Effects of repeated seasonal prescribed fire on vegetation composition in savannas and woodlands of the southeastern US

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ABSTRACT

Prescribed fire is requisite to manage pine/oak savannas and woodlands in the eastern US. Fire frequency, intensity, and timing influence plant community composition and structure. Historically, managers have applied prescribed fire primarily during the dormant season, but burning through the year is becoming more common. We report results from two relatively long-term fire seasonality studies investigating the effects of repeated seasonal prescribed fire on vegetation composition. In the first study, we examine the impact of early (April/May) and late (September/October) growing-season fire on a 1-, 2-, and 3-year fire-return interval over 15 years (2011–2025) in an oak-pine savanna on the Cumberland Plateau. In the second study, we examine the impact of four fire seasons—dormant (January/March), early growing, mid-growing (June/July), and late growing season—with an unburned control over 7 years (2020–2026) at nine sites across the southeastern US. We separated plants by flowering phenology, conservatism, heliophily, and fire-affinity to understand how these traits impact plant response to fire timing. Warm-season grasses increased in early growing-season treatments more than late growing-season treatments or unburned controls in both studies. Late growing-season fire and dormant-season fire promoted forb coverage in southeastern woodlands, and this response was driven primarily by fall-flowering forbs. In the oak-pine savanna, late growing-season fire specifically increased forb coverage for early-summer flowering forbs. Highly conservative forb species were not affected by fire timing. Increased sunlight availability was correlated with increased coverage of warm-season grasses and forbs. Frequent fire maintained open woodland and savanna conditions, especially when burning every 1–2 years in the growing season. Frequent fire during any season can be used to maintain oak/pine savannas and woodlands across the southeastern US, but managers can incorporate growing-season fire and manipulate sunlight availability to influence plant composition and structure and better meet management objectives.

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INTRODUCTION

Before European colonization, much of the southeastern US was covered with upland pine woodlands and savannas hosting a vast amount of plant and wildlife abundance and diversity (Earley 2004; Oswalt et al. 2012). Approximately 36 million acres were dominated by Southern pines including longleaf pine (*Pinus palustris*), shortleaf pine (*P. echinata*), slash pine (*P. elliottii*), and pond pine (*P. serotina*, Earley 2004; Oswalt et al. 2012). These communities hosted some of the most biodiverse ecosystems in temperate climates (Peet & Allard 1993; Earley 2004). After colonization, a combination of fire suppression and logging led to a massive decline in pine woodlands, and restoration of these ecosystems has become a priority for this region (Frost 2006; Oswalt & Guldin 2021; Guldin & Black 2018).

Frequent fire is requisite to maintain open pine woodlands and savannas in the southeastern US. Historically, both lightning strikes and human ignitions contributed to frequent fire in these ecosystems (Frost 1998; Pyne 1982). Indigenous people throughout this region set fires year-round to improve hunting and foraging grounds, prepare the land for agriculture, reduce fuel loads, and participate in ceremonies (Pyne 1982; Fowler & Konopik 2007). Lightning strikes frequently ignited fires in the summer, especially in the southeastern coastal plain (Frost 1998; Huffman 2006). The average historic mean fire-return interval in southeastern pine woodlands was 1–6 years (Frost 1998, 2006; White & Harley 2016; Rother et al. 2020; Stambaugh et al. 2020; Waters 2020). However, the US Forest Service's fire suppression campaign of the 1930s practically eliminated fire from the region, contributing to the decline of these pine systems. Reintroducing fire as a management tool began in the 1940s, and continues to this day (Fowler & Konopik 2007).

Many wildlife species thrive in areas managed with frequent fire. The federally-threatened red-cockaded woodpecker (*Leuconotopicus borealis*) declined because of fire suppression and the resultant encroachment of hardwoods into the midstory (U.S. Fish and Wildlife Service 2003). Northern bobwhite (*Colinus virginianus*, Brown & Palmer 2022), Bachman's sparrow (*Peucaea aestivalis*, Tucker et al. 2003; Jones et al. 2013), and the federally-listed gopher tortoise (*Gopherus polyphemus*, Yager et al. 2007) also require areas maintained with frequent fire. Wild turkey (*Meleagris gallopavo*) select areas that have been burned in the past two years and often forage in areas immediately after a burn (Martin et al. 2012). Fire also can be used to increase forage availability and nutritional quality for white-tailed deer (*Odocoileus virginianus*, Masters

et al. 1996; Lashley et al. 2015; Turner, Harper et al. 2020; Nichols et al. 2021). Even wildlife that are not considered fire adapted, such as *Plethodon* salamanders, persist better in areas with low-intensity fire characteristic of prescribed fires than areas with high fire-intensity fires that are more common with unplanned wildfires (Ford et al. 1999; Wilk & Peterman 2024). Direct mortality is uncommon for many wildlife species, and the positive impact of fire on vegetation cover often is more influential for many wildlife taxa that are management priorities in this region (Russell et al. 1999; Cox & Widener 2008; Keyser & Ford 2006; Harper et al. 2016). Nevertheless, timing of fire may be particularly important to minimize fire-induced mortality for some taxa, such as herptofauna (Humphries & Sisson 2012; Harris et al. 2020; Pilliod et al. 2003).

Plant species native to pine woodlands also have evolved with frequent fire. Southern pine species have developed traits such as thick bark, resprouting (in shortleaf pine), and flammable needles to not only survive fire but also increase fire frequency in their immediate surroundings to reduce competition (Bradley et al. 2016; Landers 1991; Waldrop et al. 1987; Outcalt 2000). Native shade-intolerant herbaceous plants typically increase with frequent fire, whereas understory shrub and tree species often decrease with frequent fire (Glitzenstein et al. 2003). Fire also may increase flowering in some herbaceous species, especially when the fires occur in the growing season (Abrahamson 1984; Clewell 1989).

One of the most common goals of using fire to manage pine woodlands is to set-back woody succession to maintain an open structure and herbaceous understory that is important for many endemic plant and wildlife species (Van Lear et al. 2005; Nowacki & Abrams 2008). Many hardwood species are adapted to resprouting after being top-killed by fire; therefore frequent, repeated fire is necessary to control hardwood encroachment (Boyer 1990; Olson & Platt 1995; Drewa et al. 2006). A fire-frequency of every 1–2 years is common to prevent woody dominance in the southeastern US (Waldrop et al. 1992; Glitzenstein et al. 2012; Robertson et al. 2021). Sunlight availability is as important as frequent fire to promote the herbaceous understory characteristic of woodlands and savannas, and herbaceous species often are not impacted by fire treatments if there is insufficient sunlight (Lettow et al. 2014; Vander Yacht et al. 2020; Bassett et al. 2020).

Fire seasonality impacts plant response to repeated fire. Repeated, frequent growing-season fire more effectively controls midstory hardwood stem density than similar dormant-season fire (Knapp et al. 2009). Areas burned during the growing season experience greater midstory top-kill (Ferguson 1957) and mortality (Resop et al. 2024), have lower hardwood stem density (Drewa et al. 2006), decreased woody cover (Gruchy et al. 2009), and less resprouting growth (Zeitler et al. 2025) when compared to areas burned during the dormant season. Growing-season burns repeated every 1–2 years can decrease resprouting of hardwoods by inducing complete mortality (Waldrop et al. 1992; Olson & Platt 1995). Hardwood carbohydrate storage primarily is in the root system during the dormant season, whereas more carbohydrates are stored above ground during the growing season. Thus, top-killing hardwoods during the growing season depletes more carbohydrates and, over multiple burn cycles, makes it less likely for these trees to resprout (Robertson & Hmielowski 2014). Nevertheless, single burns and burn regimes with a return interval greater than 2 years are not successful at managing hardwood saplings regardless of burn season (Boyer 1990; Waldrop et al. 1992; Olson & Platt 1995; Drewa et al. 2006; Keyser et al. 2019; Robertson et al. 2021).

Herbaceous understory response to fire also varies based on fire timing. Dormant-season and late growing-season fire tends to increase forb coverage compared to fire in the early or mid-growing-season (Resop et al. 2024; Bones et al. 2026). In contrast, early growing-season fire tends to increase grass coverage relative to late growing-season fire (Sparks et al. 1998; Lewis et al. 1964), especially for warm-season grasses (Howe 2011; Dickson et al. 2019). Howe (1995, 2011) reported early-flowering and mid-flowering species were eliminated over time in areas burned during March–April or not burned at all. In contrast, these species increased when burned in July, whereas late-flowering species decreased after July burns. These results suggest early-flowering species may be set-back by spring burns but benefit from mid-summer burns after they have finished flowering through decreased competition from late-flowering species. This result also may, in part, explain why repeated fire later in the growing season tends to increase species diversity relative to early growing-season fire (Towne & Kemp 2008; Howe 2011; Towne & Craine 2014).

Changes in flowering phenology may be responsible for some differences in species response to fire season. Many grass and forb species increase flowering after growing-season fire (e.g.,

wiregrass [*Aristida stricta*] (Clewell 1989; Platt et al. 1991; Streng et al. 1993; Fill et al. 2012), bluestems [*Andropogon* spp.] (Abrahamson 1984; Platt et al. 1991; Streng et al. 1993), golden-asters [*Pityopsis* spp.] (Streng et al. 1993; Brewer 2006), and blazingstars [*Liatris* spp. (Streng et al. 1993)). On the other hand, fewer flowers are seen on plants when they are burned during their flowering period or directly before their flowering period (Pavlovic et al. 2011), which may impact recruitment. Growing-season burns synchronize flowering of forbs and shrubs by decreasing flowering duration (Platt et al. 1988; Hiers et al. 2000; Dixon & Robertson 2025). However, these changes may not impact fruit initiation (Hiers et al. 2000) or long-term populations (Fill & Crandall 2024; Brewer 2006). More research is needed to understand the relationship between flowering phenology and fire season to determine if changes in flowering influence long-term trends in understory plant composition.

Most fire seasonality studies have been limited in temporal and geographic scope. Few studies have used repeated data collection to document how repeated fire impacts long-term changes in plant communities in the eastern US. In fact, all previous studies tracking understory plant communities for more than 10 years have been conducted in tallgrass prairie (e.g., Howe 2011; Towne & Craine 2014; Dickson et al. 2019). Studies in Southern pine systems have reported results of relatively long fire regimes but provide only one year of data collection (e.g., Lewis & Harshbarger 1976; Streng et al. 1993; Kush et al. 2000). These studies can confound effects of fire seasonality with time-since-fire and are not designed to analyze trends in vegetation response (Streng et al. 1993). Lack of replication across a geographic region also limits the generalizability of many ecological studies (Field et al. 2018; Frühstückl 2025; Filazzola & Cahill Jr 2021; Borer et al. 2014). Most fire seasonality studies examine trends in vegetation response to fire season in a single location (e.g., Howe 2011; Glitzenstein et al. 2012; Dixon & Robertson 2025). A few studies have compared results across multiple states (e.g., Drewa et al. 2006; Vaughan et al. 2022), but none except for previous work in our study system (Bones et al. 2026) has examined fire seasonality across the entire southeastern region.

This thesis aims to use (1) a long-term (15-year) case-study on the Cumberland Plateau and (2) a geographically replicated study of pine savannas to further our understanding of the impacts of repeated seasonal fire on changes in vegetation composition in pine woodlands and savannas across the southeastern US. Specifically, we aim to investigate how

1. fire-affinity impacts woody response to fire seasonality,
2. flowering phenology, heliophily, and conservatism impact herbaceous response to fire seasonality, and
3. sunlight availability affects understory response to fire seasonality.

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CHAPTER 1: FIRE FREQUENCY AND SEASON IMPACT LONG-TERM CHANGES IN VEGETATION COMPOSITION IN A DEVELOPING OAK-PINE SAVANNA

A version of this chapter has been submitted to *Restoration Ecology* for publication:

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ABSTRACT

Introduction

Understanding impacts of fire timing on plant communities is important when restoring fire-dependent ecosystems in the eastern US.

Objectives

We used a case study to document how fire frequency and seasonality influence long-term change in plant composition in a developing oak-pine savanna on the Cumberland Plateau and how those effects vary with reproductive phenology, fire affinity (pyrophobic/pyrophilic), heliophily (a measure of sunlight-affinity), and conservatism (a measure of fidelity to open, fire-adapted ecosystems).

Methods

We implemented six fire treatments consisting of early and late growing-season fire on a 1-, 2-, and 3-year fire-return interval from 2011–2025. We recorded vegetation composition annually.

Results

Warm-season grass coverage increased with early growing-season fire relative to late growing-season fire when burned every 1–2 years. Change in forb coverage differed based on flowering phenology with early summer-flowering forb coverage increasing more with late growing-season fire than early growing-season fire when burned every 1–2 years. Late summer-flowering forb coverage increased with all fire treatments. The Hill-Shannon diversity index increased in late

growing-season treatments. Midstory stem density was greatest in the 3-year treatments and the 2-year early growing-season treatment.

Conclusions

Fire seasonality impacted long-term changes in plant composition when burning every 1–2 years, but not when burning every 3 years. Reproductive phenology influenced herbaceous plant response to fire seasonality, but coverage of highly conservative species was maintained with all fire treatments.

Implications for practice

Our data indicate fire in both the early and latter portions of the growing season can be used to restore and maintain an oak-pine savanna on the Cumberland Plateau, and managers can use our results to help meet their management objectives. When burning every 1–2 years, early growing-season fire increased coverage of warm-season grasses, whereas late growing-season fire increased coverage of early-summer flowering forbs. Late growing-season fire increased diversity of commonly encountered understory species in all fire frequencies. Herbaceous plants persisted in the 3-yr interval treatments, however, when the fire-return interval exceeded 2 years, midstory stem density became too dense to represent savanna conditions.

INTRODUCTION

Oak-pine savannas are experiencing drastic decline in the eastern United States (US). As of the late 20th century, these savannas occupied less than 2% of pre-settlement distribution (Nuzzo 1986; Earley 2004). As a result, populations of wildlife that rely on or benefit from these ecosystems, such as *Picoides borealis* (red-cockaded woodpecker), *Colinus virginianus* (northern bobwhite), *Melanerpes erythrocephalus* (red-headed woodpecker), and *Pituophis melanoleucus melanoleucus* (northern pine snake), have declined. Southeastern pine savannas are known for incredible herbaceous vegetative diversity (Walker & Peet 1983; Keddy et al. 2006) and rare and endemic plant species (McMillan et al. 2002; Noss 2013). Thus, restoration and management of oak-pine savannas in fire-suppressed areas is a conservation focus in the eastern US.

Frequent, low-intensity fire is requisite when managing oak-pine savannas. Frequent fire limits encroachment of hardwood stems and stimulates herbaceous plants (Brockway & Lewis 1997; Glitzenstein et al. 2012; Vander Yacht et al. 2020). Dendrochronological studies have documented fire-return intervals of 2–4 years in central Tennessee before the fire-suppression campaign in the 20th century (Stambaugh et al. 2016, 2020). Many rare and endemic species rely on frequent fire to persist and have adapted traits, such as increased flowering following fire, to thrive in a frequent-fire environment (Slapcinsky et al. 2010; Ames et al. 2017). A fire-return interval of 1–2 years has been recommended to limit hardwood encroachment and maintain open woodland and savanna conditions (Glitzenstein et al. 2012; Robertson et al. 2021).

Fire seasonality impacts woody plant response to frequent fire. Repeated growing-season fire more effectively controls encroaching hardwood stems (Waldrop et al. 1992; Vaughan et al. 2022; Resop et al. 2024) and shrubs (Lewis & Harshbarger 1976; Drewa et al. 2006) than dormant-season fire. This relationship likely results from increased above-ground carbohydrate storage during the growing season (Robertson & Hmielowski 2014).

Sufficient sunlight is necessary to stimulate herbaceous response following fire (Lettow et al. 2014; Bassett et al. 2020), which may affect the impact of fire seasonality. Short-term studies in closed-canopy forests may not detect differences in vegetation composition (Keyser et al. 2019; Vaughan et al. 2022; Keyser & Greenberg 2024). However, with sufficient sunlight, even short-term studies can detect differences in groundcover composition with seasonal fire treatments. These studies report greater increases in warm-season grasses following early-growing season

fire (Lewis et al. 1964; Howe 1994, 2000), greater increases in forb coverage following fall and winter fire (Resop et al. 2024; Bones et al. 2026), and lower species diversity following spring fire (Roberton & Rebar 2022). Vander Yacht et al. (2020) reported minimal difference in understory composition when comparing early and late growing-season fire in oak woodlands on the Cumberland Plateau, but they suspected fire seasonality effects were confounded with fire intensity, and suggested longer monitoring may detect differences

Few studies in the eastern US have used repeated data collection to examine long-term (10+ years) effects of seasonal fire treatments on groundcover composition, and all were conducted in tallgrass prairies (e.g., Howe 2011; Towne & Craine 2014; Dickson et al. 2019). Two studies reported a greater increase in warm-season grasses following frequent early growing-season fire compared to other seasons (Howe 2011; Dickson et al. 2019). Howe (2011), Towne & Kemp (2008), and Towne & Craine (2014) reported reduced species diversity following early growing-season fire compared to burning later in the year. Howe et al. (2011) reported reduced species diversity following early growing-season fire was driven by fewer early-flowering forbs. Dickson et al. (2019) reported fire season had minimal impact on plant composition when implemented every 4 years. Other studies report results of relatively long fire regimes but provide only one year of data collection (e.g., Streng et al. 1993; Kush et al. 2000; Novak et al. 2021). Although valuable, these studies are unable to examine trends in vegetation response, are subject to annual variation, and can confound fire seasonality and time-since-fire (Streng et al. 1993).

Fire seasonality impacts flowering abundance and phenology, which may help explain long-term impacts of seasonal fire regimes. Growing-season fire delays and synchronizes flowering compared to dormant-season fire (Platt et al. 1988; Hiers et al. 2000; Dixon & Robertson 2025). Early growing-season fire increases flowering of warm-season grasses (Abrahamson 1984; Streng et al. 1993; Main & Barry 2002), and early and mid-growing-season fire can increase flowering for certain forbs (Streng et al. 1993; Brewer & Platt 1994; Hiers et al. 2000). In contrast, fire immediately prior to a plant's peak flowering period can decrease flowering (Pavlovic et al. 2011). However, changes in flowering do not always lead to changes in seed production or long-term changes in populations (Brewer 2006; Richardson & Wagenius 2022; Fill & Crandall 2024). Many species are resilient to changes in fire timing (Dixon & Robertson

2025), and seedling establishment can be slow in southeastern pine savannas (Glitzenstein et al. 2001), so persistence of a species may be influenced more by survival and resprouting than changes in flowering.

Given limited long-term fire seasonality research, we provide results of a 15-year case study implemented on the Cumberland Plateau in White County, TN to evaluate impacts of fire frequency (1-, 2-, and 3-year fire-return intervals) and growing-season fire timing (early and late) on long-term changes in plant composition. We grouped herbaceous plants by flowering phenology to test if phenology impacts long-term response to fire timing in this study system, as demonstrated in tallgrass prairie (Howe 2011). We grouped woody plants by fire affinity to determine if pyrophilic and pyrophobic species respond differently to fire season (Keyser et al. 2019; Zeitler et al. 2025). Finally, we grouped forb species by coefficient of conservatism (C-value, a measure of fidelity to intact ecosystems) and heliophily (a measure of sun-affinity) to understand how fire seasonality impacts species of conservation concern in oak-pine savanna ecosystems (Rooney & Leach 2010; Stephen et al. 2024). We hypothesized burning at different times and frequencies would lead to long-term changes in plant composition. We grouped predictions by growth form, first discussing herbaceous response, then woody response, and finally community-level species diversity metrics.

1. Herbaceous response: We predicted grasses and forbs would decrease in coverage when burned immediately before or during flowering because of reduced reproductive success (Pavlovic et al. 2011; Howe 2011). Specifically, we predicted warm-season grasses would increase in early growing-season (EGS) treatments relative to late growing-season (LGS) treatments, whereas cool-season grasses would decrease in EGS treatments relative to LGS treatments (Towne & Kemp 2003; Dickson et al. 2019). Similarly, we predicted forbs flowering spring through early-summer would decrease in EGS treatments relative to LGS treatments, whereas forbs flowering in the fall would increase in EGS treatments relative to LGS treatments (Howe 2011). We predicted highly conservative, sun-loving forbs would increase most in the 1- and 2-year interval treatments since frequent fire is necessary for many savanna conservative species (Ames et al. 2017).
2. Woody response: We predicted woody understory coverage and midstory density would increase most in the 3-year interval treatments because of increased time for woody

plants to recover following fire (Glitzenstein et al. 2012). We predicted less stem density in the LGS 3-year treatment than the EGS 3-year treatment because late growing-season fire can reduce resprouting rates (Huddle & Pallardy 1999; Meunier et al. 2021).

3. Species diversity response: Frequent fire often increases species diversity in fire-adapted ecosystems (Peterson & Reich 2008; Glitzenstein et al. 2012). We predicted species diversity indices would increase in all treatments but increase most in the 1- and 2-year fire-return intervals. We also predicted a greater increase in species diversity in the LGS treatments relative to EGS treatments considering the long-term trends reported in tallgrass prairie ecosystems (Howe 2011; Towne & Kemp 2008; Towne & Craine 2014).

METHODS

Study site

We conducted a case study at the Fire Demonstration Area (FDA) at Bridgestone-Firestone Wildlife Management Area (WMA) in White County, TN. Prior to establishment, the FDA was a *Pinus taeda* (loblolly pine) plantation that was clearcut prior to purchase by the Tennessee Wildlife Resources Agency (TWRA) in 1996. After purchase, the area was burned twice during the dormant season from 1998–2010 (pers. com. Clarence Coffey, TWRA), but there was no established fire regime or stated objective for the area during this period. The resulting plant community regenerated naturally; nothing was planted. At the start of the restoration project in 2011, the site was dominated by herbaceous groundcover with encroaching trees and shrubs, including *Pinus echinata* (shortleaf pine), *P. virginiana* (Virginia pine), *Quercus alba* (white oak), *Acer rubrum* (red maple), *Carya tomentosa* (mockernut hickory), and *Rhus copallinum* (winged sumac) with a basal area of 2.1 m^2/hectare and an average diameter at breast height (DBH) of 20 cm. The most common understory species included *Piptochaetium avenaceum* (black-seeded needlegrass), *Danthonia sericea* (fuzzy povertygrass), *Rubus flagellaris* (northern dewberry), and *Symphyotrichum dumosum* (rice button aster). Average annual precipitation was 155 cm and fairly consistent throughout each year with greatest precipitation in July (average 16 cm) and least in October (average 8.4 cm). Predominant soils were Ramsey-Lily complex and Lonewood loam (Soil Survey Staff, accessed 2026).

The FDA was established in 2011 as a collaborative effort between UT Extension and TWRA to (1) restore this area to historic pine-oak savanna conditions and (2) provide an educational field

demonstration site for professional and lay audiences to highlight effects of fire frequency and seasonality. We established six treatment units (6.5–13.8 hectares) and randomly assigned a combination of burn season (early or late growing season) and fire-return interval (1, 2, or 3 years). Treatments included 1-year interval late growing season (LGS1), 2-year interval late growing season (LGS2), 3-year interval late growing season (LGS3), 1-year interval early growing season (EGS1), 2-year interval early growing season (EGS2), and 3-year interval early growing season (EGS3; Figure 1A).

We established five fixed sampling plots placed randomly within each treatment for a total of 30 plots. We placed a metal stake at the center of each plot to define plot location. Our goal was to provide an educational demonstration area that represented long-term management at a scale relevant to agency land managers. Thus, treatment units were relatively large (6.5–12.7 ha). Although placed randomly, our sampling plots were not independent because all plots for one treatment occurred in the same unit. Thus, our study design was pseudo-replicated, which was an inevitable constraint when designing this study to be useful for demonstration and research. The consequence of pseudo-replication is our fire treatment effect could be a location effect of treatment unit. However, treatment units were large with spatially heterogeneous vegetation composition, and pre-burn conditions in each treatment unit were similar, suggesting *within* treatment unit heterogeneity was not different than *between* treatment unit heterogeneity. Thus, we expect a minimal effect of location and attribute the effects we document to fire treatment. Although our design limits extrapolation of our results to other systems, it provides useful information as a case study for managers interested in restoring oak-pine savannas in this region of the Cumberland Plateau.

Fire treatments

The growing season in this region stretches from early April through October. We conducted our EGS treatments mid-April–May and LGS treatments in September–October. We conducted the first LGS treatments in September 2011 and the first EGS treatments in April 2012. The one-year interval units were not burned in fall 2012 or spring 2013 but were burned every year since (Figure 2).

We used low- to moderate-intensity fire with flame lengths approximately 60 cm. Our objective was to burn hot enough to top-kill relatively young, encroaching trees and shrubs, consume leaf

litter, and maximize burn coverage, but not damage the relatively sparse larger trees. Beginning in 2023, we deployed UX-100 HOBO dataloggers and 12-inch Type K thermocouples (Onset Computer Corporation, Bourne, MA, USA; hereafter, "temperature loggers") on the soil surface and oriented vertically to record fire temperature at each sampling plot for 5 temperature measurements per treatment. Temperature loggers recorded temperatures from 0–900 ℃ every second. We recorded air temperature, wind speed, relative humidity, rate of spread, and flame length. Following each burn, we traced areas within a unit that did not burn using a smartphone application (OnX Maps, Missoula, MT, USA; Avenza Maps, Davisville Toronto, ON, v5.5) to calculate burn coverage.

Vegetation sampling

We sampled vegetation each year, July–August, 2011–2025, except 2013 and 2015 (Figure 2). We defined midstory as woody plants taller than 1.4 m with DBH <11.4 cm. At each sampling plot, we tallied all midstory trees and shrubs within 5 m of plot center. We determined understory (<1.4 m tall) vegetation composition using line-point sampling (Godínez-Alvarez et al. 2009). Each of our five transects intersected a fixed sampling plot and extended east-west across the entire unit (50–480 m; Figure 1B). At each 10-m mark, we identified all plants that crossed the transect to the lowest taxon possible (i.e., species or genus). Although the majority of the FDA represented upland oak-pine savanna, drainages bisected some of the units, allowing linear sections of mesic tree species to persist. We excluded mesic areas that would not burn and were not representative of our treatments from our analysis.

