Changes in spatial variance during a grassland to shrubland state transition

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Summary

1. State transitions are changes in ecosystem structure and self-reinforcing feedbacks that are initiated when an exogenous driver variable crosses a threshold. Reversing state transitions is difficult and costly. While some state transitions are relatively rapid, many take years to decades. Outside of theoretical models, very little is known about slower state transitions and how they unfold in time and space.

2. We quantified changes in spatial variance as a mesic grassland ecosystem shifts to a shrub-dominated state, using long-term experiments and simulations that maintain grasslands with annual fires or initiate a state transition to shrub dominance by decreasing fire frequency.

3. In the experiments, the susceptibility to state transitions varied substantially in space. In the less frequent fire treatment, some plots became shrub-dominated around year 20 and grass extirpations began in year 25, but a third of the plots were still grass-dominated in year 37. Variable rates of state transition resulted in increasing spatial variance of grass cover over time, whereas shrub cover variance decreased. In the annually burned treatment, grasses remained dominant and the spatial variance of grass cover declined.

4. In a separate experiment, less frequent fires were maintained for 23 years and then switched to annual fires. The switch to annual fires occurred shortly after grass variance started to increase and a majority of these plots quickly returned to a grass dominated state.

5. In simulations, spatial variance remained low and average grass cover was high under frequent fires. If fire frequency decreased below a threshold, the ecosystem transitioned to shrubland, with a transient increase in the spatial variance of grass cover during the transition between states.

6. *Synthesis*. Spatial variability in the rate and susceptibility to state transitions is indicative of a system with a patchy spatial structure, high spatial heterogeneity and low connectivity between patches. Increases in spatial variance can serve as an indication that some patches have begun a state transition and that management interventions are needed to avoid widespread transitions. This is one of the first empirical examples where altering management after an increase in spatial variance prevented state transitions.

Key-words: bush encroachment, early warning signs, forecasting, leading indicators, long-term, non-equilibrium, regime shifts, resilience, shrub encroachment, transient dynamics

Introduction

Some ecosystems exhibit multiple alternative stable states or attractors, making them capable of transitioning from one self-reinforcing state to another when an exogenous driver variable crosses a threshold (Holling 1973; Noy-Meir 1975; May 1977; Folke *et al.* 2004; Walker & Salt 2006). In ecosystems with multiple stable states, reversing changes in state becomes difficult once the system reorganizes around a new set of self-reinforcing processes, at which point the ecosystem is often said to have undergone a state transition (also known as a state shift, regime shift or catastrophic shift) (Holling 1973; Walker & Salt 2006).

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Anthropogenic activities, such as altering disturbance frequency or nutrient addition, can push driver variables across ecological thresholds, leading to the onset of state transitions (Holling 1973; Noy-Meir 1975; May 1977; Hastings 2010). While some ecosystems are capable of transitioning to an alternative state in 1–2 years (Chase 2003; Carpenter *et al.* 2011), it is increasingly recognized that many state transitions take years to decades and therefore appear gradual at human time-scales of observation (Van Geest *et al.* 2007; Bestelmeyer *et al.* 2011; Hoffmann *et al.* 2012; Hughes *et al.* 2013). During slower transitions, ecosystems or patches of a landscape are in a transient state where timely manipulations of driver variables can potentially avert a state transition (Westoby, Walker & Noy-Meir 1989; Hughes *et al.* 2013).

Outside of theoretical models, little is known about the transient dynamics of state transitions (Hastings 2010). In particular, we lack empirical assessments of how transient dynamics vary in space. Yet, most ecosystems are patchy (Levin 1992) and as a result, different locations can exhibit unique responses to the same driver (Westoby, Walker & Noy-Meir 1989; Bestelmeyer *et al.* 2013; Dai, Korolev & Gore 2013; Collins & Xia 2015). The characteristics of a given patch—such as soil properties, species composition and topography—can influence how species respond to driver variables (Van Nes & Scheffer 2005; Van Geest *et al.* 2007). Therefore, in ecosystems with greater underlying spatial heterogeneity, the susceptibility to state transitions likely varies among patches (Van Nes & Scheffer 2005; Cumming 2011; Villa Martin *et al.* 2015). In contrast, patches tend to shift to an alternative state in synchrony in ecosystems with low underlying spatial heterogeneity or high spatial connectivity between patches (Van Nes & Scheffer 2005; Cumming 2011; Villa Martin *et al.* 2015). Ecosystems with low spatial heterogeneity or high connectivity are also particularly susceptible to abrupt, large-scale state transitions (Van Nes & Scheffer 2005; Cumming 2011; Okin *et al.* 2015).

Patchiness, spatial heterogeneity and limited spatial connectivity can provide opportunities for adaptive management. For instance, transitions by the most susceptible patches can indicate that other locations might soon transition to an alternative state. Moreover, model simulations suggest that the differences between patches are elevated during the transient phase of state transitions (Guttal & Jayaprakash 2009; Fukami & Makajima 2011). Increasing differences between patches can be measured as changes in variance across a fixed set of plots (Kefi, Guttal *et al.* 2014), and therefore, an increase in the spatial variance might indicate the onset of a slow state transition (Guttal & Jayaprakash 2009).

