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RESEARCH ARTICLE

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Restoration of native-dominated plant communities on a *Centaurea stoebe*-infested site

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Abstract

Questions: Restoring native-dominated plant communities often requires controlling invasive species, reintroducing native species, and implementing continued management practices. Can single herbicide applications to control *Centaurea stoebe* L. encourage establishment of seeded native species more effectively than a single mowing? Can annual hand pulling to control *C. stoebe* favor the persistence of seeded native species? Can mid-spring burning reduce *C. stoebe* and increase native forbs and grasses? After eight years, will the restored plant communities differ from those in untreated areas?

Location: Bass River Recreation Area, Ottawa County, MI, USA.

Methods: We studied the effects of site preparation (mowing, clopyralid, glyphosate), hand pulling of *C. stoebe*, and burning on restoring native plant communities on a *C. stoebe*-infested site. Over eight years, we quantified the development of the plant communities on plots seeded with native grasses and forbs, and report on the second four years here.

Results: Native-dominated plant communities developed using both herbicides, but while clopyralid provided longer control of *C. stoebe*, clopyralid-treated plots had fewer native species than glyphosate-treated plots. Native-dominated plant communities also developed on plots that were only mowed once before seeding, achieving similar native species richness as the glyphosate treatment. Hand pulling controlled *C. stoebe*, burning increased relative cover of native graminoids and decreased that of non-native grasses, and hand pulling and burning in combination increased relative cover of native forbs. After eight years, the restored plant communities had greater native species cover and richness and higher mean Coefficient of Conservatism, Floristic Quality Index, and Shannon's Diversity Index values than untreated areas.

Conclusions: Site preparation, seeding, hand pulling of *C. stoebe*, and annual burning facilitated restoration of native-dominated plant communities on a *C. stoebe*-infested site. Effects accumulated over a period of eight years, illustrating the importance of continued management and monitoring as part of similar restoration efforts.

KEYWORDS

Centaurea stoebe L., clopyralid, glyphosate, hand pulling, invasive species, mowing, native species, prescribed burning, restoration, seeding, spotted knapweed, systemic herbicides

1 | INTRODUCTION

Restoring native plant communities on degraded sites often requires controlling invasive-species infestations, reintroducing native species, and implementing management practices to ensure persistence of native-dominated plant communities. Herbicides may initially control invasive species, but restoration may fail if the target species reinfests the site, other non-native species become secondary invaders, or native species do not reestablish from local seed sources (Rinella, Maxwell, Fay, Weaver, & Sheley, 2009; Skurski, Maxwell, & Rew, 2013; Pearson, Ortega, Runyon, & Butler, 2016). Native species often need to be reintroduced to restore a native-dominated plant community (Foster et al., 2007; Zylka, Whelan, & Molano-Flores, 2016; Mahmood et al., 2018) that will resist reinvasion by exotic species (Sheley & Half, 2006; Maron & Marler, 2007; Rinella, Pokorny, & Rekaya, 2007). Finally, seeded native species may not persist or may take years to become dominant, requiring long-term evaluation of restoration progress, an effort not included in many studies (Reid, Morin, Downey, French, & Virtue, 2009; Kettenring & Adams, 2011; Rinella, Mangold, Espeland, Sheley, & Jacobs, 2012).

Many disturbed sites and remnant natural areas in midwestern North America have been invaded by non-native grasses and forbs (e.g., Emery & Rudgers, 2012; Zylka et al., 2016). While many of these species are weak invaders, others are considered strong invaders, which may become community dominants (Ortega & Pearson, 2005). *Centaurea stoebe* L. (Spotted knapweed; USDA NRCS 2018) is a strong invader that infests many regions throughout North America (Sheley, Jacobs, & Carpinelli, 1998). *Centaurea stoebe* first entered the eastern United States in the early 1880s, and by 1920 had spread into those areas with climatic conditions similar to its native range (Broennimann, Mráz, Petitpierre, Guisan, & Müller-Schärer, 2014). *Centaurea stoebe* was first collected in Michigan in 1911, and now occurs throughout the state on disturbed and degraded sites (Michigan Flora Online 2017). Restoration of these sites requires effective control of *C. stoebe* to prevent reinvasion of the developing plant community.

We have experimented with native plant community restoration on a degraded, *C. stoebe*-infested site in western Michigan since 1997 (MacDonald, Koetje, & Perry, 2003). Sites with similar glaciofluvial landforms and coarse-textured soils in this region originally supported oak-pine forests and mixed-oak savannas, fire-adapted communities that included forbs and warm-season grasses (MacDonald, Scull, & Abella, 2007). The native plant communities at our study site were lost in the late 1800s to mid-1900s as a result of agricultural conversion and disturbance by gravel mining (MacDonald et al., 2007; MacDonald, Martin, Kapolka, Botting, & Brown, 2013). We selected the specific study location within the Bass River Recreation Area in consultation with the Michigan Department of Natural Resources, which was interested in determining if a native plant community could be re-established there. Prior to the initiation of our experiments, *C. stoebe* was the dominant invasive plant at the study site, with 60% to 70% relative cover, while the remaining plant community also comprised non-native species including *Poa pratensis* (Kentucky bluegrass), *Elymus repens* (Quackgrass), *Poa compressa* (Canada bluegrass), *Melilotus officinalis* (Sweetclover), and *Trifolium arvense (Rabbitfoot clover*; Martin, MacDonald, & Brown, 2014). For additional details on study-site characteristics, please see MacDonald et al. (2003, 2007, 2013) and Martin et al. (2014).

Our studies have focused on reducing *C. stoebe*, reestablishing native species, and using fire to align the site on a trajectory toward recovery of native species and processes. An earlier study demonstrated that native grasses could be reestablished on this site (MacDonald et al., 2003), and that annual mid-spring burning reduced *C. stoebe* density and biomass and increased native grass dominance (MacDonald et al., 2007). In 2008, we established a separate experiment at this study site to test the feasibility of restoring a more diverse native plant community by seeding experimental plots with native grasses and forbs while using factorial combinations of site preparation treatments, hand pulling of *C. stoebe*, and burning (MacDonald et al., 2013; Martin et al., 2014). Seeding allowed native species to establish on all plots, including those not treated with herbicides, burning, or hand pulling (Martin et al., 2014). While these results were encouraging, the experimental plant communities were still dominated by non-native species after four years. We therefore continued the study for another four years to determine if native-dominated plant communities would develop through time. Results presented in this paper focus on the second four years (2013–2016) of this eight-year study, since results from the first four years (2009–2012) have been published previously (MacDonald et al., 2013; Martin et al., 2014). To provide context for the most recent results, we also include discussion of previously published results where relevant.

The objective of our experiment was to test methods of restoring native-dominated plant communities on a degraded, *C. stoebe*-infested site. Experimental site preparation methods included a single mowing, alone or in combination with systemic herbicides, either clopyralid, a broadleaf-specific residual herbicide, or glyphosate, a broad-spectrum non-residual herbicide, to provide three levels of initial *C. stoebe* control (e.g., Rinella, Jacobs, Sheley, & Borkowski, 2001; Sheley, Jacobs, & Lucas, 2001). We seeded all experimental plots with a mixture of native grasses and forbs to ensure the presence of the desired propagules (e.g., Gross, Mittelbach, & Reynolds, 2005; Suding & Gross, 2006). We incorporated hand pulling of *C. stoebe* as an experimental factor to control *C. stoebe* while the seeded native species established (e.g., Lutgen & Rillig, 2004; Skurski et al., 2013). Once adequate fuel loads accumulated, we incorporated burning as another experimental factor to help reduce non-native species, while favoring the establishment and dominance of native species (e.g., Brudvig, Mabry, Miller, & Walker, 2007; Bowles & Jones, 2013). We specifically evaluated burning to control *C. stoebe*, as few studies have examined its effectiveness in controlling this species during the restoration of native plant communities containing both grasses and forbs (e.g., Emery & Gross, 2005; Martin et al., 2014). We thus employed an experimental approach incorporating multiple practices to control *C. stoebe* and thus restore native plant communities and their natural ecological processes

(Krueger-Mangold, Sheley, & Svejcar, 2006; Sheley, Mangold, & Anderson, 2006; Miller, 2016). Finally, we observed plant community development and persistence of native species across a period of eight years, incorporating a long-term evaluation of treatment effects lacking in many ecological restoration studies (e.g., Reid et al., 2009; Kettenring & Adams, 2011; Rinella et al., 2012). We considered a successfully restored plant community to be dominated by native species and to exhibit other attributes of restored ecosystems, including a species assemblage characteristic of natural plant communities, a diversity of plant functional groups, and evidence of being self-sustaining (SERI-SPWG, 2004). We hypothesized that a single application of either herbicide would control *C. stoebe* and encourage establishment and persistence of native species more effectively than a single mowing; that hand pulling, by reducing *C. stoebe* seed fall and competition, would favor the establishment and persistence of native species; and that mid-spring burning would reduce the cover of *C. stoebe* and increase that of native forbs and warm-season grasses (MacDonald et al., 2013; Martin et al., 2014). Finally, we hypothesized that the restored plant communities would differ in composition from those in adjacent untreated areas of the study site by the end of the eight-year study period.

