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Research Article

Plant Community Response and Implications for Wildlife Following Control of a Nonnative Perennial Grass

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ABSTRACT Restoration of early successional plant communities dominated by nonnative plant species is a central focus of many state and federal agencies to improve habitat for wildlife associated with these communities. Restoration efforts largely have concentrated on controlling nonnative species followed by planting native grasses and forbs. However, there are numerous establishment problems associated with planting that warrant evaluation of alternative approaches for restoration. We conducted a field experiment to compare vegetation composition and structure as related to habitat for focal wildlife among plant communities established by planting (Planted) native grasses and forbs and revegetation from the seedbank (Seedbank) without planting following control of tall fescue (*Schedonorus arundinaceus*) at 15 replicated sites in Tennessee and Alabama, USA. Planted and Seedbank treatments produced similar plant communities. Vegetation structure providing cover for nesting and brooding northern bobwhite (*Colinus virginianus*) and wild turkey (*Meleagris gallopavo*) was similar between Seedbank and Planted treatments except native grass cover was greatest in Planted, and we recorded greater openness at ground level in Seedbank than Planted or tall fescue control (Control). Abundance of northern bobwhite food plants and selected white-tailed deer (*Odocoileus virginianus*) forage were similar between Planted and Seedbank treatments, but nutritional carrying capacity for deer was greatest in Seedbank. Despite similarities in food abundance, and even though all forbs included in the planting mixtures were food plants, the majority of food plants in Planted were from the seedbank. The compositional and structural characteristics deemed most influential in previous studies to selection of breeding sites by dickcissel (*Spiza americana*), field sparrow (*Spizella pusilla*), grasshopper sparrow (*Ammodramus savannarum*), Henslow's sparrow (*Ammodramus henslowii*), and northern bobwhite were similar in Planted and Seedbank. Tall fescue Control was most similar to characteristics of eastern meadowlark (*Sturnella magna*) breeding sites. Revegetation following Seedbank produced a plant community that provided habitat for many wildlife species equal to or better than Planted and was 3.7 times less expensive than Planted. © 2021 The Wildlife Society.

KEY WORDS conservation programs, early successional communities, grassland restoration, grassland songbirds, northern bobwhite, seedbank, tall fescue, white-tailed deer, wild turkey.

Restoration of native grasslands and other early successional communities dominated by forbs, grasses, and other herbaceous plants representative of an early seral stage is a conservation focus in the eastern U.S. (Noss et al. 1995, Harper 2017, Keyser et al. 2019). Substantial land-use changes through urbanization, intensified agriculture, and commercial forestry have reduced native, early-successional plant communities (Ramankutty and Foley 1999, Drummond and Loveland 2010), and associated wildlife have experienced steep declines in recent decades (Brennan 1991, Peterjohn and Sauer 1997, Kirkland and Hart 1999, Pruitt 2000, Mcchesney and Anderson 2015). Conservation efforts have concentrated on converting row-crop agriculture and nonnative grassland to native plant communities, particularly to increase and enhance habitat for conservation-priority species,

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such as northern bobwhite (*Colinus virginianus*; hereafter bobwhite) and grasshopper sparrow (*Ammodramus savannarum*) (Johnson and Schwartz 1993, Delisle and Savidge 1997, Herkert 1998, Fletcher et al. 2006, Crosby et al. 2015).

Conversion of nonnative grasslands to native plant communities has been a major objective because of the considerable negative effects on the diversity and function of native early successional plant communities (Rudgers and Clay 2007, Barnes et al. 2013). In the eastern U.S., tall fescue (*Schedonorus arundinaceus*) is the most commonly occurring nonnative grass covering approximately 15 million hectares (Ball et al. 2003). Tall fescue is an introduced, sod-forming, cool-season grass widely promoted by forage agronomists and soil conservationists from the 1940s–1970s, and more recently through the United States Department of Agriculture-Natural Resources Conservation Service's (USDA-NRCS) Conservation Reserve Program (CRP) as a livestock forage and to aid in protection against soil erosion (Carmichael 1997, Rogers and Locke 2013). Tall fescue presents problems for various wildlife because of its growth habit and its association with an endophytic fungus (*Neotyphodium coenophialum*) that infects >90% of the grass (Bacon and Siegel 1988, Stuedemann and Hoveland 1988, Ball et al. 2003). The dense structure of tall fescue at ground level suppresses the seedbank, lowering plant diversity (GeFellers et al. 2020); restricts movement of small wildlife species, and lacks vertical structure important for bobwhite chicks, wild turkey (*Meleagris gallopavo*) poults, and numerous other ground-feeding wildlife species (Barnes et al. 1995, Washburn et al. 2000, Harper et al. 2007, Barnes et al. 2013). The endophyte fungus compounds the problem by giving tall fescue a competitive advantage over native plant species (Clay 1990, Latch 1993, Hill et al. 1996, Salminen et al. 2005, Rudgers et al. 2010), especially during drought conditions; this grass also releases toxic ergot alkaloids that have negative effects on wildlife (Betsill et al. 1979, Madej and Clay 1991, Clay et al. 1993, Coley et al. 1995, Conover and Messmer 1996).