Data from large-scale, long-term experiments are needed to determine whether the susceptibility to state transitions varies between locations. We assessed changes in spatial variance over the course of a state transition from a mesic grassland to a shrub-dominated ecosystem. Grassland to shrubland state transitions are occurring globally, with significant consequences for conservation, livestock production and other ecosystem services (Briggs *et al.* 2005; Eldridge *et al.* 2011; Anadon *et al.* 2014; Lautenbach *et al.* 2016; Ratajczak *et al.*

2016a). Many mesic grasslands occupy a climate zone capable of supporting shrublands (Knapp *et al.* 2008), but grasses are capable of generating highly flammable biomass, which facilitates frequent ground fires that damage or kill young shrubs and trees (Anderies, Janssen & Walker 2002; Heisler *et al.* 2004; Ratajczak *et al.* 2014). This positive feedback between grasses and fire can prevent a build-up of litter and the expansion of forbs and woody species (Knapp & Seastedt 1986; Gibson & Hulbert 1987), leading to persistent dominance by perennial C_4 grasses (Briggs *et al.* 2005; Collins & Calabrese 2012; Bowles & Jones 2013).

Transitions from mesic grassland to shrubland occur when the time between fire increases and grass biomass declines, which allows shrubs to reach a size capable of shading grasses and disrupting the grass-fire feedback (Briggs *et al.* 2005; D'Odorico, Okin & Bestelmeyer 2012; Ratajczak, Nippert & Ocheltree 2014). A review of observational studies and long-term experiments suggests that grassland-shrubland transitions in our study region are mediated by a threshold of c. 3 years between typical prescribed fires (Ratajczak *et al.* 2014). If the mean fire interval is increased to 3 years or greater, patches become susceptible to invasion by shrubs and trees (Briggs *et al.* 2005; Ratajczak *et al.* 2014, 2016a). Increasing the frequency of typical prescribed fires does not usually reverse transitions to shrubland, because mature shrubs and trees reduce fine fuel loads and are more resistant to fire (Heisler *et al.* 2004; Briggs *et al.* 2005; Twidwell *et al.* 2009, 2013; Wonkka *et al.* 2016). Thus, shifts to shrub and tree dominance in our study region exhibit two key features of a state transition: a threshold relationship between state and a driver variable (shrub cover vs. fire frequency) and hysteresis once woody plants are established (Twidwell *et al.* 2013; Ratajczak *et al.* 2014, 2016a).

We used data from long-term fire manipulation experiments to quantify spatial variance during a state transition to a shrub-dominated state. The experiments included both long-term fire suppression and a treatment where annual fires were reinstated after over twenty years of fire suppression. While our primary focus is on experimental results, we also developed a modified Lotka–Volterra model built on assumptions from our study site. Our primary hypothesis is that spatial variance will increase when this grassland ecosystem is pushed beyond a fire frequency threshold, but will remain low or even decrease when driver variables do not exceed a threshold or once a state transition to shrub dominance is complete.

Materials and methods

STUDY SYSTEM AND SITE

The experimental portion of this study uses field data from Konza Prairie Biological Station (KPBS), a large-scale long-term experiment manipulating fire and grazing in the Central Great Plains, North America (39′05″N, 96′35″W; more information at http://www.konza.ksu.edu/knz/pages/home/home.aspx). KPBS is native, unplowed tallgrass prairie dominated by drought-tolerant C_4 grasses. The site

has a mid-continental climate, with a mean annual precipitation of c. 840 mm year^{-1}, most of which falls during the growing season.

The site is characterized by a patchy and heterogeneous spatial structure (Koerner & Collins 2013), reflecting variability in species composition, substrate, topography and other factors (Gibson & Hulbert 1987; Collins & Smith 2006; Nippert *et al.* 2011). Without grazers, the estimated patch size of dominant grass species is c. 1–5 m in diameter (Koerner & Collins 2013). Fire behaviours between patches are partially coupled, because the flammability of nearby patches determines whether fire moves to an adjacent patch (e.g. Abades, Gaxiola & Marquet 2014). In addition, woody plants can cast shade that reduces the flammability of adjacent patches through impacts on fuel quantity and moisture (Breshears 2006). Mycorrhizal networks, plant use of groundwater and runoff should partially connect water and nutrient pools between adjacent patches (Wilson, Hartnett & Rice 2006; Logan & Brunsell 2015). Most dominant grasses and shrubs are also capable of lateral growth via clonal ramets, leading to direct associations between species composition in neighbouring patches (Benson & Hartnett 2006). For instance, once a patch transitions to shrub dominance, individual woody plants can expand clonally, creating shrub patches up to 50 m^2 (Heisler *et al.* 2004; Ratajczak *et al.* 2011).

EXPERIMENTAL DESIGN

The average fire interval for grasslands in this region is 2·5–4 years (estimated over the last several hundred years; Desantis, Hallgren & Stahle 2010; Allen & Palmer 2011; Stambaugh, Guyette & Marschall 2013). Under current conditions, this ecosystem transitions to a woody-plant dominated state when typical prescribed fires are applied at an interval greater than 3 years (Ratajczak *et al.* 2014, 2016a). Before fire experiments began, KPBS was managed primarily for cattle production, with prescribed burns every 1–2 years in most locations and some herbicide use to suppress shrubs and forbs. The fire experiments used in this study began in 1977 by splitting KPBS roughly along topographic boundaries into replicated management units (watersheds) with different fire return intervals. The first set of experimental treatments consists of watersheds that maintained 1, c. 4, and c. 20 year fire intervals through 2013 (referred to as 'continuous fire treatments'). The 4- and 20-year fire treatments eventually yielded changes in species composition that appeared to constitute a state transition (see Briggs *et al.* 2005; Ratajczak, Nippert & Ocheltree 2014; Ratajczak *et al.* 2014; Wonkka *et al.* 2016 for similar shrublands).