Assigning plant traits

We classified understory vegetation as forbs, graminoids, woody plants (shrubs and understory trees), semi-woody plants (*Rubus* spp. and lianas), and other (ferns and mosses). We assigned peak flowering months to all plants using the Lady Bird Johnson Wildflower Center Database (2025), the Southeastern Grassland Institute Species Traits Database (Southeastern Grasslands Institute 2025), and research-grade iNaturalist observations (iNaturalist community 2026). We grouped grasses into warm-season and cool-season and analyzed *Dichanthelium* spp. (low panic grasses) independently as they have two growth cycles. We grouped perennial forbs according to their months of peak flowering in the absence of fire: spring (April–mid-June), early-summer

(mid-June–mid-July), late-summer (mid-July–mid-August), and fall (mid-August–November; Table 1).

We assigned C-values and heliophily scores following the Grassland Fidelity Project (Estes et al. 2025). C-values are a well-established index developed by Swink and Wilhelm (1979) ranging from 1–10 and represent a species' fidelity to high-quality, intact ecosystems. A C-value of 1–3 represented generalist native species that can tolerate degraded conditions, 4–6 represented intermediate species, and 7–10 represented conservative species that only exist in high-quality, remnant savanna communities. A conservatism score of 0 indicated a nonnative species. Heliophily values were developed as an index of a species' fidelity to sunlight and range from 1 (species adapted to dense shade) to 9 (species requiring full sunlight; Estes et al. 2025). For our analysis, we grouped C-values and heliophily values into high (value ≥7), medium (value 6–4), and low (value 1–3). None of our forb species had low heliophily values, and all our highly conservative forb species had high heliophily values. We therefore grouped forbs by heliophily and conservatism into five categories (Table 1). A list of all understory species and their life cycle, flowering group, heliophily, and C-value are provided in Table 2.

We used a combination of previous literature (e.g., Thomas-Van Gundy & Nowacki 2013; Siskind et al. 2025), the Fire Effects Information System (U.S. Department of Agriculture, Forest Service), and botanical consultants to categorize our woody species into pyrophilic, neutral, and pyrophobic. We analyzed *Rubus* spp. and winged sumac individually in our understory analysis because of management interest in reducing these species. All understory and midstory woody species with their fire-affinity group are listed in Table 3.

Data analysis

We used R Statistical Software (v4.5.1; R Core Team 2025) and the *tidyverse* package (Wickham et al. 2019) for data cleaning and statistical analyses and the *stats* (v4.5.1; R Core Team 2025) and *lme4* (Bates et al. 2015) packages to run statistical models. We used plot or transect as our unit of replication (n=5 per treatment per year). Specifications for all models are summarized in Table 4. When applicable, we ensured model assumptions were met by visually examining residual plots and checking for overdispersion (Faraway 2006).

Understory coverage

For each transect, we calculated the percentage cover (PC) for each understory vegetation group (Table 1) by dividing the number of points containing at least one observation of the vegetation group (N_{obs}) by the total number of points on the transect (N_{tot}). We used generalized linear models with a binomial random component and a logit link function to model changes in percentage cover of our 17 understory vegetation groups over the fifteen years and weighted the model with N_{tot}. Our model was

$$N_{obs} \sim Binomial(PC, N_{tot})$$

$$logit(PC) = Year * Treatment + PostBurn$$

where *Year* was a continuous variable, *Treatment* was a factor with 6 levels (EGS1, EGS2, EGS3, LGS1, LGS2, LGS3), and *PostBurn* was a categorical predictor variable indicating if the data for a specific year was collected the year after a burn for the 2- and 3-year treatments. We included this variable because vegetation composition can differ greatly the year after a burn.

We explored several more-complex models as a sensitivity analysis. Given the lack of replication, we first explored a model including spatial autocorrelation to partially account for pseudoreplication (Supplement 1). We also explored a model that more explicitly accounted for effects of time-since-fire (Supplement 2). These models yielded near identical results to the model given above, so we chose to report results from the simpler model.

For each of the seventeen fitted understory vegetation models (one model per vegetation group), we used the model to predict percent coverage at the beginning (PC_{2011}) and end (PC_{2025}) of the study. We calculated the change in coverage ($\Delta PC = PC_{2025} - PC_{2011}$) for each treatment. To compare two treatments (given as T1 and T2 below), we calculated distribution of the pairwise difference in ΔPC between treatments using the estimated variance-covariance matrix of the coefficients from our fitted model and the standard asymptotic assumption that the sampling distribution of the coefficients followed a multivariate normal distribution (Faraway 2006). We calculated the two-tailed p-value as

$$p = 2 \times \min\{Prob(\Delta PC_{T2} - \Delta PC_{T1}) > 0, \quad Prob(\Delta PC_{T2} - \Delta PC_{T1}) < 0\}$$

correcting for multiple comparisons using the Benjamine-Hochberg procedure (Benjamini & Hochberg 1995) as implemented in the *stats* package p.adjust function (method = "fdr"). For

each treatment, we also determined if coverage was increasing or decreasing based on whether the 95% confidence interval crossed 0.

Midstory top-kill and resprouting

For each midstory plot, we calculated the number of stems per acre (SPA) for each treatment and year. Midstory stem density differed between treatments in the 2011 pre-treatment surveys. Therefore, we calculated a normalized SPA

$$nSPA_i = \frac{SPA_i}{SPA_{2011}}$$

where SPA_i is the SPA in year *i* and SPA_{2011} is the pre-treatment SPA. To capture stem density prior to each treatment, we modeled nSPA only at the end of a fire-free interval, immediately before reburning. We used a mixed effects model with a gaussian random component and log link function to model stem densities as

$$\ln(nSPA) \sim Normal(\mu, \sigma)$$

$$\mu = Treatment + (1|Year)$$

In contrast to the understory models described above, we did not include an interaction between Treatment and Year and instead included Year as a random effect because midstory stem densities across treatments varied greatly by year, likely because years with greater precipitation led to faster growth rates of young woody stems (Paine et al. 2009; Lucas et al. 2017).

To assess midstory top-kill, we calculated the percentage of midstory SPA remaining post-burn

$$pbSPA_i = \frac{SPA_i}{SPA_{i-1}}.$$

We used a mixed effects model with a gaussian random component and a log link function to model pb-SPA as

$$\ln(nSPA) \sim Normal(\mu, \sigma)$$

$$\mu = Treatment + (1|Year)$$

We used a likelihood ratio test for both midstory models to test whether the factor Treatment significantly affected our response variables. When we detected significant effects, we performed

a Tukey's post-hoc test using the *emmeans* (Lenth & Piaskowski 2025, v1.11.2-8) and *multcomp* packages (Hothorn et al. 2008) to pairwise compare the impact of treatment on midstory top-kill and stem density. We repeated this process for pyrophilic and pyrophobic trees and included an interaction term of fire-affinity and treatment in our mixed effects model such that the systematic component of our models was updated to:

$$\mu = \ Treatment * FireAffinity + (1|Year)$$

In this case, we used Tukey's post-hoc test to compare the impact of treatment within each fire-affinity group, as well as the impact of fire-affinity within each treatment.

Species diversity

Species richness (S) and Hill-Simpson diversity (D) indices provide a powerful understanding of vegetation community metrics because they allow examination of changes in rarely occurring species (S) and commonly occurring species (D; Roswell et al. 2021). We used the *iNEXT* package (Hsieh et al. 2016) to estimate S and D for the understory for each treatment in each year at double the minimum sample coverage (Chao et al. 2014) as well as the standard error SE_S and SE_D. We modeled S using linear models with a gaussian random component and weighted the models with $1/SE_S$ to account for variable uncertainty in our estimates of S. We fit two non-nested models (for clarity, the weighting component is not shown below):

$$S \sim Normal(\mu_{S,1}, \sigma)$$

$$\mu_{S,1} = \ Treatment * Year + PostBurn$$

and

$$S \sim Normal(\mu_{S,2}, \sigma)$$

$$\mu_{S,2} = \ Season * Year + \ Treatment + \ PostBurn$$

We used likelihood ratio tests to determine if fire treatment or season impacted change in S over time. When we detected differences, we performed a Tukey's post-hoc test to compare changes in treatments over time. We repeated this process for D.

Fire behavior

We modeled maximum fire temperature using a linear model with a gaussian error distribution

$$T_{max} \sim Normal(\mu_F, \sigma_F)$$

$$\mu_F = Treatment.$$

We used a likelihood ratio test to test whether maximum fire temperature differed between fire treatments. A similar analysis for fire residency time is given in Supplement 3.

RESULTS

Grasses

Flowering phenology influenced grass response to fire treatment. Warm-season grass coverage increased in all treatments (95% confidence interval [CI] lower bound >0 for all treatments). Coverage increased more in EGS1 (ΔPC=25.7, CI=[19.6, 32.4] percentage points [PP]) and EGS2 (27.6 [18.5, 36.3] PP) than LGS1, EGS3, and LGS3 (range of the means: 5.4–10.6 PP; $p<0.05$ for all pairwise comparisons between EGS1, EGS2 and LGS1, EGS3, LGS3).

Cool-season grass coverage decreased by more than 20 percentage points in all treatments but decreased more in LGS2 (-42.8 [-51.6, -33.5] PP) than EGS2 or the 3-year treatments (-24– -26 PP; $p<0.05$ for all comparisons between LGS2 and EGS2, EGS3, LGS3). Cool-season grasses also decreased more in EGS1 (-34.4 [-41.8, -26.7] PP) than the 3-year treatments ($p<0.05$ for all comparisons between EGS1 and EGS3, LGS3). *Dichanthelium* spp. coverage increased in LGS1 and LGS2 (8.8–10.2 PP) relative to the EGS treatments and LGS3 (-1.0– -9.2 PP, $p<0.05$ for all pairwise comparisons between LGS1, LGS2 and EGS1, EGS2, EGS3, LGS3, Figure 3).

Forbs

Change in forb coverage varied by flowering phenology. A likelihood ratio test (LRT) indicated change in spring-flowering forbs differed by treatment (df=5, chisq=11.2, $p<0.05$), however, after adjusting the pairwise comparisons for false discovery rate, we determined none of the treatments were different ($p>0.6$ for all pairwise comparisons). However, change in early summer-flowering forb coverage differed between treatments (LRT df=5, chisq=20.3, $p<0.002$). Early summer-flowering forbs increased in LGS1 (10.5 [3.9, 17.0] PP) and LGS2 (13.1 [6.4, 19.9] PP) more than LGS3, EGS1, and EGS2 (-2.7–1.0; $p<0.05$ for all pairwise comparisons between LGS1, LGS2 and LGS3, EGS1, EGS2). Late summer-flowering forbs increased in all

treatments except EGS2 (CI lower bound >2.3 PP for all treatments), whereas fall-flowering forbs remained stable in all treatments (Figure 4).

We did not detect a change in high-conservatism forbs in EGS1 (2.6 PP [-3.0, 8.1] PP), but we did detect an increase in all other treatments (CI lower bound ≥0 for all five treatments). Similarly, we did not detect a decrease in high-heliophily, medium-conservatism forbs in any treatment. High-heliophily, low-conservatism forbs increased in LGS3 (8.8 [5.8, 12.1] PP) relative to EGS1 and EGS2 (-0.8–2.7 PP, $p<0.07$) as well as in EGS3 (8.2 [4.7, 12.0] PP) relative to EGS1 ($p<0.07$). Medium-heliophily, medium-conservatism forbs decreased in EGS2 (-10.6 [-17.0, -4.7] PP) relative to all other treatments except EGS1 ($p<0.04$ for all comparisons between EGS2 and EGS3, LGS1, LGS2, LGS3). These forbs also increased in LGS2 (5.7 [0, 11.5] PP) relative to EGS1 (-6.1 [-12.2, 0] PP, $p<0.03$). Medium-heliophily, low-conservatism forbs remained stable or decreased in all treatments (Figure 6).

Woody understory

Woody plant coverage increased in LGS2, LGS3, and EGS3 (15.8–22.9 PP) relative to EGS1 (0.6 [-7.7, 8.7] PP, $p<0.05$). *Rubus* spp. coverage did not increase in any treatment. Winged sumac increased in EGS3, LGS1, and LGS3 (CI lower bound >0 for all three treatments) but remained stable in all other treatments. Pyrophilic woody coverage increased more in LGS2 (19.3 [11.6, 27.2] PP) than all other treatments (-2.4–6.5 PP; $p<0.05$ for comparison between LGS2 and all other treatments). Pyrophobic woody understory coverage did not differ between treatments ($p>0.07$ for all pairwise comparisons, Figure 7).

Midstory top-kill and stem density

When examining top-kill using the percentage of midstory SPA remaining post-burn (pb-SPA), the pb-SPA differed between treatments (df=5, chisq=21.2, $p<0.001$). LGS1 had greater pb-SPA than LGS2, (df=31.5, t=3.2, $p<0.04$), EGS2 (df=31.5, t=3.0, $p<0.06$), and EGS3 (df=31.6, t=3.0, $p<0.06$). EGS1 also had greater pb-SPA than LGS2 (df=31.5, t=2.9, $p<0.07$). Fire-affinity did not impact how top-kill varied by treatment (df=5, chisq=1.2, p=0.95). When examining normalized midstory stem density (nSPA) at the end of a fire-free interval, nSPA differed by treatment (df=5, chisq=35.8, $p<10^{-5}$). EGS2, EGS3, and LGS3 had greater nSPA than LGS2 and EGS1 (df=29–30, t>3.4, $p<0.02$ for all pairwise comparisons between EGS2, EGS3, LGS2, and LGS2, EGS1).

Fire-affinity influenced treatment impact on nSPA (df=5, chisq=20.8, $p<0.001$). For pyrophilic species, EGS2 and EGS3 had greater nSPA than EGS1, LGS1, and LGS2 (df=70–72, $t>3.1$, $p<0.04$ for all pairwise comparisons between EGS2, EGS3, and EGS1, LGS1, LGS2). LGS3 also had greater pyrophilic nSPA than EGS1 and LGS1 (df=70–71, $t>2.8$, $p<0.07$ for all comparisons between LGS3 and EGS1, LGS1). For pyrophobic species, LGS2 had lower nSPA than LGS1, LGS3, and EGS3 (df=70–72, $t>2.9$, $p<0.06$), and EGS2 had lower nSPA than LGS1 (df=70.8, $t=2.8$, $p<0.07$). In EGS2, nSPA was greater for pyrophilic species than pyrophobic species (df=70, $t=3.9$, $p<0.001$, Figure 8).

Species diversity

Neither fire treatment (df=5, 65, $F=0.2$, $p=0.95$) nor fire season (df=1, 69, $F=0.1$, $p=0.73$) changed species richness (S) over time. In fact, S remained constant throughout the study in all treatments (df=1, 65, $F=2.6$, $p=0.11$). Fire treatment did not impact change in Hill-Simpson diversity index (D) over time (df=5, 65, $F=1.5$, $p=0.21$). However, D increased in LGS treatments (0.41 effective species per year) relative to EGS treatments (no change; df=1, 69, $F=7.6$, $p<0.01$; Figure 5).

Fire behavior

Maximum fire temperature (T_{max}) varied by fire treatment (df=5, 39, $F=4.1$, $p<0.01$). EGS3 had a greater maximum fire temperature (T_{max} = 363 [261, 466]°C) than all other treatments (range of mean T_{max} for all other treatments = 116–155°C; df=39, $t>3.3$, $p < 0.03$ for all comparisons between EGS3 and EGS1, EGS2, LGS1, LGS2) except LGS3 (T_{max} = 193 [91.1, 297]°C; df=39, $t=2.4$, $p=0.20$).

DISCUSSION

Our 15-year case study demonstrates how reproductive phenology, fire-affinity, conservatism, and heliophily help explain how fire frequency and timing influenced long-term changes in plant composition in a developing oak-pine savanna on the Cumberland Plateau. The greatest differences between seasonal burn treatments occurred with fire every 1–2 years; most seasonal differences were not detected in the 3-year interval treatments. The largest differences in understory response to fire timing indicate herbaceous plants increased most when burned before investing energy in reproduction or after setting seed. As predicted, warm-season grasses

increased most when burned every 1–2 years in the EGS. In contrast, *Dichanthelium* spp. and early-summer flowering forbs increased more when burned every 1–2 years in the LGS, as predicted. Contrary to our expectations, cool-season grasses decreased across treatments. Midstory stem density was greatest in the 3-year interval treatments, as predicted, but there was no difference between EGS3 and LGS3. Hill-Simpson diversity increased in the LGS treatments relative to EGS treatments, as predicted. Frequent early and late growing-season fire maintained an oak-pine savanna, and our results should help fire practitioners better use fire for restoration of oak/pine savannas on the Cumberland Plateau.

As hypothesized, grass response to growing-season fire was impacted by flowering phenology. As predicted, warm-season grasses increased most (26–28 percentage points) in the EGS treatments when burned on a 1–2-year interval, which is consistent with previous studies (Lewis et al. 1964, Howe 2011; Dickson et al. 2019) studies. Fire during the EGS decreases competition by setting back early-flowering herbaceous species, and repeated burning during this time may encourage grass dominance and reduce coverage and diversity of forbs (Howe 1994, 2011; Dickson et al. 2019). Contrary to our predictions and previous work in tallgrass prairie (Towne & Kemp 2003; Dickson et al. 2019), cool-season grasses (primarily black-seeded needlegrass and fuzzy povertygrass) decreased across all treatments, especially when burned every 1–2 years. In contrast, in the 1- and 2-year treatments *Dichanthelium* spp. increased more in LGS relative to EGS. This relative increase follows our expectation that fire in the spring while *Dichanthelium* spp. are preparing to flower may discourage herbaceous spread compared to fire after seed production (Pavlovic et al. 2011). Towne and Kemp (2008) reported similar decreases in *Dichanthelium oligosanthes* (few-flowered panicgrass) when burned in spring and summer, but they did not compare the response to fall burning.

Reproductive phenology was similarly related to the effects of fire timing on changes in forb coverage. EGS treatments reduced early-flowering forbs relative to LGS treatments when burning every 1–2 years, similar to trends reported by Howe (2011) in tallgrass prairie. Previous short-term studies also report a greater increase in forb coverage following late growing-season fire (Gruchy et al. 2009; Resop et al. 2024; Bones et al. 2026). Forb response not only contributes to species diversity but is especially important for food and cover for many wildlife species on the Cumberland Plateau, including white-tailed deer (Turner et al. 2025, Harper et al.

2025), elk (Nanney et al. 2018), wild turkey (Baughman & Guynn Jr. 1993; Harper et al. 2000), northern bobwhite (Kroeger et al. 2020), songbirds (Worthington et al. 2004; Shaffer et al. 2023), and pollinators (Wilhelm et al. 2026). Contrary to our predictions, late-summer flowering forb coverage increased across all treatments, and fall-flowering forb coverage did not change in any treatment, consistent with Dixon and Robertson (2025) and Vander Yacht et al. (2020) who suggested many species are resilient to fire at a various times of the year.

Frequent fire is requisite to control woody and semi-woody encroachment in southeastern savanna ecosystems. *Rubus* spp. did not increase in any treatment over the course of the study, similar to Bones et. al (2026) who reported EGS and LGS fire controlled bramble coverage. Our results corroborate previous work suggesting fire-return intervals greater than 2 years are insufficient to reduce woody encroachment and maintain open savanna conditions in the southeastern US (Waldrop et al. 1992; Glitzenstein et al. 2012; Robertson et al. 2021). Despite the highest fire temperatures and rates of top-kill in the 3-year treatments, continuous resprouting resulted in as many or more midstory stems three years after burning as occurred when our study began (more than 1,900 stems per acre). Woody understory cover also increased approximately 15 percentage points over 15 years when burned on a 3-year interval. Woody plants dominated our 3-year interval treatments, similar to Glitzenstein et al. (2003), but in contrast to their results, we did not record a decrease in herbaceous cover despite the abundance of woody plants, which indicates fire applied every three years top-killed woody plants frequently enough to maintain coverage of herbaceous species. Midstory top-kill was least in LGS1 because the majority of this treatment unit did not burn in alternate years. For example, burn coverage was more than 90% in 2023, which resulted in a 20% decrease in midstory stems the following summer, but burn coverage was less than 10% in 2024, which resulted in a 50% increase in midstory stems the following summer. Although fire intensity in alternate years was great enough to maintain an open savanna condition, an annual return interval during the LGS may be difficult because of a lack of fine dead fuels.

The response of pyrophylic and pyrophobic woody species was complex. Pyrophilic understory woody coverage increased more in LGS2 than EGS2, but pyrophilic midstory stem density two years following fire was greater in EGS2 than LGS2 despite similar fire temperatures and midstory top-kill, suggesting these species are resprouting more often or with more stems

following EGS fire, consistent with Huddle and Pallardy (1999) and Meunier et al. (2021). Zeitler et al. (2025), however, reported greater pyrophylic resprouting following a single LGS fire. More research is needed to look at the relationship of fire affinity and hardwood resprouting after repeated seasonal fire treatments.

The FDA is in a region historically dominated by pine-oak savannas perpetuated by frequent fire (Stambaugh et al. 2020). Although the seedbank may be insufficient to restore groundcover diversity at some sites (e.g., Leicht-Young et al. 2009; Kaeser & Kirkman 2012; Ralston & Cook 2013), it is noteworthy that we documented extensive coverage of conservative forbs, including *Mimosa microphylla* (eastern sensitive-briar), *Pityopsis nervosa* (broad-leaved goldenaster), *Parthenium integrifolium* (wild quinine), *Liatris* spp. (blazingstars), *Angelica venenosa* (hairy angelica), and *Orbexilum pedunculatum* (Sampson's snake root). This highly conservative plant community reestablished naturally after establishment and removal of a loblolly pine plantation and reinstating frequent fire, and it contained many species not detected in the surrounding landscape, which indicates the seedbank and dormant rhizomes from a historically fire-maintained savanna persisted despite the intervening history of timber production. Of course, land use history may alter seedbank composition (Plue et al. 2010), but other studies have noted similar response of conservative species with savanna restoration on the Cumberland Plateau (Vander Yacht et al. 2020; Littlefield et al. 2025) and elsewhere in the eastern US (Cohen et al. 2004; Abella et al. 2020; Huebner et al. 2023).

Areas with increased fire frequency can have greater species diversity (Glitzenstein et al. 2012), which we did not document, but we did detect an increase in species diversity with LGS fire, similar to results in tallgrass prairie (Howe 2011; Towne & Craine 2014; Roberton & Rebar 2022). Although species richness remained unchanged over 15 years in all treatments, the number of commonly occurring species (Hill-Simpson diversity index) increased by almost one species every two years in LGS treatments. This increase was not represented by any single plant group (forbs, graminoids, etc.) but rather by LGS treatments preventing dominance of warm-season grasses and maintaining a moderate woody understory that allowed proliferation of early and late summer-flowering forbs. Although low-conservatism forb coverage (e.g. *Potentilla simplex* [common cinquefoil], *Solidago rugosa* [wrinkleleaf goldenrod]) was increasing, they were not overtaking treatment areas or excluding other species.

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APPENDIX A

The figures and tables referenced in the main text of the journal article associated with Chapter 1 are shown in this appendix.

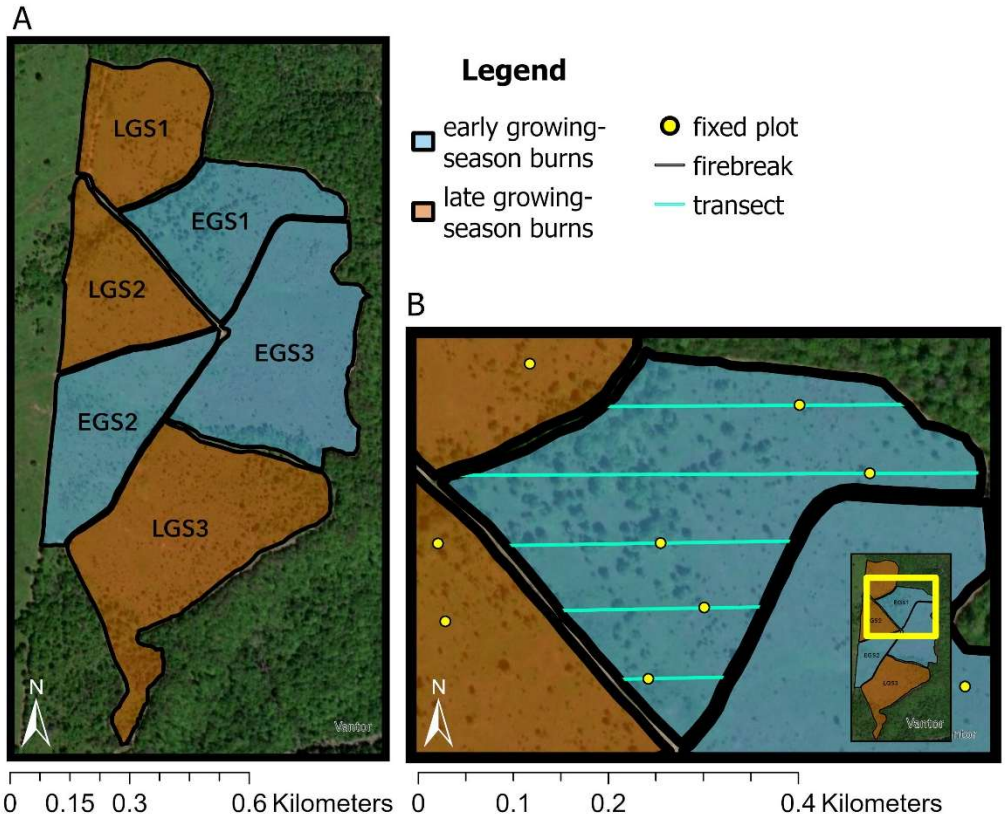


Figure 1. (A) Map of the Bridgestone-Firestone Demonstration Area treatment units. (B) Map of EGS1 treatment with sampling plots and understory transects. Fire treatments were conducted from 2011–2025.

