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# Changes in Plant Composition Following Disturbance in Restored Native Early Successional Communities☆,☆☆

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ABSTRACT

Restoration of nonnative grasslands to native early successional plant communities has been a conservation focus throughout the United States for several decades. In the eastern US, where precipitation exceeds 1 000 mm per year, disturbance is necessary following restoration to prevent early successional communities from progressing into woody-dominated midsuccessional communities. Resulting plant composition may vary among disturbance practices, and knowledge of such effects will help direct maintenance of restored native early seral plant communities. We evaluated the effects of the two most common disturbance practices, prescribed fire and mowing, following restoration of nonnative grasslands to native plant communities via two methods: 1) planting native grasses and 2) forbs and seedbank response without planting, across 11 replicated sites in Tennessee and Alabama, 2018–2020. Specifically, we evaluated how disturbance altered vegetation composition following four treatment combinations (planted mowed, planted burned, seedbank mowed, and seedbank burned) and tall fescue (*Schedonorus arundinaceus*) control from predisturbance conditions. Grass coverage increased in all treatment units, but tended to increase more in mowed treatments than burned treatments. Forb coverage declined in all treatments except seedbank burned, where it increased. Similarly, spring-, summer-, and fall-flowering forbs, which are the focus of conservation programs designed to enhance habitat for pollinators, increased most in seedbank burned. Species richness decreased across all treatments and control, except seedbank burned, where it increased. The species evenness did not differ by treatment. Our results provide insight into how disturbance techniques may alter plant community composition soon after restoration. We recommend managers use prescribed fire instead of mowing if increased forb coverage is important to meet objectives. Furthermore, our results highlight how planting native grasses and forbs is not necessary to restore native early successional plant communities on most sites dominated by nonnative grasses in the eastern United States, where precipitation is not limiting succession.



## Introduction

Restoration and maintenance of native grasslands and other native early successional plant communities is a national and global concern (Samson et al. 2004; Fuhlendorf et al. 2018; Bardgett et al. 2021; Torok et al. 2021). In the eastern United States, native early successional plant communities have been in decline for many decades, largely because of conversion to nonnative grass species, urban development, and woody encroachment (Brennan 1991; Noss et al. 1995; Noss 2013; Keyser et al. 2019). Through the midtwentieth century, tall fescue (*Schedonorus arundinaceus*) was planted for livestock forage and became the most dominant grass throughout the interior of much of the eastern United States,

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whereas bermudagrass (*Cynodon dactylon*) and bahiagrass (*Paspalum notatum*) were planted and replaced native grasses and forbs throughout the coastal plain of the southeastern US (Ball et al. 2015). Additional land was planted to nonnative grasses in the late twentieth century as part of the Natural Resources Conservation Service's (NRCS) Conservation Reserve Program (CRP), whereby retired crop lands were planted primarily to tall fescue (Buckner and Landers 1979; Carmichael Jr. 1997; Rogers and Locke 2013). Thus, nonnative grasses were vastly prevalent and dominated open areas, replacing native grasses and forbs, throughout the eastern US by the late twentieth century (Samson and Knopf 1994, Ball et al. 2015, Barnes 2004, Dykes 2005, Keyser et al. 2019). Additionally, approximately 5.7 million hectares of early successional plant communities were lost to land development in the United States from 1982–2015 (USDA 2018). Similar conditions exist in the western US where nonnative grasses have replaced native species on a majority of public and private lands and altered natural disturbance regimes and associated wildlife communities (Litt and Pearson 2013; Abella et al. 2015; Fusco et al. 2019). As a result of the vast coverage of nonnative grasses, many wildlife species associated with early successional plant communities in the eastern US have experienced dramatic population declines (Brennan 1991; Knopf 1994; Hunter et al. 2001; Brennan and Kuvlesky Jr. 2005; USDA 2009).

More recently, federal and state initiatives have increased restoration of native plant communities on private and public lands across the eastern United States. The goal is to restore ecosystem services, such as improvement of soil and water quality, provide critical components of habitat for various wildlife species that require early successional plant communities, and maintain a diverse native plant community. Stakeholders in this effort are diverse, including conservation biologists, plant ecologists (Noss et al. 2021), state and federal agencies trying to conserve pollinators and other at-risk wildlife (Mawdsley and Humpert 2016), and private landowners with interests in agriculture and livestock (Raynor et al. 2019) or big game (Harper et al. 2021). To address these varied interests, the NRCS offers cost-share programs that provide technical and financial assistance for conservation of early successional communities on private lands (Heard et al. 2000; USDA 2016). Additionally, early-succession management has been included in many State Wildlife Action Plans (Tennessee 2015; Kentucky Department of Fish and Wildlife Resources 2013; North Carolina 2005; Georgia Department of Natural Resources 2015), which guide wildlife management practices on state-owned lands.

Native early successional communities can be restored or established using different methods, and numerous studies have evaluated restoration techniques. Restoration involves converting a plant community dominated by nonnative grasses and forbs to native plants, and removal of nonnative grasses is common (Madison et al. 1995; Washburn et al. 2000; Harper and Gruchy 2009; Hall et al. 2012; GeFellers et al. 2020). Planting native grasses and forbs following treatment to control or eradicate nonnative species is ubiquitously recommended and practiced (Barnes 2004; Burger 2005; Mittelhauser et al. 2011; Wortley et al. 2013). Restoration via planting commonly costs \$450–\$900 $ha^{-1}$, and seeding mixtures designed specifically for pollinators can cost \$2 500 $ha^{-1}$ or more (Monroe et al. 2017; Williams and Lonsdorf 2018; GeFellers et al. 2020). However, recent research suggests restoration of nonnative grasslands in the eastern US using selective herbicide applications along with the seedbank response is just as effective or more so than planting and with considerable cost savings (GeFellers et al. 2020; Harper et al. 2021). This technique performs well on most sites except where soil has been removed and there is no seedbank.

