1734. https://doi.org/10.2136/sssaj2004.1729

Marshalla, D., & Fraterrigo, J. M. (2025). *Data for 'Increased fire occurrence benefits early oak regeneration in temperate deciduous forests in part by disrupting an invasive grass-fire feedback'*. University of Illinois Urbana-Champaign. https://doi.org/10.13012/B2IDB-8802487_V1

Mazerolle, M. J. (2023). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*. R package version 2.3.3. https://cran.r-project.org/package=AICcmodavg

McGranahan, D. A., Engle, D. M., Miller, J. R., & Debinski, D. M. (2013). An invasive grass increases live fuel proportion and reduces fire spread in a simulated grassland. *Ecosystems*, *16*(1), 158–169. https://doi.org/10.1007/s10021-012-9605-4

Morrison, D. A. (2002). Effects of fire intensity on plant species composition of sandstone communities in the Sydney region. *Austral Ecology*, *27*(4), 433–441. https://doi.org/10.1046/j.1442-9993.2002.01197.x

Narango, D. L., Tallamy, D. W., & Shropshire, K. J. (2020). Few keystone plant genera support the majority of Lepidoptera species. *Nature Communications*, *11*, 5751. https://doi.org/10.1038/s41467-020-19565-4

Noble, S. L., & Bauer, J. T. (2022). Canopy cover and canopy heterogeneity drive plant alpha diversity but not beta diversity in a midwest oak savanna. *Natural Areas Journal*, *42*(3), 242–251. https://doi.org/10.3375/21-55

Nowacki, G. J., & Abrams, M. D. (2008). The demise of fire and "mesophication" of forests in the eastern United States. *BioScience*, *58*(2), 123–138. https://doi.org/10.1641/B580207

NRCS, USDA, & Soil Survey Staff. (2025). *Web soil survey*. http://websoilsurvey.sc.egov.usda.gov/

Pausas, J. G., & Keeley, J. E. (2009). A burning story: The role of fire in the history of life. *BioScience*, *59*(7), 593–601. https://doi.org/10.1525/bio.2009.59.7.10

Pellegrini, A. F. A., Ahlström, A., Hobbie, S. E., Reich, P. B., Nieradzik, L. P., Staver, A. C., Scharenbroch, B. C., Jumpponen, A., Anderegg, W. R. L., Randerson, J. T., & Jackson, R. B. (2018). Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. *Nature*, *553*(7687), 7687. https://doi.org/10.1038/nature24668

Pertierra, L. R., Martínez, P. A., Rubalcaba, J. G., Richardson, D. M., & Olalla-Tárraga, M. A. (2023). Contrasting patterns in phylogenetic and biogeographic factories of invasive grasses (Poaceae) across the globe. *npj Biodiversity*, *2*(1), 1–12. https://doi.org/10.1038/s44185-023-00016-4

Pickering, B. J., Duff, T. J., Baillie, C., & Cawson, J. G. (2021). Darker, cooler, wetter: Forest understories influence surface fuel moisture. *Agricultural and Forest Meteorology*, *300*, 108311. https://doi.org/10.1016/j.agrformet.2020.108311

Pile Knapp, L. S., Dey, D. C., Stambaugh, M. C., Thompson, F. R., & Varner, J. M. (2024). Managing forward while looking back: Reopening closed forests to open woodlands and savannas. *Fire Ecology*, *20*(1), 72. https://doi.org/10.1186/s42408-024-00312-9

Pilliod, D. S., Welty, J. L., & Arkle, R. S. (2017). Refining the cheatgrass–fire cycle in the Great Basin: Precipitation timing and fine fuel composition predict wildfire trends. *Ecology and Evolution*, *7*(19), 8126–8151. https://doi.org/10.1002/ece3.3414

Pinheiro, J. C., Bates, D. M., & R Core Team. (2025). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-168. https://doi.org/10.32614/CRAN.package.nlme

Poulos, L. P., & Roy, B. A. (2015). Fire and false brome: How do prescribed fire and invasive Brachypodium sylvaticum affect each other? *Invasive Plant Science and Management*, *8*(2), 122–130. https://doi.org/10.1614/IPSM-D-14-00024.1

R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org

Ratnam, J., Bond, W. J., Fensham, R. J., Hoffmann, W. A., Archibald, S., Lehmann, C. E. R., Anderson, M. T., Higgins, S. I., & Sankaran, M. (2011). When is a 'forest' a savanna, and why does it matter? *Global Ecology and Biogeography*, *20*(5), 653–660. https://doi.org/10.1111/j.1466-8238.2010.00634.x

Rebbeck, J., Gottschalk, K., & Scherzer, A. (2011). Do chestnut, northern red, and white oak germinant seedlings respond similarly to light treatments? Growth and biomass. *Canadian Journal of Forest Research*, *41*(11), 2219–2230. https://doi.org/10.1139/x11-124

Refsland, T., & Fraterrigo, J. (2018). Fire increases drought vulnerability of Quercus alba juveniles by altering forest microclimate and nitrogen availability. *Functional Ecology*, *32*(10), 2298–2309. https://doi.org/10.1111/1365-2435.13193

Rembelski, M., & Fraterrigo, J. (2023). Drought reduces invasive grass performance by disrupting plant–microbe interactions that enhance plant nitrogen supply. *Oecologia*, *201*, 549–564. https://doi.org/10.1007/s00442-022-05307-4

