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Abrupt transition of mesic grassland to shrubland: evidence for thresholds, alternative attractors, and regime shifts

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Abstract. Ecosystems with alternative attractors are susceptible to abrupt regime shifts that are often difficult to predict and reverse. In this study, we quantify multiple system dynamics to determine whether the transition of mesic grassland to shrubland, a widespread phenomenon, represents a linear reversible process, a nonlinear but reversible threshold process, or a transition between alternative attractors that is nonlinear and prone to hysteresis. Using a 28-yr data set with annual resolution and extensive spatial replication, we found that shrub cover is correlated with distinct thresholds of fire and C_4 grass cover, resulting in temporal bimodality of shrub cover and abrupt shifts of shrub cover despite gradual changes in grass cover. These abrupt increases in shrub cover are the most rapid ever reported in grasslands, and illustrate internal thresholds that separate grasslands and shrublands. Nonlinear transitions from low to high shrub cover were also closely associated with positive feedback mechanisms that alter fire and competition ($r^2 = 0.65$), suggesting that grasslands and shrublands could show hysteresis, and by definition exist as alternative attractors. Thus, the response of this ecosystem to anthropogenic activity should tend to be rapid, nonlinear, and perhaps difficult to reverse. Regime shifts in this mesic grassland were predictable: we found that grassland and shrubland attractors were differentiated by critical thresholds of ~50–70% grass cover, 5–10% shrub cover, and a fire return interval of ~3 yr. These thresholds may provide adaptive potential for managing nonlinear behavior in socio-ecological systems in a changing environment.

Key words: alternative stable states; bi-stability; bush encroachment; catastrophic shifts; critical transitions; dynamical systems; fold bifurcation; grassland–woodland transitions; shrub encroachment; tallgrass prairie; tipping points; woody encroachment.

Introduction

A growing body of evidence suggests that many ecosystems have internal thresholds, or in more extreme cases, self-reinforcing alternative attractors. Regime shifts to an alternative attractor are typically rapid, difficult to foresee, and costly to reverse (Holling 1973, Noy-Meir 1975, May 1977, Walker et al. 1981, Folke et al. 2004). In this study, we test if the transition of mesic grassland to shrubland represents a regime shift between alternative attractors. An assessment of transitions in grasslands is needed, because woody plant expansion in grasslands is widespread, with pronounced impacts on biodiversity and ecosystem services (Anderies et al. 2002, Knapp et al. 2008, Barger et al. 2011, Eldridge et al. 2011, Ratajczak et al. 2012). This conversion of mesic grasslands to shrublands has implications for conservation and economic activity, considering the endangered status of many native grasslands (Hoekstra et al. 2005) and the important societal role of seminatural grasslands (Ellis et al. 2008).

Identifying and managing regime shifts requires knowledge of linearity and hysteresis in ecosystem dynamics. Linearity describes whether the relationship between an ecosystem's driver and state variables is defined by a single line, such that gradual changes in driver variables result in proportional changes in state (a linear system). Alternately, ecosystem dynamics may be defined by a threshold response, where the relationship between state and driver does not conform to a linear correlation, such that gradual changes in drivers can result in abrupt increases or decreases in state (a threshold system). Hysteresis captures whether a threshold response is easily reversible (hysteresis absent) or requires greater forcing to return to the original state than was required to initiate the original state transition (hysteresis present; Scheffer and Carpenter 2003, Bestelmeyer et al. 2011). For this study, "linear systems" are those where state and driver have a linear correlation, "threshold systems" are those that exhibit a threshold response between state and driver variables, but no hysteresis, and "alternative attractor systems" are those that exhibit both threshold responses and hysteresis (sensu Bestelmeyer et al. 2011).

The occurrence of internal thresholds and alternative attractors is usually the result of feedback mechanisms

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that facilitate the rapid transition between states and reinforce an ecosystem state once established (Walker and Salt 2006). Mechanistic studies suggest that grasslands and shrublands may represent alternative attractors because both grass and shrub dominance are associated with self-reinforcing feedback mechanisms. In mesic grasslands, grass dominance increases the potential for frequent and intense fires and pronounced resource competition, particularly in upper soil layers (Jackson et al. 1996, Van Wilgen et al. 2003, Baldocchi et al. 2004, Teuling et al. 2010, Nippert et al. 2012, Scheiter et al. 2012). These characteristics of grass dominance negatively impact woody plants (Scholes and Archer 1997, Roques et al. 2001, Bond 2008, Hoffmann et al. 2012), potentially explaining how grasslands persist in areas like the Central Plains, USA where the climate would otherwise allow the development of woodlands (Axelrod 1985).

Shrubs in mesic grasslands can also initiate self-reinforcing feedback mechanisms (Walker et al. 1981, Ratajczak et al. 2011, D'Odorico et al. 2012). While initial woody plant establishment in these grasslands is strongly limited by fire mortality and water limitation (Scholes and Archer 1997, Briggs et al. 2005, Bond 2008, Ratajczak et al. 2011, Scheiter et al. 2012), established shrubs can suppress and/or circumvent these limiting factors (Ratajczak et al. 2011). Adult shrubs avoid summer drought and competition with grasses because they have access to deep soil water (Walker et al. 1981, Jackson et al. 1996, Ratajczak et al. 2011, Nippert et al. 2013; Brunsell et al., *in press*). In our study system, adult shrubs transfer this deep water to their expanding rhizomatous clonal stems, which allows them to circumvent the demographic bottleneck imposed by competition with grasses, build deep root systems, and promote further clonal expansion (Ratajczak et al. 2011). Shrubs also create a microsite that deters fire transmission, lowers fire intensity, and buffers aboveground stems against fire mortality (Ratajczak et al. 2011, D'Odorico et al. 2012). Together, these shrub characteristics facilitate radial shrub expansion through a positive feedback process (Ratajczak et al. 2011, sensu D'Odorico et al. 2012).

Despite growing evidence for positive feedback mechanisms that reinforce system states in mesic grassland, the existence of thresholds and alternative attractors has not been reported. Identifying thresholds and alternative attractors in ecosystems is difficult (Scheffer and Carpenter 2003), but possible with theoretically derived analytical approaches and extensive spatial and/or temporal data sets (Fig. 1 and Holling [1973], Noy-Meir [1975], Walker [1981], May [1977], Folke et al. [2004], Scheffer et al. [2004], Schroder et al. [2005], Bestelmeyer et al. [2011], Ratajczak et al. [2011], D'Odorico et al. [2012], and Nippert et al. [2013]). Theoretical derivations and heuristic models predict that systems with thresholds and alternative attractors should undergo abrupt shifts in state over time when driver variables change gradually. Threshold and alternative attractor systems also have nonlinear relationships between state and driver variables, resulting in spatiotemporal bimodality in system states (Holling 1973, Noy-Meir 1975, May 1977, Walker et al. 1981, Scheffer and Carpenter 2003, Folke et al. 2004, Bestelmeyer et al. 2011, D'Odorico et al. 2012, Scheffer et al. 2013). We can identify hysteresis by halting and/or reversing directional change of driver variables and observing whether the system easily returns to the previous state (Bestelmeyer et al. 2011). In the absence of driver reversal experiments, quantifying the presence of positive feedbacks suggests the capacity for hysteresis (D'Odorico et al. 2012).