The second set of experimental treatments is referred to as 'fire reversal treatments'. The fire reversal treatments were also initiated in 1977 (Table 1), but were conducted in 4 watersheds separate from the continuous fire treatments. Two of the reversal watersheds started with an annual fire frequency and two started with a 20-year fire frequency. In 2001, the fire frequencies were reversed, switching the 20-year fire frequency watersheds to an annual fire frequency (referred to as 'infrequent→annual fire reversal') and switching the annually burned watersheds to a planned fire interval of 20 years (referred to as 'annual→infrequent fire reversal'). The infrequent→annual fire reversal allowed us to assess whether patches of the watersheds had reached an alternative state after over 20 years of fire suppression and if changes in variability emerge early enough to engage in management interventions that prevents patches from becoming trapped in a shrubland state. The fire reversal treatments serve as additional tests our hypotheses that spatial variability will decrease when fire is frequent (before the fire reversal in the annual→infrequent treatment and after the fire reversal in the infrequent→annual treatment) and increase when fire frequency is reduced

(after the fire reversal in the annual→infrequent treatment and before the fire reversal in the infrequent→annual treatment).

We quantified changes in plant community composition using data from permanently located long-term vegetation monitoring plots. Data collection for the continuous fire treatments began in 1984 and between 1984 and 1997 in the fire reversal experiments (see Table 1 and Appendix S1, Supporting Information for notes on the data set). The data come from four 50 m transects per watershed, with five 10 m^2 circular vegetation plots located at 10 m intervals along each transect (see Table 1 for replication). Each year, the approximate aerial cover of every species in each plot was recorded using a modified Daubenmire cover scale (Collins & Smith 2006; Appendix S1), which captures absolute cover per species with units of plant cover per unit ground area. Therefore, cover can exceed 100% due to the presence of overlapping plant canopies. All data in this study are from lowland topographies and in watersheds without grazers, as the shallow soil of uplands rarely supports shrub expansion (Ratajczak *et al.* 2014; Appendix S1) and fire reversal treatments were not available for grazed areas.

We used the long-term plant composition data to quantify trends in grass and shrub cover over time. Following our past analyses of this data set (Ratajczak, Nippert & Ocheltree 2014), we defined 'grass cover' as the summed cover of the four dominant grass species that typically comprise c. 90% of grass biomass: *Andropogon gerardi* (Big Bluestem), *Panicum virgatum* (Switchgrass), *Sorghastrum nutans* (Indian grass), and *Schizachyrium scoparium* (Little Bluestem). Shrub cover was the summed cover of woody species that typically maintain foliage above the grass canopy (>1 m tall) and therefore, are capable of negatively affecting grasses via light limitation. *Cornus drummondii* (Roughleaf dogwood), *Rhus glabra* (Smooth sumac), *Rhus aromatica* (Aromatic sumac), and *Prunus americana* (American plum) comprised most shrub cover. For both dominant grasses and shrubs and all combinations of year and fire treatment, we report mean cover and the 5th and 95th percentiles of cover.

We calculated the coefficient of variation (CV) of grass and shrub cover, and grass-shrub correlation as metrics of changing spatial heterogeneity and competitive interactions over time. We chose these metrics based on our simulations, the literature on 'early warning signs' of state transitions (Scheffer *et al.* 2012; Van Leemput *et al.* 2013; Kéfi, Guttal *et al.* 2014), and a modelling study reporting changes in spatial variance during the transient phase of state transitions (Guttal & Jayaprakash 2009). Spatial variability was measured as the CV of each combination of year and treatment, which is calculated as the standard deviation (σ) divided by the mean (μ). The CV of grass and shrub cover captures normalized changes in variance

Table 1. Description of treatments and their sample size

Treatment	Watershed	Sample size (corresponding years)
Annual fire	1d	20 (1984–2013)
Infrequent fire	4b	20 (1984–2013)
	20d	20 (1984–2013)
Annual→infrequent fire reversal	1a to r20a	20 (1997–2013)
	1c to r20b	20 (1984–1990, 1993–2010)
		10 (2011–2013)*
Infrequent→annual fire reversal	20a to r1a	20 (1997–2013)
	20d to r1b	20 (1993–2013)

*Replication in this watershed was reduced to 10 at this point due to a warm-season wildfire that burned half of the plots in this treatment in 2011.

over a fixed sample in space. We also calculated changes in variance (σ^2) to ensure that any increases in spatial CV were not related solely to changes in mean cover. Grass-shrub correlations were reported as the correlation coefficient between grass and shrub cover across plots within a fire treatment. When shrubs are rare, zero-inflation of the data can make estimates of variance and correlation coefficients misleading. Therefore, shrub CV, shrub variance and grass-shrub correlations are only reported where sufficient shrub cover occurred, which was from 1993 onwards in the intermediate fire and intermediate→annual fire reversal treatments.

We used moving windows and the nonparametric Kendall's tau rank statistic to identify potentially significant increases or decreases in the spatial CV over different time periods. For example, a window that ends in 1999 and has a length of 9 years covers 1991–1999. If the rank-statistic between time and a response variable is statistically significant for this window, then the trend in this response variable is considered to have been significant from 1991 to 1999. We used this approach because it is amenable to real-time monitoring of changes in ecological properties (Kefi, Guttal *et al.* 2014). Similar to other uses of the same moving window method (Burthe *et al.* 2015), we used a window length of 10 years because it was half the length of the shortest data set (Table 1). Pearson product-moment correlations were used to assess parametric significance of grass-shrub correlations. All statistical analyses and simulations were performed in R (www.r-project.org).

SIMULATIONS

The key features of the simulation model are logistic growth of shrubs and grasses, competition between shrubs and grasses, a fire regime that removes shrub cover as a function of grass cover and fire frequency (characterized by the fire frequency parameter, 'f'), and spatial interactions between patches. The relative parameter values are estimates for the field site, but our goal is to use the model as a general example of grass-shrub competition in fire-prone environments (similar to Anderies, Janssen & Walker 2002; Van Langevelde *et al.* 2003; D'Odorico, Laio & Ridolfi 2006).