Resco de Dios, V., Arteaga, C., Peguero-Pina, J. J., Sancho-Knapik, D., Qin, H., Zveushe, O. K., Sun, W., Williams, D. G., Boer, M. M., Voltas, J., Moreno, J. M., Tissue, D. T., & Gil-Pelegrín, E. (2020). Hydraulic and photosynthetic limitations prevail over root non-structural carbohydrate reserves as drivers of resprouting in two Mediterranean oaks. *Plant, Cell & Environment*, *43*(8), 1944–1957. https://doi.org/10.1111/pce.13781

Ruffner, C. M., & Groninger, J. W. (2006). Making the case for fire in southern Illinois forests. *Journal of Forestry*, *104*(2), 78–83. https://doi.org/10.1093/jof/104.2.78

Salemme, R. K., & Fraterrigo, J. M. (2021). Grass invasion reduces the resilience of tree regeneration to fire in the Central Hardwoods Region. *Forest Ecology and Management*, *491*, 119202. https://doi.org/10.1016/j.foreco.2021.119202

Schafer, J. L., & Just, M. G. (2014). Size dependency of post-disturbance recovery of multi-stemmed resprouting trees. *PLoS One*, *9*(8), e105600. https://doi.org/10.1371/journal.pone.0105600

Soong, J. L., & Cotrufo, M. F. (2015). Annual burning of a tallgrass prairie inhibits C and N cycling in soil, increasing recalcitrant pyrogenic organic matter storage while reducing N availability. *Global Change Biology*, *21*(6), 2321–2333. https://doi.org/10.1111/gcb.12832

Spînu, A. P., Niklasson, M., & Zin, E. (2020). Mesophication in temperate Europe: A dendrochronological reconstruction of tree succession and fires in a mixed deciduous stand in Białowieża forest. *Ecology and Evolution*, *10*(2), 1029–1041. https://doi.org/10.1002/ece3.5966

Stambaugh, M. C., Guyette, R. P., Grabner, K. W., & Kolaks, J. (2006). Understanding Ozark forest litter variability through a synthesis of accumulation rates and fire events. In P. L. Andrews & B. W. Butler, Comps., *Fuels management-how to measure success: Conference Proceedings*. 28–30 March 2006; Portland, OR. Proceedings RMRS-P-41 (pp. 321–332). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Stephens, S. L., McIver, J. D., Boerner, R. E. J., Fettig, C. J., Fontaine, J. B., Hartsough, B. R., Kennedy, P. L., & Schwilk, D. W. (2012). The effects of forest fuel-reduction treatments in the United States.

BioScience, *62*(6), 549–560. https://doi.org/10.1525/bio.2012.62.6.6

Stockdale, C. A., Macdonald, S. E., & Higgs, E. (2019). Forest closure and encroachment at the grassland interface: A century-scale analysis using oblique repeat photography. *Ecosphere*, *10*(6), e02774. https://doi.org/10.1002/ecs2.2774

Tekiela, D. R., & Barney, J. N. (2013). Quantifying Microstegium vimineum seed movement by non-riparian water dispersal using an ultraviolet-marking based recapture method. *PLoS One*, *8*(9), e63811. https://doi.org/10.1371/journal.pone.0063811

Tomat-Kelly, G., & Flory, S. L. (2023). Research gaps limit understanding of invasion-fire cycles. *Biological Invasions*, *25*(3), 693–711. https://doi.org/10.1007/s10530-022-02951-y

Varner, J. M., Arthur, M. A., Clark, S. L., Dey, D. C., Hart, J. L., & Schweitzer, C. J. (2016). Fire in eastern North American oak ecosystems: Filling the gaps. *Fire Ecology*, *12*(2), 2. https://doi.org/10.4996/fireecology.1202001

Wagner, S. A., & Fraterrigo, J. M. (2015). Positive feedbacks between fire and non-native grass invasion in temperate deciduous forests. *Forest Ecology and Management*, *354*, 170–176. https://doi.org/10.1016/j.foreco.2015.06.024

Wang, X., Zhao, J., Wu, J., Chen, H., Lin, Y., Zhou, L., & Fu, S. (2011). Impacts of understory species removal and/or addition on soil respiration in a mixed forest plantation with native species in southern China. *Forest Ecology and Management*, *261*(6), 1053–1060. https://doi.org/10.1016/j.foreco.2010.12.027

Ward, J. S. (2015). Improving competitive status of oak regeneration using stand management and prescribed fires. *Journal of Sustainable Forestry*, *34*(1–2), 105–124. https://doi.org/10.1080/10549811.2014.973606

Wepryk, O., Niklasson, M., Nordlind, E., & Drobyshev, I. (2025). Modelling of forest fuel and weather effects on fire behavior in the oak forests of southern Sweden. *Scandinavian Journal of Forest Research*, *40*, 1–14. https://doi.org/10.1080/02827581.2025.2531994

Western Regional Climate Center. (2025). *USFS Remote Automatic Weather Station (RAWS) Dixon Springs Illinois*. http://raws.dri.edu

Zhang, Q., Wei, W., Chen, L., Yang, L., Luo, Y., & Cai, A. (2020). Plant traits in influencing soil moisture in semiarid grasslands of the Loess Plateau, China. *Science of the Total Environment*, *718*, 137355. https://doi.org/10.1016/j.scitotenv.2020.137355

SUPPORTING INFORMATION

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

Appendix S1: Detailed description of the experimental design.

Appendix S2: Detailed description of resource availability measurements.

Appendix S3: Linear equations evaluated in the piecewise structural equation models.

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