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Special Feature: Long-term ecological effects of forest fuel and restoration treatments

Reducing resilience debt: Mechanical felling and repeated prescribed fires may sustain eastern oak forests

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Abstract

The misalignment of species adaptations with current environmental conditions can cause ecosystems to lose resilience, accumulate resilience debt, and transition to another state. Such a state change is evident in eastern North American broadleaf forests where dominant tree species are shifting from oaks (*Quercus* spp.) to mesophytic species such as maples (*Acer* spp.). The replacement of oaks is widespread and threatens the ecosystem services these forests provide, generating interest in using forest management to halt or reverse this change. The national Fire and Fire Surrogate (FFS) study was a large-scale study of forest management practices, and the Green River FFS site in western North Carolina (initiated in 2001) offers the opportunity to understand how management actions affect oak forest resilience. The Green River FFS site implemented three experimental treatments replicated across three spatial blocks: mechanical felling of saplings and ericaceous shrubs (Mech), prescribed fire (Fire), and a combination (Mech + Fire), which were compared to untreated controls (Control). Here, we used this long-running experiment to evaluate oak forest resilience by examining changes in overstory basal area and forest composition among overstory trees, saplings, and seedlings. We found that basal area increased in the Control and Mech treatments, was unchanged in the Fire treatment, and decreased in the Mech + Fire treatment as a result of mortality. Oak sapling abundances increased with reduced basal area, a pattern not found with the major mesophytic representative, maples.

Helen H. Mohr and Thomas A. Waldrop have retired.

This suggests that oaks are well positioned to recruit to the overstory where basal area has decreased due to overstory mortality, and at the Green River FFS site, this was best achieved in the Mech + Fire treatment. Creating conditions where oak saplings have an advantage over maples requires the mortality of some overstory trees, including desirable oaks. Taken together, our findings suggest that the misalignment of oak traits and current environmental conditions has led to resilience debt, which may be reduced when management actions mimic a severe disturbance that results in the opening of the canopy. Thus, management actions that combine mechanical felling and repeated prescribed fires may promote sustained oak dominance in the future.

KEYWORDS
ecological memory, fire severity, mesophication, organic horizon, tree recruitment, tree regeneration

INTRODUCTION

Mismatches between species traits and disturbance regimes erode ecosystem resilience and can lead to an ecosystem state change (Johnstone et al., 2016). Such a transition is evident in the broadleaf forests of eastern North America, which have dramatically changed in tree species composition over the past century. Mounting evidence demonstrates a forest shift from dominance of oaks (*Quercus* spp. L.) to dominance of maples (*Acer* spp. L.) and other mesophytic species (Fei et al., 2011; Jo et al., 2019; Knott et al., 2019), a process widely termed "mesophication" (Nowacki & Abrams, 2008). Implications of this change are widespread and include reductions in wildlife habitat, fresh water resources, and timber availability (Caldwell et al., 2016; Luppold, 2019; McShea et al., 2007). Although the need for solutions is clear, the problem has manifested slowly, as tree populations turn over gradually, and as such, science has yet to answer questions regarding which management actions may be necessary to slow down or reverse mesophication.

The current composition of broadleaf forests in eastern North America (hereafter eastern broadleaf forests) has been shaped by centuries of change. Prior to European colonization, oaks and American chestnut (*Castanea dentata* (Marshall) Borkh.) dominated much of eastern broadleaf forests (Hanberry & Nowacki, 2016), which then experienced widespread logging and clearing for agriculture (Ayres & Ashe, 1905; Thompson et al., 2013). During the last century, many lands reforested while concurrently, the regionally abundant American chestnut was functionally eliminated, atmospheric nitrogen (N) deposition increased, and most of the region experienced widespread fire exclusion (Averill et al., 2018; Boerner et al., 2008; Elliott & Swank, 2008; Nowacki & Abrams, 2008). Fire exclusion is particularly notable because it represents a modification of the disturbance regime that shaped these forests for millennia, thereby favoring fire-sensitive tree species such as maples that further suppress fire. In some regions, fire exclusion has also led to the expansion of large-statured ericaceous shrubs such as great laurel (*Rhododendron maximum* L.) and mountain laurel (*Kalmia latifolia* L.), which can reduce light availability to young trees and suppress oak regeneration (Brose, 2016; Lafon et al., 2022). As a result of these human activities and the resulting forest successional trajectories that have favored mesophytes (Wurzburger et al., 2023), eastern broadleaf forests today are less oak-dominated than they were a few centuries earlier.