State wildlife agencies across most of the eastern U.S., along with the USDA-NRCS and USDA-Farm Service Agency, actively promote conversion of nonnative grasslands to native plant communities through conservation programs, such as CRP, Conservation Reserve Enhancement Program (CREP), and Environmental Quality Incentives Program (EQIP). The conversion from nonnative to native plant communities is intended to increase and enhance habitat for species of concern that require early successional plant communities (Allen and Vandever 2012, Kentucky Department of Fish and Wildlife Resources 2013, Georgia Department of Natural Resources 2015, Tennessee Wildlife Resources Agency 2015, USDA-NRCS 2018). Although some grassland obligate songbirds, such as eastern meadowlark (*Sturnella magna*), may use fields dominated by nonnative grasses for nesting (McCoy et al. 2001, Moorman et al. 2017), conversion to native plant communities offers benefits to a broad suite of species. Species benefiting from conversion include conservation-priority species such as grasshopper sparrow and Henslow's sparrow (*Ammodramus henslowii*) as well as species commonly selected for management by private landowners, such as white-tailed deer (*Odocoileus virginianus*) and wild turkey (Nagy-Reis et al. 2019, Reiley et al. 2019, Lituma and Buehler 2020).

Enrollment in most state and federal conservation programs requires landowners to plant a native seed mixture following control of nonnative grasses such as tall fescue. Several problems are commonly associated with planting, including improper site preparation and equipment setup, lack of weed control options that will not harm planted species, and high seed costs, which are paid with taxpayer and sportsman dollars through conservation programs (Harper et al. 2007, Kettenring and Adams 2011). An alternative approach to circumvent establishment problems and cost may be to relax the planting requirement. Allowing the naturally occurring seedbank to revegetate the site following eradication of nonnative species could allow more options for controlling undesirable vegetation (e.g., nonnative invasive species), eliminate planting and site preparation issues, and reduce costs because seed purchase would not be necessary.

We conducted a field experiment to evaluate plant community response and associated effects on various habitat components for selected wildlife species following tall fescue control and revegetation via planting a native grass/forb mixture and via revegetation from the seedbank without planting. We evaluated effects on vegetation composition and structure for a number of species: 1) 5 grassland songbirds undergoing population decline and identified as priority species in conservation programs; 2) northern bobwhite, which also is undergoing population decline and requires early successional plant communities; and 3) white-tailed deer and wild turkey because they are primary focal species of private landowners in the eastern U.S. Deer and turkeys are considered generalist species, but their habitat may be improved by restoring early successional plant communities. We measured cover of food plants for bobwhite and measured forage availability for deer. We hypothesized plant community composition following planting would favor native warm-season grasses, whereas revegetation from the seedbank without planting would produce more forb cover, which would increase forage availability for white-tailed deer and food plants for northern bobwhite. We hypothesized that vegetation structure following planting and revegetation from the seedbank would be similar and would be favorable to wildlife that prefer taller structure, but that tall fescue control would provide structure more favorable to songbirds that prefer shorter structure.

STUDY AREA

We conducted our study across 15 fields dominated (>75% cover) by tall fescue in Tennessee and northern Alabama, USA (Fig. 1). The fields we used historically were hayed or grazed, but each had been idle from haying or grazing for >10 years prior to our study and maintained by annual mowing, representing standard management of such fields, which are ubiquitous in the region (Dykes 2005, Rogers and

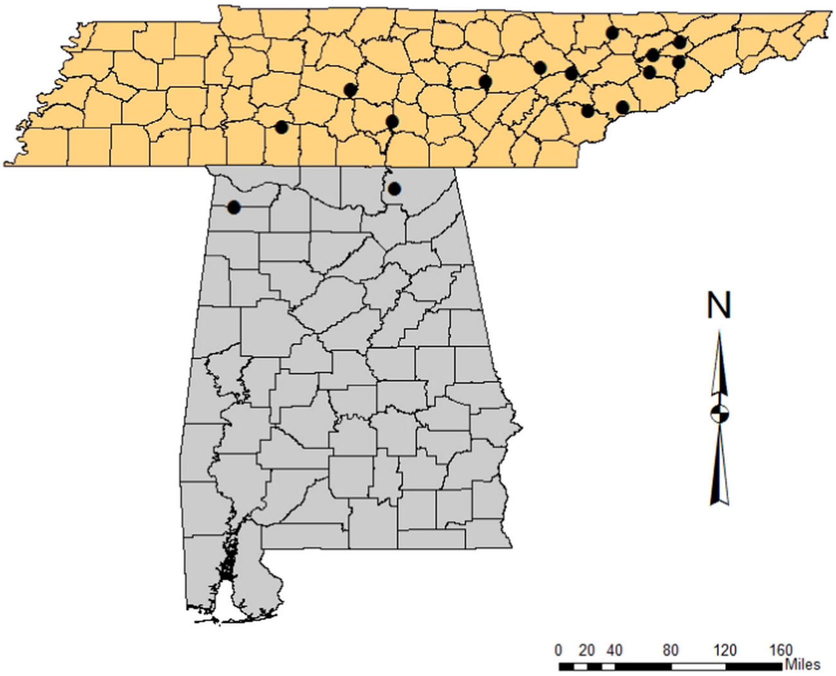

Figure 1. Map of 15 study site locations in Tennessee and Alabama, USA, 2016–2018, where we compared vegetation composition and structure as related to several components of habitat for focal wildlife.