The primary assumptions of the model are in the parameterization of competition and fire mortality (see Table S1 for parameters values). Competitive exclusion usually requires that a species limits its competitor's growth more than its own growth (Chesson 2000). In the model, grasses limit shrub growth via competition, but this effect is weaker than the limitation grasses induce on themselves. This follows empirical observations that grasses at KPBS exert some competitive effects on shrubs, but are unable to exclude shrubs through competition alone (Briggs *et al.* 2005). Fire mortality of shrubs is a function of the fire parameter (f), which captures how frequently fires occur, and the abundance of grasses, which is correlated with fire intensity and therefore determines how much shrub cover is reduced by fires. f ranges from 0 to 1, with higher values corresponding with more frequent fire. Empirical results show that grasses can exclude shrubs when grass fuels are abundant and ignition events are frequent (Briggs *et al.* 2005; Bowles & Jones 2013; Ratajczak *et al.* 2014). Therefore, the model is parameterized such that fire removes almost all shrub biomass in two time-steps when grasses are close to their carrying capacity and fires are frequent (higher values of f). With infrequent fire, shrubs are superior competitors at this site (Briggs *et al.* 2005; Ratajczak *et al.* 2014). Consequently, shrubs are parameterized to limit grass growth more than their own, allowing shrubs to exclude glasses at lower fire frequencies.

The model was implemented in a 50 by 50 lattice. Within this lattice, grasses and shrubs exhibit spatial interactions, with both functional groups dispersing from patches of high cover to patches of low cover. Spatial heterogeneity was included in the simulations by drawing grass carrying capacity for each patch of the lattice from a normal distribution. For a more detailed description of the model, including spatial interactions, see Appendix S2.

Asymptotic states for the simulations were calculated numerically by starting with different initial combinations of grass and shrub cover and values of f, and running the model for 400 time-steps to determine the equilibrium conditions (the model typically stabilized in <300 time-steps) ($n = 1000$ iterations). To explore transient dynamics, we considered three management scenarios, all with the same initial conditions of dominance by grasses and a fire frequency at which grass dominance is stable ($f = 0.8$): (i) fire frequency is increased, further favouring grasses (f changed to 1); (ii) fire frequency is decreased, but not enough to exceed the threshold needed to initiate a transition to shrub dominance (f changed to 0·6); and (iii) fire is decreased enough to cross a fire frequency threshold, initiating a transition to shrub dominance (f changed to 0·2).

Results

FIELD EXPERIMENTS

In the annually burned treatment, shrubs have remained absent and average grass cover decreased initially before settling around an average value of c. 125% cover. Both the 5th and 95th cover percentiles remained close to average grass cover for most of the experiment (Figs 1a and 2a). The grass cover CV changed little, with occasional significant decreases over time (Fig. 3, Table 2). The variance of grass cover also decreased (Fig. 3).

In the infrequent fire treatment, average grass cover decreased quickly until 1993, but slowly from 1993 to 2005. Shrub cover increased slowly until c. 2000, after which the annual rate of shrub expansion doubled (Fig. 1). Only one observer gathered data from 2000 onwards and therefore, changes in observer are unlikely to account for the sustained increase in shrub expansion rate from 2001 to 2013 (Appendix S1). After shrub expansion rate increased, average grass cover began to decline faster, decreasing from 50% cover in year 2000 to c. 21% cover by 2013. The effect of shrubs on grasses was evident in grass-shrub correlations, which were significantly negative in 1996 to 1998 and from 2000 onwards ($P < 0.05$, Fig. 3, Table 2). By the final year of sampling, shrub cover exceeded 50% in 63% of plots and grass cover was c. 0% in plots with high shrub cover (Figs 2e and 4b).