Following restoration, disturbance is necessary to maintain early successional plant communities and prevent succession to semiwoody- and woody-dominated communities. The type of disturbance, as well as the frequency, intensity, and timing of disturbance, affects vegetation composition (Fynn et al. 2004; MacDougall and Turkington 2007; Gruchy and Harper 2014; Harper 2017). Different disturbance regimes are used to benefit various wildlife species. Prescribed fire is commonly promoted to maintain early successional communities, consume thatch, and stimulate the seedbank (Buckner and Landers 1979; Gruchy and Harper 2014). Mowing is the most common method for maintaining openings, but mowing can lead to accumulated thatch and reduced plant species richness, which may have negative effects on habitat quality for some wildlife species (Dykes 2005; Golden et al. 2013; Harper 2017; Gudlin et al. 2019).

Previous research has evaluated the effects of management on early successional communities restored via planting, but no research has compared vegetation change following disturbance on sites that were planted to those restored using the seedbank only in the eastern United States, where average precipitation exceeds 1 000 mm per year (McCoy et al. 2001; Greenfield et al. 2003; Gruchy and Harper 2014). Restoration of native early successional plant communities and the effects of management following restoration have been researched in the tallgrass prairie region of the United States (Howe 1995; Collins et al. 1998; Briggs et al. 2002), but similar research has not been conducted in eastern grasslands. The composition of planted communities may be different from those comprised of seedbank response only (GeFellers et al. 2020), and disturbance thus may further lead to differential plant community composition. Various restoration or disturbance combinations may promote different plant species and influence plant species richness, evenness, and diversity, which can affect resource availability for wildlife, including availability of pollen and nectar resources (McCoy et al. 2001; Van Nuland et al. 2013; Halbritter et al. 2015). The evaluation of plant composition change following different disturbances in plant communities restored using planting or seedbank response can provide managers with valuable insight that could help them reach their management objectives.

We implemented a field experiment across Tennessee and north Alabama, United States, to assess the effects of common field management practices on plant composition and the trajectory of plant succession in fields previously dominated by tall fescue. These fields had been restored previously either by 1) eradicating tall fescue with a broadcast herbicide application in the fall, then planting a mixture of native forbs and grasses the following spring, or 2) eradicating tall fescue with a broadcast herbicide application in the fall, then allowing the seedbank to respond without planting (described below and in GeFellers et al. 2020). Following evaluation of the restoration methods (GeFellers et al. 2020), our research objective was to compare effects of the two most common practices to maintain an early successional plant community in the eastern US (burning and mowing) on vegetation composition in early successional communities that had been established using the two restoration methods. We hypothesized burning would stimulate increased forb coverage, including spring-, summer-, and fall-flowering forbs important to pollinators, because burning consumes the litter layer and stimulates germination of the seedbank (Buckner and Landers 1979; Harper 2007; Gruchy and Harper 2014). We hypothesized mowing would lead to increased grass coverage because many perennial grasses spread by tillering and do not rely necessarily on germination from the seedbank. We hypothesized that regardless of disturbance type, seedbank response units would have greater coverage of native forbs and grasses and less coverage of nonnative forbs and grasses than planted units because herbicide applications have limited application in planted units because of potential harm to planted species. Lastly, we hypothesized that burning and mowing would result