While all of these singular forms of evidence and their associated data types are important, they all have certain limitations (Scheffer and Carpenter 2003, Schroder et al. 2005, Ratajczak and Nippert 2012, Hanan et al. 2013, but see Scheffer et al. 2013). Thus, the most robust evidence for alternative attractors is when multiple analytical techniques converge on the same predicted internal dynamics, and when state and driver variables are carefully chosen based on mechanistic studies (Carpenter et al. 2001, Scheffer and Carpenter 2003, Schroder et al. 2005).

To date, we are aware of very few studies of alternative attractors in terrestrial systems that use the systematic approach recommended by theoreticians (e.g., Bestelmeyer et al. 2011, Isbell et al. 2013) and no studies on mesic grassland to woodland transitions. The unresolved and largely untested question of whether mesic grassland and shrublands represent alternative attractors leaves major gaps in theoretical and applied knowledge. To test whether the transition from mesic grassland to shrubland represents linear, threshold, or alternative attractor processes, we used multiple approaches and a unique 28-yr data set with annual resolution and a factorial design of fire and grazing manipulations. This experimental, multifaceted, long-term approach provides a more complete understanding of ecosystem dynamics and improves our predictive capacity for successful management of socio-ecological systems (Anderies et al. 2002, Folke et al. 2004, Hastings and Wysham 2010).

METHODS

Site and experimental design.—Konza Prairie Biological Station (KPBS) is a National Science Foundation long-term ecological research (LTER) site in northeastern Kansas, USA (39°05′ N, 96°33′ W). KPBS is primarily a native unplowed tallgrass prairie, situated in the Flint Hills ecoregion of the central Great Plains. Tallgrass prairie is characterized by high floristic diversity (Collins and Calabrese 2012), but four species of C_4 grass comprise >90% of aboveground net primary productivity (*Andropogon gerardii*, *Schizachyrium scoparium*, *Panicum virgatum*, and *Sorghastrum nutans*). Historical accounts describe the region as open

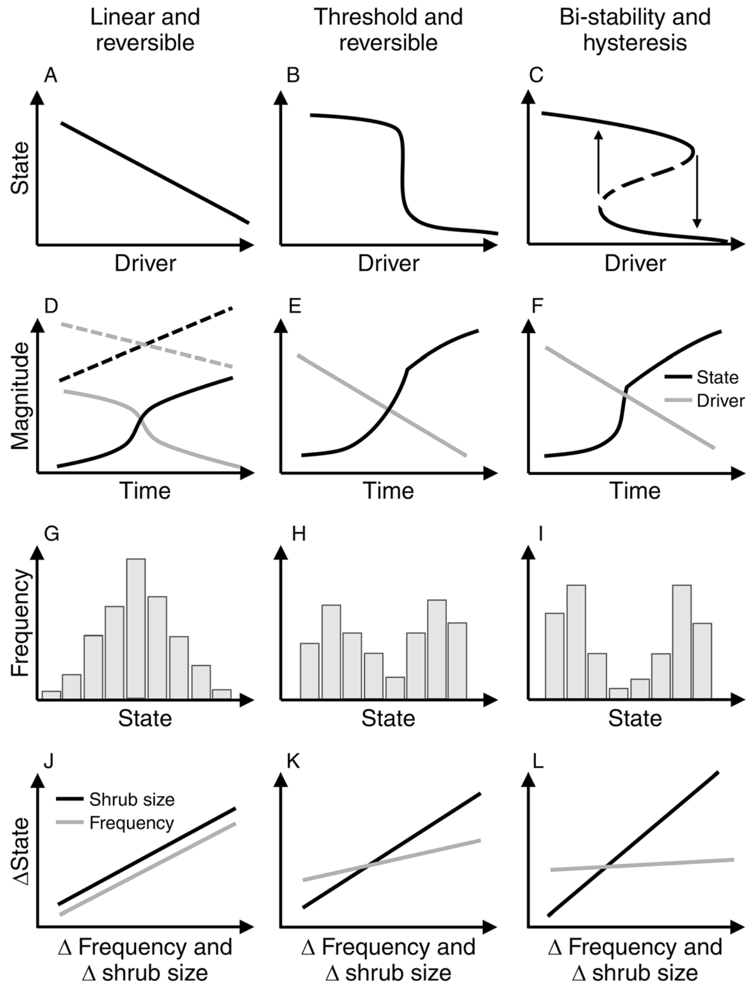


FIG. 1. Depiction of different types of (A–C) internal dynamics in ecosystems with varying linearity and hysteresis and (D–I) the expected behavior. Panels (J–L) depict hypotheses specific to our study system, linking positive feedback mechanisms to threshold transitions. The first row shows the relationship between state and driver variables in (A) linear, (B) threshold, and (C) alternative attractor systems (systems manifesting bi-stability and hysteresis). For panels (A–C), black lines depict stable equilibria, dashed lines are unstable "repellors," and arrows depict a regime shift between alternative attractors. Here, we use shrub cover as the proposed state variable (i.e., a slow changing variable) and we explore potential driver variables. Panels (D–F) show the expected temporal behavior of an ecosystem's state (black line) in the three different system types, under different scenarios of changes in driver variables over time (gray lines). Note that in panel (D), dotted lines show how a system with linear internal dynamics should respond to an abrupt shift in the driver variable. Panels (G–I) show the expected frequency (no. shrubs/plot) diagrams for the different system types. Panels (J–L) depict our hypothesis that shrub expansion in our study system should be correlated with increases in shrub size because this type of expansion is related to positive feedback mechanisms (Δ stands for "change in"). Panels (A–I) are based on Holling (1973), Noy-Meir (1975), May (1977), Walker (1981), Folke et al. (2004), Scheffer et al. (2004), Schroder et al. (2005), and Bestelmeyer et al. (2011), while panels (J–L) are based on concepts developed in Ratajczak et al. (2011), D'Odorico et al. (2012), and Nippert et al. (2013)

grassland except along riparian areas, but native woody plant cover has increased over the last half-century, typically attributed to fire suppression, overgrazing, and exurban expansion (Briggs et al. 2005). The pre-European fire frequency is estimated to be ~4 yr between fires. Prior to the mid 1970s, KPBS was burned every ~2–3 yr and grazed moderately by cattle (Briggs et al. 2005). The mean annual precipitation is 835 mm/yr and the growing season temperature (May–September) is 32.5°C, with the mean monthly maximum in July (36.1°C). From 1977 to 1983, the 3487 ha area of the KPBS was split into catchment basins with different prescribed fire frequencies (1-, 3- to 4-, or 20-yr intervals between fires; Appendix B). Grazing by bison (*Bos bison*; a large native ungulate grazer) occurs within the central approximately one-third of the site, representing a light to moderate level of grazing (approximately half the grazing intensity of commercial cattle operations [Collins and Calabrese 2012]). Thus, we had data from a factorial study with grazed and ungrazed treatments, with three fire return intervals per grazing treatment: 1-yr, 3- to 4-yr, and 20-yr fire

TABLE 1. Statistical fits of varying temporal models analyzed.

