ECOLOGICAL THRESHOLDS AND ABRUPT TRANSITIONS OF TALLGRASS PRAIRIE
TO SHRUBLANDS AND WOODLANDS

by

ZAK RATAJCZAK

B.A.,,Vassar College, 2010

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
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Abstract

Ecological thresholds are breakpoints where small increases in external pressure can generate rapid and difficult to reverse ecological transitions. Often, ecological thresholds are not recognized until they are crossed at a large-scale, leading to unintended and lasting externalities. In tallgrass prairie, we identified ecological thresholds of 3-year fire returns and ~60% grass cover, based on mechanistic field studies and long-term fire and grazing experiments. When tallgrass prairie is pushed passed these thresholds, it makes an abrupt transition to a self-reinforcing shrubland state. Demographic bottlenecks, niche partitioning, and altered fire feedback mechanisms account for both the non-linear nature of grassland-shrubland transitions and the resistance of established shrublands to fire and drought. In the last decade, only ~27% of Central Great Plains tallgrass prairie was burned every 1-2 years, and therefore ~73% of this region is susceptible to shrubland and woodland transitions in the next two to three decades. If transitions to shrublands and woodlands do occur, we expect a multi-trophic loss of grassland biodiversity, decreased cattle production, and the potential for damaging woodland fires in close proximity to human development. However, knowledge of fire thresholds, adaptive management tools, and bottom-up citizen action campaigns are creating a rare window of opportunity to avoid transformation of the remaining tallgrass prairies.

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Ecological thresholds are breakpoints where small increases in external pressure can generate rapid and difficult to reverse ecological transitions. Often, ecological thresholds are not recognized until they are crossed at a large-scale, leading to unintended and lasting externalities. In tallgrass prairie, we identified ecological thresholds of 3-year fire returns and ~60% grass cover, based on mechanistic field studies and long-term fire and grazing experiments. When tallgrass prairie is pushed passed these thresholds, it makes an abrupt transition to a self-reinforcing shrubland state. Demographic bottlenecks, niche partitioning, and altered fire feedback mechanisms account for both the non-linear nature of grassland-shrubland transitions and the resistance of established shrublands to fire and drought. In the last decade, only ~27% of Central Great Plains tallgrass prairie was burned every 1-2 years, and therefore ~73% of this region is susceptible to shrubland and woodland transitions in the next two to three decades. If transitions to shrublands and woodlands do occur, we expect a multi-trophic loss of grassland biodiversity, decreased cattle production, and the potential for damaging woodland fires in close proximity to human development. However, knowledge of fire thresholds, adaptive management tools, and bottom-up citizen action campaigns are creating a rare window of opportunity to avoid transformation of the remaining tallgrass prairies.

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Dedication

I dedicate this dissertation to my grandfather, Jack Buyce, who passed away while I was in South Africa performing fieldwork for this dissertation. Jack Buyce was an ardent conservationist in the southern Adirondacks of Upstate New York, managing much of the Sacandaga Lake. We grew up in the Sacandaga region, and one summer I even had the privledge of working on the river that connects the Sacandaga Lake to the Hudson River and the Atlantic Ocean. The boarding house he helped maintain in Pleasantville NY sold hiking gear to Harvey Fireston, Henry Ford, and Thomas Edison as they experiences life outside the city and is still the gateway for many people looking to experience the forests of the Adirondacks. In Roxburry NY he started his family and restored the home of William Burroughs, an early American Conservationist whos writing I admire and who has influenced my views on conservation ethics. Jack Buyce was also a devoted father of four and many foster children. He supported my pursuit of a degree in Environmental Sciences, philopshopically and at many times directly. I will miss him greatly and rely on his wisdom often.

Chapter 1 - Introduction, Social-Ecological Systems, and Ecological Thresholds

Ecosystems provide goods and services equal or greater in economic value than all human enterprises combined (Costanza et al. 1997), as well as many intangible benefits, such as recreation and exposure to more diverse experiences. Humans can alter the ability of nature to provide goods and services (Hardin 1968, Rockstrom et al. 2009, Chapin et al. 2011), especially when they do not fully understand how human actions translate to ecological change (Carpenter et al. 2001, 2005). However, with comprehensive knowledge of interactions between humans and the environment, outreach, and adaptive management/governance (Folke et al. 2004, Walker 2009) it will be easier to manage ecosystems for biodiversity and ecological goods and services (Biggs et al. 2009, Chapin et al. 2011). This dissertation attempts to provide some of that information for the Central Great Plains of North America, with a focus on ecological "tipping points" and the transformation of grasslands to shrublands and woodlands, a phenomenon known as woody encroachment. To this end, this dissertation has eight sections: the importance of social-ecological interactions and the concept of ecological thresholds (Chapter 1), the effects of woody encroachment on plant diversity and primary productivity in North America (Chapter 2), evidence for and against mechanistic feedbacks and demographic barriers that would create ecological thresholds in tallgrass prairie (Chapter 3), how spatial and temporal data are used to detect ecological thresholds (Chapter 4), identification of threshold relationships between shrubs, grasses, fire, and grazing at Konza Prairie (Chapter 5), the generality of thresholds in a regional context (Chapter 6), tools to predict when thresholds are changing over time (Chapter 7), and a conclusion consisting of future scenarios for the Central Great Plains and recommendations for

how humans could change their management of the region to achieve more sustainable outcomes (Chapter 8).

Social ecological systems and tipping points:

The human footprint has expanded so much that there are few, if any ecosystems that are not affected by human activities (Ellis et al. 2008, Rockstrom et al. 2009). This idea is captured by the concept of "social-ecological systems", a view that most places on earth are composed of interacting abiotic, biological, and human components (Walker et al. 2004, Folke et al. 2004). Through direct and indirect interactions, humans alter biological components (Collins et al. 2011), with resulting changes in how biological components affect humans. Thus, a critical step towards achieving sustainable outcomes requires understanding the mechanics of social-ecological networks (Levin et al. 2013).

Transitions from grasslands to shrubland or woodland are an example where humans can be the drivers of major ecological change and in turn, where ecological change has a major effect on humans. In the last century, grasslands around the world have transitioned to shrublands and woodlands, which is often attributed to human activities (Scholes and Archer 1997, Van Auken 2000, Roques et al. 2001, Briggs et al. 2005, Higgins and Schieter 2012). This transition typically results in a major structural change from dominance by grass species to dominance by native trees and shrubs, with concomitant changes in ecosystem goods and services (Knapp et al. 2008, Eldridge et al. 2011, Eldridge et al. 2011, Gray and Bond 2012, Limb et al. 2012). I used this case study to address applied issues in the Central Great Plains and to test theoretical predictions of how ecological systems respond to human pressures.

I first investigated the impacts of woody encroachment. Past studies have found that many effects of woody encroachment are context specific (e.g. carbon storage, freshwater

availability, Huxman et al. 2005, Eldridge et al. 2011, Limb et al. 2012). However, one common finding is that woody encroachment reduces grazer productivity and increases visual obstruction (Riginos and Grace 2008, Limb et al. 2012, Gray and Bond 2012). These changes hurt economies that rely on cattle production and ecotourism—two of the most important economic enterprises in many grasslands and savannas (Ellis et al. 2008).

The effects of woody encroachment on biodiversity are not as well-known. High levels of biodiversity are critical to maintaining multiple ecosystem services and resilience to unknown pressures that may emerge in the future (Maestre et al. 2011, Tilman et al. 2012, but see Adler et al. 2011). On one hand, woody encroachment might bolster biodiversity because it increases the amount of physical structure and in semi-arid regions, can increase the concentration of soil resources allowing more species to survive (Eldridge et al. 2011). However, woody encroachment can lead to very low levels of light availability at the ground level (Knapp et al. 2008) and disrupts many disturbance processes vital to maintaining high levels of diversity (*sensu* Collins and Calabrese 2012). To determine the net effects of woody encroachment on biodiversity, I performed a meta-analysis of the scientific literature, government reports, and dissertations/theses. I used climate and productivity as covariates that would aid in extrapolation to unstudied sites and explain why the relative change in biodiversity might be different between different grassland and savanna communities.

The rest of this dissertation focuses on how grasslands respond to different human-controlled pressures. Linearity and hysteresis are two key aspects of how ecosystem drivers and ecosystem state are related to each other (Scheffer and Carpenter 2004, Bestelmeyer et al. 2011). Linearity refers to whether responses to pressures are gradual, or whether ecosystems have punctuated responses to gradual forcing. Hysteresis capture whether or not changes in state are

easily reversed or require more effort to return the system to its previous state than was needed to precipitate the transition. Combining linearity and hysteresis and following May (1977), Scheffer and Carpenter (2004), and Bestelmeyer and colleagues (2011), we consider four different categories of how ecosystems can respond to human pressures (Fig 1): 1) no response (null hypothesis); 2) a gradual and reversible response (a linear system); 3) a non-linear, but reversible response (a threshold system); or 4) a non-linear response with hysteresis (regime shift, alternative attractor, alternative stable state, or "tipping point system). It is critical to discern these internal dynamics for rapidly changing driver variables; otherwise, the existence of unknown thresholds and alternative attractors can result in ecological surprises that are difficult and time-consuming to reverse (Hughes et al. 2012).

The idea that ecosystems can have thresholds and hysteresis is not new by any means. Holling (1973), Noy Meir (1975), May (1977), and Walker (1981) formally posited these ideas for ecological systems over 40 years ago, and intuitively, there are examples of tipping points and thresholds in many ecological and everyday interactions (Fig 2; Scheffer 2009, Dodds, et al. 2010, Perkins and Gido 2010, Vespignani 2012, Isbell et al. 2013, but see Schroder et al. 2005, Bestelmeyer et al. 2013). Identifying thresholds and hysteresis has been hampered by healthy skepticism, misuse of these ideas, and a lack of appropriate experiments and data (Schroder et al. 2005, Hanan et al. 2013). Thus, despite a strong theoretical basis for these phenomena, there is very little sense of just how common ecological thresholds actually are. In particular, thresholds have not been tested in terrestrial systems, perhaps because these systems response more slowly than others and are difficult to manipulate (Folke et al. 2005).

Tallgrass prairie, the focus of this dissertation, is resilient to many different pressures including species invasions (Seabloom et al. 2013), non-random extinctions (Smith and Knapp

2003), long periods of above average precipitation (Collins et al. 2012b), regional nitrogen deposition (McLauchlan et al. *in press*, but see Isbell et al. 2012), drought (Weaver 1956) and grazing (Vanderweide 2012). Tallgrass prairie of Kansas also show impressive temporal heterogeneity (Knapp and Smith 2001), which some theoretical models predict will limit the potential for thresholds (Van Nes et al. 2005, Scheffer et al. 2012, D'Odorico and Bhattachan 2013). These studies suggest that within the range of state and driver parameter space observed thus far, tallgrass prairie has linear or null relationships with these pressures, (i.e. there could be a threshold, but it has not been crossed yet).

Mechanistic studies indicate that tallgrass prairie could be capable of threshold behavior because some tallgrass prairie species are capable of instituting self-reinforcing feedbacks and/or face demographic bottlenecks . Feedback mechanisms are sets of interactions that moderate internal and external inputs, either dampening their influence (negative feedbacks) or amplifying them (positive feedbacks). Feedbacks create the potential for thresholds by making the system more sensitive to past events: once a state becomes established, it can alter the system to reinforce its own dominance and resilience. Demographic bottlenecks are population dynamics with rate limiting steps. A common example of demographic bottlenecks is when adults of a species are capable of living in an ecosystem, but suffer high mortality rates as juveniles that prevent a reproductively viable population from becoming established (De Roos et al. 2002). Similar to the presenence of feedback mechanisms, demographic bottlenecks can create alternative stable states under the same external condition (De Roos et al. 2002, Higgins and Schieter 2012).

In tallgrass prairie and other temperate grasslands, the dominant grasses institute feedbacks that facilitate high-intensity fires and draw-down resources in the upper soil layers—

conditions where large C_4 grasses are superior competitors (Ehlringer et al. 1997, Schieter and Higgins 2012). These impacts, among others, create a demographic bottleneck for other species, so much so that recruitment by seed makes up less than 1% of ramets each year (Benson and Hartnett 2006) and potentially explaining why tallgrass is resistant to invasive species (Seabloom et al. 2013). Moreover, redundancy among dominant grasses (Collins et al. 2012b), suggests the dominant C_4 grass community might be resilient to multiple types of ecological pressures (*sensu* Ehrlich and Walker 1998).

Woody plants are one functional group that might be able to disrupt the grass dominance cycle. In ecosystems with similar climates to tallgrass prairie, woody plants often have deep roots, allowing them to circumvent competition with grass species and overcome demographic bottlenecks (Jackson et al 1996, Scholes and Archer 1997, Bond 2008). Woody stems also allow shrubs and trees to develop a canopy above grasses, which may allow woody plants to reduce grass productivity, and thereby, the fine herbaceous biomass that fuels fire (Grime 1978, Dohn et al. 2012).

Given the uncertainty, but potential for thresholds in tallgrass prairie, this dissertation examines if there is evidence for ecological thresholds separating reinforcing states of grass dominance and shrub dominance. I focused on management of fire and grazers because these are two aspects of management that humans actively control in the Central Great Plains at a large scale. I approached this question from multiple angles, including a mechanistic assessment of feedback interactions and demographic bottlenecks, re-analyzing published data-sets to refine methods for detecting thresholds, and using long-term experiments that manipulate fire and grazing to test whether or not transitions from grassland to shrubland follow the expected patterns for systems with thresholds and alternative stable states (Chapter 3 through 6). The

methodological, conceptual, and theoretical basis for each angle of analysis is laid out within each chapter. Together, the goal of these chapters is to test questions in ecological theory and provide information on how humans in the Central Great Plains alter their environment. The conclusion puts these results in context, using satellite estimates of fire frequency to predict that status of Central Great Plains grasslands 30 years from now if humans continue their current fire management practices. My primary objective is to identify whether ecosystems are capable of rapid, widespread, and surprising changes in structure, and under what conditions such behavior should emerge.

The final research chapter of this dissertation (Chatper 7) follows a recent evolution in the field of dynamical systems theory and ecological thresholds: the pursuit to identify thresholds *before* they are crossed, rather than after. For these chapters, I test if theoretical derived dynamical behaviors occur when a system approaches a threshold, and quantify the contributions of demographic and feedback processes to abrupt shifts and hysteresis. These analyses also reveal changes in scales of interaction as regime shifts occur.

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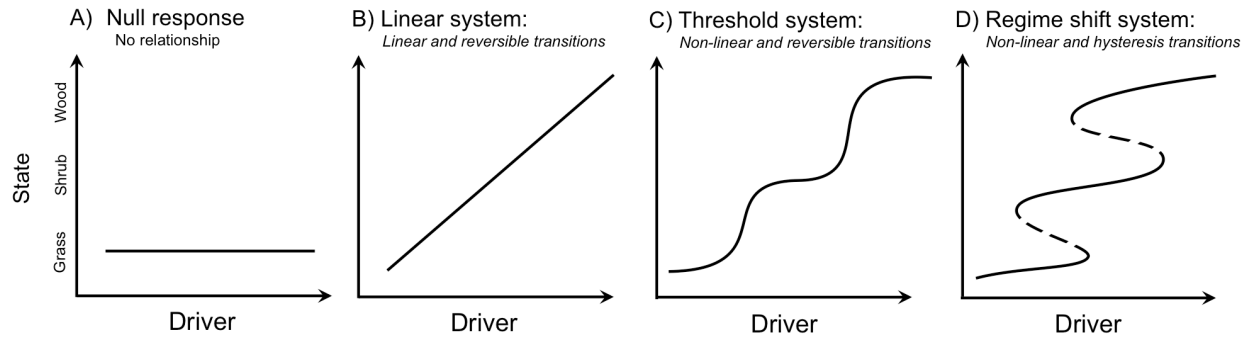
Figure 1.1 A comparison of null (A), linear (B), threshold (C), and regime shift systems (D). Solid lines depict stable states and dotted lines are unstable thresholds.
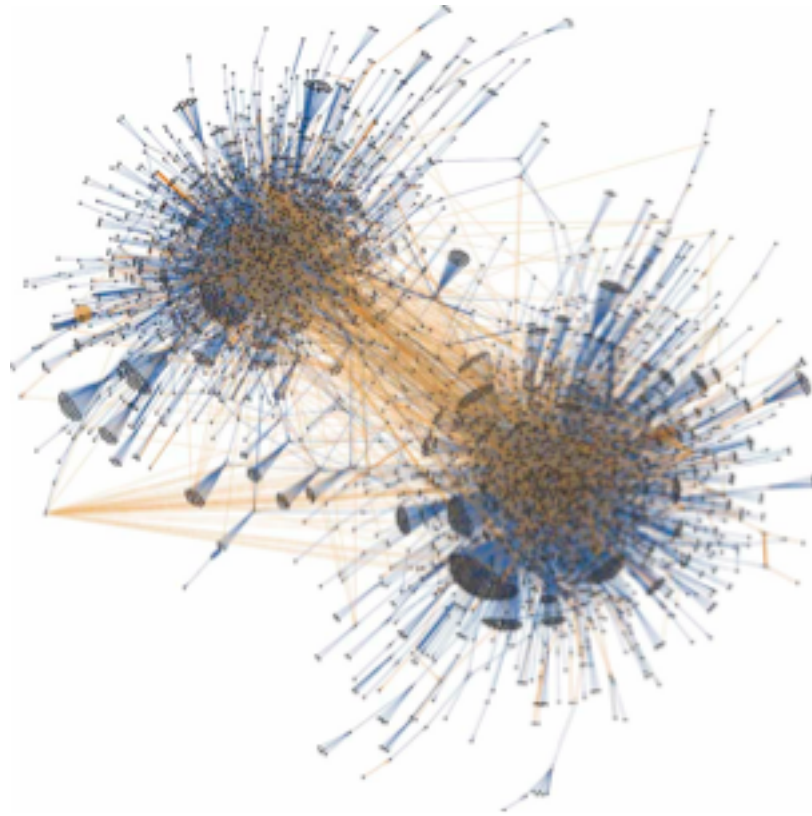
Figure 1.2 An ordered network generated by Vespignani (2012) using original tweets, retweeting, and positive/negative associations with the hashtag #GOP on "Twitter.com". This particular socio-technological network shows strong bi-modality, reflecting general partisanship of the public in the United States of America.

Chapter 2 - Woody encroachment decreases diversity across North American grasslands and savannas

Abstract:

Woody encroachment is a widespread and acute phenomenon affecting grasslands and savannas worldwide. We performed a meta-analysis of 26 studies from 13 different grassland/savanna communities in North America to determine the consequences of woody encroachment on plant species richness. In all 13 communities species richness declined with woody plant encroachment (average decline = 45%). Species richness declined more in communities with higher precipitation (r^2= 0.81) and where encroachment was associated with a greater change in annual net primary productivity (ANPP) (r^2= 0.69). Based on the strong positive correlation between precipitation and ANPP following encroachment (r^2= 0.87), we hypothesize that these relationships occur because water-limited woody plants experience a greater physiological and demographic release as precipitation increases. The observed relationship between species richness and ANPP provides support for the theoretical expectation that a trade-off occurs between richness and productivity in herbaceous communities. We conclude that woody plant encroachment leads to significant declines in species richness in North American grassland/savanna communities.

Key Words: Bush Encroachment, Shrub encroachment, Global Change, Primary productivity, Species Richness, Ecosystem structure, Biodiversity, Tree-grass coexistence, Tree encroachment, Productivity-Richness Relationship, Woody Release

Introduction:

Over the last century, the cover and dominance of native trees, shrubs and bushes has increased dramatically in grasslands and savannas globally (Archer 1995, Scholes and Archer 1997, Roques et al. 2001, Briggs et al. 2005)—a phenomenon referred to as woody encroachment. Potential causes of woody encroachment are many, including increasing atmospheric CO_2 (Bond and Midgley 2000, Wigley et al. 2010), climate change (Shaver et al. 2001, D'Odorico et al. 2010), nitrogen deposition (Kochy and Wilson 2001), fire-suppression and over-grazing (Scholes and Archer 1997, Van Auken 2000, Roques et al. 2001, Briggs et al. 2005). Understanding the consequences of woody encroachment is important because grassland and savanna communities are undergoing widespread degradation worldwide (Hoekstra et al. 2005) and woody encroachment is further reducing grassland cover through difficult to reverse state transitions (Schlesinger et al. 1990, Scheffer et al. 2001, Ratajczak et al. 2011). Here, we present a meta-analysis of how woody encroachment affects species richness in grass-dominated ecosystems of North America (grasslands and tree/shrub savannas), exploring the relationships between woody encroachment, plant species richness, climate and productivity.

Woody encroachment alters light, water and nutrient availability (Schlesinger et al. 1990, Archer 1995, Scholes and Archer 1997, Knapp et al. 2008, Brantley and Young 2009)—key resources for many herbaceous grassland/savanna species (Chapin 1980, Knapp and Smith 2001, Clark et al. 2007, Harpole and Tilman 2007). Moreover, woody encroachment has been shown to mitigate the intensity and frequency of disturbances, such as grazing and fire (Riginos and Grace

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2008, Staver et al. 2011, Ratajczak et al. 2011), which are integral to maintaining grassland and savanna diversity (Collins et al. 1998). Woody encroachment also increases aboveground net primary productivity (ANPP) far above existing levels (Knapp et al. 2008), which is often correlated with a decline in plant species diversity in many herbaceous communities (Grime 1973, Tilman and Pacala 1993, Clark et al. 2007, Harpole and Tilman 2007).

Alternatively, woody encroachment could have a neutral or positive impact on species richness in some plant communities. In some semi-arid ecosystems, shrubs create "islands of fertility" where increased nutrient availability below shrubs provides refugia for species sensitive to low nutrient availability (Maestre et al. 2009, Pugnaire et al. 2011). Indeed, shrub establishment in the Mediterranean Basin and Australia has been shown to increase species richness by stabilizing soil and attenuating water-stress (Thompson and Eldridge 2005, Maestre et al. 2009, Pugnaire et al. 2011). In North American grasslands, however, resource island formation is also accompanied by a decrease in resources in inter-shrub spaces, which might outweigh the positive effects of shrub dominance (Schlesinger et al. 1990).

Recently, Eldridge et al. (2011) conducted a comprehensive analysis of the consequences of woody encroachment into a number of grasslands around the world. They concluded that woody encroachment had no net effect on species richness globally. However, a zero net effect on richness could result from strong regional positive and negative patterns. We focused our analysis on woody encroachment in North American because North America has a unique evolutionary, disturbance and human history. Additionally, more data are available for North America across a diverse array of grassland communities because many theses and government reports have been digitized.

For our analysis, we investigated: 1) whether encroachment increased, decreased or had no net effect on species richness and; 2) if the effects of woody encroachment on species richness were moderated by mean annual temperature or precipitation, and/or changes in productivity. Our meta-analysis included data from sites that differ in edaphic conditions (e.g., coastal dunes, interior plains, montane grasslands), dominant forms of graminoid vegetation (C3/C4 graminoids), ecosystem types (grasslands, savannas and grassland/shrubland mixes) and climate (mean annual temperature and precipitation ranges of 33 °C and 800 mm, respectively). Our analysis is unique in that we: 1) had high levels of replication; 2) weighted all communities equally, allowing for more general interpretation; and 3) developed a conceptual framework based on physiological and demographic release of woody plants, which reconciles parallel changes in diversity and ecosystem function with current ecological theory.

Methods:

Literature search and meta-analysis criteria:

For this analysis, we performed searches on Scopus (scopus.com), Web of Knowledge (apps.isiknowledge.com), and Google Scholar (scholar.google.com) using relevant combinations of the words: encroachment, invasion, thicket, thicketization, succession, shrub, woody, tree, bush, cover, diversity, richness, grass, grassland, and savanna. We also followed citations within published articles and sought papers on ecosystems where encroachment has been reported. For grassland/savanna communities with richness data available, we attempted to find data for differences in ANPP between graminoid and woody dominated patches.

All studies had to meet the following *a priori* criteria in order to be included in this meta-analysis: 1) they must occur in a North American grassland or savanna; 2) species richness or raw data to calculate species richness must be presented; 3) the study site must not be a grassland

created by recent forest clearing or removal of encroaching trees/shrubs, because community recovery can be long (Lett and Knapp 2005) and probably varies considerably between ecosystems; 4) there must be evidence that native woody plants have become more numerous within the ecosystem over the last 150 years (the period when documented encroachment began; Van Auken 2000); 5) the study site must not receive >1100 mm of precipitation, because these areas are commonly forested (Hirota et al. 2011, Staver et al. 2011) making it difficult to discern between woody encroachment and naturally-occurring patch-dynamics. Following Scholes and Archer (1997), an ecosystem was considered a grassland or savanna if graminoid species were a dominant component of the community (this includes ecosystems co-dominated by grasses and trees/shrubs, such as savannas and big-sagebrush communities).

In all, our search resulted in 225 studies that were initially considered in part or in full for inclusion in the meta-analysis. Of those, 26 papers met our criteria for inclusion in this study. These papers covered 13 grassland/savanna communities and 21 different encroaching species (see supplement 1 for raw data and site information; appendix 1 for citations). ANPP data were readily available for 10 communities that also measured species richness and 2 communities without richness data (appendix 1). Appendix 2 is a list of studies that met most of our criteria for inclusion, but were eventually rejected for violating one of our inclusion criteria.

Meta-analysis metrics:

Studies varied considerably in their design and analysis. Therefore, we used the log response ratio (RR), where RR = ln (X_e / X_c) = ln (X_e) – ln (X_e), and X_e and X_c are the mean values of experimental and controls groups, respectively. Negative RR values indicate a decline in the variable of interest following encroachment, positive values indicate an increase and 0 indicates no change. Following Clark et al. (2007), we refer to this metric as "richness response".

We chose this metric because it accommodates many different experimental designs, as well as differing degrees of statistical reporting (Hedges et al. 1999). Taking the natural log of a fraction also has the beneficial property of making the resulting metric equally responsive to changes in the numerator and denominator. This was especially important because the denominator (measured unencroached richness) varies with both species richness and plot size (e.g. Adler et al. 2005), and our analysis included studies with different plot sizes. The use of this metric and the inclusion criteria above follows Hedges et al. (1999) and Whittaker (2010). Information on how data were obtained from individual studies is presented in appendix 3.

For grasslands/savannas that had multiple studies published on encroachment, we averaged the richness response of all studies for each community. This minimized bias towards grassland/savanna communities that have been studied more extensively than others (see Table 1 for levels of replication). Usually, replicates within communities showed similar responses even if study designs and plot sizes differed (supplement 1) and the relationship between plot size and richness response explained little of the overall variability ($r^2 = 0.05$). Therefore, we feel confident that differences in study design do not substantially alter our results. Tallgrass prairie had the most variable results and the highest number of studies (n=5).

Reporting of climatic data varied across studies, therefore we used the WorldClim GIS database (WorldClim.org) to obtain standardized monthly and annual temperature and precipitation for each site (supplement 1). WorldClim precipitation values were highly similar to those reported in the sub-set of papers that included local climate data ($r^2 = 0.96$, n = 10 sites). Prior to statistical analysis, temperature and precipitation were averaged within communities in the same way as "richness response" (Table 1). We analyzed "richness response" and ANPP data using a mixed-effects model ANOVA where climate variables (precipitation, temperature)

were fixed effects fit with a random intercept. Climate variables and ANPP were strongly correlated, therefore we performed separate analyses for "richness response" with either climate data or ANPP as fixed effects. Because ANPP can be scaled from different plot sizes, analysis was performed on the reported values of ANPP and on the RR transformation of ANPP, when data from both encroached and un-encroached grasslands were available. Unfortunately, comparable data on soil characteristics were not available at many sites and a recent analysis suggests that global soil databases are inadequate for such analyses (Staver et al. 2011). Therefore, we did not include soil variables in our analysis.

Results:

Woody encroachment was associated with a significant decline in species richness in the 13 grassland/savanna communities with available data (Table 1). The average richness response for all communities was -0.65 and the average proportional decline in species richness ($[X_{unencroached}-X_{encroached}]/ X_{unencroached} * 100\%$) was 45%. Richness response decreased with mean annual precipitation (MAP) (Fig 1a, $r^2 = 0.81$, $p < 0.001$). Richness response was also negatively correlated with the ANPP following encroachment ($r^2 = 0.69$, $p < 0.05$, data not shown) and the magnitude of change in ANPP following encroachment (Fig 1b, $r^2 = 0.69$, $p < 0.05$). Relationships between richness response and RR_{ANPP} were weaker ($r^2 = 0.48$), suggesting that species richness responds more closely to the magnitude of change in ANPP, rather than the proportional change in ANPP. The ANPP of encroached patches was directly related to precipitation ($r^2 = 0.87$, $p < 0.001$, data not shown), as was the difference in ANPP between encroached and un-encroached patches (Fig 1c, $r^2 = 0.81$). For both richness response and ANPP of encroached patches, April precipitation was the best monthly predictor ($r^2 = 0.71$ and 0.86, respectively). Temperature was not a significant predictor of richness response or ANPP. After

removing one statistical outlier, all reported relationships were also significant when studies are considered as single data-points, rather than community type averages (appendix 3).

Discussion:

As a whole, woody encroachment consistently resulted in a significant decline in species richness in North America grassland/savanna communities (Table 1). Moreover, most of the studies included here found that encroachment altered community composition as well (Table 1). Species richness often reflects microsite environmental conditions and the traits of species available to colonize an area (Chapin 1980, Shipley et al. 2006). The observed declines in richness, taken together with the noted impacts of woody encroachment on key resources and disturbance mechanisms (Schlesinger et al. 1990, Archer 1995, Scholes and Archer 1997, Knapp et al. 2008, Riginos and Grace 2008, Brantley and Young 2009, D'Odorico et al. 2010, Eldridge et al. 2011, Ratajczak et al. 2011), suggest that few species from the pre-existing grassland/savanna community are well-adapted to woody plant dominance in North America.