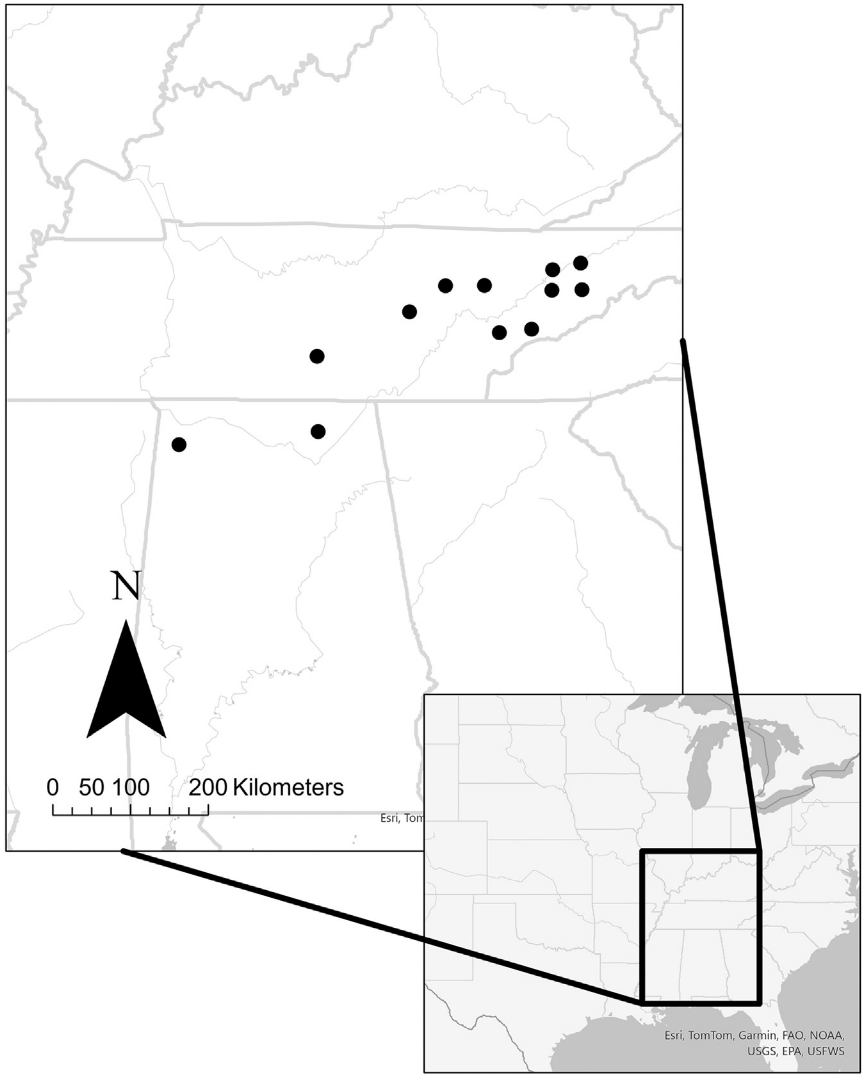


**Figure 1.** Map of 11 study site locations in Tennessee and Alabama, United States, 2018–2020.

in similar amounts of woody and semiwoody species (including brambles and vines) because those plants typically resprout following fire and mowing unless setback more than once during the growing season.

## Methods

### *Study area*

We conducted our study at 11 sites in Tennessee and Alabama, United States (Fig. 1). Each site was represented by a 0.8 ha 2.0 ha field dominated by tall fescue. State and federal agencies that owned the properties chose the sites we used in our study because they were considered representative fields under their ownership and they were dominated by nonnative grasses when the study began. Six of the study sites were on Tennessee Valley Authority property in Bedford, Hamblen, Jefferson, Monroe, and Sevier counties, TN, and Franklin County, AL. Three study sites were on Tennessee Wildlife Resources Agency (TWRA) property in Cocke, Cumberland, and White Counties, TN. One study site was in Cades Cove within the Great Smoky Mountains National Park in Blount County, TN. Another study site was on Alabama Department of Conservation and Natural Resources (ADCNR) property in Jackson, AL. Our study was initiated in 2015 by partitioning each field into three equally-sized treatment units (planted, seedbank, and tall fescue control). Tall fescue was treated with an application of glyphosate at all study areas in November 2015 prior to initiating two establishment treatments (planted and seedbank) in spring 2016 as described by GeFellers (2019). Evaluation of the establishment techniques was described by GeFellers et al. (2020) and Harper et al. (2021). Elevation at study sites ranged from 180 m at the Franklin County, AL, site to 658 m above mean sea level at the Cumberland County, TN, site. Mean daily temperature across the study area ranged from −4°C to 33°C, with mean annual precipitation ranging from 114 cm to 152 cm (National Oceanic and Atmospheric Administration 2019). Soils at 10 of the 11 sites were loam or silt or loam, whereas one site (Jackson County, AL) had silt clay (Soil Survey Staff 2021). We divided the planted and seedbank units at each site into two equal-sized units and randomly assigned mowing or burning to each in the spring of 2019. This approach created four treatment units that varied from 0.36 ha to 0.95 ha at each of the 11 sites: planted mowed, planted burned, seedbank mowed, and seedbank burned. We maintained the tall fescue-dominated control at each site with an annual late-winter mowing, which is consistent with how idle fields dominated by tall fescue are maintained in the region (Dykes, 2005; Harper 2007).

### Burning treatments

Location managers installed firebreaks around the appropriate units and implemented prescribed fire in those units at each site. We used backing fires at each site to establish a blackened area on the downwind side of the burn unit adjacent to the firebreak, and if conditions allowed, backing fires were used to burn the entire unit. Flanking and heading fires were used when conditions did not allow backing fires to consume fuel. All fires were considered relatively low intensity, with flame lengths averaging 0.8 m. We conducted all burns at each site in 2019 and 2020 during the late dormant season (February–early April), which is consistent with when most prescribed fire is implemented to maintain fields enrolled in conservation programs (Dryden 2001; Harper 2007). All burns were conducted within the following prescription parameters: relative humidity 20–50%, wind speed 0–16 km · $h^{-1}$, temperature 1–24°C, and cloud cover < 50%. Complete burn coverage was achieved during each burn event.

### Mowing treatments

Location managers or contractors mowed the appropriate units at each site in 2019 and 2020 using tractor-mounted rotary mowers during late winter. All units were mowed to a height of approximately 25 cm.

### Herbicide treatments

Throughout the study, we used selective herbicide applications to control nonnative species in all treatment units. We used 15-L backpack sprayers with wands (Solo USA, Newport News, Virginia) and a 95-L ATV sprayer (Cabelas, Sydney, Nebraska) equipped with a spray gun (Green Garde, H.D. Hudson Manufacturing Company, Chicago, IL) to make spot-spray applications of glyphosate, imazapic, imazapyr, clethodim, or triclopyr according to herbicide label recommendations. We reduced coverage of undesirable species (i.e., nonnative invasive plant species and two native species, blackberry [*Rubus* spp.] and black locust [*Robinia pseudoacacia*], if coverage exceeded 30% to remain in compliance with recommendations from state agency private lands biologists with the ADCNR, the TWRA, and NRCS biologists for conservation programs). We conducted spot-spray applications once during spring and/or once during summer to control undesirable warm-season species, such as johnsongrass (*Sorghum halepense*), sericea lespedeza (*Lespedeza cuneata*), or bermudagrass. We conducted one fall or winter application to control undesirable cool-season species, such as common henbit (*Lamium amplexicaule*) or purple deadnettle (*Lamium purpureum*), if needed. We used spot-spray applications with selective herbicides, such as imazapic, in planted units in accordance with recommendations of private lands biologists with ADCNR and TWRA to remain in compliance with what is permitted and recommended to landowners enrolled in state conservation programs. Herbicide applications were limited to control some species, such as bermudagrass or sericea lespedeza, because there is no herbicide that will kill bermudagrass without killing planted native warm-season grasses, and there is no herbicide that will kill sericea lespedeza without killing planted forbs. We controlled nonnative invasive species with spot-spray applications in seedbank units whenever they occurred, regardless of percent coverage. We used triclopyr (0.10 kg ai · $ha^{-1}$) and fluroxypyr (0.31 kg ai · $ha^{-1}$) and an ATV sprayer in May 2019 to spot-spray control units to limit woody encroachment and maintain a tall fescue control. No additional herbicide treatment or spot-spraying was used in control units.