Researchers and land managers have sought solutions to halt the trajectory of oak decline. Early recognition that young oaks failed to compete with mesophytic tree species, particularly red maple (*Acer rubrum* L.) and tulip tree (*Liriodendron tulipifera* L.) for canopy positions (i.e., regeneration failure; Lorimer, 1993) in forests that were increasingly denser, shadier, and less flammable (Alexander et al., 2021; Nowacki & Abrams, 2008; Woodall & Weiskittel, 2021) motivated studies on the use of prescribed fire and cutting to encourage oak regeneration. Results from these studies suggested that neither prescribed fire nor cutting alone is sufficient to halt the encroachment of mesophytes into areas previously dominated by oaks (Arthur et al., 2015, 2021; Hutchinson et al., 2005, 2012; Keyser et al., 2017; Schweitzer & Dey, 2011). The combination of prescribed fire and cutting seems promising, and although early results from such studies have shown an increase in oak reproduction, they also indicate that mesophytes maintain a strong presence (Albrecht & McCarthy, 2006; Brose et al., 1999, 2001; Brose & Van Lear, 1998; Cannon & Brewer, 2013; Iverson et al., 2008, 2017; Schweitzer et al., 2019; Waldrop et al., 2016).

Failure to reverse mesophyte dominance with management interventions suggests a substantial loss of oak forest resilience. When species traits and disturbance regimes are misaligned over time (e.g., fire-adapted trees in areas that no longer burn), it can lead to resilience debt, which manifests when the ecosystem fails to recover from disturbance (Johnstone et al., 2016). The successful recovery of oak forests requires oak regeneration, which often occurs when overstory trees die, leaving canopy gaps that allow sufficient light for young oaks, but the success of these young oaks depends on minimized shading from mesophytes or evergreen ericaceous shrubs (Dey, 2014; Lorimer, 1993). These findings invite the possibility that heightened overstory mortality is a necessary sacrifice for the advancement of young oaks. That is, the reduction in resilience debt through the death of overstory trees, combined with a return to the fire regime that minimizes fire-sensitive species in the understory, may result in the return of oak dominance and increased resilience if sufficient ecological memory (e.g., acorns, oak seedlings, and surviving root stocks) is held in the system (Johnstone et al., 2016; Webster et al., 2018). Indeed, a combination of canopy gaps and multiple prescribed fires that limit mesophytes can increase oak regeneration (Izbicki et al., 2020). If this is the case, understanding the interaction of management actions with resilience debt and ecological memory will be vital to our ability to promote and sustain oak forests moving forward.

One large-scale study of forest management practices that can provide information on oak forest resilience was the national Fire and Fire Surrogate (FFS) study (McIver et al., 2012), where three forest treatments, mechanical thinning or felling (Mech), prescribed fire (Fire), or a combination (Mech + Fire), were experimentally applied and compared to untreated controls (Control). One location of the FFS study within eastern broadleaf forests is the Green River site in western North Carolina, where the Mech treatment involved mechanical felling of saplings and ericaceous shrubs. After 12 years of treatment, basal area was reduced following prescribed fire and oak reproduction was higher in all Mech and Fire treatments relative to the Control (Waldrop et al., 2016). Since this initial report, another prescribed fire has been applied and forest composition has continued to be monitored, offering the opportunity for further insights into the success of management strategies and the mechanisms that may help reestablish oak dominance.

Here, we evaluated changes in forest composition and oak dominance 17 years after the initiation of the Green River FFS site to evaluate how forest management affects oak forest resilience. We investigated how changes in tree mortality, recruitment, and growth differed among management treatments. To specifically examine the interaction of forest management in the context of resilience debt and ecological memory, we examined the composition of oak overstory trees, saplings, and seedlings and their relationships with treatments. We first hypothesized that changes in overstory basal area would be positive in all treatments except the Fire and the Mech + Fire treatments, where we expected basal area losses due to mortality to exceed basal area gains associated with mesophication (H1). Second, we hypothesized that oak seedling and sapling abundance would be greatest in the Fire and Mech + Fire treatments, which we expected to have the greatest reductions in overstory basal area, thereby increasing light levels for lower strata (H2).

MATERIALS AND METHODS

Study location and design

The Green River site covers 5841 mountainous hectares in Polk County, North Carolina (35.287633, −82.327276), with elevations of 300–800 m above sea level. When the study was initiated in 2001, overstory trees averaged 80–120 years old and consisted primarily of mixed-xeric or mesic upland oak and pine species depending on topographic position. Canopy cover was near 100% and mean tree density was 558 trees per ha. Large-statured ericaceous shrubs (mountain laurel and great laurel) made up a dense midstory throughout the study area, with the former more prevalent in xeric sites and the latter more prevalent in mesic sites. Mesophytic tree species such as red maple and tulip tree were abundant in the midstory. Understory communities were comprised of many species of broadleaved forbs, ferns, graminoids, shrubs, and tree seedlings (details on pretreatment cover and change are available in Oakman et al., 2019; Waldrop et al., 2016). Soils are deep and well drained, primarily in the Evard and Cliffield soil series (fine-loamy, oxidic, mesic, and Typic Hapludults), with inclusions of the Ashe series (coarse-loamy, mixed, active, and mesic Typic Dystrudepts) found throughout. The region has a humid-subtropical climate, with hot/humid summers and cool/mild winters. Mean annual rainfall is 139 cm, with no distinct dry season.