In contrast to these results, a meta-analysis by Eldridge et al. (2011) found that across continents (~18 equivalents of the 'communities' in our study), woody encroachment tended to have a positive or neutral effect on species richness. The analysis by Eldridge et al. (2011) included less than half of the North American communities used in our analysis and this handful of shared communities comprises many of the examples of negative encroachment impacts in their analysis. Thus, the available evidence suggests that the effects of woody encroachment in North America differ from the neutral or positive effects usually observed in other regions. Region-specific variation in evolutionary history (disturbance, grazing, climate, species radiation) and anthropogenic activity (pre- and post-industrial) may account for differences between North America and other continents. For instance, in Mediterranean and Australian

grasslands, woody encroachment has been initiated by a discontinuation of pastoral activities and/or wood collection and has been followed by increases in species richness (Thompson and Eldridge 2005, Maestre et al. 2009). Whereas in North America, intensifying human activity tends to be the primary cause of woody encroachment (Van Auken 2000, Kochy and Wilson 2001, Briggs et al. 2005) and the impact on species richness is negative (Table 1). Together, these studies demonstrate that species richness is consistently greater when anthropogenic impacts are less intense.

Inter-relations between richness, productivity and precipitation across North America:

Woody encroachment in North America occurs over a large climatic and productivity gradient. We found that woody encroachment had a greater impact on species richness at sites with higher precipitation (Fig 1a) and when encroachment resulted in a greater change in ANPP (Fig 1b). Also, ANPP and changes in ANPP following encroachment were positively related to precipitation (Fig 1c; see Knapp et al. 2008, Barger et al. 2011). These results mirror other observations that the performance of woody plants in grasslands is moderated by water availability. Precipitation is correlated to maximum woody cover in Africa, Australia and South America (Williams et al. 1996, Sankaran et al. 2005, Hirota et al. 2011, Staver et al. 2011) and in encroached grasslands globally (Eldridge et al. 2011). Likewise, encroachment-related changes in light interception and litter cover are directly related to precipitation (Knapp et al. 2008, Eldridge et al. 2011). Together, these studies demonstrate that both the impact per unit area and the spatial extent of woody encroachment scale directly with precipitation.

We suggest that the parallel relationships between species richness, ANPP and MAP exist because precipitation determines the magnitude of "woody release" that occurs with woody encroachment (Fig 2). Through competition for resources in the upper soil layers and as a fuel

source for fires, grass dominance negatively impacts woody seedling survival and growth, which can suppress woody vegetation even if resource availability is adequate to support adult shrubs and trees (Higgins et al. 2000, Sankaran et al. 2004, Sankaran et al. 2005, Bond 2008, Staver et al. 2011). When factors limiting woody vegetation are attenuated by fire suppression, over-grazing or increased resource availability, water-limited woody plants undergo a release and reach a level of dominance that is determined predominately by precipitation (Fig 1 and 2; Sankaran et al. 2005, Knapp et al. 2008, Hirota et al. 2011, Staver et al. 2011, Barger et al. 2011, Eldridge et al. 2011) and to a lesser extent, local edaphic factors or grazing (e.g. Williams et al. 1996, Roques et al. 2001, Staver et al. 2011). This release is both physiological (affecting individual plants) and demographic (affecting overall cover). Since there is a greater release at sites with higher precipitation, woody encroachment also has a greater effect on resource availability and ecosystem processes, resulting in stronger declines in species richness.

This woody release hypothesis assumes that the impact of encroachment on key processes increases with woody cover and woody biomass (i.e. that per-gram competitive effects do not vary among North American grasslands). A woody-release interpretation does not tie the observed relationship between precipitation and richness response to changes in any single resource or disturbance across sites—just the magnitude of overall change, which is captured in the various metrics discussed previously. This is important because light, water, nutrients, grazing, and fire are differentially affected by woody encroachment and have divergent effects across grassland communities (Knapp and Smith 2001, Clark et al. 2007, Knapp et al. 2008, Peters et al. 2011, Staver et al. 2011).

The relationship between changes in species richness and changes in ANPP also matches general theoretical expectations. In herbaceous plant communities, the relationship between

diversity and productivity is hypothesized to be a uni-modal, hump-shaped curve (Grime 1973, Tilman and Pacala 1993). While recent work has found that uni-modal curve might not be appropriate across the natural range of productivity found in grasslands (Adler et al. 2011), several global change experiments suggest that an increase in productivity leads to a decline in species richness (Suding et al. 2005, Clark et al. 2007, Harpole and Tilman 2007). This relationship may scale-up from changes within the herbaceous community, to changes in the dominant vegetation type as well. Woody encroachment has similar effects on species richness and productivity (Fig 1a-c) and is also stimulated by a decrease in disturbance (Van Auken 2000, Briggs et al. 2005, D'Odorico et al. 2010) and/or the fertilization effects of nitrogen deposition/CO_2 emissions (Bond and Midgley 2000, Kochy and Wilson 2001, Wigley et al. 2010). Moreover, the magnitude of changes in species richness scale with the changes in aboveground productivity (Fig 1b), which is the expected relationship as increasing dominance by an individual species or functional group—in this case a strong aboveground competitor— leads to increased productivity, but decreased diversity (Tilman and Pacala 1993, Clark et al. 2007). In the one case where woody encroachment decreased productivity (Chihuahuan Desert), the theoretical patterns and mechanisms still held. In herbaceous communities, increasing abiotic stress is associated with a decrease in both productivity and diversity—this is the left half of the uni-modal curve (Grime 1973, Tilman and Pacala 1993). In the northern Chihuahuan desert, shrub encroachment has facilitated desertification, which intensifies both water and nutrient limitation (Schlesinger et al. 1990). These impacts, in turn, result in a concomitant decline in productivity and diversity (Baez and Collins 2008, Barger et al. 2011), as theory predicts.

The results of this meta-analysis suggest that in North America, species richness consistently declines following woody encroachment and that the magnitude of impact varies

along a large-scale precipitation/productivity gradient. The woody release framework (Fig 2)

explains these patterns based on observations from demographic theory and measured responses

of encroachment to precipitation (Fig 1a-c). We also found preliminary evidence that changes in

species richness are related to annual net primary productivity, which represents a scaling-up of

potential trade-offs between richness and productivity (Fig 1b). On a global scale, our results

suggest that the impacts of woody encroachment vary regionally. Given that woody plant

encroachment is a relatively recent global phenomenon, it is possible that species richness may

gradually increase over time following encroachment (e.g. Adler et al. 2005). However, woody

encroachment currently leads to altered plant communities and a loss of grassland/savannas

ecosystems. Because woody encroachment generally reflects a transition to an alternative stable

state (Schlesinger et al. 1990, Scheffer et al. 2001, D'Odorico et al. 2010, Ratajczak et al. 2011)

and efforts to reverse encroachment have had limited success (Lett and Knapp 2005), continued

encroachment will likely lead to further decreases in species richness and changes in community

structure throughout grasslands and savannas in North American.

Acknowledgements:

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Table 1. Site attributes and changes in richness and ANPP following encroachment

Biome (# studies)	MAP (mm)	MAT (°C)	Richness Response (unitless)	Encroached ANPP (g/m^2)	Changes in Community Composition*
Pinyon/Oak Savanna (2)	599	8.0	-0.67	---	F, I
Barrier Island (1)	1050	14.8	-1.11	1471	F, I
Big Sagebrush (4)	277	7.4	-0.31	---	F, I
Chihuahuan Desert (5)	248	14.5	-0.42	134	D, F, I, O
Coastal mesic grassland (1)	1028	10.2	-0.85	1340	NA
Edwards Plateau (2)	549	18.4	-0.60	---	F, I
Mediterranean Grassland (1)	598	13.8	-0.86	1125	I
Mixed Grass Prairie (3)	380	0.3	-0.49	325	D, F, I
Oak Savanna (2)	782	6.8	-0.66	950	F, I
Sonoran	304	20.8	-0.45	140	D

Desert (1)					
Subtropical Thorn- woodland (1)	682	22.2	-0.72	551	F
Tallgrass Prairie (5)	871	14.0	-1.11	1104	D, F, O
Tussock Tundra (1)	225	-11.3	-0.32	507	F, I

For changes in composition, "F" indicates composition changes within and/or between functional groups. "D" indicates changes in composition as measured by detrended correspondence or ordination analysis. "I" indicates that the frequency of individual species changes. "O" indicates change in composition through a miscellaneous methodology. "NA" indicates that no measurements of composition were reported.
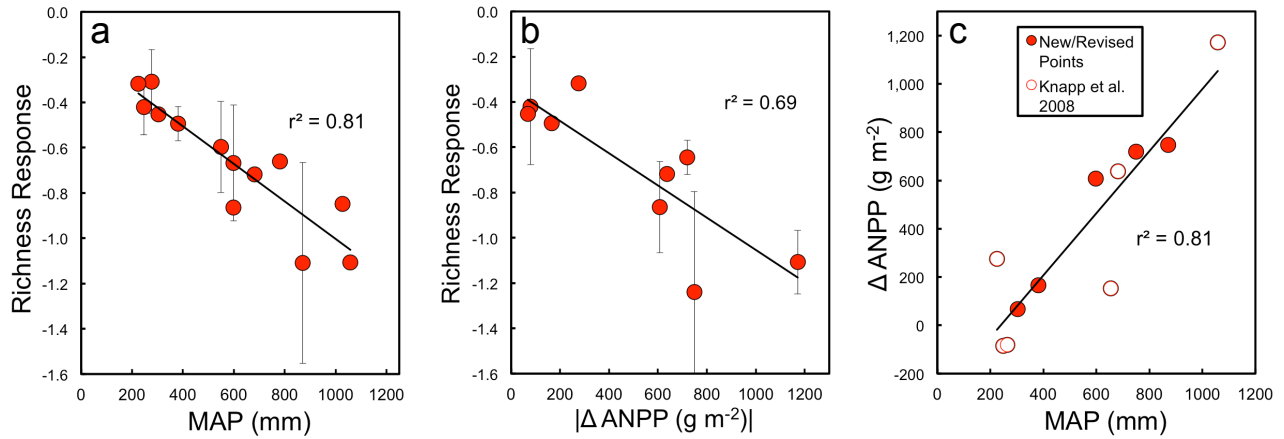
Figure 2.1 a) The relationship between "richness response" (ln[species richness in encroached plot / species richness in un-encroached plot]) and mean annual precipitation (MAP). Negative values indicate a greater decline in richness following encroachment. b) The relationship between "richness response" and the absolute value of changes in ANPP following encroachment (i.e. Δ ANPP). c) The relationship between Δ ANPP and MAP. For a-b, all error bars denote ± 1 SEM. Points without bars did not have enough replicates to calculate SEM or error bars were too small to be seen.
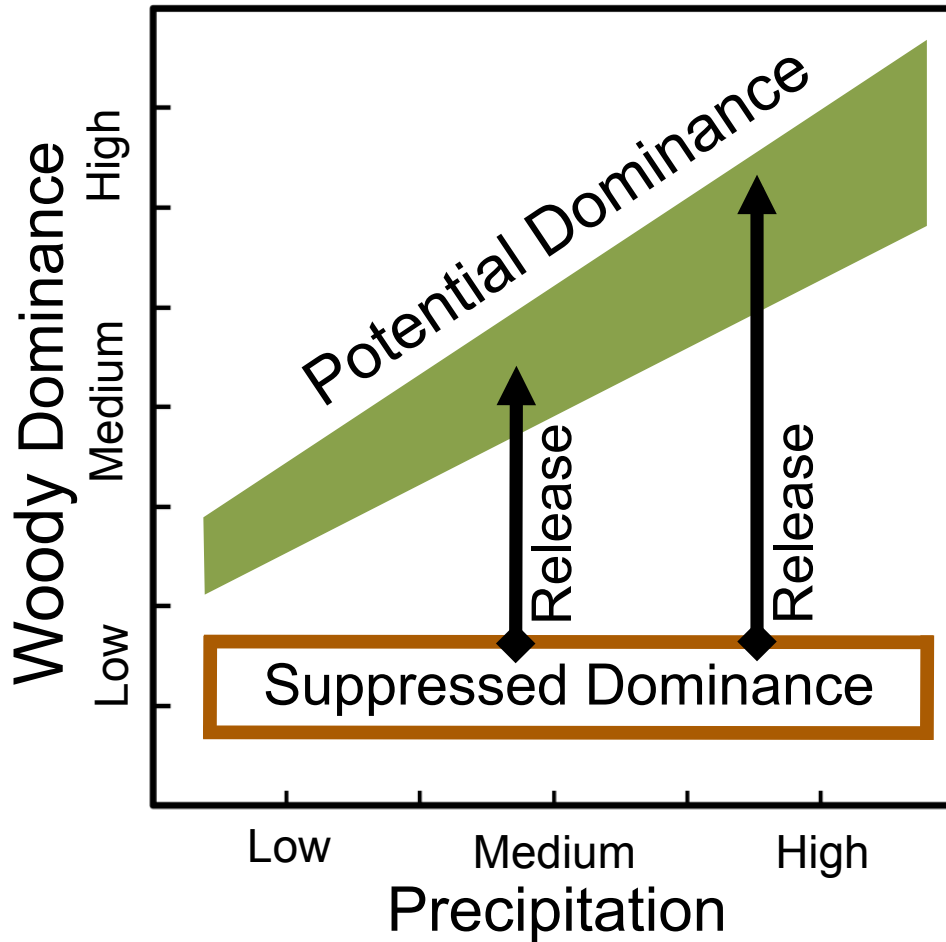
Figure 2.2 A conceptual framework of "woody release" that explains related changes in "richness response" and ANPP along the North American precipitation gradient. This framework depicts two population states, which differ in their degree of woody plant dominance. The demographically suppressed population is the level of woody dominance when a combination of grass competition and resource availability prevents recruitment of adult woody plants. The potential dominance line represents the climatic potential of woody plants when demographic barriers are attenuated. Woody release is both demographic (more individuals reach the adult stage) and physiological (individual plants become larger). The "potential dominance line" is thick to reflect the potential role of local edaphic factors and grazing as moderators of the level of woody release.

Ecological Archives Descriptions:

Supplement 1: Richness response, ANPP and climate data for all studies included in the meta-analysis.

Appendix 1: Citations for all studies used to derive data for meta-analysis.

Appendix 2: List and description of studies that met many, but not all of our inclusion criteria.

Appendix 3: Description of how data were obtained from individual studies.

Chapter 3 - Positive Feedbacks Amplify Rates of Woody Encroachment in Tallgrass Prairie

Abstract:

Over the last century, many grasslands worldwide have transitioned from a graminoid to a tree/shrub-dominated state in a short period of time, a phenomenon referred to as woody encroachment. Positive feedbacks and bi-stability are thought to be important drivers of woody encroachment, but there is little empirical evidence to suggest that positive feedbacks accelerate the woody encroachment of mesic grasslands. In mesic tallgrass prairie, shrub establishment does not directly facilitate seedling establishment. Yet, shrub establishment may facilitate the clonal spread of existing shrubs into nearby patches, because clonal reproduction might circumvent barriers that typically limit woody seedlings. Our results show that when Cornus drummondii (the predominate encroacher of mesic tallgrass prairie) extends rhizomatous stems into open grasslands, these stems use the same deep soil water sources as mature stems—thereby avoiding competition with grasses and gaining access to a reliable water source. In addition, herbaceous fuel concentrations are lower at the shrub/grass interface than in open grasslands, reducing the potential impacts of subsequent grassland fires. We propose that the release from resource and fire limitation results in a positive feedback loop as clonal stems are able to extend

into surrounding patches, circumvent demographic barriers, mature, and spread by developing their own clonal stems. Long-term data on site (26 years) corroborates this interpretation: the size of deep-rooted clonal shrub species has increased 16-fold and their cover has increased from 0 to 27%, whereas the cover of shallow-rooted species (both clonal and non-clonal) has only increased marginally. Together, these results suggest that (1) positive feedbacks can facilitate mesic woody encroachment and (2) bi-stability exists in mesic tallgrass prairie.

Key words: Andropogon gerardii, bi-stability, bush encroachment, Cornus drummondii, $\delta 18O$, fire, niche-partitioning, shrub encroachment, source water, tipping points, tree–grass coexistence, two-layer soil model

Introduction:

In the last century, woody encroachment has been reported in grasslands worldwide and across a range of evolutionary histories and climatic conditions (Archer 1995, Van Auken 2000, Roques et al. 2001, Knapp et al. 2008), resulting in changes in ecosystem structure and function (Scholes and Archer 1997, Van Auken 2000, Knapp et al. 2008). Positive feedbacks have been shown to increase the rate and extent of woody encroachment in many grasslands (Schlesinger et al. 1990, Van Auken 2000, Scheffer et al. 2001, Wookey et al. 2009, D'Odorico et al. 2010). However, the study of encroachment feedbacks has focused primarily on semi-arid and arctic grasslands (Archer et al. 1988, Schlesinger et al. 1990, Ravi et al. 2007, Wookey et al. 2009, D'Odorico et al. 2010), with examples in mesic systems restricted to theoretical models (D'Odorico et al. 2006, Baudena et al. 2010). This study addresses the potential for positive feedback mechanisms in mesic tallgrass prairie, a system in which positive feedbacks have not been previously identified.

In semi-arid and arctic grasslands, woody encroachment alters temperature and/or the availability of water and nutrients, which facilitates the establishment of other shrubs and creates a positive feedback loop (Schlesinger et al. 1990, Scheffer et al. 2001, Ravi et al. 2007, Wookey et al. 2009, D'Odorico et al. 2010; see Archer et al. 1988 for mechanisms related to seed dispersal). However, these and other mechanisms have been found to have a minimal impact on encroachment of tallgrass prairie (Briggs et al. 2005, McKinley and Blair 2008). Instead, the nature of feedbacks in tallgrass prairie may involve factors that structure mesic grasslands: pronounced belowground competition in the upper soil layers (Nippert and Knapp 2007a, b), frequent and intense fires (Knapp et al. 1998, van Wilgen et al. 2003, Briggs et al. 2005, Bond 2008) and predominance of clonal reproduction (Benson and Hartnett 2006, Dalgleish and Hartnett 2006).

Though mesic grasslands receive enough rainfall to support closed forests, woody plants are commonly excluded because grass dominance decreases water availability in the upper soil and stimulates fires (Scholes and Archer 1997, Sankaran et al. 2005, Bond 2008, Staver et al. 2011). Many adult woody plants escape resource competition because they can access deeper water sources and usually can withstand grassland fires (Walter 1971, Scholes and Archer 1997, Bond 2008). However, grasses can suppress seedling establishment and/or prohibit seedlings from reaching the adult stage, which imposes a demographic bottleneck on woody plant populations (Higgins et al. 2000, Sankaran et al. 2005, Gignoux et al. 2009, Staver et al. 2011). Specifically, when woody species are young they have a shallow and less robust root system, which overlaps with the extensive grass root systems in the upper soil (Wilson 1993, Jackson et al. 1996, Weltzin and McPherson 1997, Partel and Wilson 2002). Because grasses deplete soil moisture in the upper soil, this overlap results in high mortality rates until woody plants develop deeper roots

(Scholes and Archer 1997, Jurena and Archer 2003, Bond 2008). Likewise, the thinner bark and lower stature of young woody plants makes them more susceptible to fire than adults (Scholes and Archer 1997, Higgins et al. 2000, Bond 2008, Lawes et al. 2011). Both of these demographic barriers are especially acute in tallgrass prairie, as seedling establishment accounts for less than1% of recruitment each year (Benson and Hartnett 2006) and this system supports high levels of herbaceous productivity (Nippert et al. 2011), which leads to high-intensity fires (Gibson et al. 1990).

Considering the limitations of woody vegetation in mesic grasslands, positive feedbacks that favor encroachment in tallgrass prairie should theoretically reduce competition for water and the impacts of fire during the establishment phase of woody plants. In tallgrass prairie most reproduction occurs by clonal reproduction (Benson and Hartnett 2006), as dominant species become established and then expand radially via rhizomatous clonal stems. Therefore, to test for positive feedbacks in mesic grassland we focused on factors affecting clonal stem production. Using a 26 year species composition data-set, we first identified long-term trends in woody coverage in tallgrass prairie and determined whether changes in cover were the result of the expansion by existing shrubs and/or the establishment of new individuals. We also used this dataset, which occurs over a soil moisture gradient, to determine if water availability limits woody establishment in tallgrass prairie. Then, we explored three specific mechanisms: (1) Do clonal shrub stems use deep soil water to circumvent the competition with grasses? (2) Does shrub establishment alter drivers of fire frequency/intensity in favor of clonal shrub expansion? (3) Early in development, can clonal shrub stems limit light availability to suppress growth of competing grasses?

Methods:

Study site and organisms

The Konza Prairie Biological Station (KPBS) is a native tallgrass prairie (3487 ha) in the Flint

Hills of northeast Kansas, USA, where most of the large remnant tracts of tallgrass prairie

remain (39°05′ N, 96°35′ W). KPBS is divided into 60 hydrological catchment basins, referred to

as watersheds. Each watershed has a prescribed fire frequency (1, 2, 4, or 20 yrs) with most

being burned in late April. The estimated historical fire frequency (i.e., prior to European

settlement) for this region is every 3 to 4 years (Knapp et al. 1998). All analyses reported here

occurred in watersheds that are ungrazed by bison and burned every 3 to 4 years.

Topographic variation at KPBS is dramatic over small scales. Upland locations have thinner soils

than lowlands, resulting in lower water availability and lower primary productivity (Nippert et al.

2011). KPBS experiences weather conditions typical of mesic grassland, with 75% of annual

rainfall occurring during the growing season of April to September (Hayden 1998). The climate

of 2009 was wetter (950 mm) and cooler (11.9°C mean daily air temperature) than the long-term

site average (35 year mean: 835 mm precipitation and 12.7°C air temperature). The plant

community of KPBS is dominated by perennial C4 grasses Andropogon gerardii, Sorghastrum

nutans, Schizachyrium scoparium, and Panicum virgatum, which rely almost exclusively on soil-

water from 0–25 cm depth (McCarron and Knapp 2004, Nippert and Knapp 2007a, b). KPBS

was historically devoid of woody vegetation except in riparian areas, but in the last 26 years,

woody encroachment has occurred in areas with a fire frequency of 3 years per fire or greater

(reviewed in Briggs et al. 2005). More information on KPBS can be found at

http://www.konza.ksu.edu.

Long-term cover dynamics

We present changes in the cover dynamics of 5 native deciduous woody species in this study:

Cornus drummondii, Rhus glabra, Prunus americana, Ceanothus americanus and Amorpha canescens. Together, these 5 focal species account for 85% of woody cover in ungrazed watersheds of KPBS burned every four years. We separated these species into either "shallow" or "deep" rooting habits based on whether they obtained more water from deeper soil layers (>25 cm) than the dominant C4 grass community. Past work has shown that C. americanus, A. canescens, and P. americana rely primarily on upper 25 cm of soil for their water needs (McCarron and Knapp 2004, Nippert and Knapp 2007a, b) and so, we categorized these species as "shallow-rooted". In contrast, pre-dawn water potentials of R. glabra have been found to be strongly correlated with soil water availability at 75 cm depth (McCarron and Knapp 2004) and therefore, we categorized this species as "deep-rooted". The source water depth of C. drummondii has not been determined previously. We focused most of this study on the shrub C. drummondii because it is the predominate encroacher of natural and semi-natural tallgrass prairie in Kansas, USA. Individual C. drummondii have been observed to extend clonal rhizomatous stems (hereafter to referred to as clones) into surrounding grasslands patches. R. glabra and P. americana are also capable of clonal expansion. A summary of life-form (clonal vs. non-clonal), rooting habit and other characteristics of these species can found in Table 1.

Long-term dynamics of shrub expansion

Permanent community composition plots were established at KPBS in 1983. For each fire frequency × grazing combination, two watersheds have been sampled annually. Sampling occured in 10 m^2 circular plots, arrayed equally along 50 m long transects. Within each watershed, 4 such transects were randomly located in upland locations and 4 in lowland locations (i.e., n = 40 plots per watershed, n = 20 per topographic position, per watershed). When transects were established, shrub cover in all permanent plots was minor (<5%). Since then, woody plants

have become established throughout these plots. We analyzed this long-term dataset to track the expansion of our 5 focal woody species over the last 26 years (1983–2009). At each plot, approximate canopy cover of each species has been recorded using a permutation of the Daubenmire cover scale (Bailey and Poulton 1968). Cover was recorded as either 0–1%, 1–5%, 5–25%, 25–50%, 50–75%, 75–95%, and 95–100% of the 10 m^2 circle; we used the midpoint of these ranges for our calculations. For our analysis of C. drummondii cover dynamics, we treated uplands and lowlands separately, reporting for each year the average cover of C. drummondii across all plots, the frequency of plots containing C. drummondii, and size index of C. drummondii (n = 40 for each topographic location per year). Frequency is the percentage of plots in which C. drummondii occurs. Size index is the relative size of each shrub and is calculated as the total cover of C. drummondii divided by the number of plots in which it occurs. We consider our estimate of shrub size to be conservative because shrubs that expanded outside of the plots would not be considered as increasing the cover recorded inside the plot area. We also report changes in cover, frequency and size index for the other 4 focal woody species described above and the remaining woody species aggregated (Table 1). When we report data for all species (not just C. drummondii), the data reported are from lowlands only, because uplands have experienced minimal encroachment.

Soil water provenance of C. drummondii and A. gerardii

C. drummondii occurs as monotypic stands in the grassland matrix. In late May 2009, eight isolated C. drummondii were selected in lowlands and slopes between lowlands and uplands, within watersheds burned every 4 years (including the watersheds with permanent community composition plots). All shrubs were at least 300 m apart from each other. Shrubs were 9.5 m (± ~ 1 m) in diameter, including shrub clones. At each shrub, we established a transect

perpendicular to the prevailing hill-slope aspect and measured the diameter of the mature shrub. Using this measurement, five equidistant transect intervals were marked starting at the center of each shrub, with points 1–2 being the mature shrub, point 3 the transition from mature shrub to clones, and points 4–5 the zone where developing clonal stems, not mature stems, occur. Clones were smallest at point 5 and interspersed within the grass canopy.

During the growing season, the stable isotopic signature of groundwater on KPBS falls on the meteoric water line ($\delta D = -41.2‰$, $\delta^{18}O = -6.4‰$; Nippert and Knapp 2007a) and primarily reflects recharge by winter precipitation (Macpherson 1996, Nippert and Knapp 2007a), whereas the stable isotopic signature of shallower soils is evaporatively enriched (Nippert and Knapp 2007a). Using this gradient, we sampled surface soils and xylem tissue of C. drummondii and A. gerardii and extracted water for isotopic analysis, in order to determine source water-use over time. Sampling of xylem tissue and soil occurred during daylong sampling campaigns during the most active portion of the growing season (June 13 and 26, and July 10 and 23, 2009). During each sampling campaign, C. drummondii stem samples were collected at all five transect intervals per shrub, while A. gerardii samples were collected at intervals 3–5 along the transect because grasses were not present in the mature shrub interior (intervals 1–2). Soil samples were collected at transect intervals 1, 3, and 5, at 8 and 30 cm depth. C. drummondii samples consisted of a non-photosynthetic woody stem sample, taken from a single C. drummondii stem at about 1.25 m height. To obtain sufficient quantity of A. gerardii xylem tissue, we collected and pooled the non-photosynthetic crown tissue of 2–3 tillers at each transect interval. All plant and soil samples were immediately sealed in exetainers (Labco Ltd., UK) and iced in the field. At the end of the day, samples were placed in a freezer at $-10°C$ until they were processed.

Xylem and soil-water was extracted using cryogenic vacuum distillation (Ehleringer and

Osmond 1989, Nippert and Knapp 2007a). Samples were analyzed for their stable oxygen and hydrogen isotopic signatures using a Picarro WS-CRDS isotopic water analyzer and referenced to V-SMOW. Within-run variation of a working standard for all runs was <0.07‰ and <0.5‰ for $\delta^{18}O$ and δD, respectively. The accuracy of all runs was <0.18‰ and <0.6‰ for $\delta^{18}O$ and δD, respectively, determined from an in-house standard. Isotope ratios were expressed using δ notation: $\delta = (R_{sample}/R_{standard} - 1) \times 1000$, where R is the absolute ratio of the rare to common isotope.

To estimate varying contributions of multiple water sources to the isotopic water mixture in plant stems, we used the isotopic mixing model MixSIR (Semmens and Moore 2008). MixSIR uses a Bayesian approach to estimate probability distributions of multiple sources to the isotopic mixture of xylem samples (or any other isotope mixing model), by incorporating analytical uncertainty into the prediction. We modelled each individual plant sample for each collection period using the corresponding soil water samples, and ran 1.5 million iterations per sample (accuracy of the model increases with the number of iterations). At each individual shrub, 8 cm and 30 cm soil δD and $\delta^{18}O$ and corresponding variance were obtained by averaging data from all transect intervals for the same depth, for each sampling period, because there was no effect of transect position on the isotopic signature of soil water (see Results). Groundwater samples were not available at all locations, therefore we used the most depleted δD and $\delta^{18}O$ sample value measured at each transect as a proxy for the deepest soil water source available (>30 cm end member).

Fire fuel dynamics

To test whether C. drummondii alter fire dynamics, we compared herbaceous fuel concentrations at different landscape positions (open grassland, shrub edge or shrub center) and below shrubs of

different ages. In early June, fire fuel dynamics were assessed for 19 C. drummondii shrubs across five watersheds at KPBS with a 4-year burn frequency. In each watershed, four shrubs were chosen randomly. Three randomly placed replicate samples of litter were taken at the center and edge of each shrub island and a paired grassland plot 15 m from the edge of each shrub island. Using a 0.1 m^2 clip frame to denote each replicate, all dead plant material from the ground to 1 m height was gathered and dried at 60°C for five days before being analyzed. Replicates were sorted into woody and herbaceous components and weighed. Within shrub replicates were weighed separately and then averaged prior to statistical analysis.

At each shrub, the largest stem(s) present was harvested to approximate the age of the shrub. A cross-section of each stem was dried, cut, sanded and then scanned using a flatbed scanner at 600 dpi. The scanned images were used to determine the approximate age of oldest standing stems for each shrub by counting growth rings.