Grass cover CV in the infrequent fire treatment increased steadily over time, with over half of moving windows recording statistically significant increases (Fig. 3, Table 2). By 2013, the grass CV in this treatment was over five times larger than in the annually burned treatment. Grass variance also increased over time, indicating the increase in grass CV was not driven only by a decrease in mean grass cover (Fig. 3). The increases in grass CV and variance coincided with a fast rate of grass cover loss in some plots, shown by the steep decline in the 5th percentile of grass cover, from c. 30% in
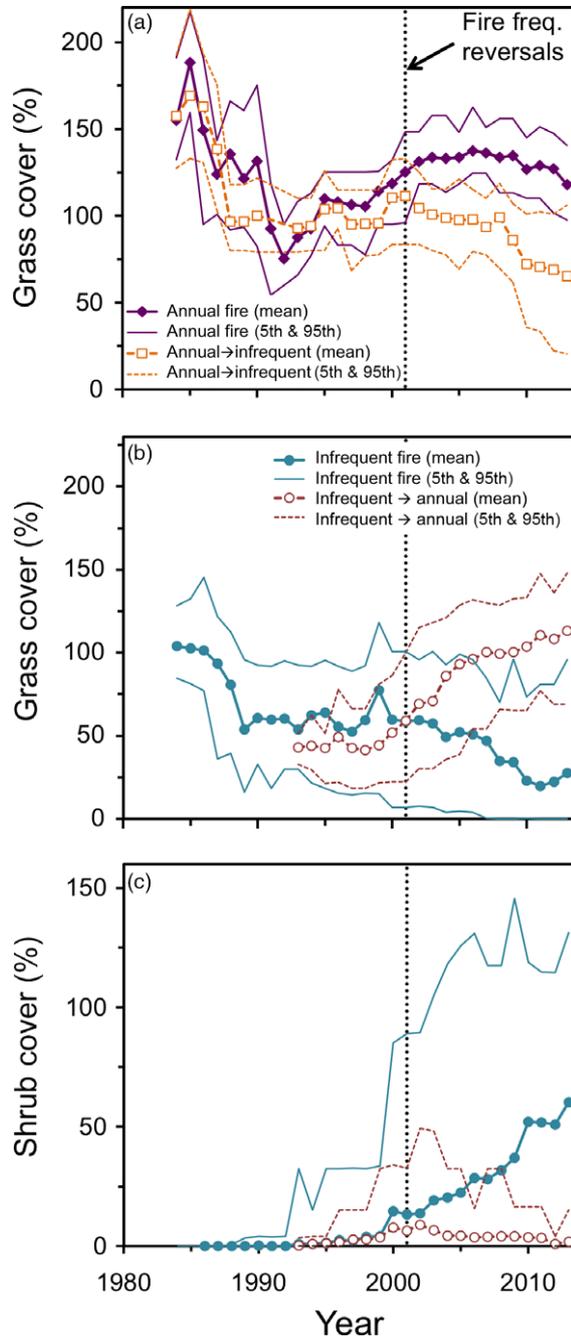
Fig. 1. Grass and shrub cover responses to long-term experimental treatments. Grass cover (a) for the annually burned continuous fire treatment (filled purple diamonds) and the annual→infrequent fire reversal (open orange triangle), grass cover (b) and shrub cover (c) for the continuous intermediate fire treatment (filled teal circles) and the infrequent→annual fire reversal (open red circles). Lines with symbols and thick lines are the average cover for each treatment and thin lines with no symbols denote the 5th and 95th percentiles for a treatment. The black dashed vertical line demarks when fire frequency reversals occurred. [Colour figure can be viewed at wileyonlinelibrary.com]
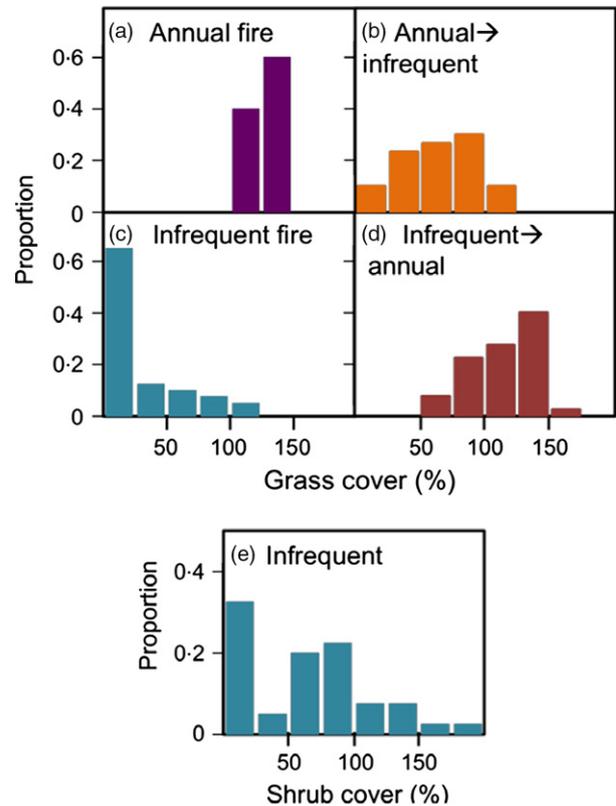
Fig. 2. Histograms of grass in 2013 for the annually burned (a), annual→infrequent fire reversal (b), infrequent fire (c), and infrequent→annual fire reversal (d), and shrub cover in the infrequent fire treatments (e). [Colour figure can be viewed at wileyonlinelibrary. com]

Until year 2000, the infrequent→annual fire reversal treatment followed a similar trajectory as the continuous infrequently burned treatment, with average grass cover decreasing at a similar rate and shrub cover increasing (Fig. 1). After reinstating annual fires, grass cover increased and shrub cover decreased in most plots, but as of 2013, c. 30% of plots have still not returned to a state of high grass cover (Fig. 2a, d). Plots with <50% grass cover in year 2000 were more likely to recover slowly, whereas plots with >50% and <100% grass cover saw large increases (Fig. 4c) and plots with >100% grass cover were relatively stable, suggesting an upper limit for grass cover.

The CV of grass cover increased while the infrequent→annual reversal treatment was under an infrequent fire frequency, but not as quickly as in the continuous infrequent fire treatment (Fig. 3, Table 2). After annual fires were reinstituted, grass cover CV and variance plateaued and then decreased. Increases in grass cover CV were significant for windows ending in 2002 and 2003 and decreases were significant for windows ending in 2007–2013 (Table 2). Shrub cover CV decreased, with statistically significant values for windows ending in 2002 and 2003 (Fig. 3, Table 2). The correlation between grass and shrub cover was significantly negative in 2013, but this relationship was driven by one plot with high shrub cover and low grass cover.

The annual→infrequent fire reversal treatment initially followed a similar trajectory as the continuous annually burned