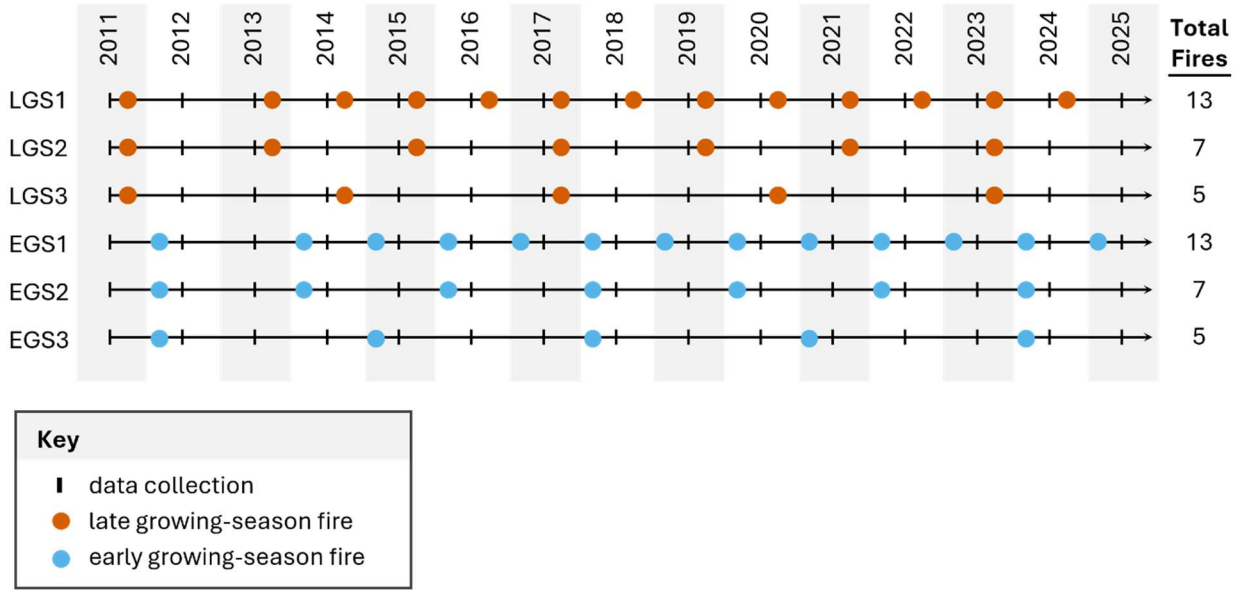


Figure 2. Timeline of data collection and fire implementation for early and late growing season fire treatments on a 1-, 2-, and 3- year fire return interval in a developing oak-pine savanna on the Cumberland Plateau in Tennessee (2011–2025).

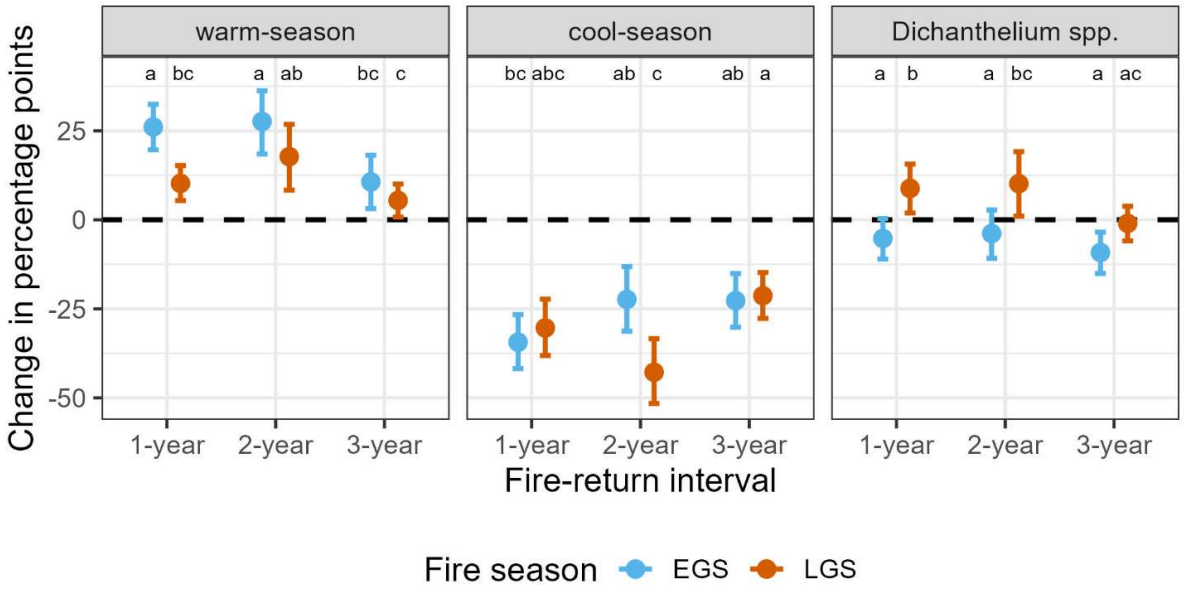


Figure 3. Model predicted change in percentage points (ΔPC) for understory cover over 15 years (2011–2025) for warm-season grasses, cool-season grasses, and *Dichanthelium* spp. when burning in the early and late growing season on a 1-, 2-, and 3- year fire return interval in a developing oak-pine savanna on the Cumberland Plateau in Tennessee. Error bars indicate the 95% confidence interval. Treatments that do not share a letter have different changes in percentage points ($p<0.05$).

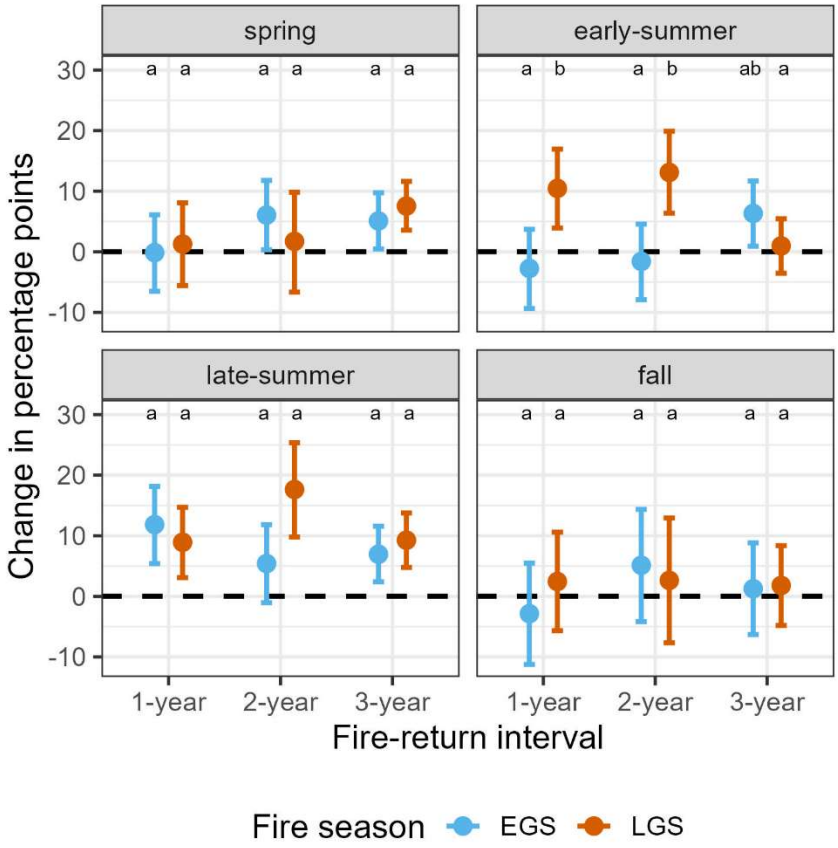


Figure 4. Model predicted change in percentage points for understory cover over 15 years (2011–2025) for perennials in four flowering-periods when burning in the early and late growing season on a 1-, 2-, and 3- year fire return interval in a developing oak-pine savanna on the Cumberland Plateau in Tennessee. Error bars indicate the 95% confidence interval. Treatments that do not share a letter have different changes in percentage points ($p<0.05$).

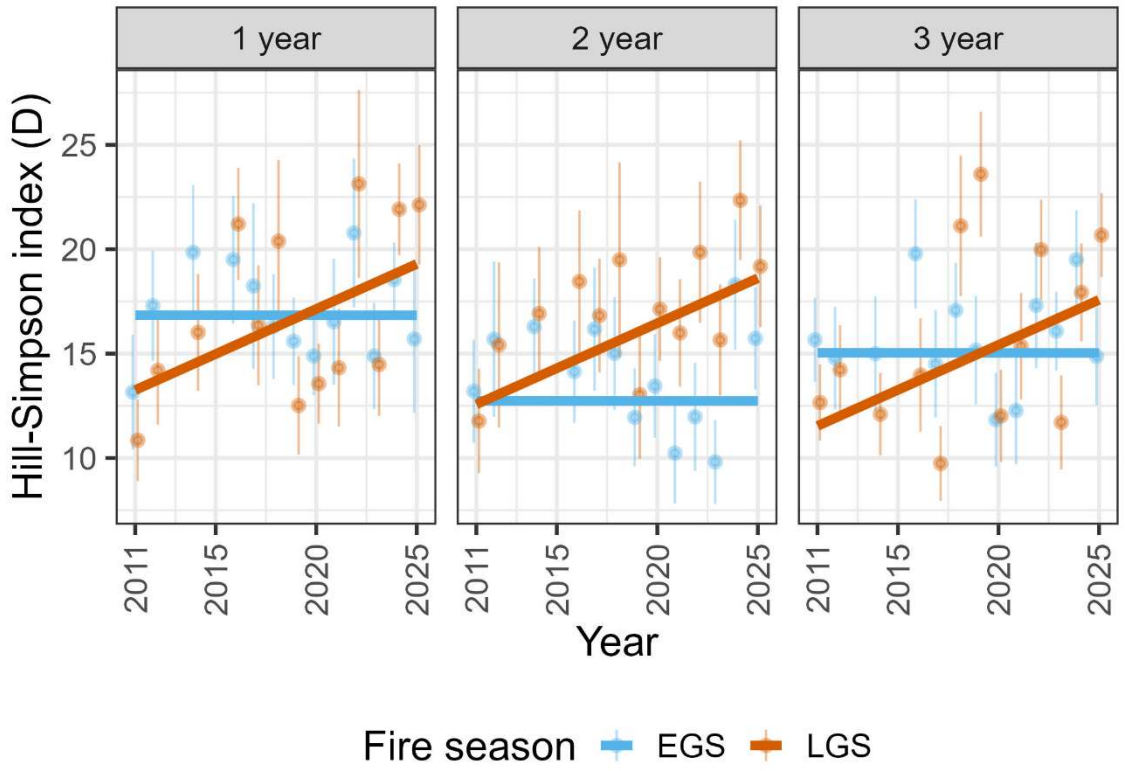


Figure 5. Hill-Shannon diversity index (D) and 95% confidence intervals over 15 years (2011–2025) of burning in the early and late growing season on a 1-, 2-, and 3- year fire return interval in a developing oak-pine savanna on the Cumberland Plateau in Tennessee. The solid lines are the model fit for change in D over time when including an interaction term for fire season and year.

Table 1. Percent of all understory sampling points containing at least one observation of each vegetation group used during analysis. Data was collected annually for 15 years (2011–2025) in a developing oak-pine savanna on the Cumberland Plateau in Tennessee.

Vegetation group	Definition	Percent of understory sampling points
Grasses		
Cool-season	Flower April–July	49%
Warm-season	Flower August–November	20%
Dichanthelium spp.	*Dichanthelium* spp.	15%
Forbs		
Spring-flowering perennials	Peak flower April–mid-June	15%
Early-summer flowering perennials	Peak flower mid-June–mid-July	17%
Late-summer flowering perennials	Peak flower mid-July–mid-August	15%
Fall-flowering perennials	Peak flower mid-August–November	49%
HH/HC	High heliophily, high conservatism	8%
HH/MC	High heliophily, medium conservatism	56%
HH/LC	High heliophily, low conservatism	11%
MH/MC	Medium heliophily, medium conservatism	13%
MH/LC	Medium heliophily, medium conservatism	6%
Woody and semi-woody plants		
Woody plants	Shrubs and understory trees	41%
Rubus spp.	*Rubus* spp.	15%
Winged sumac	Rhus copallinum	16%
Pyrophillic trees	Understory trees adapted to fire	15%
Pyrophobic trees	Understory trees not adapted to fire	4%

APPENDIX B

The figures, tables, and supplements referenced in the supporting information of the journal article associated with Chapter 1 are given in this appendix.

Table 2. Vegetation class, heliophily and conservatism scores, life cycle, and flowering group for all understory species found from 2011–2025 in a developing oak-pine savanna on the Cumberland Plateau in Tennessee.

Scientific name	Common name	Vegetation class	Heliophily	C-value	Life cycle	Flowering group
Acer rubrum	red maple	woody	med	med	perennial	spring
Achillea gracilis	common yarrow	forb	high	med	perennial	summer
Agalinis tenuifolia	slender gerardia	forb	high	med	annual	fall
Ageratina aromatica	white snakeroot	forb	high	med	perennial	fall
Ailanthus altissima	tree of heaven	woody	med	low	perennial	summer
Alnus serrulata	hazel alder	woody	med	med	perennial	spring
Ambrosia artemisiifolia	common ragweed	forb	high	low	annual	fall
Amelanchier spp. (arborea, laevis, canadensis)	serviceberry spp.	woody	N/A	med	perennial	spring
Amphicarpaea bracteata	hog peanut	forb	med	med	perennial	fall
Andropogon gerardii	big bluestem	graminoid	high	med	perennial	warm-season
Andropogon virginicus	broomsedge	graminoid	high	low	perennial	warm-season

Table 2 continued

Scientific name	Common name	Vegetation class	Heliophily	C-value	Life cycle	Flowering group
Andropogon spp. (gyrans, ternarius)	Elliot's bluestem, bushy bluestem	graminoid	high	med	perennial	warm-season
Angelica venenosa	hairy angelica	forb	high	high	perennial	summer
Antennaria spp. (plentaginifolia, parlinii)	plantain leaf pussytoes, Parlin's pussytoes	forb	med	med	perennial	spring
Apocynum cannabinum	hemp dogbane	forb	high	low	perennial	summer
Aralia spinosa	devil's walkingstick	woody	med	med	perennial	late-summer
Aronia melanocarpa	black chokeberry	woody	high	high	perennial	spring
Asclepias amplexicaulis	clasping milkweed	forb	high	med	perennial	summer
Aureolaria flava	smooth yellow false foxglove	forb	med	high	perennial	fall
Aureolaria pectinata	combleaf yellow false foxglove	forb	high	high	annual	fall
Aureolaria spp. (pectinata, flava, virginica)	yellow false foxglove spp.	forb	med	high	perennial	fall
Baptisia tinctoria	eastern wild indigo	forb	high	med	perennial	summer
Bidens spp.	beggartick spp.	forb	high	low	annual	fall
Calystegia catesbeiana	Catesby's false bindweed	forb	high	high	perennial	spring
Carex hirsutella	hairy-leaved sedge	graminoid	high	med	perennial	cool-season

Table 2 continued

Scientific name	Common name	Vegetation class	Heliophily	C-value	Life cycle	Flowering group
Carya glabra	pignut hickory	woody	med	med	perennial	spring
Carya ovata	shagbark hickory	woody	med	med	perennial	spring
Carya spp. (glabra, ovata, tomentosa)	hickory spp.	woody	med	med	perennial	spring
Carya tomentosa	mockernut hickory	woody	med	med	perennial	spring
Ceanothus americanus	New Jersey tea	woody	high	high	perennial	summer
Cercis canadensis	eastern redbud	woody	med	med	perennial	spring
Chamaecrista fasciculata	showy partridge pea	forb	high	low	annual	fall
Chamaecrista nictitans	sensitive partridge pea	forb	high	low	annual	fall
Chasmanthium laxum	spike uniola	graminoid	med	med	perennial	cool-season
Chrysopsis mariana	Maryland goldenaster	forb	high	med	biennial	fall
Cirsium spp. (discolor, carolinianum)	field thistle, Carolina thistle	forb	high	low/high	perennial	spring/fall
Clitoria mariana	butterfly pea	forb	med	med	perennial	late-summer
Coreopsis major	greater coreopsis	forb	med	med	perennial	summer
Coreopsis tripteris	tall coreopsis	forb	high	med	perennial	fall
Cornus amomum	silky dogwood	woody	med	med	perennial	summer
Cornus florida	flowering dogwood	woody	med	med	perennial	spring
Crataegus macrosperma	bigfruit hawthorn	woody	high	med	perennial	spring

Table 2 continued

Scientific name	Common name	Vegetation class	Heliophily	C-value	Life cycle	Flowering group
Croton capitatus	woolly croton	forb	high	low	annual	fall
Croton willdenowii	elliptical rushfoil	forb	high	high	annual	late-summer
Cyperus spp. (echinatus, retrofractus)	nut sedge spp.	graminoid	high	med	perennial	cool-season
Danthonia sericea	fuzzy poverty grass	graminoid	high	med	perennial	cool-season
Desmodium laevigatum	smooth ticktrefoil	forb	high	med	perennial	fall
Desmodium marilandicum	Maryland ticktrefoil	forb	high	med	perennial	fall
Desmodium obtusum	stiff ticktrefoil	forb	high	med	perennial	fall
Desmodium rotundifolium	round-leaf ticktrefoil	forb	high	med	perennial	fall
Desmodium spp.(ciliari, marilandicum, natalii, obtusum, laevigatum, paniculatum)	ticktrefoil spp.	forb	high	med/high	perennial	fall
Dichanthelium aciculare	needleleaf rosette grass	graminoid	high	med	perennial	spring and summer
Dichanthelium clandestinum	deer tongue	graminoid	med	med	perennial	spring and summer
Dichanthelium laxiflorum	openflower rosette grass	graminoid	med	med	perennial	spring and summer

Table 2 continued

Scientific name	Common name	Vegetation class	Heliophily	C-value	Life cycle	Flowering group
Dichanthelium polyanthes	small-fruited witchgrass	graminoid	high	med	perennial	spring and summer
Dichanthelium spp.	rosette grass spp.	graminoid	med/high	med	perennial	spring and summer
Diodia virginiana	Virginia buttonweed	forb	high	low	perennial	late-summer
Diospyros virginiana	common persimmon	woody	med	low	perennial	spring
Doellingeria umbellata	flat-topped white aster	forb	high	med	perennial	fall
Elaeagnus umbellata	autumn olive	woody	med	low	perennial	spring
Eleocharis tenuis	slender spikesedge	graminoid	high	med	perennial	warm-season
Elephantopus carolinianus	Carolina elephants foot	forb	med	low	perennial	fall
Elephantopus tomentosus	common elephants foot	forb	med	low	perennial	fall
Elymus glabriflorus	southeastern wild rye	graminoid	med	med	perennial	cool-season
Erechtites hieraciifolius	American burnweed	forb	med	low	annual	fall
Erigeron canadensis	horseweed	forb	high	low	annual	fall
Erigeron strigosus	prairie fleabane	forb	high	low	perennial	summer
Euonymus americanus	strawberry bush	woody	low	med	perennial	spring
Eupatorium hyssopifolium	hyssop-leaf thoroughwort	forb	high	med	perennial	fall
Eupatorium perfoliatum	common boneset	forb	high	med	perennial	fall
Eupatorium pilosum	rough boneset	forb	high	med	perennial	fall

Table 2 continued

Scientific name	Common name	Vegetation class	Heliophily	C-value	Life cycle	Flowering group
Eupatorium rotundifolium	roundleaf thoroughwort	forb	high	med	perennial	late-summer
Eupatorium serotinum	late boneset	forb	high	low	perennial	fall
Eupatorium spp.	boneset spp.	forb	high	med/high	perennial	fall
Euphorbia corollata	flowering spurge	forb	high	med	perennial	late-summer
Eutrochium spp. (fistulosum, purpureum)	hollow joepye weed, purple joepye weed	forb	med/high	med	perennial	fall
Fagus grandifolia	American beech	woody	low	med	perennial	spring
Fragaria virginiana	wild strawberry	forb	high	low	perennial	spring
Frangula caroliniana	Carolina buckthorn	woody	med	med	perennial	spring
Fraxinus americana	green ash	woody	med	med	perennial	spring
Galium pilosum	hairy bedstraw	forb	med	med	perennial	summer
Gamochaeta spp. (purpurea, argyrinea)	purple everlasting, silvery cudweed	forb	high	low	biennial	spring
Geum canadense	white avens	forb	med	med	perennial	summer
Helianthus angustifolius	swamp sunflower	forb	high	med	perennial	fall
Helianthus atrorubens	purpledisk sunflower	forb	high	med	perennial	fall
Helianthus hirsutus	rough-haired sunflower	forb	high	med	perennial	late-summer
Helianthus microcephalus	small woodland sunflower	forb	high	med	perennial	fall

Table 2 continued

Scientific name	Common name	Vegetation class	Heliophily	C-value	Life cycle	Flowering group
Helianthus spp. (angustifolius, atrorubens, hirsutus, microcephalus)	sunflower spp.	forb	high	med	perennial	late-summer/fall
Hexasepalum teres	poorjoe	forb	high	low	perennial	fall
Hieracium gronovii	beaked hawkweed	forb	high	med	perennial	fall
Houstonia spp. (caerulea, longifolia)	azure bluet, long-leaf bluet	forb	med/high	med	perennial	spring/ late-spring
Hylodesmum nudiflorum	naked-flowered tick trefoil	forb	med	med	perennial	late-summer
Hypericum gentianoides	orangegrass	forb	high	med	annual	late-summer
Hypericum hypericoides	St. Andrew's cross	woody	med	med	perennial	late-summer
Hypericum punctatum	spotted St. John's-wort	forb	med	low	perennial	summer
Hypericum virgatum	coppery St. John's-wort	forb	high	high	perennial	late-summer
Ilex opaca	American holly	woody	med	med	perennial	spring
Ipomoea pandurata	bigroot morningglory	forb	high	low	perennial	late-summer
Iris verna	dwarf violet iris	forb	high	med	perennial	spring
Kalmia latifolia	mountain laurel	woody	med	med	perennial	late-spring
Kummerowia striata	Japanese clover	forb	high	low	annual	fall
Lactuca spp. (hirsuta, canadensis)	tall hairy lettuce, Canada lettuce	forb	high	low/med	biennial	summer

Table 2 continued

Scientific name	Common name	Vegetation class	Heliophily	C-value	Life cycle	Flowering group
Lechea spp. (racemulosa, minor, mucronate, tenuifolia)	pinweed spp.	forb	high	high	perennial	summer
Lespedeza bicolor	bicolor lespedeza	forb	high	low	perennial	fall
Lespedeza capitata	round-headed bush clover	forb	high	med	perennial	fall
Lespedeza cuneata	sericea lespedeza	forb	high	low	perennial	fall
Lespedeza hirta	hairy lespedeza	forb	high	med	perennial	fall
Lespedeza spp. (procumbens, repens)	creeping lespedeza, trailing lespedeza	forb	high	med	perennial	fall
Lespedeza violacea	violet lespedeza	forb	high	med	perennial	fall
Lespedeza virginica	slender lespedeza	forb	high	med	perennial	fall
Leucanthemum vulgare	oxeye daisy	forb	high	low	perennial	summer
Liatris microcephala	small-headed blazing star	forb	high	high	perennial	fall
Liatris spicata	dense blazing star	forb	high	high	perennial	late-summer
Liatris spp. (microcephala, spicata, squarrosa)	blazing star spp.	forb	high	high	perennial	late-summer/ fall
Ligusticum sp. nov.	N/A	forb	high	high	perennial	summer
Lilium philadelphicum	prairie lily	forb	high	high	perennial	summer

Table 2 continued

Scientific name	Common name	Vegetation class	Heliophily	C-value	Life cycle	Flowering group
Linum spp. (curtissii, virginianum)	woodland yellow flax, Texas yellow flax	forb	high	high	perennial	summer
Liquidambar styraciflua	sweetgum	woody	med	low	perennial	spring
Liriodendron tulipifera	yellow poplar	woody	med	med	perennial	spring
Lobelia inflata	Indian tobacoo	forb	med	low	annual	late-summer
Lobelia puberula	downy lobelia	forb	high	med	perennial	fall
Lobelia spicata	pale spiked lobelia	forb	high	med	perennial	summer
Lobelia spp. (spicata, puberula, inflata)	Lobelia spp.	forb	high	high	perennial	summer/ late-summer/fall
Lolium arundinaceum	tall fescue	graminoid	high	low	perennial	cool-season
Lonicera japonica	Japanese honeysuckle	semi-woody	med	low	perennial	late-spring
Ludwigia alternifolia	rattlebox	forb	high	med	perennial	late-summer
Lygodium palmatum	Japanese climbing fern	Other	med	med	perennial	N/A
Lysimachia lanceolata	lance-leaf loosestrife	forb	high	med	perennial	summer
Lysimachia quadrifolia	whorled yellow-loosestrife	forb	med	med	perennial	summer
Magnolia acuminata	cucumber magnolia	woody	med	med	perennial	spring
Maianthemum racemosum	false Solomon's seal	forb	med	med	perennial	spring