Treatments	Single line (r^2/AIC)	Logistic (r^2/AIC)	Split line (r^2/AIC)			Slope		Change in intercept (percent cover)
			Individual slopes	Individual intercepts	Individual slopes and intercepts	1983–1999	2000–2012	
4-yr grazed	0.86/274	0.95/219	0.88/265	0.94/231	0.96/213	0.26	1.38	4.4
4-yr ungrazed	0.90/208	0.98/160	0.96/180	0.95/192	0.99/135	0.79	2.60	19.1
20-yr grazed	0.87/301	0.93/270	0.9/289	0.92/280	0.95/260	0.57	2.00	9.2
20-yr ungrazed	0.79/218	0.98/150	0.81/217	0.97/162	0.97/159	0.24	3.74	5.0

Notes: Treatments are a combination of grazing (or not), and intervals between fires (4 or 20 yr). AIC is Akaike's information criterion.

frequencies, henceforth referred to as 1-yr, 4-yr, and 20-yr treatments.

Across these treatments, we assessed the cover of different plant functional groups using a long-term data set (Konza LTER data set PVC02, watersheds N1B, N4D, N20B, 1D, 4B, and 20B). In 1983, permanent plots were established in each combination of grazing, fire frequency, and three different topographic positions (uplands, slopes, and lowlands). The initial goal of this data set was to quantify herbaceous plant dynamics. Therefore, plots were located in areas that typify herbaceous communities (away from drainage ditches, rock outcrops, and any existing woody vegetation). Plots were evenly spaced along 50-m transects, with five 10-m^2 circular plots per transect, and four transects per treatment (treatment described a combination of fire, grazing, and topography). Exceptions to this design include the ungrazed treatments and the 1-yr fire grazed treatment, where continuous data sets for slope transects are absent. Since data collection began, the cover of each species has been measured annually in each plot, recording species cover using a Daubenmire scale, with cover classes of 0–1%, 4–5%, 5–25%, 25–50%, 50–75%, 75–95%, or 95–100% aerial coverage. We used the midpoint of these ranges to calculate cover, reporting changes in cover (percentage of area), frequency (no. shrubs/plot), and size index (cover of shrubs in the plots in which they occur; total cover × frequency). See Ratajczak et al. (2011) and Collins and Calabrese (2012) for more information on this data set and these metrics.

We used only slope and lowland transects, because upland plots have little woody encroachment (Ratajczak et al. 2011). Half of the plots for grazed 4-yr and 20-yr treatments were started in 1993 (Table 1). The inclusion of data from these plots collected in the same catchment basin did not affect the results and thus, the analyses here include data from all plots. In addition to the data discussed thus far, there is a second data set in different catchment basins than those reported in the main text for 1993. These plots were started in largely herbaceous-dominated plots and therefore, are similar to the core data set as of 1983. As such, this data set is not yet of sufficient length for robust analyses. However, preliminary data are summarized in *Results* and Appendix A.

For all woody plant dominance metrics, we made the a priori decision to only include tree and shrub species that grow taller than the grass canopy (average height >1 m). Compared to sub-shrubs (e.g., *Amorpha canescens*, *Rosa arkansas*, etc.), these woody species have more woody tissue, reach a greater height, and have a dense canopy, making them more likely to escape fire mortality and initiate positive feedback mechanisms by altering fire dynamics (Ratajczak et al. 2011). For grass cover, we used the cover of the dominant C_4 grasses (*A. gerardii*, *S. scoparium*, *P. vigratum*, and *S. nutans*). We also included two other functional groups to determine whether observer biases might account for rapid changes in cover in specific years or if the cover class categories used account for jumps across certain ranges of cover. Specifically, we looked at whether target and nontarget functional groups (1) were prone to nonlinear behavior at the same time as shrub and grass cover, and (2) tended to show nonlinear behavior and/or show bimodality over similar cover ranges as shrub cover. We used members of the genus *Solidago* (goldenrod; a group of forb species) and the second most common group of grasses (*Bouteleau* and *Sprobolis* spp., hereafter "subdominant grasses") because these two functional groups have dynamic behavior, include a similar number of species as the dominant C_4 grass and shrub functional types, and encompass similar cover ranges.

Temporal tests.—To compare models describing changes in shrub cover over time, we used Akaike's information criterion (AIC), a maximum likelihood approach. AIC balances obtaining a better fit of the data against over-fitting the model, such that lower AIC values are considered to be most representative of internal dynamics (see Bestelmeyer et al. 2011, Scheffer et al. 2013 on using AIC in ecology). We compared AIC values of models where time × shrub cover was linear, a standard three parameter logistic model, and split linear models. For split linear models, splits were induced following the greatest increase in woody cover, and we tested models where each line segment had independent slopes, independent intercepts, or independent slopes and intercepts. If the linear model has the lowest AIC, it generally indicates that the system has linear internal dynamics (Bestelmeyer et al. 2011). If the logistic model had the lowest AIC, it is evidence for logistic growth associated with rapid alteration of a driver variable, followed by logistic growth (sensu May 1977). Logistic growth can occur in systems with both linear and nonlinear internal dynamics (threshold and alternative attractors) and is often associated with rapid changes in driver variables. If the split linear model with different slopes for each line segment has the lowest AIC, this is evidence for a threshold or alternative attractor system (Hughes et al. 2012). If the lowest AIC is for the split linear model with independent intercepts or the split linear model with independent slopes and intercepts, then it usually indicates that the system has alternative attractors, because the change in intercept signifies a jump from one stable root of the equation to another when the system crosses a fold bifurcation (Fig. 1; Scheffer and Carpenter 2003). This scenario can also potentially indicate the existence of a threshold system under some conditions (Bestelmeyer et al. 2011).

State–driver relationships.—We considered the following variables as potential drivers of shrub cover: grass cover and mean seasonal temperature and total precipitation (winter [Dec–Feb], spring [Mar–May], summer [Jun–Aug], and fall [Sep–Nov]). Climate data are from the Manhattan, Kansas National Oceanic and Atmospheric Administration weather station, located ~6.5 km from KPBS. These predictor variables were chosen based on the role of climate and grass dominance for woody plant performance in many grass-dominated systems (Walker et al. 1981, Scholes and Archer 1997, Roques et al. 2001, Anderies et al. 2002, Briggs et al. 2005, Bond 2008, Staver et al. 2011, Collins and Calabrese 2012, Scheiter et al. 2012, Scheffer et al. 2013). We assessed linear relationships between shrub cover and potential driver variables using a general linear model and used a standard three parameter logistic model to quantify the existence of a nonlinear relationship between shrub cover and potential driver variables. If both linear and logistic models were significant for a given driver variable ($P < 0.05$), we compared models using AIC values. If a system has linear internal dynamics, we expected linear models to have the lowest AIC values, whereas threshold and alternative attractor systems usually have a nonlinear fit (i.e., logistic) between driver and response.