The Green River study utilized a randomized complete block design (Appendix S1: Figure S1), with four treatment units in each of three replicate blocks for a total of 12 treatment units. Each treatment unit covered an average of 12 ha, each surrounded by a treated but unsampled 4 ha buffer. Within the replicate blocks, each of the four treatment units was randomly assigned to one treatment. Treatment units were of sufficient size to include all prevailing combinations of elevation, aspect, slope, and landscape position.

The Fire treatment was applied in February–March of 2003, 2006, 2012, and 2015. All fires were ignited using a spot fire technique; the first was done by helicopter ignition and the others were done by hand ignition. Fire intensity was generally low, with flame lengths typically ≤1 m, and fire severity (defined as the consumption of soil organic horizons) was also low. However, some locations burned with higher intensity (flame lengths up to 10 m), particularly during the 2003 and 2006 fires (details of fire behavior are reported in Waldrop et al., 2010). The Mech treatment was applied in the winters of 2001–2002 and 2011–2012 and included cutting of all woody vegetation >1.4 m tall and <10.2 cm in dbh with a chainsaw. The Mech + Fire treatment had the first mechanical cutting in 2001–2002 and was treated with prescribed fire in 2003, 2006, 2012, and 2015. Slash resulting from mechanical felling was left in place. A second mechanical cutting was not implemented in the Mech + Fire treatment. Localized areas of higher fire intensity (flame lengths >2 m) were occasionally observed in the Mech + Fire treatment, presumably due to higher fuel loading created by that treatment. Visual estimates indicated near 100% burn coverage in both the Fire and Mech + Fire treatments during each fire. Further details on fire characteristics (e.g., flame lengths, fuel loadings) are available in Waldrop et al. (2016).

Sampling

A permanently marked, 50 m × 50 m grid was established in each treatment unit. Modified Whitaker plots, 20 m × 50 m in size (Waldrop et al., 2016), were established at 10 randomly selected grid points within each treatment unit. Each plot consisted of 10, 10 m × 10 m subplots. For vegetation sampling within each plot, the forest was divided into three strata: overstory, sapling, and understory. Overstory and sapling data were collected in five subplots along one side of the plot, and seedling data were collected in two, 1 m × 1 m quadrats in opposite corners of each subplot (Appendix S1: Figure S1). The overstory was defined as all woody vegetation, excluding mountain laurel and great laurel, greater than 10 cm dbh. In 2001, overstory trees were marked with numbered tags, identified to species, and dbh was measured to the nearest 0.1 cm. Trees were remeasured in subsequent years, recorded as alive or dead, and any trees newly recruited into the overstory size class were identified and tagged. Saplings were defined as trees in the midstory taller than 137 cm, but less than 10 cm dbh. Seedlings were defined as all woody stems less than 137 cm in height. All strata were identified to species and grouped into genera for analyses.

Data on saplings and seedlings were collected in 2001 (pretreatment) and 2016. Overstory data were collected in 2001 and 2018. To calculate relative growth rate (RGR) in overstory trees over the course of the study, we used the formula: $\text{RGR} = (\ln \text{dbh}_{2018} - \ln \text{dbh}_{2001})/(2018 - 2001)$. Changes (Δ) in basal area and tree density were calculated by subtracting the latest values from the 2001 values. Duff depth was also measured in 2001 and 2014 (details in Appendix S1).

Statistical analyses

We analyzed changes in basal area and tree density with a linear mixed-effects model (all analyses were conducted using R version 4.3.2; R Core Team, 2023), with treatment as a fixed effect and block and treatment unit as nested random intercepts (lmer function in lme4 package; Bates et al., 2015). To further understand the patterns among overstory *Quercus* species, we analyzed changes in oak basal area using a linear mixed model with treatment and species as interacting fixed effects and block, treatment unit, and plot as nested random intercepts. We analyzed the mortality of overstory trees with a logistic regression model that included treatment and genus as interacting fixed effects and block, treatment unit, and plot as nested random intercepts (glmer function in lme4 package). We analyzed RGR using a linear mixed-effects model with treatment and genus as interacting fixed effects and block, treatment unit, and plot as nested random intercepts.

Count data (overstory recruits, saplings, and seedlings) were analyzed with a generalized linear mixed-effects model with treatment and genus as interacting fixed effects and block, treatment unit, and plot as nested random intercepts. To further understand the patterns among *Quercus* saplings and seedlings, we analyzed these similarly, but with treatment and species as interacting fixed effects. To compare saplings and seedlings to changes in basal area, we constructed two generalized linear mixed-effects models for saplings and seedlings, respectively. The first analyzed total sapling/seedling abundance with changes in basal area as a fixed effect and block, treatment unit, and plot as nested random intercepts. The second analyzed sapling/seedling abundance with changes in basal area and genus as interacting fixed effects and block, treatment unit, and plot as nested random intercepts. To further understand the patterns among *Quercus* saplings and seedlings with changes in basal area, we constructed similar models, but with changes in basal area and species as interacting fixed effects. An additional observation-level random intercept was added to models of count data to correct overdispersion as needed (Harrison, 2014).