### Data collection

We recorded vegetation composition in each treatment unit and control mid-June through early August 2020. We used line-point intercept sampling along four 50-m transects in all treatment units to measure vegetation coverage. Each transect was systematically placed equal distance from one another, and each transect was at least 10 m from the edge of each unit. We identified vegetation to species at 2-m intervals along each transect with each transect, providing 25 sampling points per transect. We recorded all species present at each sampling point if more than one plant occurred in the vertical space above or below the transect sampling point. We calculated percent coverage of various plants and plant groups by dividing the total no. of detections on each transect by the no. of sampling points on the transect. We then calculated the average species or plant group coverage across each unit by averaging the percent coverage estimates of all the transects in that unit. We used the USDA plants website (plants.usda.gov) to divide plant species into four plant groups and to further divide plant groups into other categories, such as native or nonnative. Our four main plant groups were grass, forb, semiwoody, and woody. Semiwoody included all bramble (e.g., *Rubus* spp.) and vine species detected. Woody included all tree and shrub species detected. We also divided plants into native and nonnative species groups. We further divided grass into cool-season (CSG) or warm-season grasses (WSG) and forbs into spring-, summer-, and fall-flowering groups. Flowering season was determined for each species using the USDA plants website.

We calculated Simpson's *E* index and Shannon–Weiner index values for each treatment at each site to determine average plant species evenness and diversity. We calculated Simpson's *E* index by summing the no. of detections of a species along the transects within each treatment. We divided the no. of detections for each species by the no. of total detections of all species, and then squared that value. We summed the squared values for all species within each treatment and divided one by that value. We then divided that value by the total no. of plant species detected in each treatment to obtain the index score. Simpson's *E* index indicates how evenly abundance is distributed among species, whereas the Shannon–Weiner index evaluates species richness and evenness to calculate a diversity score. The maximum value for Simpson's *E* index is one, and values nearer one represent greater evenness in the plant community. Greater values for the Shannon–Weiner index represent greater plant diversity.

### Data analysis

We used coverage data collected in 2018 (GeFellers et al. 2020; Harper et al. 2021) in the same fields prior to disturbance (prescribed fire or mowing) to calculate the percent difference in plant group coverage and assess how each disturbance practice affected the plant community after 2 yr of management. We subtracted percent coverage of plant groups in 2018 from the percent coverage of plant groups in 2020 to calculate the percent difference in each treatment following disturbance. We used percent change for species richness, Simpson's evenness, and Shannon's diversity indices because these metrics were not already in percentages. We calculated the percent change by subtracting the 2018 means from the 2020 means and then dividing that calculation by the original (2018) mean and multiplying by 100. We provide both percent coverage values as well as percent change calculations when appropriate in the results text. The data from 2018 were collected during the same time period (midjune–early August) in the same fields using the same sampling protocol as used by GeFellers et al. (2020).

**Table 1**
Mean percent (%) coverage[1] and standard error (SE) of all species groups detected in five early successional plant community treatments across all study sites (n = 11) in Tennessee and Alabama, United States, 2018–2020.