State modality.—A bimodal distribution of system state provides support for the existence of thresholds and alternative attractors (Fig. 1; Bestelmeyer et al. 2011, Scheffer et al. 2013). In systems with alternative attractors, higher frequencies are indicative of system stability (an attractor) and low frequencies are indicative of instability (a repellor; Scheffer et al. 2013). We compared AIC values of shrub cover distribution models that were unimodal (linear system), followed the Johnson SI distribution (linear system), and bimodal (threshold or alternative attractor system). The unimodal fit is a standard normal distribution. The Johnson SI fit is a flexible normal distribution that allows both skewness and kurtosis to vary, as might be expected in a growing population or zero-inflated data set. The bimodal model fits two normal distributions with fixed skewness and kurtosis, allowing the proportion of observations that fall into each distribution to vary. We considered each value of shrub cover per treatment, per year as a replicate (Bestelmeyer et al. 2011). For shrub cover distribution analyses we used 5% cover classes (0 to <5%, etc.) for 4-yr grazed and 20-yr grazed treatments, and 10% cover classes for 4-yr ungrazed and 20-yr ungrazed treatments. Bin sizes reflect the common approach where the number of classes is equal to $n^{1/2}$ (smaller/larger cover classes yielded equivalent results). For the other functional groups considered, we used 5% cover classes in the analyses to assess the possibility that the Daubenmire scale was responsible for jumps in cover class.

Positive feedbacks.—We assessed if changes in shrub cover were related to expansion of shrubs into new patches or expansion by existing shrubs. Expansion into new patches occurs when seedlings become established in a new area, and is captured by the shrub frequency metric (no. of shrubs/number of plots). At our study site, changes in frequency are not considered evidence of positive feedbacks (sensu Archer 1995), because the woody plant seed rain has been increased by habitat fragmentation and exurban expansion (Briggs et al. 2005). In contrast, shrub expansion within patches is related to a positive feedback process whereby existing shrubs spread locally via clonal rhizomatous stems (Ratajczak et al. 2011). The shrub size index indicates if shrubs are expanding within patches (percent shrub cover/number of shrubs). We compared whether changes in shrub cover were associated with changes in frequency and/or size using delta values where $\Delta(\text{cover}) = \text{cover}_{t+1} - \text{cover}_t$. Here, t refers to the time such that cover_t is shrub cover in a given year and cover_{t+1} denotes shrub cover in the next year. We used the same general equation for Δfrequency and the Δsize index, and compared the r^2 values of general linear models with Δ(cover) as the response variable, and Δ(frequency) and Δ(size index) as predictor variables (r^2 values were used because both models have an equal number of parameters).

Statistical analyses.—Statistical analyses were performed using JMP (SAS Institute). Shrub cover of 1-yr ungrazed was excluded from temporal state × driver, modality, and positive feedback analyses because shrub cover in this treatment was 0% in all years.

RESULTS

Temporal dynamics.—Over the course of the long-term experiment, annual fire returns maintained low rates of shrub cover expansion, with only minor increases in grazed treatments (to a ~7% cover) and zero shrub cover expansion in ungrazed 1-yr fire treatments. In all treatments with a fire frequency >1 yr, shrub cover increased slowly for the first 17 yr, with

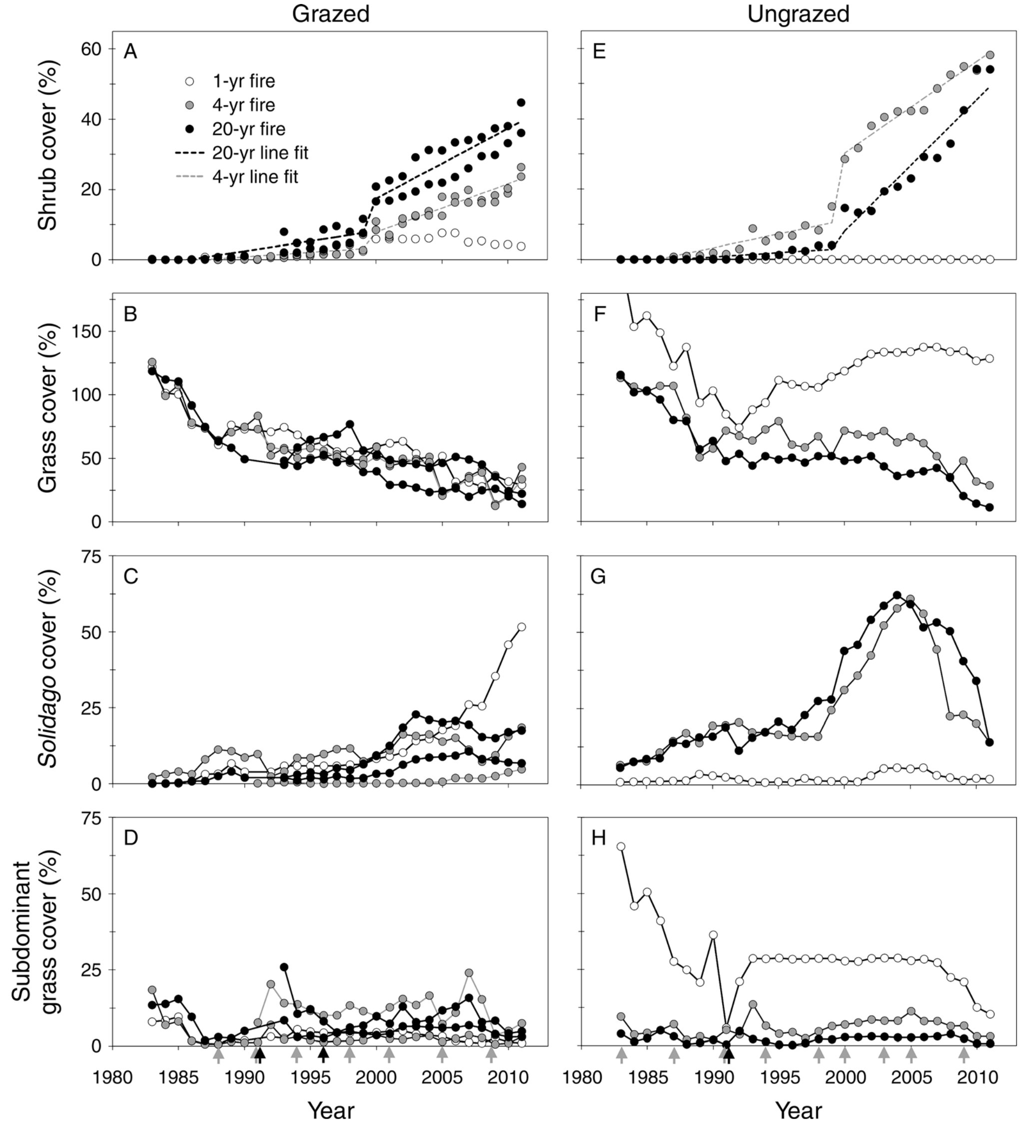


FIG. 2. Temporal patterns of (A, E) shrub cover, (B, F) dominant C_4 grass cover, (C, G) *Solidago* spp. cover, and (D, H) subdominant grass cover, for grazed (left column) and ungrazed treatments (right column). The 20-yr-between-fires (20-yr fire) treatments appear as black circles, 4-yr-between-fires (4-yr fire) treatments as gray circles, and 1-yr-between-fires (1-yr fire) treatments as open circles. In panels (A) and (E), dashed lines show split linear fits for treatments with fire frequency >1-yr-fire (black for 20-yr fire and gray for 4-yr fire). Arrows below panels (D) and (H) demark the timing of prescribed fires in 4-yr (gray arrows) and 20-yr fire treatments (black arrows). Note that there are two replicates for the 4- and 20-yr grazed treatments because data from slope transects was available for almost the entirety of the experiment.

an average slope of ~0.5% cover increase per year. In these treatments, the dynamics of shrub cover changed between 1998 and 2001, with a large increase in shrub cover of ~5–10 % over just 1–3 yr, followed by more than a decade of rapid shrub expansion (the new rate of shrub expansion ranges from 1.4 to 2.7 % cover/yr, depending on treatment). This change took place from 1999 to 2001 in 4-yr grazed, 1998 to 2000 in 4-yr ungrazed, and 1999 to 2000 in 20-yr grazed and ungrazed. For shrub cover over time in these treatments, the model with the lowest AIC values and the greatest predictive capability was a split linear model with independent slopes and intercepts for each line segment. The one exception was the 20-yr ungrazed treatment, where the logistic model had the lowest AIC values (Table 1).

