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Effects of experimental prescribed fire and tree thinning on oak savanna understory plant communities and ecosystem structure

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ABSTRACT

In the Midwestern United States, oak savannas have been reduced in area by at least 99% since European settlement, mirroring global trends for savannas, grasslands, and shrublands. Most remaining patches are highly degraded following decades of fire suppression and other anthropogenic impacts, and subsequent tree and shrub encroachment. Yet, reintroducing fire alone may not be sufficient to restore these ecosystems on desired timelines and mechanical thinning may be an important step in the restoration process, to increase understory light and promote the ground layer community. However, it is unclear how plant community dynamics develop under burn-only compared to thin-and-burn restoration scenarios. We investigated the impacts of prescribed fire and mechanical tree thinning on ecosystem structure and plant community dynamics over eight years in an oak savanna restoration experiment in southern Michigan. Established in 2010, this experiment utilized 15 0.4–1.2-hectare treatment units receiving either repeated prescribed fire alone, a combination of repeated prescribed fire and mechanical thinning, or no management. We used this design to test how differences in management affect understory and overstory structure, specifically understory vegetative cover and light availability associated with canopy openness, and plant community dynamics, specifically ground layer plant species richness and composition. We found that, over eight years of restoration, the response of ecosystem structure and the plant community was greatest in units where mechanical thinning was combined with prescribed fire. Thinned and burned units had greater canopy openness, vegetative cover, and plant species richness. Plant species composition also diverged between managed and unmanaged units. Canopy openness increased rapidly, within two years of restoration, while vegetative cover increased more gradually, over five years, and increases in richness were less pronounced overall. Composition diverged initially between managed and unmanaged units and continued to shift throughout the study period. Some effects of management peaked after four years, but were transient by the end of the study. Additional management will be necessary to capitalize on the initial response to restoration toward an oak savanna ecosystem. We predict that additional thinning will further increase light availability and development of graminoid fuels and in combination with prescribed fires will continue to promote open canopy structure and a ground layer dominated by savanna-associated species.

1. Introduction

Temperate grasslands, savannas, and shrublands are among the most imperiled ecosystems on the planet (Hoekstra et al., 2005). Nearly half of the global area of these ecosystems has been converted for human land uses and remaining patches often face alterations to key ecological processes (Nuzzo, 1986; Hoekstra et al., 2005; Veldman et al., 2015). For example, alterations to disturbance regimes like fire and grazing result in tree and shrub encroachment, modified ecosystem structure, altered species composition, and losses of native diversity (Leach and Givnish, 1999; Briggs et al., 2005; Brudvig, 2010; Ratajczak et al., 2012; Smith et al., 2016; Ladwig et al., 2018). As a result, restoration of temperate grassland, savanna, and shrubland ecosystems is a high priority. However, restoration may not be achievable solely through the reintroduction of historical processes such as disturbance regimes, owing to thresholds that ecosystems may cross during periods of altered disturbance (Suding and Hobbs 2009). In such instances, successful restoration may require structural interventions like tree

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thinning, in combination with reintroduction of key disturbances (Nielsen et al., 2003; Lettow et al., 2014; Vander Yacht et al., 2017). Here, we evaluate the effects of reinstating a key disturbance, fire, either alone or coupled with overstory tree thinning, in fire-suppressed oak savannas in the Midwestern USA.

Midwestern oak savannas historically occurred along the prairie-forest ecotone, from Minnesota to Missouri, and as far east as Ohio (Anderson, 1998). The structure and species composition of both the canopy and ground layer varied widely, occupying a continuum bracketed on one end by prairie grasslands with scattered trees and on the other by closed-canopied oak-hickory forests (Curtis, 1959). Within this variation, three features define oak savannas: (1) a discontinuous oak-dominated overstory of fire-tolerant trees, resulting in higher understory light availability than in closed-canopied forests; (2) a continuously vegetated ground layer dominated by herbaceous species and shrubs; and (3) a disturbance regime characterized by frequent fire (~3 fires/decade; Abrams, 1992; Peterson and Reich, 2001), and to a lesser extent, grazing by native herbivores and windfall. Both overstory structure and fire maintain plant diversity and composition in savannas (Cottam, 1949; Leach and Givnish, 1999; Pavlovic et al., 2006). A discontinuous overstory creates a ground layer with both high and low light availability, and as a result the coexistence of shade-tolerant and -intolerant species (Pavlovic et al., 2006). Frequent fire reduces leaf-litter, encourages a unique fire-tolerant flora, and reduces woody encroachment (Abrams, 1992; Peterson and Reich, 2001).

Midwestern oak savannas have declined by at least 99% since European settlement in the 1800s (Nuzzo, 1986). Most savannas were converted to anthropogenic land uses (e.g., agriculture and urban development), and remnant savannas typically persist in a degraded state due to decades of livestock grazing and fire suppression. These remnants are characterized by modified structure and composition. Signs of degradation include a closed overstory canopy, a dense mid-story of shrubs and tree saplings, and reduced ground layer plant diversity composed of shade-tolerant species typical of forest communities and few typical of savanna communities (Bowles and McBride, 1998; Brudvig and Mabry, 2008; Ladwig et al., 2018).

Given the central role of overstory structure and fire in maintaining ground layer diversity and composition in savannas, restoration must consider both. Historically, frequent fire maintained the canopy and ecosystem structure of Midwestern oak savannas (Abrams, 1992; Peterson and Reich, 2001) and the diversity of ground layer forbs and grasses that they supported (Bowles and McBride, 1998; Leach and Givnish, 1999; Ladwig et al., 2018). However, simply reintroducing fire may not be sufficient to restore the structure, composition, and diversity of savannas (Nielsen et al., 2003; Bowles et al., 2017; Vander Yacht et al., 2017). Extensive tree and shrub encroachment, due to decades of fire suppression, may limit the effectiveness of fire for achieving target structure and composition. Mechanical thinning is often used in combination with prescribed fire, to increase canopy openness and associated light availability to the savanna understory, remove non-savanna trees that have exceeded fire-sensitive size thresholds, and facilitate fuel accumulation (Lettow et al., 2014; Bowles et al., 2017).