2 | METHODS

2.1 | Experimental design

We established the study in 2008 within the Bass River Recreation Area, Ottawa County, MI, USA (43°00′49″ N, 86°01′47″ W; Appendix S1), as previously described by MacDonald et al. (2013) and Martin et al. (2014). We used a fully crossed factorial arrangement of treatments in a randomized complete block design, including three levels of initial site preparation, two levels of hand pulling of *C. stoebe* (with or without), and two levels of burning (burned or unburned) to produce twelve treatment combinations (for details, see Martin et al., 2014). The study was replicated in four complete blocks, for a total of 48 5-m × 5-m plots, and all treatment combinations were randomly assigned to plots at the beginning of the experiment. All four blocks were mowed in July, 2008 to facilitate plot layout, herbicide treatment application, and subsequent seeding. The three site preparation treatments consisted of the single mowing only, or mowing plus the application of either clopyralid (Transline®; Dow Agrosciences, Indianapolis, IN) or glyphosate (Roundup Concentrate Plus®; Monsanto, Marysville, OH). The herbicides were applied to randomly selected plots in mid-August (clopyralid, 0.6 kg ae/ha, $n = 16$ plots) or early September (glyphosate, 9.9 kg ae/ha, $n = 16$ plots), 2008. All 48 plots were seeded (22 kg/ha) in May, 2009, with a seed mix containing five warm-season grasses and 18 forbs representative of native species found in Michigan dry-mesic prairies, dry sand prairies, and oak barrens (Martin et al., 2014; Appendix S2). We included 5-m buffers around each experimental block with 2.5-m buffers between plots, and mowed these buffers once each year in late June or early July to minimize *C. stoebe* seed fall from adjacent untreated areas. While there was no true "control" treatment combination in the sense of including plots with no treatments whatsoever, in the context of the factorial experiment the plots that were only mowed once without receiving herbicide application, hand pulling, or burning provide a minimally managed and practical comparison to the other 11 more intensively managed treatment combinations (Martin et al., 2014).

We hand pulled *C. stoebe* from 24 randomly selected plots in early July each year from 2009 to 2016, as detailed by MacDonald et al. (2013). From 2009 to 2011, we removed only adults, but from 2012 on we also removed seedlings and juveniles since few adults remained. A *C. stoebe* plant was considered a seedling if it had one to four primary leaves, a juvenile if it was still in the rosette stage, or an adult if it had bolted. All adult *C. stoebe* plants were removed before seed dispersal each year.

In 2012, 2014, 2015, and 2016, 24 randomly selected plots were burned in early to mid-spring. The 2 Apr 2012 burn took place during sub-optimal weather conditions, and burn intensity was fairly low (MacDonald et al., 2013; Martin et al., 2014). In subsequent years, we visually estimated the percent of each plot burned following the burn, and the percent bare soil in July. We conducted the 11 May 2014, 7 May 2015, and 20 May 2016 burns under more optimal weather conditions, and burning effects were more pronounced. The mean percent of plot area burned increased from 75% in 2014 to over 87% in 2015 and 2016, while the mean bare soil exposure on burned plots in July increased from 14.5% in 2014 to 28.4% in 2016. On non-burned plots, mean bare soil exposure was consistently <1%.

2.2 | Plant community measurements

Nomenclature follows that in the USDA PLANTS Database (USDA NRCS 2018). From 2011 to 2016, we visually estimated percent cover of all species on each experimental plot in July of each year. We divided each 5-m × 5-m plot into quarters, and made separate visual cover estimates of all species in each quarter. To standardize these visual estimates, we referred to published cover charts (Anderson, 1986) and used 0.1- and 0.25-m^2 frames as standard area references. As a measure of relative dominance, we calculated the relative percent cover of each species on each plot by dividing the summed total cover of each species by the summed total cover of the plot (Barbour, Burk, & Pitts, 1980). In 2016, we also made cover estimates on 12 randomly located 25-m^2 plots in untreated areas adjacent to the experimental plots that never had been mowed, seeded, or otherwise treated (Appendix S1). These untreated plots were established in 2009 just beyond the mowed buffers by using random distances along the borders of the mowed buffers to locate the plots, with an equal number of plots closely associated with each experimental block (MacDonald et al., 2013). Initial plant communities in these untreated areas comprised the same non-native species present in the areas used for the experimental plots, and also were dominated by *C. stoebe* (MacDonald & Bottema, 2014). Mature *C. stoebe* densities measured in untreated areas of the study site in 2013 (46.3 ± 7.7 plants/m^2; MacDonald & Bottema, 2014) were very similar to adult *C. stoebe* densities present on minimally treated experimental plots at the initiation of the current study in 2009 (45.6 ± 4.7 plants/m^2; MacDonald et al., 2013).

Based on the relative cover data, we determined the native and non-native species richness on each plot, following the USDA PLANTS Database (USDA NRCS 2018) for species native to Michigan. Using our relative cover data, we calculated Shannon's Diversity Index (H'), and expressed this as $e^{H'}$ to simplify interpretation since $e^{H'}$ represents the functional number of species in the community (Peet, 1974; Morris et al., 2014). Shannon's Diversity Index is sensitive to the presence of both rare and abundant species, combines richness and evenness components, and can discriminate between plots better than simpler diversity measures (Morris et al., 2014). We calculated the mean Coefficient of Conservatism ($\bar{C}$) for each plot using Coefficients of Conservatism for native herbaceous species determined for Michigan (Michigan Flora Online 2017), and calculated the native Floristic Quality Index (FQI) by multiplying $\bar{C}$ by the square root of the number of native species on the plot (Spyreas, Meiners, Matthews, & Molano-Flores, 2012). $\bar{C}$ and FQI distinguish among plant communities containing ubiquitous native plants and those containing more conservative native species, with $\bar{C}$ representing the average tolerance to disturbance and degree of fidelity to habitat integrity of the native species present, and FQI incorporating the additional effect of native species richness on community quality (Taft, Wilhelm, Ladd, & Masters, 1997). FQI and $\bar{C}$ have been shown to be effective at distinguishing qualitative differences in floristic integrity among plant communities, and can be more effective in this respect than traditional diversity measures (Taft, Hauser, & Robertson, 2006). Since few species were present on all plots, we summed relative cover by six life-form groups, including native graminoids (grasses and sedges), native forbs, non-native grasses, non-native forbs (exclusive of *C. stoebe*), *C. stoebe*, and woody species to allow more robust statistical analyses.

To assess the long-term effectiveness of *C. stoebe* control efforts, in 2015 and 2016 we estimated densities of four *C. stoebe* life stages (seed bank, seedling, juvenile, and adult) on the 48 experimental and 12 untreated plots. To estimate seed-bank densities, we collected five cores from the upper 5 cm of soil on each plot using a 4.5-cm diameter metal corer on 3 Apr 2015 and 1 Apr 2016. The five soil cores were combined into one sample for each plot, spread on top of sterile potting soil in 15-cm diameter plastic pots in a greenhouse, and watered regularly. We counted and removed germinated *C. stoebe* seedlings several times a week from April through June. Whenever germination rates slowed to zero, approximately once every two weeks, we stirred the soil to bring additional viable seeds toward the surface to germinate.

In mid-July of 2015 and 2016, we quantified seedling, juvenile, and adult *C. stoebe* densities on the experimental and untreated plots. On the 24 hand-pulled plots, densities were determined each year by total counts of the plants removed from each plot. On the 24 non-hand-pulled plots and 12 untreated plots, densities were estimated at a minimum of five random locations per plot. In 2015, seedling and juvenile densities were counted inside a 0.5-m × 0.5-m quadrat at each random location and adult densities were counted in 1-m × 1-m quadrats. In 2016, seedling and juvenile counts were made within a 1-m × 1-m quadrat at each random location, and adult densities were counted on entire 25-m^2 plots, except for a few of the untreated plots with high adult densities (>20 plants/m^2 on average). On these plots, adult density estimates were made on at least five 1-m × 1-m quadrats per plot.

2.3 | Statistical methods

Data for most variables did not consistently meet parametric assumptions, so we used nonparametric permutational analyses of variance (PERMANOVA+ for PRIMER, PRIMER-e, Plymouth, UK; Anderson, 2001; Anderson, Gorley, & Clarke, 2008; Anderson & Walsh, 2013) to analyze species diversity, floristic quality, and life-form group cover. For analyses of data from the experimental plots, we included the four years, three site-preparation treatments, two hand-pulling levels, and the two burning levels as fixed-effect factors in permutational factorial repeated-measures analyses of variance. Block effects were included in these analyses as a random factor.