For each described model, significance was assessed using the Wald χ^2 test (Anova function in car package; Fox & Weisberg, 2019) and nonsignificant ($p > 0.05$) interactions were removed from final versions of the models. Post hoc comparisons were conducted using estimated marginal means (emmeans or emtrends function in emmeans package; Lenth, 2022). To facilitate model convergence where genus was a variable, we included the top seven genera (*Acer*, *Carya*, *Liriodendron*, *Nyssa*, *Oxydendrum*, *Pinus*, and *Quercus*), which represented 96.7% of overstory trees, 79.9% of saplings, and 86.2% of seedlings (Appendix S1: Table S1).

RESULTS

Overall, we found that basal area decreased in the Mech + Fire treatment due to overstory mortality, and this was associated with increasing abundance of oak saplings. Changes in basal area were positive and higher in the Control and Mech treatments relative to the Mech + Fire treatment ($\chi^2 = 51.11$, df = 3, $p < 0.01$; Figure 1). In contrast to our hypothesis (H1), however, basal area did not decrease in the Fire treatment, and instead, only the Mech + Fire treatment was sufficient to reduce basal area over the 17 years of the study. We also examined changes in tree density and found that it was less in the Fire and the Mech + Fire treatments compared to the Control treatment ($\chi^2 = 99.22$, df = 3, $p < 0.01$; Appendix S1: Figure S2).

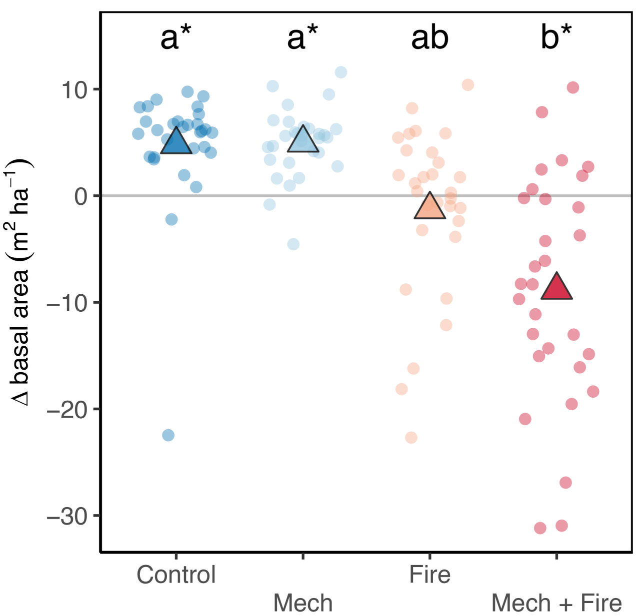

FIGURE 1 Changes (Δ) to overstory basal area at the Green River Fire and Fire Surrogate Study site 2001–2018. Each point represents one plot in each of the four treatments. Triangles represent model predictions for each treatment. Absence of the same letter signifies treatment differences ($p \leq 0.05$) and asterisks signify model predictions that differ from zero.

Examining forest composition from 2001 to 2018, we found that 211 trees recruited to the overstory, over half of which were in the Control treatment. Overstory recruitment was highest in the Control treatment relative to the others ($\chi^2 = 63.34$, df = 3, $p < 0.01$; Figure 2a), suggestive of advancing mesophication in these forests. However, we did not find support for recruitment to be higher for mesophytes in the Control compared to other treatments (interaction of treatment and genus; $p > 0.05$). Overall, overstory recruitment varied by genus, where *Quercus* had greater recruitment than *Liriodendron*, but did not differ from other genera ($\chi^2 = 49.92$, df = 6, $p < 0.01$; Appendix S1: Figure S3). Further, *Oxydendrum* had greater recruitment than *Pinus*, *Carya*, *Nyssa*, and *Liriodendron*, and *Acer* had greater recruitment than *Carya* and *Liriodendron*. When we evaluated the overstory tree RGR, we did not find support for an interaction of treatment and genus or any treatment differences. However, RGR differed by genus, where it was higher for *Quercus* relative to *Carya* and *Oxydendrum* ($\chi^2 = 25.17$, df = 6, $p < 0.01$; Appendix S1: Figure S4).

Over the course of the study, we found that 303 overstory trees died, a third of which were in the Mech + Fire treatment. Accordingly, the probability of overstory tree mortality was highest in the Mech + Fire treatment relative to the other treatments ($\chi^2 = 32.30$, df = 3, $p < 0.01$; Figure 2b). We did not find evidence that genus-specific mortality differed by treatment (interaction of treatment and genus; $p > 0.05$). The probability of overstory tree mortality varied by genus ($\chi^2 = 58.64$, df = 6, $p < 0.01$), where it was higher for *Pinus* relative to other genera, and higher for *Quercus* relative to *Acer* (Appendix S1: Figure S5). Collectively, these findings indicate that recruitment explained the positive basal area gains in the Control treatment, while mortality was responsible for reductions in basal area in the Mech + Fire treatment.