In contrast to shrub cover, climate showed essentially no statistically significant trends over time, grass cover declined in a linear to log-linear fashion, and fire frequencies were effectively constant for their respective treatments (Figs. 2 and 3, Appendices A and B). The only significant trend in climate was a slightly significant increase in temperature in fall ($P = 0.048$, $r^2 = 0.13$), and the primary exception for fire frequency was in the 4-yr ungrazed treatment, which had an approximately biennial fire frequency from 1998 to 2005. *Solidago* spp. and subdominant grasses had complex dynamics. *Solidago* spp. had peak-like dynamics emerging in 1996–1999 for ungrazed treatments, and after 2004 in grazed treatments. Depending on the treatment and time of year, subdominant grasses showed a mix of temporal dynamics, but none that were similar to trends in shrub cover, in terms of exhibiting nonlinear behavior from 1998 to 2001 or following logistic or split linear dynamics. Thus, dominant C_4 grasses, *Solidago* spp., and subdominant C_4 grasses differ from shrubs in that they (1) do not generally conform to split linear dynamics, (2) do not show any nonlinear temporal behavior (peaks or otherwise) that corresponds with changes in shrub cover, and (3) do not show consistent dynamic behavior across all treatments.

State–driver relationships.—Among the driver variables considered for shrub cover, grass cover was the only consistently significant predictor of shrub cover for both linear and logistic models ($P < 0.05$ and $r^2 = \sim 0.60$ for treatments with a fire frequency >1 year between fires). Summer temperature had a slightly significant relationship with shrub cover in some treatments, but was not significant after controlling for the effects of grass cover. The logistic fit between grass and shrub cover had a lower AIC value than the linear model, and increased shrub cover coincided with declines in grass cover to 40–70% (Fig. 4).

State modality.—Shrub cover was unimodal when all treatments were combined in one analysis (data not shown). However, shrub cover was bimodal within treatments (i.e., the bimodal distribution had the lowest AIC), again with the exception of the 20-yr ungrazed treatment where a Johnson SI fit had the lowest AIC (Fig. 5). *Solidago* spp. and subdominant grasses had diverse distributions depending on the treatment (Appendix B). The cover ranges that were rare for shrub cover (5–15%), were not rare for the other functional groups assessed (Appendix B), indicating that it is unlikely that shrub cover bimodality is an artifact of sampling methodology.

Positive feedback analyses.—ΔFrequency and Δsize index were unrelated ($r^2 = 0.03$), suggesting these two metrics represent different aspects of system behavior. Abrupt increases in shrub cover were correlated with size index ($r^2 = 0.63$), whereas the relationship between changes in frequency and changes in shrub cover was very weak ($r^2 = 0.05$, Fig. 6).

Supplementary data sets.—In the supplementary data set, portions of the grazed 4-yr and 20-yr treatments underwent a nonlinear transition to higher shrub cover in 2011, associated with similar shrub cover thresholds as those in the core data set. Supplemental 1-yr grazed treatments followed similar trends as this treatment in the core data set. Shrub cover in the 4-yr ungrazed treatment has not exhibited nonlinear behavior, but cover is still below the threshold where nonlinear behavior would be predicted to emerge.

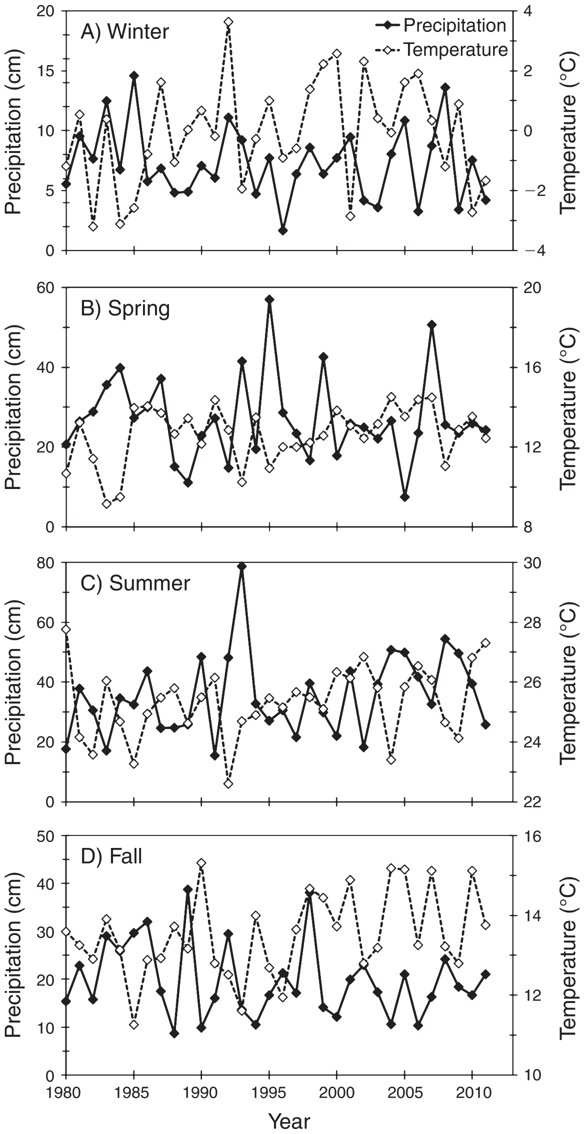


FIG. 3. Trends in precipitation (solid diamonds and line) and temperature (open diamonds and dashed line) over the study period for (A) winter, (B) spring, (C) summer, and (D) fall.