Locke 2013). Although the fields were dominated by tall fescue, each was undergoing succession with various forbs (e.g., Canada goldenrod [*Solidago canadensis*], wingstem [*Verbesina alternifolia*]), and brambles (*Rubus* spp.) pioneering from the seedbank, providing a different structure than that present in tall fescue fields maintained for hay or pasture production. Fields ranged in size from 2.2 to 5.3 ha (3.4 ± 0.2 [SE], $n = 15$). Seven study sites were on Tennessee Wildlife Resources Agency property in Cocke, Cumberland, Lawrence, Roane, Union, White, and Williamson counties. Six study sites were located on Tennessee Valley Authority properties in Bedford, Hamblen, Jefferson, Monroe, and Sevier Counties, Tennessee, and Franklin County, Alabama. One study site was on Alabama Department of Conservation and Natural Resources property in Jackson County, and one was in Cades Cove within the Great Smoky Mountains National Park (hereafter Park) in Blount County, Tennessee. Elevations ranged from 181 m to 658 m. Mean daily temperature across the study area ranged from −4°C to 33°C, with mean annual precipitation that ranged 114 cm to 152 cm (National Oceanic and Atmospheric Administration 2019). Soils were classified as silt loam or silty clay at all sites (USDA-NRCS 2019).

METHODS

Study Design

Our experimental design was a randomized complete block design with replication. We divided each field into 3 similar-sized treatment units, and we randomly assigned 1 of 3 treatments (control [Control], seedbank response without planting [Seedbank], and planted [Planted]) to each unit. No treatment was made to change plant community composition in Control units, and we mowed Control units annually in late winter to represent pretreatment conditions throughout the study and represent default management practices common in idle tall fescue fields (Dykes 2005). Treatment units varied in size from 0.8 to 1.6 ha (1.1 ± 0.1, $n = 45$).

Treatment initiation.—We mowed all study sites in October 2015 and allowed them to regrow to 15.2–25.4 cm (Harper 2017). We then broadcast-sprayed glyphosate (2.8 kg active ingredient (ai)/ha) herbicide in Planted and Seedbank units to control tall fescue in November–December 2015. We used spot-spray glyphosate applications in February–March 2016 to control any tall fescue missed during initial applications. We made herbicide applications when temperatures were at or above 10°C to ensure effectiveness of the herbicide because tall fescue actively grows at temperatures as low as 3°C (Gastal et al. 1992, Rogers and Locke 2013).

Planting treatment.—We planted a native warm-season grass and forb seed mixture in Planted treatment units in April–May 2016 (Table S1, available online in Supporting Information). Planted units simulated plantings made on lands enrolled in conservation programs (e.g., CRP and EQIP), and the seed mixture and planting rate were determined by Private Lands Wildlife Biologists with Tennessee Wildlife Resources Agency and Alabama Department of Conservation and Natural Resources who implement their conservation programs. We planted all sites with the same seed mixture excluding the Park site because the National Park Service prohibits introduction of outside genotypic seed sources. Seeds planted at the Park site were collected from within Cades Cove by National Park Service personnel (Table S2, available online in Supporting Information). We used no-till drills (Truax$^{\text{TM}}$ Flex II Series drills, Truax Company Inc., New Hope, MN, USA, and Haybuster® drills, Duratech Industries International Inc., Jamestown, ND, USA) to plant seed. We calibrated and adjusted drills to ensure seed were planted at the recommended seeding rate of 7.3 kg/ha pure live seed and that planting depth was ≤0.64 cm. We made preemergence imazapic (Plateau®, BASF, Research Triangle Park, NC, USA) applications (0.07–0.105 kg ai/ha) within 7 days of planting to control competition (Washburn et al. 1999, Harper et al. 2007).

Natural revegetation treatment.—We allowed the seedbank to revegetate Seedbank units following treatment initiation in October 2015. We later used herbicide applications described below as necessary to remove undesirable vegetation and promote a desirable early-successional, native plant community.

Herbicide applications in Seedbank and Planted treatment units.—To control undesirable plant species during each year of establishment, we made spot-spray applications using 15-L backpack sprayers (Solo USA, Newport News, VA, USA) and/or a 95-L ATV sprayer (Cabelas, Sydney, NE, USA) equipped with a spray gun (Green Garde®, H.D. Hudson Manufacturing Company, Chicago, IL, USA). We used spot-spray applications most often (69% and 86% of all applications made in Seedbank and Planted, respectively). We defined spot-spraying as any herbicide application that did not impact the entire treatment unit. Spot-spray applications on average impacted <20% of any single treatment unit. Broadcast applications impacted 100% of any single treatment unit (31% and 14% of all applications made in Seedbank and Planted, respectively). We made broadcast applications with a tractor and 3-point boom sprayers, ATV sprayer with boom attachment, or 4-nozzle handheld booms (R&D Sprayers, Opelousas, LA, USA). We used broadcast applications during fall/winter when ≥50% of the treatment unit was comprised of undesirable cool-season species and during summer when ≥90% of a treatment unit was comprised of undesirable warm-season species. We used spot-spray applications otherwise. We determined herbicides, application rates, and application timing based on plant species targeted for removal. All herbicide applications were made in accordance with label recommendations and federal laws governing their use. We recorded the number of herbicide applications made and how much of each herbicide was applied to later calculate average costs.

We maintained Planted units throughout the study consistent with what is required to remain in compliance with conservation program rules and according to Private Lands Biologists' recommendations. If we detected >30% cover of johnsongrass (*Sorghum halepense*), crabgrass (*Digitaria* spp.), or Japanese stiltgrass (*Microstegium vimineum*), we spot-sprayed these species with imazapic because they are controlled by this herbicide whereas the planted species are resistant to it. Bermudagrass (*Cynodon dactylon*) also was a common problem in Planted units. We sprayed bermudagrass regardless of percent cover, and we sprayed woody species (i.e., trees and shrubs) in Planted treatment units if they reached 5% cover.

