LETTER

Fire frequency, state change and hysteresis in tallgrass prairie

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Abstract

Hysteresis is a fundamental characteristic of alternative stable state theory, yet evidence of hysteresis is rare. In mesic grasslands, fire frequency regulates transition from grass- to shrub-dominated system states. It is uncertain, however, if increasing fire frequency can reverse shrub expansion, or if grass-shrub dynamics exhibit hysteresis. We implemented annual burning in two infrequently burned grasslands and ceased burning in two grasslands burned annually. With annual fires, grassland composition converged on that of long-term annually burned vegetation due to rapid recovery of grass cover, although shrubs persisted. When annual burning ceased, shrub cover increased, but community composition did not converge with a long-term infrequently burned reference site because of stochastic and lagged dispersal by shrubs, reflecting hysteresis. Our results demonstrated that annual burning can slow, but not reverse, shrub encroachment. In addition, reversing fire frequencies resulted in hysteresis because vegetation trajectories from grassland to shrubland differed from those of shrubland to grassland.

Keywords

Alternative stable states, prescribed fire, regime shift, resilience, woody encroachment.

INTRODUCTION

Although most terrestrial ecosystems are highly dynamic, they typically persist within a range of environmental conditions that fluctuate over multiple time scales (e.g. diurnal, seasonal, interannual). In many cases, these ecosystems change gradually and predictably as they track variability in environmental drivers. State change can occur, however, when an ecosystem exhibits a relatively abrupt, non-linear response as environmental drivers cross an ecological threshold or tipping point (Scheffer *et al.* 2001). Under these conditions ecosystems may exhibit two or more alternative states (Scheffer *et al.* 2001; Ratajczak *et al.* 2014). Each state can exist under a range of overlapping environmental conditions, making them prone to transition from one alternative state to another as conditions change, due to environmental stochasticity, or a change in disturbance regimes (Beisner *et al.* 2003; Walker & Salt 2006; Ridolfi *et al.* 2011).

When exogenous drivers weaken self-reinforcing feedbacks and push an ecosystem across a threshold, the ecosystem can diverge to an alternative state that persists even if environmental conditions return to their previous range and dynamics (Holling 1973; Noy-Meir 1975; May 1977; Folke *et al.* 2004; Scheffer *et al.* 2009). One indicator of alternative states is hysteresis, where changes in an ecological driver result in an alternative ecosystem state but reversing that driver does not immediately restore the previous ecosystem state (Beisner *et al.* 2003). Instead, the eventual pathway back to the original state differs from the pathway to the alternative state. Importantly, not all alternative states are equally stable. That is, it may be easier to move from a grassland to a shrubland state, but the reverse may be more difficult. As a consequence, reversing state changes can be challenging once the system reorganises around a new set of self-reinforcing feedbacks (Holling 1973; Walker & Salt 2006).

Although alternative stable state theory typically focuses on relatively rapid transitions and their indicators (e.g. Carpenter *et al.* 1999; Carpenter & Brock 2006), many state changes are slow and exhibit time lags (Smith *et al.* 2009; Hughes *et al.* 2012; Karssenberg *et al.* 2017), often as a consequence of acute vs. gradual change in drivers (Ratajczak *et al.* 2017a). Examples of slow change include transitions from semi-arid grassland to shrubland (D'Odorico *et al.* 2012) and from tropical forest to savanna (Staver *et al.* 2011). Thus, slow regime shifts may exhibit properties that differ (e.g. easier to reverse; Ratajczak *et al.* 2017a) from more rapid state transitions. Moreover little is known about how abrupt changes in system drivers affect ecosystem structure over the long-term, including how long systems exhibit hysteresis during state change.

Many grassland ecosystems worldwide are undergoing state transitions from C_4-dominated grasslands to C_3-dominated shrublands and woodlands (van Auken 2000; Eldridge *et al.* 2011; Ratajczak *et al.* 2014; Hempson *et al.* 2019). Alternative stable state theory provides a theoretical underpinning to explain how and why woody plant encroachment occurs and persists in many formerly grass-dominated ecosystems (D'Odorico *et al.* 2012, 2013; Ratajczak *et al.* 2017a). Shrub encroachment can be attributed to multiple factors, including overgrazing, changing precipitation regimes, increased atmospheric CO_2 concentrations and altered fire regimes (van Auken 2000; Kulmatiski & Beard 2013; Moncrieff *et al.* 2014; Wilcox *et al.* 2018). For example, historical livestock overgrazing resulted in loss of grass cover and increased cover of

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shrubs and trees in arid grasslands of the U.S. Southwest (Peters *et al.* 2004; Browning *et al.* 2014; Porensky *et al.* 2016; Pierce *et al.* 2019), whereas fire suppression promoted woody encroachment in more mesic grasslands (Staver *et al.* 2011; Ratajczak *et al.* 2017b; Hempson *et al.* 2019). These transitions may be long-lasting, even after grazing is relaxed or more aggressive fire regimes are reintroduced (Bestelmeyer *et al.* 2011; Ratajczak *et al.* 2014; Case & Staver 2017; but see Twidwell *et al.* 2016).

Key factors that interact to drive structure and function in mesic grasslands are well documented – fire, grazing by megaherbivores, and climate variability and change (Knapp *et al.* 1998; Lehmann *et al.* 2014; Smith *et al.* 2016; Bond & Zaloumis 2016; Scholtz *et al.* 2018). For example, early growing season burning in North American tallgrass prairie enhances grass production and forage quality (Knapp & Seastedt 1986; Raynor *et al.* 2015), and limits woody plant encroachment (Collins & Calabrese 2012). Lower fire intensity can feedback to increase susceptibility to invasion by woody plants (Twidwell *et al.* 2013a). Together, these factors impact the frequency of fire needed to maintain a grassland state in the face of enhanced rates of woody encroachment (Case & Staver 2017). Although grazing pressure has been implicated as a potential mechanism driving shrub encroachment globally (van Auken 2000; Eldridge *et al.* 2011), shrub encroachment continues in many mesic grasslands in the absence of grazing (Ratajczak *et al.* 2014), suggesting that other factors, such as fire frequency, also regulate the rate of shrub encroachment in these ecosystems.