We investigated the impacts of prescribed fire and mechanical thinning on ecosystem structure and plant community dynamics over eight years in an oak savanna restoration experiment in southern Michigan. Descriptions of the overstory and understory structure and composition in Michigan savannas as fire-dependent communities with a sparse canopy (10–60%) of oak species (particularly *Quercus alba*, *Q. macrocarpa*, and *Q. velutina*) and a diverse ground layer with a significant graminoid component (Cohen, 2001, 2004; Chapman and Brewer, 2008), are consistent with descriptions of savannas throughout the Midwestern USA (e.g., Nuzzo, 1986; Leach and Givnish, 1999). Established in 2010, this experiment utilizes 15 0.4–1.2-hectare treatment units which receive either repeated prescribed fire alone (burn-only), a combination of repeated prescribed fire and mechanical tree thinning (thin-burn), or no management. We used this design to test how differences in management affect key aspects of ecosystem structure, specifically canopy openness and understory vegetative cover; and plant community dynamics, specifically ground layer plant species richness and composition.

We asked whether thin-burn and burn-only treatments altered the following factors, compared to unmanaged controls and to each other, and whether the magnitude of these differences changed over time:

1) Structural characteristics (canopy openness and understory vegetative cover).
2) Plant species richness (total, native, exotic).
3) Plant species composition.
4) Individual species or groups of species.

2. Material and Methods

2.1. Study site

This study took place at Michigan State University's ~165 ha MacCready Reserve in Jackson County, Michigan (42°07′36″N, 84°23′38″W). A portion of this site features an esker ridge, which historically supported open-canopy oak savannas, presumably maintained by the site's coarse soils, periodic surface fires, and grazing (Lettow et al. 2014). Following decades of fire suppression and exclusion of grazing animals, however, these oak savannas were invaded by fire-sensitive tree species (e.g., *Acer rubrum*, *Prunus serotina*). This resulted in closed canopy conditions at the onset of our experiment, with intermixed remnant large-canopy oak trees (primarily *Quercus alba* and *Q. velutina*) and smaller diameter fire-sensitive trees filling former canopy gaps. Prior to restoration treatments, the understory supported species characteristic of oak savannas (e.g., *Ceanothus americanus*, *Krigia biflora*), as well as species with savanna affinities that also occur in oak-hickory woodland and forest (e.g., *Galium circaezans*, *Hepatica americana, Hylodesmum glutinosum*) (Cohen, 2001, 2004; Chapman and Brewer, 2008; Lettow et al., 2014). Additional site description details are available in Lettow et al. (2014).

2.2. Experimental design

In 2010 we identified 10 areas of fire suppressed oak savanna along the esker (each 0.4–1.2 ha) and randomly assigned these to two restoration treatments. The long-term target for restoration treatments were guided by historical descriptions of Michigan's savanna communities, in particular reducing canopy cover below 60%, increasing dominance of oaks both in the canopy and in recruitment classes, encouraging a diverse herbaceous ground layer with a significant graminoid component containing savanna indicator species, and the reintroduction of fire as a natural disturbance (Cohen, 2001, 2004; Chapman and Brewer, 2008). Five units were assigned a burn-only treatment and received prescribed low intensity surface fire every 2–3 years. Five units were assigned a thin-burn treatment and received two rounds of canopy thinning to remove encroaching fire sensitive trees, along with prescribed low intensity surface fire every 2–3 years. A first round of thinning conducted in late fall 2010 (after plant senescence) cut all non-oak stems < 10.2 cm DBH (diameter at 1.4 m height) and a second round of thinning conducted in late fall 2011 (again, after senescence) cut all non-oak stems < 17.8 cm DBH. In 2010 prior to thinning, mean basal area was 26.9 m^2/ha (117.1 ft^2/A) and 29.1 m^2/ha (126.6 ft^2/A) in burn-only and thin-only plots, respectively. Stocking rates were 802.3 trees/ha (334.3 trees/A) and 814.6 trees/ha (339.4 trees/A), respectively. Thinning reduced basal area in thin-burn units to 22.0 m^2/ha (95.7 ft^2/A), and stocking to 268.9 trees/ha (112.0 trees/A) by summer 2012. We conducted thinning in two phases using these diameter cutoffs for logistical reasons and focused on non-oak stems to encourage oak regeneration because oaks dominate similar systems in our region and throughout the Midwest (Abrams, 1992; Cohen, 2001, 2004; Peterson and Reich, 2001; Dey et al., 2017). Thus, the goal of this particular thinning treatment was to increase understory light availability by reducing woody stem densities in favor of oak species (Abrams, 1992; Dey et al., 2017). All cut stems were left in place and stumps were treated with glyphosate-based herbicide (Cornerstone Plus, mixed according to manufacturers specifications) to prevent resprouting.

The goals of prescribed fires were to increase understory light availability, through mortality of non-oak woody stems, and to provide recruitment opportunities for understory plants, by consuming leaf litter and exposing mineral soil. To achieve these goals, we conducted prescribed fires in early spring, after initiation of leaf out by many fire sensitive tree species, but before initiation of oak leaf out. We ignited fires at the top of the esker ridge and allowed fires to burn slowly downhill, backing into the wind when possible. Fires consumed leaf litter, understory plants, and some downed woody material, but did not burn into tree canopies. Each management unit was burned between three and five times over the duration of this study, with approximately equal variation between the set of burn-only and thin-burn units (burn only: one unit burned three times, three units burned four times, one unit burned five times; thin-burn: one unit burned three times, four units burned four times).