We spot-sprayed undesirable species in Seedbank units on average once/year regardless of coverage. Undesirable vegetation most often included species identified by the Southeast Exotic Pest Plant Council as nonnative invasive species. Commonly occurring undesirable nonnative species included johnsongrass, bermudagrass, crabgrass, sericea lespedeza (*Lespedeza cuneata*), narrowleaf plantain (*Plantago lanceolata*), musk thistle (*Carduus nutans*), and common chickweed (*Stellaria media*). The areas opened by herbicide applications revegetated naturally again. Certain native species, including *Rubus* spp., broomsedge bluestem (*Andropogon virginicus*), and black locust (*Robinia pseudoacacia*), also can dominate open areas. To promote plant species diversity, we reduced these species with the appropriate herbicide application if they exceeded 30% cover, as assessed by our transect data.

Response Variables

Vegetation composition.—We collected all vegetation data from June–August 2016–2018 along 5, 50-m systematically-spaced transects across and throughout each treatment unit at each site and maintained a minimum 10-m buffer from unit edges. We conducted line-point intercept sampling to quantify vegetation composition in all treatments (Herrick et al. 2009). Every plant species that intercepted each line point along each transect was recorded at 2-m intervals. We calculated percent cover of species and vegetation life form (bramble, forb, grass, and woody) by dividing the number of hits of each species or life form by the total number of sampling points per transect. We then averaged percent cover of each species or life form across all transects for each treatment to calculate percent cover.

Vegetation structure.—We measured visual obstruction of vegetation using a modified vegetation profile board (Nudds 1977). The vegetation profile board was 2-m tall and divided into 5 alternating-colored rectangular sections. The bottom 0.5 m was divided into 2, 0.25-m × 0.25-m sections, whereas the upper 1.5 m was divided into 3, 0.5-m × 0.25-m sections. The bottom 0.25 m represented visual obstruction at the level where bobwhite and other small ground-dwelling wildlife species occur. Visual obstruction 0–0.5 m represented that occurring at the upper end of vegetation height important to brooding wild turkey (Metzler and Speake 1985, Peoples et al. 1996, Wood et al. 2019). Huegel et al. (1986) indicated that visual obstruction ≥1 m was important at deer fawn bedsites because taller vegetation may maintain more stable temperatures than shorter vegetation. We recorded 2 visual-obstruction measurements along each transect 10 m on either side of center. One person knelt at plot center and estimated visual obstruction by placing each of the 5 sections into 1 of 6 categories (0 = no vegetation, 1 = 1–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, and 5 = 81–100% visual obstruction). We qualitatively compared visual obstruction measurements across treatment units to that reported as used by wild turkey, bobwhite, and deer in other studies.

We used measurements from a ground-sighting tube to provide an index of openness at ground level (Gruchy and Harper 2014). We recorded 2 sight-tube measurements along each transect at 14 and 34 meters. The observer looked through the sighting tube while another team member placed a 5.1cm-diameter PVC pole in front of the tube. The pole was moved away until the bottom 15 cm was completely obscured by vegetation and then the distance from the pole to the sighting tube was recorded. Openness at ground level is an important habitat component for several wildlife species, as it allows mobility to access food resources and escape predation (Rosene 1969, Harper et al. 2007). We measured litter depth at the 15 m and 35 m intercept along each transect. We collected measurements using a 30.5-cm metal ruler to the nearest 0.5 centimeter from mineral soil to the top of accumulated plant litter.

Structural characteristics of grassland and shrubland bird breeding sites.—Treatment and control units were too small to monitor actual bird use in response to the establishment practices. However, to evaluate the suitability of the vegetation characteristics in treatment and control units to areas actually selected by birds for breeding, we used the same vegetation composition and structural data from 2 published studies located in the same ecoregion. These studies were conducted in relative proximity to our study sites and identified variables characteristic of actual breeding sites selected by dickcissel (*Spiza americana*), eastern meadowlark, field sparrow (*Spizella pusilla*), grasshopper sparrow, Henslow's sparrow, and bobwhite. Vegetation characteristics surrounding songbird and bobwhite nest sites were collected at Fort Campbell Army Installation in Hopkinsville, Kentucky, USA (Giocomo 2005, Giocomo et al. 2008) and Peabody Wildlife Management Area in west-central Kentucky (Brooke et al. 2017). Given the area and landscape requirements of the species we considered, we did not use breeding-site data to speculate on bird use of our study fields, per se, but rather to aid in comparison of treatment and control units as potential breeding sites by the grassland songbirds and bobwhite.

Food availability for bobwhite and forage selectivity by deer.—We classified bobwhite food plants as those producing seed and/or soft mast commonly consumed by bobwhite (Rosene and Freeman 1988, Johnson et al. 2018). We inspected each plant recorded along point-intercept transects to determine if the plant had been eaten by deer. We divided the number of stems that had been eaten by the number of stems available on that plant to measure deer browse intensity and selectivity using the Chesson index (Chesson 1983, Shaw et al. 2010). A fifteenth percentile cut-off value was used to rank species selection because that cut-off value closely matched field observations of deer selectivity and has been used by previous researchers (Nanney et al. 2018). Species determined to be selected by deer were included in nutritional carrying capacity calculations.

Deer forage availability.—We randomly placed 2, 1-m^2 frames along each transect and all vegetation ≤2 m in height within each frame was cut with a hedge trimmer (Stihl HS 45, Virginia Beach, VA, USA) at ground level (Lashley et al. 2014). We placed all cut vegetation in a cloth sack and assigned unique labels to each sample. Forage samples were separated into selected and non-selected deer forages. We separated selected forages by species and by young and old plant portions because deer are concentrate selectors and select the youngest and most nutritious portions of plants (Hewitt 2011, Lashley et al. 2014). We dried all forage samples for 72 hours at 50°C in a forced-air oven dryer. We weighed each sample with calibrated digital scales to the nearest 0.1 g. We then packaged samples and shipped them to the Agriculture Service Laboratory at Clemson University for wet chemistry nutritional analysis.