We also used PERMANOVA to compare plant communities between experimental plots and untreated plots. Since the experimental plant communities differed in various ways related to the hand pulling by burning interaction, but without any significant three-way interactions including site preparation, we grouped the experimental data into the four hand pulling by burning treatment combinations (n = 12 each), which allowed balanced comparisons with the plant communities on the 12 untreated plots using one-way permutational analyses of variance. For all one-way analyses, the plant community category (n = 5, four experimental and one untreated) was considered a fixed effect and blocks were included as a random factor. We performed univariate analyses for species richness, Shannon's Diversity Index, $\bar{C}$, FQI, and the densities of the four *C. stoebe* life stages. To provide an overall comparison of plant community composition between experimentally restored and untreated plant communities, we also used PERMANOVA to conduct a one-way permutational multivariate analysis of variance incorporating the six life-form groups as multiple response variables. To evaluate the magnitude of differences in the relative cover of individual plant groups between the four treatment combinations and the untreated areas in 2016, we calculated effect sizes (d = mean difference/pooled standard deviation) for these comparisons following Nakagawa and Cuthill (2007). To further characterize differences in plant species composition among the four experimental treatment combinations and the untreated areas in 2016, we used a canonical analysis of principle coordinates (CAP; Anderson & Willis, 2003; Anderson et al., 2008) incorporating normalized relative percent cover data (Euclidean distances) for 27 common species from the 60 restored and untreated plots (Appendix S2). All 27 species were recorded as present from 2011 to 2016 on restored plots, occurred on at least 25% of these plots in 2016, and constituted >95% relative cover for all treatment combinations (Appendix S2).

All analyses of variance were conducted using Euclidean distances and were based on permutation of residuals under a reduced

TABLE 1 Variation in characteristics (mean ± *SE*) of restored plant communities at the Bass River Recreation Area, Ottawa County, Michigan, through time (2013–2016) and as affected by experimental treatments

		Year					
Community Characteristic	**Year effect $F_{3,9}$; p**[†]	**2013**	**2014**	**2015**	**2016**	**Treatment effects**[‡]	**Treatment effect F_{df}; p**[§]
Native species (no. per 25-m^2 plot)	7.8; 0.0082	14.6a[¶] ± 0.5	14.5ab ± 0.5	14.2ab ± 0.4	13.6b ± 0.4	Prep	$F_{2,33}$ = 3.9; 0.0318
Non-native species (no. per 25-m^2 plot)	76.7; 0.0001	14.2a ± 0.4	12.1b ± 0.3	9.5c ± 0.3	7.4d ± 0.3	—	—
Shannon's Diversity Index ($e^{H'}$)	10.2; 0.0016	9.1 ± 0.5	8.7 ± 0.3	7.8 ± 0.2	6.8 ± 0.2	Pull × Burn	$F_{1,33}$ = 4.7; 0.0371
Mean coefficient of conservatism ($\bar{C}$)	9.0; 0.0040	3.52 ± 0.05	3.56 ± 0.06	3.64 ± 0.05	3.71 ± 0.05	Burn	$F_{1,33}$ = 4.3; 0.0489
Floristic Quality Index (FQI)	6.0; 0.0178	13.3 ± 0.2	13.4 ± 0.2	13.6 ± 0.3	13.5 ± 0.2	—	—
Native graminoids (% cover)	56.8; 0.0001	37.0d ± 1.9	43.1c ± 2.3	53.2b ± 2.4	60.6a ± 2.6	Year × Burn	$F_{3,99}$ = 37.4; 0.0001
Native forbs (% cover)	3.3; 0.0527	10.4 ± 1.1	10.4 ± 1.1	12.0 ± 1.2	14.0 ± 1.4	Pull × Burn	$F_{1,33}$ = 6.9; 0.0129
Non-native grasses (% cover)	11.9; 0.0030	23.9a ± 2.8	24.2a ± 2.6	23.7a ± 2.2	18.5b ± 2.4	Year × Burn	$F_{3,99}$ = 9.6; 0.0001
Non-native forbs (% cover)	37.1; 0.0003	13.0a ± 1.6	12.9a ± 1.5	5.4b ± 0.8	2.0c ± 0.4	Year × Prep Year × Pull Year × Burn	$F_{6,99}$ = 3.2; 0.0067 $F_{3,99}$ = 4.2; 0.0075 $F_{3,99}$ = 11.9; 0.0001
Centaurea stoebe (% cover)	133.0; 0.0001	14.7a ± 3.0	9.3b ± 2.0	5.7c ± 1.3	4.9c ± 1.2	Year × Prep × Pull	$F_{6,99}$ = 12.3; 0.0001

[†] Pseudo-*F* and permutational *p*-value for year effects from factorial repeated-measures analysis of variance. [‡] Significant treatment main and interaction effects from the permutational factorial repeated-measures analysis of variance. Year = year in study, Prep = site preparation treatments (applied once in 2008), Pull = hand-pulling treatment (applied annually 2009–2016 to remove *Centaurea stoebe*), Burn = burning treatment (applied in 2012, 2014, 2015, 2016). [§] Pseudo-*F* and permutational *p*-value for treatment main and interaction effects from factorial repeated-measures analysis of variance. [¶] Year means with different letters differ significantly at $p < 0.05$. Letters a, b, c, d compare means between years for a single variable; $n = 48$ for each mean.

model using 9,999 permutations, which would allow the determination of permutational *p* values to a level of 0.0001 (1/9999). Analyses of variance used untransformed data, except for *C. stoebe* density data which were analyzed as ln(X + 1) to reduce dispersion. We used pairwise tests within PERMANOVA to identify differences among means where multiple comparisons were necessary. While permutation *p*-values from pairwise tests in PERMANOVA provide statistically exact tests for each individual comparison (Anderson et al., 2008), Type I error rates might be inflated because results are from an ongoing experiment, and the probability of replicating a previous result could be increased. In addition, the various diversity indices were calculated using species presence and relative cover data, resulting in multiple tests using similar data. Therefore, we applied a sequential Bonferroni correction (Holm, 1979) to the results of multiple comparisons as a conservative measure, using Monte Carlo *p*-values for comparisons involving year effects where the number of unique permutations was <450 (Anderson et al., 2008). Spearman rank correlation (r_s) analyses between plant group relative cover variables were performed with SPSS (IBM Statistics for Windows version 22.0. Armonk, New York). We concluded significance for all effects at $p < 0.05$, as adjusted for multiple comparisons as noted above. Raw data are included in Appendices S3 and S4.

3 | RESULTS

Numeric results presented in the text represent mean ± *SE* unless otherwise specified. Presentation of results focuses on statistically significant effects that also have practical implications for restoration of similar sites. All comparative statements in the Results indicate statistically significant differences unless otherwise stated.

3.1 | Trends in characteristics of restored plant communities

The restored plant communities on the experimental plots followed a definite developmental trajectory through the four years (Table 1). When averaged across all treatment combinations, the number of non-native species declined substantially from 2013 to 2016, while the number of native species declined only slightly. PERMANOVA also indicated significant year effects for Shannon's Diversity Index, $\bar{C}$, and FQI, but the sequential Bonferroni procedure did not distinguish among means. The relative cover of native graminoids increased from 2013 to 2016, while relative cover of non-native grasses, non-native forbs, and *C. stoebe* decreased. Relative cover of native forbs also tended to increase through time, although not significantly ($p = 0.053$).

3.2 | Treatment effects on experimental plant community characteristics

The experimental treatments had several effects on plant community characteristics or composition that did not significantly interact with year (Table 1). The number of native species on the clopyralid treatment averaged across all four years was 12.7 ± 0.3 species/25 m^2, which was less than the average number of native species on the glyphosate treatment (15.3 ± 0.2 species/25 m^2). The number of native species on the mowed-only treatment (14.7 ± 0.2 species/25 m^2), however, did

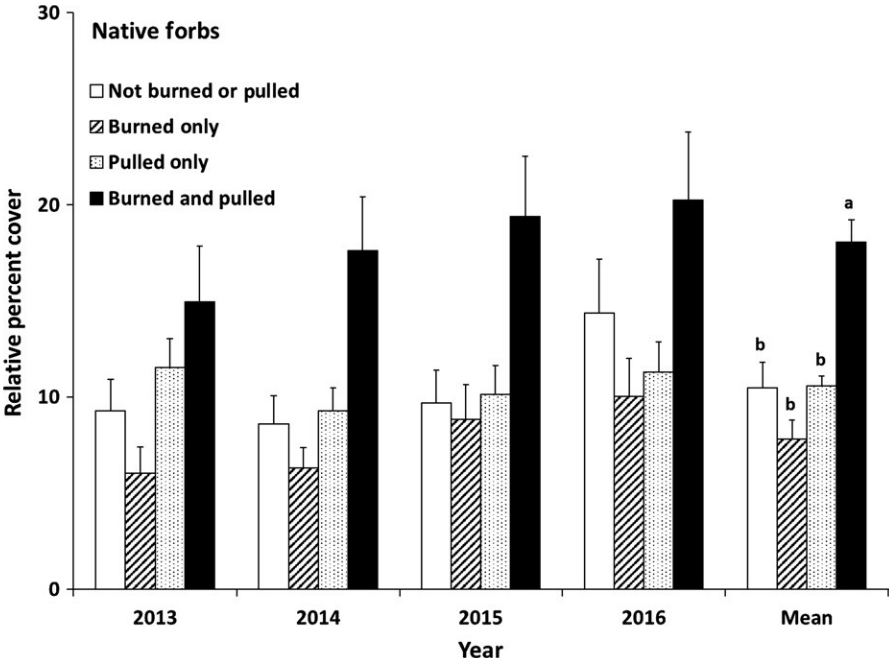

FIGURE 1 Hand-pulling and burning effects on native forb relative percent cover (mean + *SE*), Bass River Recreation Area, Ottawa County, Michigan, 2013–2016. All means are averaged across the levels of the site preparation factor, which did not interact with the hand-pulling or burning treatments (n = 12 each for within-year means). Mean bars on the right, averaged across the four years (n = 48 each), show the significant interaction between hand pulling and burning; bars with different letters differ significantly at $p < 0.05$