Canopy development

To determine the effects of woody expansion on light availability, we measured the leaf area index (LAI), which reflects changes in canopy density per unit ground area. At the same locations used for isotopic analysis, we measured LAI at 8 cm height every two weeks from June11 to August 28, 2009 using a Li-Cor LAI 2000 Plant Canopy Analyzer (Li-Cor, Lincoln, Nebraska, USA). At each transect interval, five individual readings were averaged for each LAI measurement.

Statistical analyses

The stable isotopic signature (δ^{18}O and δD) of xylem water was analyzed using a mixed-effects model ANOVA in R (www.r-project.org). In the analysis, date of sampling, species (grass or shrub), transect interval, elevation, and their interactions were fixed effects. Data were log-

transformed as needed to meet the assumption of normality. Analysis of litter and LAI was performed separately using a mixed-effects model ANOVA with date of sampling, species, transect interval, topographic position, years since last burn, and their interaction as fixed effects. Biomass data was not normally distributed, so a (log + 1) transformation was used. Statistical trends did not vary statistically when analyzed for $\delta^{18}O$ and δD. To simplify the presentation, we present the results of $\delta^{18}O$ rather than δD because oxygen isotopes have been shown to be a more robust indicator of plant source-water use (Ellsworth and Williams 2007).

Results:

Long-term C. drummondii demography and dynamics

Since 1983, cover of C. drummondii in lowlands has increased from ~0% to ~19%, while cover in uplands has remained at or close to 0% throughout the 26-year period (Fig. 1A). In lowlands, the frequency and size of C. drummondii has increased, more or less linearly throughout the entire 26-year period (Fig. 1B, C). Notably, there were two punctuated increases in C. drummondii cover, from 1999 to 2002 and 2006 to 2009. Both of these increases are commensurate with increases in shrub size over the same period.

In lowlands, species that are clonal and deeply rooted have increased substantially in cover (Fig. 2A) and have become an increasing higher percentage of the total woody community (Fig. 2B). P. americana, a shallow-rooted clonal species, has increased slightly, and non-clonal shallow rooted species have not increased significantly (Table 1, Fig. 2A).

Soil water provenance of C. drummondii and A. gerardii

The $\delta^{18}O$ of soil water varied significantly by sample period (p < 0.01), soil depth (p < 0.01) and their interaction (p < 0.05), but did not vary by transect interval (p = 0.69) (Fig. 3). C. drummondii had lower $\delta^{18}O$ values than A. gerardii for all 4 sampling intervals (p < 0.0001, Fig.

3). For most sampling periods, the highest proportion of water used by C. drummondii came from >30 cm soil depths, while the lowest source contribution was from the 8 cm soil (Fig. 4A). In contrast, A. gerardii obtained most of its water from sources at 8 cm and 30 cm depths (Fig. 4B). The source fraction of water-use did not vary along the transect interval for C. drummondii ($p = 0.88$) or A. gerardii ($p = 0.20$). $\delta^{18}O$ of A. gerardii xylem water was significantly lower on slopes, compared to lowlands ($p < 0.05$).

Fuel dynamics

Herbaceous fuel (i.e., dead herbaceous biomass) was lower at the shrub edge and center than in open grasslands, and declined significantly ($p < 0.05$) with age at the shrub edge (Fig. 5). At the shrub edge, declines in herbaceous biomass were best explained by an exponential curve ($r^2 = 0.60$, compared to $r^2 = 0.47$ for linear). Herbaceous biomass was greater at the shrub edge immediately following fires than in open grasslands ($p < 0.01$ for interaction between location and years post-burn). Age of nearby shrubs had no effect on herbaceous biomass in paired grassland sites.

Canopy development and light limitation

LAI varied significantly by transect interval ($p < 0.0001$) and sample date × transect interval ($p < 0.001$) (Fig. 6). Transect intervals 1 through 3 (the mature shrub) had the most similar values across the growing season and high LAI values early in the season. LAI values at points 4 and 5 (the area dominated by shrub clones) were significantly lower than points 1–3 ($p < 0.05$). LAI values for all transect locations converged by mid-August (Fig. 6).

Discussion:

In lowlands the aerial coverage of encroaching C. drummondii has increased from 0% to 19% over the last 26 years, and notably, the size index of C. drummondii has increased more than 16-fold. However, C. drummondii has not become established in uplands (Fig. 1). Compared to lowlands, uplands have thinner soils and significantly lower water availability (Knapp et al. 1998, Nippert et al. 2011). As a result, uplands also support lower levels of herbaceous biomass (Nippert et al. 2011) and because herbaceous biomass is the primary fuel for fire (van Wilgen et al. 2003), these areas also have lower fire intensities (Gibson et al. 1990). Thus, despite the key role of fire in preventing C. drummondii establishment in tallgrass prairie (Heisler et al. 2003, Briggs et al. 2005), water limitation prevents woody establishment under drier conditions, either through outright resource limitation or reducing growth rates to the point at which woody seedlings cannot survive fires of even low intensity.

While resource limitation might constrain establishing C. drummondii, our results show that mature C. drummondii on slopes and in lowlands avoid competition for water by accessing deeper water sources than primary grass competitors. Across all transect intervals and all sampling periods, $\delta^{18}O$ of xylem water in C. drummondii was significantly lower than A. gerardii (Fig. 3) and on average, C. drummondii relied on the upper 30 cm soil for 53% of its water-uptake, compared to 79% in A. gerardii (Fig. 4). This represents a substantial degree of niche partitioning, considering Nippert and Knapp (2007a, b) found that forbs and other woody species in tallgrass prairie usually relied on the upper 25 cm of soil for 70–90% of their water uptake.

The source-water partitioning between C. drummondii and A. gerardii is consistent with a large number of studies that have found a vertical separation of tree and grass root systems (Jackson et

al. 1996, Weltzin and McPherson 1997, but see Scholes and Archer 1997, Bond 2008, Kulmatiski et al. 2010). However, it is surprising that C. drummondii clones measured in the grassland matrix were accessing the same soil water source as the mature shrubs, even up to 5 m from the center of the shrub island ($p > 0.88$ for difference between mature shrub and clones; Fig. 4). We suspect that clonal stems initially access deep soil water through rhizomatous transfer. Survival rates of woody plants in many types of grassland are usually low until root development extends beyond concentrated grass roots in surface soils (Jackson et al. 1996, Partel and Wilson 2002), resulting in competitive release (Walter 1971, Weltzin and McPherson 1997, Jurena and Archer 2003, Bond 2008; Z. Ratajczak unpublished data). At KPBS, deep soil water is recharged by winter precipitation and because it is not a primary water source for grasses, this soil-water source is abundant and intra-annually stable (Macpherson 1996, Nippert and Knapp 2007b). Therefore, access to deep soil water should allow clonal stems to circumvent the period of water limitation that prevents woody seedling establishment. This can potentially result in a positive feedback system, as niche partitioning allows clonal stems to colonize new patches and then develop their own clonal stems, which can circumvent water competition as well (i.e., Fig. 4). To test this proposed feedback loop, we compared long-term rates of expansion by species with different rooting depths and clonal and non-clonal life forms.

In tallgrass prairie, the two species that account for the majority of woody encroachment (C. drummondii and R. glabra) are both clonal and more deeply rooted than the dominant grass species (Table 1, Fig. 2). In contrast, there has only been a marginal increase in cover by the clonal, shallow-rooted P. americana (McCarron and Knapp 2004) and there has been no increase in cover by non-clonal shallow-rooted species (Table 1, Fig. 2). The increased cover of clonal species was the result of both new shrub establishment, as indicated by an increase in frequency,

and the widening of individual shrubs, as indicated by an increase in size index. In fact, all clonal species—even the shallow-rooted P. americana—have increased in size index, suggesting that clonality is a key trait for determining whether woody species spread within the areas they colonize (rather than enhanced seedling establishment). However, P. americana has only increased half as much in size index and frequency as its more deeply-rooted counterparts. These differences are likely attributable to the increased competition with grasses that is inherent to having a shallower root system (Jackson et al. 1996, Nippert and Knapp 2007a, b). Together, these results suggest that both clonality and deep roots are needed for woody plants to colonize tallgrass prairie and expand substantially within individual patches.

In addition to changes in competition for water, we also found evidence that individual C. drummondii may facilitate their own expansion through localized changes in fire frequency/intensity. The short stature of C. drummondii does not permit escape from fire through vertical growth, therefore the most likely way for C. drummondii to escape fire is to alter fire dynamics. We found that following fire, large portions of fuel goes un-burned at the shrub edge and center, suggesting that few fires carry into the center of the shrub islands (i.e., fire frequency is effectively reduced). Just preceding fires, fuel loads are lower around C. drummondii compared to open grasslands and as C. drummondii ages, the amount of herbaceous fuel declines at the shrub grass/interface where clones emerge (Fig. 5). Given the key role of herbaceous biomass in determining fire intensity in tallgrass prairie (Gibson et al. 1990) and elsewhere (Ansley et al. 1998, van Wilgen et al. 2003, Tidwell et al. 2009), these changes in fuel should also reduce fire intensity around shrub islands. Since fire is one of the primary factors limiting shrub establishment in tallgrass prairie and other grasslands (Scholes and Archer 1997, Roques et al. 2001, Briggs et al. 2005, Bond 2008), the creation of a low fire frequency/intensity zone

around shrubs should decrease the mortality of mature and clonal shrub stems, which would contribute to the clonal expansion described above. Indeed, reductions of fuel by woody vegetation have been shown to result in positive feedbacks in savanna models (Scholes and Archer 1997, D'Odorico et al. 2006) and localized fuel alterations have been shown to reduce fire mortality for woody plants in other grasslands (Tidwell et al. 2009).

In contrast to changes in water competition and fire, we found that changes in light availability do not appear to contribute directly to clonal stem establishment. If emerging C. drummondii clones could reduce light availability early in their development, this would limit grass growth and thereby, total water and nutrient uptake by grasses (e.g., Knapp and Seastedt 1986). However, LAI values were low where developing clones predominated (Fig. 6) and similar to those measured in open tallgrass prairie during the same time (Nippert et al. 2011). Although light interception might not have a direct effect, changes in light availability may indirectly contribute to the subsequent expansion of shrubs. LAI values inside the mature shrub and at the shrub edge were high early in the growing season (Fig. 6), which is a critical growth period for competing C4 grasses (Knapp et al. 1993, Nippert and Knapp 2007a). Because light availability limits productivity in tallgrass prairie (Knapp and Seastedt 1986), these differences in LAI are probably partially responsible for the observed decline in fuel outlined above (Fig. 5).

Conclusion

The combination of long-term and physiological data presented in this study provides evidence that positive feedbacks contribute to the woody encroachment of tallgrass prairie, but by different mechanisms than those reported in other systems. The cover of deep-rooted clonal species—C. drummondii and Rhus glabra—has increased substantially over the last 25 years, whereas the cover of non-clonal and shallow-rooted species has not (Table 1). Clonal expansion

has been an important driver of this increase in cover; if the average size of C. drummondii were the same size as it was from 1983–1985 (the beginning of the data-set) the contemporary aerial coverage would be only 6% of its current site coverage. Thus, the increasing cover of woody plants in tallgrass prairie is largely the result of expansion by established shrubs, rather than the more commonly reported pattern where encroachment facilitates establishment of new individuals (i.e., Archer et al. 1988, Schlesinger et al. 1990, Ravi et al. 2007, Wookey et al. 2009, D'Odorico et al. 2010).

Many potential positive feedback mechanisms in tallgrass prairie have already been explicitly or implicitly refuted, including grazing pressure and shrub-mediated changes in water/nitrogen availability (reviewed in Briggs et al. 2005). Based on the shared rooting characteristics of encroaching species and noted changes in herbaceous fuels, we propose the following positive feedback loop for shrub encroachment of tallgrass prairie: (1) global change facilitates initial C. drummondii establishment; (2) C. drummondii develops deep roots and reduces herbaceous fuel concentrations; (3) C. drummondii extends clonal stems into surrounding patches; (4) a high percentage of clonal stems survive and mature because they can use deep soil water and are less susceptible to fire; (5) now mature clonal stems develop deep roots and produce new clonal stems, allowing them to expand into new patches. To date, some shrubs have reached an area of 200 m^2 in this way (Z. Ratajczak, unpublished data). As far as we are aware, these mechanisms have not been reported for other systems where woody encroachment of grasslands is occurring. This disparity reflects the unique demographic barriers of mesic North American grasslands (Dalgleish and Hartnett 2006) and that most studies of encroachment feedbacks have focused on drier ecosystems or modeled fire-feedbacks for larger scales (Schlesinger et al. 1990, Scheffer et

al. 2001, D'Odorico et al. 2006, Ravi et al. 2007, Wookey et al. 2009, Baudena et al. 2010, D'Odorico et al. 2010).

While the mechanisms underlying encroachment of different grasslands may vary, many examples of encroachment exhibit a pattern of rapidly increasing woody coverage and sustained encroachment (Schlesinger et al. 1990, Briggs et al. 2005, Wookey et al. 2009), which is diagnostic of bi-stability (Scheffer et al. 2001). Notably, the mechanisms that facilitate woody encroachment of tallgrass prairie represent an inversion of the mechanisms that maintain grass dominance in mesic grasslands (i.e., intensified competition for water and increased fire intensity; Scholes and Archer 1997, Knapp et al. 1998, Sankaran et al. 2005, Bond 2008, Staver et al. 2011). Taken together with the observation that current encroachment of tallgrass prairie occurs despite historical fire frequencies (Briggs et al. 2005), this contrast highlights the likely possibility that tallgrass prairie is a bi-stable system as well.

This and other studies (Schlesinger et al. 1990, D'Odorico et al. 2006, Ravi et al. 2007, Wookey et al. 2009, Baudena et al. 2010, D'Odorico et al. 2010, Staver et al. 2011) suggest that woody plants have a strong propensity for expansion into grasslands following initial shrub establishment. Therefore, to separate the mechanisms of initial establishment from trajectories of woody encroachment, future work needs to identify how global change phenomena are affecting rates of recruitment from seedling to adult stages. Because woody encroachment of tallgrass prairie occurs even in areas with greater fire intensities than those that existed prior to European settlement (e.g., Knapp et al. 1998, Briggs et al. 2005), we suspect that global drivers such as CO_2 emissions and N-deposition may be inciting the initial establishment of shrubs in tallgrass

prairie.

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Table 2. Woody species characteristics and long-term cover dynamics

Table 1. Woody species characteristics and long-term cover dynamics.

Species	Life form	Rooting depth§	N-fixing	Cover (%)		Frequency (%)		Size index (%)	
				1983–1985	2007–2009	1983–1985	2007–2009	1983–1985	2007–2009
Cornus drummondii	clonal	deep	no	0.0	18.5	0	35	0	47
Rhus glabora	clonal	deep[1]	no	0.0	8.2	0	28	0	27
Prunus americana	clonal	shallow[1]	no	0.0	4.0	0	13	0	16
Ceanothus americanus	non-clonal	shallow[2]	no	0.0	0.1	0	5	0	2
Amorpha canescens	non-clonal	shallow[2]	yes	4.2	4.7	43	46	5	6
Other species‡	various	unknown	various	0.3	5.7	3 (±2)	8 (±5)	1 (±0.4)	6 (±4)

Note: Sources are: 1, McCarron and Knapp (2004); 2, Nippert and Knapp (2007*a, b*).

§ Species were considered to have a shallow rooting depth if they obtained the majority of their water from 0–30 cm, where grass roots predominate.

‡ For 'Other species', cover is the aggregate cover of species in this group, whereas frequency and size index are averages of all species. This group is made up of 7 species total. Numbers in parentheses denote ±1 SEM.
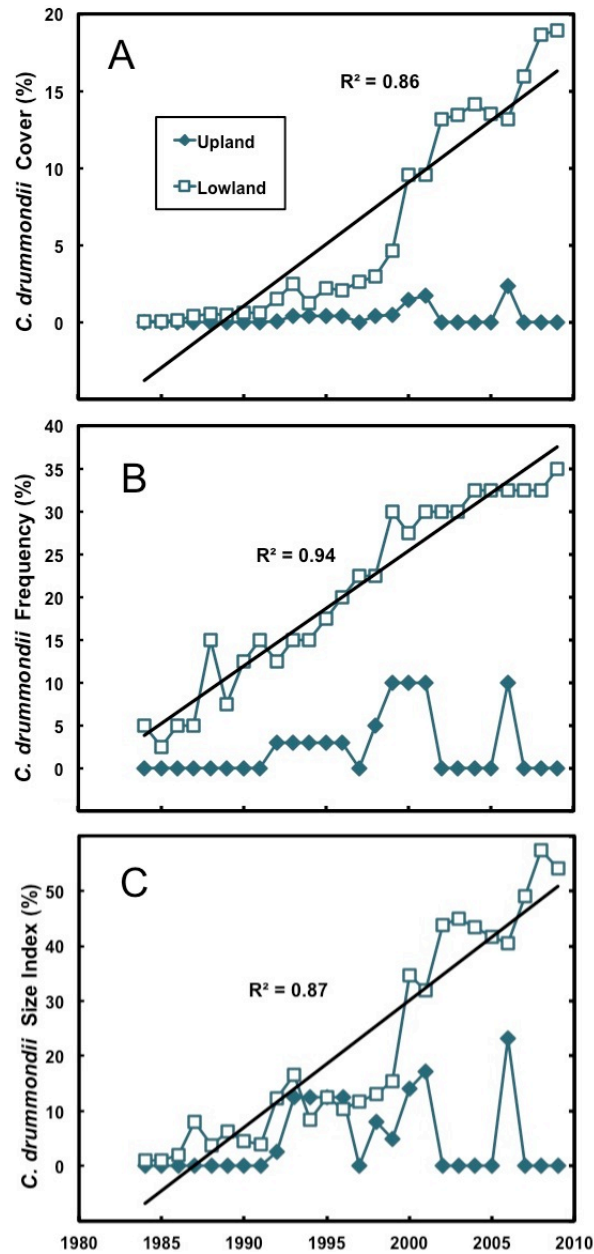
Figure 3.1 The long-term trends in (A) aerial cover of the shrub *Cornus drummondii* (B) the percentage of plots with *C. drummondii* and (C) size index of *C. drummondii* within the permanent community plots (n= 80, 10 m^2 plots), measured in uplands (circles) and lowlands (squares). For this analysis, the size index is calculated as the aerial coverage divided by the number of plots containing *C. drummondii*.
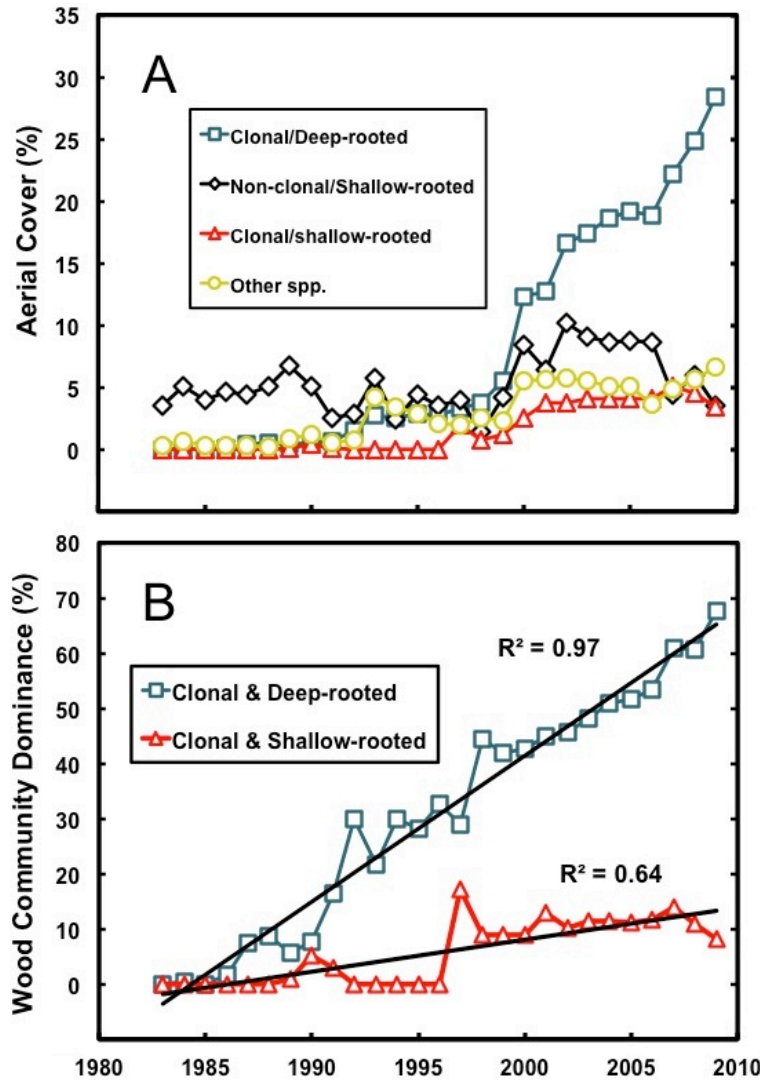
Figure 3.2 (A) The long-term changes in cover for 4 woody functional groups over time: species that are clonal and deep-rooted (squares), clonal and shallow-rooted (diamonds), non-clonal and shallow-rooted (triangle) and the remaining species (circles). (B) Change in the % of total woody cover that is clonal deep-rooted species (squares) and clonal shallow-rooted species (triangles). Woody Community Dominance = % cover of woody functional group / % cover of all woody plants.
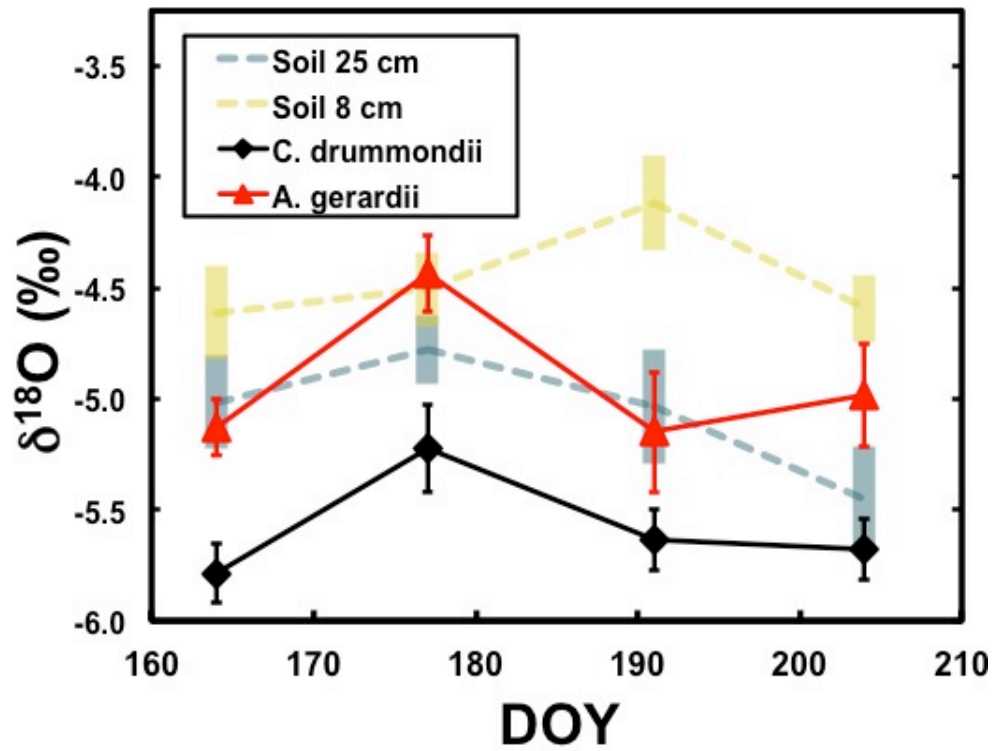
Figure 3.3 Temporal trends in δ¹⁸O of soil water at 8 cm and 30 cm depth and *Cornus drummondii* (triangles) and *Andropogon gerardii* (diamonds) xylem water. Data are all transect intervals combined. Shaded bars denote (± 1SEM) and correspond to data series of the same color.
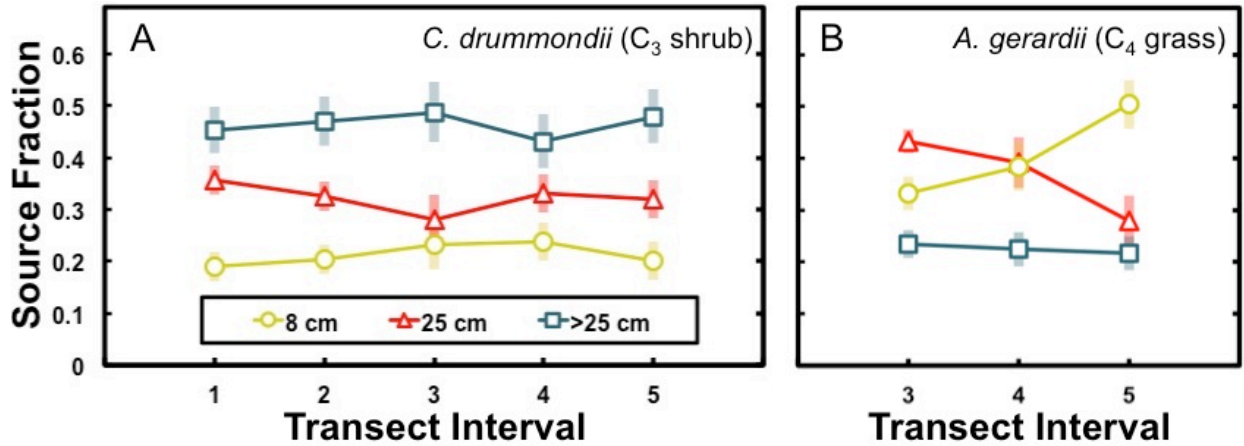
Figure 3.4 Mean proportional contributions (± 1SEM) of soil water from different depths to the isotopic mixture of xylem-water for (A) *Cornus drummondii* **and (B)** *Andropogon gerardii*. **Source fraction is the Bayesian estimate of the proportion of source water obtained from each depth by each species, at each transect interval. Transect interval 1 = the center of the mature shrub, 2 = point between the center and edge of the mature shrub, 3 = the edge of the mature shrub, 4 = shrub clones, 5 = shrub that are younger and further away than those at interval 4.**

Fig 5.
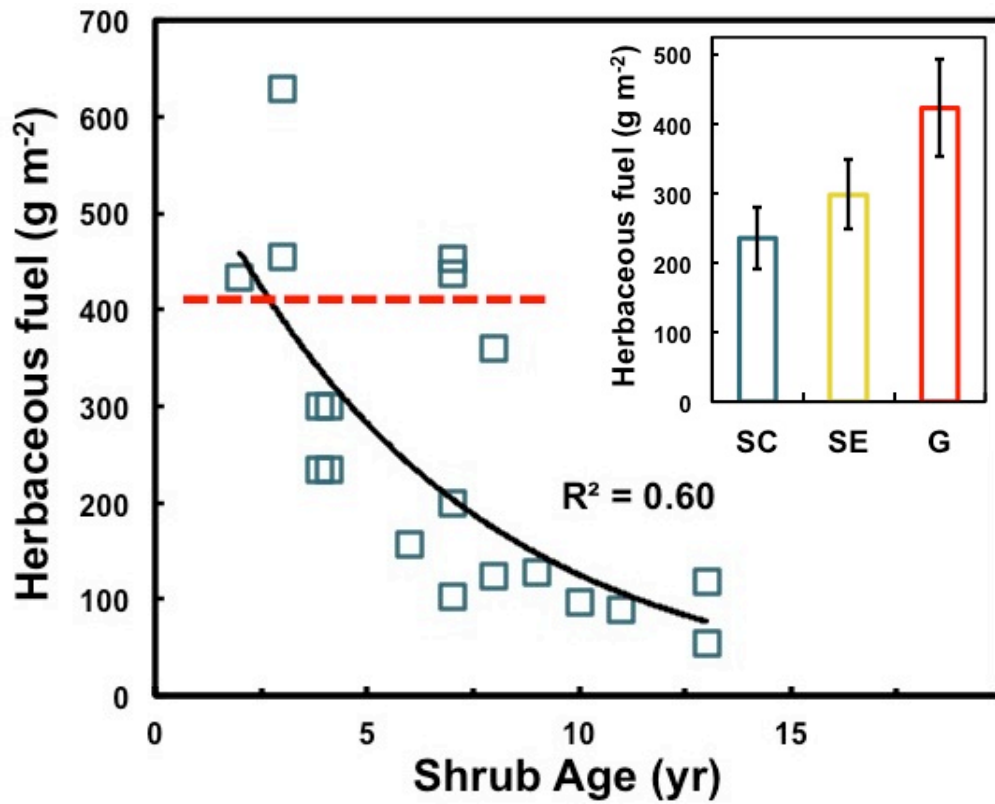
Figure 3.5 Herbaceous fuel at the shrub edge (interval 3) in relation to shrub age. The horizontal red line denotes fuel levels in open grassland before burning. Some points are jittered to make them visible. (Inset) average herbaceous fuel at the shrub center (SC), shrub edge (SE) and open grassland (G). Error bars denote ± 1SEM.
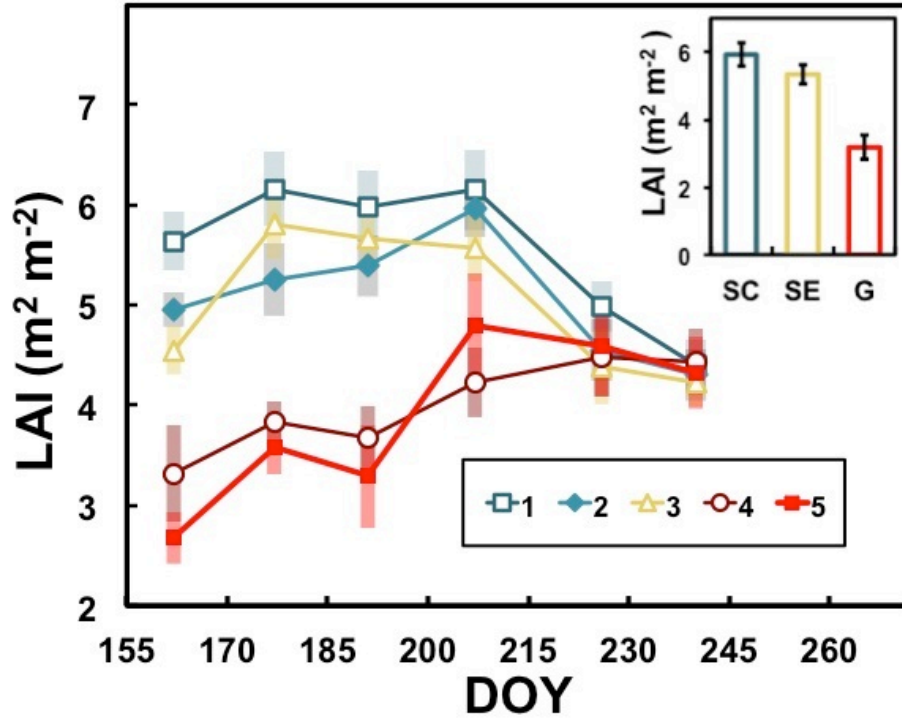
Figure 3.6 Mean changes (± 1SE) in LAI from June-September, 2009 for each equidistant transect interval. Intervals 1-3 are the mature shrub while 4-5 are developing clonal stems in the surrounding grass matrix. (Inset) average LAI values for the first 3 sampling periods at the shrub center (SC), shrub edge (SE) and open grassland (G). Error bars denote ± 1SEM.