1993 to <10% in 2000. In contrast, the 95th percentile of grass cover changed little until 2007 (Fig. 1). The CV of shrub cover decreased over time, but shrub cover variance increased (Fig. 3).
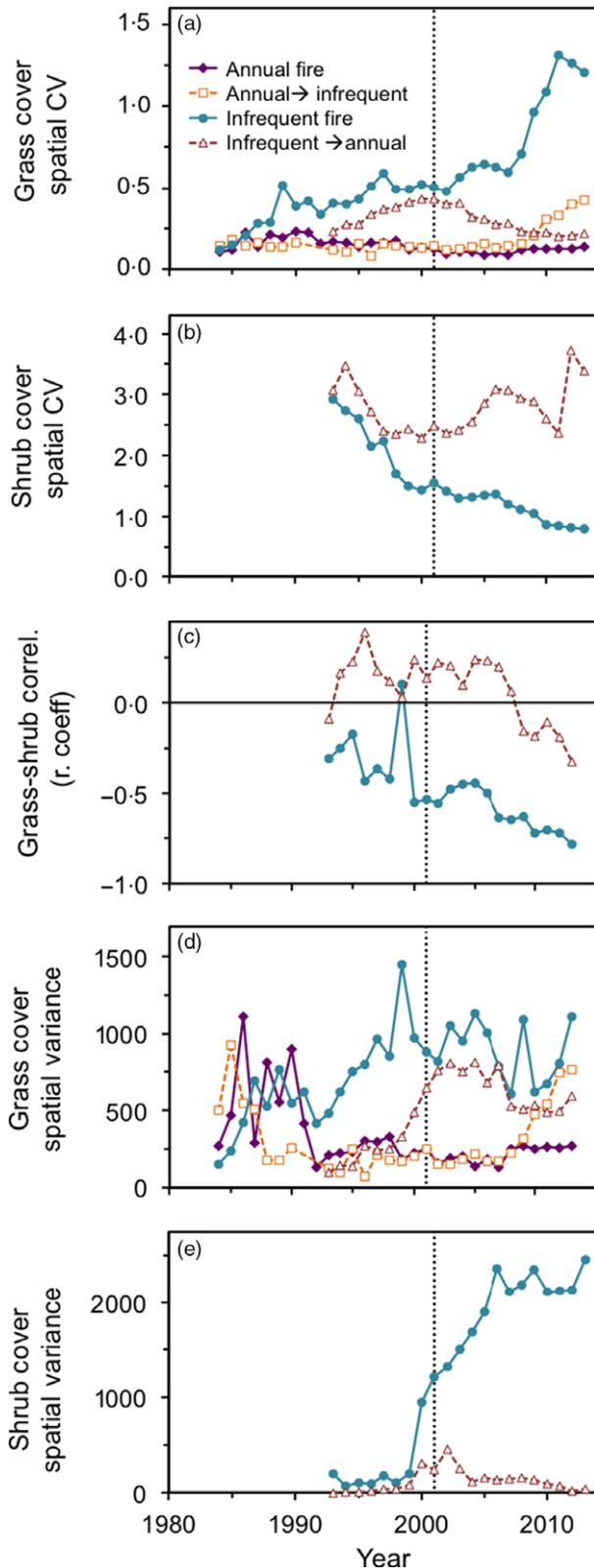
Fig. 3. The coefficient of variation (CV) (a) and spatial variance for grass cover (d), the CV (b) and spatial variance shrub cover (e), and the correlation between grass and shrub cover across space (c) for each year. The CV of shrub cover and grass-shrub correlations are not reported when few plots have shrubs present in a treatment. Symbols follow Fig. 2. [Colour figure can be viewed at wileyonlinelibrary.com]

treatment, settling around a value of 100% grass cover and 0% shrub cover. From 1984 to 2000, grass cover CV and variance decreased (Table 2, Fig. 3). After annual burning ceased, grass cover was relatively stable from 2001 to 2008, but decreased from 2009 to 2013. By 2013, shrubs were present in three plots, but mean shrub cover was still low (<3% cover, not shown). Once fire suppression began, grass CV and variance eventually increased, recording significant trends for moving windows ending in 2009–2013 (Fig. 3, Table 2). Increases in grass CV and variance coincided with rapid grass cover decreases in some plots: the 5th percentile of plots went from c. 80% to c. 20% grass cover, whereas the 95th percentile decreased slightly, from c. 120% to c. 100% cover.

SIMULATION MODEL

In the simulation model, the system was generally attracted to either a low or high grass cover state for $f > 0.4$. When the fire frequency parameter (f) decreased below 0.4, the system consistently converged on a shrub-dominated state (Fig. 5). When $f > 0.4$, differences between patches were minor, reflecting differences in grass carrying capacity between patches (Fig. 6). After initiating a transition to shrub dominance by decreasing f from 0.8 to 0.2, patches with lower grass carrying capacity tended to transition to shrubland faster. When f was decreased and maintained at a value of 0.2, grass CV increased over time, peaked, and then decreased (Fig. 6). Shrub CV, in contrast, decreased over time. Grass and shrub cover CV both followed unimodal patterns over time (Fig. 6). Grass-shrub correlations became negative and increased in absolute value, indicating that competitive effects were becoming stronger or more apparent (Fig. 6). If frequent fires are reinstated shortly after grass CV peaks (by returning f to 0.8), shifts to shrub dominance were restricted to a few patches (Fig. 7).

The average ecosystem state and grass cover CV changed little when f was moved away from the fire frequency threshold (increased fire frequency) or when f was decreased but did not cross the fire frequency threshold (Fig. 6). Shrub CV decreased with both decreases in f (to 0.2 or 0.6), whereas shrub CV increased when f increased. Grass-shrub correlations increased slightly when f increased and decreased slightly when f was decreased to 0.6 (Fig. 6).

Discussion

Rapid changes in driver variables, as a consequence of global change or otherwise, can initiate lasting state transitions (Holling 1973; Smith, Knapp & Collins 2009; Hughes *et al.* 2013). Most work on state transitions has focused on systems near equilibrium conditions (Hastings 2010) and research on non-equilibrium dynamics has typically focused on questions related to range shifts and community assembly (Svenning & Sandel 2013), whereas experiments addressing the transient dynamics of state transitions are rare. In this study, we quantified the behaviour of an ecosystem that is suddenly out of equilibrium and approaching a new self-reinforcing state due