TABLE 2 Site preparation, hand-pulling, and burning effects on relative percent cover of non-native forbs (mean ± *SE*), Bass River Recreation Area, Ottawa County, Michigan, 2013–2016

		Percent cover in year			
Experimental factor	**Treatment**	**2013**	**2014**	**2015**	**2016**
Site preparation	Mowed only	10.4 ± 2.0	12.3ab ± 2.1	6.2 ± 1.6	0.9 ± 0.1
	Clopyralid	17.7 ± 3.5	18.0a ± 3.3	5.6 ± 1.5	2.2 ± 0.8
	Glyphosate	10.7 ± 2.1	8.3b ± 1.9	4.5 ± 0.7	2.6 ± 0.8
Hand pulling	Not pulled	9.8 h ± 1.6	12.2 ± 2.3	6.5 ± 1.3	1.6 ± 0.5
	Pulled	16.1 g ± 2.6	13.6 ± 2.0	4.4 ± 0.7	2.3 ± 0.6
Burning	Not burned	8.1y ± 1.3	9.7 ± 1.4	7.2x ± 1.3	1.6 ± 0.4
	Burned	17.8x ± 2.5	16.0 ± 2.6	3.7y ± 0.6	2.3 ± 0.6

Effects of each experimental factor interacted significantly with year ($p < 0.01$, Table 1). Means with different letters differ significantly at $p < 0.05$. Letters a, b compare site preparation means within a single year. Letters g, h compare hand-pulling means within a single year. Letters x, y compare burning means within a single year. Means for each experimental factor are averaged across the levels of the other two non-interacting experimental factors; $n = 16$ each for site preparation means and 24 each for hand pulling and burning means.

not differ from either herbicide treatment. $\bar{C}$ was slightly reduced on burned plots, averaging 3.54 ± 0.06 across the four years as compared to 3.68 ± 0.03 on non-burned plots. Native forb cover was affected by a significant interaction between hand pulling and burning, and averaged across all four years was greatest on the hand-pulled and burned treatment combination (Figure 1). Shannon's Diversity Index displayed a similar interaction between hand pulling and burning, but significant effects were restricted to the burned treatment, where the four-year average index was lowest on the non-hand-pulled, burned combination (7.3 ± 0.5) and highest on the hand-pulled, burned combination (8.9 ± 0.9).

The experimental treatments also interacted with year to affect the development of the restored plant communities in both subtle and substantial ways (Table 1). For example, clopyralid treatment, hand pulling, and burning all favored greater non-native forb cover in either 2013 or 2014, but none of these effects persisted as relative cover of these species declined to low levels on all treatments by 2016 (Table 2). In contrast, burning effects on both native graminoid and non-native grass cover became more pronounced through time, with burning producing increased native graminoid cover in 2015 and 2016 (Figure 2a), while it produced decreased cover of non-native grasses in 2014, 2015, and 2016 (Figure 2b). Finally, residual herbicide application effects on *C. stoebe* relative cover were significant only on the non-hand-pulled treatment combinations, where a single application of clopyralid in 2008 maintained lower *C. stoebe* cover compared to either mowed-only or glyphosate-treated plots in 2013. This effect did not persist as *C. stoebe* relative cover subsequently declined on the mowed-only and glyphosate treatments (Table 3). In contrast, hand pulling maintained greatly reduced *C. stoebe* relative cover regardless of site preparation treatment in all years. Burning had no significant effects on *C. stoebe* relative cover in any year. For example, in 2016 *C. stoebe* relative cover on the non-hand-pulled treatment did not differ between non-burned plots (8.6 ± 2.0%) and burned plots (11.1 ± 3.2%). In contrast, the relative cover of *C. stoebe* on non-hand-pulled plots ($n = 24$) became progressively more negatively correlated with that of native graminoids through time ($r_s = -0.36$, $p = 0.09$ in 2013; $r_s = -0.39$, $p = 0.06$ in 2014; $r_s = -0.44$, $p = 0.03$ in 2015; $r_s = -0.47$, $p = 0.02$ in 2016), an effect that included both burned and non-burned treatments.

Annual hand pulling maintained greatly reduced densities of seedling, juvenile, and adult *C. stoebe* as compared to the non-hand-pulled treatments in both 2015 and 2016 (Table 4). When combined with burning, hand pulling also produced reduced seed-bank densities in 2015 compared to densities on non-pulled, non-burned plots, but this effect was not significant in 2016. Burning reduced adult *C. stoebe* densities on non-hand-pulled plots in 2015, but burning did not affect seedling or juvenile densities in either year (Table 4).

3.3 | Comparisons of experimentally restored and untreated plant communities

By 2016, the experimentally restored plant communities differed significantly from adjacent untreated areas in most measures. Densities of seedling, juvenile, and adult *C. stoebe* in the restored plant communities were substantially less than those in the untreated plant community in both 2015 and 2016, especially on hand-pulled plots (Table 4). *Centaurea stoebe* seed bank densities were reduced below those on untreated plots in the hand-pulled treatment combinations in 2015, and also tended to be lower in both burned treatment combinations than in untreated areas in 2016 (Table 4), but this effect was not significant in 2016. Restored plant communities had greater native species richness, as well as higher values of Shannon's Diversity Index, $\bar{C}$, and FQI than the untreated plant community (Table 5). The untreated plant community also tended to contain higher numbers of non-native species than all of the experimental treatment combinations, but the sequential Bonferroni procedure did not differentiate among means (Table 5). Based on the multivariate analysis incorporating the six life-form groups as multiple response variables, the composition of all of the experimentally restored plant communities differed significantly from that of the adjacent untreated plant community