In 2012 we identified five additional areas of fire suppressed oak savanna along the esker ridge, to serve as unmanaged controls for this study. These areas were selected to match site characteristics to the pre-restoration conditions in the 10 burn-only and thin-burn units. In particular, we ensured that all 15 units were underlain by similar soils (on or adjacent to the esker), were on similar aspects (south, south-east, or south-west facing), supported similar overstory tree compositions and configurations (near closed-canopy, oak dominated), and the same land-use history (tree cutting and livestock grazing, but no known agricultural cultivation). The three treatments were spatially intermixed among across the 15 units, with no geographic bias with respect to treatment (see Fig. 1 in Lettow et al., 2014).

2.3. Sampling methods

Within each unit, we established 1–2 permanently marked sampling transect(s), initiated at the base of the esker ridge and running uphill to the top of the esker. Owing to variation in the height and slope of the esker, transects varied in length from 20 to 100 m. In instances where transects were < 40 m, we established two transects in a unit to provide sufficient number of sampling plots.

Each transect was 10 m wide and composed of contiguous 10 m × 10 m plots. We sampled trees within each 10 m × 10 m plot by measuring DBH and recording species identity of all live woody stems ≥ 5 cm DBH. We measured saplings within 4 m × 10 m plots centered on the sampling transect by measuring DBH and recording species of all live woody stems < 5 cm DBH, but at least 140 cm tall. For this current study, we combine tree and sapling data to calculate basal area. We sampled understory plants by recording species identity and aerial percent cover for all herbaceous species and woody species < 1 m height rooted within or overhanging 1 × 1 m plots located every 10 m along each transect. We quantified canopy cover using a spherical densiometer above each 1 m × 1 m plot; we took four readings above each plot, oriented in each of the four cardinal directions. We collected each of these types of data annually in August or early September, once plants were fully emerged and identifiable, but prior to senescence. We initiated sampling of burn-only and thin-burn units in 2010, one season prior to initiation of treatments, and in 2012 for unmanaged units.

2.4. Data analysis

All analyses were conducted using R 3.5.2 (R Core Team, 2018).

2.4.1. Structure and diversity response to management

Prior to analyzing the effects of management, we averaged values across all 1-m^2 plots within a treatment unit for both structural variables (percent canopy openness and percent vegetative cover) and diversity variables (native, exotic and total species richness). We then tested for the effects of management treatments on each of these variables by conducting repeated measure ANOVAs using *lme* function in the *nlme* package in R. For each response variable, we constructed a model with treatment and year as fixed effects, site as a random effect, and a first-order autoregressive correlation structure. While we used $\alpha = 0.05$ throughout to determine statistical significance, when the treatment effect was marginally significant at $p < 0.10$, we further explored pairwise comparisons among treatment effects with Tukey's HSD, with the *glht* function in the *multcomp* package in R. To estimate the amount of variation explained by the fixed effects in each model, we calculated marginal pseudo-R^2 using the *r.squaredGLMM* function in the *MuMIn* package in R (Nakagawa and Schielzeth, 2013). We conducted repeated measures analysis only on data from 2012 to 2018, because no data were collected in unmanaged controls in 2010 and 2011. When analyzing canopy openness, we omitted data from 2014, due to missing data for some plots, and from 2017, because densiometer readings were anomalously high.

To better understand the temporal dynamics of changes in ecosystem structure and plant species diversity, we followed up repeated measures analysis with individual one-way ANOVAs testing the effect of treatment types on all structural and diversity variables for each individual year of the study. When treatment effects were significant at $p < 0.10$, we conducted pairwise comparisons among treatment effects with Tukey's HSD.

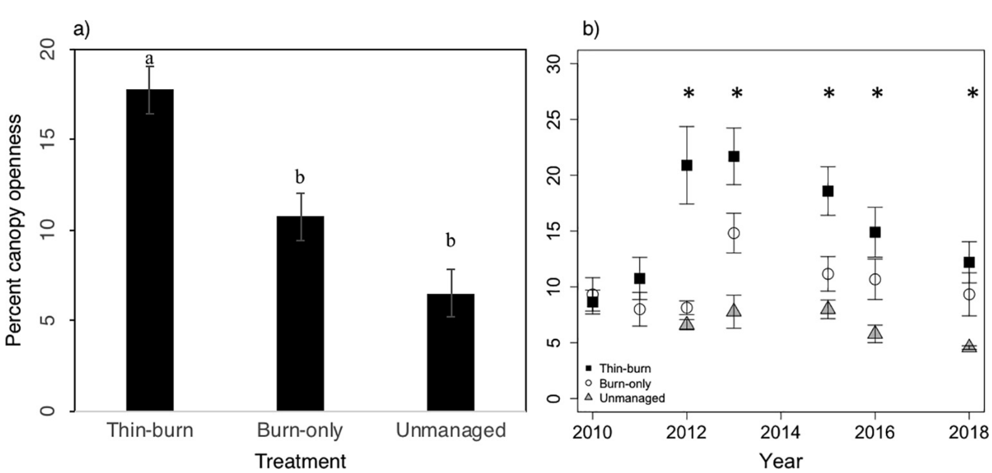

Fig. 1. Percent canopy openness is higher in thin-burn units than in unmanaged units. Least-square means of percent light availability from repeated measures ANOVA on data from 2012 to 2018 (a); and means (+/- SE) for individual years of study (b). In (a), bars with different letters are significantly different at $p < 0.05$; significance assessed using Tukey's HSD with Bonferroni corrections. (Note: burn-only and unmanaged plants are significantly different at $p < 0.10$.) In (b), a significant effect of treatment from ANOVA; $^*p < 0.05$, $^{\cdot}p < 0.10$. Data from 2014 (missing values) and 2017 (anomalously high values) are omitted (see *Methods*).