Theoretical and empirical analyses support the idea of grass-shrub alternative stable states in some grassland ecosystems (D'Odorico *et al.* 2012; Ratajczak *et al.* 2017b). However, testing hypotheses associated with woody plant encroachment and alternative stable states in grasslands requires long-term data and is best done in an experimental context (Schröder *et al.* 2005). Such experiments are rare because they require decades of experimental manipulation due to slow rates of change in many terrestrial ecosystems (Hughes *et al.* 2012). Here we used multi-decade measurements (20–40 years) from experimental watersheds in tallgrass prairie under annual and infrequent fire regimes to determine (1) how reversing long-term fire regimes affected vegetation structure and community composition, (2) if implementing annual fire frequency can reverse shrub encroachment in long-term infrequently burned watersheds, and (3) if characteristics of this grassland-shrubland system exhibit hysteresis in response to abrupt changes in long-term fire frequency. Thus, we hypothesised that restoring annual spring burning to watersheds with a history of infrequent burning would increase grass and reduce shrub cover, resulting in convergence of community composition with other long-term annually burned watersheds. Alternatively, annual burning may not be sufficient to reduce cover of established woody plants because shrubs reduce fine fuel loads causing lower fire intensity and many shrubs can resprout following burning (Heisler *et al.* 2003; Ratajczak *et al.* 2011). Given that long-term annually burned tallgrass prairie has little to no shrub cover, is dominated by perennial C$_4$ grasses, and has low species richness (Collins & Calabrese 2012; Ratajczak *et al.* 2014), we hypothesised that shrub encroachment would occur slowly primarily due to dispersal limitation when fires were suppressed. Finally, based on differences in species composition and relative grass and shrub cover under contrasting fire regimes, we hypothesised that reversing fire treatments would result in large-scale changes in vegetative structure (shrub or grass cover), but that community composition would exhibit hysteresis driven by feedbacks between fuel loads and fire intensity, as well as stochastic processes, such as dispersal and time lags.

METHODS

Site description

The Konza Prairie Biological Station (KPBS; 39°05′ N, 96°35′ W) is located in the Flint Hills ecoregion (25,708 km^2) of eastern Kansas, USA, the largest remaining region of unplowed, native tallgrass prairie. KPBS is a 3487-ha native tallgrass prairie characterised by uplands with shallow limestone soils and lowlands with deep silty-clay loams separated by rocky hillslopes. The elevation varies from 320 to 444 m above sea level. The site is divided into 57 'watersheds' based on topography, each assigned to a specific fire frequency (1, 2, 4, or 20-year intervals) and grazing treatment (bison, cattle, or no large mammalian grazers). None of the watersheds in the current study have been grazed by cattle or bison in the past 50 years. Mean annual precipitation (1982–2019) is ~ 835 mm, with approximately 75% falling during the growing season (April–September). Monthly diurnal temperature means (1982–2019) range from a low of −1.2 °C in January to a high of 26.1 °C in July.

The vegetation at KPBS is predominantly native unplowed tallgrass prairie, with some woody vegetation in gallery forests along drainages (Knight *et al.* 1994) as well as in infrequently burned sites (Briggs *et al.* 2002). The grassland is dominated by C$_4$ perennial grasses, including *Andropogon gerardii*, *Sorghastrum nutans*, *Schizachyrium scoparium* and *Panicum virgatum*, while interstitial forb species comprise more than 75% of the species richness (Towne 2002). Common shrubs, all of which are clonal, include *Cornus drummondii*, *Rhus glabra*, *R. aromatica* and *Prunus americana*.

Experimental design

We used six watersheds at KPBS (Table 1) to investigate the dynamics of state transitions following changes in fire frequency (data in Hartnett & Collins 2019). The fire treatments of two watersheds that were burned annually from 1978 to 2000 were altered in 2001 to an infrequent fire return interval of once every 20 years, although unplanned wildfires do occur (Table 1). The fire treatments of two additional watersheds that were infrequently burned from 1978 to 2000 were switched to annual burning beginning in 2001. For comparison to these fire reversal treatments, we used data from two reference watersheds that have received consistent fire treatments, one that has been burned annually and another that has only burned twice since 1978.

Table 1 Watershed code, size (ha), fire history and burning treatment for the six watersheds used in this study. Two watersheds had consistent fire treatments from 1978 to the present. Watershed 1D was burned annually and watershed 20B was burned infrequently (twice). Four watersheds experienced fire reversal treatments. Two watersheds (subscripts a and b) were burned infrequently (I) from 1978 to 2000 and burned annually (A) thereafter. Two other watersheds (subscripts c and d) were burned annually from 1978 to 2000 and burned infrequently thereafter

Watershed code	Size (ha)	Fire history	Vegetation data	Treatment code
1D	41.6	Annually burned since 1978	1984-present	Annually burned reference site
20B	23.8	1991, 2017	1984-present	Infrequently burned reference site
R1A	14.4	1980, 1984, annually starting in 2001	1997-present	$I_a \rightarrow A_a$
R1B	39.7	1980. 1991, annually starting in 2001	1993-present	$I_b \rightarrow A_b$
R20A	26.3	Annually from 1978 to 2000, 2008	1997-present	$A_c \rightarrow I_c$
R20B	12.3	Annually from 1978 to 2000, 2008, 2011	1984-present	$A_d \rightarrow I_d$

Vegetation sampling

Plant species composition was sampled in May and August each year to capture within season vegetation dynamics (e.g. spring ephemerals, peak growth). Because upland areas were limited in two of the fire reversals we used only vegetation data from lowland topographic positions on all watersheds for all analyses. Vegetation was sampled in five 10-m^2 permanently located circular plots equally spaced along each of four 50 m transects in lowland areas in each watershed, for a total of 4 transects and 20 plots (200 m^2) per treatment. Vegetation sampling started 4–16 years prior to reversal treatments (Table 1). Cover of plant species rooted in each plot was estimated using a Daubenmire scale (1 = < 1%, 2 = 2–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–95%, 7 = 95–100%). We determined abundance by converting the Daubenmire scale to the midpoint of the cover range and then averaging by species across 5 plots per transect or 20 plots per site, depending on the analysis (see below). The maximum cover value for each species (May or August sample) was used in all analyses, which results in total cover exceeding 100% in this highly productive ecosystem with multiple overlapping canopies. See Collins & Smith (2006) and Collins & Calabrese (2012) for details.