In the lower strata, we found that treatment effects on both sapling and seedling abundances varied by genus (saplings: $\chi^2 = 174.34$, df = 18, $p < 0.01$; seedlings: $\chi^2 = 75.21$, df = 18, $p < 0.01$; Appendix S1: Tables S2 and S3). In contrast to our hypothesis (H2), *Quercus* sapling abundance was not higher in the two prescribed fire treatments relative to the other treatments. Instead, *Quercus* saplings were more abundant in the Mech + Fire treatment relative to both the Mech and Fire

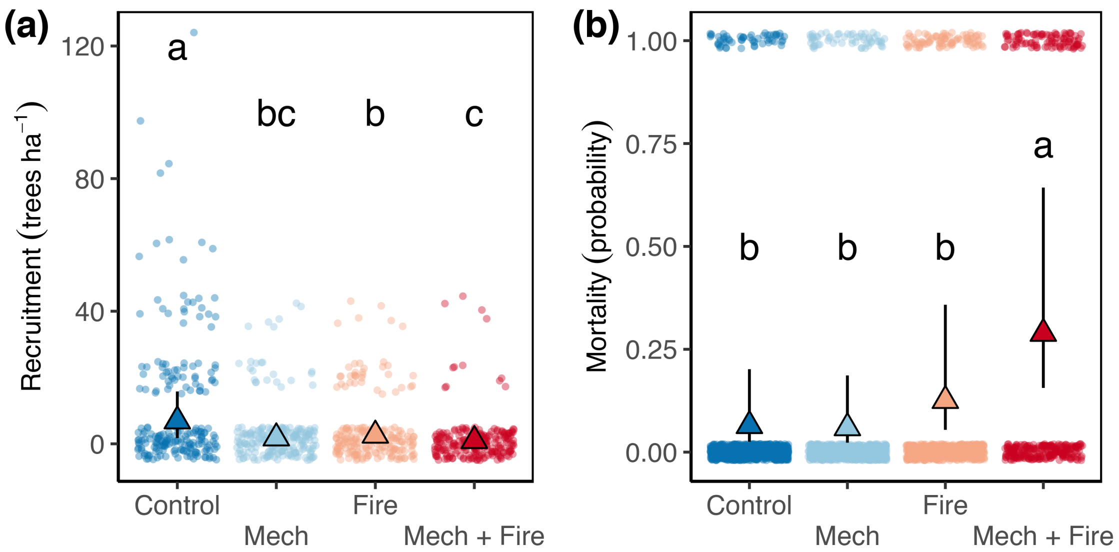

FIGURE 2 Overstory tree recruitment and mortality at the Green River Fire and Fire Surrogate Study site 2001–2018. (a) Recruitment of overstory trees in each of the treatments. Points represent each of seven tree genera in each plot (30 per treatment). (b) Mortality probability of overstory trees in each of the treatments. Points represent trees that lived (0) and died (1) by 2018. In both (a) and (b), triangles represent model predictions for each treatment and lines represent the range of model predictions across genera. Absence of the same letter signifies treatment differences ($p \leq 0.05$).

treatments and were higher in the Control treatment relative to the Fire treatment. Comparing the two most abundant genera of saplings, *Acer* and *Quercus*, we found no significant differences in their abundances in any treatment except for the Fire treatment, where *Acer* saplings were more abundant (Appendix S1: Table S2). For *Quercus* seedling abundances, we did not find support for treatment differences ($p > 0.05$). Comparing the two most abundant genera of seedlings, *Acer* and *Quercus*, we found no significant differences in their abundances in any treatment (Appendix S1: Table S3).

When examining sapling abundance in the context of overstory basal area, we found that saplings increased with decreasing basal area (indicated by more negative Δ basal area values; Figure 3a), but this relationship was dependent upon genus ($\chi^2 = 2331.03$, df = 6, $p < 0.01$). *Quercus*, but not *Acer*, sapling abundance increased with decreasing basal area (Figure 3b), providing partial support for our hypothesis (H2). Reduced overstory basal area also increased the abundance of less abundant genera (Appendix S1: Figure S6), but the lack of response from *Acer*, the main mesophytic representative, suggests that overstory mortality may be a mechanism for improving oak regeneration. In contrast to saplings, total seedling abundance had no relationship with changes in basal area ($p > 0.05$); however, we did find relationships that varied by genus ($\chi^2 = 549.46$, df = 6, $p < 0.01$). In contrast to our hypothesis (H2), we found no relationship between *Quercus* seedling abundance and changes in basal area, although *Acer* seedling abundance increased with larger increases in basal area, and *Liriodendron*, *Nyssa*, *Oxydendrum*, and *Pinus* seedling abundances decreased with larger increases in basal area (Appendix S1: Figure S7).