2.4.2. Composition response to management

We used a series of multivariate tests to assess how management treatments influenced plant species composition, and how plant species composition responded to treatments over time. We constructed two sets of site × species matrices for these analyses, using average percent cover per 1-m^2 plot for species at each site. The first set included one matrix for each year that included all treatments, to test whether composition differed between treatments within each year (i.e., treatment was the grouping factor). The second set included one matrix for each treatment that included all years to test whether composition differed within each treatment over time (i.e., year was the grouping factor).

We evaluated whether composition differed among treatments and years with PERMANOVA, using the *adonis* function in the *vegan* package in R. For each matrix, we calculated Bray-Curtis dissimilarities, then conducted PERMANOVAs using treatment as a grouping factor. We calculated Bray-Curtis dissimilarities on these matrices and conducted PERMANOVAs using year as a grouping factor. To assess between-group differences, we calculated Bonferroni-corrected p values with the *pairwise.adonis* function in the *pairwiseAdonis* package in R (Martinez Arbizu, 2019), and compared group centroids visually in NMDS plots. The test statistic in PERMANOVA is robust to the heterogeneity of multivariate dispersion with balanced designs, so we do not present analyses of multivariate dispersion (Anderson and Walsh 2013).

Finally, we evaluated species responses to treatments, by conducting indicator species analysis using the *indval* function in the *labdsv* package in R. The indicator value (IV_{ij}) is the product each species *specificity* (A_{ij}) to a grouping factor ($A_{ij}=\frac{\bar{x}_{ij}}{\sum_j \bar{x}_{i.}}$) and the *fidelity* ($B_{ij}$) of that species to a grouping factor ($B_{ij}=\frac{n_{ij}}{n_{.j}}$), where x_{ij} = mean abundance of species i in group j, and n_{ij} = the number of samples where species i occurs in group j. We then permuted ($n = 1000$) each IV_{ij} and asked whether each IV_{ij} was at least as great as the calculated value ($p = 0.05$). Using the first set of matrices, we assessed whether the indicator species for each treatment was consistent across years (j = treatment), and using the second set we assessed whether the indicator species for each year was consistent across treatments (j = year).

3. Results

Canopy openness, vegetative cover, and ground layer plant species richness (especially native species) were generally higher in thin-burn units, than in burn-only and unmanaged units.

3.1. Question 1: Structure

Both percent canopy openness (partial-η^2 = 0.56, pseudo-R^2 = 0.56; Fig. 1) and percent vegetative cover (partial-η^2 = 0.20, pseudo-R^2 = 0.25; Fig. 2) differed among treatments (Table 1). Canopy openness in thin-burn units was 7.0% greater than burn-only and 11.3% greater than unmanaged units (Table 1). Canopy openness was also 4.3% higher in burn-only than unmanaged units, although the difference was marginally significant (Table 1). After the second round of thinning in 2011, percent canopy openness differed among treatments in every subsequent year (2012–2018) (Fig. 1b; Table S1). Percent canopy openness was significantly higher in thin-burn than unmanaged units in each of these years, while the significance of other pairwise comparisons (thin-burn vs. burn-only, burn-only vs. unmanaged) differed from year to year (Table S1). Percent vegetative cover was 12.5% higher in thin-burn and 11.5% higher in burn-only than unmanaged units, although the difference was marginally significant in burn-only units (Table 1). Percent vegetative cover was similar in burn-only and thin-burn units (Table 1). Percent vegetative cover never differed significantly among treatments in individual years, but differences were marginally significant from 2013 to 2015 (Fig. 2b; Table S1). Thin-burn units had 22.5% greater percent vegetative cover than unmanaged units in 2014, and 22.8% greater vegetative cover in 2015, although the difference was marginally significant in 2014 (Fig. 2b; Table S1). No other pairwise comparisons were significant for percent vegetative cover in any other year (Fig. 2b; Table S1).

3.2. Question 2: Species richness

Species richness differed among treatments (partial-η^2 = 0.43, pseudo-R^2 = 0.39), and was highest in thin-burn units (Fig. 3a,b, Table 1). There were on average 4.8 more vascular plant species in thin-burn units than in unmanaged units while other pairwise comparisons did not differ (Table 1). Treatment effects on richness were significant from 2014 to 2018, although this trend was apparent starting in 2012, with marginally significant differences in 2012 and 2013 (Fig. 3b; Table S1). Across years, there were between 3.7 and 6.2 more species in thin-burn units than unmanaged units, peaking in 2015 (Table S1). Treatment effects on native richness (partial-η^2 = 0.41, pseudo-R^2 = 0.36) were consistent with the pattern seen for overall richness (Fig. 3c,d), while exotic richness did not differ significantly among treatments (partial-η^2 = 0.24, pseudo-R^2 = 0.21) (Table 1). There were on average 4.4 more species in thin-burn units than in unmanaged units, while other treatments did not differ (Tables 1, S1). Exotic richness was similar among all treatments (Table S1).

3.3. Question 3: Composition

Species composition differed among treatments in 5 of 9 years, 2013–2017, although the difference was marginally significant in 2016 (Table 2, Fig. S1). In 2013, 2014 and 2016 burn-only units differed from unmanaged units, although the difference was marginally significant in 2013 and 2014. In 2014 and 2015, thin-burn units differed from unmanaged units, although the difference was marginally significant. In 2017, there were no differences in pairwise comparisons. Species composition differed among years in both thin-burn sites and burn-only sites, but not unmanaged sites (Table 2, Fig. 4).

3.4. Question 4: Individual species responses

Eleven plant species were significant indicators of at least one of the treatments in at least one year (Table 3). Only one species, the native forb *Polygonatum biflorum*, was associated with unmanaged units, and only in 2015. Two native perennial forbs were consistently associated with the same treatment in multiple years. *Galium triflorum*, a native habitat-generalist typical of a variety of forests, was an indicator of burn-only units in the years 2014–2017. *Potentilla simplex*, a native species of sandy open forests and old-fields, was an indicator of thin-burn units in the years 2013–2016 (Voss and Reznicek, 2012). In Michigan, *Potentilla simplex* is also considered an indicator species for oak barrens, a savanna community typical of droughty soils referred to elsewhere as sand savanna (Cohen, 2001; Bowles et al., 2011).