Table 2 continued

Scientific name	Common name	Vegetation class	Heliophily	C-value	Life cycle	Flowering group
Malus coronaria	sweet crabapple	woody	high	med	perennial	spring
Microstegium vimineum	Japanese stiltgrass	graminoid	med	low	perennial	warm-season
Mimosa microphylla	eastern sensitive-briar	forb	high	high	perennial	late-spring
Monarda fistulosa	wild bergamont	forb	med	med	perennial	summer
Morus rubra	red mulberry	woody	med	med	perennial	spring
Muhlenbergia schreberi	nimblewill	graminoid	med	low	perennial	warm-season
Nyssa sylvatica	blackgum	woody	med	med	perennial	spring
Oenothera fruticosa	narrowleaf evening primrose	forb	high	med	perennial	late-spring
Orbexilum pedunculatum	Sampson's snakeroot	forb	high	high	perennial	spring
Ostrya virginiana	eastern hophornbeam	woody	med	med	perennial	spring
Oxalis dillenii	slender yellow woodsorrel	forb	med	low	perennial	spring
Oxydendrum arboreum	sourwood	woody	med	med	perennial	summer
Oxypolis rigidior	cowbane	forb	med	med	perennial	fall
Packera anonyma	Small's ragwort	forb	high	med	perennial	spring
Panicum anceps	beaked panicgrass	graminoid	high	med	perennial	warm-season
Panicum virgatum	switchgrass	graminoid	high	med	perennial	warm-season
Parthenium integrifolium	wild quinine	forb	high	high	perennial	summer

Table 2 continued

Scientific name	Common name	Vegetation class	Heliophily	C-value	Life cycle	Flowering group
Parthenocissus quinquefolia	Virginia creeper	semi-woody	med	low	perennial	summer
Paspalum setaceum	thin paspalum	graminoid	high	med	perennial	warm-season
Passiflora lutea	yellow passionflower	forb	med	med	perennial	summer
Persicaria pensylvanica	Pennsylvania smartweed	forb	high	low	annual	fall
Phlox amoena	hairy phlox	forb	high	high	perennial	spring
Phytolacca americana	pokeweed	forb	high	low	perennial	summer
Pinus echinata	shortleaf pine	woody	high	med	perennial	N/A
Pinus taeda	loblolly pine	woody	med	low	perennial	N/A
Pinus virginiana	Virginia pine	woody	high	low	perennial	N/A
Piptochaetium avenaceum	black seeded needlegrass	graminoid	med	med	perennial	cool-season
Pityopsis nervosa	broad-leaved goldenaster	forb	high	high	perennial	fall
Plantago lanceolata	narrow leaf plantain	forb	high	low	perennial	late-spring
Platanthera ciliaris	orange fringed orchid	forb	high	med	perennial	late-summer
Platanus occidentalis	American sycamore	woody	med	med	perennial	spring
Polygala curtissii	Curtiss' milkwort	forb	high	med	annual	late-summer
Polygala sanguinea	purple milkwort	forb	high	med	annual	late-summer
Polygala verticillata	whorled milkwort	forb	high	med	annual	late-summer

Table 2 continued

Scientific name	Common name	Vegetation class	Heliophily	C-value	Life cycle	Flowering group
Maianthemum racemosum/ Polygonatum spp. (biflorum, pubescens)	Solomon's seal spp.	forb	med	med/high	perennial	spring
Polygonum cespitosum	oriental lady's thumb	forb	high	low	perennial	summer
Potentilla canadensis	dwarf cinquefoil	forb	med	med	perennial	spring
Potentilla simplex	common cinquefoil	forb	med	low	perennial	late-spring
Prunus serotina	black cherry	woody	med	low	perennial	spring
Pseudognaphalium obtusifolium	sweet everlasting	forb	high	med	annual	fall
Pycnanthemum loomisii	Loomis' mountain mint	forb	high	med	perennial	summer
Pycnanthemum muticum	clustered mountain mint	forb	high	high	perennial	late-summer
Pycnanthemum spp. (loomisii, muticum, tenuifolium)	mountain mint spp.	forb	high	med/high	perennial	summer
Pycnanthemum tenuifolium	narrowleaf mountain mint	forb	high	med	perennial	summer
Quercus alba	white oak	woody	med	med	perennial	spring
Quercus coccinea	scarlet oak	woody	med	med	perennial	spring
Quercus falcata	southern red oak	woody	med	med	perennial	spring
Quercus montana	chestnut oak	woody	med	med	perennial	spring

Table 2 continued

Scientific name	Common name	Vegetation class	Heliophily	C-value	Life cycle	Flowering group
Quercus stellata	post oak	woody	high	med	perennial	spring
Quercus velutina	black oak	woody	med	med	perennial	spring
Rhexia mariana	Maryland meadowbeauty	forb	high	med	perennial	summer
Rhus copallinum	winged sumac	woody	high	low	perennial	late-summer
Rhus glabra	smooth sumac	woody	high	low	perennial	summer
Rhynchosia tomentosa	twining snoutbean	forb	high	med	perennial	summer
Robinia pseudoacacia	black locust	woody	high	low	perennial	spring
Rosa carolina	Carolina rose	woody	high	med	perennial	summer
Rosa multiflora	multiflora rose	woody	med	low	perennial	late-spring
Rubus flagellaris	northern dewberry	semi-woody	high	med	perennial	spring
Rubus occidentalis	black raspberry	semi-woody	med	med	perennial	spring
Rubus spp. (flagellaris, steelei, argutus, allegheniensis)	Rubus spp.	semi-woody	high	med	perennial	spring
Rubus trivialis	southern dewberry	semi-woody	high	med	perennial	spring
Rudbeckia hirta	black-eyed Susan	forb	high	low	perennial	summer

Table 2 continued

Scientific name	Common name	Vegetation class	Heliophily	C-value	Life cycle	Flowering group
Rudbeckia spp. (hirta, fulgida)	black-eyed Susan, orange coneflower	forb	high	med	perennial	summer/ late-summer
Saccharum alopecuroides	silver plumegrass	graminoid	high	med	perennial	warm-season
Sambucus canadensis	American black elderberry	woody	med	med	perennial	summer
Sassafras albidum	sassafras	woody	med	low	perennial	spring
Schizachyrium scoparium	little bluestem	graminoid	high	med	perennial	warm-season
Scutellaria incana var. punctata	downy skullcap	forb	high	high	perennial	summer
Senna marilandica	Maryland senna	forb	high	med	perennial	fall
Smilax bona-nox	saw greenbriar	semi-woody	med	low	perennial	spring
Smilax glauca	cat greenbriar	semi-woody	med	med	perennial	spring
Smilax rotundifolia	roundleaf greenbriar	semi-woody	med	med	perennial	spring
Smilax smallii	lanceleaf greenbriar	semi-woody	med	med	perennial	spring
Solanum carolinense	Carolina horsenettle	forb	high	low	perennial	summer
Solanum emulans	Eastern black nightshade	forb	high	med	annual	late-summer

Table 2 continued

Scientific name	Common name	Vegetation class	Heliophily	C-value	Life cycle	Flowering group
Solidago altissima	tall goldenrod	forb	high	low	perennial	fall
Solidago gigantea	giant goldenrod	forb	high	low	perennial	fall
Solidago hispida	hairy goldenrod	forb	med	med	perennial	fall
Solidago juncea	early flowering goldenrod	forb	high	med	perennial	late-summer
Solidago nemoralis	field goldenrod	forb	high	low	perennial	fall
Solidago odora	fragrant goldenrod	forb	high	med	perennial	fall
Solidago rugosa	wrinkleleaf goldenrod	forb	high	low	perennial	fall
Solidago speciosa	showy goldenrod	forb	high	med	perennial	fall
Solidago spp.	goldenrod spp.	forb	high	med/high	perennial	fall
Spiranthes tuberosa	little lady's tresses	forb	med	med	perennial	fall
Stellaria media	common chickweed	forb	med	low	perennial	spring
Symphyotrichum dumosum	rice button aster	forb	high	med	perennial	fall
Symphyotrichum patens	late purple aster	forb	high	med	perennial	fall
Tephrosia virginiana	goat's rue	forb	high	med	perennial	late-spring
Toxicodendron radicans	poison ivy	semi-woody	med	low	perennial	summer
Ulmus alata	winged elm	woody	med	low	perennial	spring
Vaccinium arboreum	sparkleberry	woody	med	med	perennial	spring
Vaccinium corymbosum	highbush blueberry	woody	med	med	perennial	spring

Table 2 continued

Scientific name	Common name	Vegetation class	Heliophily	C-value	Life cycle	Flowering group
Vaccinium pallidum	hillside blueberry	woody	med	med	perennial	spring
Vaccinium spp. (arboreum, corymbosum, pallidum, stamineum)	blueberry spp.	woody	med	med	perennial	spring
Vaccinium stamineum	deerberry	woody	med	med	perennial	spring
Verbena urticifolia	white vervain	forb	med	low	perennial	summer
Verbesina alternifolia	wingstem	forb	high	med	perennial	fall
Viburnum acerifolium	mapleleaf viburnum	woody	low	med	perennial	late-spring
Viburnum alabamense	Alabama arrowwood	woody	med	high	perennial	spring
Viola lanceolata	lanceleaf violet	forb	high	med	perennial	spring
Viola pedata	bird's foot violet	forb	high	med	perennial	spring
Viola primulifolia	primrose-leaf violet	forb	med	med	perennial	spring
Viola sagittata	arrowleaf violet	forb	med	med	perennial	spring
Viola sororia	wood violet	forb	med	low	perennial	spring
Viola spp.	violet spp.	forb	med/high	med	perennial	spring
Vitis aestivalis	summer grape	semi-woody	med	med	perennial	late-spring
Vitis spp. (rotundifolia, aestivalis)	muscadine, summer grape	semi-woody	med	med	perennial	late-spring

Table 3. Fire affinity for all woody midstory and understory species documented from 2011–2025 in a developing oak-pine savanna on the Cumberland Plateau in Tennessee. We excluded neutral, neutral/pyrophobic, and neutral/pyrophilic species from our analysis because there were very few observations of these species.

Scientific name	Common name	Vegetation class
Acer rubrum	red maple	pyrophobic
Ailanthus altissima	tree of heaven	pyrophobic
Alnus serrulata	hazel alder	neutral
Amelanchier spp. (arborea, laevis, canadensis)	serviceberry spp.	pyrophilic
Aralia spinosa	devil's walkingstick	neutral
Aronia melanocarpa	black chokeberry	pyrophilic
Asimina triloba	pawpaw	pyrophobic
Carya glabra	pignut hickory	pyrophilic
Carya ovata	shagbark hickory	pyrophobic
Carya spp.	hickory spp.	pyrophilic
Carya tomentosa	mockernut hickory	pyrophilic
Ceanothus americanus	New Jersey tea	pyrophilic
Celtis tenuifolia	dwarf hackberry	neutral
Cercis canadensis	eastern redbud	neutral
Cornus amomum	silky dogwood	neutral

Table 3 continued

Scientific name	Common name	Vegetation class
Cornus florida	flowering dogwood	pyrophilic
Crataegus macrosperma	bigfruit hawthorn	neutral/pyrophobic
Diospyros virginiana	common persimmon	neutral
Elaeagnus umbellata	autumn olive	neutral
Euonymus americanus	strawberry bush	pyrophobic
Fagus grandifolia	American beech	pyrophobic
Frangula caroliniana	Carolina buckthorn	neutral
Fraxinus americana	white ash	pyrophobic
Hypericum hypericoides	St. Andrew's cross	pyrophilic
Ilex opaca	American holly	pyrophobic
Kalmia latifolia	mountain laurel	pyrophilic
Liquidambar styraciflua	sweetgum	neutral/pyrophobic
Liriodendron tulipifera	yellow-poplar	pyrophobic
Lonicera maackii	bush honeysuckle	pyrophobic
Magnolia acuminata	cucumber magnolia	pyrophobic
Malus coronaria	sweet crabapple	neutral/pyrophobic
Morus rubra	red mulberry	pyrophobic
Nyssa sylvatica	blackgum	neutral/pyrophilic
Ostrya virginiana	eastern hophornbeam	pyrophobic
Oxydendrum arboreum	sourwood	pyrophilic

Table 3 continued

Scientific name	Common name	Vegetation class
Pinus echinata	shortleaf pine	pyrophilic
Pinus spp.	pine spp.	pyrophilic
Pinus taeda	loblolly pine	neutral/pyrophilic
Pinus virginiana	Virginia pine	pyrophilic
Platanus occidentalis	American sycamore	pyrophobic
Prunus serotina	black cherry	neutral
Quercus alba	white oak	pyrophilic
Quercus coccinea	scarlet oak	pyrophilic
Quercus falcata	southern red oak	pyrophilic
Quercus montana	chestnut oak	pyrophilic
Quercus stellata	post oak	pyrophilic
Quercus velutina	black oak	pyrophilic
Rhus copallinum	winged sumac	pyrophilic
Rhus glabra	smooth sumac	pyrophilic
Robinia pseudoacacia	black locust	neutral
Rosa carolina	Carolina rose	pyrophilic
Rosa multiflora	multiflora rose	pyrophobic
Sambucus canadensis	American black elderberry	pyrophobic
Sassafras albidum	sassafras	pyrophilic

Table 3 continued

Scientific name	Common name	Vegetation class
Ulmus alata	winged elm	pyrophobic
Vaccinium arboreum	sparkleberry	pyrophilic
Vaccinium corymbosum	highbush blueberry	pyrophilic
Vaccinium pallidum	hillside blueberry	pyrophilic
Vaccinium spp.	blueberry spp.	pyrophilic
Vaccinium stamineum	deerberry	pyrophilic
Viburnum acerifolium	mapleleaf viburnum	pyrophobic
Viburnum alabamense	Alabama arrowwood	pyrophilic

Table 4. Specifications for generalized linear models used to analyze understory and midstory vegetation response to 15 years of seasonal fire treatments (2011–2025) in a developing oak-pine savanna on the Cumberland Plateau in Tennessee.

Model description	Response variable	Random component	Link function	Systematic component	Weights
Understory percent coverage	Num. observed	Binomial	Logit	Treatment * Year	# points
Midstory stem density	ln(nSPA)	Gaussian	Identity	Treatment + (1|Year)	N/A
Midstory stem top-kill	ln(pb-SPA)	Gaussian	Identity	Treatment + (1|Year)	N/A
Fire-affinity stem density	ln(nSPA)	Gaussian	Identity	Treatment*FireAffinity + (1|Year)	N/A
Fire-affinity stem top-kill	ln(pb-SPA)	Gaussian	Identity	Treatment*FireAffinity + (1|Year)	N/A
Species richness	S	Gaussian	Identity	Treatment*Year	1/SE
Species richness	S	Gaussian	Identity	Season*Year + Treatment	1/SE
Hill-Simpson diversity	D	Gaussian	Identity	Treatment*Year	1/SE
Hill-Simpson diversity	D	Gaussian	Identity	Season*Year + Treatment	1/SE

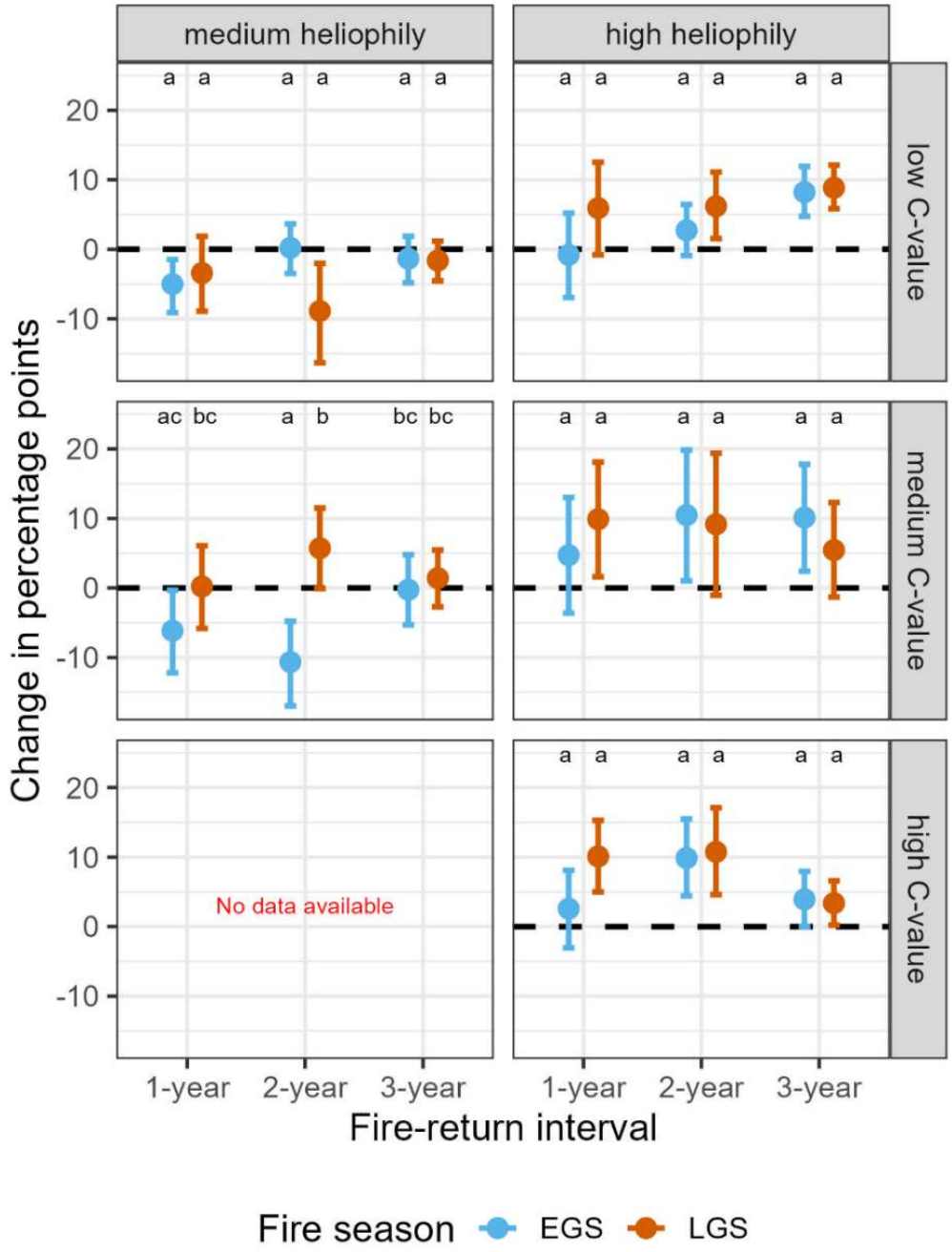


Figure 6. Model predicted change in percentage points for understory cover over 15 years (2011–2025) for forbs grouped by heliophily score and coefficient of conservatism (C-value) when burning in the early and late growing season on a 1-, 2-, and 3- year fire-return interval in a developing oak-pine savanna on the Cumberland Plateau in Tennessee. Error bars indicate the 95% confidence interval. Treatments that do not share a letter have different changes in percentage points ($p<0.05$).

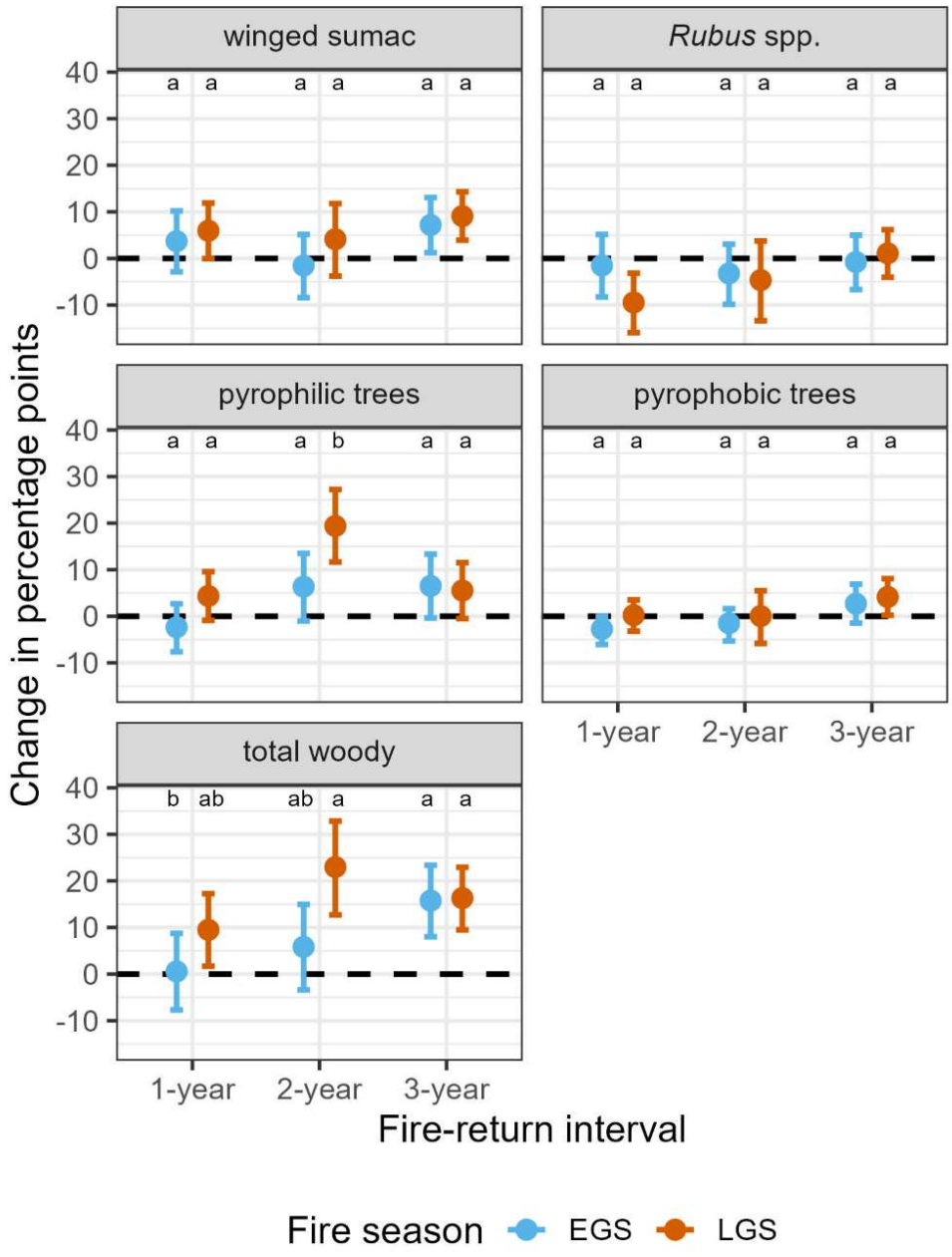


Figure 7. Model predicted change in percentage points for understory cover over 15 years (2011–2025) for woody plant groups when burning in the early and late growing season on a 1-, 2-, and 3- year fire-return interval in a developing oak-pine savanna on the Cumberland Plateau in Tennessee. Error bars indicate the 95% confidence interval. Treatments that do not share a letter have different changes in percentage points ($p<0.05$).

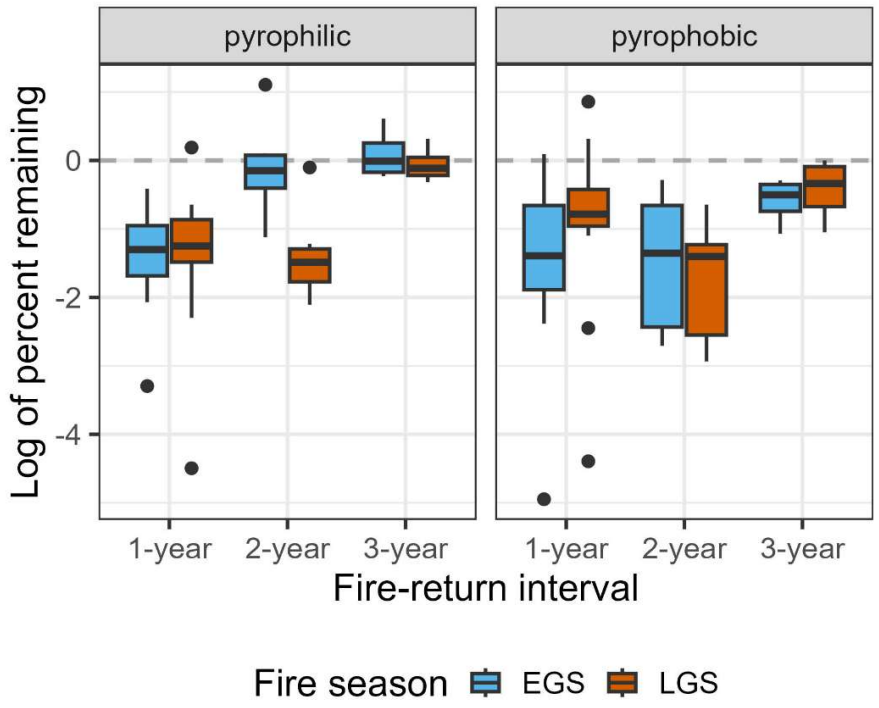


Figure 8. Percent of pre-treatment stems remaining the year before reburning for pyrophilic and pyrophobic woody species when burning for 15 years (2011–2025) in the early and late growing season on a 1-, 2-, and 3- year fire-return interval in a developing oak-pine savanna on the Cumberland Plateau in Tennessee.

Supplement 1: Spatial Autocorrelation Model

Alternative model to test the sensitivity of our understory vegetation results to spatial autocorrelation.

To investigate how including spatial autocorrelation affects the sensitivity of our results, we repeated our analysis for each understory vegetation group (Table 1) using a Bayesian model with the package *brms* (Burkner 2017). We modeled spatial autocorrelation using a Gaussian Process where transects that were closer together in space could have higher levels of correlation. Note that transects within a sampling unit often were closer to each other than to transects in other treatment units, but along treatment unit edges, transects could be closer to transects in other treatment units. This approach allowed us to partially (but not completely) account for the pseudo-replicated nature of our study.