Nutritional carrying capacity.—We calculated estimates of nutritional carrying capacity for deer using a mixed-diet approach with nutritional constraints according to Hobbs and Swift (1985). We used a nutritional constraint of 14% crude protein with a 2.4 kg/day intake rate to represent nutritional needs of a 50-kg doe at peak lactation with twin fawns (National Research Council 2007, Hewitt 2011, Lashley et al. 2011, Nanney et al. 2018).

Data Analysis

We analyzed data collected in 2018 (third growing season) to compare treatment effects and the resulting habitat quality of established vegetation for the wildlife species considered in our analysis. We used 2018 data because restoration of native plant communities commonly requires 2–3 years (Fransen et al. 2006, Harper et al. 2007, Rushing 2014). We used mowing and broadcast herbicide applications as part of the establishment process during the growing seasons of 2016–17, which highly altered vegetation composition and structure during those growing seasons, to promote native plant communities in both Seedbank and Planted treatment units. We fit analysis of variance (ANOVA) models with blocking using program R (v. 3.5.1, R. Core Team 2018) to detect differences among treatments in percent cover of brambles, forbs, grasses, woody plants, and quail food plants, litter depth, ground-sighting distance, visual obstruction, deer forage availability, and deer nutritional carrying capacity across 15 replicate fields at significance level $\alpha = 0.05$. We used post-hoc Tukey HSD tests to compare treatment estimates when a significant effect of treatment was observed. We met assumptions of normality and equal variance using arcsine square root transformations on percent cover of brambles, forbs, woody species, and visual obstruction data. Additionally, we used square root transformations on forage availability.

We determined vegetation characteristics that best explained selection of breeding sites by grassland and shrubland birds using multivariate factor analyses (FA) in R. We first performed principal component analysis to determine how many factors to include in the FA. We then plotted vegetation characteristics assigned to factors 1 and 2 by FA on a biplot with 95% confidence ellipses around the multivariate centroid for each species. We standardized treatment data from our study with data from the Ft. Campbell and Peabody WMA bird nest datasets and conducted identical FA procedures, so results were comparable across the 2 datasets. We plotted factor scores for treatments with 95% confidence ellipses on the biplot with the bird nest-site factor scores. Using ArcMap 10.5 (ESRI, Redlands, CA, USA), we calculated the percent of each treatment ellipse that was contained within the 95% nest-site ellipses for each species. We plotted factor 1 on the x-axis and factor 2 on the y-axis of biplots for all species, except grasshopper sparrow, for which factor 2 was explained by vegetation height variables that were not measured in our study. We plotted factor 3 instead because it was explained by variables that were collected in our study and explained nearly as much variability (12.8%) as did factor 2 (14.8%).

RESULTS

Vegetation Composition

Tall fescue cover was greatest ($F_{2,28} = 213.11$, $P \leq 0.001$) in Control (75% ± 2.1%), with minimal cover in Seedbank (6% ± 1.1%) and Planted (2% ± 0.6%). Forb cover in Seedbank (72% ± 2%) and Planted (64% ± 3%) was increased 50% and 33% over that in Control (48% ± 3%), respectively (Table 1). Overall grass cover was greatest in Control (92%). Native warm-season grass cover in Planted (61% ± 2%) and Seedbank (49% ± 4%) was increased 85% and 48% over that in Control (33% ± 4%), respectively. Percent cover of brambles and woody species was ≤12% and ≤9% across all treatments, respectively (Table 1). Percent cover of plant species producing bobwhite foods was approximately 30% greater ($F_{2,28} = 2.93$, $P = 0.070$) in Seedbank (43% ± 3%) and Planted (41% ± 3%) than Control (32% ± 3%).

Vegetation Structure

Visual obstruction 0–0.25 m above ground did not vary among treatments (all 99–100% cover), and it did not vary between Seedbank and Planted from 0.25 m up to 2 m. However, there was less visual obstruction in Control from 0.25 m to 1.5 m than Seedbank and Planted, and less in Control than Planted from 1.5 m to 2.0 m (Table 2). Of particular importance was a minimum 28–51% increase in visual obstruction from 0.5 m to 1.5 m in Seedbank and Planted over Control. We detected a treatment effect ($F_{2,28} = 4.79$, $P = 0.016$) for ground-sighting distance. Average ground-sighting distance was similar in Planted (66 ± 3 cm) and Control (63 ± 2 cm; $P = 0.916$), but approximately 30% farther in Seedbank (85 ± 5 cm). Litter depth (Control = 3.5 ± 1.2 cm; Seedbank = 2.6 ± 1.5 cm; Planted = 3.5 ± 2.2 cm) was similar among treatments ($F_{2,28} = 2.83$, $P = 0.076$).

Suitability of Vegetation Among Treatments for Breeding Birds

Ellipses identifying compositional and structural variables most influential to selection by breeding birds were similar between Seedbank and Planted but varied by bird species (Table S3 and Figs. S1–S6, available online in Supporting Information). Treatment and control ellipses were 94–100% contained within the dickcissel and grasshopper ellipses. The Seedbank ellipse was most similar (90%) to the field sparrow ellipse. The Seedbank ellipse also was most similar (82%) to the Henslow's sparrow ellipse. The Control ellipse was most similar (98%) to the eastern meadowlark ellipse with regard to vegetation composition and structure. Seedbank (86%), Control (85%), and Planted (79%) ellipses all were relatively similar to the bobwhite ellipse with regard to vegetation composition and structure.