DISCUSSION

This study provides the first empirical evidence that the transition between mesic grasslands and shrublands is nonlinear, representing either a threshold transition or regime shift between alternative attractors (Fig. 1). Terrestrial ecosystems have long been theorized to have thresholds (Holling 1973, Noy-Meir 1975, Walker et al. 1981), but these phenomena have rarely been documented within an empirical framework. Identifying and understanding nonlinear transitions in this ecosystem were enabled by long-term high-resolution data, which is

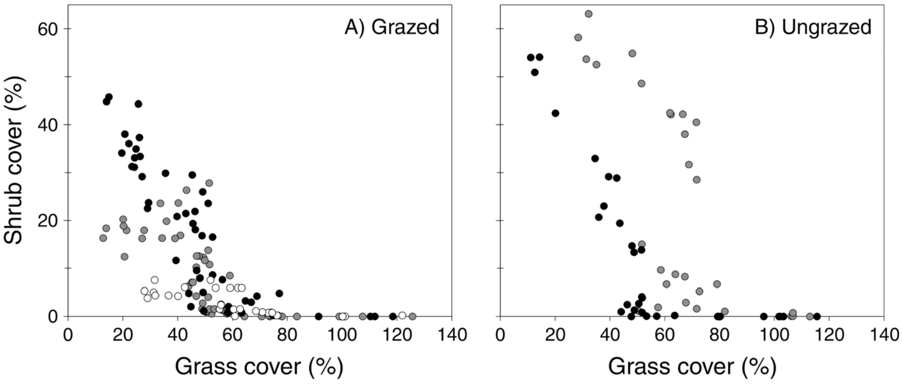


FIG. 4. Relationship between grass cover and shrub cover in (A) grazed and (B) ungrazed treatments. Fire treatment symbols are as in Fig. 2. In grazed treatments, the 4-yr-fire treatment has linear AIC/r^2 of 344/0.45; logistic AIC/r^2 of 325/0.63. The 20-yr-fire treatment has linear AIC/r^2 of 348/0.64; logistic AIC/r^2 of 319/0.82. In the ungrazed treatments, the 4-yr-fire treatment has linear AIC/r^2 of 257/0.49; logistic AIC/r^2 of 257/0.53. The 20-yr-fire treatment has linear AIC/r^2 of 239/0.56; logistic AIC/r^2 of 200/0.90.

a basic prerequisite for testing ecosystem transitions, but is currently unavailable for many terrestrial ecosystems.

Nonlinear changes in system state are often the first observed evidence for thresholds and alternative attractors. Shrub cover in the 4-yr and 20-yr fire treatments showed discontinuous shifts of ~10% shrub cover from 1998 to 2001 (Fig. 2), which were followed by a fivefold increase in shrub expansion rates, from ~0.5% to ~2.5% cover per year (Table 1). Rates of woody plant expansion in other grasslands are typically 0.5% cover per year and rarely exceed 1.5% cover per year (Barger et al. 2011, Ratajczak and Nippert 2012), suggesting that

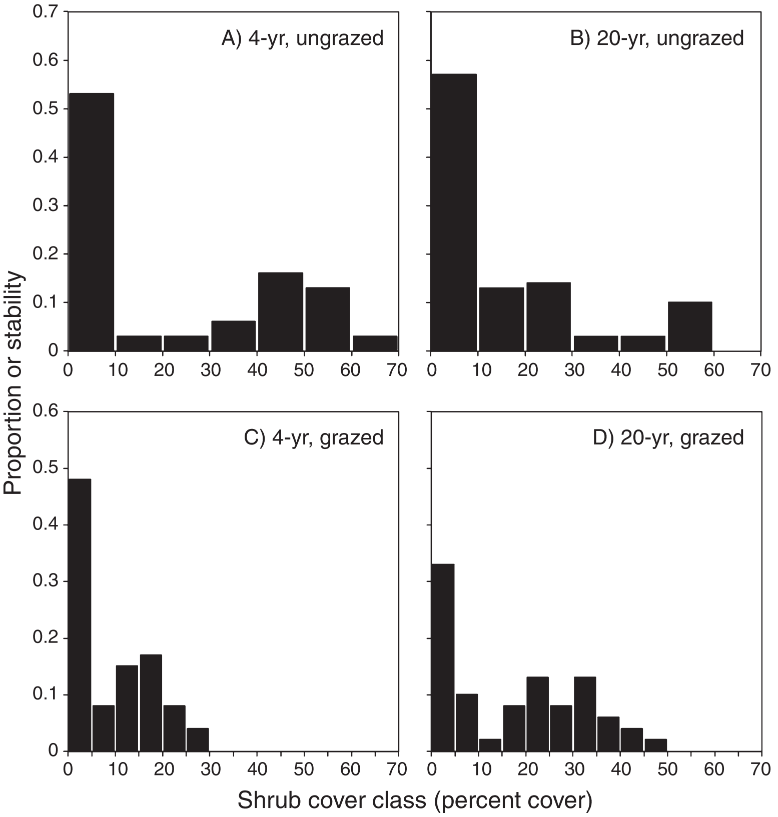


FIG. 5. Histograms of shrub cover in ungrazed (A) 4-yr and (B) 20-yr treatments, and in grazed (C) 4-yr and (D) 20-yr treatments. AIC values for the three distributions are (A) unimodal 373, bimodal 330, Johnson SI 339; (B) unimodal 392, bimodal 378, Johnson SI 392; (C) unimodal 274, bimodal 248, Johnson SI 250; and (D) unimodal 257, bimodal 225, Johnson SI −1025.