This model was identical to the models used in the main text except i) we fit it using a Bayesian method and weakly regularizing our flat priors and ii) we included random effects for transects that were drawn from a multivariate normal distribution where the correlation among random effects was determined by a distance decay function (see below). The model is given by

$$Num.observed \sim Binomial(PC, Num.points\ on\ transect)$$

$$logit(PC) = (Year * Treatment + PostBurn) + \gamma_{transect}$$

where the variables in paratheses are the fixed effects with an associated intercept parameter α and fixed effect coefficients β. *Year* was a continuous variable, *Treatment* was a factor with 6 levels (EGS1, EGS2, EGS3, LGS1, LGS2, LGS3), and *PostBurn* was a categorical predictor variable indicating if the data for a specific year were collected the year after a burn for the 2- and 3-year treatments.

The $\gamma_{transect}$ gives the random effect of transect or plot defined as

$$\gamma_{transect} \sim MVN\left((0, \ldots, 0), \boldsymbol{K}\right)$$

$$K_{ij} = \sigma^2 \exp\left(-\frac{D_{ij}^2}{2l^2}\right)$$

where D_{ij} gives the distance between transects i and j. The parameters σ^2 and l^2 give the variance and shape parameters of the distance decay function. 'MVN' stands for Multivariate Normal. The priors we used were

$$\ell \sim InvGamma(2.422857, 0.255167)\ [when\ distance\ was\ scaled\ from\ 0\ to\ 1\ for\ ease\ of\ fitting]$$

$$\sigma \sim Half - t_3(0, 2.5)$$

$$\alpha \sim t_3(0, 2.5)\ [Intercept]$$

$$\beta \sim Flat\ prior\ on\ support\ [Fixed\ effects]$$

All models were run with 1000 warm-up iterations and 1000 samples with four chains run and convergence was assessed using $\hat{R}$ and traceplots. Overall, the results from analyzing these models were virtually identical to the model presented in the main text (see Figure 9–Figure 12) with slightly more uncertainty around the modeled effects, but not to an extent that altered our conclusions.

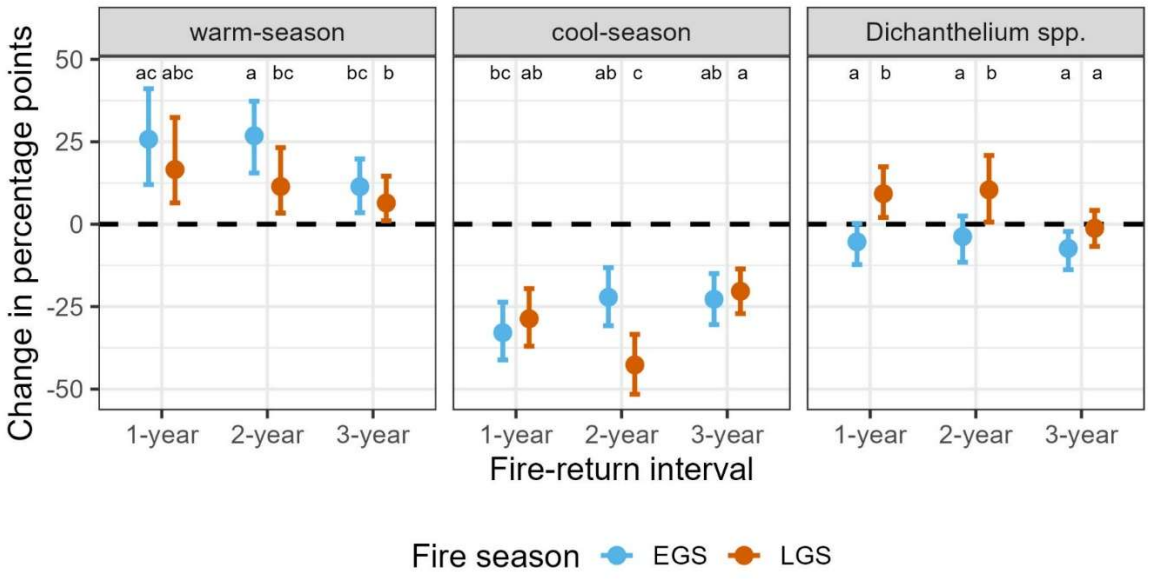


Figure 9. Spatial Autocorrelation Model predicted change in percentage points (ΔPC) for understory cover over 15 years (2011–2025) for warm-season grasses, cool-season grasses, and *Dichanthelium* spp. when burning in the early and late growing season on a 1-, 2-, and 3-year fire-return interval in a developing oak-pine savanna on the Cumberland Plateau in Tennessee. Error bars indicate the 95% confidence interval. Treatments that do not share a letter have different changes in percentage points ($p<0.05$).

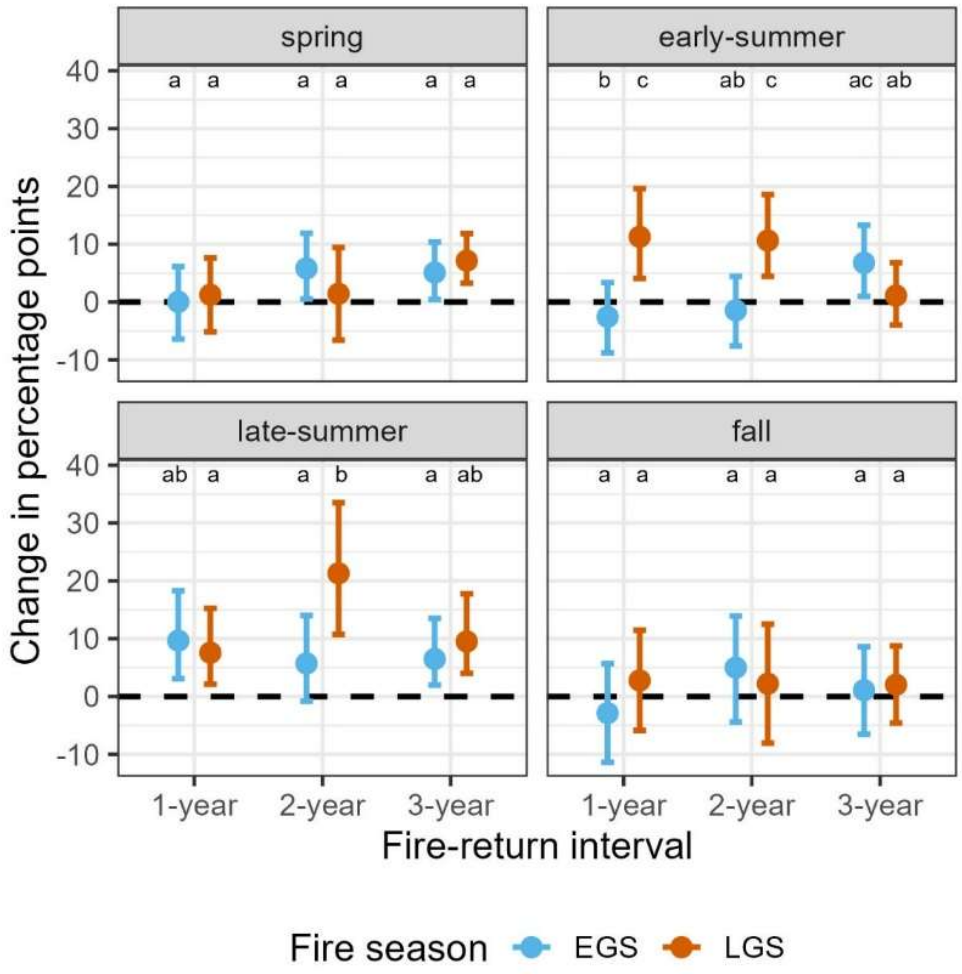


Figure 10. Spatial Autocorrelation Model predicted change in percentage points (ΔPC) for understory cover over 15 years (2011–2025) for perennials in four flowering-periods when burning in the early and late growing season on a 1-, 2-, and 3-year fire-return interval in a developing oak-pine savanna on the Cumberland Plateau in Tennessee. Error bars indicate the 95% confidence interval. Treatments that do not share a letter have different changes in percentage points ($p<0.05$).

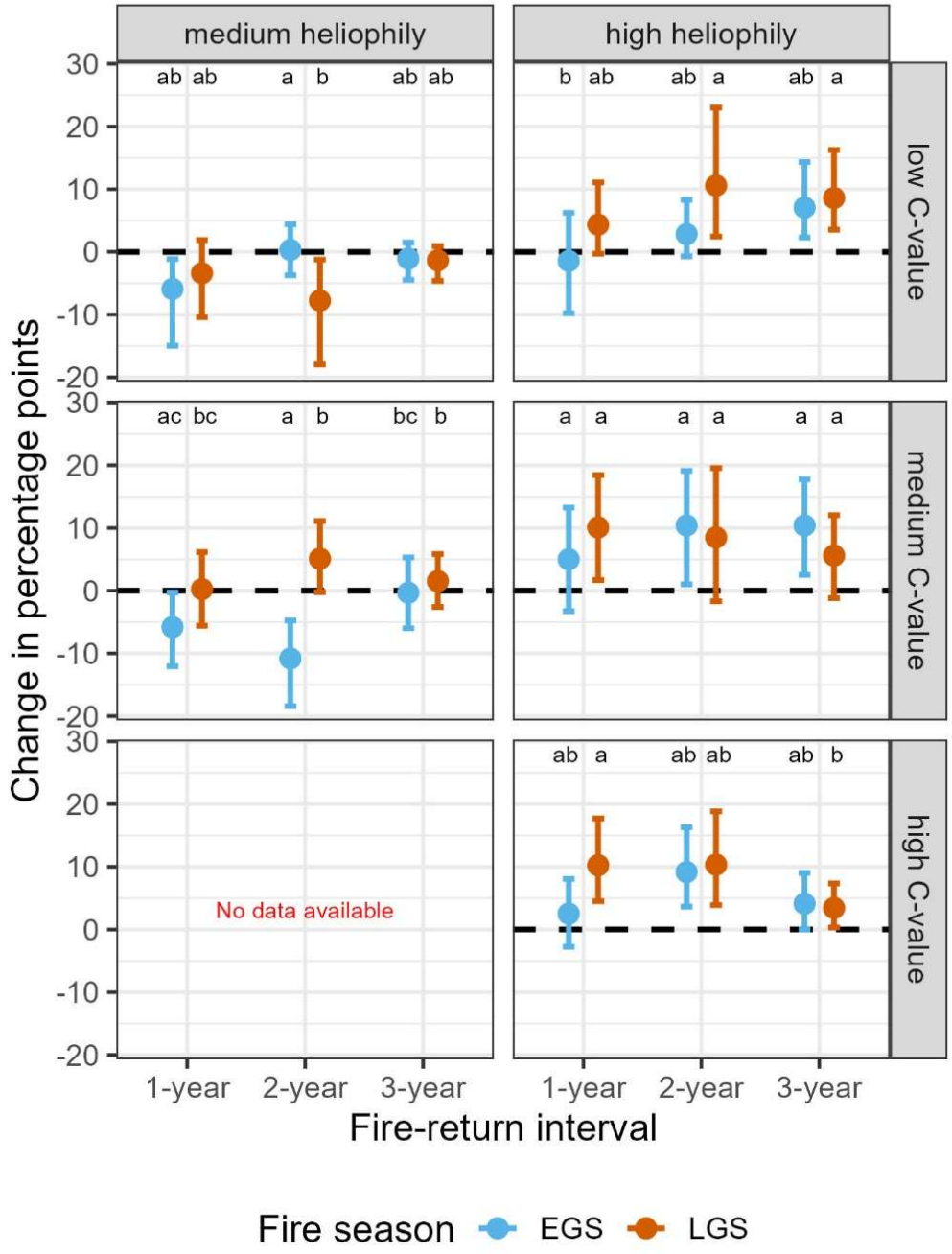


Figure 11. Spatial Autocorrelation Model predicted change in percentage points (ΔPC) for understory cover over 15 years (2011–2025) for forbs grouped by heliophily score and coefficient of conservatism (C-value) when burning in the early and late growing season on a 1-, 2-, and 3-year fire-return interval in a developing oak-pine savanna on the Cumberland Plateau in Tennessee. Error bars indicate the 95% confidence interval. Treatments that do not share a letter have different changes in percentage points ($p<0.05$).

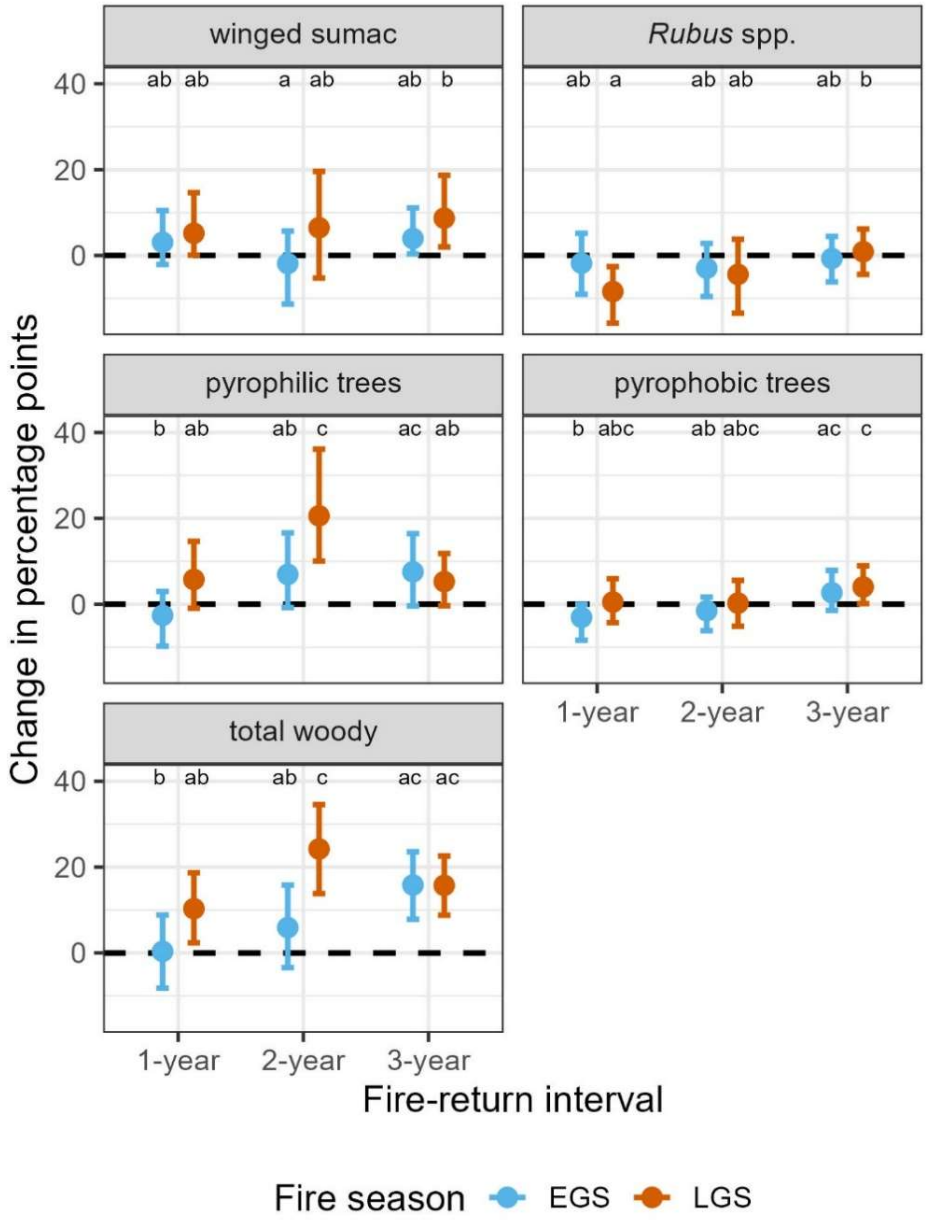


Figure 12. Spatial Autocorrelation Model predicted change in percentage points (ΔPC) for understory cover over 15 years (2011–2025) for woody plant groups when burning in the early and late growing season on a 1-, 2-, and 3-year fire-return interval in a developing oak-pine savanna on the Cumberland Plateau in Tennessee. Error bars indicate the 95% confidence interval. Treatments that do not share a letter have different changes in percentage points ($p<0.05$).

Supplement 2: Time-Since-Fire Model

Alternative model to test the sensitivity of our understory vegetation results to time-since-fire.

To investigate how including time-since-fire affects the sensitivity of our results, we repeated our analysis for each understory vegetation group (Table 1) using the model

$$Num.observed \sim Binomial(PC, Num.points\ on\ transect)$$

$$logit(PC) = Year * Treatment + PostBurn * season + 2YrsPostBurn * season$$

where *Year* was a continuous variable, *Treatment* was a factor with 6 levels (EGS1, EGS2, EGS3, LGS1, LGS2, LGS3), and *PostBurn* was a categorical predictor variable indicating if the data for a specific were was collected the year after a burn for the 2- and 3-year treatments and *2YrsPostBurn* is a categorical predictor variable indicating if the data for a specific year were collected 2 years after a burn for the 3-year treatments. The results from analyzing these models were virtually identical to the model presented in the main text (see Figure 13–Figure 16).

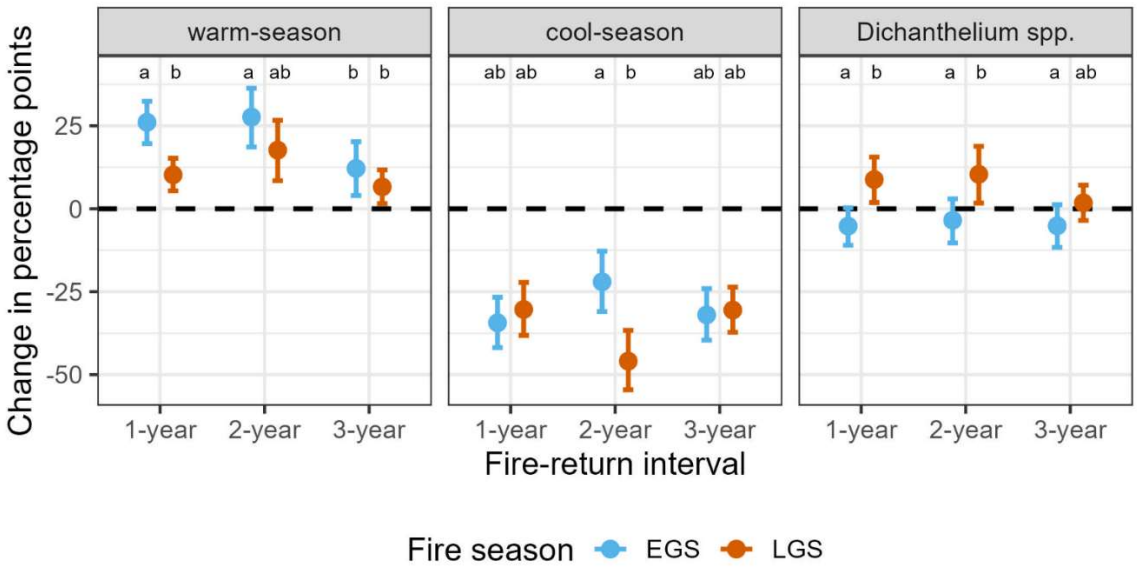


Figure 13. Time-Since-Fire Model predicted change in percentage points (ΔPC) for understory cover over 15 years (2011–2025) for warm-season grasses, cool-season grasses, and *Dichanthelium* spp. when burning in the early and late growing season on a 1-, 2-, and 3-year fire-return interval in a developing oak-pine savanna on the Cumberland Plateau in Tennessee. Error bars indicate the 95% confidence interval. Treatments that do not share a letter have different changes in percentage points ($p<0.05$).

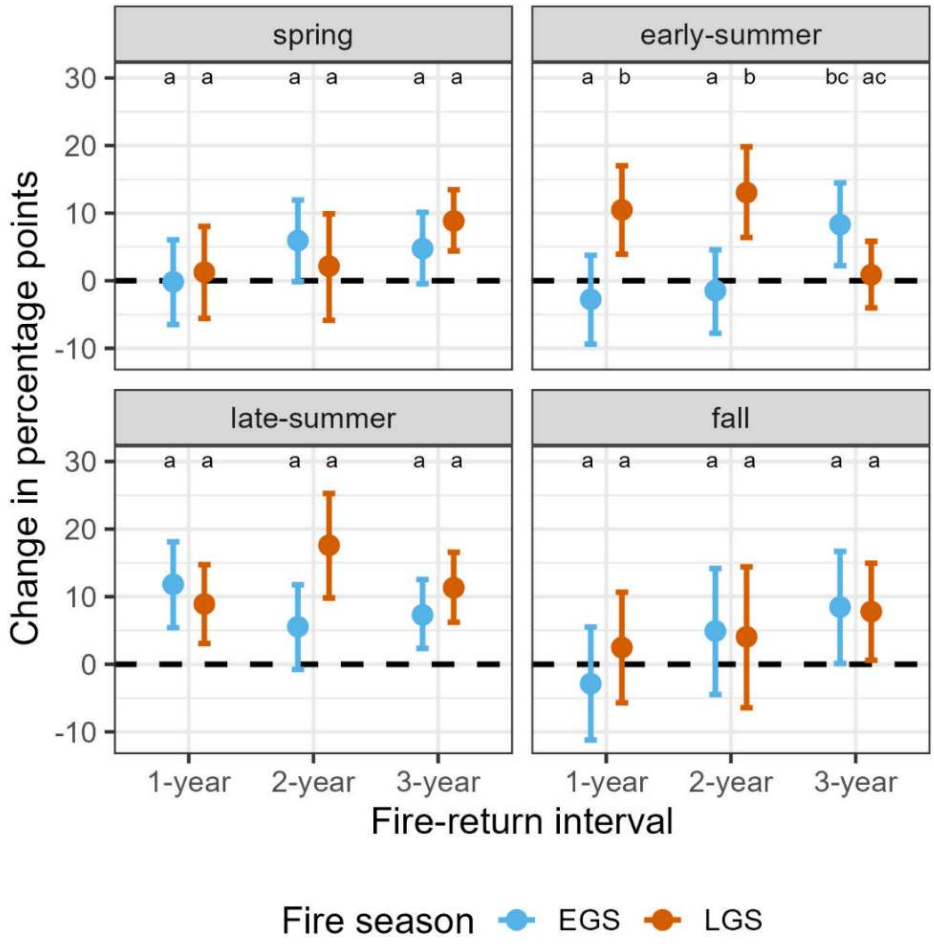


Figure 14. Time-Since-Fire Model predicted change in percentage points for understory cover over 15 years (2011–2025) for perennials in four flowering-periods when burning in the early and late growing season on a 1-, 2-, and 3-year fire-return interval in a developing oak-pine savanna on the Cumberland Plateau in Tennessee. Error bars indicate the 95% confidence interval. Treatments that do not share a letter have different changes in percentage points ($p<0.05$).

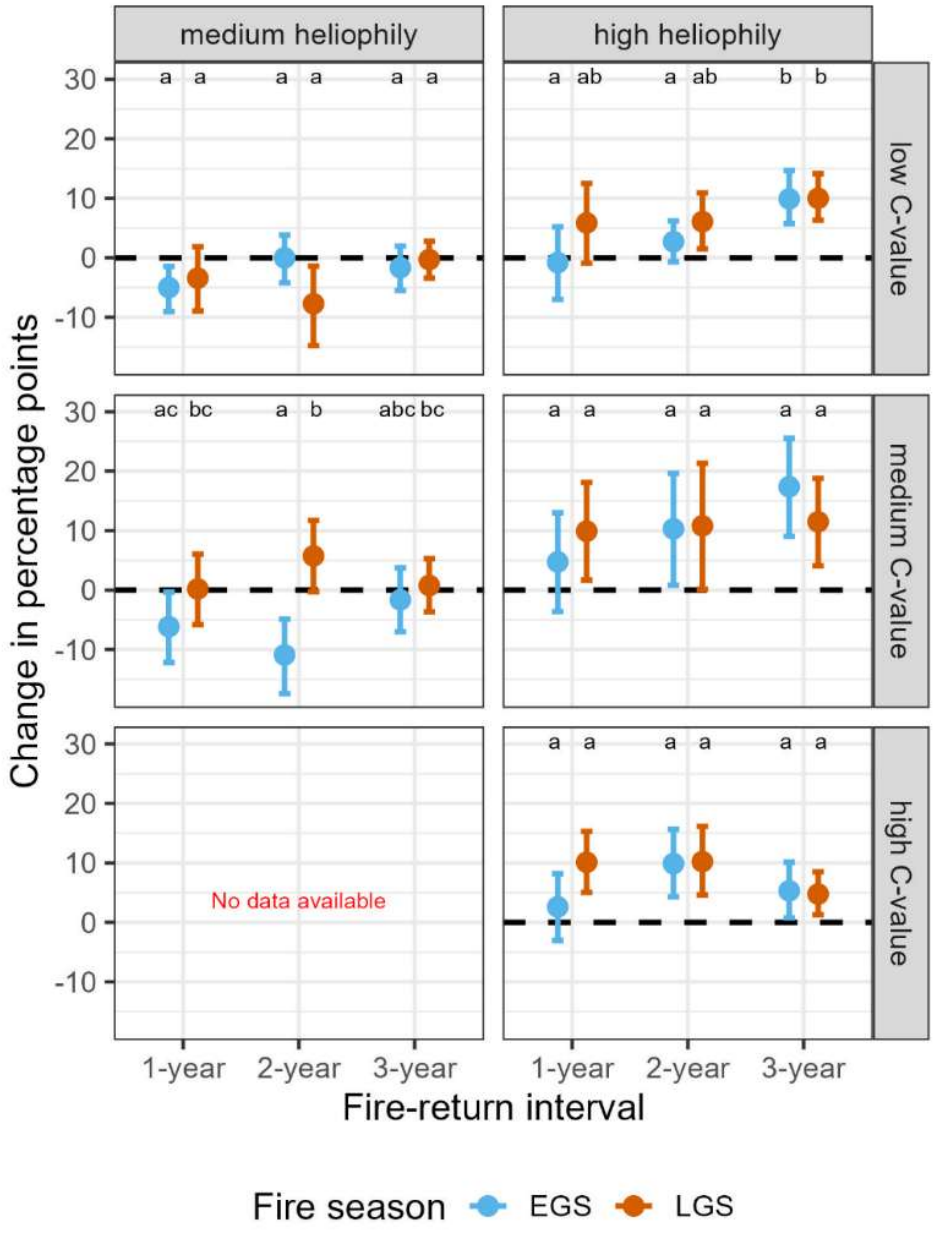


Figure 15. Time-Since-Fire Model predicted change in percentage points for understory cover over 15 years (2011–2025) for forbs grouped by heliophily score and coefficient of conservatism (C-value) when burning in the early and late growing season on a 1-, 2-, and 3-year fire-return interval in a developing oak-pine savanna on the Cumberland Plateau in Tennessee. Error bars indicate the 95% confidence interval. Treatments that do not share a letter have different changes in percentage points ($p<0.05$).