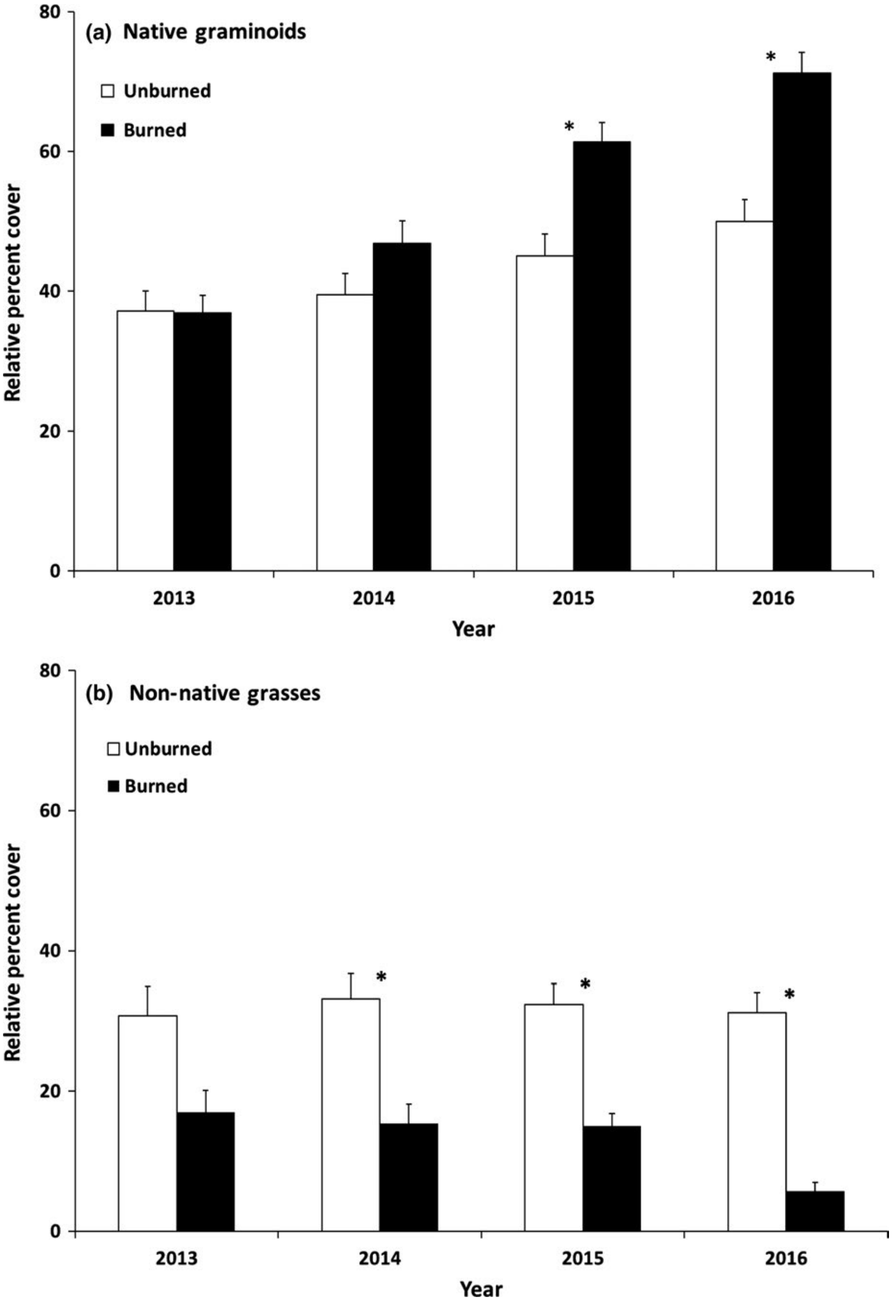

FIGURE 2 Burning effects on (a) native graminoid and (b) non-native grass relative percent cover (mean + *SE*), Bass River Recreation Area, Ottawa County, Michigan, 2013–2016. Means are averaged across the levels of the site preparation and hand pulling factors, which did not interact with the burning treatment; $n = 24$ for each mean.
* Adjacent non-burned/burned pairs of means differ significantly ($p < 0.05$) within a single year

(Figure 3). Differences in relative cover of individual plant groups between restored and untreated plant communities were substantial ($d > 0.8$, Nakagawa & Cuthill, 2007) for native graminoids ($d = 3.5$–4.7), non-native grasses ($d = 1.3$–3.6) and *C. stoebe* ($d = 1.1$–2.3), but were less pronounced for native forbs ($d = 0.4$–1.2), non-native forbs ($d = 0.4$–0.8), and woody species ($d = 0.6$–0.8). Canonical analysis of principal coordinates (Figure 4) clearly revealed the separation of the restored plant communities from that in the surrounding untreated areas along canonical axis 1, and the more subtle separation between burned and unburned restored plant communities along canonical axis 2. Cross-validation produced from 50% to 75% correct classification for restored plant communities and 100% correct classification for untreated plant communities. Only one experimental plot, with 34% relative cover of *C. stoebe*, was misclassified as untreated. The vector overlay of representative species portrays the strong association of native graminoid and forb species with the restored plant communities, and the similarly strong association of non-native species, including *C. stoebe*, with the untreated plant community. The differential effects of burning on native forb species (e.g., *Asclepias* spp. vs *Monarda* spp.) and native and non-native grasses (e.g., *Sporobolus cryptandrus*, Sand dropseed vs. *Poa compressa*, Canada bluegrass) also were apparent.

4 | DISCUSSION

Others have reported the effects of single management practices such as herbicide treatments (e.g., Rice, Toney, Bedunah, & Carlson,

TABLE 3 Site preparation and hand-pulling effects on *Centaurea stoebe* relative percent cover (mean ± *SE*), Bass River Recreation Area, Ottawa County, Michigan, 2013–2016

Treatment combination	Percent cover in year 2013	2014	2015	2016
Mowed, not pulled	41.4a ± 7.4	25.9a ± 5.4	13.3a ± 3.7	11.4a ± 3.3
Clopyralid, not pulled	12.7b ± 3.1	8.3a ± 1.5	6.7a ± 1.7	8.6a ± 2.7
Glyphosate, not pulled	34.0a ± 6.3	21.2a ± 5.2	14.0a ± 4.0	9.6a ± 4.0
Mowed, pulled	0.04c ± 0.01	0.02b ± 0.02	0.01b ± 0.01	0.01b ± 0.01
Clopyralid, pulled	0.05c ± 0.02	0.05b ± 0.03	0.01b ± <0.01	0.0b ± 0.0
Glyphosate, pulled	0.01c ± <0.01	0.01b ± 0.01	0.01b ± 0.01	0.0b ± 0.0

Effects of site preparation and hand pulling interacted with year ($p = 0.0001$, Table 1). Means within a single year with different letters differ significantly at $p < 0.05$. Treatment combination means are averaged across the levels of the burning factor, which was not significant and did not interact with site preparation or hand pulling; $n = 8$ for each mean.

1997), burning (e.g., Heslinga & Grese, 2010), or seeding (e.g., Rinella et al., 2012) on plant community composition over multiple years, but few studies have reported the effects of multiple management practices for more than a few years (Reid et al., 2009; Kettenring & Adams, 2011; Pearson et al., 2016). Our study followed the development of native-dominated plant communities established using an initial seeding and factorial combinations of site preparation treatments, hand pulling of *C. stoebe*, and burning over a period spanning eight years. Our results thus provide practical insights into the long-term impacts of these practices on native plant community restoration on similar degraded, *C. stoebe*-infested sites in midwestern North America (e.g., Emery & Gross, 2005; Emery & Rudgers, 2012; Mahaney, Gross, Blackwood, & Smemo, 2015), as well as in eastern and central North American mixed-grass and tallgrass prairies (e.g., Brudvig et al., 2007; Foster et al., 2007; Bowles & Jones, 2013), and on grasslands and rangelands in western North America (e.g., Sheley et al., 1998, 2006; Krueger-Mangold et al., 2006; Rinella et al., 2012). While most applicable to restoration of fire-adapted plant communities in North America, our results may relate to restoration of temperate grasslands in other parts of the world, which also are becoming increasingly rare as a result of fragmentation, abandonment, intensification of agricultural use, and invasion by

TABLE 4 Hand-pulling and burning effects on densities (mean ± *SE*) of four *Centaurea stoebe* life stages at the Bass River Recreation Area, Ottawa County, Michigan, 2015–2016

Life stage	Year	Experimental treatment combination: Not pulled Not burned	Not pulled Burned	Pulled Not burned	Pulled Burned	Untreated	$F_{4,52}$; p[†]
Seed bank (no./m^2)	2015	231ab ± 71	137abc ± 62[‡]	73.4bc ± 28.8	31.4c ± 22.6	472a ± 112	5.3; 0.0016
	2016	52.4 ± 36.2	10.5 ± 10.5	115 ± 104	10.5 ± 10.5	178 ± 91	1.1; 0.3747
Seedlings (no./m^2)	2015	18.0b ± 4.5	22.3b ± 9.9	0.02c ± 0.01	0.01c ± <0.01	118.8a ± 24.0	61.2; 0.0001
	2016	4.9b ± 1.7	1.4b ± 0.7	0.00c ± 0.00	0.00c ± 0.00	35.1a ± 10.6	43.7; 0.0001
Juveniles (no./m^2)	2015	12.7b ± 5.5	6.6b ± 2.1	0.04c ± 0.02	0.06c ± 0.02	30.0a ± 4.7	34.6; 0.0001
	2016	7.5b ± 2.5	8.1b ± 2.6	<0.01c ± <0.01	0.01c ± 0.01	42.6a ± 14.5	44.1; 0.0001
Adults (no./m^2)	2015	4.8b ± 1.5	1.4c ± 0.4	<0.01d ± <0.01	0.01d ± <0.01	12.9a ± 2.6	53.6; 0.0001
	2016	3.9b ± 1.0	2.2b ± 1.3	0.00c ± 0.00	0.00c ± 0.00	16.4a ± 4.0	32.2; 0.0001

Means within a single life stage and year followed by different letters differ significantly at $p < 0.05$. Experimental treatment combination means are averaged across the levels of the site preparation factor, which did not interact with hand pulling or burning.

[†] Pseudo-*F* and permutational *p*-value from one-way analysis of variance comparing untreated and experimental plant communities.

[‡] To more accurately represent the relatively low seed-bank densities on most plots ($n = 11$) in the non-hand-pulled and burned treatment combination in 2015, the mean excludes data from one plot with a seed-bank density of >33,000 germinants/m^2; $n = 12$ each for all other means. Lettering showing mean separation is based on analyses of the complete dataset including the ln-transformed outlier, and accurately represents the relationships between the means of the ln-transformed data.