4. Discussion

Oak savanna management by thinning and burning led to shifts in key aspects of ecosystem structure as well as shifts in native plant species diversity and composition, while burning alone had more limited impacts. In particular, canopy openness was dramatically higher after mechanical thinning, in units where thinning was applied. Percent vegetative cover was also higher in managed units, although the response was delayed, perhaps due to slower responses of light- and fire-adapted species. Species richness among treatments was higher in thin-burn units after management, particularly of native species, shifting largely in parallel with differences among structural characteristics. Finally, species composition shifted through time with management, and not in unmanaged units. Effects on composition played out over

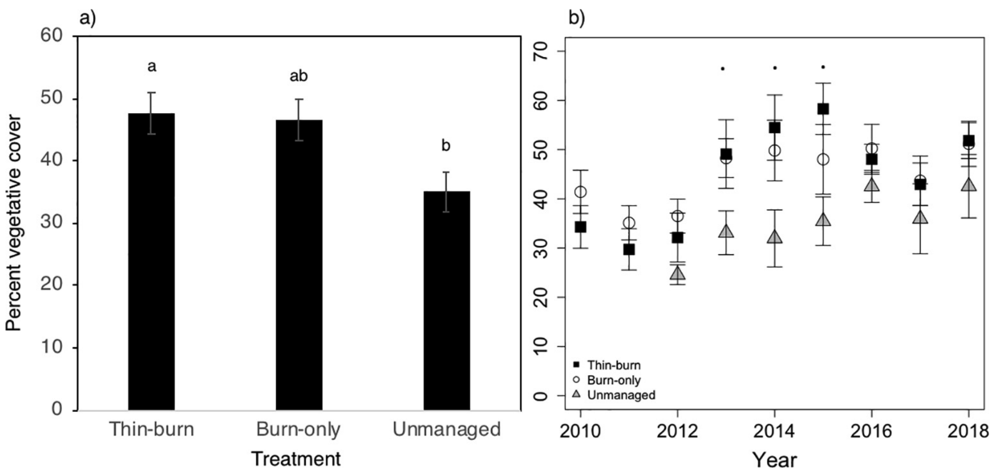

Fig. 2. Percent vegetative cover is higher in thin-burn units than in unmanaged units. Least-square means of percent understory vegetative cover from repeated measures ANOVA on data from 2012 to 2018 (a); and means (+/- SE) for individual years of study (b). In (a), bars with different letters are significantly different at $p < 0.05$; significance assessed using Tukey's HSD with Bonferroni corrections. In (b), a significant effect of treatment from ANOVA; $^{\cdot}$ $p < 0.10$.

years, with managed and unmanaged units beginning to diverge after half a decade. By the end of the study period, however, differences between managed and unmanaged units had begun to decline. While managed units all appeared to move along a trajectory toward the structure, richness, and composition typical of savanna (Cohen 2001, 2004; Chapman and Brewer, 2008) in response to management, achieving this goal long-term will require continued and likely more intensive management.

4.1. Canopy openness and vegetative cover increased in response to management

Canopy openness increased in response to management, with differences in canopy openness developing between all treatment types. Predictably, the largest and most consistent differences were observed in units that included a mechanical thinning treatment. While the first round of thinning (up to 10 cm DBH) resulted in limited increases, canopy openness doubled from ~10% to ~20% in thin-burn units between 2011 and 2012, following the second round of thinning (up to 20 cm DBH). Burn-only units, in contrast, generally lagged behind thin-burn units, nearly doubling in canopy openness from ~8% to ~15% instead over two years between 2011 and 2013 (following a second round of prescribed fire). It is intuitive that thinning in the absence of fire should increase canopy openness and associated light availability. Fire in the absence of thinning, in contrast, may also open canopies to those typifying savannas (e.g., < 60% cover), shifting overstory and understory composition and increasing understory diversity, but only over decades of repeated burns (~50 yr; Nowacki and Abrams, 2008; Peterson and Reich, 2008; Knapp et al., 2015). However, maintaining canopy openness via mechanical thinning, even with fire, may require repeated interventions (Nowacki and Abrams, 2008). In our study, canopy openness decreased to close to pre-thinning levels within 8 years of thinning. This may be due to lateral branching in both thin-burn and burn-only units as trees that remain grow to fill space and access available light (e.g., Mäkinen, 2002). Long-term maintenance of canopy openness may not be possible until a threshold of tree density is crossed, below which the herbaceous ground layer develops sufficient fuels and regular prescribed fire controls woody encroachment (Suding and Hobbs, 2009; Feltrin et al., 2016).

Vegetative cover also increased in response to management, but more gradually than canopy openness. A difference in vegetative cover was only detectable between thin-burn and unmanaged units, and only after the second round of fires in 2013. Lacking a 'thin-only' treatment, we cannot entirely disentangle the individual contributions of fire and thinning to this response. However, vegetative cover increased in response to a second round of fire (and not the first) which directly followed the dramatic increase in canopy openness after the second round of thinning. This suggests that vegetative cover is dependent on the combined effects of both fire and increased canopy openness. For example, nitrogen-fixing species often decline in the absence of fire and may increase rapidly with the reintroduction of fire to fire-suppressed ecosystems (Leach and Givnish, 1996). Fire also reduces the cover and depth of leaf litter, the accumulation of which can suppress the growth of long-lived graminoids such as the clonal sedge *Carex pensylvanica*, and reduce microsite availability for many small-seeded forbs (Bowles et al., 2011). While fire may create these 'windows of opportunity' for savanna-associated species, substantive increases in growth may not be possible without increased light availability. Finally, vegetative cover remained high relative to pre-management levels. This may be because, despite gradual reductions in canopy openness following an initial peak in 2012, the continued use of prescribed fire maintained the growth of light- and fire-dependent ground layer species. However, vegetative cover gradually increased in unmanaged units as well, resulting in an erosion of management treatment effects by 2016. It is possible that an

Table 1
Response of plant species richness (native, exotic and total richness) and ecosystem structure (canopy openness and total percent vegetative cover) to oak savanna management treatments over 2012–2018. Results of repeated measures ANOVA with treatment and year as fixed variables, and site nested within year as random variables. Chi-squared values (χ^2) and effect size (partial-η^2) for model coefficients are shown. We assessed the statistical significance of Tukey's HSD for pairwise comparisons between treatment types (BO = Burn-only, TB = Thin-burn, UN = Unmanaged) with Bonferroni corrections. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{\cdot}$ $p < 0.10$.