Chapter 4 - Comment on "Hirota et al. 2011, Global Resilience of tropical forest and savanna to critical transitions'

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Abstract: Hirota et al. (1) used spatial data-sets to quantify a largely temporal phenomenon: tree-cover bi-stability. We reanalyzed their data to determine the frequency of unstable states and found that unstable states are common in low precipitation regions. Taken together with the existing literature, we argue that spatial data-sets might under-estimate bi-stability in semi-arid ecosystems.

Comment:

Determining the thresholds between grassland, savanna and forest states is critical to forecasting how terrestrial ecosystems will respond to global change. Hirota et al. (1) reported in this journal that tree-cover in the southern hemisphere is distinctly tri-modal: areas with a tree-cover of 0-5% (grassland), 10-50% (savanna) or 60-80% (forest) predominate, whereas ecosystems with a tree-cover of ~5-10% and ~50-60% are often rare. The authors propose that the frequency of these tree-cover ranges is proportional to stability, and thus, rare ranges of tree-cover constitute unstable intermediates situated between stable states. While spatial data-sets can reach unparalleled levels of replication, this type of analysis cannot distinguish between environmental variability and the error due to substituting space for time. We have tested assumptions made by Hirota et al (1) by re-analyzing their data to determine the frequency of

unstable states, a potential indicator of error induced by spatial techniques. These results, in combination with the existing literature on stable state dynamics, strongly suggest that spatial tools do not accurately quantify bi-stability in semi-arid ecosystems (~300-600 mm precipitation/yr).

Spatial patterns of bi-stability ultimately reflect processes that operate across time. Even if most vegetation patches of the landscape are strictly bi-stable, "unstable" states will occur as patches transition from one stable state to another across the landscape. As a whole, the frequency of "unstable states" will be common when: 1) state changes occur slowly; 2) when state change occur more often, and; 3) when more patches are not actually bi-stable. The first two factors are confounding because they make unstable intermediates appear stable across the space, even when they are unstable over time. The third factor captures is the variable of interest, and captures the percentage of the landscape that does not conform to stable-state dynamics. However, the limited temporal scale of MODIS data makes it impossible to differentiate these patches from those that are transitioning from stable states.

To test the potential influence of these factors, we re-analyzed frequency diagrams of tree-cover from Hirota et al. (1), who only reported the frequency of stable states and included unstable intermediates as part of the "savanna" biome. Here, we report the frequency of unstable ranges as their own discrete states, with respect to precipitation(2). The data show that the frequency of both unstable intermediates peaks when the proportion of two opposing stable states is equal (Fig 1). Peaks in instability likely occur at these cover classes because: 1) more ecosystems are undergoing state-transitions when conditions equally favor two opposing stable states and; 2) the unstable intermediates are slightly more stable at these junctures, indicating a shifting gravity between two stable states.

While the position of unstable peaks is expected, the magnitude of the grassland/savanna intermediate is surprisingly high. The grassland/savanna intermediate reaches a frequency of ~13.5% for 600 and 900 mm precipitation/yr, which is 30% of either stable state and equivalent to ~1053 km^2 within the area analyzed by (1). This frequency is impressive considering that the grassland/savanna intermediate only encompasses a 5% range of tree-cover, compared to an average range of 25% for stable states. In contrast, the savanna/forest intermediate only reaches a maximum frequency of 7% and for just a single MAP value, which constitutes 15% of the opposing forest/savanna states.

Several lines of evidence suggest that the grassland/savanna intermediate is common because grassland/savanna transitions occur slowly in semi-arid ecosystems. Maximum population growth rates, especially for trees, should be slow in semi-arid regions due to decreased soil-moisture (1,3,4,5). In addition, the primary feedback mechanism that facilitates state-shifts in semi-arid ecosystems is grass and tree-mediate changes in soil properties (6). These mechanisms typically take at least a decade to act (6). In contrast, grassland/savanna transitions in mesic ecosystems (3) and savanna/forest transitions (7) usually involve fire feedbacks, which have an almost immediate effect, but are more reversible than soil-reinforced stability. The greater reversibility of these feedbacks may explain why the unstable state is so common at 900 mm precipitation, because greater reversibility increases the likelihood of frequent state shifts.

The available literature on tree-cover change over time supports our hypothesis that grassland/savanna transitions occur more quickly in wetter ecosystems (see 8 for inclusion criteria). Although the number of temporal studies is limited, the general trend is that drier ecosystems usually have much slower transition rates (Table 1). For example, it can take ~35 yrs

for Chihuahuan desert to increase from 5 to 10% shrub cover, which is inconsistent with the view that all grassland/savanna transitions are abrupt (1). In contrast, the fire-driven transitions in mesic tallgrass prairie can cross the 5-10% window in 2 years (14). We also found that many temporal studies support the idea that 5-10% tree cover is also unstable across time. For instance, the cover of shrubs in southern Africa usually increases slowly from 0-5% cover, but increases quickly when it enters the 5-10% tree-cover window (12). A strikingly similar pattern was observed recently in the mesic tallgrass prairie (14). However, studies in the Sonoran and Chihuahuan deserts found that that shrub cover can oscillate in the 5-10% cover range for 5 to 35 years (9,11). These examples illustrate the need for further work to determine if 5-10% cover is consistently unstable across time.

Hirota and colleagues (1) have greatly expanded the understanding of stable state dynamics in terrestrial ecosystems. This re-analysis of their data has revealed distinct patterns of unstable state-state frequency that are of theoretical and applied significance. Combined with temporal studies in the existing literature, these data suggest that the use of spatial techniques is potentially confounded by slow rates of state-transition in semi-arid ecosystems. This feature of semi-arid state shifts makes unstable states appear common across space, even though such states are probably unstable across time. With only 12 years of MODIS data, it will would take 20 more years for spatial tools to create a data-set capable of quantifying semi-arid state-shift rates. These results highlight the necessity to identify existing temporal data-sets in order to predict when and where semi-arid state shifts will occur.

References and Notes:

1. M. Hirota, M. Holmgren, E. H. Van Nes, M. Scheffer. *Science* 334, 232 (2011).

2. We reanalyzed data from figure 1 in Hirota et al. (1) to determine the frequency of unstable states. In keeping with the analysis by Hirota et al. 2011, we used 5-10% tree-cover as the grassland/savanna intermediate and 50-60% tree-cover as the savanna/forest intermediate. Even though the unstable range for savanna/forest is smaller for some continents (for example 55-60%), we used this wider range of 50-60% because the results presented by (1) consider all continents together. Thus, the frequency of the savanna/forest intermediate should be considered to be an overestimate. 0-5% tree-cover was considered grassland, 10 to 50% was considered savanna, and 60-80% was considered forest. Curves are fit to frequency diagrams using the same logistic regression model as Hirota and colleagues (1).

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8. We identified studies using the ISIS web of knowledge (wokinfo.com) and searching for "tree cover time". We only used studies with reasonably small time-steps between sampling, because it is difficult to accurately transition rates when time-steps between sampling are long. Table 1 includes the minimum time step so that minimum observed transition rates can be compared to the minimum transitions rates detectable by each study. In many studies, different minimum and maximum transition rates were possible and observed.

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Table 3 A summary of existing fine-scale studies on grassland/savanna transitions over time.

Country	MAP (mm precip/yr)	Transition type	Min. transition time (yrs)	Max. transition time (yrs)	Min. time-step (yrs)	Transition Mechanism	Tree/Shrub	Reference
North America	300	Grassland→ Savanna	5	37	5	Soil feedbacks	Shrubs	9
North America	600	Savanna→ Grassland	2	>2	2	Acute drought	Trees	10
North America	635	Savanna→ Grassland	5	>5	5	Fire/soil feedbacks	Trees	11
Swaziland	675	Grassland→ Savanna	8	50	8	---	Shrubs	12
Botswana	680	Grassland→ Savanna	3	---	3	---	Trees	13
North America	850	Grassland→ Savanna	2	---	1	Fire feedbacks	Tall shrubs	14
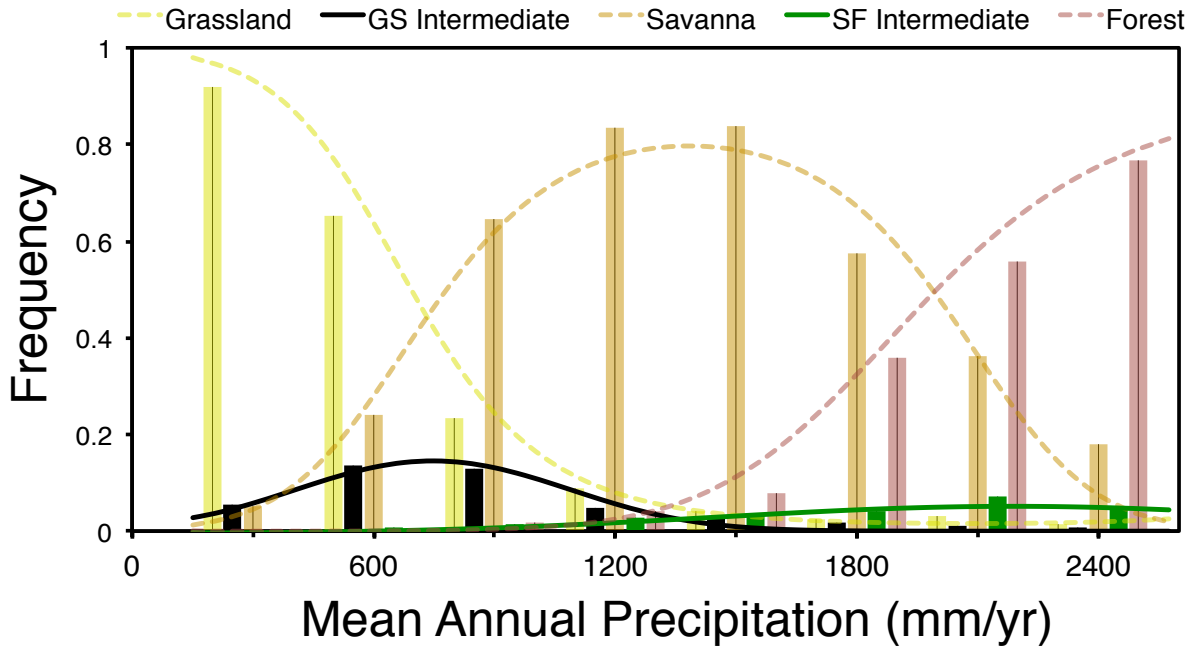
Figure 4.1 The frequency of unstable states: grassland/savanna intermediate (black) and savanna/forest intermediate (green), compared to the frequency of stable states: treeless (yellow), savanna (orange) and forest (red). The grassland/savanna intermediate is all areas with a tree-cover of 5-10%, the savanna/forest intermediate is 50-60%, the grassland state is 0-5%, the savanna state is 10-50%, and the forest state is 60-80%. Data encompass a precipitation gradient covering primarily the non-mountain, non-arctic, and non-developed areas of Africa, Australia, and South America.

Chapter 5 - Abrupt shifts of mesic grassland to shrubland: evidence for thresholds, alternative attractors, and regime shifts

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 non-linear but reversible threshold process, or a transition between alternative attractors that is non-linear and prone to hysteresis. Using a 28 year dataset 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. Non-linear 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, non-linear, 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 years. These thresholds may provide adaptive potential for managing non-linear behavior in socio-ecological systems in a changing environment.

Keywords: Alternative Stable States, Bi-Stability, Bush encroachment, Catastrophic Shifts, Critical Transitions, Dynamical Systems, Fold Bi-Furcation, 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. 2003, Knapp et al. 2008, Eldridge et al. 2011, Barger 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. 2008) and the important societal role of semi-natural grasslands (Ellis et al. 2009).

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 2004, 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; "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 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, Baldocchi et al. 2004, Van Wilgen et al. 2004, Tueling 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 promotes 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 2004), but possible with theoretically derived analytical approaches and extensive spatial and/or temporal datasets (Fig 1 and references therein). 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 non-linear 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 2004, Folke et al. 2005, 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 2004, Schroder et al. 2005, Ratajczak and Nippert 2012, Hanan et al. *in press*, 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 2004, 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-year dataset with annual resolution and a factorial design of fire and grazing manipulations. This experimental, multi-faceted, 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 & Experimental Design: Konza Prairie Biological Station (KPBS) is a National Science Foundation Long-Term Ecological Research Site in northeastern Kansas, USA (39°05' N, 96°33' W; konza.ksu.edu). 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 grassland except along riparian areas, but native woody plant cover has increased over the last half-century, typically attributed to fire suppression, over-grazing, and exurban expansion (Briggs et al. 2005). The pre-European fire frequency is estimated to be ~4 yr/fire. Prior to the mid 1970's, KPBS was burned every ~2-3 years and grazed moderately by cattle (Briggs et al. 2005). The mean annual precipitation is 835 mm/yr and the growing season temperature (May-Sept.) is 32.5°C, with the mean monthly maximum in July (36.1 C). From 1977 to 1983 the 3,487 ha area of the KPBS was split into catchment basins with different prescribed fire frequencies (1, 3 to 4, or 20 yr/fire; Appendix B). Grazing by bison (*Bos bison;* a large native ungulate grazer) occurs within the central ~1/3 of the site representing a light to moderate level of grazing (~1/2 grazing intensity of commercial cattle operations; Collins and Calabrese 2012). Thus, we had data from a factorial study with grazed and ungrazed treatments, with 3 fire return intervals per grazing treatment: 1 yr, 3 to 4yr, and 20 yr fire frequencies.

Across these treatments, we assessed the cover of different plant functional groups using a long-term dataset (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

dataset was to quantify herbaceous plant dynamics, and 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 long transects, with five 10 m^2 circular

plots per transect, and four transects per treatment (treatment = 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 (% area), frequency (# 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, and references therein, for more information on this dataset 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 4yr 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 in 1993. These plots were started in largely herbaceous-dominated plots

and therefore, are similar to the core data-set in 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 (*Andropogon gerardii, Schizachyrium scoparium, Panicum vigratum, and Sorghastrum 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 accounts for jumps across certain ranges of cover. Specifically, we looked at whether target and non-target functional groups: 1) were prone to non-linear behavior at the same time as shrub and grass cover; and 2) tended to show non-linear behavior and/or show bi-modality 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. 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 non-linear 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 bi-furcation (Fig 1; Scheffer and Carpenter 2005). 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 (March-May), summer (Jun.-Aug.), and fall (Sep.-Nov.). Climate data are from the Manhattan, KS 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 non-linear 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 non-linear 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), 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 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 4yr grazed and 20yr grazed treatments, and 10% cover classes 4 yr ungrazed and 20 yr ungrazed. Bin sizes reflect the common approach where the # 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 "shrub frequency" (# of shrubs/ # 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 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). "Shrub size index" indicates if shrubs are expanding within patches (% shrub cover / # of shrubs). We compared whether changes in shrub cover were associated with changes in frequency and/or size using delta values where: Δ(cover) = cover_{t+1} – cover_t. We used the same general equation for Δfrequency and 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 (N.C. USA, Cary 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 years, with an average slope of ~0.5% cover increase yr^{-1}. In these treatments, the dynamics of shrub cover

changed between 1998 to 2001, with a large increase in shrub cover of ~5-10 % over just 1 to 3 years, followed by more than a decade of rapid shrub expansion (the new rate of shrub expansion ranges from 1.4 to 2.7 % cover year^{-1}, 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 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 (Fig 2 and 3, Appendix 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 to 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 non-linear behavior from 1998-2001 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 non-linear 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 = $ ~0.60 for treatments with a fire frequency >1 year/fire). 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 bi-modal within treatments (i.e. the bi-modal 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 sub-dominant grasses had diverse distributions depending on the treatment (Appendix B). The cover ranges that were rare for shub cover (5 to 15%), were not rare for the other functional groups assessed (Appendix B), indicating that it is unlikely that shrub-cover bi-modality 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 non-linear 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 non-linear behavior, but cover is still below the threshold where non-linear behavior would be predicted to emerge.

Discussion:

This study provides the first empirical evidence that the transition between mesic grasslands and shrublands is non-linear, 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 non-linear transitions in this ecosystem was enabled by long-term high-resolution data, which is a basic prerequisite for testing ecosystem transitions but is currently unavailable for many terrestrial ecosystems.

Non-linear 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 was followed by a 5-fold 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 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 non-linear, 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 to 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 to 2001 are consistent with 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 non-linear 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 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 4 and 20 yr fire treatments. These results suggest 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 to 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 &

Archer 1997, Anderies et al. 2002, Van Wilgen et al. 2003, Bond 2008, Tueling et al. 2010,

Higgins and Schieter 2012, Hoffmann et al. 2012, Nippert et al. 2012, Schieter 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 Schieter 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, non-linear 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 datasets (Staver et al. 2011, Scheffer et al. 2013, but see Hanan et al.

2013). When an ecosystem shows bimodality of state and a non-linear 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 non-linearities 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 1yr 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 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 2002). We suspect grazing has created favorable micro-sites 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 observations). 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 "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 (Fig 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, similar to the decline in grass cover that occurs 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. 2005). 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 2 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, Folke et al. 2004, Scheffer and Carpenter 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 fire (2 yrs per fire) 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. 2009)— must consider that this system is capable of abrupt and sometimes difficult to reverse transitions.

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Table 4 Statistical fits of varying temporal models analyzed.

Treatments	Single Line (r2/AIC)	Logistic (r2/AIC)	Split Line Ind. Slopes (r2/AIC)	Split Line Ind. Intercepts (r2/AIC)	Split Line Ind. Slopes & Intercepts (r2/AIC)	Slope 1983-1999	2000-2012	Change in Intercept (% cover)
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

Fig 1.

| Linear & Reversible | Threshold & Reversible | Bi-Stability & Hysteresis |
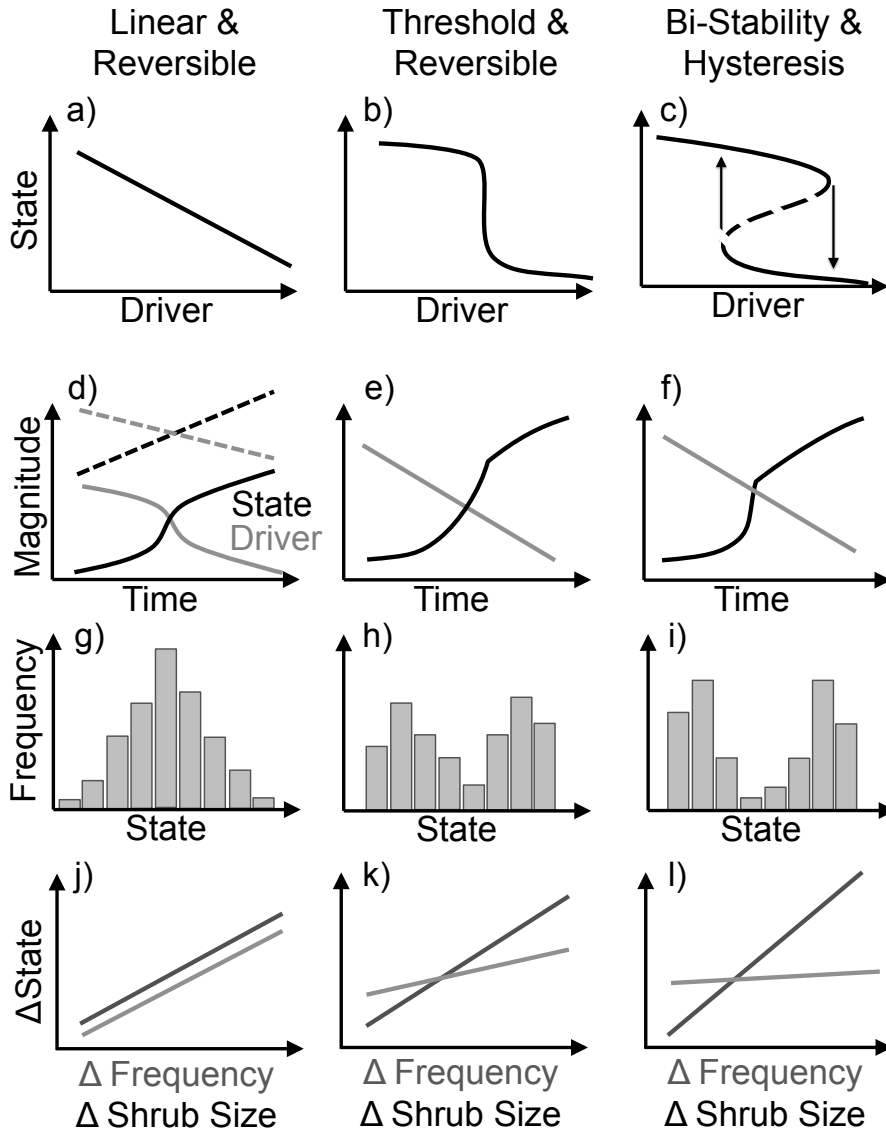
Figure 5.1 Depiction of different types of internal dynamics in ecosystems with varying linearity and hysteresis (a-c) and their expected behavior (d-i). Panels (j-l) depict hypotheses specific to our study system, linking positive feedback mechanisms to threshold transitions. The first row shows the relationship between state and driver variables in: linear (a), threshold (b), and alternative attractor systems (c). For a-c, black lines depict stable equilibria, dotted 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. 'slow' variable) and we explore potential "driver" variables. Panels (d-f) show the expected temporal behavior of an ecosystems state (black line) in the three different system types,

under different scenarios of changes in driver variables over time (grey lines). Note that in (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 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. Panels (a-i) are based on (Holling 1973, Noy-Meir 1975, Walker 1981, May 1977, Scheffer et al. 2004, Folke et al. 2005, Schroder et al. 2005, and Bestelmeyer et al. 2011), while (j-i) are based on concepts developed in (Ratajczak et al. 2011, D'Odorico et al. 2012, Nippert et al. 2013)

Fig 2
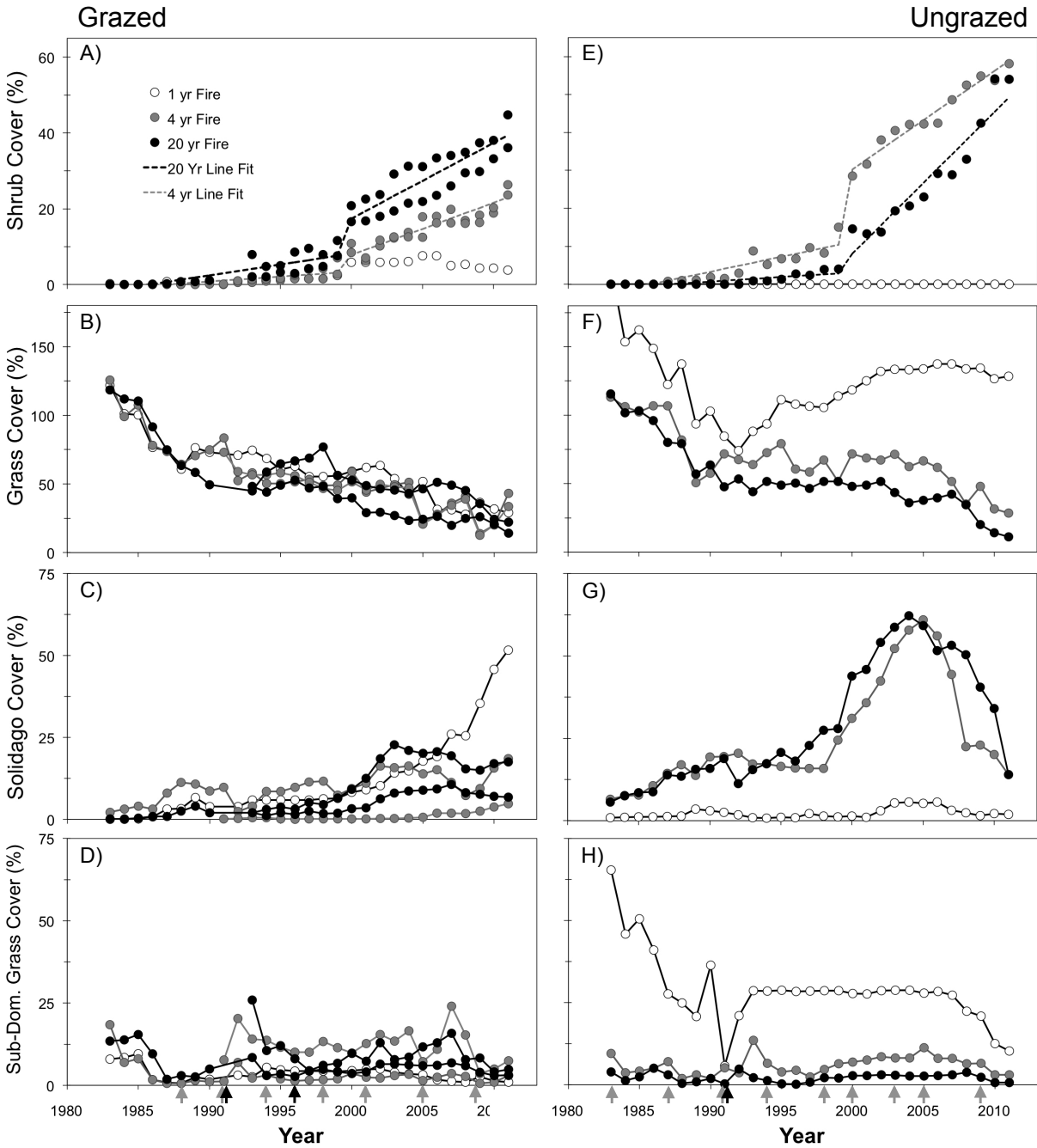
Figure 5.2 Temporal patterns of shrub cover (a and e), dominant C$_4$ grass cover (b and f), *Solidago* spp. cover (c and g), and subdominant grass cover (d and h), for grazed (first column) and ungrazed treatments (second column). 20 yr fire treatments appear as black circles, 4 yr fire treatments as grey circles, and 1 yr fire treatments as open circles. In panel a and e, dashed lines show split linear fits for treatments with fire frequency >1 yr/fire

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(black for 20 yr fire and grey for 4 yr fire). Arrows below panel (d) and (h) demark the timing of prescribed fires in 4 yr (grey arrows) and 20 yr fire treatments (black arrows).

Fig 3.
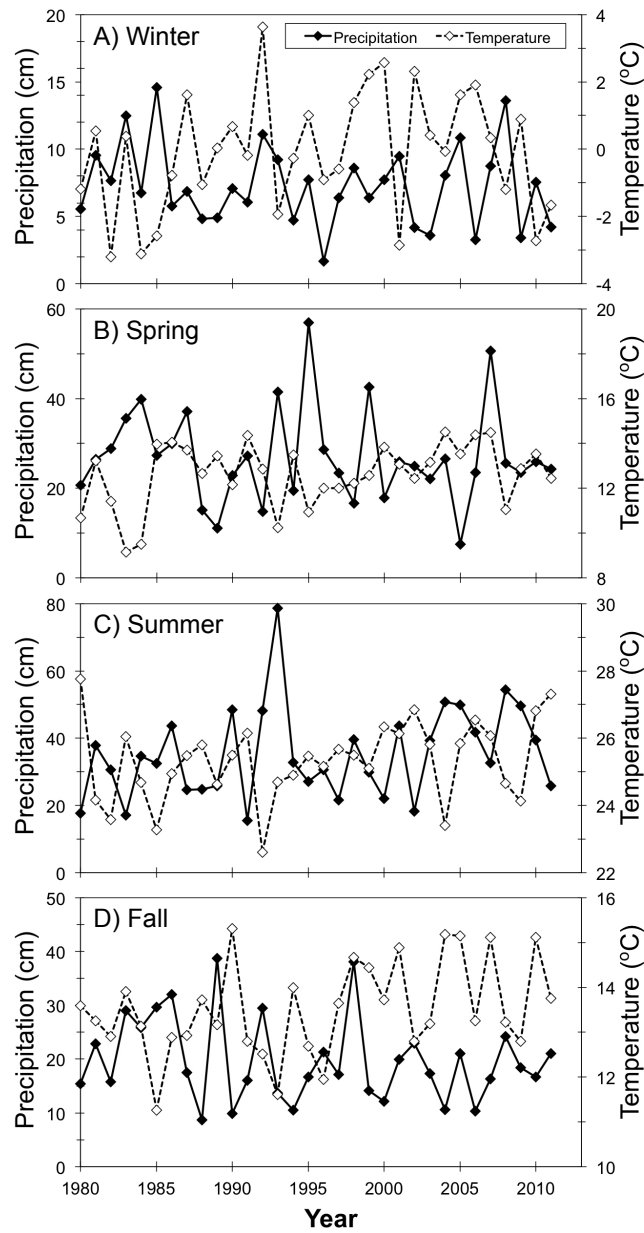
Figure 5.3 Trends in precipitation (black and solid line) and temperature (open circles and dashed line) over the study period for winter (a), spring (b), summer (c), and fall (d).