Deer Forage Availability and Nutritional Carrying Capacity

We documented 290 plant species across all sites and years. We classified 14 documented species as moderately and highly selected by deer using a selection index and a cut-off value of $\alpha = 0.005$ (Chesson 1978). Selected species included 9 forbs, 2 brambles, 2 trees, and 1 vine. No grasses were selected (Table 3). All 14 plant species were included in nutritional carrying capacity calculations. Forage availability did not differ ($F_{2,28} = 2.49$, $P = 0.101$) among treatments (Seedbank = 570 ± 54 kg/ha; Planted = 452 ± 58 kg/ha; Control = 429 ± 60 kg/ha). The 5 forb species in mixtures seeded in Planted all were considered selected deer forages, but contributed only 26 ± 9 kg/ha, indicating 94.2% of the deer forages in Planted occurred naturally from the seedbank. Nutritional carrying capacity was 2.2 times greater in Seedbank (145 ± 14 deer days/ha) than Control (66 ± 10 deer days/ha, $n = 15$; $P = 0.013$) and 1.7 times greater than Planted (88 ± 11 deer days/ha; $P = 0.090$).

Treatment Costs and Effort

Considering cost for seed and herbicide, the average cost for Planted treatments was $468.98 per hectare. Glyphosate applications to prepare Planted treatments were $20.26 per hectare, the preemergence imazapic application was $16.61 per hectare, seed cost $400.38 per hectare, and post-planting herbicides for weed control averaged $31.73 per hectare. Costs of herbicide application in Seedbank were variable because of differences in seedbank responses at each site. The range of costs for Seedbank was $55.74–$289.28

Table 1. Percent cover of plant groups detected (mean ± SE) in 3 early successional plant community treatments across all study sites (n = 15) in Tennessee and Alabama, USA, June–August 2018.

	Treatment							
Life form	**Control**		**Seedbank**		**Planted**		$F_{2,28}$	P
Bramble[a]	9 ± 2	A	10 ± 2	A	12 ± 2	A	2.35	0.114
Forb	48 ± 3	B	72 ± 2	A	64 ± 3	A	7.53	0.002
Grass	92 ± 2	A	63 ± 3	B	76 ± 3	B	10.96	≤0.001
NWSG[b]	33 ± 4	C	49 ± 4	B	61 ± 3	A	15.11	≤0.001
Woody[c]	9 ± 2	A	7 ± 1	A	7 ± 1	A	0.57	0.575

[a] Row means with the same letter were not different ($\alpha = 0.05$).

[b] NWSG = native warm-season grass.

[c] Woody = shrubs, trees, and woody vines.

Table 2. Vegetation profile board estimates (mean ± SE) by treatment for individual strata at all study sites (n = 15) in Tennessee and Alabama, USA, June–August 2018.

Treatment	0–25 cm[a]		25–50 cm		50–100 cm		100–150 cm		150–200 cm	
Control	100 ± 0.2	A	88 ± 2	B	60 ± 3	B	35 ± 3	B	20 ± 3	B
Seedbank	99 ± 0.6	A	95 ± 1	A	77 ± 3	A	54 ± 3	A	34 ± 3	AB
Planted	100 ± 0.1	A	99 ± 1	A	82 ± 2	A	53 ± 3	A	37 ± 3	A
$F_{2,28}$	1.70		11.17		6.82		4.52		4.45	
P	0.201		0.004		0.004		0.020		0.021	

[a] Column means with the same letter are not different (α = 0.05).

per hectare and averaged $126.69 per hectare, including the initial $20.26 per hectare glyphosate application. On average, Planted units required 0.4 (SE = 0.11; range 0–3) entries per site per year (excluding the initial herbicide treatment to control tall fescue) for herbicide applications, whereas Seedbank units required 1.3 (SE = 0.18; range 0–4) entries per site per year.

DISCUSSION

Our study documents similar results following 2 approaches to restore a native plant community on sites previously dominated by a nonnative grass and indicated that planting native grasses and forbs is not necessary on a majority of sites when the objective is to improve those sites for grassland songbirds, bobwhite, wild turkey, and white-tailed deer. We measured treatment effects in fields approximately 2–5 ha in size, but we stress that managers can use these results at the appropriate management scale while considering the area requirements of focal species to simultaneously benefit multiple conservation-priority species as well as the 2 most-popular game species in the eastern U.S. In particular, eradicating tall fescue with a single herbicide application and allowing the seedbank to respond without planting anything more than doubled nutrition available for white-tailed deer, improved potential brooding cover for turkeys and quail, and provided structure consistent with that selected by several grassland birds.

Plant composition and structure in Seedbank and Planted treatments were similar despite the use of different establishment approaches. However, openness at ground level was greatest in Seedbank, and native grasses were more prevalent in Planted, which supported our hypotheses related to structure. Forage availability for deer did not differ between Planted and Seedbank, which did not support our hypothesis, but the majority of deer forage in Planted was from species germinating from the seedbank.