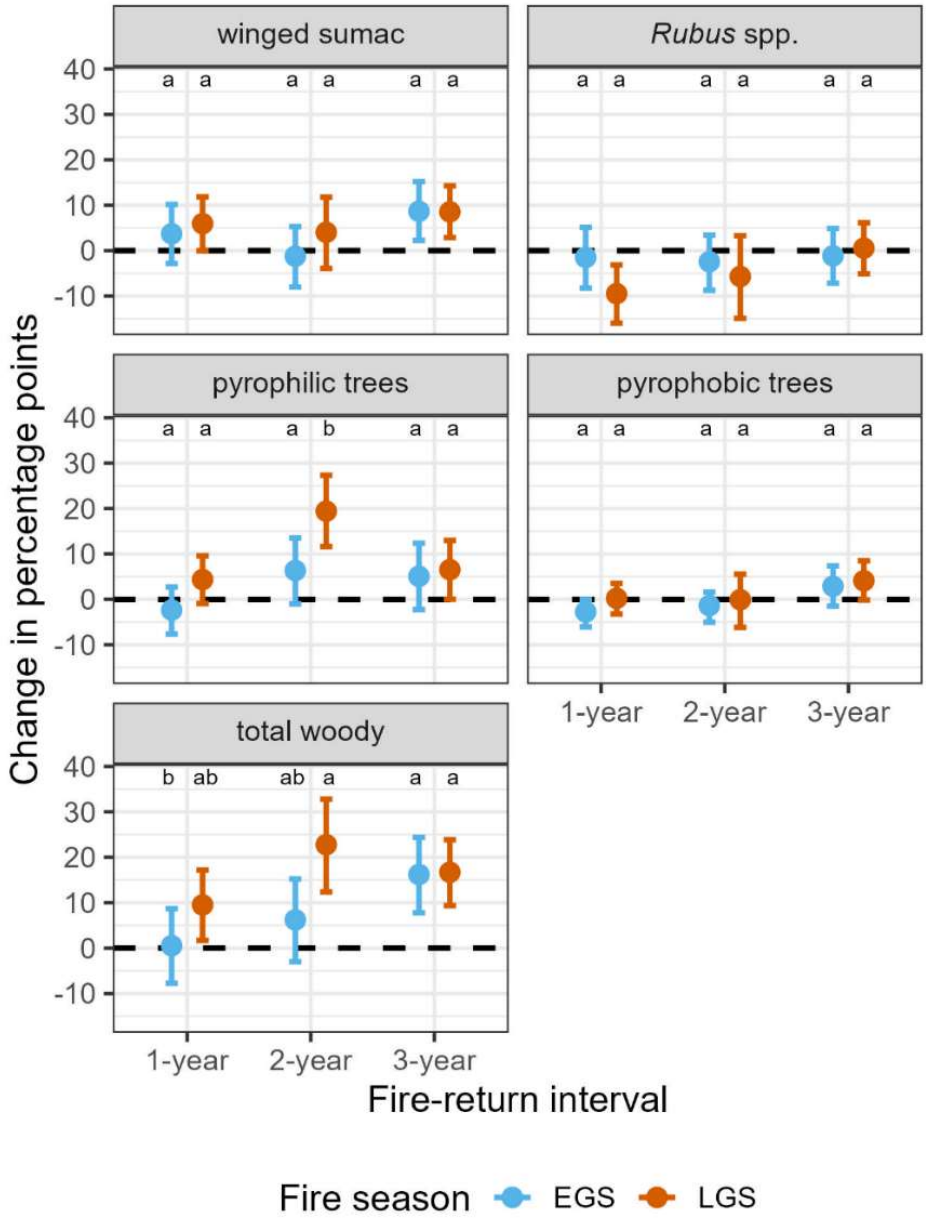


Figure 16. Time-Since-Fire Model predicted change in percentage points for understory cover over 15 years (2011–2025) for woody plant groups when burning in the early and late growing season on a 1-, 2-, and 3-year fire-return interval in a developing oak-pine savanna on the Cumberland Plateau in Tennessee. Error bars indicate the 95% confidence interval. Treatments that do not share a letter have different changes in percentage points ($p<0.05$).

Supplement 3: Fire residency time analysis

We defined fire residency time (R) as the number of seconds fire temperatures were above 60˚C, given the maximum temperature reached 60˚C. We modeled fire residency time using a linear model with a gaussian error distribution

$$R \sim Normal(\mu_F, \sigma_F)$$

$$\mu_F = Treatment.$$

We used a likelihood ratio test to test whether fire residency time differed between fire treatments. A likelihood ratio test indicated fire residency time did not differ between treatments (p=0.75).

CHAPTER 2: EFFECTS OF REPEATED SEASONAL PRESCRIBED FIRE AND SUNLIGHT AVAILABILITY ON VEGETATION COMPOSITION IN SOUTHEASTERN PINE WOODLANDS

ABSTRACT

Prescribed fire is a requisite disturbance practice to maintain pine woodlands in the southeastern US. Fire timing influences plant community composition and structure. Historically, managers have applied prescribed fire primarily during the dormant season, but burning through the year is becoming more common. We evaluated change in plant composition over seven years (2020–2026) of biennial fire in the dormant (January–March), early (April/May), mid- (June/July), and late (September/October) growing season with an unburned control in nine pine woodlands in four states of the southeastern US. Warm-season grasses increased most in the early growing-season and dormant-season treatments. Forbs increased most in the late growing-season and dormant-season treatments, and this pattern was driven by fall-flowering forbs. Unburned controls had the greatest increase in midstory stems whereas early growing-season treatments most effectively reduced woody encroachment. Dormant-season treatments had the greatest fire intensities, which top-killed larger midstory stems, but these treatments also had the greatest woody resprouting. Sunlight availability increased herbaceous coverage for warm-season grasses and forbs, but not for cool-season grasses. All fire treatments promoted open woodland conditions, but fire seasonality impacted vegetation response, and sufficient (>40%) sunlight penetration was necessary to promote an herbaceous understory component.

INTRODUCTION

Fire-maintained pine woodlands and savannas are a focus for restoration in the southeastern US (Earley 2004; Guldin & Black 2018). Many species that depend on these ecosystems, including red-cockaded woodpecker (*Picoides borealis*, Stephens et al. 2019), Bachman's sparrow (*Peucaea aestivalis*, Tucker et al. 2003; Jones et al. 2013), northern bobwhite (*Colinus virginianus*, Weber et al. 2022), and gopher tortoise (*Gopherus polyphemus*, Yager et al. 2007) have faced severe population decline because of habitat loss, but they have responded well to restoration of these ecosystems. Frequent fire plays an important role in the restoration process by setting back woody succession and promoting an herbaceous understory (Brockway & Lewis 1997; Glitzenstein et al. 2012). A fire-return interval of 1–2 years is necessary to control hardwood encroachment in this region (Waldrop et al. 1992; Glitzenstein et al. 2012; Robertson et al. 2021). Frequent fire also increases vegetative diversity (Walker & Peet 1983; Glitzenstein et al. 2003; Keddy et al. 2006) and promotes many rare and endemic plant species that have adapted to fire in these ecosystems (Walker 1993; McMillan et al. 2002; Ames et al. 2017).

Fire seasonality impacts vegetation response to fire treatments. Growing-season fire reduces hardwood resprouting more effectively than dormant-season fire (Waldrop et al. 1992; Knapp et al. 2009; Resop et al. 2024; Zeitler et al. 2025) because of increased root carbohydrate storage during the dormant season (Robertson & Hmielowski 2014). However, different hardwood species respond differently to fire season (Waldrop et al. 1992; Resop et al. 2023; Turner, Bones et al. 2025), which may be related to variation in root carbohydrate storage between pyrophilic and pyrophobic species (Brose & Van Lear 1998; Huddle & Pallardy 1999; Zeitler et al. 2025). Warm-season grasses increase more with dormant and early-growing season fire (Lewis et al. 1964; Howe 2011; Dickson et al. 2019), whereas forbs increase more with dormant and late growing-season fire (Towne & Kemp 2003; Resop et al. 2024; Bones et al. 2026). However, many fire-adapted species are shade-intolerant, and sunlight penetration with repeated fire is necessary to detect an herbaceous response to fire management (Vander Yacht et al. 2020). Fire in closed-canopy forests often do not result in major changes in herbaceous understory composition (Elliott & Vose 2005; Lettow et al. 2014; Bassett et al. 2020), which may partially explain why these forests do not display major differences in vegetation composition with seasonal fire treatments (Keyser et al. 2019; Vaughan et al. 2022; Keyser & Greenberg 2024).

Flowering phenology also is impacted by fire seasonality, which may influence long-term herbaceous response to fire season. Early growing-season fire increases flowering for warm-season grasses (Abrahamson 1984; Streng et al. 1993; Main & Barry 2002) and some forb species (Streng et al. 1993; Brewer & Platt 1994; Hiers et al. 2000), but burning immediately before a plant's flowering period can decrease flowering (Pavlovic et al. 2011). Most species in pine savannas appear resilient to fire in different seasons (Dixon & Robertson 2025), and often delay and synchronize flowering when burned during the growing season (Platt et al. 1988; Hiers et al. 2000; Dixon & Robertson 2025). Changes in flowering phenology only leads to changes in seed production for some species (Hiers et al. 2000; Brewer 2006; Richardson & Wagenius 2022), and long-term herbaceous composition may be driven more by survival and resprouting than seedling establishment (Glitzenstein et al. 2001; Brewer 2006; Fill & Crandall 2024). Nevertheless, long-term studies of understory populations have documented greater increases in warm-season grasses with early growing-season fire and greater increases in early-flowering forbs with fire later in the growing season (Howe 2011; Dickson et al. 2019). Forbs flowering later in the growing season appear more resilient to a variety of fire seasons (Howe 2011; Lapp et al. *in revision*).

Few fire seasonality studies in the eastern US compare fire effects in all four seasons of the year (Streng et al. 1993; Dixon & Robertson 2025; Zeitler et al. 2025) and only one (Bones et al. 2026) compared vegetation responses across the southeastern US. Zeitler et al. (2025) and Dixon and Robertson (2025) investigated short-term vegetation response to fire seasonality. Streng et al. (1993) reported minimal difference in understory composition after ten years of annual or biennial fire in four seasons, but they collected only one year of understory data, which they acknowledge limited their ability to examine changes in the understory plant community.

We implemented biennial fire treatments three times in four fire seasons (dormant, early growing, mid-growing, and late growing) across four states in the southeastern US (Mississippi, Alabama, South Carolina, and Tennessee) to examine how fire seasonality impacts changes in plant community composition over seven years. Previous work in this study system examined broad-scale vegetation group response to these fire treatments (Bones et al. 2026). After an additional burn cycle, we now expand on this study to examine how various plant traits impact understory and midstory response to fire season. We grouped herbaceous plants by flowering

phenology to determine if reproductive timing impacts plant response to fire season, as has been documented in tallgrass prairie (Howe 2011) and pine-oak savanna (Lapp et al. *in revision*). We group woody plants by fire affinity to evaluate whether pyrophilic and pyrophobic species respond differently to fire treatments (Keyser et al. 2019; Zeitler et al. 2025). We also grouped forbs by coefficient of conservatism (C-value, a measure of fidelity to intact ecosystems) to determine how these fire treatments impact species of conservation concern in southeastern pine ecosystems (Rooney & Leach 2010; Larson et al. 2020; Stephen et al. 2024). Finally, we analyzed how sunlight availability changes the impact of fire seasonality. We hypothesized that fire seasonality would impact vegetation response to fire timing, and that flowering phenology, fire-affinity, conservatism, and sunlight availability would influence plant response to fire season.

1. **Graminoid response:** We predicted warm-season grasses would increase most in early growing-season (EGS) and dormant-season (DOS) treatments because of reduced competition from early-flowering species (Streng et al. 1993; Howe 2011; Dickson et al. 2019), whereas cool-season grasses would increase most when burned in the late growing season (LGS) or DOS (Hover & Bragg 1981; Howe 2000).
2. **Forb response:** We predicted forbs would increase in all fire treatments compared to the unburned control (CON) regardless of flowering period. We predicted forbs flowering in the spring and early summer would decrease in coverage in EGS treatments relative to all other fire treatments, but that forbs that flower in late summer and fall would increase similarly in all fire treatments (Howe 2011; Lapp et al. *in revision*). We predicted highly conservative plants would increase in burned treatments relative to CON, given many woodland and savanna conservative species are adapted to frequent fire (Ames et al. 2017).
3. **Woody response:** We predicted woody understory coverage and midstory stem density would be greatest in the CON where they are not being top-killed by fire and in the DOS where hardwoods are more likely to resprout after fire (Knapp et al. 2009; Resop et al. 2024). Additionally, we predicted pyrophylic species would decrease more in EGS treatments than LGS treatments, but pyrophobic species would decrease similarly regardless of timing within the growing season (Zeitler et al. 2025)

4. **Sunlight:** Finally, we predicted herbaceous species would increase more regardless of treatment with greater sunlight penetration (Elliott & Vose 2005; Lettow et al. 2014; Bassett et al. 2020).

METHODS

Study site

Our study covered nine sites dominated by loblolly or shortleaf pine in Tennessee, South Carolina, Alabama, and Mississippi, US (Figure 17A). The two Tennessee sites, managed by the Tennessee Wildlife Resource Agency (TWRA), included Foothills Wildlife Management Area (WMA) in Blount County and the Bridgestone-Firestone Centennial Wilderness WMA in Van Buren County. The two South Carolina sites, managed by the South Carolina Department of Natural Resources, included Belfast WMA in Laurens County and Webb WMA in Hampton County. Of the three Alabama sites, Barbour County WMA was managed by the Alabama Wildlife and Freshwater Fisheries Division. Folsom in Perry County and Mason Bend in Hale County were privately owned. The two Mississippi sites included Copiah County State WMA, managed by the Mississippi Department of Wildlife, Fisheries, and Parks, and Triple Creek, which was privately owned.

Five sites (Webb, Belfast, Barbour, Mason Bend, and Folsom) were planted as loblolly stands between 1990–2010. Two sites (Copiah and Foothills) were naturally regenerated stands. The Bridgestone-Firestone site was planted with shortleaf pine in 2014. Excluding Bridgestone-Firestone WMA, all eight sites were dominated by a loblolly or shortleaf pine overstory and were logged before the study to a basal area between 7.3–11.7 m^2/ha (32–51 ft^2/ac). No site was burned for at least 3 years prior to our study. For further details on site conditions prior to 2020—including fire history, understory composition, and soil type—see Turner and Harper (2024).

We used a randomized complete block design with each site as a treatment replicate (n = 9). We created four treatment units per site, each of which was approximately two hectares and was randomly assigned to the following treatments: dormant-season burn (DOS; January–March), early growing-season burn (EGS; April–May), mid-growing-season burn (MGS; June–July), late growing-season burn (LGS; August–October), and an unburned control (CON). We established

four permanent sampling plots within each unit, for a total of 36 plots per treatment (Figure 17B). We chose these sampling plots at random in areas representative of the upland pine sites.

Fire implementation

We implemented fire treatments on a two-year rotation. We conducted burns with 44±13(sd)% relative humidity, 2.4±1.7 m/s surface winds, and 26±7°C ambient temperatures. We used low-intensity fire with flame lengths of 1.7±0.9 m that aimed to be hot enough to top-kill woody midstory trees and shrubs, consume leaf litter, and maximize burn coverage, but not damage overstory trees. We conducted the first iteration of treatments in October 2020 for LGS and 2021 for all other treatments. Challenges with burn bans forced us to delay 6 of our 108 burns (<6%) past their normal burn window. Of these, four were burned within a week and the remaining two were burned within four weeks of our planned schedule. We collected fire behavior data (flame length, rate of spread, fire temperature, and burn coverage) and weather data (temperature, humidity, wind speed and direction) as described by Bones et al. (2026).

Vegetation sampling

We collected vegetation data annually June–early August beginning in 2020. We did not collect data at Webb WMA or Mason Bend in 2026 because these sites were thinned in the months prior to data collection, which disrupted the understory vegetation. We recorded diameter at breast height (DBH) of all overstory species (trees with DBH > 11.4 cm) within 11.3 m of each plot center. We defined the midstory as all woody plants taller than 1.4 m with DBH < 11.4 cm. We tallied all midstory trees within 5 m of each plot center. We recorded understory composition (plants < 1.4 m tall) using line-point-intersect sampling (Caratti 2006) along a randomly generated 50-m transect centered on the sampling point. At each meter mark (2023–2026) or every other meter mark (2020–2022) we identified each plant crossing the tape to the lowest taxon possible (i.e., species or genus).

Sunlight availability

At each sampling plot, we measured the percentage of photosynthetically active radiation (PAR) reaching the understory using paired readings from two ACCUPAR LP-80 ceptometers (Meter Group, Pullman, WA, USA). At each sampling point, one device was used to take readings every meter for 20 meters, centered on the sampling point, while the other device was used outside of

the stand with no canopy obstruction to take 20 simultaneous readings. Timing of readings were coordinated among observers using a radio or cell phone. We divided each reading taken in-stand with their associated reading outside the stand to get a percent PAR filtering through the canopy (Wall et al. 2010; Turner & Harper 2024; Bones et al. 2026). We calculated a site's Sunlight Availability Index (SAI) by calculating average percent PAR at each site (range: 23–79%).

Assigning plant traits

Plant traits were assigned following the protocol in Lapp et al. (*in revision*). We classified understory vegetation as forbs, graminoids, shrubs, trees, *Rubus* spp., and other (lianas, ferns, mosses). We assigned peak flowering months to all herbaceous plants using the Lady Bird Johnson Wildflower Center Database (2025), the Southeastern Grassland Institute Species Traits Database (Southeastern Grasslands Institute 2025), and research-grade iNaturalist observations (iNaturalist community 2026). We used flowering period to group grasses into warm-season and cool-season and analyzed *Dichanthelium* spp. (low panic grasses) independently as they have two growth cycles. We grouped perennial forbs according to their months of peak flowering in the absence of fire: spring (April–mid-June), early-summer (mid-June–mid-July), late-summer (mid-July–mid-August), and fall (mid-August–November).

We assigned all forbs C-values following the Grassland Fidelity Project (Estes et al. 2025). C-values are an index first developed by Swink and Wilhelm (1979) that range from 1–10 and represent a species' fidelity to high-quality, intact ecosystems. A C-value of 1–3 represented generalist native species that can tolerate degraded conditions, 4–6 represented intermediate species, and 7–10 represented conservative species that only exist in remnant savanna communities. Non-native species are given a C-value of 0.

We used a combination of previous literature (e.g., Thomas-Van Gundy & Nowacki 2013; Siskind et al. 2025), the Fire Effects Information System (U.S. Department of Agriculture, Forest Service), and botanical consultants to designate fire affinity. We categorize our woody species into pyrophilic, neutral, and pyrophobic. Definitions of all plant groups are listed in Table 5.

Data analysis

We used R Statistical Software (v4.5.1; R Core Team 2025) and the *tidyverse* package (Wickham et al. 2019) for data cleaning and statistical analyses and the *brms* (Bürkner 2017) package to run

statistical models. We used plot or transect as our unit of replication (n=4 per treatment per year). Specifications for all models are summarized in Table 6. We used weakly regularizing priors for all models as described in Appendix D. All models were run with 1000 warm-up iterations and 2000 samples with four chains run, convergence was assessed using $\hat{R}$ and traceplots, and density overlay plots and zero-inflation plots were used as posterior predictive checks.

Understory coverage

For each of our fourteen understory vegetation groups (Table 5) we used a zero-inflated (ZI) generalized linear mixed effects Bayesian model with a binomial random component and a logit link function to model changes in percentage cover for each transect over the course of the study. The model is given by

$$V \sim ZIBinomial(p_z, p, N)$$

$$logit(p_z) = \beta_z$$

$$logit(p) = Year * Treatment + PostBurn * Treatment + Year * SAI + \alpha_{site} + \alpha_{transect}$$

where N was the number of points on the transect, V was the number of points that have at least one observation of the vegetation group, *Year* was a continuous variable (0,6) indicating the year since the start of the study, *Treatment* was a factor with 5 levels (CON, DOS, EGS, MGS, LGS), and SAI was the Sunlight Availability Index for a site. *PostBurn* was a categorical predictor variable indicating if the data for a specific year were collected the year after fire treatments were implemented to account for the impacts of time-since-fire (i.e. years 1, 3, and 5). The parameter p_z was the zero-inflation probability, which we assumed was independent of any covariate and had the value β_z on the logit scale. We also explored models including the interaction of *SAI* and *Treatment*, but the interaction did not improve model predictions, so we did not include it in our final models. Finally, α_{site} and $\alpha_{transect}$ were random effects of site and transect.

For each of the fourteen fitted understory vegetation models (one model per vegetation group), we sampled the model posteriors to get a distribution of the expected percentage cover at the beginning (PC_0) and end (PC_6) of the study for a low (25%), medium (50%), and high (75%) SAI. MGS treatments were always implemented after summer data collection, so PC_6 was extrapolated twelve months for this treatment. We used these distributions to determine the distribution of the change in percent cover for a specific treatment and SAI ($\Delta PC_{T,SAI} = PC_0 -$

PC_6). We calculated the mean and 95% credible intervals (CI) for $\Delta PC_{T,SAI}$ from this distribution. If T_1 and T_2 are two treatments, we considered treatment to have a differential impact on ΔPC when the 95% CIs of $\Delta PC_{T_1,50}$ and $\Delta PC_{T_2,50}$ did not overlap. Similarly, we considered SAI to have an impact on ΔPC for treatment T_1 when the 95% CIs of $\Delta PC_{T_1,25}$ and $\Delta PC_{T_1,75}$ did not overlap. Finally, we considered a $\Delta PC_{T_1,SAI}$ to be increasing if the 95% CI did not overlap zero.

Midstory stem density

We used negative binomial linear mixed effects Bayesian models with a log link function to model the number of stems per plot (S) for all midstory trees, midstory trees with DBH >5cm, and shrubs. We excluded data from years immediately following fire to focus on understanding changes in midstory stem density over time, rather than the immediate impacts of fire on midstory top-kill. Our model was

$$S \sim NegativeBinomial(\mu, \phi)$$

$$\ln(\mu) = Treatment * Year + \alpha_{site} + \alpha_{transect}$$

where ϕ is the dispersion parameter of the negative binomial distribution.

We repeated this process while categorizing midstory trees by fire-affinity (pyrophilic, pyrophobic, or neutral) and included a three-way interaction term of fire-affinity, treatment, and year in our mixed effects model such that the systematic component of our models was updated to:

$$\ln(\mu) = Treatment * Year * FireAffinity + \alpha_{site} + \alpha_{transect}.$$

For each of our four fitted midstory models (all trees, trees with DBH> 5 cm, trees including fire-affinity, all shrubs), we sampled the model posteriors to get a distribution of the expected midstory stems at the beginning (S_0) and end of the study (S_6). We extrapolated S_6 for MGS treatments. We used these distributions to determine the distribution of the change in expected stem density $\left(\Delta S = \frac{S_6}{S_0}\right)$ for each treatment. For two treatments *T1* and *T2*, we considered treatment to have an impact on stem density when the 95% CI of $\log_{10}(\Delta S)_{T1} - \log_{10}(\Delta S)_{T2}$ did not overlap zero.

Fire behavior

We log-transformed maximum fire temperature (˚C, T_{max}), average rate of fire spread (m/hr, R), and flame length (L_f). We used gaussian linear mixed effects Bayesian models to model these transformed metrics. Our model was

$$\ln(T_{max}), \ln(R), \ln(L_f) \sim Normal(\mu)$$

$$\mu = Treatment + \alpha_{site}.$$

We also used a linear mixed effects Bayesian model with a beta random component and a logit link function to model burn coverage (C_{burn}). Our model was

$$C_{burn} \sim Beta(\mu, \phi)$$

$$\text{logit}(\mu) = Treatment + \alpha_{site}$$

where ϕ is the dispersion parameter of the Beta distribution. For each of our fire behavior models, we sampled the model posteriors to get a distribution of the expected response variables μ for $\ln(T_{max})$, $\ln(R)$, $\ln(L_f)$, and C_{burn}. For two treatments *T1* and *T2*, we considered treatment to have an impact on a fire behavior metric when the 95% CI of the difference between the response variable (e.g., $\ln(T_{max})_{T1} - \ln(T_{max})_{T2}$) did not overlap zero.