	Treatment		Year		Pairwise comparisons			
Response	χ^2	η^2	χ^2	η^2	R^2	BO-UN	TB-UN	TB-BO
Species richness	**$11.25_{2,12}$****	**0.43**	$0.73_{2,12}$	0.001	0.39	2.47	**4.84***	2.37
Native species richness	**$9.83_{2,12}$****	**0.41**	$1.04_{2,12}$	0.002	0.36	2.63	**4.36***	1.73
Exotic species richness	$4.81_{2,12}$$^{\cdot}$	0.24	$4.35_{2,12}$	0	0.21	−0.20	0.41	0.62
Percent canopy openness	**$37.94_{2,12}$*****	**0.56**	**$16.06_{2,12}$*****	**0.13**	0.36	4.25$^{\cdot}$	**11.25*****	**7.01****
Percent vegetative cover	**$8.93_{2,12}$***	**0.2**	**$11.59_{2,12}$*****	**0.08**	0.25	11.53$^{\cdot}$	**12.54***	1.01

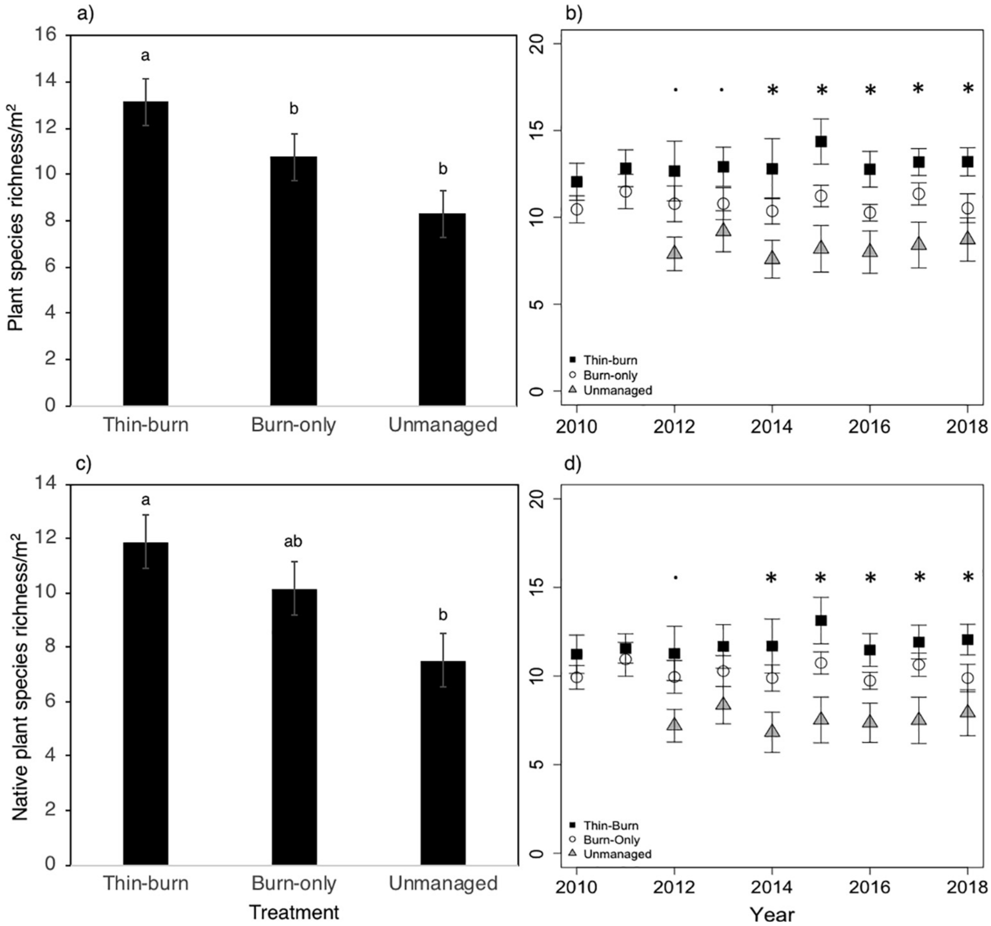

Fig. 3. Native and total plant species richness is higher in thin-burn units than in unmanaged units. Least-square means of understory species richness in 1 × 1 m plots from repeated measures ANOVA on data from 2012- Least-square means of percent vegetative cover from repeated measures ANOVA on data from 2012 to 2018 for total (a) and native (c) richness; and means (+/- SE) for individual years of study for total (b) and native (d) richness. In (a,c), bars with different letters are significantly different at $p < 0.05$; significance assessed using Tukey's HSD with Bonferroni corrections. In (b,d), a significant effect of treatment from ANOVA; *$p < 0.05$, $^{\cdot}$ $p < 0.10$.

Table 2

Response of species composition to oak savanna management treatments over 2012–2018. PERMANOVA with associated p-values for each year. Years with at least a marginally significant PERMANOVA ($p < 0.10$) in bold; pairwise comparisons at least marginally significant ($p < 0.10$) in bold. *p-values for pairwise comparisons are adjusted with Bonferroni correction. BO = Burn-only, TB = Thin-burn, UN = Unmanaged.