| Life form | Treatment | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Planted mowed | | | | Planted burned | | | | Seedbank mowed | | | | Seedbank burned | | | | Control | | | |
| | 2018 | (SE) | 2020 | (SE) | 2018 | (SE) | 2020 | (SE) | 2018 | (SE) | 2020 | (SE) | 2018 | (SE) | 2020 | (SE) | 2018 | (SE) | 2020 | (SE) |
| Grass[2] | 78.6 | 5.3 | 89.0 | 3.5 | 78.6 | 5.3 | 80.7 | 4.2 | 60.8 | 9.2 | 72.2 | 5.8 | 60.8 | 9.2 | 67.2 | 2.8 | 95.4 | 2.2 | 98.0 | 1.8 |
| NG[3] | 61.3 | 6.7 | 70.3 | 5.5 | 61.3 | 6.7 | 57.0 | 6.6 | 46.9 | 9.4 | 57.8 | 7.0 | 46.9 | 9.4 | 52.8 | 5.0 | 35.5 | 8.4 | 9.9 | 3.2 |
| NNG[4] | 21.1 | 6.9 | 26.1 | 5.4 | 21.1 | 6.9 | 30.0 | 7.1 | 12.0 | 2.8 | 17.7 | 5.3 | 12.0 | 2.8 | 15.5 | 3.5 | 86.5 | 4.0 | 96.5 | 2.3 |
| NNCSG[5] | 5.3 | 2.2 | 5.0 | 2.8 | 5.3 | 2.2 | 1.4 | 0.4 | 6.7 | 2.0 | 6.6 | 3.1 | 6.7 | 2.0 | 1.0 | 0.4 | 85.0 | 3.7 | 95.8 | 2.3 |
| NWSG[6] | 61.0 | 6.6 | 69.2 | 5.5 | 61.0 | 6.6 | 56.6 | 6.6 | 45.1 | 9.2 | 54.6 | 6.9 | 45.1 | 9.2 | 50.7 | 5.2 | 33.8 | 8.5 | 9.7 | 3.2 |
| CSG[7] | 5.3 | 2.2 | 6.0 | 2.8 | 5.3 | 2.2 | 1.72 | 0.6 | 6.8 | 2.5 | 9.8 | 3.7 | 6.8 | 2.5 | 3.1 | 1.4 | 85.0 | 2.9 | 95.8 | 2.3 |
| WSG[8] | 75.9 | 5.2 | 85.0 | 3.4 | 75.9 | 5.2 | 79.5 | 4.0 | 55.3 | 8.6 | 66.9 | 5.6 | 55.3 | 8.6 | 65.6 | 3.1 | 48.2 | 7.2 | 15.1 | 3.8 |
| Forb[9] | 64.3 | 6.7 | 44.6 | 6.6 | 64.3 | 6.7 | 52.3 | 7.2 | 71.1 | 3.5 | 60.9 | 6.4 | 71.1 | 3.5 | 81.9 | 4.8 | 40.6 | 7.3 | 12.1 | 4.6 |
| NF[10] | 48.7 | 7.8 | 34.7 | 6.1 | 48.7 | 7.8 | 40.5 | 6.6 | 51.6 | 5.7 | 49.2 | 6.4 | 51.6 | 5.7 | 75.2 | 5.2 | 26.5 | 7.6 | 9.4 | 4.2 |
| NNF[11] | 25.8 | 6.0 | 14.8 | 4.2 | 25.8 | 6.0 | 20.5 | 7.2 | 30.1 | 5.1 | 25.3 | 4.5 | 30.1 | 5.1 | 25.6 | 6.7 | 18.2 | 2.9 | 3.3 | 1.2 |
| SPFF[12] | 11.1 | 4.7 | 12.6 | 3.1 | 11.1 | 4.7 | 19.3 | 5.2 | 9.7 | 2.7 | 29.8 | 5.9 | 9.7 | 2.7 | 42.4 | 5.2 | 1.7 | 0.8 | 5.5 | 1.8 |
| SUFF[13] | 15.7 | 2.7 | 30.9 | 4.3 | 15.7 | 2.7 | 43.7 | 6.5 | 12.8 | 2.5 | 48.5 | 6.2 | 12.8 | 2.5 | 72.2 | 5.0 | 11.6 | 3.8 | 8.5 | 2.5 |
| FAFF[14] | 28.0 | 7.0 | 37.5 | 5.8 | 28.0 | 7.0 | 28.1 | 7.3 | 35.7 | 7.2 | 48.7 | 6.5 | 35.7 | 7.2 | 74.6 | 5.0 | 16.8 | 6.7 | 9.4 | 3.1 |
| Semiwoody[15] | 13.1 | 3.9 | 16.5 | 3.7 | 13.1 | 3.9 | 15.6 | 3.9 | 11.5 | 3.7 | 21.5 | 4.0 | 11.5 | 3.7 | 22.6 | 4.8 | 8.7 | 3.4 | 2.6 | 1.2 |
| Woody[16] | 0.5 | 0.1 | 3.8 | 1.3 | 0.5 | 0.1 | 2.3 | 0.8 | 0.2 | 0.1 | 5.8 | 1.7 | 0.2 | 0.1 | 5.4 | 1.8 | 0.4 | 0.2 | 2.3 | 1.2 |
| NS[17] | 85.9 | 4.9 | 87.4 | 3.8 | 85.9 | 4.9 | 81.2 | 6.0 | 82.0 | 4.3 | 85.6 | 3.4 | 82.0 | 4.3 | 95.6 | 1.2 | 56.4 | 5.9 | 22.0 | 6.0 |
| NNS[18] | 41.9 | 7.0 | 38.6 | 6.2 | 41.9 | 7.0 | 45.6 | 8.0 | 39.7 | 5.8 | 38.4 | 6.4 | 39.7 | 5.8 | 39.5 | 6.3 | 90.9 | 2.9 | 96.8 | 1.8 |

[1] Coverage of the different plant types does not sum to 100 because multiple plant types commonly occur in the same vertical space as detected and recorded at the sampling point using the line-point intercept sampling method.
[2] All grasses present in each treatment.
[3] NG consists of all native grasses present in each treatment.
[4] NNG consists of all nonnative grasses present in each treatment.
[5] NNCSG consists of all nonnative cool-season grasses present in each treatment.
[6] NWSG consists of all native warm-season grasses present in each treatment.
[7] CSG consists of all cool-season grasses in each treatment.
[8] WSG consists of all warm-season grasses in each treatment.
[9] All forbs are present in each treatment.
[10] NF consists of all native forbs present in each treatment.
[11] NNF consists of all nonnative forbs present in each treatment.
[12] SPFF (spring-flowering forbs) consists of all forb species detected that flower in spring.
[13] SUFF (summer-flowering forbs) consists of all forb species detected that flower in summer.
[14] FAFF (fall-flowering forbs) consists of all forb species detected that flower in fall.
[15] Semiwoody consists of bramble and vine species.
[16] Woody consists of tree and shrub species.
[17] NS consists of all native plant species present in each treatment.
[18] NNS consists of all nonnative plant species present in each treatment.

We used a randomized block study design with the treatment unit serving as the experimental unit. The response for plant groups was the difference between averaged measurements from 2018 and 2020 in each treatment unit. The response for species richness, Simpson's evenness, and Shannon's diversity was the percent change between averaged measurements from 2018 and 2020 in each treatment unit. We conducted analysis of variance analysis of variance in program R (R Core Team 2020) to determine the effects of treatment on vegetation composition and diversity indices. If treatment effects were significant, we used package "emmeans" (Lenth 2018) to compare means using Tukey's Honest Significant Difference (HSD) $P$-value adjustment. We used a significance level of $\alpha = 0.05$ for all contrasts.

## Results

Change in total grass coverage from 2018 to 2020 did not differ by treatment ($F = 0.7$, $P = 0.55$). Total grass coverage increased in all management treatments as well as control (Table 1). Total grass coverage increased 13.2% and 18.8% in planted mowed and seedbank mowed, and 2.7% and 10.5% in planted burned and seedbank burned, respectively.