RESULTS

Understory

Grass response to fire season

Grass response to fire seasonality varied by flowering phenology. Warm-season grass coverage increased more in the EGS (ΔPC_{50} = 5.5%, CI = [1.8%, 12.6%] percentage points [PP]) and DOS (3.1 [0.9, 8.0] PP) treatment units compared to decreases in LGS (-1.3 [-4.6, 0.3] PP) and CON (-1.3 [-4.5, -0.2] PP). MGS (1.7 [0.2, 5.8] PP) also had a greater increase in warm-season grasses than CON (Figure 18A). Cool-season grass coverage increased more in DOS (20.0 [8.2, 32.4] PP) and CON (14.9 [5.9, 24.7] PP) than MGS (0.4 [-2.8, 4.2] PP) and more in DOS than LGS (2.6 [0.5, 7.2] PP, Figure 18B). *Dichanthelium* spp. coverage increased more in MGS (18.6 [11.9, 25.3] PP) than CON (-11.8 [-18.1, -7.0] PP), DOS (3.0 [0.3, 6.3] PP), and EGS (7.4 [4.1, 11.6] PP) and also increased more in LGS (14.3 [9.4, 19.5] PP) than CON or DOS (Figure 18C).

Forb response to fire season

Total forb coverage increased more in the LGS (29.5 [23.5, 34.6] PP) and DOS (28.2 [22.2, 33.2] PP) treatment units than in the CON (-0.9 [-3.6, 1.7] PP) or MGS (12.3 [7.6, 17.7] PP) treatment units. Forb coverage also increased more in EGS (21.8 [23.5, 34.6] PP) and MGS than CON (Figure 19A). These trends were driven primarily by fall-flowering forbs, which were the most abundant forbs at our sites. Fall-flowering forb coverage increased more in LGS (24.0 [18.5, 29.9] PP) and DOS (21.0 [15.9, 26.7] PP) than MGS (8.8 [5.1, 13.6] PP) and EGS (10.1 [6.6, 14.4] PP), but all treatments had greater increases in fall-flowering forb coverage than CON (0.3 [-2.6, 1.7] PP, Figure 20D). Early-summer flowering forb coverage increased more in EGS (2.5 [1.0, 5.7] PP) and LGS (2.4 [1.0, 5.4] PP) than CON (-0.1 [-0.9, 0.7] PP, Figure 20B). Late-summer flowering forb coverage increased more in DOS (3.4 [1.6, 6.7] PP) and EGS (2.0 [0.9,4.3] PP) than CON (0.1 [-0.8, 0.9] PP, Figure 20C). We did not detect an impact of treatment on spring-flowering forb coverage (Figure 20A).

Low conservative forb coverage increased in all fire treatment units (LGS: 7.6 [4.3, 12.2] PP; EGS: 6.5 [3.6, 10.9] PP; DOS: 5.8 [3.4, 9.7] PP; MGS: -0.6 [-3.0, 1.8] PP;) compared to CON (-6.4 [-11.5, -3.6] PP, Figure 21C). Medium conservative forb coverage increased in DOS (18.5 [13.3, 24.2] PP), LGS (17.5 [12.4, 23.4] PP), and EGS (10.6 [6.8, 15.2] PP) compared to CON (3.4 [1.4, 6.0] PP, Figure 21B). We did not detect an effect of treatment on highly conservative forb coverage (Figure 21A).

Understory woody response to fire season

Coverage of tree species in the understory increased more in the DOS (5.5 [2.4, 10.4] PP) treatment units than in the CON (-5.5 [-10.2, -2.2] PP), MGS (-5.7, [-11.7, -2.2] PP), and EGS (-1.3, [-4.3, 0.4] PP) treatment units (Figure 22A). Coverage of shrub species in the understory increased more in DOS (16.7 [9.9, 25.6] PP) than CON (1.9 [-0.3, 4.9] PP), but increased over time with all fire treatments (LGS: 7.3 [3.8, 12.6] PP; EGS: 6.1 [3.0, 10.8] PP, MGS: 4.5 [1.7, 9.3] PP, Figure 22B). *Rubus* spp. coverage increased more in DOS (18.4 [12.4, 23.3] PP), LGS (9.0 [5.0, 13.5] PP) and EGS (4.8 [1.7, 8.7] PP) than MGS (-4.6 [-9.0, -0.8] PP) and CON (-1.4 [-4.6, 1.5] PP). *Rubus* spp. also increased more in DOS compared to EGS (Figure 22C).

Understory response to sunlight availability

Sunlight availability impacted warm-season grass and forb coverage. Warm-season grass coverage increased more at sites with high SAI than low SAI in the DOS, EGS, and MGS treatment units (Figure 18A, all 95% CIs comparing $\Delta PC_{75} - \Delta PC_{25}$ for each treatment did not overlap 0). Forb coverage was greater at sites with high SAI than low SAI for all fire treatments (Figure 19A, all 95% CIs comparing $\Delta PC_{75} - \Delta PC_{25}$ for each fire treatment did not overlap 0) but not CON. This result again was driven by fall-flowering forbs, which had greater coverage at sites with high SAI than low SAI for all fire treatments and CON (Figure 20D, all 95% CIs comparing $\Delta PC_{75} - \Delta PC_{25}$ for each treatment did not overlap 0). Medium conservative forb coverage was greater at sites with high SAI than low SAI for all treatments and CON (Figure 21B, all 95% CIs comparing $\Delta PC_{75} - \Delta PC_{25}$ for each treatment did not overlap 0). Cool-season grass coverage increased in MGS with high SAI and decreased with low SAI (Figure 18B, 95% CIs comparing $\Delta PC_{75} - \Delta PC_{25}$ did not overlap 0) but were not affected in other treatments. *Rubus* spp. coverage increased more with high SAI than low SAI in CON and MGS only (Figure 22C, 95% CIs comparing $\Delta PC_{75} - \Delta PC_{25}$ did not overlap 0 for these treatments). We did not detect an influence of SAI on spring, early-summer, and late-summer flowering forbs, low and high conservative forbs, or *Dichanthelium* spp. (Figure 18C, Figure 20A–C, Figure 21A,C).

Midstory

Midstory tree stem density increased more in CON (284% increase, $\log_{10}(\Delta S) = 0.58$ [0.43, 0.74]) units compared to all fire treatment units (DOS: 0.15 [-0.02, 0.31]; MGS: 0.14 [-0.13, 0.41]; LGS: -0.03 [-0.18, 0.13]; EGS: -0.23 [-0.40, -0.06]). DOS and MGS had a greater increase in stem density ($(10^{0.14} - 1) \times 100 \approx (10^{0.15} - 1) \times 100 \approx$ 40% increase) than EGS, which was the only treatment in which we detected a decrease in midstory tree stem density (41% decrease, Figure 23A). Density of midstory stems >5 cm DBH decreased in DOS (75% decrease, -0.60 [-0.97, -0.26]) relative to all other burn treatments and CON (MGS: 0.81 [0.20, 1.4]; CON: 0.37 [0.15, 0.58]; EGS: 0.18 [-0.18, 0.51]; LGS: 0.08 [-0.24, 0.40], Figure 23B). Shrub stem density increased less in the EGS (36% increase, 0.13 [-0.19, 0.47]) relative to all burn treatments and CON (DOS: 1.02 [0.69, 1.35]); CON (0.93 [0.61, 1.23]); MGS: 0.79 [0.26, 1.34]; LGS: 0.68 [0.34, 1.02], Figure 23C). CON had a greater increase in pyrophobic tree stem density (358% increase, 0.66 [0.34, 0.98]) than EGS (79% decrease, -0.68 [-1.17, -0.19]), LGS (46% decrease, -

0.27 [-0.66, 0.10]), or DOS (21% decrease, -0.10 [-4.9, 0.26]) and had a greater increase in pyrophilic tree stem density (156% increase, 0.41 [0.09, 0.73]) than EGS (49% decrease, -0.29 [-0.65, 0.07]) or LGS (41% decrease, -0.23 [-0.61,0.13])). Trees with neutral fire affinity increased more in the DOS (85% increase, 0.27 [-0.04, 0.57]) and CON (49% increase, 0.17 [-0.12, 0.47]) than the EGS (50% decrease, -0.39 [-0.64, 0.04], Figure 23D).

Fire behavior

Fire behavior metrics were consistently greatest in the DOS treatment units and least in the MGS treatment units. Maximum temperature was higher in DOS (T_{max} = 153 [129, 182]℃) than all growing-season treatments (℃, MGS: 85 [71, 101] ℃; LGS: 103 [85, 125]; EGS: 104 [87, 123] ℃, Figure 24A). Flame length was greater in DOS (L_f = 86 [65, 112] cm) than all growing-season treatments (EGS: 55 [42, 72] cm, LGS: 56 [42, 73] cm) and was least in MGS (37 [28, 47] cm , Figure 24B). Rate of spread also was greater in DOS (R = 59 [38, 89] m/hr) than all growing-season treatments (MGS: 26 [17, 39] m/hr; LGS: 30 [19, 46] m/hr, EGS: 36 [24, 54] m/hr, Figure 24C). Burn coverage was greater in DOS (C_{burn} = 94 [91, 97]%) and EGS (93 [89, 96]%) than LGS (89 [84, 93]%) and was least in MGS (81 [74, 87]%, Figure 24D).

DISCUSSION

In our seven-year study, we documented how sunlight availability and repeated fire in four fire seasons impacted changes in woody and herbaceous plant composition in nine pine woodlands across the southeastern US. As predicted, all fire treatments successfully set-back succession and reduced woody encroachment compared to CON, and growing-season fire reduced woody resprouting more than DOS fire despite lower fire intensity. Shade-intolerant herbaceous response was greater in fire treatments and at sites with more sunlight penetration, but differed depending on fire timing, as predicted. As expected, we documented a greater increase in warm-season grass coverage with EGS and DOS fire and a greater increase in forb coverage with LGS and DOS fire. The increase in forb coverage was represented primarily by fall-flowering forbs. We did not detect an impact of fire season on forbs flowering earlier in the growing season, which was contrary to our expectations. Biennial fire may be used in different seasons of the year to maintain pine woodlands in the southeastern US, and managers may adjust timing of

prescribed fire and sunlight availability through thinning to influence plant composition and structure to better meet management objectives.

A primary objective when using fire to maintain pine woodlands is to set-back woody encroachment and promote an open, herbaceous plant-dominated understory (Block et al. 2016; Greene et al. 2016; Nordman et al. 2021). All fire treatments set-back succession compared to the unburned control, but EGS fire was most effective at controlling woody encroachment. The EGS treatment decreased midstory tree stem density (41% decrease over 7 years). The DOS treatments had the highest fire intensities, as expected in this region (Sparks et al. 2002; Bones et al. 2026), and were more successful at top-killing larger midstory stems (DBH>5 cm), but midstory tree stem density and coverage of tree, shrub, and *Rubus* species in the understory increased because of resprouting stems, as predicted. Dormant-season fire often is used when reintroducing fire to long unburned areas to reduce fuel loads and duff accumulation (Outcalt 2006; Rankin & Herbert 2014), and our results indicate DOS fire is beneficial to top-kill larger midstory stems before switching to growing-season fire to reduce resprouting. All growing-season fire treatments had less woody understory resprouting than DOS treatments, consistent with previous literature (Waldrop et al. 1992; Knapp et al. 2009; Resop et al. 2024). Inconsistent with Zeitler et al. (2025), fire-affinity did not impact trends in midstory tree response to fire season.

Open pine woodlands are characterized by an herbaceous understory that requires sunlight penetration and is perpetuated with frequent fire (Nordman et al. 2021; Hanberry et al. 2018). In our study, sunlight availability had the strongest impact on warm-season grasses, which are shade-intolerant (Lin et al. 1998; Awada et al. 2003; Charles-Dominique et al. 2018). After three iterations of fire treatments, sites with a SAI < 40% had less than 6% coverage of warm-season grasses, regardless of fire treatment. The majority of the forb species we detected also were shade-intolerant. Total forb coverage was not as dramatically impacted by sunlight availability as warm-season grasses but still were more common at sites with more sunlight penetration. In the burn treatments, forb coverage in the final year of the study was 8–9% greater with every 10% increase in sunlight availability (Figure 19B). Warm-season grasses and forbs also increased more in our fire treatments, which set-back woody plants and maintained greater sunlight penetration, than in the CON where by 2026 there was approximately 40% less sunlight because

of midstory growth. This result is consistent with previous literature that reports areas with lower basal area and canopy cover (metrics used as proxies for sunlight penetration) have greater forb coverage or biomass (McConnell & Smith 1965; Peitz et al. 2001; Keene et al. 2021). Overstory trees expand following thinning and thus reduce sunlight penetration. More intense thinning or repeated thinning over time can be used to maintain enough sunlight to promote relatively shade-intolerant forbs. Cool-season grasses were not strongly impacted by sunlight availability and were not hindered by lack of fire, which may reflect that many cool-season grasses (including *Chasmanthium* spp. which were the most common cool-season grass species) are shade-tolerant (Charles-Dominique et al. 2018; Szakacs et al. 2022). We also did not detect an impact of sunlight availability on *Dichanthelium* spp. which contain a mix of shade-tolerant and shade-intolerant species, but as a clade may be less dependent on full sunlight than warm-season grasses (Szakacs et al. 2022).

Fire seasonality impacted herbaceous response to repeated fire. Total forb coverage increased in all fire treatments, but increased most in the DOS and LGS treatments, consistent with previous fire seasonality literature (Lewis et al. 1964; Towne & Kemp 2003; Resop et al. 2024; Bones et al. 2026). This pattern was driven primarily by fall-flowering forbs, which were the most abundant forbs at our study sites and southeastern pine savannas generally (Platt et al. 1988; Dixon & Robertson 2025). Many wildlife species, including bobwhite (Kroeger et al. 2020), wild turkey (Peoples et al. 1995; Nelson et al. 2022), songbirds (Worthington et al. 2004; Shaffer et al. 2023), deer (Nanney et al. 2018; Turner, Harper, et al. 2025), and pollinators (Waters et al. 2024; Powell et al. 2025) rely on forb species for food and cover and may benefit from increased forb coverage with LGS and DOS fire. Our work also corroborated the existing body of literature that DOS and EGS fire increase native warm-season grass coverage relative to LGS fire and the CON (Ehrenreich & Aikman 1963; Lewis et al. 1964; Howe 2011; Dickson et al. 2019). Fire during the EGS can reduce competition from early-flowering species and increase sunlight availability for warm-season grasses (Hulbert 1988) as well as promote flowering in some of these species (Abrahamson 1984; Streng et al. 1993; Main & Barry 2002). *Dichanthelium* spp. increased in all fire treatments and increased most when burned later in the growing season, after they have finished flowering, similar to Lapp et al. (*in revision*).

Longer monitoring may be necessary to detect differences in some of our vegetation groups. For forb species that flower early in the year, we detected greater increases in forb coverage in our burned treatments relative to the CON, but we did not detect differences between the timing of fire. Previous studies examining the interaction of flowering phenology and fire seasonality in this region have reported early-flowering species more sensitive to fire seasonality than late-flowering species (Howe 2011; Lapp et al. *in revision*). Given these species were relatively uncommon at our study sites, more burn cycles and longer monitoring may be necessary to detect differences in seasonal response for these flowering groups. The same may be true for highly conservative forbs; we did not see an impact of fire season on those forbs, as expected (Lapp et al. *in revision*), but they also were relatively uncommon at our sites and longer monitoring should continue to see if this trend remains.

All fire treatments maintained open pine woodland conditions and promoted an herbaceous plant community. Growing-season fire, especially EGS fire, reduced woody encroachment more than DOS fire, but DOS fire may be more effective in areas where greater fire intensity is needed to top-kill larger midstory trees. Fire timing can be used to promote desired herbaceous species; however, sunlight penetration must be sufficient (>40%) to allow an herbaceous response.

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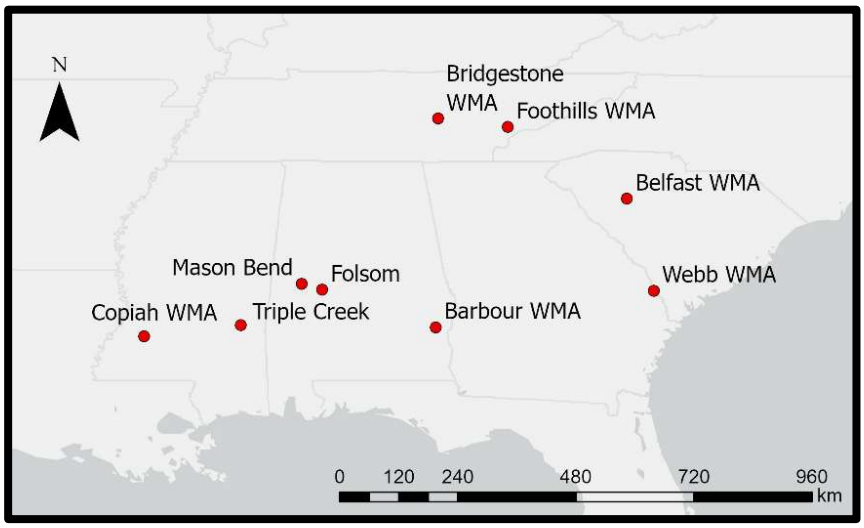
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APPENDIX C

This appendix contains all tables and figures for Chapter 2.

(A)



(B)

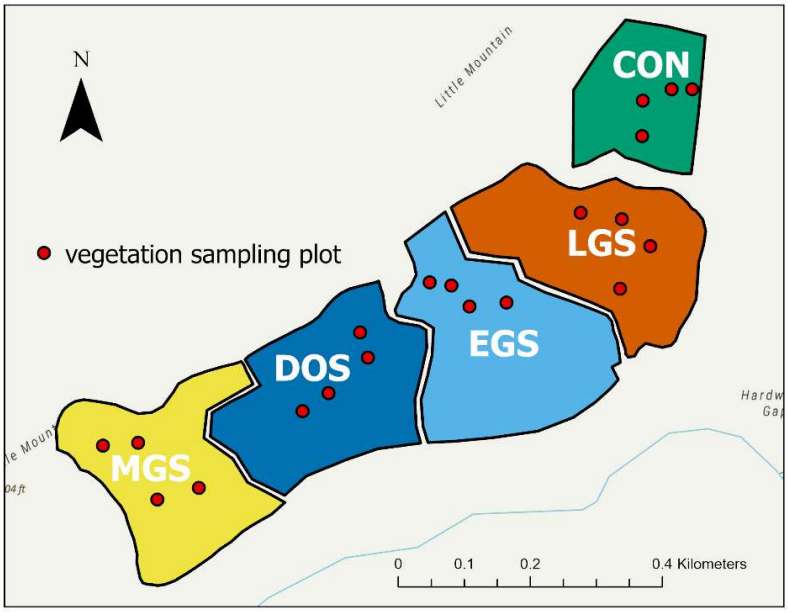


Figure 17. (A) Nine study site locations in Tennessee, Mississippi, Alabama, and South Carolina, USA where we studied fire effects on vegetation in pine woodlands during four fire seasons over seven years (2020–2026). (B) Example layout of four burn treatments (DOS = dormant season, EGS = early growing season, MGS = mid-growing season, LGS = late growing season) and an unburned control (CON) at Foothills WMA in Tennessee.

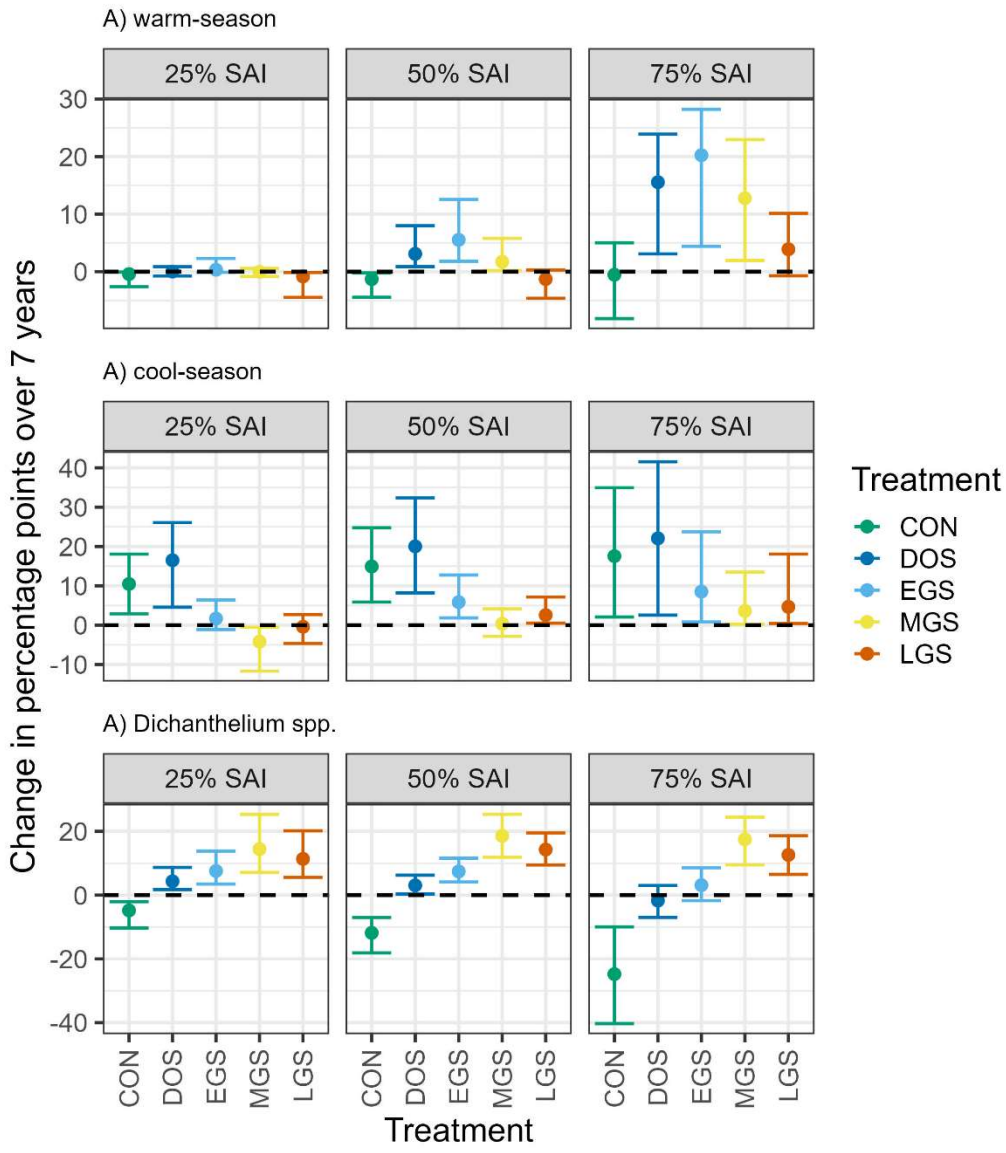


Figure 18. Model predicted change in percentage points (ΔPC) for understory coverage over 7 years (2020–2026) for (A) warm-season grasses, (B) cool-season grasses, and (C) *Dichanthelium* spp. in sites with three Sunlight Availability Indices (SAI) for an unburned control (CON) and burning in the dormant season (DOS), early growing season (EGS), mid-growing season (MGS), and late growing season (LGS) on a 2-year fire-return-interval in pine woodlands in the southeastern US. Error bars indicate the 95% credible interval.

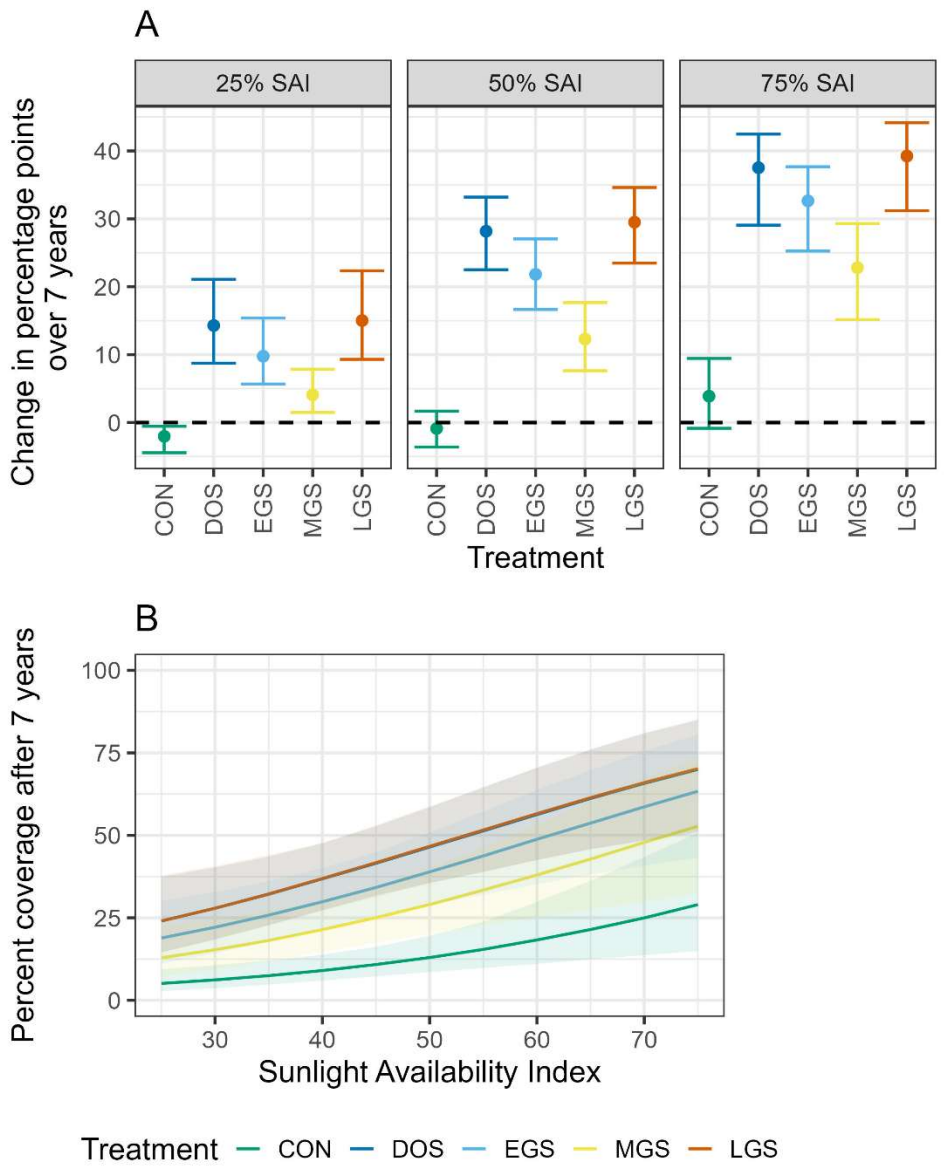


Figure 19. (A) Model predicted change in percentage points (ΔPC) for understory coverage of all forbs over 7 years (2020–2026) in sites with three Sunlight Availability Indices (SAI) and (B) total forb coverage after 7 years for an unburned control (CON) and burning in the dormant season (DOS), early growing season (EGS), mid-growing season (MGS), and late growing season (LGS) on a 2-year fire-return-interval in pine woodlands in the southeastern US. Error bars indicate the 95% credible interval.