TABLE 5 Comparison of diversity and floristic quality (mean ± *SE*) between restored plant communities and adjacent untreated plant communities at the Bass River Recreation Area, Ottawa County, Michigan in 2016

	Experimental treatment combination					
Variable	Not pulled Not burned	Not pulled Burned	Pulled Not burned	Pulled Burned	Untreated	$F_{4,52}$; *p*†
Non-native species (no. per 25-m^2 plot)	8.5 ± 0.6	6.9 ± 0.7	7.0 ± 0.6	7.0 ± 0.7	10.1 ± 1.0	5.0; 0.0017
Native species (no. per 25-m^2 plot)	13.6a ± 0.7	12.8a ± 1.0	13.3a ± 0.9	14.5a ± 0.8	5.6b ± 0.6	21.6; 0.0001
Shannon's Diversity Index ($e^{H'}$)	7.4a ± 0.4	6.0a ± 0.3	6.6a ± 0.2	7.0a ± 0.4	4.4b ± 0.3	12.8; 0.0001
Mean Coefficient of Conservatism ($\bar{C}$)	3.8a ± 0.1	3.6a ± 0.1	3.8a ± 0.1	3.7a ± 0.1	2.6b ± 0.2	17.6; 0.0001
Floristic Quality Index (FQI)	13.8a ± 0.5	12.7a ± 0.2	13.7a ± 0.6	13.8a ± 0.3	5.8b ± 0.5	64.2; 0.0001

Experimental treatment combination means are averaged across levels of the site preparation factor, which did not interact with the hand-pulling or burning treatments; *n* = 12 for each mean. † Pseudo-*F* and permutational *p*-value from one-way analysis of variance comparing untreated and experimental plant communities. Means within a single row followed by different letters differ significantly at $p < 0.05$.

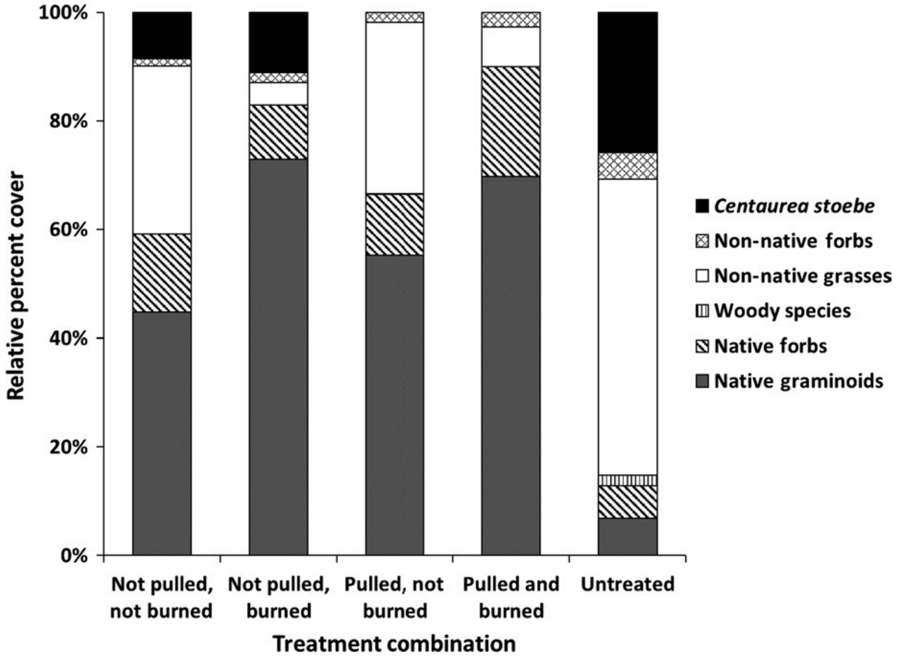

FIGURE 3 Plant community composition on experimentally restored and adjacent untreated areas in the Bass River Recreation Area, Ottawa County, Michigan, 2016. Experimental treatment combination means are averaged across the three levels of the site preparation factor, which did not interact with the hand-pulling or burning treatments (*n* = 12 each for all five categories). All experimental treatment combinations were seeded with a mixture of five native grasses and 18 native forbs. Plant communities in untreated areas differed from all experimentally restored plant communities based on permutational multivariate analysis of variance incorporating the six plant groups as multiple response variables ($F_{4,52}$ = 29.1; *p* = 0.0001)

exotic species (e.g., Europe: Bakker & Berendse, 1999; Bartha et al., 2014; Klaus et al., 2017; Australia: Cole, Koen, Prober, & Lunt, 2018; Johnson, Catford, Driscoll, & Gibbons, 2018; Mahmood et al., 2018).

4.1 | Site preparation effects

When averaged across the second four years of the study, native species richness was lower on the clopyralid treatment than on the glyphosate treatment. Native forbs that exhibited reduced frequency and relative cover on clopyralid-treated plots included *Ratibida pinnata* (Pinnate prairie coneflower) and *Symphyotrichum pilosum* (Hairy white oldfield aster; Appendix S2). Like *C. stoebe*, these species are members of the Asteraceae family, which has a known sensitivity to clopyralid (Tyser, Asebrook, Potter, & Kurth, 1998). While Rice et al. (1997) concluded that the effects of clopyralid on plant community diversity were negligible, they also noted decreased frequency of native forbs from the Asteraceae and Fabaceae families on clopyralid-treated plots. Similarly, Tyser et al. (1998) observed that native forb cover declined on clopyralid-treated plots, while non-native grass cover tended to increase. In our study, while clopyralid provided extended *C. stoebe* control, it also was associated with increased non-native grass cover in 2011 and 2012 (Martin et al., 2014), and greater non-native forb cover in 2014, although these secondary invasion effects (Pearson et al., 2016; Reid et al., 2009) did not persist into 2016. Clopyralid is considered to have low toxicity to humans and other organisms, so the potential impacts on non-target plant species appear to be the greatest acute risk associated with its use (Durkin & Follansbee, 2004).

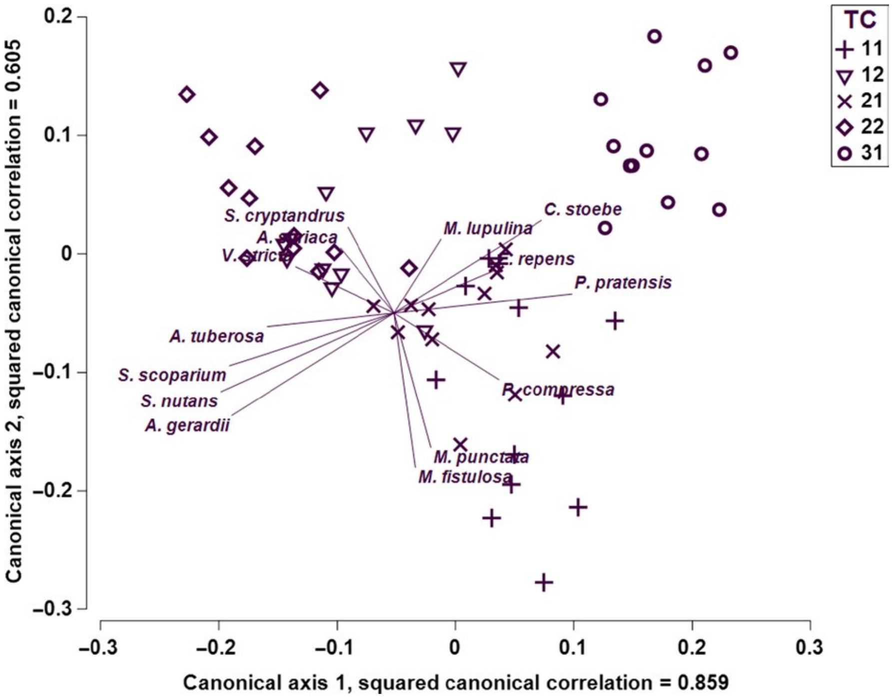

FIGURE 4 Canonical analysis of principal coordinates (CAP) characterizing differences between restored and untreated plant communities at the Bass River Recreation Area, Ottawa County, Michigan, 2016. CAP included normalized relative percent cover data (Euclidean distances) for 27 common plant species from 60 5-m × 5-m plots, 12 from each treatment combination (TC; 11 = not pulled, not burned; 12 = not pulled, burned; 21 = pulled, not burned; 22 = pulled and burned, 31 = untreated). Vector overlay shows the degree and direction of correlation with the canonical axes for representative species variables

In contrast to the reduced native species richness on clopyralid-treated plots, we found that the glyphosate treatment was associated with greater richness of native species. While relative cover of both *C. stoebe* (MacDonald et al., 2013) and non-native forbs (Martin et al., 2014) initially increased on the glyphosate treatment, these effects disappeared through time, while most native species established on this treatment persisted. Gross et al. (2005) also found that native midwestern forb and grass species successfully recruited into glyphosate-treated plots, although the effect was short-lived for many species. Many of the native species seeded in our study, including *Asclepias tuberosa* (Butterfly milkweed), *Monarda punctata* (Spotted beebalm), *Ratibida pinnata*, *Rudbeckia hirta* (Blackeyed Susan), *Andropogon gerardii* (Big bluestem), and *Schizachyrium scoparium* (Little bluestem) were well-established on the glyphosate treatment by 2011 (Martin et al., 2014), and all persisted on glyphosate-treated plots through 2016 (Appendix S2). While glyphosate is widely used, it has the potential for chronic toxicity to animals and humans (Van Bruggen et al., 2018) and its use may be restricted or regulated in some jurisdictions.