Fig 4.
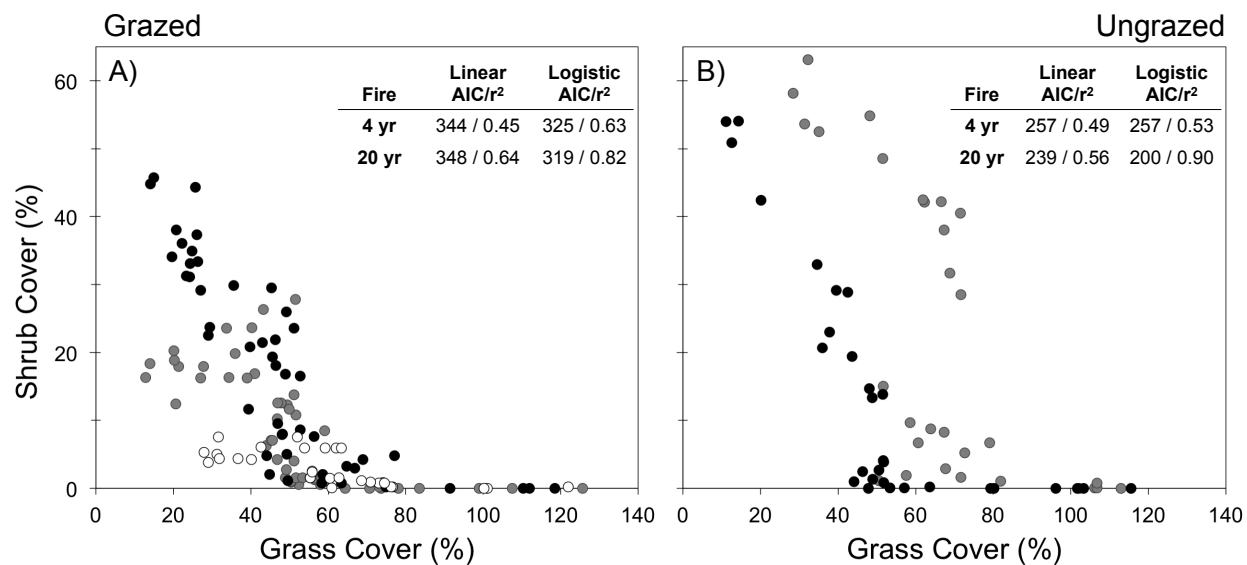
Figure 5.4. Relationship between grass cover and shrub cover in grazed (a) and ungrazed (b) treatments. Fire treatment symbols are as in figure 2 and AIC values of linear and logistic fits are shown as insets.
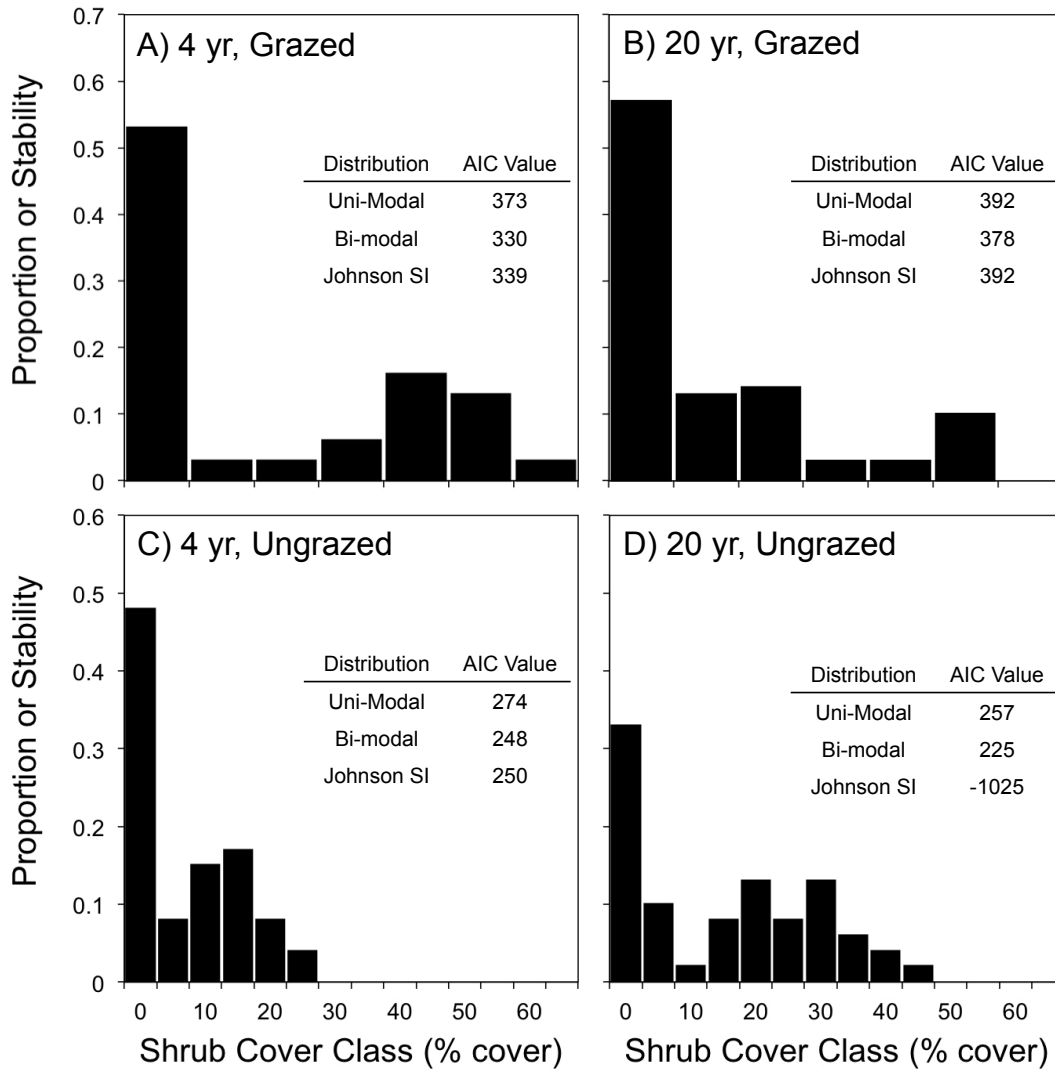
Figure 5.5 Histograms of shrub cover in grazed 4 yr (a) and 20 yr treatments (b), and in ungrazed 4 yr (c) and 20 yr treatments (d). AIC values of different distribution fits are shown as insets.

Fig 6.
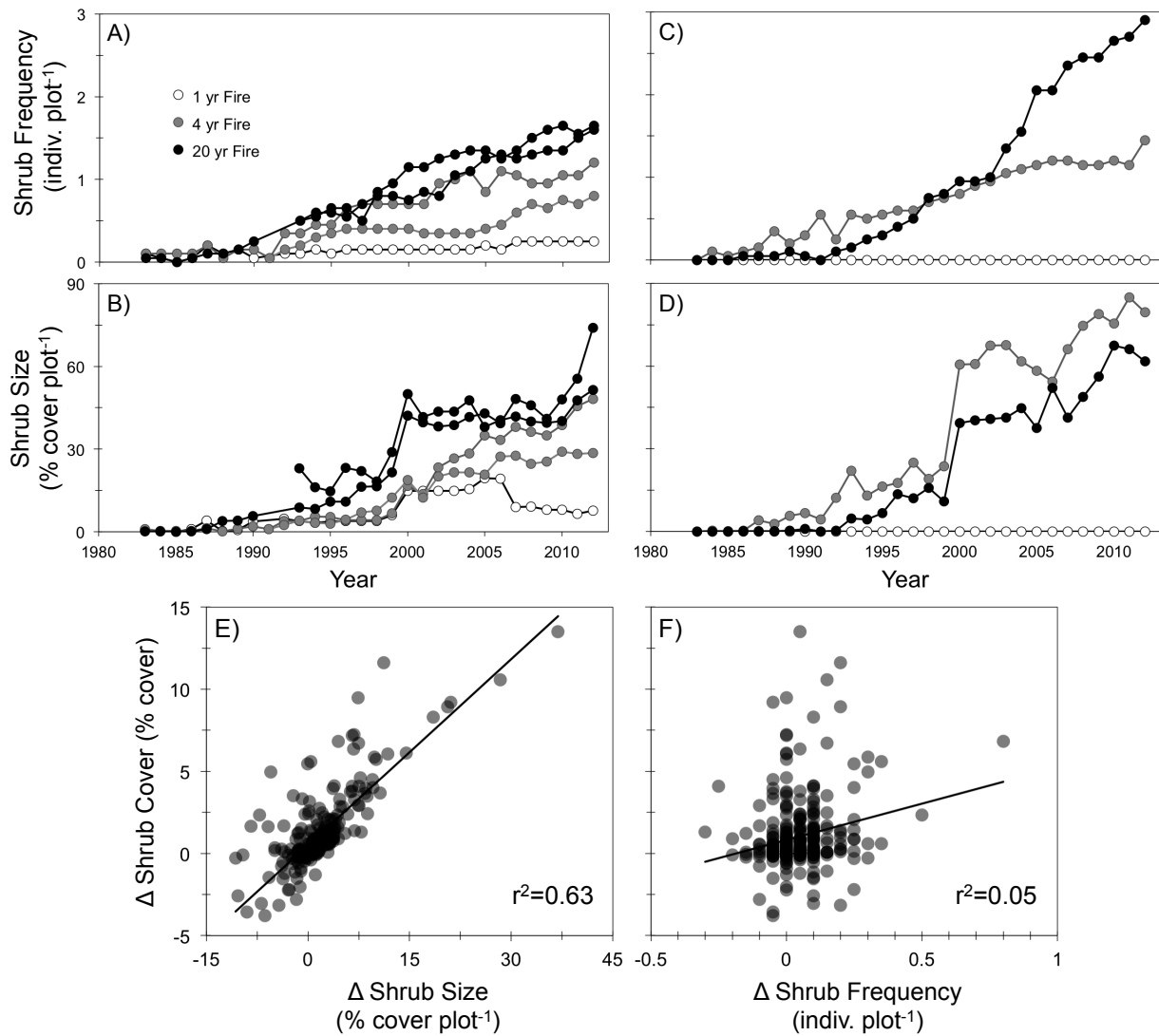
Figure 5.6 The trends in shrub frequency (a and c) and shrub size index (b and d) in grazed (a and b) and ungrazed treatments (c and d). Panel (e) shows the relationship between year to year changes in shrub size index and shrub cover, (f) shows the relationship between year to year changes in shrub frequency and shrub cover. For (e) and (f), all treatments are shown together because relationships were similar across treatments.

Fig 7.

Figure 5.7 Photos at KPBS in 2012 following prescribed burns in a 4 yr fire ungrazed treatment (a) and in a 20 yr fire grazed treatment (b and c). Note that in (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 (b). In contrast to these large shrub clusters, small shrubs and single-stemmed shrubs (c) are exposed to more intense fire and experience higher rates of mortality.

Appendix Items:

Appendix A. History of Data-sets and Analyses of Temporally Limited Data-Sets

Appendix B. Temporal dynamics and modality of non-target functional groups and climate.

Chapter 6 - Fire dynamics control transitions between grassland, shrubland, and woodland basins of attraction in North American Central Plains

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Running Header: Tri-Stability of Grasslands, Shrublands, and Woodlands

Abstract:

1. The climate of many mesic grasslands can also can also support altered states of grass and shrub co-dominance and tree-dominated woodlands. The historical prevalence of mesic grasslands, therefore, has been attributed to competition with C_4 grasses and their ability to facilitate intense and frequent fires.

2. Long-term fire manipulations show that grassland to shrubland transitions in deeper soils is triggered by fire-free intervals ≥ 3 years, and mechanisms that reduce competition of shrubs with grasses for water (deep rooting and clonal expansion). Drought tolerant tree species can establish in a broader range of soil types and depths than shrubs, but require longer fire suppression (~10 year returns). Once transitions to shrublands and woodlands occur, frequent fires do not usually return the system to grasslands.

3. Transitions from grassland to shrubland are consistent with a regime shift, including abrupt state changes, hysteresis, and non-linear relationships between state and driver variables. Once established, the dominant growth forms of each state no longer face demographic bottlenecks and create self-reinforcing feedback mechanisms that modify fire dynamics and competitive interactions.

Synthesis: Mesic grasslands, shrublands, and woodlands constitute opposing basins of attractions, delineated by fire frequency thresholds. Therefore, when maintaining one of these states is preferably, preventing transitions using knowledge of fire frequency thresholds will be more cost-effective than restoration attempts.

Key Words: Alternative Stable States, Bi-Stability, Bush Encroachment, Dynamical Systems, Plant population and community dynamics, Positive Feedbacks, Resilience, Restoration, Tallgrass Prairie, Woody Encroachment

Introduction:

Increases in the density and aerial extent of woody plants (i.e., woody encroachment) are occurring across diverse types of North American grassland ecosystems (Archer *et al.* 1988, Briggs *et al.* 2005, Morgan *et al.* 2007, Van Auken and McKinley 2008, Barger *et al.* 2011, Ratajczak, Nippert & Collins 2012), and in many other grasslands globally (Eldridge *et al.* 2011, Gray & Bond 2013). This recent widespread increase in shrub and tree cover in grasslands and savannas, often referred to as an ecosystem transition, can lead to states of co-dominance of shrubs and grasses or complete conversions of grasslands to shrublands or tree-dominated woodlands (where the climate supports these vegetation types).

Woody encroachment into grasslands has been attributed to a variety of potential drivers operating at global (e.g. elevated CO_2, climate change; Bond & Midgley 2012, Kulmatiski & Bear 2013), regional (e.g. nitrogen deposition, fragmentation; Kochy & Wilson 2001, Briggs *et al.* 2005) and local scales (e.g. over-grazing, fire; Walker *et al.* 1981, Roques *et al.* 2001, Fuhlendorf *et al.* 2008, Van Auken & McKinley 2008). Within mesic grasslands, including North American tallgrass prairie, changes in the timing, intensity and frequency of fire have been implicated as an important proximate driver of transitions from grasslands to shrubland or woodland (Briggs *et al.* 2005, Fuhlendorf *et al.* 2008, Bond 2008, Gibson 2009, Twidwell *et al.* 2013a).

The ramifications of these ecosystem transitions are manifold, with impacts on community composition and vegetation structure (Eldridge *et al.* 2011, Ratajczak *et al.* 2012), ecosystem function (Knapp *et al.* 2008a, Barger *et al.* 2011), ecohydrology (Huxman *et al.* 2005, Awada *et* al. 2012, Brunsell, Nippert & Buck *in press)* and long-term conservation of biodiversity (Gray & Bond 2012). Woody encroachment into mesic grassland also has potential

impacts on regional economies. The replacement of C_4 grasses by shrubs or trees results in loss of forage for large grazers (Hoch, Briggs &Johnson 2002, Briggs *et al.* 2005, Limb *et al.* 2010) and directly impacts livestock production, which is the primary economic enterprise in North American rangelands (Limb *et al.* 2011).

Conceptual Framework:

The process of woody encroachment into grasslands has been described using many different conceptual and theoretical frameworks, including directional succession, gradual linear dynamics, alternative stable states, rapid changes in ecosystem drivers, and physiological thresholds (Walker *et al.* 1981, Archer *et al.* 1988, Scholes & Archer 1997, Frehlich *et al.* 1999, Roques *et al.* 2001, Anderies et al. 2002, Folke *et al.* 2004, Briggs *et al.* 2005, Briske, Fuhlendorf, & Smeins 2006, Briske *et al.* 2008, Elliot 2012, Hoffman *et al.* 2012, Bestelmeyer *et al.* 2013, Twidwell *et al.* 2013a). Distinctions among these frameworks are based largely on determining what types of pressures elicit ecological responses, the severity of said responses to changes in salient pressures, and the temporal dynamics of drivers (i.e. press vs. pulse temporal change) (Bestelmeyer *et al.* 2011, Collins *et al.* 2011). For drivers that do elicit a response, some ecosystems may show gradual, linear responses to external forcing (linear systems), whereas systems with threshold responses may be initially resilient, but eventually undergo an abrupt, non-linear transition in response to continued forcing (threshold systems) (Noy-Meir 1975, May 1977, Holling 2001, Walker 1981, Folke 2006, Briske *et al.* 2008, Scheffer 2009, Bestelmeyer *et al.* 2011). In more extreme cases (termed "critical transitions" or "regime shifts"), some threshold transitions also exhibit hysteresis (Fig. 1), where after a critical threshold is crossed eliminating the external forcing or returning driving variables to their pre-transition state or rate

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may be insufficient to reverse the state transition (Noy-Meir 1975, May 1977, Walker *et al.* 1981).

Discerning the internal dynamics of ecosystems is not just an exercise in categorization; if an ecosystem is capable of regime shifts, then management to maintain a desired state must incorporate the potential for thresholds or risk costly efforts to reverse regime shifts (Holling 2001, Folke *et al.* 2004, Walker & Salt 2006, Scheffer 2009). Knowledge of potential thresholds is also critical for successful ecosystem restoration, because in systems with thresholds minor pushes on the system will rarely return the ecosystem to its previous state and instead, more significant action may be required to achieve the desired state transition (Briske et al. 2008, Suding and Hobbs 2009).

Determining if system responses to changing drivers are linear, threshold, or critical thresholds is challenging and requires multiple lines of inference, including but not limited to mechanistic studies and experimental manipulations (Scheffer & Carpenter 2004, Schroder *et al.* 2005, Bestelmeyer *et al.* 2011, D'Odorico *et al.* 2012). Mechanistic studies of ecological thresholds typically focus on demography and feedback processes (e.g. Archer *et al.* 1988, Roff & Mumby 2012, Higgins & Scheiter 2013), because ecological thresholds occur primarily in systems with demographic barriers and/or strong feedback mechanisms (De Roos and Persson 2002, Walker & Salt 2006, D'Odorico *et al.* 2012, Boerlijst, Oudman, & Roos 2013, Higgins & Schieter 2013). In particular, demographic bottlenecks, either as a result of evolved life history traits or ecological constraints (Grime 1979), can suppress a potentially dominant functional group (De Roos & Persson 2002, Higgins & Schieter 2012). The difference between feedbacks and demographic bottlenecks can be difficult to disentangle, because feedbacks by one group can create demographic bottlenecks for another group or species. However, feedbacks generally refer

to sets of interactions that amplify (positive feedbacks) or dampen external pressures (negative feedbacks; Walker & Salt 2006, D'Odorico *et al*. 2012). Experimental approaches can identify thresholds by altering driver variables and determining whether a system exhibits linear or threshold relationships between driver and state (Scheffer & Carpenter 2004, Bestelmeyer *et al*. 2011). Reversing the change in drivers can identify hysteresis (different trajectories of change in a reversible process, depending on initial state; Fig. 1)

Here, we synthesize and expand upon recent research investigating the role of fire as a driver of woody encroachment in mesic grasslands (i.e., tallgrass prairies) of the North American Central Great Plains (CGP). We review the evidence for whether altering fire frequency results in threshold transitions and hysteresis, and provide a mechanistic overview of how grass, shrub, and trees respond to and alter fire and competition dynamics. We draw heavily upon more than 30 years of extensive research manipulating grazing and fire frequency in a North American tallgrass prairie at the Konza Prairie Biological Station (KPBS), as well as data from other tallgrass prairie sites in the region. For the purpose of this review, we define the Central Great Plains as an ecoregion bounded to the south by the Cross-Timbers region, to the north by transition from C_4 grass dominance to C_3 grass dominance, to the west by the transition to mixed grass prairie, and to the east by deciduous forest (similar to Barger *et al.* 2011). Our review first addresses the effects relationship between fire frequency and transitions to shrubland, and then transitions to tree-dominated woodlands.

The focus on temperate mesic grassland transitions is timely and novel, given the need for increased conservation efforts in temperate grasslands (Hoekstra et al. 2005) and because many of the paradigms for grassland to woodland transitions are based on studies from tropical and semi-arid climates (e.g. Folke *et al*. 2004, Van Auken & McKinley 2008, Hirota *et al.* 2011,

Staver, Archibald & Levin 2011, Hoffman *et al.* 2012). Moreover, mesic grasslands are particularly responsive to shifts in climate, land management and fire regimes (Knapp *et al.* 2001, Hoch *et al.* 2002, Briggs *et al.* 2005, Brudvig *et al.* 2007, Knapp et al. 2008a, Fuhlendorf *et al.* 2009, Gibson 2009), making this system ideal for studying transitions between multiple ecosystem states. Temperate mesic grasslands are also one of the most widespread coupled human-ecological systems (Ellis *et al.* 2008) and fire is one of the most commonly manipulated components of these ecosystems along with grazing (Mohler & Goodin 2012, Twidwell et al. 2013b).

Grassland to shrubland transitions:

Background:

Historically, much of the CGP was tallgrass prairie vegetation, an herbaceous plant community dominated by rhizomatous C_4 grasses (i.e. warm-season grasses), but also including a diverse subdominant community of C_3 grasses, forbs, and legumes (Fig 2, Collins & Adams 1983, Gibson & Hulbert 1987, Collins & Calabrese 2012). The C_4 grasses of the CGP are well adapted to drought and plentiful light (Knapp 1993), and rely primarily on shallow soil water resources (Nippert and Knapp 2007). Dominant C_4 grass species have high concentrations of roots in the upper soil layers (Jackson *et al.* 1996, Nippert & Knapp 2007, Nippert *et al.* 2012) and are able to maintain stomatal conductance at low soil moistures, and high light environments, and at elevated temperatures and vapor pressure deficits (Knapp 1993, Epstein *et al.* 1997, Knapp *et al.* 2001, Bredenkamp, Spada, & Kazmierczak 2002, Ocheltree *et al.* 2013, 2014). These attributes allow C_4 grasses to achieve rapid water uptake during times with high water availability, withstand drought, and draw down shallow soil moisture to low water potentials, thereby limiting infiltration to deeper soil layers (Nippert *et al.* 2011).

The dominant C_4 grasses are also pyrogenic, capable of producing large quantities of curable herbaceous biomass over short periods of time, which creates substantial quantities of fine fuel to support frequent and intense fires (Gibson, Hartnett, & Merrell 1990, Van Wilgen *et al.* 2002, Bond 2008). Dominant C_4 grasses respond positively to fire, resprouting from belowground meristems and growing vigorously in the post-fire high light environment (Knapp *et al.* 1998, Benson & Hartnett 2006, Schieter & Higgins 2012) (Fig. 2).

The unique physiological traits of C_4 grasses have the potential to create demographic bottlenecks for other species. In many areas of the CGP historically dominated by tallgrass prairie, the balance of precipitation and evapotranspiration is capable of supporting woody vegetation (Borchert 1950, Hayden 1998). Yet, woody plant cover in the region historically was minimal, except along riparian corridors and certain other landscape features (e.g., limestone outcrops, seeps, etc.) (Weaver 1954, Wells 1970, Axelrod 1985, Abrams 1985). Where fire frequency is higher in tallgrass prairie, and perhaps other mesic grasslands, establishment of new individuals by seed, including small shrubs and trees, is rare and may be episodic because over 99% of stem recruitment by herbaceous plants in tallgrass prairie is due to asexual clonal reproduction (Benson & Hartnett 2006). These patterns suggest mechanisms by which C_4 grass species can create powerful demographic barriers to shrub recruitment: they grow quickly in the early growing season particularly in post-fire windows (Briggs & Knapp 2001), they are capable of rapid clonal spread (Weaver 1954, Benson & Hartnett 2006), and they are effective at competing for light aboveground and for water and nutrients in the upper soil layers (Nippert et al. 2012). By producing large quantities of nutrient-poor fine litter upon senescence, the grasses suppress the growth of other plants through reduced light and nutrient availability when surface litter accumulates (Knapp & Seastedt 1986) and by stimulating frequent and intense fires, which

results in direct mortality of unprotected meristems (Benson & Hartnett 2006). As a result, the establishment of shrubs in frequently burned grasslands is rare (Benson & Hartnett 2006, Ratajczak *et al.* 2011).

Once shrubs become established in grasslands, the competitive dynamics between grasses and shrubs change dramatically. Initially, shrub seedlings recruit as single stemmed ramets, which are highly susceptible to top-kill by fire. If seedlings persist for sufficient time to establish a canopy and root system that reduces competition from grasses, expansion for many shrub species occurs via clonal ramet recruitment from rhizomes (Fig 2). Encroaching shrub species in CGP tallgrass prairie, such as *Cornus drummundii* and *Rhus glabora*, form clonal multi-stem clusters in the grassland matrix ("shrub islands") that increase in both height of individual stems and radial extent over time, reaching diameters of up to 15 meters in some instances (Petranka & McPherson 1979, Collins & Adams 1983, Anderson *et al.* 2000, Harrell *et al.* 2001, McCarron & Knapp 2003, Brudvig *et al.* 2007, Ratajczak, Nippert & Ocheltree *in press*). Increasing shrub dominance is negatively correlated with grass cover and biomass, resulting in less fine fuel accumulation (Heisler *et al.* 2004, Lett & Knapp 2005, Ratajczak *et al.* 2011). Decreases in grass biomass are linked to the properties of shrub cluster canopies, which are taller than grasses and very dense, rivaling light interception levels of deciduous forest canopies (Heisler *et al.* 2004, Knapp *et al.* 2008a, Ratajczak *et al.* 2011). Because low fuel microsites occurs at the center and edge of shrub clusters, newer clonal recruits near the edge of growing shrub clusters can benefit from parent ramet effects on micro-site fire suppression. With time these impacts minimize the potential for C_4 grasses to return to pre-transition productivity in short time frames (2 years or less), possibly through meristem limitation (Lett & Knapp 2005). In the rare instances where fire does penetrate mature shrub clusters, shrub stems are capable of resprouting and can reach their

former height and actually increase in density in as little as one or two years (Heisler *et al.* 2004, Hajny, Hartnett & Wilson 2011). Under these circumstances, fire may no longer be a viable filter for reducing shrub expansion and restoring grasses (Fig. 2).

Established shrubs can also circumvent physiological barriers related to summer drought and competition with grasses. In contrast to C_4 grasses (Nippert & Knapp 2007), mature clonal shrubs are deep-rooted, and obtain a larger percentage of their water from deeper soils (< 50 cm), allowing them to reduce competition for water with grasses (Fig. 2) (McCarron & Knapp 2001, Ratajczak *et al.* 2011). Reliance by shrubs on deeper water sources mitigates susceptibility to summer drought, climate variability, and competition with grasses (Nippert *et al.* 2013) and alters landscape energy balance and ecohydrology (Brunsell *et al. in press*). Critically, deep-rooted parent stems also can transfer water to developing clonal stems in the grassland matrix, allowing them to avoid competition with grasses and increase in size until they can access deep soil moisture, suppress grass growth via shading, and begin developing their own clonal recruits (Ratajczak *et al.* 2011, Killian 2012). Combined with effects of shrubs on fire suppression, the clonal growth form and rooting properties of these shrubs creates a positive feedback loop with fire intensity and alters the demographic bottleneck related to shrub recruitment, both of which facilitate shrub cluster expansion (Ratajczak *et al.* 2011, similar to De Roos and Persson 2002, D'Odorico *et al.* 2012).

Considering the competitive interactions between C_4 grasses and shrubs, resource competition and high fire frequencies with sufficient fuel loads are considered the primary filters that regulate woody plant expansion into mesic grasslands (Briggs *et al.* 2005, Ratajczak *et al.* 2011). In the CGP, limited landscape connectivity means fire frequency is largely controlled by the number of ignition events, which occur via lightning strikes or increasingly, by humans

(Allen & Palmer 2011, Stambaugh, Guyette & Marschall 2013, Twidwell *et al*. 2013b). We have

limited evidence regarding pre-settlement fire regimes in CGP grasslands, however, best

estimates of historic fire frequencies in and near CGP grasslands range from 3-5 years (lightning

and/or indigenous humans; Wright and Bailey 1982, Allen and Palmer 2011, Desantis, Hallgren

& Stahle 2010, Strambaugh *et al*. 2013). Fire frequency now varies across the region (Mohler

and Goodin 2012) from annually or biennially in many grasslands managed primarily for cattle

production (Smith & Owensby 1978) to 3-4 years in areas managed to balance cattle production

and biodiversity (Fuhlendorf *et al*. 2009, Allred *et al*. 2011), to long-term fire suppression of 20

years or more associated with a cessation of ranching and use or sub-urban development (e.g.

Hoch *et al*. 2002, Briggs *et al*. 2005, Mohler and Goodin 2012). The mechanistic evidence

presented thus far indicates that decreasing fire frequency should facilitate a transition to

shrublands. The presence of feedback mechanisms and demographic potential associated with

clonal life history traits in both grasses and shrubs foreshadows that this transition could be

abrupt and capable of hysteresis (Walker & Salt 2006).

Experimental and observational evidence for shrubland fire thresholds and regime shifts:

 Long-term fire return intervals of two years or less have prohibited shrub expansion in CGP

grasslands (Bragg & Hulbert 1976, Briggs and Gibson 1992, Kettle *et al*. 2001, Bowles & Jones

2013, Ratajczak, *et al*. *in press*; Fig. 3), whereas fire returns of 3 years result in a mix of

grassland persistence and transitions to shrublands, and fire returns ≥3 years allow rapid shrub

expansion (Brudvig et al. 2007, Bowles et al. 2013, Ratajczak, et al. *in press*). Two to three years

between fires is the average amount of time needed to regenerate maximum fuel loads, indicating

that 2-3 year fire frequencies will also generate high-intensity fire (Knapp & Seastedt 1986,

Gibson *et al*. 1990, Knapp *et al*. 1998, Fuhlendorf *et al*. 2009).