Table 2. Moving window and grass-shrub correlation statistics results

Moving window end year[†]	Grass CV[‡]				Shrub CV[‡]	
	Annual	Infreq	Annual→infrequent	Infrequent→annual	Infreq	Infrequent→annual
1993		↑**	NA	NA	NA	NA
1994		↑*	NA	NA	NA	NA
1995		↑*		NA	NA	NA
1996			↓*	NA	NA	NA
1997	↓*			NA	NA	NA
1998				NA	NA	NA
1999		↑*		NA	NA	NA
2000		↑*		NA	NA	NA
2001		↑*		NA	NA	NA
2002	↓*			↑***	↓***	↑***
2003	↓*			↑**	↓***	↑*
2004	↓*				↓***	
2005	↓**				↓**	
2006	↓**				↓**	↑*
2007		↑*		↓*	↓**	↑**
2008		↑*		↓**	↓**	↑**
2009		↑**	↑*	↓***	↓**	↑**
2010		↑**	↑**	↓***	↓**	
2011	↑*	↑**	↑***	↓***	↓**	
2012	↑*	↑**	↑***	↓***	↓**	
2013	↑**	↑**	↑***	↓***	↓***	

[†]This column reports the last year of a moving window. For instance, "2000" would denote a window from 1991 to 2000

[‡]The presence of a "↑" indicates a significant increase in the response variable for a given moving window, "↓" indicates a significant decrease in the response variable for a given moving window, the presence of an "NA" indicates that there was not enough data to run a tau test for that time window.

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

to changes in disturbance frequency. The long-term fire experiments reported here suggest that structural differences between patches increased over the course of a state transition, resulting in greater spatial variability in the grasses that defined the grassland state. A simple simulation model produced similar dynamics (Figs 5 and 6).

Transient dynamics should be a common component of many changes in ecosystem structure, including state transitions (Smith, Knapp & Collins 2009; Hastings 2010; Fukami & Makajima 2011). After experimentally increasing the time between fires beyond a threshold for this system, grass cover declined over time, eventually reaching low enough levels that shrubs were able to establish and expand (Fig. 2). Shrub expansion was slow at first, but accelerated around year 2000, which was followed by a rapid decline in grasses (Fig. 1). We previously attributed this acceleration to the experiment crossing a threshold in the ratio of shrubs to grasses (Ratajczak, Nippert & Ocheltree 2014). Results from the infrequent→annual fire treatment further reinforce the idea that the year 2000 roughly demarcates a divergence in ecosystem dynamics for this grassland. After instating annual fires in the infrequent→annual fire treatment, grass cover increased in most plots. However, 30% of the infrequent→annual fire plots have still not reached grass cover similar to the long-term annually burned treatment (Fig. 2a, d), potentially indicating that these plots were close to a critical threshold (Wissel 1984). Moreover, recent mapping of an entire infrequent→annual fire watershed found that several large shrub patches have persisted through 2015 (S.L. Collins, J.M. Blair, J.M. Briggs & Z. Ratajczak, et al. in prep, Z. Ratajczak, P. D'Odorico, S.L. Collins, B. Bestelmeyer, F.I. Isbell & J.B. Nippert, in revision). This hysteresis reinforces the argument that a bistable model is appropriate for this system (Fig. 5, Appendix S2) (Walker & Salt 2006; Bestelmeyer et al. 2011).

The transient dynamics of the fire experiments largely reflect the responses of two dominant species. On average, the grass species *A. gerardii* comprised 60% of grass cover and accounted for most of the resistance to shrub expansion (Fig. S1). While the other dominant grass species were effectively extirpated from the infrequent fire treatment by the year 1985, *A. gerardii* cover remained high in this treatment until 2007 (Fig. S1). Similarly, the species *C. drummondii* accounted for 74% of shrub cover and the acceleration in shrub expansion around year 2000 (Fig. S2, Ratajczak et al. 2011). *Cornus drummondii* possesses a combination of traits that facilitate woody plant expansion in grass-dominated communities (Bond 2008; Hoffmann et al. 2012): high canopy density, growth of meristems above the height of ground fires, the ability to spread clonally, and a deep root system that reduces competition with grasses and sensitivity to summer drought (Heisler et al. 2004; Briggs et al. 2005; Ratajczak et al. 2011; Nippert et al. 2013). The next most dominant shrub species (*R. glabra*, *P. americana*) possess some, but not all of these traits (see Ratajczak et al. 2011). Critically, all of these woody species are capable of resprouting, which

Fig. 5. Simulation results (1000 iterations) showing the relationship between the fire parameter and average grass cover after 400 time-steps. Grass and shrub cover had a different randomly chosen value at the beginning of each iteration (i.e. in an iteration where initial values of grass and shrub cover are chosen to be 40% and 60%, respectively, the initial values of grass cover were 40% in all plots and the initial value of shrub cover was 60% in all plots).

shrub expansion (Figs 1–4). The CV of grass cover consistently decreased when areas were exposed to annual fires, whereas grass CV increased when areas were exposed to infrequent fires (Fig. 3). Shrub cover CV tended to decrease with infrequent fire (Fig. 3), indicating increasingly homogenous shrub cover across patches. However, we caution that the variance of shrub cover has increased over time and the initially high values of shrub CV were partially due to low mean shrub cover (Fig. 3).

Increases in grass cover CV after crossing a fire threshold agree with model-based predictions (Guttal & Jayaprakash 2009), including our own simulations (Fig. 6). A key question is whether the experimental increases in spatial variance resulted from deterministic interactions between biological feedbacks and underlying heterogeneity in the system (soils, topography, etc.) or stemmed from other, unrelated factors. Climatic variation probably explains some year-to-year fluctuations in spatial variance, but is an unlikely explanation for differences between treatments, because all treatments were exposed to the same weather. Statistical artefacts are also unlikely, as variance often scales with the mean, but grass cover CV and variance were lower in the annually burned treatment, despite a higher average grass cover in annually burned plots (Figs 1 and 3).