	PERMANOVA	Pairwise comparison	SS	F	R^2	p*
2012	0.13	BO vs. TB	0.12	0.66	0.08	1.00
		BO vs. UN	0.38	1.75	0.18	0.31
		TB vs. UN	0.32	1.43	0.15	0.42
2013	**0.03**	BO vs. TB	0.05	0.64	0.08	1.00
		BO vs. UN	**0.25**	**2.51**	**0.24**	**0.08**
		TB vs. UN	0.23	2.33	0.23	0.11
2014	**0.02**	BO vs. TB	0.03	0.35	0.04	1.00
		BO vs. UN	**0.32**	**3.15**	**0.28**	**0.05**
		TB vs. UN	**0.33**	**2.99**	**0.27**	**0.06**
2015	**0.02**	BO vs. TB	0.05	0.77	0.09	1.00
		BO vs. UN	0.31	2.98	0.27	0.11
		TB vs. UN	**0.34**	**3.33**	**0.29**	**0.06**
2016	**0.07**	BO vs. TB	0.09	0.47	0.06	1.00
		BO vs. UN	**0.45**	**1.89**	**0.19**	**0.02**
		TB vs. UN	0.42	1.67	0.17	0.12
2017	**0.02**	BO vs. TB	0.04	0.55	0.06	1.00
		BO vs. UN	0.25	2.83	0.26	0.11
		TB vs. UN	0.28	3.03	0.27	0.16
2018	0.14	BO vs. TB	0.11	0.65	0.08	1.00
BO vs. UN	0.33	1.44	0.15			0.49
		TB vs. UN	0.36	1.63	0.17	0.24

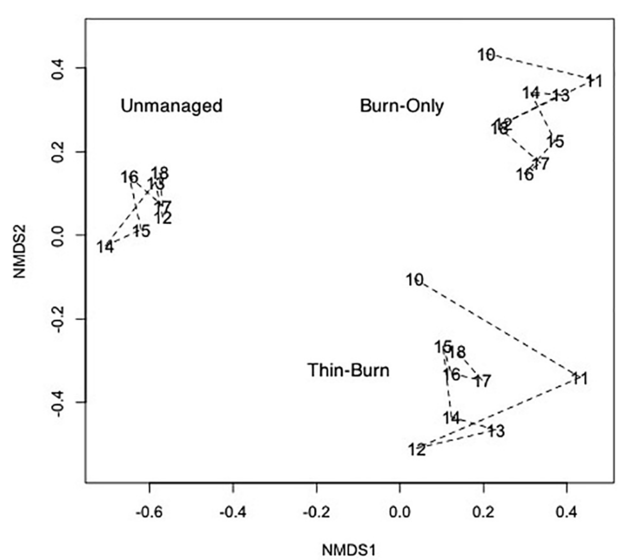

Fig. 4. Plant species composition in both thin-burn and burn-only units shifted in response to management, followed by convergence within treatment types toward pre-treatment composition. Non-metric multidimensional scaling of abundance averages among sites within each treatment type in each year, based on Bray-Curtis dissimilarity; K = 3, Stress = 0.097. Line segments added to facilitate visual tracking of difference in composition between years (10 = 2010, 11 = 2011, etc.). Composition in both thin-burn units and burn-only units differed between years (PERMANOVA, $p < 0.05$), while unmanaged units did not. See Table 2 and Fig. S1 for within-year differences between treatment types.

Table 3
Indicator species for each treatment type for each year. *Exotic species.

Species	Treatment Types		
	thin-burn	burn-only	unmanaged
Conyza canadensis	2012		
Galium triflorum		2014–2017	
Geum canadense	2018		
Hepatica americana	2012		
Polygonatum biflorum			2015
Potentilla simplex	2013–2016		
Quercus velutina	2018	2014	
Rubus flagellaris		2011, 2013	
Solidago canadensis	2015, 2017		
*Taraxacum officinale**	2018		
Viola sp.		2016	

additional factor contributing to maintaining vegetative cover in unmanaged units also maintained higher vegetative cover in thin-burn and burn-only units. For example, 2012 was a major drought year in the Midwestern United States, and may have led to a delayed mortality effect on shrub and tree species in the ground layer that gave a competitive advantage to drought-resistant herbaceous species that comprise vegetative cover, regardless of management history (Mallya et al., 2013; Mariotte et al., 2013; Hoover et al., 2014).

4.2. Species richness was consistently higher in thin-burn units

Management augmented underlying differences in diversity among units. Species richness varied only slightly within each treatment type across the study period, but was always higher in thin-burn than unmanaged units. Therefore, richness in unmanaged units prior to the initiation of management (e.g., in 2010 and 2011) may have been similar to post-management levels. After management, richness in thin-burn units was initially higher in both unmanaged units and burn-only units (61% and 17% higher in 2012, respectively), but peaked in 2015 (at 75% and 28% higher, respectively) and subsequently decreased, suggesting a transient response to the combination of thinning and burning. Other studies conducted over longer time scales have reported increases in richness specifically due to the combination of regular prescribed fire and increased light availability, whether light availability was due to mechanical thinning (e.g., Bowles et al., 2017) or the long-term impacts of prescribed fire (e.g., Peterson and Reich, 2008).

The response of native species richness to management mirrored that of total species richness. That is likely because the ground layer plant community in these sites, regardless of management, is overwhelmingly dominated by native species. Management can lead to short term increases in the relative proportion of exotic species in savanna, but even in these cases native species are overwhelmingly dominant (Brudvig, 2010; Bowles et al., 2011). In the current study, the proportion of native-to-exotic richness varied throughout the study period, but native species richness remained high (Table S2). Barring dramatic increases in the richness of exotic relative to native species within a treatment type, the response of total species richness to management will continue to reflect the response of the native community.