Change in coverage of total native grasses from 2018 to 2020 was greater in control than in all of the management treatments ($F = 8.96$, $P < 0.0001$). Total native grass coverage decreased to −72.7% in control. The change in total native grass coverage was much less and similar ($P > 0.3$) in all management treatments. The change in coverage of total nonnative grasses from 2018 to 2020 did not differ by treatment ($F = 0.3$, $P = 0.86$). However, the resulting coverage of total nonnative grasses in 2020 remained greater in planted treatments averaged together (28.1% coverage) than in seedbank treatments averaged together (16.6% coverage).

Change in total warm-season grass coverage differed by treatment ($F = 14.69$, $P < 0.0001$). Total warm-season grass coverage increased in all management treatments similarly ($P > 0.78$), but decreased in control. Change in native warm-season grass coverage differed by treatment ($F = 12.7$, $P < 0.0001$). Change in native warm-season grass coverage was similar ($P > 0.65$) among management treatments but decreased in control.

Change in nonnative cool-season grass coverage differed by treatment ($F = 5.07$, $P < 0.001$). Seedbank burned ($P < 0.002$) and planted burned ($P < 0.007$), contained less nonnative cool-season grass than control by 2020, but change in nonnative cool-season grasses was similar between control, seedbank mowed ($P > 0.06$), and planted mowed ($P > 0.06$). All management treatments reduced coverage of nonnative cool-season grasses similarly ($P > 0.65$), but burning tended to reduce them more than mowing.

Change in total forb coverage differed by treatment ($F = 8.31$, $P < 0.0001$) following disturbance from 2018 to 2020. Total forb coverage decreased in seedbank mowed, planted burned, planted mowed, and control (−14.3%, −18.7%, −30.6%, and −70.2%, respectively), but forb coverage increased 15.2% in seedbank burned. Change in coverage of native forbs differed by treatment ($F = 13.35$, $P < 0.0001$), which decreased similarly ($P > 0.15$) among seedbank mowed, planted burned, and planted mowed (−4.7%, −16.8%, and −28.7%, respectively), but increased 45.7% in seedbank burned.

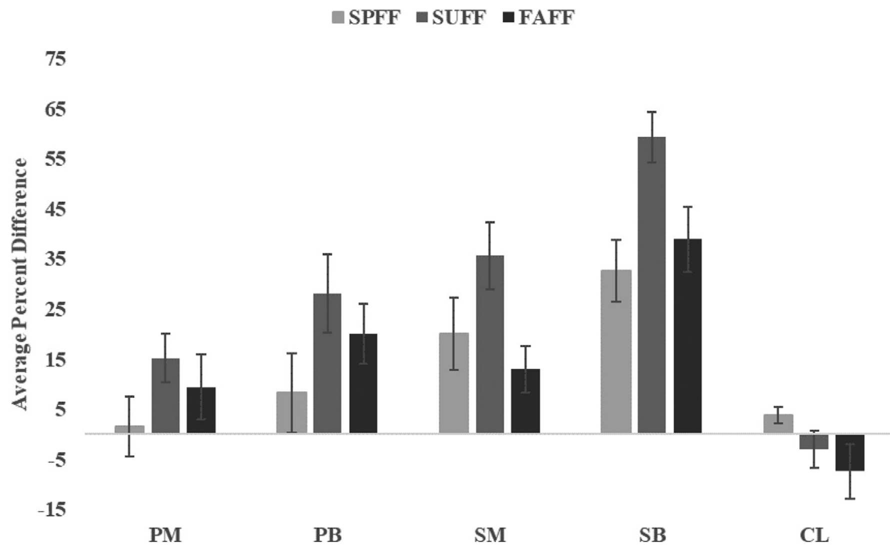


**Figure 2.** Mean percent difference (standard error) in SPFF, SUFF, and FAFF coverage from June–August 2018 to 2020 at all study sites (n = 11) in Tennessee and Alabama following burn and mow treatments. CL indicates control; FAFF, fall-flowering forb; PB, planted burned; PM, planted mowed; SB, seedbank burned; SM, seedbank mowed; SPFF, spring-flowering forb; SUFF, summer-flowering forb.

Change in nonnative forb coverage did not differ by treatment ($F = 0.74$, $P = 0.567$).

Change in coverage of spring- ($F = 8.72$, $P < 0.0001$), summer- ($F = 18.08$, $P < 0.0001$), and fall- flowering forbs ($F = 11.14$, $P < 0.0001$) differed by treatment. Coverage of spring-flowering forbs increased more in seedbank burned than planted burned, planted mowed, and control ($P < 0.002$), which corresponded with an increase in grass in those treatments (Fig. 2). Coverage of summer-flowering forbs increased more in seedbank burned, seedbank mowed, and planted burned than control ($P < 0.0022$). The increase in coverage of summer-flowering forbs in planted mowed did not differ from control ($P = 0.14$). Coverage of summer-flowering forbs increased most in seedbank burned, and the increase was greater ($P < 0.03$) in seedbank burned than seedbank mowed, planted burned, and planted mowed. Coverage of fall-flowering forbs increased more in seedbank burned, seedbank mowed, and planted burned than control ($P < 0.05$). Coverage of fall-flowering forbs increased more ($P < 0.006$) in seedbank burned than seedbank mowed, planted mowed, and control.

Change in coverage of semiwoody species differed by treatment ($F = 4.29$, $P < 0.001$). Coverage of semiwoody plants increased more in seedbank burned and seedbank mowed than control ($P < 0.012$), but change of coverage of semiwoody plants was similar among all management treatments ($P > 0.36$). Change in coverage of woody species did not vary among treatments ($F = 1.86$, $P = 0.13$).