Surprisingly, in the second four years of the study, the mowed-only site preparation treatment did not differ from the glyphosate treatment in native species richness, demonstrating that interseeding native species on *C. stoebe*-infested sites can be successful without chemical site preparation, although additional management practices favored native species dominance. Emery and Gross (2006) also found that seeded native species successfully established on untreated *C. stoebe*-dominated plots, although another attempt to establish native grasses and forbs by seeding directly into *C. stoebe*-infested sites in Michigan was less successful (Carson, Bahlai, & Landis, 2014). In our study, a single mowing had minimal impacts on *C. stoebe* densities (MacDonald et al., 2013) or initial plant community development (Martin et al., 2014). In contrast, annual mowing during the flowering stage has been shown to reduce the density of *C. stoebe* (Rinella et al., 2001), and we observed that several native grasses and forbs originally seeded on the experimental plots, including *Schizachyrium scoparium*, *Andropogon gerardii*, *Sorghastrum nutans* (Indiangrass), *Monarda fistulosa (Wild bergamot)*, *Monarda punctata*, *Rudbeckia hirta*, *Coreopsis lanceolata* (Lanceleaf tickseed), and *Asclepias tuberosa*, became well established in the annually mowed buffers around our experimental plots without supplemental seeding or any other management. Repeated cutting, twice a year each year for 10 years, also was effective in controlling *Pteridium aquilinum* (brackenfern) infestations and increasing species richness on acid grassland sites in Great Britain (Stewart et al., 2008). Any site preparation method selected to facilitate restoration of an invasive species-dominated site will have both advantages and drawbacks. In general, herbicide applications provide the most effective reductions in invasive plant cover, density, and biomass across a variety of plant communities (Kettenring & Adams, 2011), but may do so at the risk of non-target effects (Skurski et al., 2013) and/or secondary invasion by other non-native species (Pearson et al., 2016; Reid et al., 2009). Mechanical methods such as mowing avoid the use of herbicides, but may provide less successful initial control of targeted invasives without conferring greater positive effects on native plant communities than herbicides (Kettenring & Adams, 2011; Pearson et al., 2016). Ultimate selection of an initial site preparation method may depend not only on its anticipated effect on a target invasive species, but also on its facilitation of subsequent practices intended to maintain control of invasives while favoring the development of native-dominated plant communities (Krueger-Mangold et al., 2006; Miller, 2016).

4.2 | Hand pulling and burning effects

Annual hand pulling reduced *C. stoebe* relative cover to almost zero by 2016, and maintained similarly reduced densities of seedling, juvenile, and adult *C. stoebe* as compared to either non-hand-pulled treatments or adjacent untreated areas. While Lutgen and Rillig (2004) and Skurski et al. (2013) reported mixed results using this method, complete removal of the taproot of hand-pulled *C. stoebe* plants along with a persistent effort over multiple years is needed for effective control (MacDonald et al., 2013). In contrast, hand pulling of other invasive species may not be effective, especially if a species has a clonal habit. For example, repeated hand pulling of *Asclepias syriaca* (Common milkweed) over two growing seasons did not eliminate it from a grassland site in Hungary (Szitár, Kröel-Dulay, & Török, 2018).

While using hand pulling alone to control extensive, dense populations of *C. stoebe* can be prohibitive in terms of time and effort, hand pulling can be an effective practice for treating small infestations or as a follow-up treatment after other means have reduced *C. stoebe* population densities to manageable levels (MacDonald et al., 2013). For example, in our study, a single clopyralid treatment greatly reduced the number of adult *C. stoebe* that needed to be hand pulled during the initial years of the study (MacDonald et al., 2013). Where herbicide use is restricted, delaying hand pulling until adult *C. stoebe* densities are reduced to lower levels by burning and/or competition from the restored native vegetation also may be effective. For example, by 2015 adult *C. stoebe* densities on non-hand-pulled burned plots, where native graminoid relative cover was high (63.3 ± 4.9%), had declined to 1.4 ± 0.4 plants/m^2. This *C. stoebe* density was below the maximum 3.3 ± 0.9 plants/m^2 removed from hand-pulled, clopyralid-treated plots in 2010 and substantially below the 44.2 ± 6.6 plants/m^2 removed from the hand-pulled, mowed-only plots in 2009 (MacDonald et al., 2013).

Skurski et al. (2013) observed that a single hand pulling of *C. stoebe* had no other effects on any plant community characteristic, while we found that annual hand pulling of *C. stoebe*, when combined with burning, increased the relative cover of native forbs as a group. Hand pulling combined with burning also produced a higher mean value of Shannon's Diversity Index (expressed as $e^{H'}$) than on burned plots that were not hand pulled, suggesting that the combination of treatments increased the effective number of species within the plant community compared to the less intensively managed plant community (Peet, 1974). The values of $e^{H'}$ we observed (7.3–8.9), however, were typical of plant communities still recovering from past disturbance when compared to the range of <6 to >20 found in temperate grasslands in Germany by Morris et al. (2014). Others have found that hand pulling directly reduced competition from *C. stoebe* (e.g., Maron & Marler, 2008), while burning reduced competition from non-native grasses and favored the establishment and persistence of native forbs (Maret & Wilson, 2000; Suding & Gross, 2006; Bowles & Jones, 2013). Native forbs that displayed strong positive responses to hand pulling and burning in our study (Figure 4, Appendix S2) included *Asclepias syriaca*, *Asclepias tuberosa*, *Coreopsis lanceolata*, *Rudbeckia hirta*, and *Verbena stricta* (Hoary verbena), all mid- to late-season nectar sources that would provide this resource in the absence of *C. stoebe* (Carson et al., 2014).

In our study, burning increased the relative cover of native graminoids and decreased that of non-native grasses, while burning combined with hand pulling increased the relative cover of native forbs. Brudvig et al. (2007) and Bowles and Jones (2013) also observed that burning produced a shift from cool-season grasses and exotic forbs to communities dominated by native species. In contrast, Heslinga and Grese (2010) found that burning a prairie remnant in the absence of seeding did not increase native species richness because of a limited native seed bank and minimal colonization from nearby remnants. We did observe a subtle negative effect of burning on floristic quality as $\bar{C}$ was slightly lower on the burned treatment, probably as a result of several native forbs occurring less frequently on burned plots, including *Monarda fistulosa*, *Monarda punctata*, and *Ratibida pinnata* (Figure 4; Appendix S2).

In contrast to findings of an earlier study on this site (MacDonald et al., 2007), mid-spring burning had no significant effects on *C. stoebe* cover. In our earlier study, plots were dominated by dense stands of native grasses, and annual burning significantly reduced *C. stoebe* density, biomass, and dominance. In the current study, burning did reduce adult *C. stoebe* densities on non-hand-pulled plots in 2015, suggesting that mid-spring burning may reduce adult density and seedfall by inhibiting bolting of juveniles, even though *C. stoebe* cover was not directly affected. The results of our study were similar to those of Emery and Gross (2005), who found only subtle effects of early spring burning on *C. stoebe* populations in remnant prairies in southern Michigan. Restored or remnant plant communities containing both native grasses and forbs may burn with less uniform intensity than those dominated by native grasses, resulting in less effective control of *C. stoebe*.

Consistent with reduced adult density and lower seedfall on burned plots in 2015, however, the *C. stoebe* seed bank density observed on the burned plots in 2016 (10.5 ± 7.2 germinants/m^2) was below that reported for annually burned native grass plots by MacDonald et al. (2007; 52 ± 17 germinants/m^2), and also below the six-year average seed bank density in untreated areas of the study site (400 ± 54 germinants/m^2, MacDonald et al., 2013 and this study). Persistence of the seed bank on non-burned hand-pulled plots (Table 4), with little change since 2012 (68 ± 26 germinants/m^2; MacDonald et al., 2013), suggests that the sparse seed bank on burned plots in 2016 also may reflect a direct burning effect on *C. stoebe* seed viability, as observed by MacDonald, Bosscher, Mieczkowski, Sauter, and Tinsley (2001) and Vermeire and Rinella (2009).

Burning also can have indirect effects that may help suppress *C. stoebe*, at least in midwestern North America. Burning strongly favored native graminoids in our study, and when combined with hand pulling also favored native forbs. Once established, native species strongly compete with *C. stoebe* (Maron & Marler, 2007; Rinella et al., 2007; MacDonald & Bottema, 2014). Native warm-season grasses in particular are more competitive at low nutrient availability than *C. stoebe*, and can reduce nitrogen availability, decreasing invasion by non-native species (Mahaney et al., 2015). In our study, the increasing negative correlation between the relative cover of *C. stoebe* on non-hand-pulled plots and that of native graminoids, along with the inverse association between *C. stoebe* and seeded native grass species portrayed in Figure 4, also were consistent with competitive suppression of *C. stoebe* as the cover of native graminoids increased through time.