Does increased fire frequency reverse shrub encroachment in long-term infrequently burned watersheds?

To address this question data were aggregated by transect (N = 5 plots per transect and 4 transects per watershed) to provide spatial replication within each watershed. Following Isbell et al. (2013) and Wilmer et al. (2020), we used a flexible time series model, specifically generalised additive mixed models (GAMMs; Wood 2017), to compare changes in total plant cover, grass cover and shrub cover across treatments in each watershed over time. GAMMs can combine smooth and factor functions, including time-variant estimations of error, making them well-suited for complex time series with multiple treatments. For each response variable (grass and shrub cover), we considered all data from all reversal watersheds separately in our GAMMs because we do not consider them to be true replicates at this spatial scale. We constructed two competing GAMMs: (1) a model with year (time) considered as a smooth function, and (2) a model with year as a smooth function, watershed included as a main effect and watershed as a factor that interacts with the smoothing function for each watershed. Our link function for the response variable was identity and the distribution was Gaussian. To compare models we used adjusted R^2 values. A maximum likelihood approach was unnecessary because the first model had adjusted R^2 values < 0.05 for all response variables, whereas adjusted R^2 values were > 0.60 for the second model.

For all transect-based response variables, watershed effects were statistically significant. When a predictor in a GAMM is statistically significant, one way to determine when model fits from different factors (e.g. watersheds) overlap with respect to the smoothing variable (year) is to calculate confidence intervals and determine when confidence intervals visually overlap. For each combination of response variable, year, and watershed we calculated the 99% confidence interval. We used the more conservative 99% confidence interval rather than 95% because we performed multiple comparisons of groups for each response variable and because a 99% CI is appropriate for two-sided tests for significance. For a given response variable and year, data were considered to be significantly different when CIs from different watersheds did not overlap. In the context of hysteresis, this makes our approach conservative because it is less likely to determine that treatments are significantly different. Models were implemented using the 'mgcv' package in R (R Core Team 2019).

To further address changes in shrub cover under altered fire frequency, we used hand held GPS units with 2 m or better accuracy (Juno3B and Trimble GEO7X) to record the position, diameter and identity of each shrub in two reversal watersheds, one changed from infrequent to annual fire and one changed from annual to infrequent fire (R1A and R20A in Table 1). Measurements were done in 2000 prior to the start of the fire reversal treatments, then again nine (2010) and 16 years (2017) after initiation of the reversal treatments. We chose these two watersheds because they are adjacent to one another with similar topography and soils. For comparison, we also mapped shrubs in the infrequently and annually burned long-term reference watersheds in 2001, 2012 and 2019. We used ArcGIS 10.7 software (Environmental Systems Research Institute Inc., Redlands, CA) to quantify changes in shrub aerial cover by species over the three measurement periods in each watershed.

Do changes in community composition exhibit hysteresis under altered burning regimes?

Following Lamothe et al. (2019), to identify hysteresis we used non-metric multidimensional scaling ordination based on

a Bray–Curtis dissimilarity metric to assess long term community trajectories in response to fire reversal treatments in each watershed. NMDS is a highly flexible ordination technique suitable for data that deviate from normality (Dexter *et al.* 2018), which is common with vegetation data. In this analysis, we used average species composition across all 20 plots rather than transects because the larger total sample area includes a larger species pool that provides a more conservative estimate of convergence, if it occurs. We then used permutational multivariate analysis of variance (perMANOVA) with a Bray-Curtis dissimilarity metric to determine if plant community composition at different time intervals (e.g. pre- vs. post-reversal on a treatment watershed, or pre-reversal to relevant reference watershed) differed in response to changes in fire frequency. Different community composition along with different temporal trajectories would indicate hysteresis in response to changing fire regimes. The perMANOVA analyses were followed by indicator species analysis (SIMPER) to determine the species that differentiated community composition between treatments. NMDS, perMANOVA and SIMPER analyses were done with PRIMER v6.1.11.

RESULTS

Does increased fire frequency reverse shrub encroachment in long-term infrequently burned watersheds?

Total plant cover on the annually burned reference watershed averaged 164 ± 7.4% (mean ± SD) from 1984 to 2019 (Table S2; Fig. 1a,b). *A. gerardii*, *S. scoparium*, *S. nutans* and *P. virgatum* were the dominant grasses accounting for 82% of total plant cover, whereas common shrubs accounted for only 0.1% of total cover. In contrast, total cover in the long-term infrequently burned reference watershed from 1984 to 2019 averaged 197.2 ± 7.3% as woody plants increased in abundance resulting in multiple layers of vegetation. While initially low, shrub cover increased rapidly on the infrequently burned reference watershed, averaging 44.8 ± −3.4% from 2009 to 2019 (Fig. 1). By 2019, the four dominant grasses comprised only 26.2% of total cover on this watershed, while shrubs accounted for 70.6% of total cover.

GAMMs with just year as a smoothing function (model 1), provided a poor fit for total cover, dominant grass cover and dominant shrub cover (adj. $R^2 < 0.04$; Table 2), because watershed trajectories differed over time. A second model, which included watershed as a variable, explained much more variation in grass, shrub and total cover (adj. $R^2 > 0.63$; Table 2). Grass cover in the reversal treatments responded rapidly to changes in fire regime (Fig. 1c,d). On the two watersheds switched from infrequent to annual fires, grass cover increased under annual burning from an average of about 50% to over 100%. Grass cover on these infrequent-to-annually burned watersheds is now significantly greater than on the long-term infrequently burned reference site, and not significantly different from the long-term annually burned reference site, as confidence intervals overlap in recent years. On the two watersheds switched from annual to infrequent fires, however, grass cover was stable for the first eight years following the reversal treatment, but then exhibited a sharp

decline. After 19 years of fire suppression, grass cover remains higher in the annual-to-infrequent fire reversal treatments compared to the long-term infrequently burned reference site (Fig. 1a,b). This pattern is similar to long-term dynamics on the infrequently burned reference site. That is, grass cover was ∼ 50% after 20 years on the infrequently burned reference site (1980–2000), and grass cover was ∼ 60% after 19 years on the annual to infrequent fire reversal treatment (2001–2019).