The transition from grassland to shrubland has the hallmarks of a threshold transition (e.g. Scheffer & Carpenter 2004, Bestelmeyer *et al*. 2011): abrupt shifts in shrub cover over time, spatiotemporal bi-modality of system state, and non-linear correlations between state and drivers (Fig. 3; Ratajczak *et al*. *in press*). The transition to shrub-grass co-dominance typically takes 20 years, with gradual increases in shrub cover at first, but rapid rates of expansion rates in the process (Collins & Adams 1983, Ratajczak *et al*. *in press*). Analysis of 28 years of annual plant composition measurements under different fire regimes at KPBS indicates that abrupt shifts in shrub cover are not related to abrupt shifts in climate or intermittent fire suppression (i.e. pulses), but instead are correlated with gradual changes in grass cover (a proxy for fire intensity and the effects of grasses on resource availability). This suggests the transition from grassland to shrubland is defined by an internal threshold, rather than internal linear dynamics responding to an abrupt change in salient driver variables (Bestelmeyer *et al*. 2011). Demographic rates, in particular the altered demographic bottleneck, might also contribute to the abruptness of grassland to shrubland transitions (Ratajczak *et al*. 2011).

For the transition from grassland to shrubland to be considered a regime shift, shrublands must also show hysteresis with respect fire frequency and grass dominance (Fig 1). Exposing clonal oak shrublands to bi-annual fires leads to initial declines in cover, but shrub cover recovers to previous levels within 2 years (Harrell *et al.* 2001, Boyd & Bidwell 2002). In these circumstances, the shrubs that survive also increase in size, reducing long-term fire susceptibility (Harrell *et al.* 2001, Boyd & Bidwell 2002). Data from KPBS also show hysteresis, where directly after a transition to shrubland, ungrazed grasslands were burned twice within four years, but did not return to a grassland state (Ratajczak *et al. in press*). As an additional example, the dominant shrub *Rhus glabra* has shown the capacity to withstand annual fires once established

(Hajny *et al*. 2011). We attribute these examples of hysteresis to physiological reistance of larger shrubs to fire, the ability of shrubs to suppress grasses (and thereby fine fuels), and the high probability of resprouting in the rare event that shrubs are top-killed.

Similar to regime shifts reported elsewhere (Staver *et al.* 2011, Roff & Mumby 2012), thresholds in CGP grasslands appear to be context-specific. Fire intensity and frequency play an interactive role, whereby less frequent but more intense fires can exclude woody plants and are more likely to reverse shrubland transitions (Fuhlendorf *et al.* 2008, Twidwell *et al.* 2013a) and vise versa (Ratajczak et al. *in press*). Resource availability and other disturbance processes are also important. For instance, most establishment and expansion of shrub species at KPBS and elsewhere occurs in areas with deeper soils, while thin-soil upland locations are rarely colonized by shrubs, even with long-term fire suppression (Fig 3, Bragg & Hulbert 1976, Ratajczak *et al.* 2011, Bowles & Jones 2013). This result is surprising, because uplands have lower fires intensities and grass cover below the threshold required for shrub transitions in lowlands (Gibson et al. 1990). These observations suggest that other factors limit shrub populations in upland locations, such that shrubs cannot grow fast enough to reach a fire resistant size (*sensu* Hoffmann *et al.* 2012). Depressed shrub growth in uplands is probably related to shallower soil depth, which results in lower surface soil moisture for all species (Nippert *et al.* 2011) and forces shrubs to compete directly with grasses in upper soil layers (Nippert & Knapp 2007, Ratajczak *et al.* 2011).

Herbivory can also modify thresholds. Contemporary browsing pressure in CGP grasslands does not appear limit shrubland transitions, considering that the species most preferred by browsers are the same species that have increased the most in cover (Van Der Hoek *et al.* 2002 *vs.* Heisler, Briggs & Knapp, 2003, Ratajczak *et al*. 2011). We are unaware of studies

that have reintroduced larger browsers into shrublands of the CGP. Grazing, however, has modified fire thresholds (e.g. Walker *et al.* 1981, Fuhlendorf *et al.* 2008). The conventional wisdom is that grazing enhances shrub establishment by reducing grass cover, unless grazing is associated with aridification (Walker *et al.* 1981, Scholes &Archer 1997, Fuhlendorf *et al.* 2008). Recent research in the CGP has not supported this hypothesis. If anything, grazing appears to suppress dominant shrub establishment (Kettle *et al.* 2000, Brudvig *et al.* 2007, Ratajczak *et al.* *in press*), perhaps because native grazers may physically damage woody species (Coppedge & Shaw 1997) and create more bare ground which, increases sensible heat and reduces surface soil moisture (*sensu* Walker *et al.* 1981, Nippert *et al.* 2013).

Uncertainties and Opportunities for Further Study

The mechanisms of initial shrub seedling establishment and persistence are not well documented, hindering theoretical modeling and prediction regarding the initiation of grassland-shrubland transition. For example, can we predict the conditions required for shrubs to transition from seedlings to fire-immune shrubland? To provide insight into the underlying demographic mechanisms driving different trajectories of woody expansion (e.g. closed canopy *Juniperus* woodland vs. clonal-shrubland mosaics), we recommend field studies of size-specific growth, reproduction, bud bank dynamics and survivorship of encroaching shrub species. Similarly, rooting depth alone does not explain niche separation (e.g. Jackson et al. 1996), as considerable overlap occurs among grass and shrub roots (McCarron & Knapp 2001, Nippert *et al.* 2012). The degree of vertical niche partitioning between shrubs and grasses has only been tested in a few ecosystems (e.g. Sala *et al.* 1989, Kulmatiski & Beard 2013), but understanding the plasticity of this resource partitioning is imperative to developing theoretical competition models (Chesson 2000) and predicting community structure and function across broad spatial scales.

With global change pressures growing in number and magnitude, more research is needed to identify thresholds responses in complex and evolving environments. Recent research examining climate warming and altered precipitation suggests increased frequency and/or intensity of drought in the growing-season may reduce the competition from dominant C_4 grasses, reducing mortality of woody plants (Volder *et al.* 2010, 2013). Larger rainfall events sizes and seasonal shifts to greater winter precipitation may increase the availability of deep soil-water resources upon which shrubs rely (Brunsell *et al. in press*, Nippert *et al.* 2013), leading to a competitive advantage for shrub species (e.g. Kulmatiski & Beard 2013). Elevated CO_2 may also facilitate increased growth and water-use efficiency in C_3 species, as has been reported in herbarium specimens from the CGP (McLauchlan *et al.* 2010), nearby semi-arid steppe (Morgan *et al.* 2007), and savannas with precipitation similar to the CGP (Bond & Midgley 2012).

Transitions to woodlands:

*Background***:**

The final state of woody plant expansion and grass exclusion that we consider is conversion to woodlands. There are two primary types of woodlands in the CGP—Juniper woodlands dominated by coniferous evergreen species (primarily *Juniperus virginiana* in the portion of the CGP defined here) (reviewed in Briggs *et al.* 2005) and broadleaf woodlands, dominated by a larger species pool, but typically including several different oak (*Quercus*) species and sometimes a minor and/or growing *Juniperus virginiana* component (Engle *et al.* 2006, Desantis *et al.* 2011). We focus on *Juniperus virginiana* woodlands (subsequently referred to as Juniper woodlands) because these woodlands are expanding more than other in the CGP (Twidwell et al. 2013b) and others have reviewed *Juniperus* savannas and woodlands of the semi-arid southern CGP (Van Auken & McKinley 2008).

Woodland trees are especially sensitive to fires at small sizes (Fig. 2,4). Unlike grasses and shrubs, *J. virginiana* trees do not resprout when top-killed, making them susceptible to fire induced mortality until they develop thick bark and/or suppress fire (Hoch, *et al.* 2002, Fuhlendorf *et al.* 2008, Vanderweide & Hartnett 2011). Compared to deciduous woody species *J. virginiana* takes longer to reach a size that permits fire survival, because these species have low hanging flammable branches (Fig 2) and develop bark more slowly than many other CGP tree species (Vanderweide & Hartnett 2011). For these reasons, we expect that greater fire suppression is needed for woodland formation, relative to shrublands. We further predict that like shrublands, the transition from grasslands to woodlands will exhibit hysteresis, based on evidence that *J. virginiana* can suppress grass and shrub growth via their ability to form dense canopies that intercept light and alter other micro-site characteristics (Hoch *et al.* 2002, McKinley *et al.* 2008, Limb *et al.* 2010, Van Els *et al.* 2010). Mature Juniper stands can reach 75-100% tree cover, with significant reductions in herbaceous biomass and shrub establishment concentrated directly below tree canopies (Hoch *et al.* 2002, Myster 2009, Limb *et al.* 2010, Van Els *et al.* 2010).

Unlike transitions to shrubland, low water availability is less important for excluding *J. virginiana* trees from grasslands and shrublands (Volder *et al.* 2010, 2013). Evergreen trees are very drought resistant and create a microsite where water availability might be even lower than in grass-dominated patches (Awada *et al.* 2012). As a result, *J. virginiana* has high seedling survivorship even in biodiverse and grass-dominated patches (Ganguli *et al.* 2008), allowing them to colonize shallow soils and exist in locations susceptible to periodic drought (Fig. 2) (Eggemeyer *et al.* 2006, Engle *et al.* 2006).

Experimental and observational evidence for woodland fire thresholds and regime shifts:

Despite identifying the mechanistic basis for transitions to woodlands (i.e., drought tolerance, microsite modification, fire suppression), determining if Juniper woodland formation constitutes a regime shift is constrained by logistics and population dynamics of tree species. Statistical indications of regime shifts (e.g. abrupt shifts, state bi-modality) require experiments and observational data-sets that are scaled with the life span and spatial footprint of organisms involved (van Nes & Scheffer 2005, Bestelmeyer *et al.* 2011). Based on these criteria, observing a threshold transition woodland would require an experiment that increases fire returns slowly, allowing tree species to equilibrate with their changing equilibrium until a potential threshold is crossed. However, most observations of woodland transitions lack temporal resolution and lean towards complete fire suppression or reintroduction of fire to woodlands (Fig. 4, 5- references therein). In these instances, the driver (fire) goes from far below any potential threshold to far beyond the threshold. Under these conditions, both linear and threshold systems should show logistic growth of shrubs and trees reacting to an abrupt change in carrying capacity (Ganguli *et al.* 2008 *versus* Myster 2009). Consistent with these theoretical expectations (May 1977, Hughes *et al.* 2012), fire suppression in the CGP results in patterns of logistic growth by shrubs and trees over a 40-50 year period (e.g., Fig. 3, 4) (Hoch *et al.* 2002, Ratajczak *et al. in press*) with eventual dominance of trees at the expense of grasses, herbaceous eudicots and shrubs (Anderson *et al*. 2000, Peterson, Reich & Wrage 2007, Limb *et al*. 2010, Van Els *et al*. 2010, Twidwell et al. 2013). Thus, it is difficult to distinguish between linear and threshold transitions based on observational data under fire suppression only.

While we lack the experimental data to test for "abrupt shifts", state-modality, and other features of linear vs. threshold responses, we can ask: is there a fire frequency threshold that prohibits transitions from shrubland to woodland? And if so, does increasing fire frequency

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reverse the transition or does the system show hysteresis? Detailed mapping of tree

establishment and analyses of shrub cover at the Konza Prairie shows that 30 years of prescribed

3-4 year fire frequencies allows establishment of shrubs, but not trees (Fig. 3). The lack of tree

establishment over a 30 year period, and the prevalence of functionally similar shrublands

throughout the region (Petranka & McPherson 1979, Collins & Adams 1983, Anderson *et al*.

2000, Harrell *et al*. 2001, Brudvig *et al*. 2007, Ratajczak *et al*. 2011), suggests that the shrubland

state is a separate basin of attraction and that longer fire-free intervals are needed to precipitate a

transition to woodland. Contrary to 3-4 year fire frequencies, infrequent burning (~ 20 year

returns) or complete fire suppression allows tree establishment (Fig. 4, 5; Briggs & Gibson 1992,

Briggs, Knapp & Brock 2002) and eventually, formation of closed-canopy woodland (Bragg &

Hulbert 1976, Kettle *et al.* 2000, Norris *et al.* 2001, Hoch *et al.* 2002, Engle *et al.* 2006,

Twidwell et al. 2013a).

A process-based approach suggests that woodland transitions may be possible at lower

fire frequencies than the 20-year fire experiment presented here (Fig 4, 5). *Juniperus virginiana*

is resistant to typical grassland fires once it reaches diameter at breast height of ~17 cm and a

height of ~2.5 m (Owensby, Eaton, & Russ 1973, Hoch *et al.* 2002, Vanderweide & Hartnett

2012). Connecting these thresholds to reported *J. virginiana* growth rates (Owensby *et al.* 1973,

Engle & Kulbeth 1992, Schmidt & Wardle 2002), we estimate that fire free intervals of 15 to 20

years would allow consistent tree establishment, although this interval may be as low as 6-10

years for locations more amendable to rapid tree growth or subject to over grazing (Owensby *et

al.* 1973, Hoch *et al.* 2002, Fuhlendorf *et al.* 2008). These estimates closely match modeling by

Fuhlendorf and colleagues (2008), as well as historical observations that *J. virginiana* are more

common in pyrrhic woodlands with a fire frequency >5 years (Batek *et al.* 1999, Stambaugh *et

al. 2013). Similarly, a wildfire at Konza after 15 years of fire suppression killed ~3/4 of *Juniper* trees, but did not stop the transition to woodland when it was followed by 20 years of fire suppression (Fig 4), further indicating that transitions to a *Juniper* woodland are possible at a fire frequency of 15 years. However, the rate of transition will be significantly suppressed at these higher fire frequencies (Fig 4, Hoch et al. 2002).

Like grassland-shrubland transitions, the transition to woodlands potentially shows hysteresis. Woodlands can revert to shrubland or grassland with physical or chemical removal of *J. virginiana* trees to remove shading and fire suppressing feedbacks, combined with frequent burning to foster grass dominance and fire promoting feedbacks (Engle *et al*. 2006, Pierce & Reich 2010, Alford *et al.* 2012). To achieve this management goal, tree removal and reintroduction of fire should coincide, otherwise community recovery can be long (Alford *et al.* 2012) and legacy effects of woodland dominance can facilitate a rapid return to the woodland state (Kettle *et al.* 2000).

Unlike tree removal and fire, prescribed burns alone have not proven as effective at returning woodlands to a grassland state or reinstating fire feedbacks. In mixed deciduous/Juniper woodlands, re-introduction of 3-year fire returns and certain chemical controls allows *J. virginiana* to maintain ~20% cover (Engle *et al.* 2006). In both the southern and northern extent of the CGP, reintroducing fire returns of ~2-3 years for a duration of 20 to 30 years has only marginal effects on tree cover and increased grass cover to only 10-20% (Peterson et al. 2007, Burton, Hallgren & Palmer 2010, Burton *et al.* 2011). Lastly, historical records of fire scars indicate that many woodlands persisted in areas with fire returns ranging from 2 to 6 years (Batek *et al.* 1999, Desantais *et al.* 2010, Strambaugh *et al.* 2013). However, studies by Burton *et al.* (2010, 2011) and Peterson *et al.* (2007) were performed in primarily deciduous

woodlands, and these results may not be directly transferable to Juniper woodlands. Moreover, it may be possible to achieve faster reversals to grasslands using novel burning techniques that stimulate high-intensity, high-risk fires (Twidwell et al. 2013a).

Woodland fire thresholds are also context specific, but in ways that differ from thresholds differentiating grasslands and shrublands. A unique attribute of woodland trees (particularly Juniper), relative to the species that define the shrubland state, is their ability to establish in more xeric and thin soils (Engle *et al*. 2006, Eggemeyer *et al*. 2006, Knapp *et al*. 2008b, McKinley et al. 2008). The drought tolerance of Juniper and its ability to assimilate carbon year-round allows for woodland formation even in very exeric conditions (Fig 4). Establishment of woodlands on thin-soils requires some degree of fire suppression, but it is unknown if grassland-woodland fire thresholds and hysteresis differ based on topo-edaphic conditions.

Uncertainties and Opportunities for Further Study:

Grazers can alter thresholds for grassland-woodland conversion, but in complex, unpredictable ways. Conventional cattle grazing generally favors greater tree establishment by reducing fuel loads, and thereby, fire intensity (Hoch *et al*. 2002, Fuhlendorf *et al*. 2008, Twidwell *et al.*2013a). Grazing can also create microsite conditions that facilitate woodland seedling establishment (Owensby *et al.* 1973). In contrast to conventional grazers, native grazers such as *Bos bison* can significantly restrict woodland development. At moderate densities at KPBS, bison exclude *J. virginiana* trees from grasslands by scratching, breaking, and imposing complete aboveground damage (personal observations). This set of behavioral traits have also been observed in *Bos bison* of other North American grasslands (Bork *et al*. 2013, but see Coppedge & Shaw 1997). At KPBS, this effect is so strong that *Gleditsia triacanthos*—a thorned tree—is the primary species that persists with bison (unpublished data, Z. Ratajczak). These

observations underlie the significance that traditional models of grassland to woodland transition

must consider grazer impacts as a whole, not just their indirect effects on trees via grass

abundance and soil characteristics. They also open up the possibility of using native grazers to

meet the economic needs of food production, while building resilience to woodland transitions.

This possibility merits significant further testing before it is implemented at large scales.

A key difference between shrublands and woodlands is their potential for "intra-state

transitions". CGP shrublands are typically comprised of clonal deciduous shrubs, often of the

genera *Cornus*, *Rhus*, *Quercus*, and/or *Prunus*, whereas woodlands can be composed of

functionally distinct evergreen *J. virginiana* and/or deciduous trees. At Konza, the *Quercus*

species that dominate deciduous riparian woodlands have yet to appear in fire suppression plots

~3 km from a large propagule source. A possible explanation for this pattern is that some

deciduous trees are dispersal limited because they rely on woodland mammals as a dispersal

vector, whereas *J. virginiana* trees are bird dispersed and, show little dispersal limitation (Yao *et

al.* 1999). Conversely, some broadleaf species are more fire resistant than Juniper (Batek *et al.*

1999, Desantis *et al.* 2011, Stambaugh *et al.* 2013) due to their thick bark (Vanderweide &

Hartnett 2011) and ability to resprout (Briggs *et al.* 2002). Taken together, we speculate that the

likelihood that CGP woodland composition depends largely on the distance to source

populations, water limitation and degree of fire suppression.

Synthesis and opportunities for management

We propose a conceptual framework of tri-stability in the CGP that treats grasslands, shrublands,

and woodlands as basins of attraction moderated by fire frequency thresholds (Fig. 5).

Experimental and mechanistic evidence to date strongly supports mesic grasslands and

shrublands as opposing basins of attraction. Evidence for woodlands as a discrete basin of

attraction is less developed compared to the grassland-shrubland basin of attraction, but robust none-the-less based on a rich understanding of mechanistic species interaction, microclimatic changes, and demography. In areas with thin soils that restrict access to deep or reliable soil moisture, only two basins of attraction are likely to exist—grasslands and woodlands—because shrublands are rare in these soil types (Fig 3). In general, events that facilitate grass growth, greater fire intensity, or reduce tree/shrub growth will favor the grassland state (Fig. 3), requiring longer fire-free intervals to force a transition to a shrubland or woodland, and perhaps reducing hysteresis when trying to restore grasslands (Fig. 5).

The grassland-shrubland-woodland transition framework for the CGP may serve as a valuable management tool, allowing landowners to avoid unwanted state changes or return ecosystems to preferred states by managing fire frequency. The tri-stability framework suggests that preventing transitions to shrublands and woodlands is more cost effective than post-encroachment restoration because returning fire will not necessarily return the system to a grassland state on management-relevant time scales. Therefore, reversing unwanted transitions will likely require costly inputs, such as physical and chemical removal (Lett & Knapp 2004, Engle *et al.* 2006, Pierce & Reich 2010, Alford *et al.* 2012).

The potential for preventing woody encroachement in the CGP is significant. In the Flint Hills (the largest remaining area of CGP grasslands, 28,000 km^2) it is estimated that from 2000 to 2010, 27% of grasslands were burned every 1-2 years, 35% were burned every 3-6 years, and 38% were burned at >6 year fire returns (Mohler & Goodin 2012). Considered with thresholds identified here (Fig 5), the CGP could see widespread ecosystem transition to shrublands and woodlands in the next 20-50 years, unless new management regimes are adopted (see Twidwell *et al.* 2013b for management options in the CGP).

While our framework identifies fairly consistent thresholds, we also urge caution that critical fire thresholds can be variable (Bestelemeyer & Briske 2012), such as in years with above or below average precipitation, and thresholds may also change over time. Initial evidence suggests that fire thresholds have already changed in the CGP prior to European arrival. Data from the Konza Prairie over the past 30 years indicate that a 3 to 4 year fire frequencies are often insufficient to prevent the transition to shrublands (Fig 3), even though this same fire frequency used to be common in CGP tallgrass prairie (Wright & Bailey 1982, Allen & Palmer 2011). Similarly, modeling by Fuhlendorf and colleagues (2008) predict woodland exclusion with moderate grazing and 10-15 year fire frequencies, and yet these fire frequencies now allow substantial woodland expansion (Fig 5). These observations suggest that local thresholds have responded to global and/or regional pressures, such as climate change (Polley *et al.* 2011), elevated CO_2 (McLauchlan *et al.* 2010, Bond & Midgley 2012), loss of larger browsers and native grazers, and exurban expansions that have enhanced woody plant seed rain (Briggs *et al.* 2005). These recent changes indicate CGP fire frequency thresholds are not fixed over long time series, requiring adaptive management (Bestelmeyer & Briske 2012), such as coupling burning with drought events, alteration of seasonal burn timing (Hajny *et al.* 2011), and removing grazers prior to burning to allow fuel accumulation (Fuhlendorf *et al.* 2008).

This synthesis has identified ecosystem thresholds, hysteresis, and the mechanisms behind these processes—one of the major challenges in ecosystem and community ecology (Sutherland *et al.* 2013). Yet, much work remains to describe grassland-shrubland-woodland transition in the CGP. While we are developing a better mechanistic understanding of grassland-shrubland-woodland transitions under contemporary conditions, we still have very limited ability to predict how these systems will respond to novel future conditions that may occur as a result of

regional or larger-scale global changes. Moving forward, we advocate further tests of the context specificities of thresholds identified here as well as a synthesis of the dynamics of major vegetation types across broader regions, with the goal of creating a framework for regional and cross-regional generalizations of grassland-shrubland-woodland transitions.

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A) Linear system:
Linear and reversible transitions

B) Threshold system:
Non-linear and reversible transitions

C) Regime shift system:
Non-linear and hysteresis transitions

State — Wood, Shrub, Grass

Fire Suppression   Fire Suppression   Fire Suppression
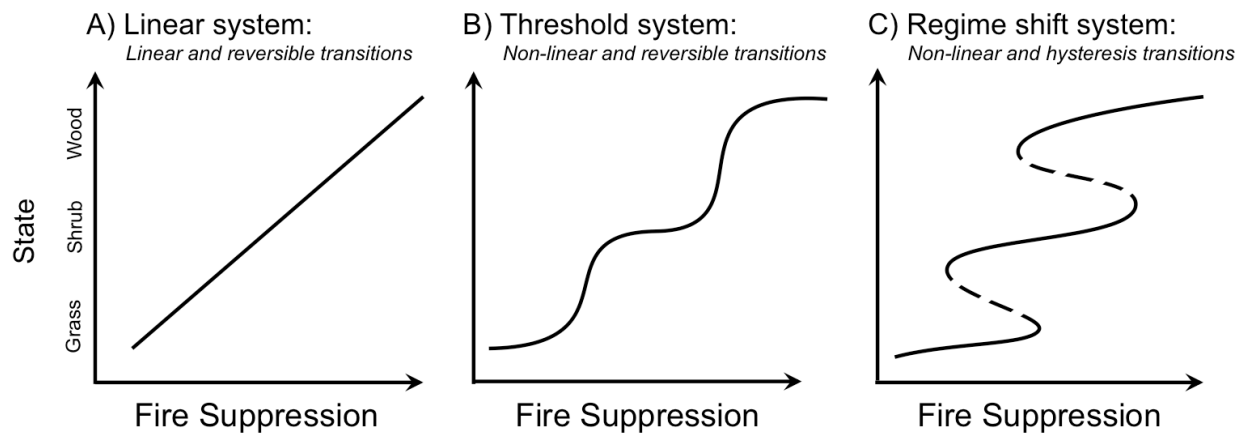
Figure 6.1 A depiction of potential internal ecosystem dynamics in response to fire. For all panels, solid lines denote stable equilibria, and in C) dotted lines delineate unstable repellors. A) shows the null hypothesis where fire does not result in ecosystems transitions (grey line) and a scenario where CGP ecosystems respond gradually to fire (black). B) shows a threshold system where small changes in fire can lead to disproportionate, but reversible change in system state. In systems with alternative basins of attraction (C) shifts between states show threshold behavior as in B), however, returning drivers to their pre-transition values does not reverse the transition. In a regime shift system, the different stable equilibria are referred to as basins of attractor of alternative attractors. This figure is based on works by Noy-Meir (1975), Walker *et al.* (1981), Holling (2001), Folke *et al.* (2004), Scheffer (2009), and Bestelmeyer *et al.* (2011).
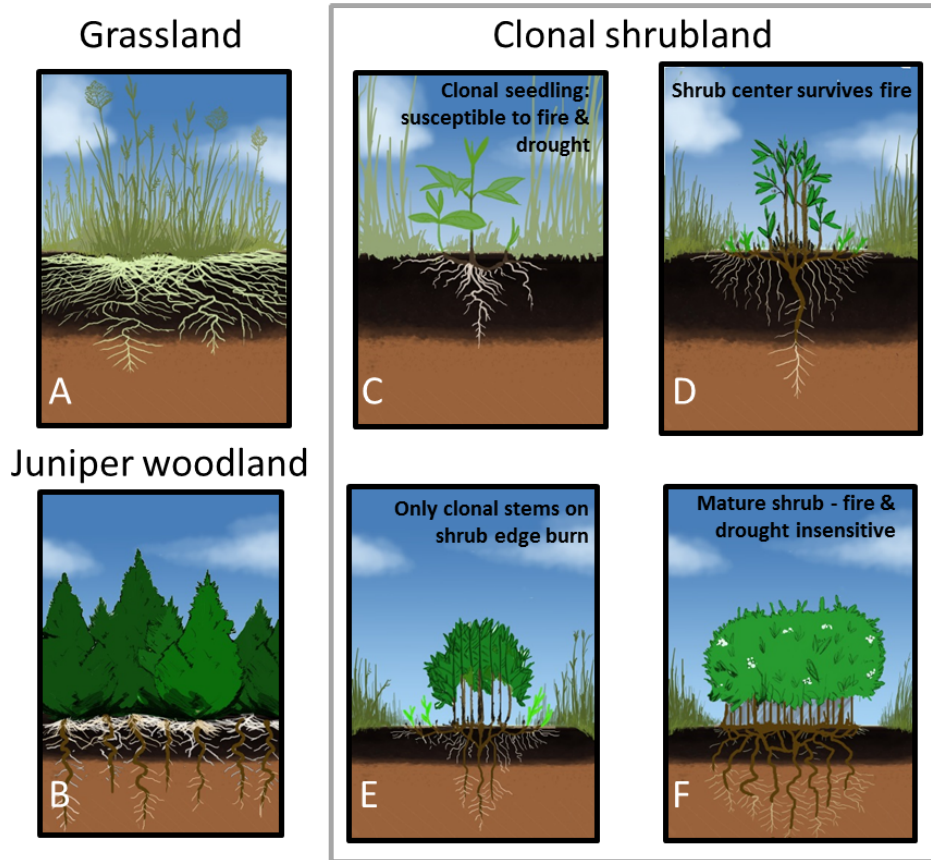
Figure 6.2 Conceptual illustration of grassland- clonal shrubland – woodland states in mesic North American grassland. In the illustration, soil zones are depicted as zones with the highest grass root biomass (surface) and deeper soil. With frequent fire (≤ 2 years), the grassland state is maintained (panel A). With fire suppression, the ecosystem transitions into a woodland within decades (B). If fire recurs infrequently (3-10 year frequency), clonal shrubland develops (C-F). Shrub seedlings are sensitive to fire and low soil moisture in shallow soil layers (C-D). If seedlings survive, high leaf biomass shades grasses, reducing growth (and subsequent fire susceptibility on shrub margins) while rhizomatous transfer of water among clonal stems from deeper soil layers minimizes susceptibility to drought (E). Mature shrubs are decoupled from seasonal drought via reliance on deep-soil water and from the effects of fire (F).
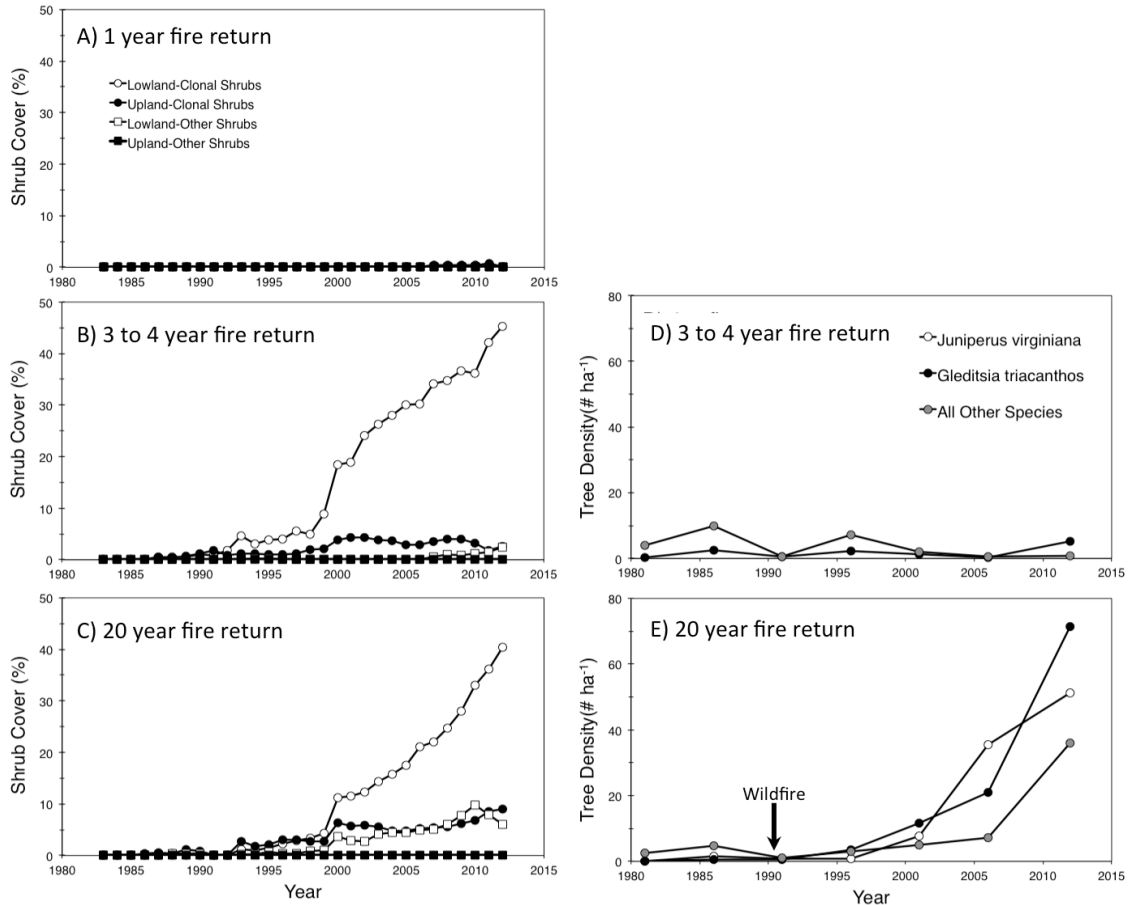
Figure 6.3 Measurements of shrub and tree dynamics at Konza Prairie across landscape positions exposed to different prescribed frequencies starting in the late 1970's. "Clonal shrubs" refer to *Cornus drummondii*, *Rhus glabra*, and *Prunus americana* cover and "other shrubs" are the cover of all other shrub species with a canopy that exists above the grass layer. Shrub cover estimates include upland and lowland measurements for (A) 1, (B) 3-4, and (C) ~20 year fire returns and averaged across grazed and ungrazed treatments (n = 40, 10 m² plots per combination of fire and topography, derived equally from grazed and ungrazed areas). In (A-C), points depict clonal shrub cover values in uplands (black) and lowlands (white), and squares depict cover values for all other shrubs in uplands (black) and lowlands (white). Tree density (D and E) come from detailed mapping of a (D) 4- and (E) 20-year fire return catchment basins in ungrazed locations on Konza Prairie. In (D-E), white points show *Juniperus virginiana* densities, black points are *Gleditsia triacanthos*, and grey points are all other tree species combined. The arrow in E indicates the timing of a wildfire that affected the 20 year fire treatment.