Plant phenology is an important consideration when making any herbicide application, and November glyphosate applications effectively controlled tall fescue. Long-term commitments often required to control nonnative invasive species can be a discouraging factor for wildlife managers. However, similar to Harper and Gruchy (2009), our data indicated that tall fescue can be controlled with a single herbicide application made after the initial frosts in autumn when most desirable warm-season plants are dead or dormant. Smith (1989) also reported better control of tall fescue with fall applications than spring applications. Subsequent spot-spray applications greatly affect restoration success by controlling undesirable competition as it occurs. Whether planting or using the seedbank to revegetate without planting, controlling competing vegetation is requisite to restoration success (Mitchell and Britton 2000, Bakker et al. 2003, Harper et al. 2007). One advantage of using the seedbank for revegetation is that a wide variety of herbicides are available to control undesirable species,

Table 3. Plant species determined to be moderate- to highly-selected deer forages by selectivity index (Chesson 1983) across all study sites (n = 15) in Tennessee and Alabama, USA, June–August 2017–2018.

Common name	Scientific name	Life form	IV[a]	CP%[b]
Common hackberry	*Celtis occidentalis*	Tree	0.034	11.9
Stiff ticktrefoil	*Desmodium obtusum*	Forb	0.025	19.7
Common selfheal	*Prunella vulgaris*	Forb	0.025	12.1
Old-field aster	*Symphyotrichum pilosum*	Forb	0.022	14.7
American pokeweed	*Phytolacca americana*	Forb	0.014	28.0
Trumpet creeper	*Campsis radicans*	Vine	0.013	12.6
Panicled-leaf ticktrefoil	*Desmodium paniculatum*	Forb	0.011	17.0
Ticktrefoil	*Desmodium* spp.	Forb	0.011	18.4
Aster	*Symphyotrichum* spp.	Forb	0.009	14.7
Northern dewberry	*Rubus flagellaris*	Bramble	0.008	10.6
Red clover	*Trifolium pretense*	Forb	0.008	21.6
Common persimmon	*Diospyros virginiana*	Tree	0.008	16.2
White clover	*Trifolium repens*	Forb	0.006	22.1
Blackberry	*Rubus* spp.	Bramble	0.006	13.2

[a] Index value (IV) cut-off—0.005.

[b] Reported crude protein (CP) values from only selected (i.e., young) portions of plants averaged across site and year.

whereas herbicide options may be limited or nonexistent to control undesirable competing vegetation following planting without killing planted species (Harper 2017). Managers using spot-spraying apply less chemical than with broadcast applications. Spot-spraying also has less negative effect on desirable species that might be susceptible to the herbicide used in a broadcast application, promoting increased colonization and spread of desirable species after undesirable species are controlled (GeFellers et al. 2020).

Nest-site ellipses for all 6 bird species occupied a larger area on biplots than did treatment and control ellipses, indicating these species breed in areas with a wider range of structural and compositional conditions than those represented at our study sites. Variability in selection is common for many species, especially across a large geographic area (Winter 1999, Dechant et al. 2002*a*, *b*). Because treatment and control ellipses were largely or entirely contained within 95% nest-site ellipses of all bird species, it was evident that Seedbank and Planted treatments provided plant community characteristics consistent with nesting cover selected by all 6 species at Ft. Campbell Army Installation and Peabody WMA. In particular, the Seedbank and Planted ellipses were centrally located on the nest-site ellipses for dickcissel, field sparrow, and Henslow's sparrow.

The overlap of treatment and control ellipses does not indicate whether these birds would have nested at our study sites, but it does indicate that both Planted and Seedbank provided similar compositional and structural variables important to selection by these species. Dickcissels select areas with relatively tall vertical cover, including tall forbs, brambles, or sparse woody vegetation that provide singing perches, and less bare ground (Dechant et al. 2002*a*). Relatively tall structure of forbs, grasses, and even scattered shrubs were characteristic of field sparrow nest sites in Missouri (Burhans and Thompson 1998) and North Carolina (Moorman et al. 2017). Forb and grass cover dominate Henslow's sparrow nest sites (Schulenberg et al. 1994, Winter 1999), a species with little preference for warm- or cool-season grasses (Herkert 1994). Heterogenous structure with forb and grass cover and more openness at ground level were influential characteristics at grasshopper sparrow nest sites (Hovick et al. 2012), but cool-season grasses also may be selected by this species (Moorman et al. 2017). The presence of litter and widespread cover of relatively short grasses, such as tall fescue or broomsedge bluestem, are widely considered important characteristics of eastern meadowlark nest sites (Roseberry and Klimstra 1970, Hull 2002, Moorman et al. 2017).

Although metrics of bobwhite habitat, including food plant cover, forb cover, and litter depth were not different between Seedbank and Planted, ground-sighting distance was greatest in Seedbank and native grass cover greatest in Planted. Openness at ground level under a canopy of forbs is required by bobwhite chicks for movement and to gain access to invertebrates during the first 2 weeks of life (Taylor et al. 1999, Collins et al. 2009, Moorman et al. 2013). The 49% cover of native grass in Seedbank more closely resembled that documented at bobwhite nest sites in previous studies than the 61% cover in Planted (Taylor and Burger 2000, Collins et al. 2009, Martin et al. 2009, Brooke et al. 2017). Furthermore, our data clearly indicate native grasses do not need to be planted to meet nesting requirements for bobwhite because there are no data that suggest bobwhite need more than 35% cover of grass for nesting, and forb cover typically may be the more limiting factor (Collins et al. 2009, Brooke et al. 2016, Richardson et al. 2020). Although all 5 forb species planted in Planted treatment units were considered bobwhite food plants, they represented only 4% of the quail food plants detected in Planted, with the majority of food plants arising from the seedbank. Cover of forbs in Seedbank and Planted were in the upper portion of the 25–75% cover of food plants identified at sites selected by bobwhite (Schroeder 1985, Rosene and Freeman 1988, Martin et al. 2015, Johnson et al. 2018). Even though we detected 32% cover of bobwhite food plants in Control units, any seed produced or insects associated with the plants are not readily accessible in fields dominated by tall fescue because of the dense structure at ground level (Barnes et al. 1995, Harper et al. 2007).