In contrast to grass cover, shrub cover was initially slow to respond to the fire reversal treatments (Fig. 1e,f). Within monitoring plots, shrub cover was relatively low on all reversal watersheds when the reversal treatments started, and cover of shrubs changed little after 19 years of annual burning on the infrequent-to-frequent burning treatments (Fig. 1c). In contrast, on the frequent-to-infrequently burned watersheds, shrub cover increased slightly during the first 10 years, reflecting a lagged response similar to that seen in the infrequently burned watershed. However, shrub cover in one of the reversals more than doubled over the last seven years (Fig. 1f).

Plotting temporal dynamics in grass-shrub phase space highlights the strong negative correlation between grass and shrub cover as regulated by fire frequency. The clear inflection point indicates that two stable states (grass- and shrub-dominated) occur in this system driven by fire frequency (Fig. 2). As shrub cover increases, grass cover declines to ∼ 50% or less in infrequently burned treatments. Once shrubs establish, their cover can increase rapidly while grass cover remains around 40–50%. However, if shrub cover continues to increase, grass cover eventually declines to < 20% (Fig. 1). Finally, when fire is reintroduced to infrequently burned watersheds, grass cover can increase rapidly even though shrub cover may remain relatively constant over time.

Mapping shrubs on one of the annual to infrequently burned reversal treatments showed a greater increase in shrub cover following the cessation of annual burning than is evident in the more spatially-distributed 10-m^2 permanent plots (Fig. 3a–c). In particular, cover of *C. drummondii* and *R. glabra* increased on this watershed after annual burning stopped. As of 2017, the percent of watershed area with shrub cover on this reversal treatment was 47.5% compared to 18% on the long-term infrequently burned reference watershed after a similar length of fire suppression (data from year 2001). Moreover on the infrequent-to-annually burned watershed, *C. drummondii* and *R. glabra* remain not only widespread but they have expanded in cover after annual burning was introduced in 2001. However, shrub stems are much shorter and intermixed with the grass canopy, except near topographic features, where taller shrubs persist (Fig. 3d).

Do changes in community composition exhibit hysteresis under altered burning regimes?

Axis 1 of a two-dimensional NMDS ordination separated the long-term annually burned and the long-term infrequently burned reference watersheds along the first axis (perMANOVA $t = 8.68$, $P < 0.001$; Fig. 4). Based on indicator species analysis (Table S1), abundance of *P. virgatum* and *A. gerardii* was higher on the long-term annually burned reference
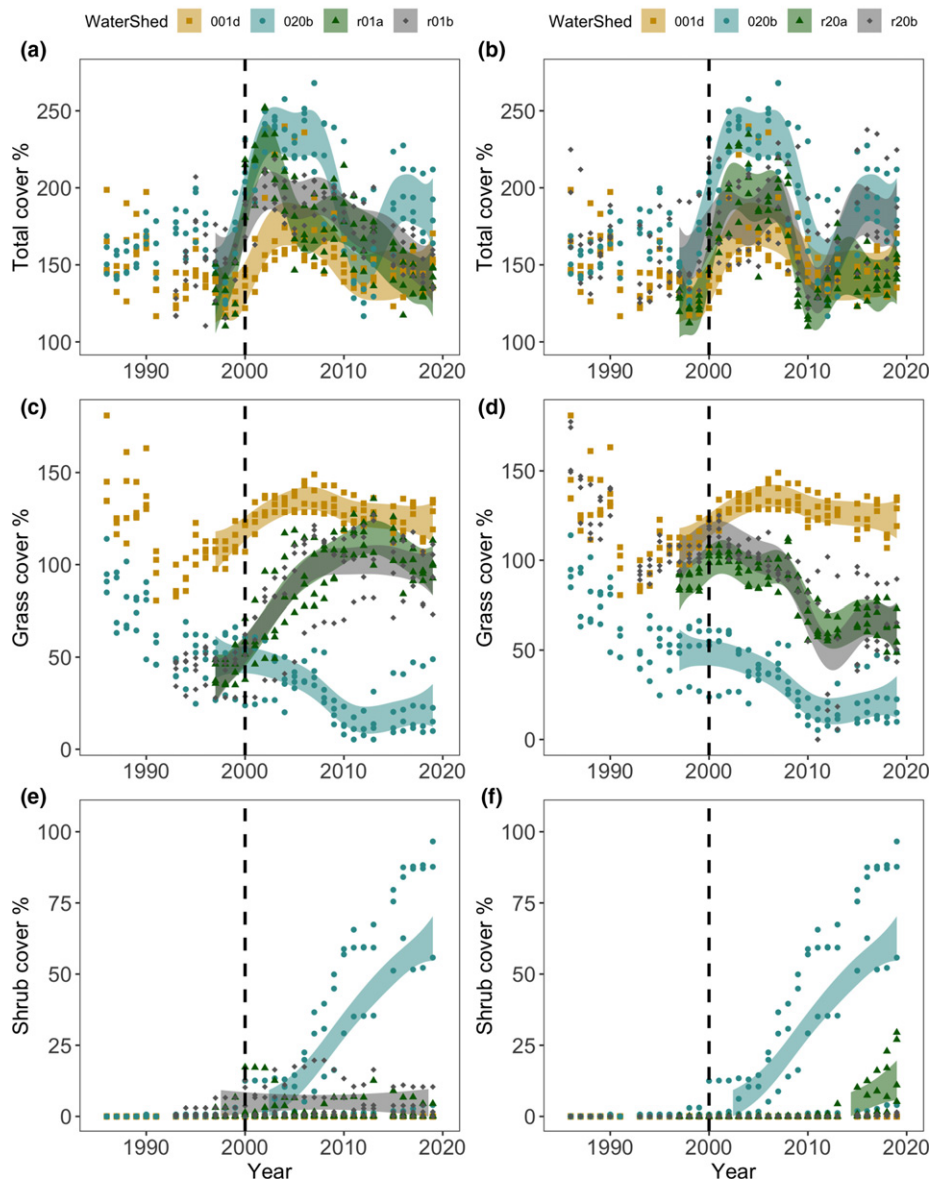
Figure 1 Trends in (a, b) total, (c, d) grass and (e, f) shrub cover on four fire reversal watersheds and two long-term reference watersheds with consistent fire regimes (Annual and Infrequent) since 1978. Two watersheds (R1A and R1B) were infrequently burned for 22 years prior to introducing annual burning in 2001. Two other watersheds (R20A and R20B) were burned annually for 22 years prior to switching to infrequent burning. Shaded areas are 99% confidence intervals based on four replicate transects each of which has five 10-m^2 permanent vegetation plots evenly spaced along each transect. See Table 1 for watershed codes and fire histories.