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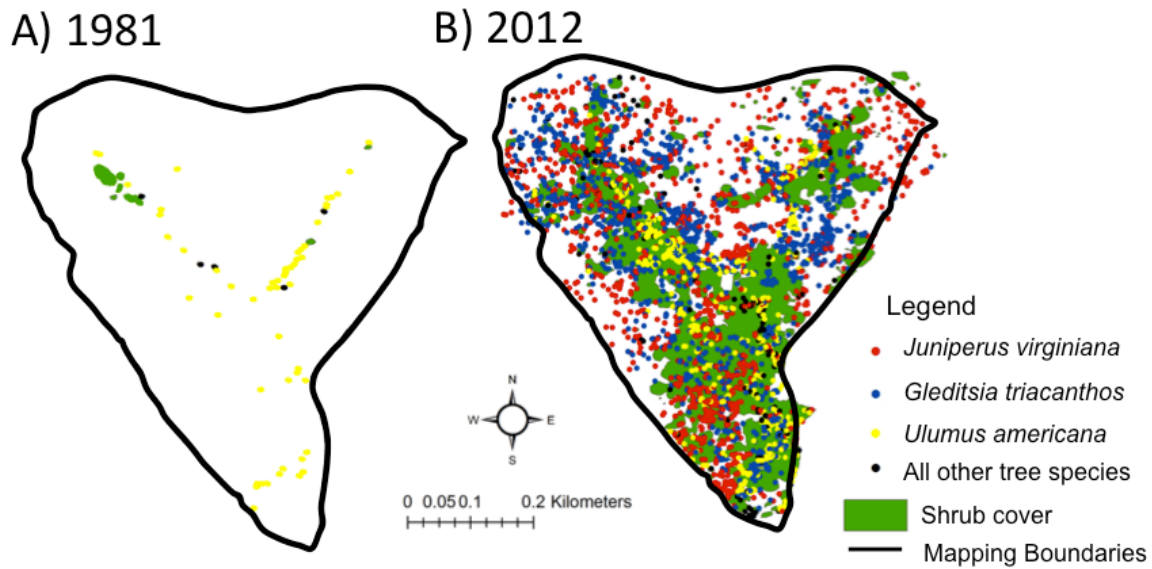
Figure 6.4 Results illustrating changes in woody species occurrence on an ungrazed catchment basin at Konza Prairie in A) 1981 and B) 2012, with only one fire since 1983. In both 1981 and 2012, coordinates of all tree stems and shrubs above the grass canopy were recorded. Trees were mapped as points and shrubs as polygons (see Briggs et al. 2002 for more details). For symbols, *Juniperus virginiana* = red dots, *Gleditsia triacanthos* = blue dots, *Ulumus americana* = yellow dots, all other tree species = black dots, and shrub cover = green poloygon. Note that the watershed boundaries changed between 1981 and 2012, therefore, the original mapping boundaries are delimited with a black line.
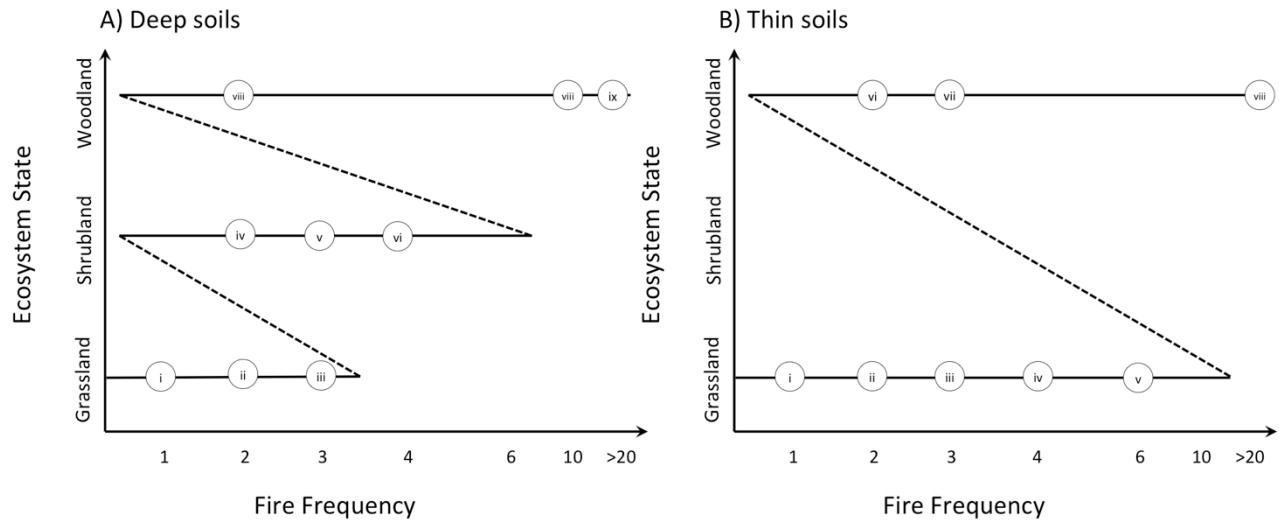
Figure 6.5 The CGP tri-stability framework for grassland, shrubland, and woodland basins of attraction in (A) deep and (B) thin soils. Horizontal black lines denote basins of attraction and dotted lines denote unstable states. Circles with roman numbers represent contrasting ecosystem states identified by experimental or observational studies showing CGP ecosystem has existed at the respective state and fire frequencies indicated on the x- and y-axes. Following thresholds from Ratajczak et al. *in press*, grasslands were those ecosystems with <10 shrub cover and C₄ grasses present, shrublands were 10-60% shrub cover, with minimal trees present, and woodlands were those ecosystems with many trees above the 2.6 m tall, 17 cm diameter at breast height fire-mortality thresholds (Owensby 1973, Hoch et al. 2002, Vanderweide and Hartnett 2011). Note that shifts from grassland to shrubland were discrete (occurring in 2-5 years), whereas transitions are more gradual between between grassland and woodland, and shrubland and woodland. Supporting citations: Bowles and Jones 2013: A) i, ii, iii, v, B) i, ii, iii, iv, v; Boyd and Bidwell 2002: A) iv; Bragg and Hulbert 1976: A) ii, ix; Briggs and Gibson 1992, Briggs et al. 2002, Fig 3 & 4: A) i, ii, v, xi; B) i, iii, viii; Fuhlendorf et al. 2008: A) viii; Fuhlendorf et al. 2009: A) iii; Harrell et al 2001: A) ii; Kettle et al. 2000: A) ii, xi; Hoch et al. 2002: A) ix B) viii; Owensby et al. 1973: A) i, ii; Peterson et al 2007: A) vii, viii, ix; Process-based estimates (described in text): A) viii; Ratajczak et al. 2011, Ratajczak et al. in press, Fig 3: A) i, iv, v, vi; B) i, iv, viii; Engle et al 2006: B) vii, viii; Burton et al. 2010, 2011: B) vi, viii.

Chapter 7 - Leading—and misleading—indicators of critical slowing down before grassland to shrubland regime shifts

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Techniques for *a priori* detection of ecological thresholds could help landowners and policy makers avoid dramatic and difficult to reverse regime shifts. In a long-term grassland fire experiment, we found evidence for critical slowing down, a phenomenon where systems near a threshold show less resistance and slower repair rates. Approaching a threshold, grassland sequentially lose the abilities to exclude species that define the alternative stable state (shrubs), remove theses species, and prevent them from reaching competitive and demographically stable size-classes. By altering fire frequency when critical slowing down became evident regime shifts were prevented, whereas plots without adaptive management underwent an abrupt transition to shrub dominance. This represents the first successful example of detecting and preventing a terrestrial regime shift using critical slowing down. However, spatial "leading indicator" statistics meant to capture critical slowing down did not occur before the regime shift. Thus, while critical slowing down may precede many terrestrial regime shifts, we still need to bridge the disconnect between theoretical models and real-world systems if there will be a chance to generate truly generic leading indicators. The relative roles of demography and feedback strength present a means to move this theoretical-empirical synthesis forward.

Key Words: Alternative Stable States, Fold Bi-Furcation, Tipping Points, Warning Signs, Woody Encroachment

Abstract:
A priori detection of ecological thresholds could help landowners and policy makers avoid dramatic and difficult to reverse regime shifts. In a long-term grassland fire experiment, we found evidence for critical slowing down, a phenomenon where systems near a threshold show less resistance and slower repair rates. Approaching a threshold, grassland sequentially loses the abilities to exclude species that define the alternative stable state (shrubs), remove theses species, and prevent them from reaching competitive and demographically stable size-classes. Increasing fire frequency when critical slowing down became evident prevented regime shifts, whereas plots without adaptive management underwent an abrupt transition to shrub dominance. This represents the first successful example of detecting and preventing a terrestrial regime shift using critical slowing down. However, spatial "leading indicator" statistics meant to capture critical slowing down did not occur before the regime shift. Thus, while critical slowing down may precede many terrestrial regime shifts, to generate truly generic leading indicators we still need to bridge theoretical models and real-world systems. The relative roles of demography and species interactions present a means to move this theoretical-empirical synthesis forward.

Introduction:

Some ecosystems exhibit two alternative stable configurations, making them prone to abrupt

shifts from one self-reinforcing state to another in response to changes in environmental

conditions or disturbance regime (e.g., Walker and Salt, 2006). When external pressure push

such systems across a critical threshold the dynamics diverge from their initial state and shift to

an alternative attractor. Transitions to an alternative attractor are typically discontinuous and

difficult to reverse, because the system organizes around a new set of relationships between state

and driver variables (e.g., Holling 1973, Noy Meir, 1975; May, 1977; Carpenter, 2003; Scheffer,

2009). In anticipation and/or possible prevention of unwanted critical transitions, proactive

natural resource management requires reliable and easy to detect leading indicators within

ecosystems that are approaching critical thresholds (Carpenter and Brock, 2006; Van ness and

Scheffer, 2007; Scheffer et al., 2009).

Current theoretical models suggest that as a system with two alternative attractors (hereafter "bi-stable" systems) approaches a critical threshold, its resistance to perturbations decreases and it exhibits critical slowing down, defined as a slower return to equilibrium after a perturbation (Fig 1A; Stogartz 1993, Van Nes and Scheffer 2007, Scheffer et al. 2012, Dakos et al. 2014). If decreased resistance and critical slowing down are near-universal properties of systems close to a threshold, we could possibly use mechanistic assessments of critical slowing to predict when well-studied systems are getting closer to a threshold or when thresholds are changing.

For systems where little is known about the potential existence of alternative attractors and their mechanistic basis, statistical signatures of critical slowing down termed "leading indicators", may serve as surrogates for changes in declining resistance and critical slowing down. The critical slowing down effect is typically shown as an increase in the repair time, variance, and temporal autocorrelation of the state variable (Carpenter and Brock 2006; Carpenter et al. 2009). Systems near a critical threshold may also exhibit oscillations between the old and new state, a phenomenon known as "flickering" (e.g., Dakos et al. 2012). Likewise, in spatially extended systems critical slowing down entails an increase in spatial correlation between adjacent patches because slower return to equilibrium results in spatial interactions having a greater influence on patches dynamics (Dakos et al. 2010).

Leading indicators have been successful predictors of regime shifts in lakes (Biggs et al. 2009, Carpenter et al. 2011), paleoclimate records (Dakos et al. 2008), experimental yeast communities (Drake et al. 2010), and marine continental shelves (Litzow et al. 2008). Yet, modeling and empirical tests suggest that critical slowing down and leading indicators might not consistently precede critical transitions in many bi-stable systems and/or that these dynamic

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behaviors may give false positive and false negative warning signs (Hastings and Wysham 2010, Dakos et al. 2012, Boereljist et al. 2012, Boetiger et al. 2013, Kefi et al. 2013).

Despite fairly widespread testing in theoretical dynamical models, leading indicators have rarely been applied to terrestrial systems and spatial leading indicators have yet to be applied in ecological systems in general (Scheffer et al. 2012, Kefi et al. 2014). As a result, we do not know whether this body of theory reliably applies to terrestrial systems. This study provides one of the first assessments of critical slowing down in a terrestrial system before, during, and after crossing a threshold. We also test if mechanistic evidence for critical translates to changes in leading indicators metrics (spatial auto-correlation, variance, etc.) and if coupling critical slowing down with adaptive management can prevent regime shifts.

Mesic grassland to shrubland transitions, the focus of this study, presents a rare opportunity to test leading indicator theory in terrestrial systems. In the last century, shifts from grasslands to shrubland have been abrupt (Ratajczak et al. *in press*), driven by positive feedback mechanisms (Ratajczak et al. 2011, D'Odorico et al. 2012), difficult to reverse (Schlesinger et al. 1992; Havstad, et al. 1999, Briggs et al. 2005), and exhibit non-linear relationships between shrub cover and several drivers (i.e. grass cover, topography, and fire frequency; Ratajczak et al. *in press*). Based on this evidence, mesic grasslands and shrublands are likely alternative attractors differentiated by a critical threshold (Walker et al. 1981, Westoby et al., 1989; Anderies et al., 2002; D'Odorico et al. 2012, Ratajczak et al. *in* press). Predicting thresholds in grassland ecosystems has applied value, because transitions to shrublands alter biodiversity and livestock production (Limb et al. 2011, Ratajczak et al. 2012).

We first performed a mechanistic assessment of critical slowing down. In many mesic climates, the ability of grasslands to resist transitions to shrub dominance is attributed to the

capacity of grasses to facilitate frequent and intense fires that result in high mortality of shrub and tree species (Bond 2008, Ratajczak et al. 2011, in press, D'Odorico et al. 2012). Grasses are also strong interference competitors, monopolizing resources in the upper soil and thereby imposing a demographic bottleneck on establishment by shrubs (Higgins et al. 2000, Benson and Hartnett 2006). However, when shrubs reach a larger size they have a deeper root system and thicker bark (Ratajczak et al. 2011, Vanderweide et al. 2011), which allows them to resist fire and resource competition with grasses and overcome demographic bottlenecks. Adult shrubs can also disrupt the grass-fire feedback and stabilize their own dominance if they can increase the importance of vertical competition for light, exert strong enough pressures on grasses (typically via shading), and replace high quantities of flammable herbaceous biomass with low quantities of less flammable material (Anderies et al., 2002; Breshears 2009, Ratajczak et al., 2011).

Based on this mechanistic understanding, we define grassland resistance as the ability to exclude shrub seedlings from the system and to withstand negative effects of shrubs. When resistance declines and shrubs enter the system, critical slowing down is captured by the ability of grasses to inflict high mortality rates on shrubs and prevent them from reaching larger sizes. We were able to measure all of these variables and how they chance over time. After assessing critical slowing down, we explored changes in spatial-autocorrelation as a leading indicator that terrestrial grassland systems are approaching a critical threshold. We focused on spatial correlation because it is more appropriate for systems with long-lived organisms and experiments with shorter time series (Dakos, et al., 2010, Kefi et al. 2014).

Our multi-scale analysis takes advantage of a well-documented regime shift from mesic grassland to shrubland in the Central Great Plains of North America (Briggs et al. 2005, Ratajczak et al. 2011, Nippert et al. 2013, Ratajczak et al. *in press*), using data from the Konza

Prairie Long Term Ecological Research (LTER) site. Konza LTER is a unique 35-year experiment that manipulates fire frequency (1-, 4-, and 20 year fire returns) and grazing (large native herbivores present or absent) across diverse topography (lowlands, slopes and uplands). The fire treatments were initiated in 1977, and in 1983, a series of 200 plots, arrayed across 50 m transects with 5 plots per transect, have recorded vegetation dynamics every year.

Using this design we quantified shrub frequency (proportion of plots occupied by shrubs), shrub mortality, shrub size, and the effect of shrubs on grasses (the correlation between proportional rates of grass cover change and shrub cover). We assessed the leading indicator of spatial autocorrelation of grass*grass and shrub*shrub cover between adjacent plots on these transects (between-plot scale). These correlation coefficients capture whether adjacent plots tend to be similar. We were not able to directly measure auto-correlation at smaller scales, and instead had to rely on grass*shrub correlation within single plots (Fig 1B). The logic for this measurement is that shrubs encroach either by filling bare space or displacing grasses. When approaching a critical threshold, shrubs could displace grasses, rather than just filling bare space. Thus, a negative correlation between grasses and shrubs suggests that shrub cover is increasing within patches previously occupied by grasses and if so, a decrease in grass-shrub auto-correlation is analogous to an increase in shrub auto-correlation within plots (Fig 1C). Correlations between grass and shrub cover also can indicate changes in the strength of competition between these two key functional groups.

In addition to multiple potential leading indicators, we also tested for false positive by comparing spatial autocorrelation in high resilience treatments that have remained grasslands (shallow soils and/or fire return of 1 yr) to spatial autocorrelation in low resilience treatments that make an abrupt transition to shrub dominance (treatments with deep soils and a fire return of

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>2 years) (Fig 1B). To determine if leading indicators could be successfully used in an adaptive management framework, we need to test whether leading indicators occur early enough to enact new management decisions and prevent the regime shifts. To meet this goal, annual fires were reintroduced to subset of plots shortly after statistical significant changes resistance and critical slowing down.

Results and Discussion:

Resistance and Critical Slowing Down before Abrupt Transitions:

After almost three decades, shrub cover only increased marginally in treatments with thin soils and/or fire returns of <2 years (high resilience plots). In contrast, shrub cover within treatments with a fire frequency >2 years and deep soils (low resilience plots) increased slowly for the first two decades, but underwent an abrupt regime shift from grassland to shrubland from 1999-2001, characterized by an initial increase in shrub cover and a quadrupling of shrub expansion rates (Fig 2). Statistical analyses support this transition as a regime shift between alternative attractors (Ratajczak et al. *in press*).

Before the regime shift to shrubland began resistance declined and critical slowing down began. In 1983, 6 years after the fire experiment was initiated, the proportion of plots occupied by shrubs was ~0.02, but at this point, plots began to be filled in a pattern of logistic growth. At first, mortality rates of shrubs were very high (%50), but began a steep decline around 1995 (Fig 3). Shrub size began to increase around 1995 as well, corresponding to an inability of grasses to reduce shrub size and prevent positive deviations in shrub growth rate (Fig 3). Thus, three out of four of metrics for declining resilience and critical slowing down showed statistically significant changes at least 6 years before the beginning of the regime shift.

Negative relations between grass cover growth rates and shrub cover also emerged over the course of the experiment, but not until the regime shift began in year 2000 (Fig 3). These results support the argument that shrubs can indeed alter fire feedbacks and competition for light in tallgrass prairie (Briggs et al. 2005, Ratajczak et al. 2011, *in press*), but not until shrubs reach a larger size. Assessments of resistance and critical slowing down that only relied on the active role of shrubs in feedback processes would fail to predict the existence of an approaching threshold.

Declining resistance and critical slowing down not only warn of the potential for a regime shift, they also emerged with sufficient time to enact adaptive management. In the year 2001, two areas that were previously burned every twenty years were switched to an annual fire frequency. This action, taken about 5 years after noticeable declines in resistance and critical slowing, was sufficient to prevent the transition to shrubland (Fig 4). Without management intervention, it is highly likely an abrupt transition to shrubland would have occurred, as seen by trends in plots without management interventions (Fig 2). This is an important distinction, because measurements of whether critical slow down occurs before regime shifts does not necessarily speak to whether the warning sign occurs early enough to engage in adaptive management that will prevent a transition (Biggs et al. 2009, *sensu* Hughes et al. 2012).

Leading indicators:

Considered against current theoretical derivations of leading indicators, we expected to see an increase in spatial-autocorrelation as long as there are spatial interactions between adjacent patches before the regime shift occurs.

In this experiment, measurements of spatial auto-correlation provided either false warning signs or no warning signs at all. Between plot correlations of grasses, shrubs, and shrubs

and grasses were all inconsistent leading indicators, with similar correlation coefficients in both

high and low resilience plots leading up to abrupt increases in shub cover (Fig 5). In fact, some

grass*grass and shrub*shrub correlation were greater in high resilience plots. We suspect that

these trends reflect the nature of spatial interactions in mesic grasslands. The distance between

neighboring plots is 6.5 meters, but mechanistic studies suggest that spatial interactions in

vegetation occur at smaller scales early in the shrub expansion process (Fig1, Heisler et al. 2004,

Ratajczak et al. 2011). This disparity suggests that between plot measurements are probably

ineffective because at the scale of between plots interactions are too weak for spatial correlation

to provide effective warning signs of regime shift.

Compared to between-plot measurements, within plot grass-shrub correlation was a more

consistent leading indicator. In the six years preceding the transition to shrubland, within plot

correlation between grasses and shrubs fluctuated around zero in high resilience plots, but

became negative and continued to decline in low resilience treatments in 1996 (Fig 5). If the

expansion of shrubs was occurring at the expense of grasses, the negative correlation between

grasses and shrubs potentially indicates an increase in small-scale shrub-shrub correlation.

However, grass*shrub correlation alone cannot discern whether the negative correlation between

these two groups is the result of shrubs displacing grasses.

A negative grass*shrub correlations can arise from demographic mechanisms if shrubs

colonize patches with low grass cover first (as we would expect) and then grow in size. Negative

effects of shrubs on grasses can also generate negative grass*shrub correlations if shrubs begin to

displace grasses, and thereby—this is the same rationale for how plot-scale grass*shrub

correlation can act as a surrogate for autocorrelation at the plot scale. To quantify if the negative

grass*shrub correlation was due to shrubs displacing grasses we compared the proportional rate

of grass cover change ($\ln[\text{grass cover}_t / \text{grass cover}_{t-1}]$) to the proportional rate of shrub cover

change ($\ln[\text{shrub cover}_t / \text{shrub cover}_{t-1}]$). This analysis tests if increases in shrub cover are

correlated with decreases in grass cover.

Until the year 2000, plots with higher shrub cover were no more or less likely to increase

or decrease in grass cover and similarly, increases in shrub cover were not correlated with

concomitant decreases in grass cover (Fig7). Thus, it is unlikely that grass*shrub correlation

reflected an increase in shrub-shrub auto-correlation at smaller scales. Instead, it is the growing

resistance of shrubs to the influence of grasses (i.e. demographic mechanisms) that lead to the

initial decrease in grass*shrub correlation we used as a statistical leading indicator.

Weighing the evidence for and against leading indicators, we conclude that there is little

evidence that declining resistance and critical slowing down resulted in increase in spatial auto-

correlation. Instead, negative correlations between grasses and shrubs occurred because shrubs

colonize low grass cover patches and then start to show increasing resistance to grasses and

greater demographic stability. Once shrubs overcome demographic barriers they begin to have

negative effects on neighboring patches, and at this point, there is the potential for an increasing

in spatial autocorrelation. This discrepancy suggests that spatial models of critical slowing down

need to consider the roll of demography and cannot assume that the potential for cells to

influence one another is constant. Instead, a transition can be precipitated by demographic shifts

and then reinforced through an alteration of fundamental feedback processes. In these instances,

spatial auto-correlation may be a poor indicator of critical slowing down.

Conclusion:

To our knowledge, this is the first example of declining resistance and critical slowing down

before a terrestrial regime shift and the first instance of combining resistance and critical slowing

down metrics with adaptive management to prevent a regime shift. However, declining resistance and critical slowing down did not lead to easily measured increases in spatial auto-correlation, because the potential for spatial interactions between adjacent patches did not emerge until the regime shift began. Therefore, to predict if less studied systems have alternative attractors and are approaching a threshold, it is necessary to access whether demographic mechanisms could possibly give rise to alternative attractors. In instances with demographic alternative stable states, other metrics of critical slowing down are likely to out-perform spatial auto-correlation. Thus, while we may not yet have truly "generic leading indicators" we are definitely getting closer.

Methods:

Konza Prairie LTER is a long-term ecological research site in the Central Great Plains of the United States. The site is native, unplowed tallgrass prairie characterized by high floristic diversity and dominance by C_4 grass species (more information on the specific data-set found at konza.ksu.edu and in Collins and Calabrese 2012). The region has seen an increase in woody cover over the last 50 years, attributed to fire suppression, grazing, exurban expansion and associated habitat fragmentation (Briggs et al. 2005), and potentially elevated CO_2 or other large-scale anthropogenic pressures (Ratajczak et al. 2011, Bond and Midgley 2012).

The Konza Prairie is a factorial cross of fire frequency (1, 4, or 20 yr fire returns) and grazing (grazed or ungrazed by large native ungulates *Bos bison*) in a topographically heterogeneous landscape. Vegetation is measured across all fire treatments and grazing treatments and in three landscape positions (thin-soiled uplands, deep-soiled lowlands, and slopes of variable soil-depth connecting uplands and lowland). Slope position data are only available for 4 and 20 year fire grazed treatments (other treatments either had no data for slopes

or were temporally limited for slopes with only two years of sampling from 2000 onwards). Vegetation plots are 10 m^2 circles arrayed along 50 m long transects with equal space between all plots. Each combination of fire, grazing, and landscape position has 4 such transects. Plots were positioned in order to typify tallgrass prairie plant communities, and therefore, were placed away from riparian regions and in areas without woody vegetation.

Each year, the plots are re-visited at the end of the growing season (late August/early September) and the approximate cover of every species is categorized into size classes of 0%, 0-1%, 1-5%, 5-25%, 25-50%, 50-75%, 75-95%, or 95-100%. We used the mid-point of these classes to calculate cover (see Ratajczak et al. *in press* for more details, including information on how the cover class system does not create false non-linear transitions). Following past studies (Ratajczak et al. 2011 and Ratajczak et al. *in press*), we defined shrub species as all woody species that typically grow taller than the grass-canopy.

Measurements of shrub occupancy were calculated at the proportion of plots with at least one shrub species present. Shrub mortality at time t was calculated as (m_t /n_t), where m_t is the number of mortality events at time t, and n_t is the number of plots occupied by shrubs. Mortality events were recorded as an instance where shrubs were present in a given plot at time t-1, but not time t. Shrub size is the cover of shrubs, only in the plots where they occur. Changes in grass and shrub cover (Δ grass and Δ shrub) where calculated as proportional rates of increasing using a natural log response ratio (ln [grass cover$_t$/grass cover$_{t-1}$]). To measure the shrub-mediated feedback strength, we used the correlation coefficient of Δ grass*shrub cover, with each plot as a replicate.

The reversal experiment was initiated in the year 2001 and switched the fire frequency from once every 20 years, to one fire per year in two geographically and hydraulically separated

catchment basins. All measurements in these fire-reversal treatments follow those for non-reversal treatments.

To calculate plot-scale auto-correlation, we compared shrub and grass cover within plots (Fig 1). This follows the assumption that each plot has a limited amount of space that can be filled by grasses, shrubs, bare ground, or other species. A decrease in the correlation between grasses and shrubs within a plot suggests that the shrub component is expanding at the expense of the grass component. This would be indicative of growth if the correlation between the space occupied by shrubs and adjacent areas was previously unoccupied by shrubs. Grass*shrub correlations between plots are used to correct for background correlation between grasses and shrubs and to quantify if and when the influence of grasses or shrubs in one plot affects grasses or shrubs in neighboring plots. To calculate auto-correlation at large scales we calculated correlation coefficients of shrub cover*shrub cover, and grass cover* grass cover cover in adjacent plots. Unlike past studies (Dakos et al. 2010), we did not need to use Moran's I index to calculate correlation coefficients because we were not considering a 2-D matrix of cells.

Treatments were grouped into low and high resilience groups using a post hoc assessment of shrub cover in each treatment and shrub-cover cut-off established in Ratajczak et al. (*in press*). This classification placed treatments with slope or lowland soils and 4 and 20 year returns in the low resilience group and all other treatments (shallow soil or annual fire) in the high resilience group. Data were also analyzed at either treatment scale, yielding similar results.