When examining the response among oak species to treatments, we found that species differences in basal area change depended on treatment ($\chi^2 = 78.51$, df = 18, $p < 0.01$), where *Quercus coccinea* had decreased basal area over the course of the study (represented by negative basal area change) in the Mech + Fire treatment compared to the other treatments, and *Quercus montana* had increased basal area over the course of the study in the Mech treatment compared to the Mech + Fire treatment (Appendix S1: Figure S8). Oak sapling abundance differed by species such that *Q. montana* and *Q. coccinea* were more abundant than *Quercus rubra*, *Quercus marilandica*, and *Quercus stellata* ($\chi^2 = 304.91$, df = 6, $p < 0.01$; Appendix S1: Table S4), but we observed no species by treatment interactions. With oak seedling abundances, we did not find support for an interaction of species and treatment or any treatment effects, but we found that seedling abundances differed by species ($\chi^2 = 689.16$, df = 4, $p < 0.01$); *Quercus alba*, *Q. coccinea*, and *Q. montana* were more abundant than *Q. rubra* and *Quercus velutina* (Appendix S1: Table S5).

In our comparison of oak saplings with overall change in basal area, we found support for an interaction of species and changes in basal area ($\chi^2 = 28.76$, df = 6, $p < 0.01$). Four species had significant negative slopes (*Q. alba*, *Q. coccinea*, *Q. montana*, and *Q. velutina*; Figure 4), showing that these species drove patterns