watershed while *Poa pratensis* and *Solidago altissima* characterised vegetation on the long-term infrequently burned reference watershed. Species composition on the long-term annually burned reference watershed exhibited transient fluctuations but little directional change. In contrast, clear directional change occurred along the first and second NMDS axes on the long-term infrequently burned reference watershed. These reference watersheds provided the endpoints against which we assessed the effects of the fire reversal treatments on compositional trajectories and the occurrence of hysteresis.

perMANOVA revealed significant differences in vegetation composition across all treatment comparisons (Table S1).

First, vegetation prior to the reversal treatments was significantly different from vegetation after treatments were reversed in all four cases (Table S1). On the two infrequent-to-annually burned treatments, cover of *A. gerardii*, *S. nutans* and *P. virgatum* increased after annual burning started, whereas on the two annual-to-infrequently burned treatments cover of these and other dominant grasses declined and abundance of forbs, such as *S. altissima*, *Symphyotrichum ericoides* and *Ambrosia psilostachya*, increased once annual burning ceased.

Species composition of the two annual-to-infrequently burned treatments overlapped that of the long-term annually burned reference site in NMDS space prior to the reversal of

Table 2 Results of two generalized additive models (GAMM) comparing changes in total plant cover, grass cover and shrub cover across treatments over time. The first model (w/out Watershed) treated year (time) as a smooth function, and the second model (w/ Watershed) included year as a smooth function, watershed included as factor, and watershed as a factor that adjusts the smoothing parameters for each watershed. See Table 1 for watershed codes.

Response variable	Adj R^2		F-statistic for watershed effect on smoothing parameter[1]						
	w/out Watershed	w/ Watershed	Year	1D	20B	R1A	R1B	R20A	R20B
Total cover	0.03	0.64	8.3***	1.7	7.6***	3.6***	0.4	4.9***	5.8***
Grass cover	0.03	0.86	5.8***	0.8	7.6***	4.7***	4.6**	2.0*	7.7***
Shrub cover	0.03	0.66	5.7*	3.7ˆ	47.2***	4.9*	2.7ˆ	2.6ˆ	3.3ˆ

[1]F-statistics for these columns correspond to the model that includes year and watershed.
***$P < 0.001$,
**$P < 0.01$,
*$P > 0.05$,
ˆ$P < 0.10$.

treatments (Fig. 4a). Once burning stopped, vegetation in the two annual-to-infrequent reversal treatments diverged in compositional space from the long-term annually burned reference watershed, as well as from each other. Forb cover increased and grass cover decreased in the absence of fire. Moreover neither site is on a trajectory toward current vegetation composition on the long-term infrequently burned reference watershed. That is, community composition on the annual-to-infrequently burned treatments exhibited hysteresis as reflected by novel compositional trajectories that differ from both the annually burned and infrequently burned reference watersheds (Table S1).

In contrast, species composition on the infrequent-to-annually burned treatments exhibited trajectories in compositional space that are moving towards that of the long-term annually burned reference site (Fig. 4b). This occurred despite the fact that plant composition on these two reversal treatments differed prior to the start of the experiment (Table S1). These changes were driven primarily by a small decline in shrub (*C. drummondii*) and forb cover, along with an increase in the dominant grasses characteristic of the long-term annually burned reference site.

DISCUSSION

Using a 20 to 40-year long watershed-scale fire reversal experiment, we found that returning annual fire frequency to formerly infrequently burned grasslands that had been encroached by shrubs significantly increased cover of the dominant perennial C_4 grasses but did not eliminate woody vegetation after 19 years of annual burning. Indeed, the response by shrubs at the transect and watershed scales appears to be contradictory. This may be because the plots were originally established in grassy areas where shrubs are now expanding, whereas the mapping data reflect vegetation across the entire watershed. The mapping data, on the other hand, denote aerial cover of clonal shrub patches, but not shrub height and stem density. Thus, these two data sets provide complimentary evidence that reintroducing fire increased grass cover, but annual burning did not prevent clonal shrub expansion within the grass canopy despite a fire management regime specifically prescribed to promote grass abundance and

reduce the spread of shrubs (Twidwell *et al.* 2013b). The persistence of short- and tall stature clonal shrubs in a long-term high-frequency fire environment is consistent with alternative stable state theory in which alternative states may persist even after a change in driver, and also implies that reducing fire frequency would likely lead to a rapid transformation back to shrubland.

Our results support our hypothesis that woody encroachment would be delayed in formerly annually burned grassland (e.g. Ratajczak *et al.* 2017b). Overall, species diversity and nitrogen availability are much lower in annually burned grassland (Blair 1997; Collins & Calabrese 2012) and annual burning prevents the establishment of woody vegetation in mesic grasslands (Twidwell *et al.* 2013a). Combined, these factors result in dominance by competitive C_4 grasses that exhibit high nutrient-use efficiency and competitive superiority for shallow soil moisture (O'Keefe & Nippert 2018). As fire frequency declines, litter accumulates, altering the soil and surface microenvironment, delaying grass growth in the spring and ultimately reducing grass abundance (Knapp & Seastedt 1986). A similar phenomenon has been observed with fire in *Leymus chinensis* grasslands (Yu *et al.* 2015). As litter accumulates, soil resources increase in grasslands (Blair 1997; Pellegrini *et al.* 2018) altering the competitive landscape (Pierce *et al.* 2019). Moreover patchy dispersal by shrubs into formerly annually burned areas takes time (Briggs *et al.* 2005), but once established woody vegetation approaches a threshold where cover and abundance increase rapidly, especially for clonal shrubs (Ratajczak *et al.* 2014, 2017b). All of these mechanisms create time-lags, and as a result, the ultimate effects of fire suppression can take decades to become apparent.