4.3. Compositional differences between managed and unmanaged units faded over time

Both management regimes caused composition to diverge from unmanaged units, but these effects were transient, consistent with and potentially tracking shifts in ecosystem structure. Changes in community composition may have been due to several factors, including increases in existing species abundances through vegetative growth or seedling recruitment or via recruitment of new species from the seedbank or dispersal from outside the units. Since species richness varied only slightly within each management type throughout the study period, it seems unlikely that compositional shifts reflect the introduction of new species. If new species were introduced to units, that must have coincided with losses of other species. Changes in composition and vegetative cover appeared to track each other over time, the largest shifts in both occurring during 2013–2015. Therefore, changes in composition reflect shifting abundances of key species that contributed significantly to vegetative cover. Finally, the convergence of composition among treatment types by the end of the study period likely mirrors the convergence in canopy openness among treatment types, and a concomitant homogenization of light conditions across treatment types.

Indicator species analysis provides some additional evidence to explain compositional shifts. Only one species was an indicator of unmanaged units, and only in a single year (the forest herb *Polygonatum biflorum* in 2015). This may be because unmanaged units, which were consistently less species-rich than managed units, are composed of a shade-tolerant subset of the managed units. Several species were indicators of thin-burn and burn-only units in only one or two years, presumably representing ephemeral shifts in composition in response to management, or variability in treatment effects or underlying composition among units of a given treatment type. Overall, indicator species were either associated with forested habitats, or disturbed open habitats. The two species that were consistent indicators of management were a common forest herb (*Galium triflorum* in burn-only units) and a common species of sandy old fields (*Potentilla simplex* in thin-burn units) (Voss and Reznicek, 2012). While *P. simplex* is considered an indicator species for one savanna type in Michigan, oak barrens (Cohen, 2001), it is also typical of early-successional disturbed habitats in savanna landscapes so its importance in tracking the development of savanna communities should not be overestimated. The low number of consistent indicators for treatment types is further evidence that shifts in composition represent changes in the abundance of existing species, as opposed to colonization or extinction in response to management.

4.4. Future directions – Are the impacts of management transient or incremental?

The way plant communities in degraded ecosystems respond to restoration is complex, with both immediate and incremental responses (Suding and Hobbs, 2009; Brudvig, 2011). Through reintroducing fire to a fire-suppressed system, and doubling canopy openness from 10% to 20%, we saw moderate shifts in richness and composition. Shifting composition toward higher richness and abundance of savanna-associated species likely requires even greater light availability and repeated fires (Cohen, 2001, 2004; Chapman and Brewer, 2008; Nowacki and Abrams, 2008; Peterson and Reich, 2008; Bowles et al., 2017). While our results suggest that the effects of management appeared transient over the course of this study, increased canopy openness and frequent fire was initially associated with shifts in understory structure and composition toward a savanna plant community. Increasing the intensity of management may result in larger shifts, and further progress toward restoring a savanna plant community.

Moving forward, we recommend a third round of canopy thinning within these units. This is primarily for two reasons. First, canopy openness, vegetative cover, and community composition responded to the first two rounds of canopy thinning, yet these effects appear to be transient. These key variables should respond to further thinning. Second, we have yet to see pronounced effects of burning alone on overstory structure or light availability. Repeated fires can, over the long term, elicit significant increases in species richness and shifts in community composition from forest-associated to savanna-associated species (Peterson and Reich, 2008). The lack of graminoid fuels and other ecosystem structure changes associated with a history of fire suppression limit the intensity of fires in ours and other systems

(Bowles and McBride, 1998). Repeated fires may result in mortality in canopy and large-diameter subcanopy trees due to stress and disease, gradually increasing canopy openness. As a result, the impact of fire alone on reducing the density of both canopy and subcanopy woody species is likely to be limited in the short-term, with large-scale reductions in woody species densities requiring decades. Expanded thinning, through increased light availability, can stimulate the growth of graminoid fuels and increase the effectiveness of future fires.

How intensive should a third round of thinning be? For future thinning to yield levels of light availability necessary to support and expand savanna-associated species, it will be necessary to target larger diameter woody stems than those cut to date. Despite the potential for increasing ground layer herbaceous density, the impacts of a very intensive thinning, for example immediately increasing canopy openness to 50% or more, could be undesirable. Both problematic native (e.g., *Rubus* spp., *Sassafrass albidum*) and invasive (e.g., *Elaeagnus umbellata*, *Rosa multiflora*) species often respond quickly via root-suckering and seedling recruitment to fill light gaps and may rapidly outcompete light-dependent savanna ground layer species if additional thinning suddenly increases light availability, particularly in the absence of grazing (Bowles and McBride, 1998; O'Connor et al., 2006; Brudvig and Asbjornsen, 2007; Harrington and Kathol, 2009). In contrast, increasing the intensity of thinning incrementally may result in a sustainable, gradual transition to more savanna-like conditions that can be maintained through prescribed fire alone. Through nearly a decade of management, this community underwent reorganization prior to the convergence toward pre-treatment conditions. More intensive management may therefore result in a similar, but more pronounced response from the plant community. A thinning prescription that removes shade from the mid-story and subsequently targets smaller diameter canopy trees (e.g., similar to a shelterwood cut aimed at oak regeneration) will likely provide the conditions suitable for a savanna understory, especially when combined with prescribed fire (Dey et al., 2017). We thus recommend a third round of thinning to return understory light levels at least to 2012–13 levels, but perhaps as high as 20–40% canopy openness, coupled with continued prescribed fire and monitoring to evaluate responses.

CRediT authorship contribution statement

Tyler J. Bassett: Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing. **Douglas A. Landis:** Conceptualization, Methodology, Investigation, Writing - original draft, Writing - review & editing, Project administration. **Lars A. Brudvig:** Conceptualization, Methodology, Investigation, Writing - review & editing, Project administration.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118047.

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