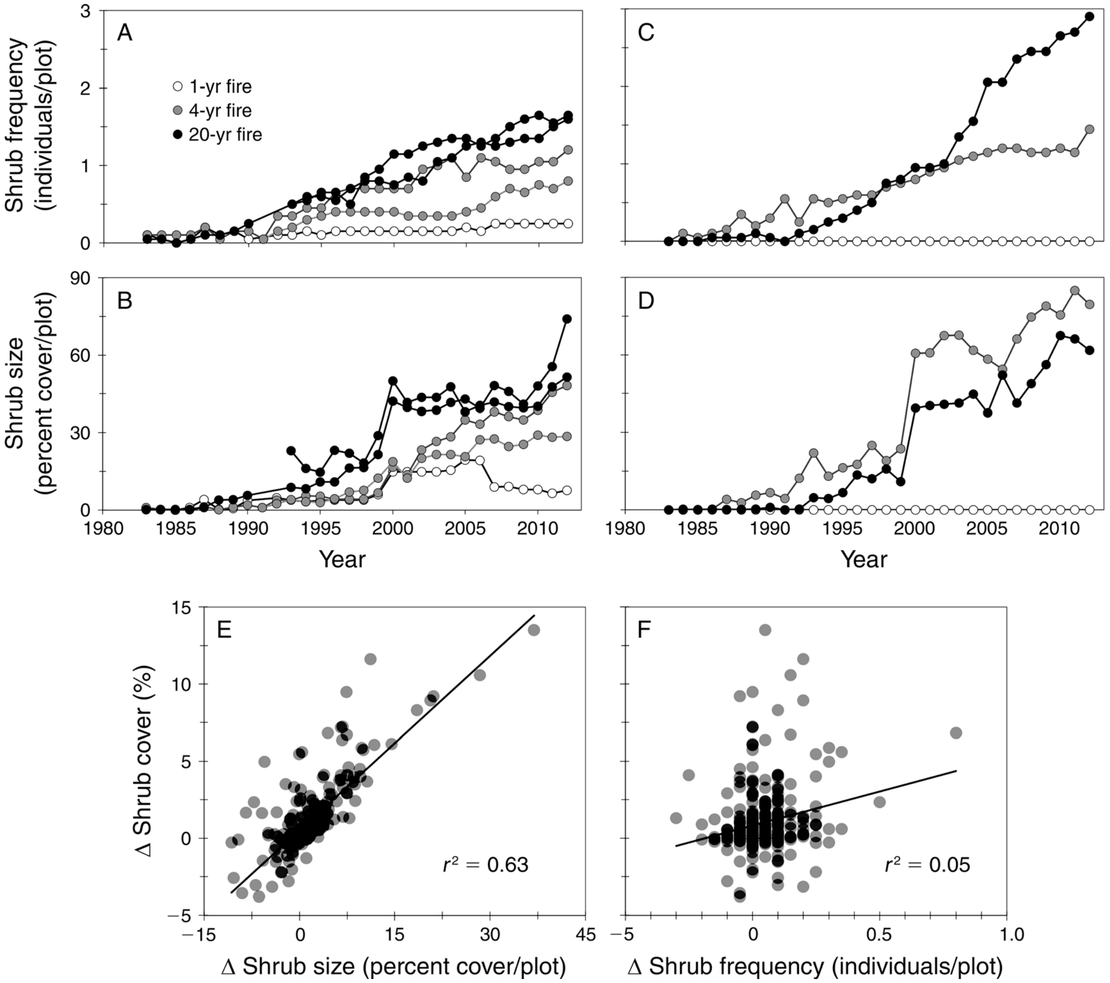


FIG. 6. The trends in (A and C) shrub frequency and (B and D) shrub size index in (A and B) grazed and (C and D) ungrazed treatments. Also shown is (E) the relationship between year-to-year changes in shrub size index and shrub cover, and (F) the relationship between year-to-year changes in shrub frequency and shrub cover. For panels (E) and (F), all treatments are shown together because relationships were similar across treatments.

the jump in shrub cover we observed is abrupt compared to other studies, and that the expansion rates that follow are anomalously high.

Statistical analyses of shrub cover over time support our interpretation of temporal shrub dynamics as abrupt and nonlinear, rather than linear tracking or logistic growth. Among the three types of temporal models we considered (linear, logistic, and split linear), we observed the lowest AIC values for split linear models that allowed each line segment to have a unique slope and intercept (Table 1). The split linear model captures the discontinuous jump in cover and the greater growth rates after 1998–2001. When a statistically significant change in intercept occurs over time, these transitions have been labeled as evidence of abrupt transitions, especially when a transition occurs within the single life span of the organisms involved, as in this study (Bestelmeyer et al. 2011, Hughes et al. 2012). Similarly, the faster rates of expansion after 1998–2001 are consistent with the definition of regime shift, where a system becomes defined by new feedbacks and dynamics once a threshold is crossed. The one exception to the abrupt shift in shrub cover was the 20-yr fire ungrazed treatment, where logistic growth had the lowest AIC values (Fig. 4). We suspect that the 20-yr ungrazed treatment is on a trajectory towards a closed woodland, as has been observed elsewhere in areas with complete fire suppression and a lack of grazers (Hoch et al. 2002, Briggs et al. 2005) and in accord with theoretical expectations (Scheffer et al. 2013).

Systems with linear internal dynamics are also capable of nonlinear transitions over time when abrupt changes in driver variables occur (Bestelmeyer et al. 2011). In our study, climate changed little over time, and shrub cover was uncorrelated with climate, even though precipitation and temperature have been linked to woody plant performance in other grass-dominated systems (Bond 2008, Knapp et al. 2008, Barger et al. 2011, Staver et al.

2011, Ratajczak et al. 2012, Scheffer et al. 2013). However, it may be that longer-term climate trends are more important for shrub performance, or that the magnitude of climatic variation necessary to elicit a response has yet to occur. In contrast to climate variables, grass cover showed a consistent, significant, and gradual decline over time, and there was a strong logistic fit between grass cover and shrub cover in the 4- and 20-yr fire treatments. These results suggest that shrub cover is defined by a threshold relationship with C_4 grass cover (Fig. 4), where shrub cover increases once grass cover remains below 50–70%, depending on the treatment.

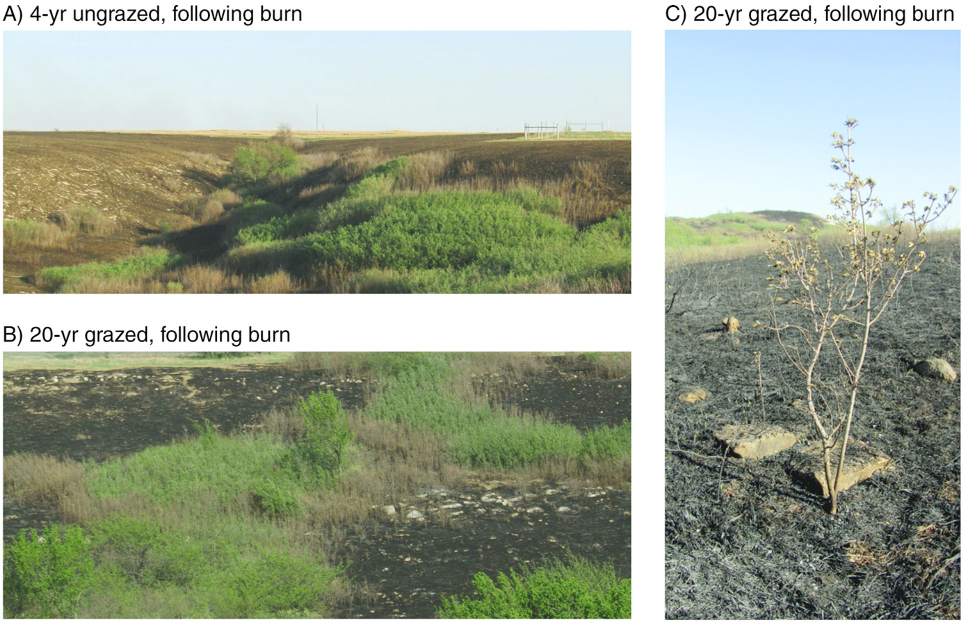
A negative relationship between C_4 grasses and shrubs is accordant with a large number of mechanistic and biogeographic studies that have addressed the interactions of C_4 grasses and woody species (reviewed in Scholes and Archer 1997, Bond 2008). These studies have generally found that C_4 grasses negatively impact woody plants in mesic environments by increasing flammability and facilitating depletion of shallow soil-water (Walker et al. 1981, Scholes and Archer 1997, Anderies et al. 2002, Van Wilgen et al. 2003, Bond 2008, Teuling et al. 2010, Higgins and Scheiter 2012, Hoffmann et al. 2012, Nippert et al. 2012, Scheiter et al. 2012). These effects of C_4 grasses disproportionately impact smaller woody plants, excluding woody plants completely from many mesic ecosystems (Bond 2008, Higgins and Scheiter 2012). A sigmoidal relationship between grass and shrub cover is also consistent with theoretical modeling of grassland–shrubland alternative attractors, with grasses and shrubs as fast and slow changing variables, respectively (Walker et al. 1981, Carpenter 2001). Thus, nonlinear increases in shrub cover may reflect an interaction between a grass cover threshold and a long-term trend of decreasing C_4 grass cover. The local and/or global factors reducing grass cover are yet unknown, but may be related to elevated CO_2 or the interaction of current management and land-use legacies (Collins and Calabrese 2012, Higgins and Scheiter 2012).