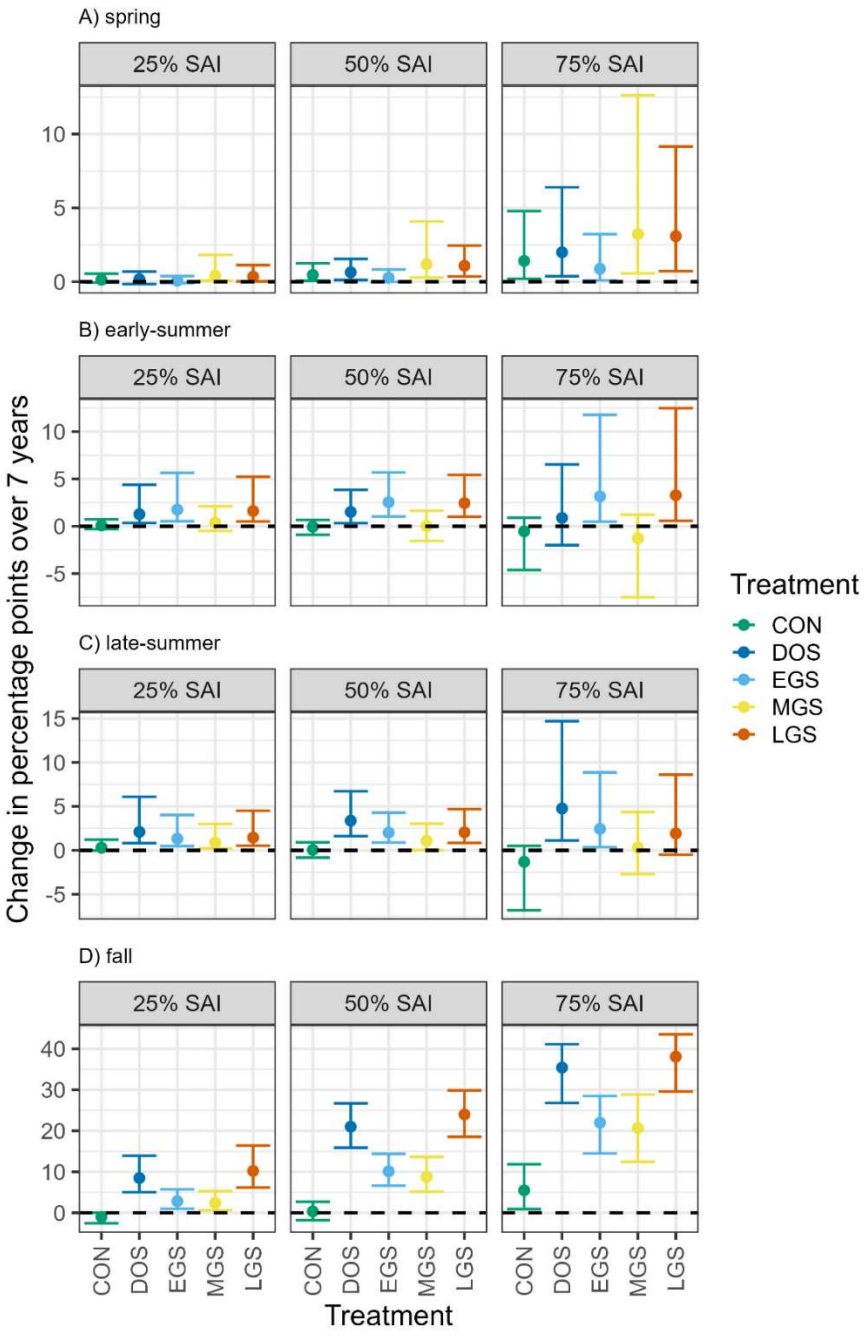


Figure 20. Model predicted change in percentage points (ΔPC) for understory coverage over 7 years (2020–2026) for (A) spring-, (B) early-summer-, (C) late-summer-, and (D) fall-flowering forbs in sites with three Sunlight Availability Indices (SAI) for an unburned control (CON) and burning in the dormant season (DOS), early growing season (EGS), mid-growing season (MGS), and late growing season (LGS) on a 2-year fire-return-interval in pine woodlands in the southeastern US. Error bars indicate the 95% credible interval.

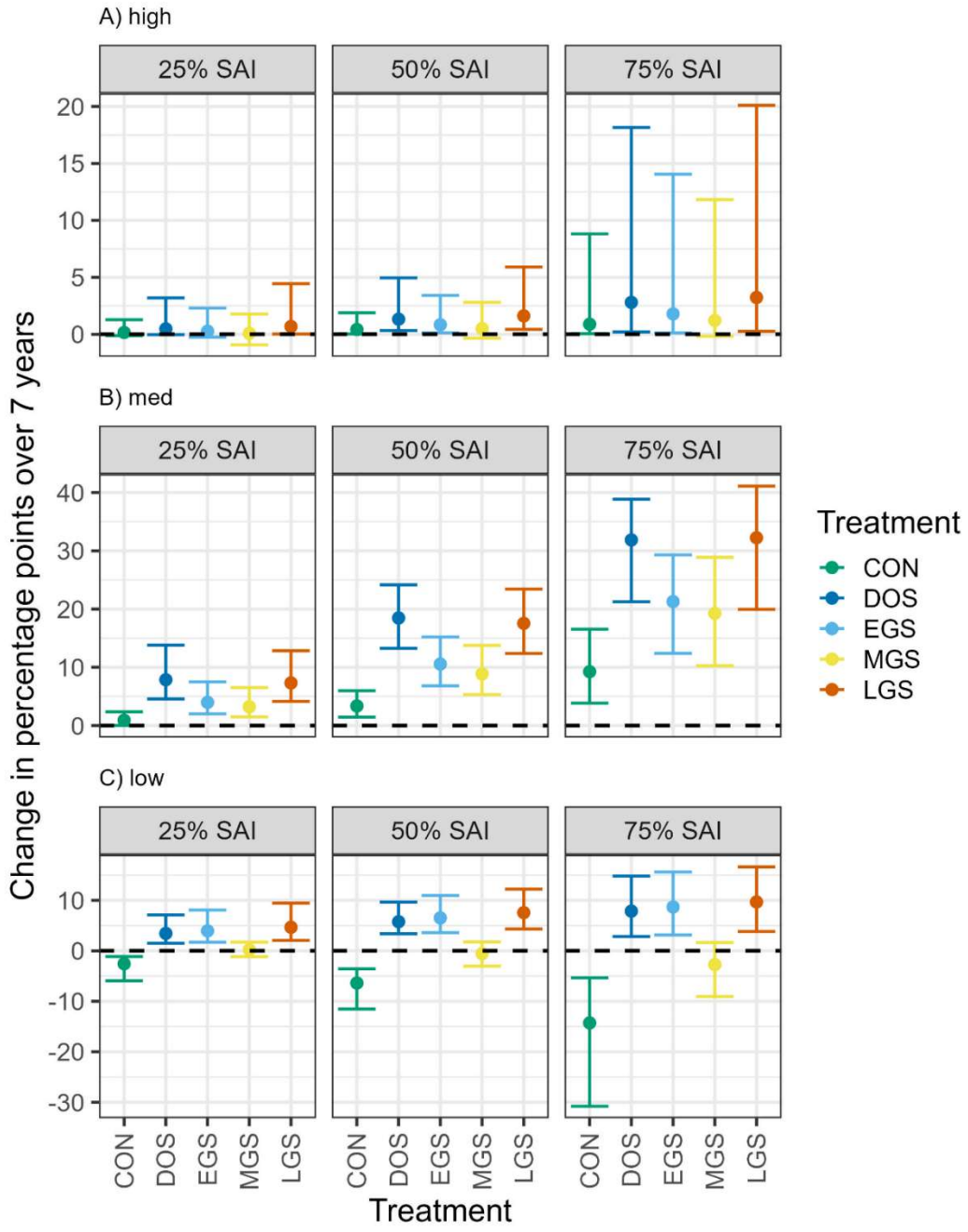


Figure 21. Model predicted change in percentage points (ΔPC) for understory coverage over 7 years (2020–2026) for (A) high, (B) medium, and (C) low coefficient of conservatism. in sites with three Sunlight Availability Indices (SAI) for an unburned control (CON) and burning in the dormant season (DOS), early growing season (EGS), mid-growing season (MGS), and late growing season (LGS) on a 2-year fire-return-interval in pine woodlands in the southeastern US. Error bars indicate the 95% credible interval.

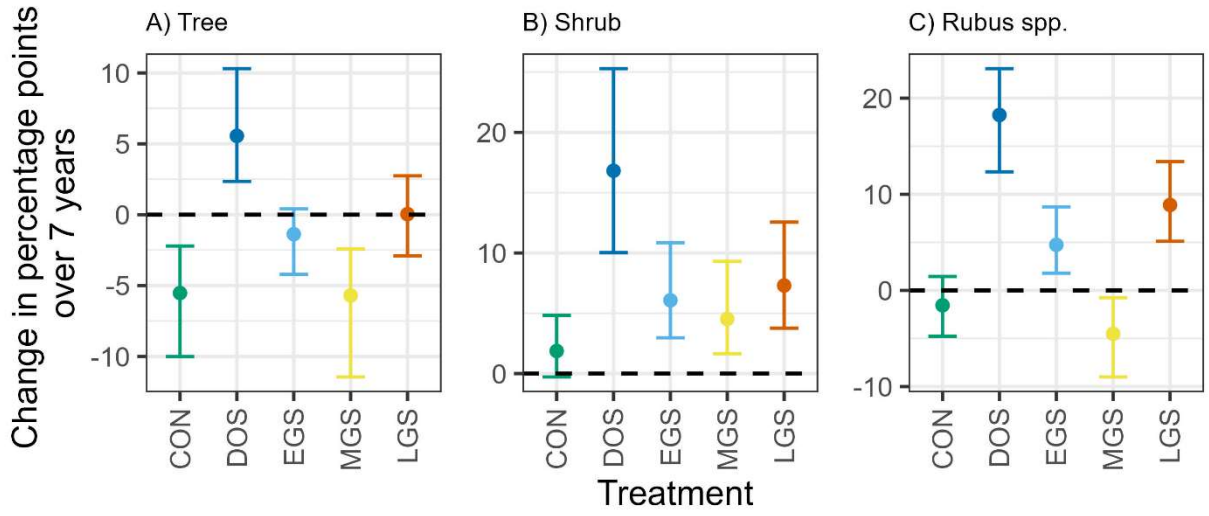


Figure 22. Model predicted change in percentage points (ΔPC) for understory coverage over 7 years (2020–2026) (A) tree, (B) shrub, (C) Rubus species in an unburned control (CON) and burning in the dormant season (DOS), early growing season (EGS), mid-growing season (MGS), and late growing season (LGS) on a 2-year fire-return-interval in pine woodlands in the southeastern US. Error bars indicate the 95% credible interval.

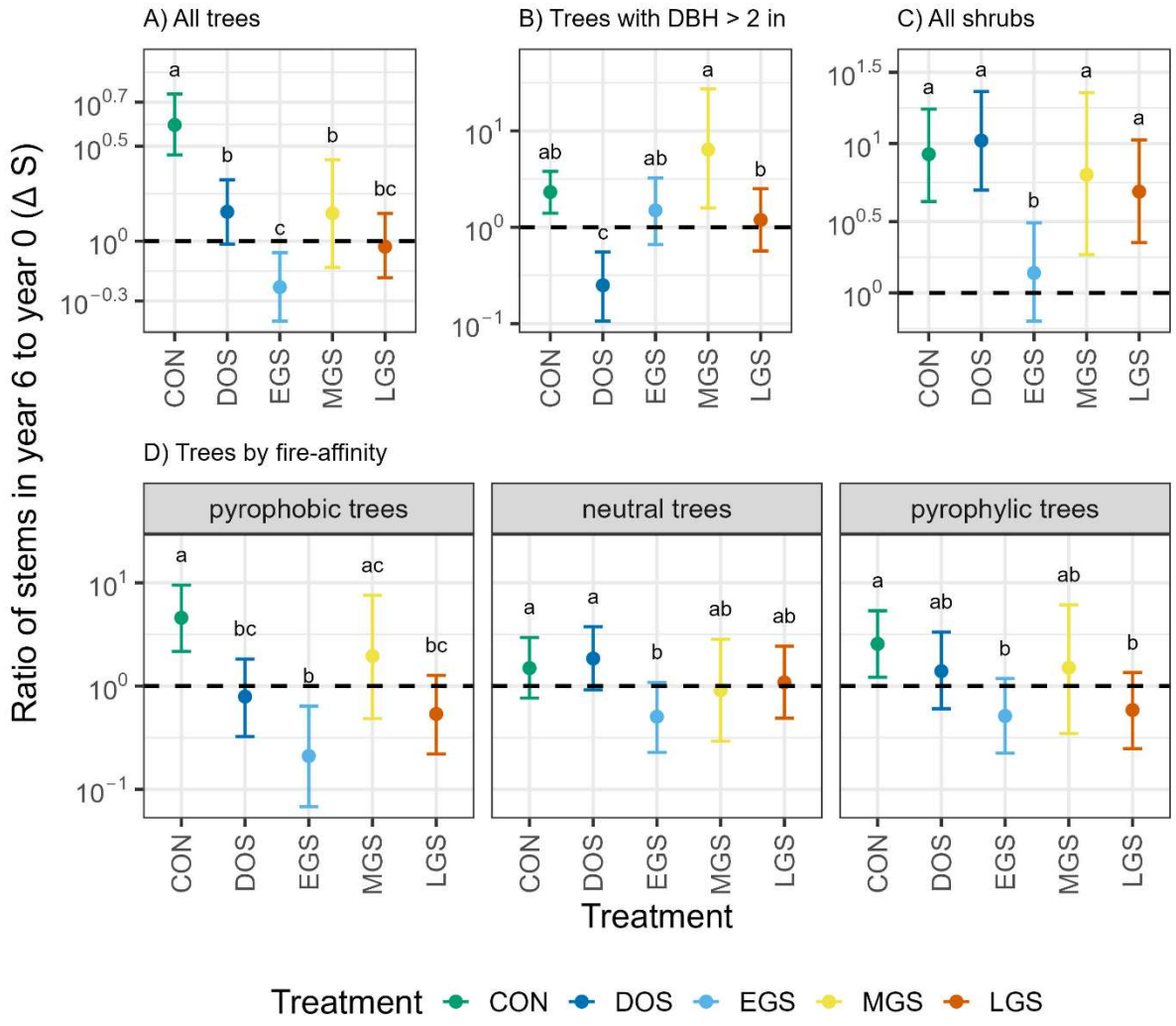


Figure 23. Model change in stem density $\left(\Delta S = \frac{S_6}{S_0}\right)$ over 7 years (2020–2026) for (A) all tree species, (B) trees with DBH > 2 in, (C) all shrub species, and (D) trees separated by fire-affinity in an unburned control (CON) and burning in the dormant season (DOS), early growing season (EGS), mid-growing season (MGS), and late growing season (LGS) on a 2-year fire-return-interval in pine woodlands in the southeastern US. Error bars indicate the 95% credible interval. For a given woody plant group, treatments that do not share a letter were statistically different.

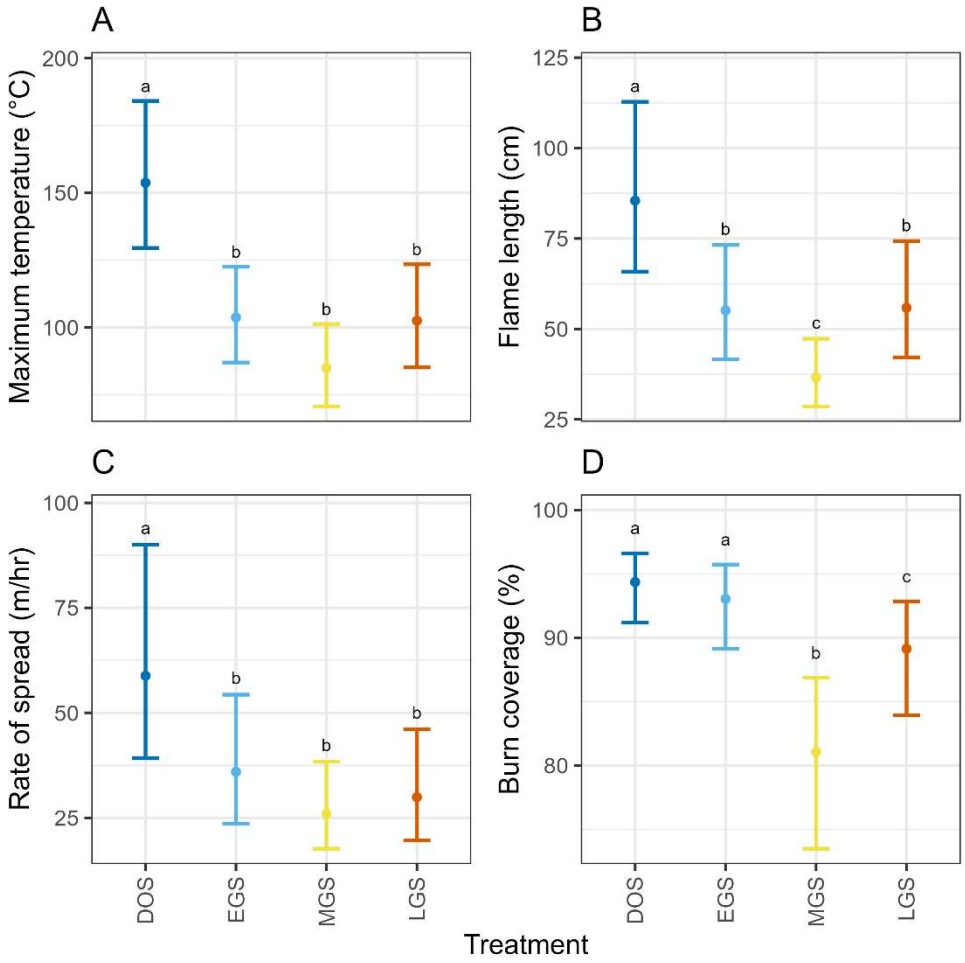


Figure 24. Average (A) maximum temperature (˚C), (B) flame length (m/hr), (C) rate of spread (cm), and (D) burn coverage for dormant season (DOS), early growing season (EGS), mid-growing season (MGS), and late growing season (LGS) fire in nine pine woodlands in the southeastern US. Error bars indicate the 95% credible interval. For a fire behavior metric, treatments that do not share a letter were statistically different.

Table 5. Vegetation groups used for analysis of vegetation response to 7 years of seasonal fire treatments (2020–2026) in nine pine woodlands in the southeastern US.

Vegetation group	Definition
Grasses	
Cool-season	Flower April–July
Warm-season	Flower August–November
Dichanthelium spp.	*Dichanthelium* spp.
Forbs	
Spring-flowering perennials	Peak flower April–mid-June
Early-summer flowering perennials	Peak flower mid-June–mid-July
Late-summer flowering perennials	Peak flower mid-July–mid-August
Fall-flowering perennials	Peak flower mid-August–November
High C-value	Conservatism score of 7–9
Medium C-value	Conservatism score of 4–6
Low C-value	Conservatism score of 1–3
Woody and semi-woody plants	
Trees	Understory tree species
Shrubs	Understory shrub species
Rubus spp.	*Rubus* spp.

Table 6. Specifications for generalized linear models used to analyze understory and midstory vegetation response to 7 years of seasonal fire treatments (2020–2026) in nine pine woodlands in the southeastern US.

Model description	Response variable	Random component	Link	Systematic component
Understory percent coverage	V	Zero-inflated Binomial	logit	$Year * Treatment + PostBurn * Treatment + Year * SAI + \alpha_{site} + \alpha_{transect}$
Midstory stem density	S	Negative binomial	ln	$Treatment * Year + \alpha_{site} + \alpha_{transect}$
Midstory stem density (including fire-affinity)	S	Negative binomial	ln	$Treatment * Year * FireAffinity + \alpha_{site} + \alpha_{transect}$
Fire behavior	$\ln(T_{max})$ $\ln(L_f)$ $\ln(R)$	Gaussian	none	$Treatment + \alpha_{site}$
Burn coverage	C_{burn}	Beta	ln	$Treatment + \alpha_{site}$

APPENDIX D

This appendix contains the weakly regularizing priors used for our Bayesian models.

Understory vegetation models

We used the following weakly regularizing priors where β_z was the zero-inflation probability on the logit scale, β_0 was the intercept, $\boldsymbol{\beta}$ was a vector of the coefficients of the covariates, α_{site} was the coefficient of the site random effect, and $\alpha_{transect}$ was the coefficient of the transect random effect.

$$\beta_z \sim Normal(0,2)$$

$$\beta_0 \sim Normal(0,5)$$

$$\boldsymbol{\beta} \sim Normal(0, 2)$$

$$\alpha_{site} \sim Normal(0, \sigma_{site})$$

$$\sigma_{site} \sim StudentT(3, 0, 2.5)$$

$$\alpha_{transect} \sim Normal(0, \sigma_{transect})$$

$$\sigma_{transect} \sim StudentT(3, 0, 2.5).$$

Midstory stem density models

We used the following weakly regularizing priors where β_0 was the intercept, s_0 was the mean number of stems in all treatments at year 0, $\boldsymbol{\beta}$ was a vector of the coefficients of the covariates, ϕ was the shape parameter of the negative binomial distribution, α_{site} was the coefficient of the site random effect, and $\alpha_{transect}$ was the coefficient of the transect random effect

$$\beta_0 \sim Normal(s_0, 5)$$

$$\boldsymbol{\beta} \sim Normal(0, 2)$$

$$\phi \sim Exp(1)$$

$$\alpha_{site} \sim Normal(0, \sigma_{site})$$

$$\sigma_{site} \sim StudentT(3, 0, 2.5)$$

$$\alpha_{transect} \sim Normal(0, \sigma_{transect})$$

$$\sigma_{transect} \sim StudentT(3, 0, 2.5).$$

Fire behavior metrics

We log-transformed fire maximum fire temperature (˚C, T_{max}), average rate of spread (m/hr, R), and flame length (L_f). For these models we used the following weakly regularizing priors where β_0 was the intercept, β_1 was the coefficient of the Treatment covariate, α_{site} was the coefficient of the site random effect, and x is the average transformed maximum temperature, rate-of-spread or flame length

$$\beta_0 \sim Normal(x, 5)$$

$$\beta_1 \sim Normal(0, 2)$$

$$\alpha_{site} \sim Normal(0, \sigma_{site})$$

$$\sigma_{site} \sim StudentT(3, 0, 2.5)$$

For burn coverage we used the following weakly regularizing priors where ϕ is the shape parameter of the Beta distribution and c_{avg} is the average burn coverage for all burns

$$\beta_0 \sim Normal\left(c_{avg}, 5\right)$$

$$\beta_1 \sim Normal(0, 2)$$

$$\phi \sim Exp(1)$$

$$\alpha_{site} \sim Normal(0, \sigma_{site})$$

$$\sigma_{site} \sim StudentT(3, 0, 2.5)$$

CONCLUSION

Fire seasonality impacts changes in plant community response to frequent, repeated fire in southeastern pine/oak savannas and woodlands. Certain patterns emerged that were supported in both studies reported herein. Frequent fire (every 1–2 years) in the early growing season increased coverage of warm-season grasses. Fire in the latter portion of the growing season and in the dormant season increased coverage of forbs, especially early-summer flowering forbs at our oak-pine savanna site and fall-flowering forbs at our pine woodlands sites. Highly conservative forb species were not detrimentally impacted by fire in any season. Growing-season fire reduced woody resprouting relative to dormant-season fire despite greater fire temperatures in the dormant season, but response of woody plants to fire within the growing-season remains unclear and should be investigated further.

Frequent fire during any season was effective to maintain open woodland and savanna conditions, and fire seasonality only impacted the plant response under certain conditions. Frequent fire (every 1–2 years) was necessary to detect seasonal responses to fire treatments. In our oak-pine savanna study, we did not detect major differences in vegetation response to fire season when burning every 3 years even after 15 years of fire treatments. Sunlight availability also affected the impact of fire on shade-intolerant herbaceous species. Without sufficient (>40%) sunlight penetration in pine woodlands, relatively shade-intolerant species will not respond strongly to fire. Although seasonal impacts of fire may persist, differences may not be relevant because a lack of sunlight is inhibiting growth and spread of relatively shade-intolerant plant species. Thus, reducing canopy coverage to provide adequate sunlight and implementing fire frequently (every 1–2 years) should be priorities when using fire to maintain open pine systems. Within such a fire regime, fire season can be manipulated to further promote desired plant communities.

VITA

Maya Lapp received a Bachelor of Arts degree in Mathematics from the College of Wooster, OH. She first became interested in prescribed fire and wildlife management when working as a Wildlife Technician with the Georgia Department of Natural Resources. She went on to work various jobs in wildlife sciences and ecosystem management in North Carolina, California, and Pennsylvania before returning to school to pursue a Master of Science degree in Wildlife Sciences in the School of Natural Resources at the University of Tennessee.