Visual obstruction measurements in Seedbank and Planted were consistent with sites selected by brooding wild turkeys (Healy 1985, Metzler and Speake 1985, Badyaev 1995, Peoples et al. 1996, Spears et al. 2007). Visual obstruction <0.5 m with minimal obstruction above 0.5 m and openness at ground level allows hens to detect predators and facilitates movement of poults. Both treatments had ≥95% visual obstruction below 0.5 m, and averaged ≥57% above 0.5 m. However, openness at ground level in Planted was similar to Control, and the increased openness at ground level in Seedbank facilitates more usable space by turkey poults. Frequent management to set back succession is necessary to maintain desirable brooding cover, whereas less frequent management will increase shrubby vegetation height and cover important for wild turkey nesting structure (Harper 2007, Moore et al. 2010, Isabelle et al. 2016, Wood et al. 2019).

Quantity of selected deer forages was similar among treatments. Blackberry and goldenrod were among the selected forages, and both occurred in Control at most sites, resulting in greater forage estimates in Control than might be expected in fields dominated by tall fescue. Although all of our sites were dominated by tall fescue, they were undergoing succession, as is typical of idle hayfields or pasture no longer in production. Although all of the forb species included in planting mixtures are considered selected forages by deer, they contributed only 26 of the 452 kg/ha detected in Planted units. Spot-spray applications to reduce cover of undesirable species in Seedbank units allowed high-quality annual forbs to establish and contribute to the greater nutritional carrying capacity in Seedbank. Dominance of native grasses in Planted units led to reduced forb cover, which has been reported commonly (Weber 1999, Dickson and Busby 2009, Gruchy and Harper 2014), thus reducing nutritional carrying capacity for deer and necessitating a reduction in grass cover to improve forage availability (Brooke and Harper 2016). We underscore the importance of including variables important to white-tailed deer and wild turkey in our evaluation because they are the primary species of interest to private landowners, and if restoration of nonnative grassland to native, early-successional plant communities benefits these species, state and federal agencies likely can impact additional acres for species of conservation concern, including pollinators (GeFellers et al. 2020).

Planting was 3.7-times more expensive than using the seedbank only, providing additional evidence that planting may not be an efficient use of conservation funds. Although we made fewer entries into Planted units than Seedbank units, more entries into Planted units would have allowed greater control of undesirable vegetation. However, conservation program policy stating that cover of undesirable vegetation should be ≥30% before herbicide applications are warranted reduced the average number of entries into Planted units (GeFellers et al. 2020). Because our study sites were widely distributed geographically and occurred in areas with differing site histories and soil types, establishment costs from our study should be representative of the cost to restore native early successional communities in tall fescue fields previously used for haying and grazing throughout a large portion of the eastern U.S. Planting costs vary greatly depending on species planted. Forbs are more expensive than grasses, and forb-dominated mixtures for pollinators now are commonly planted in many CRP and EQIP projects. Pollinator seed mixtures require a minimum of 9 flowering species (3 flowering in spring, summer, and fall), and the cost is considerably greater than the general wildlife seed mixtures used in our study, often exceeding $1,000/ha. Our data indicated that even when planting a more traditional (i.e., relatively low cost) wildlife seed mixture, 3.7-times more land could have been converted to native early successional plant communities by using the seedbank without planting for the same cost of planting per unit area. Cost and effort required to maintain an early successional native plant community obviously depend on prevalence of undesirable plant species by site, but the disturbance regime otherwise should be similar following planting or using the seedbank. However, planting often results in excessive grass cover for most wildlife species and may necessitate additional herbicide applications or disking to reduce grass cover (Brooke and Harper 2016, Harper 2017).

MANAGEMENT IMPLICATIONS

Managers working to increase or enhance early successional plant communities for wildlife should consider using the seedbank without planting. Even with considerable variation in site histories, vegetation characteristics were similar between Seedbank and Planted treatments. Perennial cool-season grasses should be treated in fall with 2.8 kg ai/ha of glyphosate following the first couple of frosts in autumn, followed by a preemergence application of imazapic in early spring where warranted for controlling undesirable plant species. Strategic spot-spray herbicide applications should be used at least once each growing season to reduce undesirable warm-season species for 2–3 years following initial control of nonnative grass cover and, optimally, once during the dormant season to reduce competition by undesirable nonnative cool-season species. Planting should be considered at sites with severely depleted seedbanks, such as reclaimed mine sites and other sites with highly erodible soils. Based on our study across a wide array of sites and management histories, planting native grasses should be avoided where species such as broomsedge bluestem, little bluestem, splitbeard bluestem (*Andropogon ternarius*), purpletop (*Tridens flavus*), or other native grasses are present in the seedbank. A 49% cover of native grass in Seedbank treatment units indicated native grasses are readily available and prevalent on most sites within 3 years after initial control of nonnative grass and do not need to be included in seed mixtures for most management objectives. Managers wishing to increase forb cover to increase nutritional carrying capacity for deer, food-producing plants for bobwhite, and brooding cover for bobwhite and wild turkey may need to reduce native grass cover even in areas revegetated from the seedbank following tall fescue control.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's web-site. Supporting materials include 2 tables that list the plant species included in the planting mixtures used at our study sites, and 1 table provides the factor loading results of our multivariate factor analyses for nest-site data of the 6 bird species we used in analysis. Also included are the multivariate biplots of vegetation variables considered most important at nest sites for the bird species used in our analyses.