Our second hypothesis that annual burning would increase grass cover and decrease shrub cover following shrub encroachment in previously infrequently burned watersheds was only partially supported, but this again reflects a form of hysteresis. Annual burning increased grass cover significantly and relatively rapidly; however, shrubs remain widespread at the watershed scale despite annual burning (Fig. 3). Similar results were observed with annual burning in Missouri grasslands (Miller *et al.* 2017), and in spinifex grasslands in Australia (Wright *et al.* 2019). In our system, the fire reversal
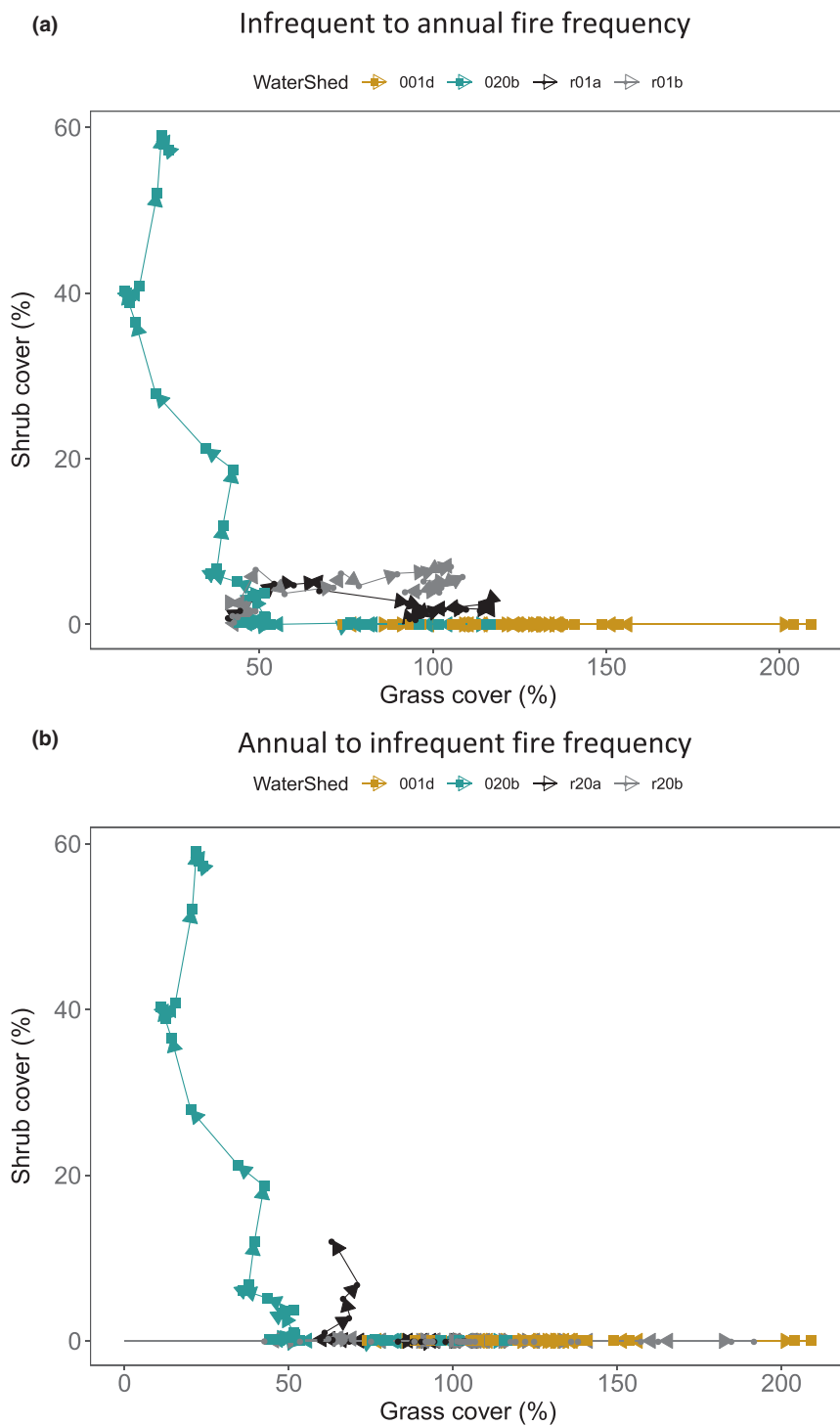
(a)
Infrequent to annual fire frequency

(b)
Annual to infrequent fire frequency

Figure 2 Grass-shrub phase space plots from four fire reversal watersheds and two long-term reference watersheds with consistent fire regimes (Annual and Infrequent) since 1978. Two watersheds (R1A and R1B) were infrequently burned for 22 years prior to introducing annual burning in 2001. Two other watersheds (R20A and R20B) were burned annually for 22 years prior to switching to infrequent burning. See Table 1 for watershed codes and fire histories.

treatments were initiated as woody cover approached a threshold beyond which encroachment is rapid and persistent (Ratajczak et al. 2017b). Shrubs were not eliminated because they spread clonally and grass cover is reduced at clone boundaries, reducing fuel loads and fire intensity such that clones persist (Briggs et al. 2005; Ratajczak et al. 2011).