Change in species richness differed by treatment ($F = 13.53$, $P < 0.0001$) following disturbance from 2018 to 2020 (Table 2). Species richness decreased similarly ($P > 0.7$) in seedbank mowed, planted mowed, and planted burned, but increased in seedbank burned. Species richness decreased more in control than in all management treatments ($P < 0.003$). We detected treatment effects for the Shannon–Weiner index ($F = 17.84$, $P < 0.0001$). Diversity decreased similarly ($P > 0.32$) in all treatments, but the decrease was greatest ($P < 0.0001$) in control. Simpson's evenness index increased similarly among treatments ($F = 0.63$, $P < 0.63$).

**Table 2**
Species diversity (Shannon–Wiener index), evenness (Simpson's E index), and richness (mean ± standard error) calculated in five early successional plant community treatments across all study sites (n = 11) in Tennessee and Alabama, United States, 2018–2020. Column means with the same letter group within each metric indicate the change in that metric from 2018 to 2020 is not different ($\alpha = 0.05$).

| Treatment | Shannon–Weiner index | | F | *P*-value |
|---|---|---|---|---|
| | 2018 | 2020 | | |
| Planted mowed | 2.6 ± 0.04 | 2.4 ± 0.07 A | 17.84 | ≤ 0.001 |
| Planted burned | 2.6 ± 0.04 | 2.2 ± 0.07 A | | |
| Seedbank mowed | 2.7 ± 0.05 | 2.5 ± 0.08 A | | |
| Seedbank burned | 2.7 ± 0.05 | 2.6 ± 0.07 A | | |
| Control | 2.2 ± 0.04 | 0.9 ± 0.15 B | | |
| | Simpson's E index | | F | *P*-value |
| | 2018 | 2020 | | |
| Planted mowed | 0.26 ± 0.01 | 0.32 ± 0.02 A | 0.63 | 0.6 |
| Planted burned | 0.26 ± 0.01 | 0.29 ± 0.04 A | | |
| Seedbank mowed | 0.31 ± 0.01 | 0.38 ± 0.04 A | | |
| Seedbank burned | 0.31 ± 0.01 | 0.35 ± 0.06 A | | |
| Control | 0.22 ± 0.01 | 0.23 ± 0.02 A | | |
| | Species Richness | | F | *P*-value |
| | 2018 | 2020 | | |
| Planted mowed | 32 ± 1 | 25 ± 1.4 AB | 13.53 | ≤ 0.001 |
| Planted burned | 32 ± 1 | 24 ± 1.9 B | | |
| Seedbank mowed | 31 ± 1 | 27 ± 1.4 AB | | |
| Seedbank burned | 31 ± 1 | 34 ± 1.7 A | | |
| Control | 25 ± 1 | 9 ± 1.4 C | | |

## Discussion

Our study compared the effects of mowing and burning on the trajectory of succession and plant composition in restored early successional plant communities. Burning led to increased native forb coverage in communities responding from the seedbank, but not in areas that were restored by planting native forbs and grasses, which partially supported our hypothesis that burning would increase forb coverage. Burning also resulted in increased coverage of spring-, summer-, and fall-flowering forbs in both seedbank response and planted communities, but the increase in coverage was much greater in seedbank units. Notably, neither burning nor mowing increased coverage of the forb species that were planted in the planted units. Grass coverage increased in all treatment units, but mowing tended to increase it at a greater rate than burning. Plant communities restored using planting and seedbank restoration responded differently to disturbance; hence, restoration method and disturbance type should be considered in efforts to meet management objectives. These results are the first published describing how type of disturbance can influence plant composition following restoration of native early successional plant communities using the seedbank only. Additionally, our study demonstrated that planting is not necessary to restore and maintain native early successional plant communities on a majority of sites dominated by perennial nonnative grasses in the eastern US, regardless of the type of disturbance implemented.

Total grass coverage increased at a similar rate in all management treatment units, consistent with other studies that used dormant- and early growing-season fire to maintain early successional plant communities (Whitehead and McConnell 1980; Manley 1994; Brockway et al. 2002; Gruchy and Harper 2014). In 2018, grass coverage was greater in planted units than in seedbank units, and grass coverage remained greater in planted units following disturbance. In fact, grass coverage in all treatments was in excess of what is selected by most wildlife that use early successional communities (Herkert 1994; Granfors et al. 1996; Warren and Anderson 2005; Unger et al. 2015; Brooke et al. 2016). The coverage of native grass that was maintained in the seedbank units (approximately 50%) substantiated that planting native grasses is not necessary when restoring native plant communities on most sites in the eastern US where tall fescue or other nonnative grasses dominate the site. In fact, following planting, native grasses commonly become too dense for management objectives within 2–3 yr, necessitating management to decrease grass coverage and increase forb coverage and overall plant diversity (Gruchy and Harper 2014; Brooke and Harper 2016).

The occurrence of nonnative plant species, especially nonnative grasses, is a common management concern when restoring and managing early successional plant communities, and periodic disturbance can favor the establishment of nonnative species (Kuebbing et al. 2014). In summer 2020, following the initial application of glyphosate in autumn of 2015 to eradicate tall fescue in the treatment units, nonnative cool-season grass coverage was only 1–6.5%, indicating a single fall herbicide application was effective at controlling this nonnative perennial cool-season grass (GeFellers et al. 2020). Following eradication of tall fescue in 2015, coverage of nonnative grasses remained greater in planted units than seedbank units from 2018 to 2020 because of the inability to spot-treat various nonnative warm-season grasses, notably bermudagrass, in planted treatments because any herbicide treatment that controls bermudagrass also kills planted native grass species. Spot-spraying nonnative forbs once per year in each of the management units was effective at preventing nonnative forbs from exceeding 30% coverage.