The existence of threshold behavior is further supported by our analyses of shrub cover modality. When data are analyzed across all treatments, shrub cover was unimodal, but within treatments shrub cover was bimodal with a low frequency zone separating high-frequency nodes of high and low shrub cover (Fig. 5). This result, based on temporal changes, mirrors analyses reported using spatial data sets (Staver et al. 2011, Scheffer et al. 2013, but see Hanan et al. 2013). When an ecosystem shows bimodality of state and a nonlinear response to gradual changes in driver variables (i.e., grass cover), these responses are generally interpreted as evidence for thresholds or alternative attractors (Scheffer et al. 2013). In this framework, we would categorize 6–15% shrub cover as an unstable state (or repellor), situated between alternative attractors of 0–5% and >10–15% shrub cover (i.e., basins of attraction; Scheffer et al. 2013). The "infrequent" shrub cover ranges varied slightly between treatments, and the ranges of cover that were rare for shrubs were not rare for the other functional groups, further suggesting that nonlinearities in shrub cover are not artifacts of methodology (Daubenmire cover classes or changes in investigator; Appendix A).

Interactions among fire and grazing treatments at Konza have influenced the relationship of shrub and grass cover thresholds. In the grazed 1-yr fire treatment, grass cover has declined well below 55%, but shrub cover has stayed below 7%. These results demonstrate the role of both fire frequency and intensity; increased fire frequency can compensate for lower fire intensities in grazed areas because shorter fire-free intervals do not leave enough time for woody plants to achieve sufficient biomass to resist even weak fires (see Hoffman et al. 2012). The slightly lower rates of encroachment in the 4- and 20-yr grazed treatments are more puzzling, because grazers typically favor woody species expansion by selectively grazing C_4 grass species (Walker et al. 1981, Scholes and Archer 1997, Roques et al. 2001, Anderies et al. 2002). We suspect grazing has created favorable microsites for seedling establishment, while simultaneously decreasing the average soil moisture across the landscape by creating bare patches of soil (Walker et al. 1981). Grazers on site have also been observed to cause physical damage to some woody saplings (*personal observation*). In these ways, large grazers may enable minor shrub establishment in 1-yr fire treatments, but suppress maximum growth rates in 4- and 20-yr fire treatments. The complex effects of grazers highlight the utility of having multiple metrics to delineate thresholds and the need for a more holistic understanding of how grazers affect shrub expansion.

Finally, we assessed if threshold transitions were associated with positive feedback mechanisms by determining if increases in shrub cover were correlated with changes in shrub frequency or shrub size. An association between positive feedbacks and thresholds is considered evidence for alternative attractors in ecological systems (D'Odorico et al. 2012). Shrub expansion in tallgrass prairie occurs by two mechanisms: (1) shrubs can become established as new seedlings, which increases shrub frequency, or (2) established shrubs can expand radially via rhizomatous clonal stems, which increases the size index. In this study, increases in shrub cover were directly correlated with increases in size index, not frequency, corroborating previous research linking changes in size index with positive feedback processes as a mechanism for woody encroachment at this site (Figs. 6 and 7; Ratajczak et al. 2011, D'Odorico et al. 2012).

The positive feedback between fire and shrub cover occurs because as shrubs get larger, fine fuel is reduced and fires seldom penetrate into shrub clusters (Fig. 7). This response is attributed to the exponential decline in grass biomass that occurs once shrubs begin to expand,


A) 4-yr ungrazed, following burn

B) 20-yr grazed, following burn

C) 20-yr grazed, following burn

FIG. 7. Photos at Konza Prairie Biological Station (KPBS) in 2012 following prescribed burns in (A) a 4-yr fire ungrazed treatment and in (B) and (C) a 20-yr fire grazed treatment. Note that in panels (A) and (B), green vegetation is primarily the shrub species *Cornus drummondii* and mortality is confined to the shrub island perimeter, despite fuel accumulation over a decade in the case of panel (B). In contrast to these large shrub clusters, in panel (C) small shrubs and single-stemmed shrubs are exposed to more intense fire and experience higher rates of mortality.

similar to the decline in grass cover that occurred around 2005 in this study (Fig. 2; Lett and Knapp 2005, Knapp et al. 2008, Ratajczak et al. 2011). Shrub expansion also has reinforcing legacy effects; in the rare instances where established shrubs are top-killed by fire, they can resprout vigorously (Heisler et al. 2004). If shrubs are completely killed by fire or by physical removal from the landscape, grasses have been shown to recover to ~30% of their previous cover two years after removal (Lett and Knapp 2005). Finally, while C_4 grasses are highly responsive to ambient climate fluctuations in tallgrass prairie, established shrublands illustrate reduced physiological sensitivity to changes in climate, including seasonal drought (Nippert et al. 2013; Brunsell et al., *in press*). Similar decoupling between driver and response variables has been seen in systems with hysteresis, including open oceans, coral reefs, lakes, Antarctic consumers, species invasions, and other grazing systems (May 1977, Walker et al. 1981, Carpenter et al. 2001, Scheffer and Carpenter 2003, Folke et al. 2004, Bestelmeyer et al. 2011, Isbell et al. 2013, but see Bestelmeyer et al. 2013). Thus, our results and supporting studies identify the strong possibility of hysteresis in shrub cover with respect to fire and grass cover, a response supported by the observation that short periods of more frequent fires (2 yr between fires) did not reverse shrub expansion in the 4-yr ungrazed treatment. However, the potential for hysteresis will require further examination with either natural or experimental reversals of key driver variables.

Synthesis.—Our results provide multiple lines of evidence that mesic grasslands and shrublands are bounded by thresholds of grass cover, shrub cover, and fire frequency. Over time, altered fire frequency and declining grass cover resulted in a rapid regime shift to higher shrub cover, associated with positive feedback mechanisms. These types of system behavior have long been theorized to be important in grasslands and shrublands, but have not been observed empirically in these systems (Walker et al. 1981, Ratajczak and Nippert 2012). The thresholds identified in this study, as well as their context specificities, may serve as valuable metrics for regional managers to diagnose the potential for regime shifts to shrublands (Hastings and Wysham 2010). However, to extend upon our correlative analyses, we recommend additional driver reversal experiments to quantify hysteresis, and grass and water manipulation experiments to test thresholds and determine how shrub cover responds to future climate scenarios and no-analog management scenarios (e.g., Bestelmeyer et al. 2013, Isbell et al. 2013).

It remains to be tested if the results of this study are generalizable to other mesic grasslands or to grasslands in general. Transitions from grassland to shrubland are an ongoing global phenomena and many instances exist where woody plant expansion occurs without abrupt changes in known driver variables (Walker et al. 1981, Roques et al. 2001, Ratajczak and Nippert 2012). Thus, based on the data reported here and in the context of woody grassland encroachment from other systems, mesic grassland exhibits thresholds of state change with the strong possibility of alternative attractors. If further evidence supports the likelihood of grasslands and shrublands as alternative attractors, these results suggest that the management of temperate grasslands, one of the largest socio-ecological systems (Ellis et al. 2008), must consider that this system is capable of abrupt and sometimes difficult to reverse transitions.

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SUPPLEMENTAL MATERIAL

Appendix A

History of data sets and analyses of temporally limited data sets (*Ecological Archives* E095-229-A1).

Appendix B

Temporal dynamics and modality of nontarget functional groups and climate (*Ecological Archives* E095-229-A2).