Importantly, we found evidence for compositional hysteresis (Lamothe et al. 2019). Specifically, returning annual fire to infrequently burned grassland caused the vegetation to move along a compositional trajectory toward that of a long-term annually burned reference grassland even though shrubs remained. This comes with the caveat that composition plots were in areas that had low shrub cover when annual fires were reintroduced. In contrast, removing fire from annually burned grassland led to hysteresis as composition of both reversal watersheds diverged from that of the grassland and shrubland endpoints, as well as from each other (Fig. 4). In fact, we see little evidence, thus far, that these communities are on a trajectory that will converge with the long-term infrequently burned reference watershed. On the other hand, vegetation
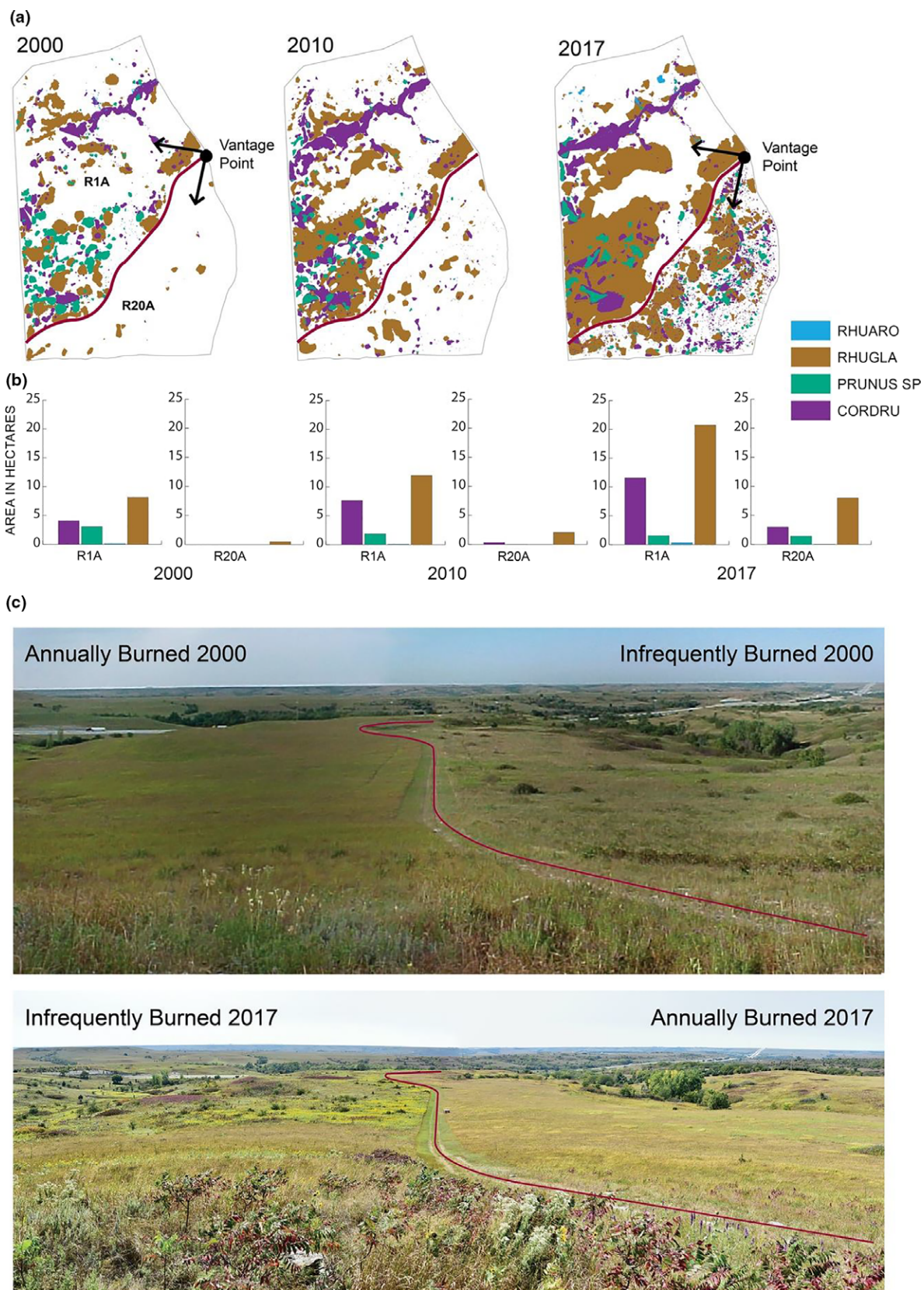
Figure 3 (a) Maps of woody plant expansion on two fire reversal watersheds in 2000, 2010, and 2017. One watershed (R1A) was infrequently burned for 22 years prior to the introduction of annual burning in 2001. An adjacent watershed (R20A) was burned annually for 22 years and then switched to infrequent burning in 2001. (b) Percent of each watershed covered by one of four clonal shrub species. (c) Photographs of annual to infrequently burned site (left) and infrequent to annually burned site (right) in 2000 prior to the fire reversal treatments and again in 2017. See Table 1 for watershed codes and fire histories.
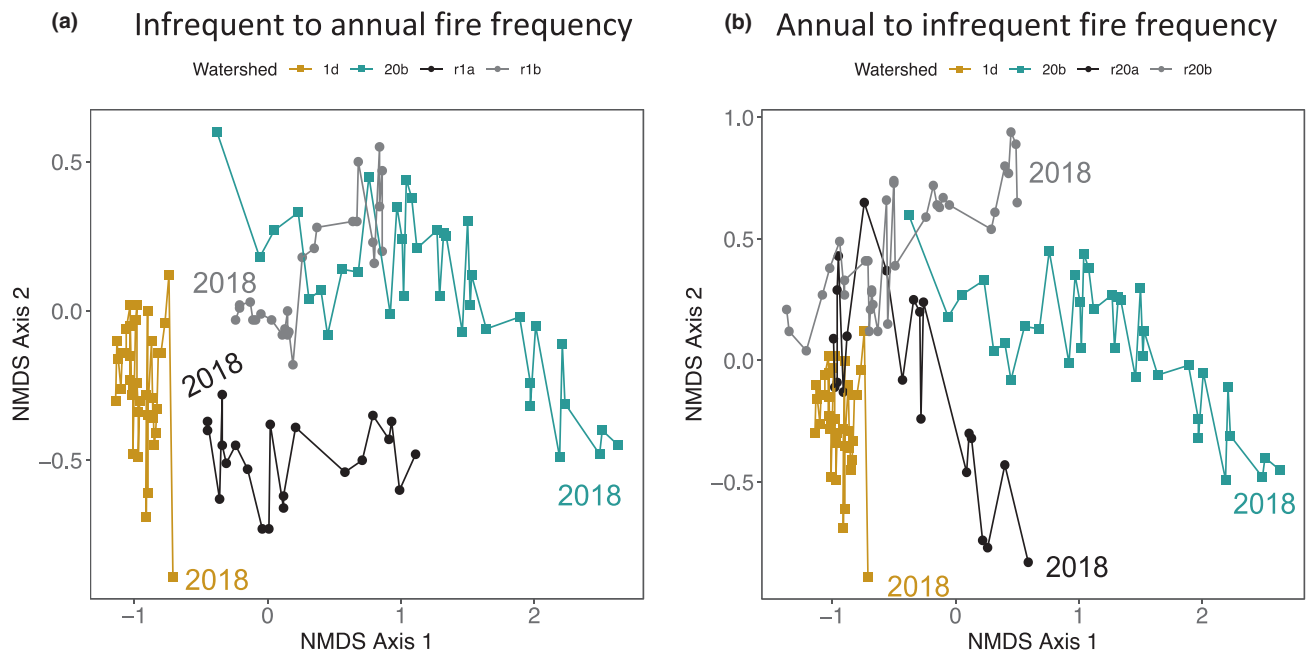
(a) Infrequent to annual fire frequency