A desirable forb component usually is an objective when managing early successional plant communities (Harper 2017; Meissen et al. 2020). Forbs provide forage, seed, cover, and nectar for a wide variety of wildlife species (Robel 1963; Healy 1985; Steffan-Dewenter and Tscharntke 2001; Lashley et al. 2011; Nanney et al. 2018). In seedbank and planted units, mowing reduced forb coverage, whereas burning increased forb coverage in seedbank units. Native forb coverage increased (47.5%) only in the seedbank burned treatment. Forb coverage did not increase in planted burned, likely because there was 80% grass coverage in planted burned by 2020. Grman et al. (2021) also reported that planted native grasses suppressed forb coverage. Mowing in planted mowing led to nearly 90% grass coverage by 2020. Mowing typically promotes thatch buildup (Gruchy 2007) and could further suppress forb response in both seedbank mowed and planted mowed.

The combination of seedbank restoration and burning increased coverage of spring-, summer-, and fall-flowering forbs at a greater rate than any other restoration or management combination, providing pollinators with more food and nest structure resources. Many species of pollinators are dependent on early successional plant communities, and forb coverage is critical for pollinator food resources (Ginsberg 1983; Teer 1996; Althoff et al. 1997; Hunter et al. 2001; Wilkerson et al. 2014). Greater coverage of forbs provides more pollen and nectar resources to a wide range of insect pollinators, but the availability of pollen and nectar resources throughout the growing season should be considered when restoration focuses on pollinators (Steffan-Dewenter and Tscharntke 2001). Insect pollinators also require nest sites, and many species nest in forb stems (Black et al. 2011).

A variety of plant species with relatively even distribution can be an important consideration when managing early successional plant communities, as increased species diversity and evenness may provide more food or cover resources with better distribution for wildlife through the year with different timing of plant phenology (Levine and D'Antonio 1999; Wilsey and Potvin 2000; Steffan-Dewenter and Tscharntke 2001; Tracy and Sanderson 2004; Fontaine et al. 2006). Plant species richness has been linked to more diverse insect populations as well as increased nutritional carrying capacity for species such as white-tailed deer (*Odocoileus virginianus*; Knops et al. 1999; Harper et al. 2021). Although relatively few private landowners may be interested in plant species richness or insect populations per se, we stress how management of early successional communities on private land is important because more private landowners manage their land for deer than any other species (McShea 2012). As private landowners learn the value of promoting increased diversity of native plants, enhanced habitat for pollinators and their populations may result by default. Species evenness increased following all management treatments, and evenness was greater in 2020 than in 2018 prior to any management treatment (GeFellers et al. 2020). Evenness may be especially important for pollinators that rely on floral resources in spring, summer, and fall. However, we documented an increase in species richness only in seedbank burned where litter was consumed and grass dominance was reduced, allowing the seedbank to germinate. There was a negative trend in species diversity following all treatments, but the change was least in seedbank burned ($< 1\%$). The combination of seedbank restoration and burning may help with plant community persistence, productivity, and overall function by increasing species richness and evenness. The reduction in species richness in control from 2018 to 2020 was the result of the herbicide application in 2019 to control encroaching woody and semiwoody plants, which also reduced coverage of some forbs present and maintained a tall fescue-dominated control.

There were no trends in the change of coverage of semiwoody or woody plants. Coverage of both semiwoody and woody species was relatively low prior to treatment, but after 2 yr of management, semiwoody plants increased to approximately 22% coverage in seedbank treatments. The presence of various semiwoody plants, such as blackberry and northern dewberry (*Rubus flagellaris*), provides additional food and cover resources for many wildlife species (Badyaev 1995; Moore et al. 2010; Nanney et al. 2018). Although we primarily used low-intensity backing fire in the burn treatments, fire intensity was sufficient to at least top-kill semiwoody or woody plant species. In both fire and mow treatments, semiwoody and woody species continued to resprout and persist. These results are consistent with other studies that reported dormant-season fire or annual mowing may control but not eradicate woody species (Drewa et al. 2002; Dykes 2005; Gruchy et al. 2009; Robertson and Hmielowski 2014).

## Management Implications

Disturbance is required to maintain early successional communities in the eastern US, regardless of establishment or restoration technique. After documenting the change in vegetation composition following the two most common disturbance practices used to manage fields and other open areas in the eastern US, we recommend managers consider using prescribed fire instead of mowing if increased forb coverage is important in helping meet their management objectives. Forb coverage is important with regard to forage for white-tailed deer, nectar for pollinators, insect and seed production for birds, and cover for gamebird broods and many songbird species. Where increased grass coverage is desirable, planting and mowing can be used to achieve management goals. However, few if any management objectives would warrant more grass coverage than what we documented following establishment from the seedbank and prescribed fire. Although we used fire and mowing for 2 yr in succession, the frequency and timing (season of burning) of disturbance may be altered depending on management objectives and plant community response. We encourage managers not only in the eastern US but in other systems as well to consider using the seedbank response instead of planting when restoring native plant communities following eradication of nonnative grasses where they dominate the site because flexibility in herbicide use is an important consideration when many herbicides required to control undesirable plants also would kill planted species.

## Data Availability Statement

Data will be made available by C. Harper upon reasonable request.

## Ethical Approval

No ethical approvals were needed for this project.

## CRediT authorship contribution statement

**Bonner L. Powell:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **J. Wade GeFellers:** Writing – review & editing, Validation, Methodology, Data curation. **David A. Buehler:** Writing – review & editing, Validation, Investigation. **Christopher E. Moorman:** Writing – review & editing, Validation, Investigation. **John M. Zobel:** Writing – review & editing, Validation, Investigation, Formal analysis. **Craig A. Harper:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2024.10.006.

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