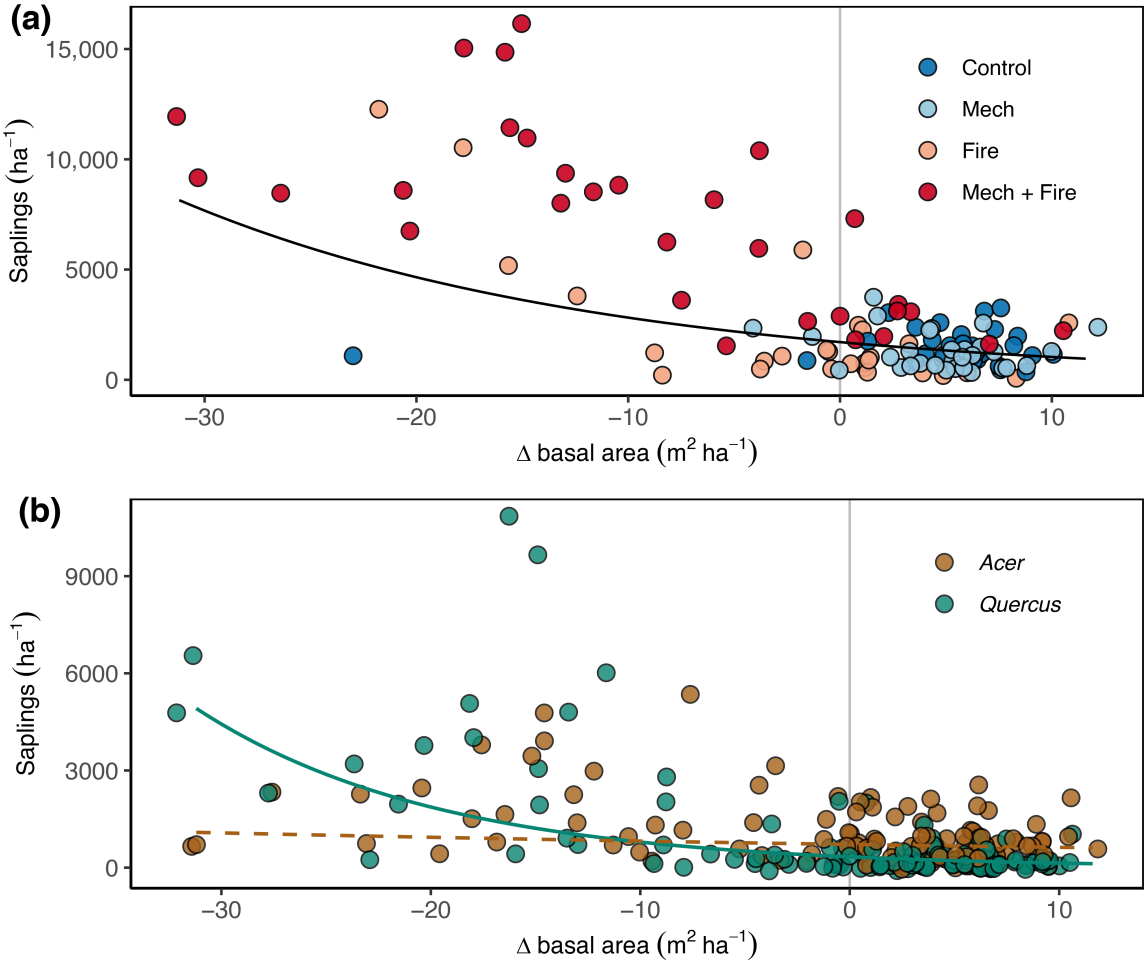

FIGURE 3 Sapling abundances compared to changes (Δ) in basal area over 17 years of treatments at the Green River Fire and Fire Surrogate Study site. (a) Total saplings. The treatment which each point represents is provided for reference. (b) Saplings of the two most abundant genera. Points in both figures are jittered slightly to aid visualization. Lines are model predictions, and solid lines denotes that the estimated slope differs ($p \leq 0.05$) from zero. Slopes of lines in (b) differ from each other.

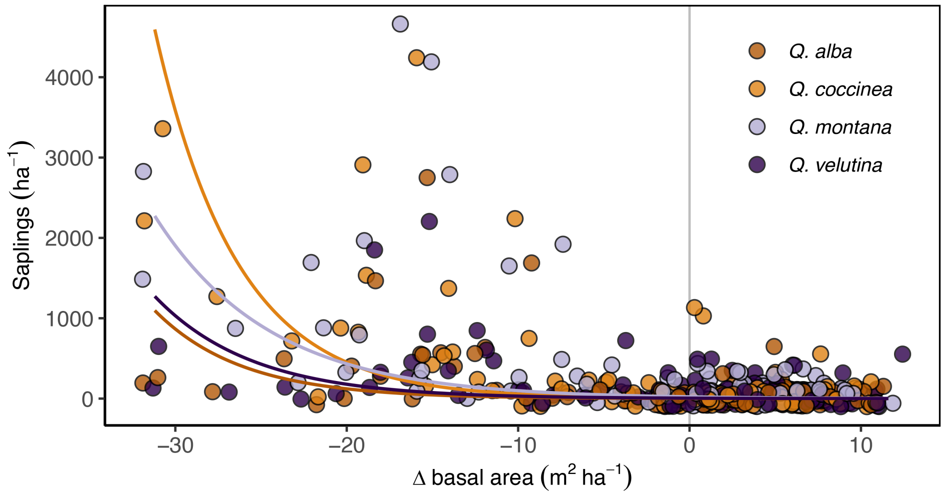

FIGURE 4 Sapling abundances of *Quercus* species compared to changes (Δ) in basal area at the Green River Fire and Fire Surrogates site. Lines are model predictions. Slope estimates for each line differ ($p \leq 0.05$) from zero. Data for three nonsignificant species (*Quercus marilandica*, *Quercus rubra*, and *Quercus stellata*) were excluded to aid visualization. Slope estimates for each line do not differ from each other.

across oaks overall, while three showed no relationship (*Q. marilandica*, *Q. rubra*, *Q. stellata*). While oak seedlings did not respond to changes in basal area at the genus level (Appendix S1: Figure S7a), in our species-level analysis, we found support for an interaction of species and changes in basal area ($\chi^2 = 12.07$, $df = 4$, $p = 0.02$) such that two species had significant negative slopes (*Q. coccinea* and *Q. velutina*; Appendix S1: Figure S9) and three showed no relationship (*Q. alba*, *Q. montana*, and *Q. rubra*).

DISCUSSION

Resilience debt accumulates over time when species adaptations are misaligned with disturbance regimes (Johnstone et al., 2016). Understanding how management actions interact with accrued resilience debt and remaining ecological memory in eastern broadleaf forests may be key to our ability to promote and sustain resilient oak forests. At the Green River FFS site, we found that decreased basal area due to overstory mortality, combined with repeated prescribed fires, was associated with increasing abundance of oak but not maple saplings. These findings indicate that a combination of treatments created conditions in which oaks are well positioned to recruit to the overstory, suggesting that long-term management actions can reduce resilience debt. Mechanical felling and repeated prescribed fire over decades may be a viable strategy to diminish resilience debt and sustain oak dominance in eastern broadleaf forests.

Our findings from the Green River FFS site demonstrate that over time, forest management treatments can halt or reverse the ongoing accretion of forest basal area associated with mesophication. Over the 17-year observation period, basal area increased in the Control treatment, largely due to overstory recruitment. This increase in basal area was unabated by the Mech treatment, suggesting that two mechanical felling treatments over the study period were insufficient to halt biomass accretion. While the Fire treatment halted gains in basal area, only the Mech + Fire treatment reduced basal area, suggesting that over 17 years, the synergistic effects of mechanical felling and multiple prescribed fires on overstory mortality were necessary to counteract mesophication. Although we found treatment effects on recruitment and mortality, we failed to find support for genus-specific treatment effects on either process (i.e., no interactions of treatment and genus). It may be possible that 17 years was not long enough to induce genus-specific treatment effects on recruitment. Further, the lack of genus-specific treatment effects on mortality suggests that mortality, which was largely in the Mech + Fire treatment, was not linked to any one tree genus's lack of adaptation to withstand fire. Most of the overstory trees that died during the study were oaks (56%), and this likely reflects the strong representation of oaks in the overstory at the outset of the study.