We applied hand pulling and burning as follow-up treatments to the initial site preparation treatments because we anticipated that both would further reduce *C. stoebe*, while potentially interacting with the site preparation treatments to differentially affect native plant community development. Hand pulling physically removes an invasive plant, which effectively controls the targeted species, but also opens up unoccupied areas that could allow the subsequent establishment of either native or non-native species (e.g., Abella, Suazo, Norman, & Newton, 2013; Hasselquist, Hasselquist, & Rogers, 2013; Heckman, McColley, Slater, & Carr, 2017). In contrast, burning involves the destruction of biomass of most if not all species inhabiting a site, has well-documented positive effects on native plant communities in North America (e.g., Brudvig et al., 2007; Bowles & Jones, 2013), and also may favor the persistence of certain native species (e.g., Howe, 2011; Young, Porensky, Wolf, Fick, & Young, 2015). Hand pulling allows the targeted control of an invasive species without the use of herbicides, but is labor-intensive and difficult to apply at large scales (Hasselquist et al., 2013; Heckman et al., 2017). In contrast, burning can be effectively applied at a large scale, but may be much less selective in its impact on a targeted invasive species and must be carefully timed to achieve the desired results (e.g., Emery & Gross, 2005; Howe, 2011; Bowles & Jones, 2013).

Prescribed burning also may facilitate active management of semi-natural grasslands in Europe, but its use is uncommon and tightly regulated in many areas (Valkó, Török, Deák, & Tóthmérész, 2014). In North America, fire is used to manage prairies dominated by C4 grasses, while in Europe many grasslands are dominated by C3 grasses that may not respond as positively to frequent fires, and its use for invasive species control has not been extensively studied (Ruprecht, Enyedi, Szabó, & Fenesi, 2016; Valkó et al., 2014). Responses to fire also differed between South African and North American grassland communities, with frequent burning in North America favoring a less diverse community dominated by native C4 grass species, while frequent burning in South Africa favored the development of a more diverse community including a range of shorter grass species (Kirkman et al., 2014). In Australia, the use of prescribed fire may help maintain competitive populations of native grasses and forbs while helping to control exotic species in temperate grasslands (Cole et al., 2018; Johnson et al., 2018). Invasive species can differentially affect fire frequency and intensity, however; the presence of *C. stoebe* decreases fire intensity in North American plant communities, while the invasive African perennial grass *Andropogon gayanus* (Bluestem) increases fire frequency and intensity in Australian grasslands (Brooks et al., 2004).

A variety of other management practices including grazing, biological controls, and seeding have potential applications in controlling invasive species and facilitating restoration of native plant communities. For example, traditional practices including mowing and grazing historically maintained semi-natural grasslands throughout Europe (Bakker & Berendse, 1999; Ruprecht et al., 2016; Klaus et al., 2017). Brudvig et al. (2007) suggested that combining grazing with targeted removal of problematic invasives, or combining burning with seeding or transplanting of desired native species warranted further testing on prairies in the Iowa loess hills of North America. Biological controls also help control a variety of invasive species including *C. stoebe*, especially when combined with other methods to increase native species such as seeding (e.g., Stephens, Krannitz, & Meyers, 2009; Cutting & Hough-Goldstein, 2013; Carson et al., 2014). Propagule supply often limits the restoration of native plant communities, so seeding after site preparation or interseeding into remnant plant communities is a necessary practice in many restoration attempts in North America (e.g., Foster & Tilman, 2003; Foster et al., 2007; Mazzola et al., 2011) and Europe (e.g., Bakker & Berendse, 1999; Klaus et al., 2017; Török et al., 2018). Combining seeding with other management methods is often successful (e.g., Klaus et al., 2017; Johnson et al., 2018; Mahmood et al., 2018), as we found by seeding native species followed by hand pulling of *C. stoebe* for eight years and annual burning for three out of the last four years of our study.

4.3 | Seeding effects

By the eighth growing season after seeding experimental plots with native species, relative cover of native graminoids and forbs ranged from 59.1 ± 3.8% on plots that only received site preparation to 89.9 ± 2.4% on plots that also were both hand pulled and burned (Figure 3). In comparison, relative cover of native graminoids and forbs was only 12.7 ± 3.7% on untreated plots. Seeded species comprised 18 of 41 native species and an average 87% of the total native relative cover on restored plots (Appendix S2). In contrast, only five of 20 native species and an average 9.7% of the total native relative cover on untreated plots represented species included in the experimental seed mix. Seeded species apparently established in untreated areas from seed produced on nearby experimental plots, as few of the species included in the native seed mix were present before the initiation of the experiment (MacDonald et al., 2007; Martin et al., 2014).

Without the initial seeding, it is unlikely that the experimental treatments alone would have produced similar native-dominated plant communities, since a lack of native propagules can constrain the diversity of restored plant communities (Foster et al., 2007; Johnson et al. 2018; Zylka et al., 2016). For example, on mowed-only plots that were neither hand pulled nor burned, relative cover of native graminoids and forbs increased from 8.0 ± 2.5% in 2011 to 60.1 ± 5.8% in 2016, representing an effect of seeding in the absence of any additional management other than the single mowing in 2008. Of the 23 native species included in our seed mix, five grasses and 13 forbs persisted through eight growing seasons (Appendix S2), surviving severe drought conditions in summer, 2012 (Martin et al., 2014). We also observed that many of the seeded native species successfully reproduced on the experimental plots and spread into both mowed and unmowed areas around the plots, evidence that the restored native plant communities would become self-sustaining, as demonstrated for native grass communities established in an adjacent area in 1999 (MacDonald & Bottema, 2014).

The restored plant communities contained assemblages of native species common to dry-mesic prairies in southern Michigan (Kost et al., 2007), being dominated by *Andropogon gerardii*, *Schizachyrium scoparium*, and *Sorghastrum nutans*, but also containing other native forbs and graminoids representing a variety of plant functional groups (Figure 4; Appendix S2; USDA NRCS 2018). Combining data for all 48 experimental plots produced a site $\bar{C}$ of 3.4 and FQI of 21.6 in 2016, similar to values found in dry-mesic prairie remnants (e.g., Taft et al., 1997) and other experimental prairie restorations (e.g., Taft et al., 2006; Foster et al., 2007), but below values for intact natural areas ($\bar{C}$ = 5 to 6, FQI = 45 to 55; Taft et al., 1997; Spyreas et al., 2012). After excluding the seeded native species from the experimental plot data, however, $\bar{C}$ fell to 2.3, while FQI fell to 10.8, similar to $\bar{C}$ (2.7) and FQI (11.9) calculated for the combined untreated plot data and typical of values for other unrestored old-field sites (Taft et al., 1997).

5 | SUMMARY AND CONCLUSIONS

The treatments we employed facilitated the restoration of native-dominated plant communities on a degraded, *C. stoebe*-infested site. The eight-year length of our study revealed the transient nature of most site preparation effects, the continued effect of persistent hand pulling on *C. stoebe* cover and density, and the increasingly pronounced effects of repeated burning on plant community composition. All three site preparation treatments, followed by seeding with a mixture of native grasses and forbs, produced native-dominated plant communities even without subsequent management. Hand pulling, while labor intensive, reduced *C. stoebe* cover and density to almost zero after eight years of treatment. Burning increased the relative cover of native graminoids, reduced that of non-native grasses, and when combined with hand pulling, also produced the greatest relative cover of native forbs. Any reinvasion by *C. stoebe* or expansion of other secondary invaders in response to experimental treatments was short lived as competition from native species increased. The restored plant communities resembled those found in southern Michigan dry-mesic prairies, contained a variety of plant functional groups, and experimentally introduced native species successfully reproduced on experimental plots and actively seeded into mowed and unmowed areas surrounding the plots. The restored plant communities also responded positively to fire as a restored natural process, persisted through periodic stress events such as drought, and had greater diversity and higher floristic quality than adjacent untreated areas. These results demonstrated that seeding native species, in combination with integrated management strategies to control *C. stoebe* and to favor native species, produced native-dominated plant communities that possessed many of the desired attributes of restored ecosystems. The length of our study, allowing the evaluation of treatment effects through time, highlights the importance of continued management and monitoring to fully implement and assess successful restoration of native plant communities on similar disturbed, invasive species-infested sites.

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AUTHOR CONTRIBUTIONS

N.M. designed the study; N.M., L.M., & K.D. conducted fieldwork; N.M. & K.D. conducted the seed bank study; N.M. performed the statistical analyses; N.M. developed the initial draft; and N.M., L.M., & K.D. collaborated on revisions of the manuscript.

DATA ACCESSIBILITY

Original data files are included as Appendices S3 and S4.

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SUPPORTING INFORMATION

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

Appendix S1 Aerial view of the study site, showing the four experimental blocks of 12 5-m × 5-m plots each.

Appendix S2 Frequency of occurrence and mean relative percent cover of common and seeded species.

Appendix S3 Plant cover, diversity, and floristic quality data.

Appendix S4 Knapweed lifestage density data.

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