(b) Annual to infrequent fire frequency

Figure 4 Nonmetric multidimensional scaling (NMDS, stress = 0.15) ordination of vegetation change on four fire reversal watersheds, two that were infrequently burned from 1978 to 2000 and then switched to annual burning, and two that were annually burned from 1978 to 2000 and are now infrequently burned. Two long-term reference watersheds with consistent fire regimes (frequent and infrequent) represent endpoints for compositional trajectories under reversed fire frequencies. Symbols represent years and lines connect samples over time, with 2018 marking the most recent data point. The ordination is broken into two panels for clarity. (a) infrequent to annually burning watersheds. (b) Annual to infrequently burned watersheds. Reference watershed (1D) has been burned annually since 1978 and reference watershed 20B has burned twice since 1978 (see Table 1 for watershed codes and fire histories).

structure does show a pattern similar to that of the infrequently burned reference watershed, with a delayed but eventual decline of grass cover, followed by a rapid expansion of shrub cover after about 20 years with low fire frequency (Fig. 1).

Changes in fire frequency resulted in hysteresis for more than half of the metrics we considered, close to our predictions. Hysteresis occurs when the trajectory from state A to B differs from that of B to A following a change in driver (Beisner *et al.* 2003). In our case, grassland and shrubland states are governed by fire frequency and an abrupt change in fire frequency resulted in hysteresis. Because of the stochastic nature of dispersal by shrubs into compositionally homogeneous grass-dominated areas (Collins & Smith 2006; Ratajczak *et al.* 2017b), community trajectories can differ once annual burning stops. In contrast, dominant C_4 grasses remained throughout the infrequently burned site, albeit at lower cover, and their cover doubled with the introduction of annual burning. This suggests that with frequent fire, community composition is somewhat deterministic, moving towards dominance by C_4 grasses despite differences in initial conditions. Thus, vegetation trajectories from the annually-burned grass-dominated state to the infrequently burned shrub-dominated state differed significantly from the trajectories of the shrub-dominated to grass-dominated state with annual burning, providing clear evidence for hysteresis. Shrub cover also exhibited hysteresis, remaining low in long-term annually burned vegetation but persisting and even expanding despite the introduction of annual burning (Fig 1 and 3).

Although numerous examples of alternative stable states have been described (DeYoung *et al.* 2008; Bestelmeyer *et al.* 2011; Scheffer *et al.* 2012; D'Odorico *et al.* 2012), evidence for hysteresis is much less common and few long-term experimental studies of state change have been conducted in natural terrestrial ecosystems at large spatial scales (Schröder *et al.* 2005; Fletcher *et al.* 2014). Yet, hysteresis is one of the underlying assumptions of alternative stable state theory (Scheffer *et al.* 2001; Beisner *et al.* 2003). One limitation to demonstrating hysteresis is the need for long-term, high frequency data within the context of changes in driver variables. Although modelling studies are useful (e.g. Cipriotti *et al.* 2019), experiments to test for existence of hysteresis within the context of alternative stable states are essential but rare, especially in slowly transitioning ecosystems (Hughes *et al.* 2012; Ratajczak *et al.* 2017a). To the best of our knowledge, this study is one of only a handful of long-term experiments that have demonstrated hysteresis in terrestrial ecosystems (e.g. Schmitz 2004; Bestelmeyer *et al.* 2011; Isbell *et al.* 2013b).

Through this long-term experiment we demonstrated the existence of alternative states and hysteresis under abrupt changes in fire regimes in mesic grassland. The existence of alternative states and hysteresis driven by fire regimes has important implications for grassland conservation and management (Dantas *et al.* 2015), and the provisioning of ecosystem services (Miller *et al.* 2011). Under current climate trajectories as well as continuing pressure for fire suppression (Twidwell *et al.* 2013a), mesic grasslands will continue to transition to shrub and woodland states (Briggs *et al.* 2005;

Twidwell *et al.* 2013b). And yet future management of mesic grasslands will likely require fires to occur at frequencies or intensities that are higher than historical regimes (e.g. Twidwell *et al.* 2013a; Case & Staver 2017). Once woody plants become well established, annual burning as a management tool can increase grass cover despite further shrub encroachment, but annual burning greatly reduces diversity in these grasslands (Collins *et al.* 1998; Collins & Calabrese 2012; Koerner *et al.* 2014) and this long-term study illustrates that annual fire may not eliminate shrubs once established. Thus, early warning indicators (e.g. Carpenter & Brock 2006; Ratajczak *et al.* 2017b) are essential to determine if shrub abundance is approaching a critical threshold because once established annual burning may not return these hysteretic systems to a highly diverse grassland state.

AUTHORSHIP

JMBlair, JMBriggs and SLC designed the fire reversal experiment. Data were collected by JMBriggs, SLC and the Konza LTER Field Crew. ZR, SLC and PB analysed the data. SLC drafted the manuscript, and all authors contributed to writing and editing the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All raw data are freely available at https://doi.org/10.6073/pasta/4e83f17c1fdab90b952e754265edaaaf

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