Ultimately, the future composition of eastern broadleaf forests will depend upon the current composition of lower strata and how they are impacted by management actions. At the Green River FFS site, we found that treatment effects on these lower strata were dependent upon genus. Half of inventoried saplings and over 75% of seedlings were in the genera *Acer* and *Quercus*, suggesting that at the Green River FFS site, maples are the major mesophytic representative. We found that total sapling abundance increased with increasing loss of basal area, a pattern likely driven by increased light availability with decreasing plot basal area. However, we observed contrasting relationships among oaks and maples, where oak sapling abundance increased with increasing losses of basal area, whereas maple sapling abundance had no such relationship. These contrasting responses are likely due to differing shade tolerances among the two genera, as oaks are generally considered less shade tolerant than maples (Abrams, 1992, 1998; Burns & Honkala, 1990). At Green River, this pattern was consistent among four oak sapling species, demonstrating that it was not solely attributable to one species. However, red maple was the only maple representative at the Green River FFS site, making it unclear if other *Acer* species or other mesophytic species in other forests would show a similar response. Our findings suggest that oaks are well positioned to compete with maples in plots where basal area has decreased, especially if prescribed fire treatments continue, corroborating previous work (Brewer, 2015; Brose et al., 2001; Brose & Van Lear, 1998; Iverson et al., 2017).

In the current conditions of eastern broadleaf forests, oaks are increasingly replaced by mesophytic trees (Fei et al., 2011; Knott et al., 2019). The crux of the problem is one of regeneration, that is, moribund overstory oaks cannot be replaced by oak saplings that are unable to reach canopy positions in dense, shady, nutrient-rich forests (Jo et al., 2019; Lorimer, 1993). As such, low levels of oak regeneration have been found to be the key comorbidity to oak recovery across several canopy-opening disturbances (Vickers et al., 2023). Our results suggest that young oaks have an advantage over the major mesophytic representative (maples) at the Green River FFS site in plots that have had basal area reduced through overstory mortality, most of which are in the Mech + Fire treatment. Collectively, these findings represent the intersection of forest management actions with resilience debt and ecological memory (Jõgiste et al., 2017;

Webster et al., 2018). That is, the misalignment of past and current fire regimes led to oak forests incurring resilience debt, which was reduced through the death of overstory oaks when management actions (in this case the Mech + Fire treatment) mimicked a severe disturbance. Ecological memory was held in this system by the life history traits of oak seedlings, and then saplings, which when presented with the fire regime in which they evolved, became abundant in the high light availability offered through the decline and death of their ancestors. Further, in forests like the Green River FFS site that have dense ericaceous midstories due to fire exclusion (Lafon et al., 2022), reducing this resilience debt may also depend on the felling of these shrubs, thereby increasing fuel loadings for subsequent prescribed fires, as was accomplished in the Mech + Fire treatment. Although it seems that young oaks are positioned to overtake maples in plots where forest basal area decreased at the Green River FFS site, a test of this hypothesis will only be possible once this cohort of saplings recruits to the overstory.

A limitation of this study is that it consists of only one site in the southern Appalachians and may not be representative of all eastern broadleaf forests. For example, at another FFS site in Ohio where treatments have continued, basal area accretion was dampened by the Mech treatment (Hutchinson et al., 2024), in contrast to our results. The Ohio FFS site differs from the Green River FFS site in two apparent ways that may explain this difference. First, the Ohio FFS site used an overstory thinning method for the mechanical treatments, rather than the sapling/shrub felling used at the Green River FFS site. Second, the Ohio FFS site lacked much of the evergreen ericaceous shrub component found at Green River. These shrubs present novel understory dynamics and fuel conditions that may differ from some eastern broadleaf forests (Elliott & Miniat, 2021). An additional potential limitation of this study is that the prescribed fires were only ignited in the dormant season. Evidence from other studies suggests that prescribed fires conducted in the growing season may be advantageous for reductions in red maple density (Vaughan et al., 2022).

Tree assemblages change slowly, challenging researchers to make recommendations to land managers with limited data that likely represent pieces of a multigenerational puzzle. Here, we used a long-term (in the human sense) study of forest management applications to show forest changes due to repeated applications of prescribed fire and mechanical felling. We found that a combination of prescribed fire and mechanical felling is the best treatment of those tested for oak regeneration, although it comes with the cost of overstory tree mortality. Such studies are invaluable to researchers and land managers alike hoping to manage forests today such that subsequent generations can benefit from oak-dominated forests and the ecosystem services they provide.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Taylor et al., 2025) are available in the USDA Forest Service Research Data Archive at https://doi.org/10.2737/RDS-2024-0024.

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SUPPORTING INFORMATION

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

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