We propose that grass variance increased primarily because a weakening of the grass-fire feedback amplified underlying differences among patches, such that patches with properties favouring grasses either remained devoid of shrubs or transitioned slowly to shrub dominance. For instance, from 1992 to 1999, grass cover decreased primarily in plots with initially lower grass cover (Fig. 4a). Non-woody species and litter build-up were probably responsible for initial decreases in grass cover (Knapp & Seastedt 1986; Gibson & Hulbert 1987; Collins & Glenn 1991; Bowles & Jones 2013). However, grass cover only fell to

Fig. 4. Grass cover averaged over 1992–1994 vs. grass cover averaged over 1997–1999 (a), illustrating that grass cover was more likely to decrease in plots with initially low grass cover. The relationship between grass and shrub cover in the infrequent fire treatment at the end of the experiment (b). Grass cover at the beginning of the infrequent→annual year fire reversal, vs. cover at the end of the experiment (c). In (a) and (c), the dotted line is the 1:1 line. [Colour figure can be viewed at wileyonlinelibrary.com]

allows them to persist if they are top-killed by fire and build carbon stores over time (Bond 2008).

While the average system state and species composition changed gradually after crossing a fire frequency threshold, some patches exhibited markedly higher susceptibility to

Fig. 6. Simulations results where the fire frequency parameter, *f*, drop below the fire frequency threshold (black lines), fire frequency decreases but does not drop below the fire frequency threshold (dark grey lines), and increases and remains above the fire frequency threshold (light grey lines). (a) Change in the fire frequency parameter over time; (b) grass cover; (c) shrub cover; (d) coefficient of variation (CV), for grass cover; (e) CV for shrub cover; and (f) correlation between grass and shrub cover. In rows (b) through (f), thick lines are the average of all simulation runs and thin lines are the 5th and 95th percentiles of all runs. Each fire frequency was run for 100 iterations.

Fig. 7. Simulation results where the fire parameter, *f*, is brought below the fire frequency threshold to a value of 0·2 for 105 time steps. This timing of when to return *f* to frequent fires (*f* = 0·8), is shortly after grass CV peaked (marked by a vertical dashed line in both panels). Panel (a) is the change in *f* over time and (b) is average grass cover over time, with the thick line representing the average of 100 simulations, and thin black lines representing the 5th/95th percentiles.

reflecting the stochastic nature of seed dispersal and survival in this grassland ecosystem (Briggs & Gibson 1993; Myster 2009).

RAMIFICATIONS

The susceptibility to state transitions tends to vary between patches when spatial heterogeneity is high and spatial connectivity is weak (Van Nes & Scheffer 2005; Villa Martin *et al.* 2015). While multiple mechanisms are known to promote connectivity between patches in tallgrass prairie—including clonal growth, mycorrhizal networks, fire dynamics and herbivore movement (Benson & Hartnett 2006; Wilson, Hartnett & Rice 2006; Fuhlendorf *et al.* 2009; Abades, Gaxiola & Marquet 2014)—these processes clearly were not strong enough to result in spatially synchronized shifts of this grassland to a shrub-dominated state (Figs 1 and 3). Grass-fire feedbacks, like those at the centre of our study, play an important role in many state transitions from grass to woody plant dominance and native herbaceous plants to fire-prone invasive species (Van Langevelde *et al.* 2003; Folke *et al.* 2004; D'Odorico, Laio & Ridolfi 2006; Bond 2008; Hoffmann *et al.* 2012). Therefore, spatial variance might also increase during state transitions in other fire-prone ecosystems, with limited spatial connectivity.

c. 0% in plots with high shrub cover (Fig. 4b), suggesting that shrubs eventually became the primary cause of grass cover declines. Patches that persisted in a grass dominated state or transitioned more slowly to shrub dominance probably had greater nitrogen availability (a key limiting resource for grasses; Blair 1997), lower water holding capacity (a key limiting resource for shrub seedlings; Bond 2008), or have not received viable shrub propagules,

This study presents caveats for forecasting in ecosystems with multiple stable states. Based on model simulations, several authors have proposed that increasing spatial variance is an indication that a driver variable is approaching a threshold (Guttal & Jayaprakash 2009; Scheffer *et al.* 2012; Kefi, Guttal *et al.* 2014; but see Burthe *et al.* 2015). Our results suggest that spatial variance might also increase when an ecosystem is already beyond a driver threshold and undergoing a slow state transition (Figs 3 and 6). Fortunately, lasting changes in ecosystem structure might be avoided if management is altered partway through a slow state transition (Hughes *et al.* 2013). The switch to annual fires in the infrequent→annual treatment occurred shortly after grass cover CV started to increase (Fig. 3) and this intervention largely limited further shrub expansion (Fig. 2; Collins *et al. in prep*). The simulation model shows a similar capacity for recovery, with most patches returning to grass dominance if frequent fires are reinstated shortly after grass cover CV peaks (Fig. 7).

Conclusions

The long-term experiments and simulations in this study find that when a mesic grassland was pushed past a disturbance frequency threshold, spatial variance of dominant grasses increased as patches of the ecosystem transitioned to a fire-resistant shrub state. Our results provide a rare empirical assessment of how non-equilibrium dynamics vary over time and space in a system with strong ecological feedback mechanisms. This study also provides one of the first examples where altering management after a change in spatial variance helped avoid long-lasting state transitions. This type of recovery potential has been hypothesized to exist in slower dynamical systems (Hughes *et al.* 2013), but has not been explicitly demonstrated in field experiments. Being able to identify slow state transitions could help prioritize efforts to avoid or prepare for an understudied class of largely irreversible changes in ecosystems.

Authors' contributions

All authors contributed to study design and revisions. Z.R. performed the simulations and data-analyses, and wrote the first draft of the manuscript.

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Data accessibility

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Information about long-term data set and its analysis.

Appendix S2. Description of spatial interactions and noise in the simulation model.