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Chapter 8 - Science based thresholds and bottom-up citizen action: will we manage fire to prevent large-scale loss of tallgrass prairie to shrublands and woodlands?

Up to the section "looking forward", this chapter is formatted for and will be submitted to: "FRONTIERS IN ECOLOGY AND THE ENVIROMENT" as a "Peer-Reviewed Letter".

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Letter:

All too often, humans do not identify ecological thresholds and tipping points until after they are crossed, whether it is the transformation of grasslands to deserts, native to invasive dominated communities, eutrophication of ecosystems, or depleted consumer populations (Folke et al. 2004). In other cases, tipping points are identified early, but large-scale action is restricted by institutional control, or local stakeholders lack the means or motivation to enact preventative measures (Walker and Salt 2006, Chapin et al. 2011). All of these scenarios can result in widespread ecological regime shifts that are rapid and difficult to reverse (Fig 1) (Scheffer 2009). In this letter, we project that almost 70% of remaining Central Plains grassland could be pushed past a tipping point and transition to shrublands and woodlands if our more frequent burning regimes aren't quickly adopted. These findings highlight the importance of a paper recently published in this journal—"The Great Plains fire campaign" by Twidwell and colleagues—which is part of an effort to enable landowners to manage and understand fire.

Recent studies have identified fire frequency and intensity thresholds in tallgrass prairie, as well as the potential for tallgrass prairie to yield ecological surprises: abrupt shifts in ecosystem state after years with little change in vegetation patterns. Specifically, 30 year long fire manipulations at Konza Prairie Biological Station and elsewhere show that fire returns greater than 2 to 3 years leads to rapid and unexpected expansions of shrub cover (Fig 1, Briggs et al. 2005, Bowles and Jones 2012, Ratajczak et al. *in press*), although adaptive grazing techniques may facilitate burning every three years without promoting changes in shrub cover (Fuhlendorf et al. 2009). Formation of shrub thickets alters local biodiversity and reduces available forage for economically important grazers (Briggs et al. 2005, Limb et. al 2011). Once shrublands are established, reintroducing frequent fires does not quickly return the system to a

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grassland state and transitions to (Ratajczak et al. *in press*). Further suppression of fire intensity and frequency (>6 to 10 year fire frequencies) leads to encroachment by evergreen Juniper trees, with exacerbated impacts on biodiversity and ecosystems goods and services (Fig 1, Briggs et al. 2005, Fuhlendorf et al. 2008). As with shrublands transitions, rates of woodland expansion can appear slow initially, but then accelerate as trees reach a fire-resistant size (Fig 1, Briggs et al. 2005). At this point, only physical removal or high-intensity high-risk fires will restore the ecosystem to grassland (Fuhlendorf et al. 2008, Twidwell et al. 2013b).

Humans are pushing tallgrass prairie beyond these fire thresholds at a large scale. Recent satellite estimates of fire frequency in the Flint Hills, the eco-region with much of the remaining tallgrass prairie in North America, indicate that 35 % of remaining tallgrass prairie of this region is burned every 3-8 years and susceptible to shrubland transitions, and 38% is burned less frequently than ever 8 years and susceptible to woodland transitions (Mohler and Goodin 2012). Thus, over 73% of this region could be susceptible to abrupt and difficult to reverse transitions in the coming decades (Mohler and Goodin 2012 *sensu* Briggs et al. 2005, Fuhlendorf et al. 2008, Bowles and Jones 2013, Ratajczak et al. *in press*). For perspective, this is an area equivalent to roughly the size of the state of New Jersey or Sicily, Italy. Some of the areas burned >8 years are in close proximiated to settlements, increasing the potential for dangerous forest crown fires in close proximity to humans—a sharp contrast to the smaller more manageable fires typical of tallgrass prairie.

Preventing these transitions will entail a large-scale increase in fire frequency. However, prescribed burning requires large groups, equipment, expertise in the field, and the ability to navigate and alter regulations (Twidwell et al. 2013a). In this journal, Twidwell and colleagues (2013a) describe the recent emergence of a bottom-up social network—the Great Plains fire

campaign—that has overcome the substantial hurdles associated with implementing prescribed burning in tallgrass prairie. Sharing expertise, time, and materials between landowners, the Great Plains fire campaign is fostering innovative adaptive management and allowing landowners to control fire frequency and intensity.

Thus, while there is strong potential for a widespread loss of tallgrass prairie, we have the ability, knowledge, foresight, and the motivation to avoid the transformation of this region (Walker and Salt 2006). A convergence of all these factors opens a rare window of opportunity to engage in preventative management of the Central Great Plains and maintain both ecological integrity and cultural resilience of this region (Folke et al. 2006, Chapin et al. 2011). The success of this initiative will require communication between landowners and scientists to raise awareness and mange externalities, continued experiments to identify if fire thresholds are changing, and innovation by landowners and scientists to adapt to future challenges. Reintroducing fire to this region is a substantial undertaking, and will certainly face challenges, such as successful scientific outreach and managing air quality. However, increasing fire frequencies in the Central Great Plains is crucial to conserving this ecosystem for future generations, avoiding the potential for dangerous wildfires, and preventing declines in cattle production and biodiversity.

Looking forward:

There are still many unanswered question to understand the theoretical basis of ecosystem transitions in grasslands and manage these transitions sustainably. In the near future, it is imperative to determine what factors encourage people to adopt more frequent fires and how human choices alter the risk:benefit ratio of maintaining native ecosystems. Another question that ties together conservation, theoretical ecology, and social-ecological interaction is how

biodiversity and management for biodiversity affects ecosystem thresholds. If managing for biodiversity increases resilience, then it would be possible for humans to meet social and conservation goals at the same time.

Surprisingly, there are few theoretically derived hypotheses of how biodiversity and should alter ecosystem thresholds and in turn, how biodiversity will change when thresholds are crossed. My primary hypothesis is that functional and demographic diversity, modular network connections, and niche complementarity among species will increase the linearity of community responses (i.e. threshold are unlikely) (Fig 2A). When thresholds are present, I predict that more diverse systems will have a lower probability of transitioning to a new self-enforcing state because these systems have higher stability (Fig 2B).

The basis for these hypotheses is the importance of non-linear demographic traits and reinforcing feedback mechanisms in systems with internal thresholds (with hysteresis or otherwise). These demographic and feedback qualities facilitate the rapid transition from one state to another and sustain states once established. Among the many potential explanations for why biodiversity is correlated with ecosystem function, it could be that these systems have greater demographic stability and/or more diverse feedback mechanisms. These properties might also allow diverse communities to ameliorate their environment in their favor and/or make more complete use of available resources. In contrast, high abundance of species with non-linear demographic rates will make thresholds more likely because they create demographic bottlenecks that make binary ecological outcomes more likely.

There are many more analytical approaches that need to be explored, but early tests of these hypotheses using data from tallgrass prairie, (Konza LTER) do not provide obvious support for the idea that naturally occurring biodiversity confers resilience to regime shifts. Plot-scale (10

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m^2) species richness early in the Konza experiment does predict shrub cover 20 years later (Fig 3) or even shortly before regime shifts from grassland to shrubland (Fig 4). The diversity of dominant grasses (specifically, the Shannon-index) does not predict transition probability either (not shown). These counterintuitive results show that we need theoretical modeling of how biodiversity should translate to ecosystem resilience, and in parallel, empirical tests of developing theories. Exploring the connection between resilience and biodiversity will contribute to leveraging regulations and local management to increase social-ecological resilience and avoid losses of biodiversity.

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A) Resilience map of the Flint Hills, Central Great Plains, USA

Future State | Fire Return
Woodland | Unburned (black)
Woodland | 10 years (dark red)
Shrubland | (orange-red)
Shrubland | 4 years (orange)
Grass/Shrubland | 3 years (light yellow-orange)
Grassland | (yellow-green)
Grassland | 2 years (light green)
Grassland | (teal)
Grassland | (blue)
Grassland | 1 year (purple)

0   100 km

Kansas
Oklahoma
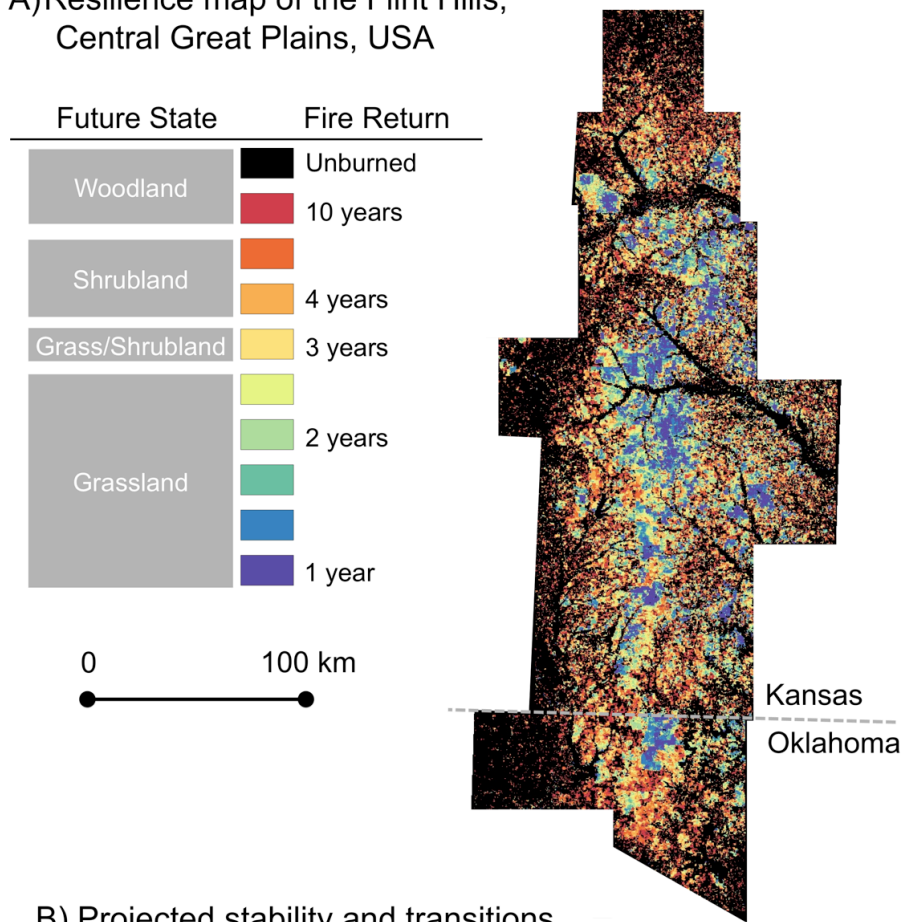
B) Projected stability and transitions in the next 2-3 decades

Grassland (28%)   Shrubland (42%)   Woodland (30%)

Area (ha) vs Fire Frequency (years per fire)
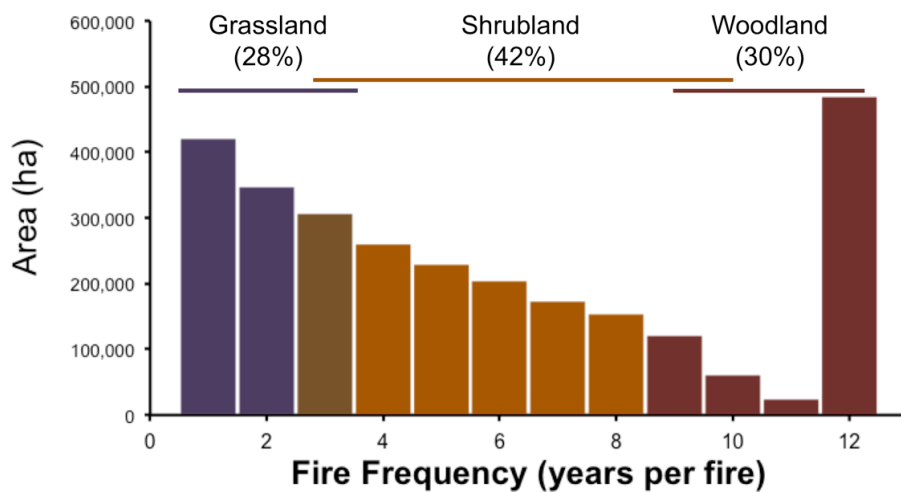
Figure 8.1 A spatial distribution (A) and total projected area (B) of ecosystems in the Flint Hills ecoregion, USA. Only areas that are classified as "grasslands" were used in (B) (see Mohler and Goodin 2012 for details), but on the current map (A), all unburned features

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are shown in black. Translating fire frequencies to future states was based on Ratajczak et al. (*in* review) and references therein. The future of ecosystems burned every 3 years is uncertain, and requires other aspects of management to determine if these areas will remain grassland or transition to shrubland. Similarly, burn frequencies of 6 to 10 years comprise a large area where the ecosystem may either transition to shrubland or woodland. Note that low fire frequencies surround a set of core areas with high burn frequency, similar to the argument by Engle and colleagues (2009) that a "Green Glacier" is approaching the Flint Hills.
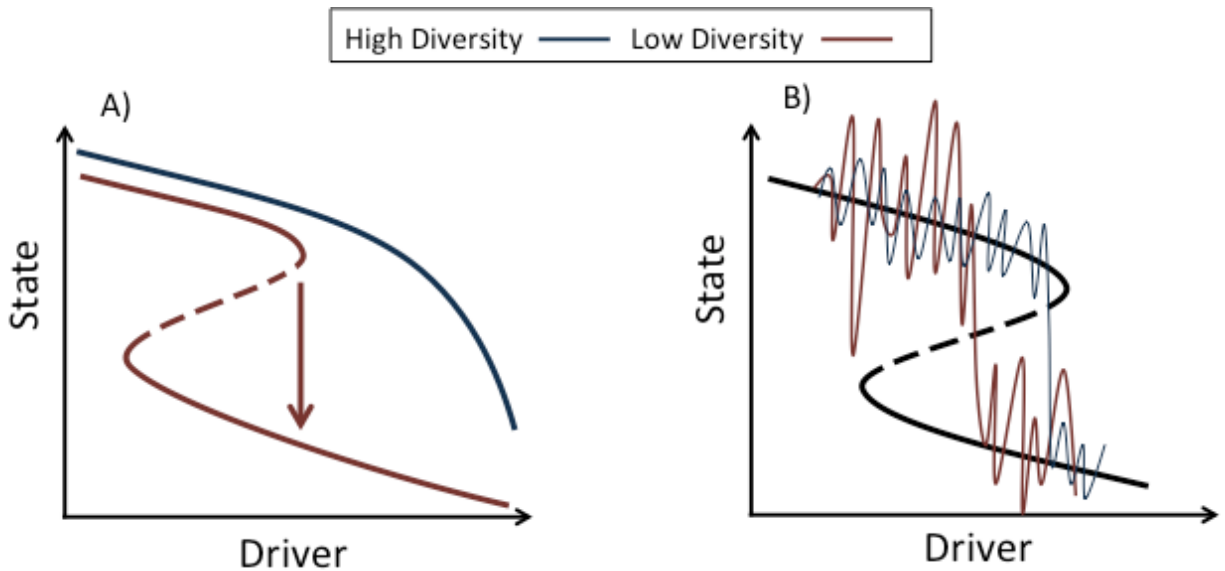
Figure 8.2 (A) Depiction of how biodiversity can result in greater resilience by altering the presence of thresholds. In this instance, the more diverse scenario (blue) lacks a critical threshold, whereas the low diversity scenario retains a critical threshold (red). Solid lines depict stable state, dotted lines predict unstable thresholds, and arrows show where a critical transition will occur. (B) Depiction of how the relationship of biodiversity and stochasticity can alter resistance and the probability of threshold transitions. In this instance both ecosystems scenarios (low and high diversity) have the same thresholds value, where solid black lines depict stable equillibria and dotted black lines depicts the unstable threshold separating equillibria. High amplitude fluctuations in the lower diversity scenario (red) increases the probability of crossing the unstable thresholds at a lower value of the driver variable, compared to the high diversity ecosystem (blue).
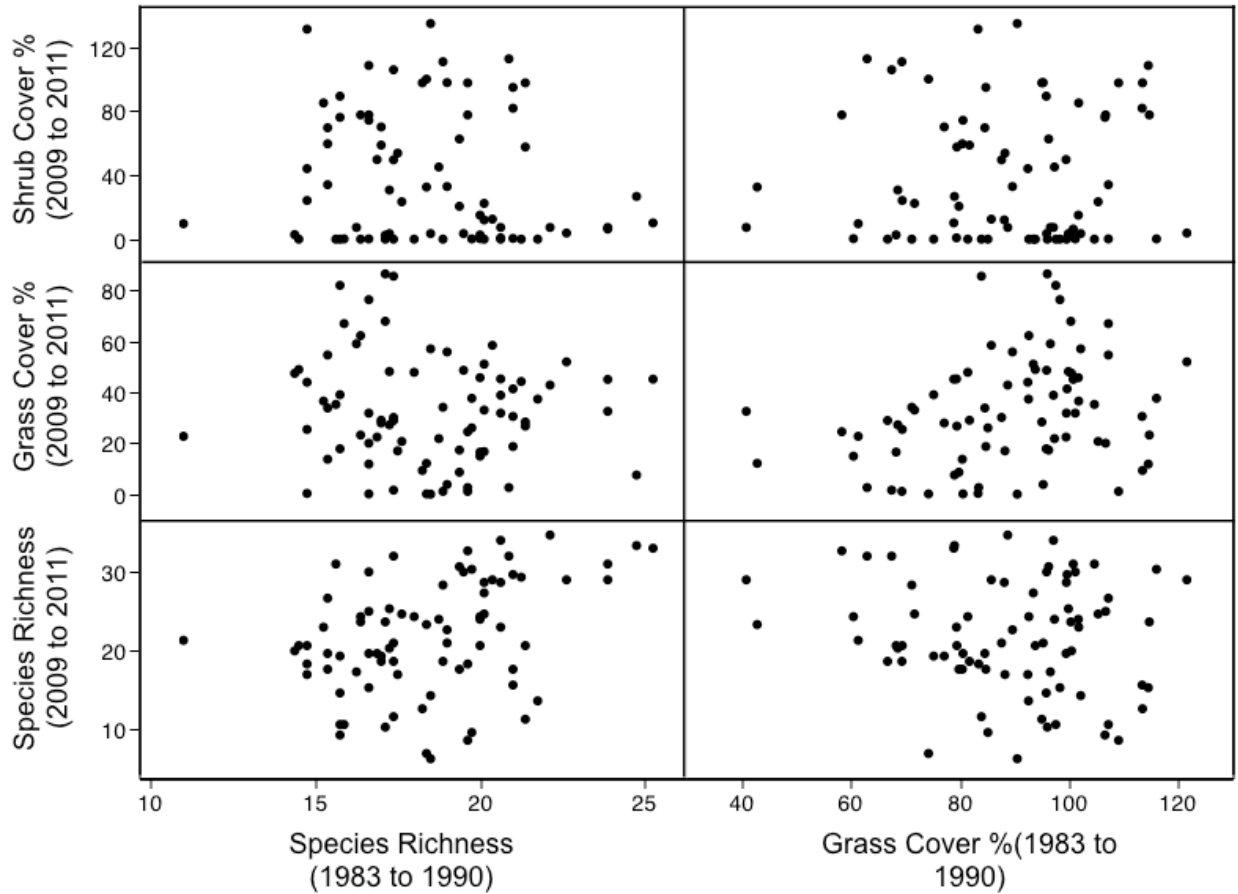
Figure 8.3 Relationships between species richness and grass cover early in the Konza experiment (left and right respectively), vs shrub cover (row 1), grass cover (row 2), and species richness (row 3) in the three most recent years of the Konza experiment and after regime shifts. These are all treatments with lowland soils and fire frequencies >4 years. In these treatments ~50% of plots transition to shrub dominance (>35% shrub cover, see figure 3). Note, the only significant relationship is between grass cover at the beginning and end of the experiment.
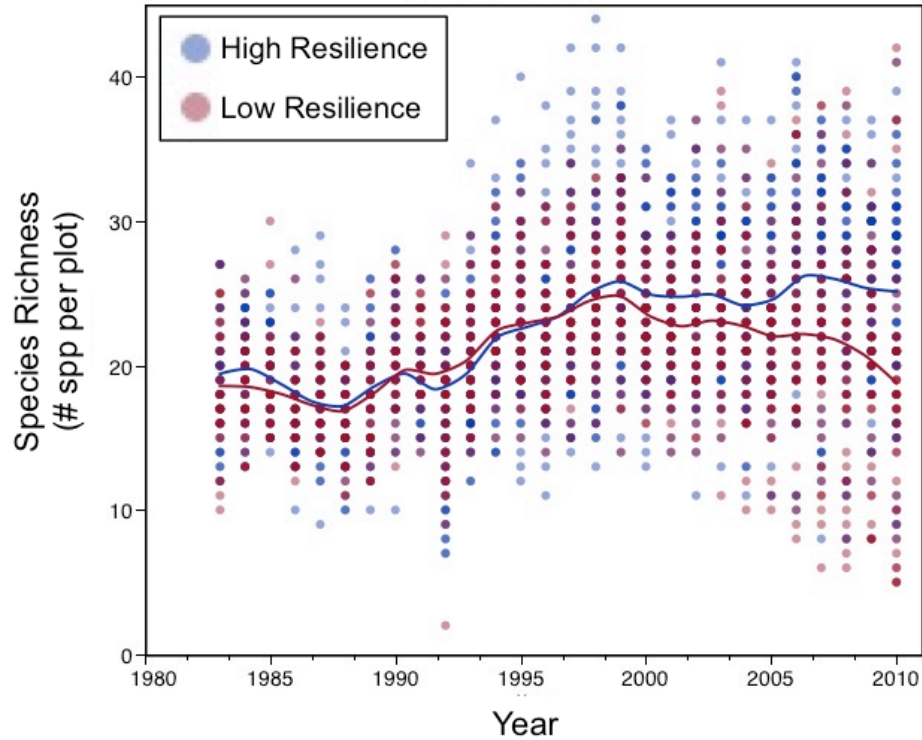
Figure 8.4 A comparison of species richness each year (x-axis) versus richness in each year (y-axis), for plots that remain grasslands (blue; high resilience), and those that transition to shrubland (red; low resilience). The cut-off separating high and low resilience plots is 35% shrub cover, based on a bi-modal distribution of plot-scale shrub cover in 2010 and 2011. In this analysis, <30% (high resilience) and >40% shrub cover (low resilience) are high frequency states (i.e. they are common), whereas 30-40% is an infrequent, uncommon or unstable state. The species richness comparison of these two categories does not diverge until ~2000-2003. At this point, shrubs start exerting a negative impact on other species, resulting in differences between the two classes of plot-level resilience.

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Please see individual chapters for references.

Appendix 2- Appendix Items for Chapter 2

Appendix A.1 Species richness references:

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Appendix A.2:

We included one study from the arctic Tundra, where encroachment was instigated by a fertilization treatment, because this site was an integral part of previous assessments of woody encroachment on aboveground biomass (Knapp et al. 2008) and woody encroachment is projected to occur over a very large area in the Arctic over the next century (Tape et al. 2006). Inclusion of this site does not alter relationships between "richness response" and MAP. Removing this site would strengthen the relationship between "richness response" and ANPP variables. The following are studies that were initially considered, but eventually reject for not meeting one of our inclusions for criteria. For each study, justifications for not including are given.

1. Bork and Burkinshaw 2009: This study only reports results from diversity indices.

2. Brewer and Vankat 2006: Changes between woody and grass dominance are results in soil hydrology, not human activity (i.e. edaphic factors structure the distribution of woody species, which is not indicative of increasing woody plant abundance).

3. Briggs et al. 2002: This article is the same article as Hoch et al. 2002. Citations as Briggs et al. 2002 are incorrect.

3. Briggs et al. 2005: Numbers that appear in this article are quoted other articles. We only included the original studies.

4. Brockway and Lewis 1997: The study site received 1200 mm of precipitation per year, which is higher than our pre-determined criteria for inclusion.

5. Brockway et al. 2000: The gradient in woody coverage at this site was created by recent forest clearing.

6. Burkhardt and Tisdale 1969: Including this study would not change r^2 of reported relationships and would increase replication within the Big Sagebrush community. However, right now the distribution of grassy and woody patches is determined by edaphic factors, which makes it difficult to parse out the effects of changes in canopy vs soil. Therefore, we did not include this study.

7. Burley et al. 2010: This study site receives 1200-1400 mm of precipitation per year, which is higher than our pre-determined criteria inclusion.

8. Cushman et al. 2010: Including this study would not change r^2 of reported relationships and would add another community type to our study. It addressed diversity in grass and woody dominated patches, but we can find no evidence of shrub cover increasing in this ecosystem. Study site has an MAP of ~300 mm and richness response of ~ -0.5.

9. Everett and Koniak 1982: Including this study would increase r^2 of reported relationships slightly and would add a replicate to the Big Sagebrush community. However, the comparisons reported here are species richness differences between widely distributed sites that differ from each other in woody cover. As such, soil characteristics and elevation vary considerably between sites. For this reason, it is difficult to say whether changes in species are related to tree cover or these edaphic differences. The study has an MAP of ~250 mm and a richness response of ~-0.22.

10. Johnson and Cushman 2007: This study addressed the effects of grazing removal and species richness of multiple functional groups. However all sampling occurred only in plots with <5% shrub cover, which is not comparable to other studies.

11. Johnson et al. 1996: The gradient in woody coverage in this site was created by recent application of herbicides.

12. Ko and Reich 1993: A large number of species were identified by genera, rather than species, making it impossible to generate a species richness measurement that is comparable to those in other studies.

13. Koniak and Evertt 1982: Including this study would increase the r^2 of reported relationships and add a replicate to the Big Sagebrush community. However, a few species were lumped together in the analysis, because reporting richness of the seedbank community, not the standing community, was the primary goal of this study.

14. Marchand and Houle 2006: Plots in this study span from the center of forests to grassland/forest ecotone, but not into pure grassland. Also, there is little evidence for increasing woody cover in this community.

15. Mata-Gonzalez et al. 2007: This study site was subject to recent shrub clearing.

16. McPherson et al. 1991: A large number of species were identified by genera, rather than species, making it impossible to generate a species richness measurement that is comparable to those in other studies.

17. Morgan et al. 2007: encroachment of this community was instigated by a free-air CO_2 experiment. However, because the experiment had only been running for several years the max shrub canopy cover was 5% in very small plots. Since most other studies assesses shrub cover of 80% or more, we did not think it was appropriate to include this study.

18. Oberndorger and Lundholm 2009: Changes in woody coverage are highly dependent on soil types, making cross-site analyses difficult. Areas without woody vegetation are predominately moss, lichen, fern, and sedge dominated (i.e. evidence for grass dominance is low).

19. Ratliff 1995: Including a response ratio of the diversity indices reported here would increase r^2 of our data and add another community type. However only diversity indices are reported, which is not consistent with other studies. Also, there is little evidence for active encroachment in the immediate area, just the region at large.

20. Rentch and Fortney 1997: The "Bald" communities described in this study are predominately forb dominated. Also, only changes in the occurrence of a select set of species are reported, making it impossible to generate a species richness measurement that is comparable to those in other studies.

21. van Els et al. 2010: Including this study as a tallgrass prairie replicate (as would be most appropriate) would increase the r^2 of reported relationships and add a replicate to this community type. However, this site appears to be more representative of a forest or woodland, as described by the authors.

22. Warren et al. 2007: the study site receives 1200-1400 mm of precipitation per year, which is higher than our pre-determined criteria inclusion.

23. West and Hassan 1985: This study accesses changes in vegetation directly after a wildfire, which decreased the cover of encroaching sagebrush. However, wildfire returns in this ecosystem are infrequent (~100 yrs), which it makes it difficult to discern between the effects of wildfire versus a moderate decrease in shrub coverage (much in the same way that a restoration study would be difficult to interpret).

24. Westman 1981: Including this study would not change the r^2 of reported relationships and would add another community type to our analysis. However, the evidence for encroachment in this ecosystem has become tenuous, because the fire-sensitive woody species are is now being

over-taken by invasive grasses. The study sites has an MAP ~400 mm and a richness response of ~-0.615.

25. Xia et al. 2010: Including this study would increase r^2 of relationships and add a replicate to the Chihuahuan desert community. However, this study only reports richness of annual species (this functional group is the focus of the paper). Annuals make up a significant portion of diversity in this ecosystem (see Baez and Collins 2008 in citations of appendix 2), but perennials do exist, so we did not think it was appropriate to include this study.

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Xia, Y, D. I. Moore, S. L. Collins, and E. H. Muldavin. 2010. Aboveground production and species richness of annuals in Chihuahuah desert grassland and shrubland plant communities. Journal of Arid Environments 74: 378-385.

Appendix A.3: Obtaining data from individual studies:

We used the response ratio on four types of data: 1) categorical woody dominated (X_e) vs. grassland dominated plots (X_c); 2) historical richness (X_c) vs. encroached richness (X_e) and; 3) regression data, where species richness was regressed with woody coverage; 4) inventory data, reporting the total number of species occurring in a large number of plots. We used the value of the regression line at the highest woody coverage reported as X_e and at the lowest coverage reported as X_c. When numbers were not reported in tables, text, or as regression-line equations, we used the program ImageJ to extract values from graphs.

In many instances, pulling data from studies was straightforward. However, there were exceptions, which are catalogued below. In general, we attempted to analyze data in way that represented a balanced assessment of woody encroachment impacts. This was achieved by always averaging data from near the base of the tree/shrub with data from the mid-canopy as

well when appropriate (i.e. number 2 and 5 below). The outlier referenced in results was Hoch et al. (2002), from appendix 2. This study was removed because it was greater than 4.4 standard deviations from the population mean.

1.Schwarz and Wein 1997, Colberg 2007: These studies report inventory data for several sites. We compared the total number of species in sites without trees to sites with the highest tree densities.

2. Archer et al. 1995: This study reports richness as a function of depth into mature woody clusters. We averaged all values occurring within the cluster edge.

3. Hobbs et al. 1986: This study reports inventory-style data for individual species across a chronosequence of shrub encroachment. We averaged values for the 8-9 yrs old and >10 yrs clusters, because >9 yr clusters tend to collapse, but may eventually be re-colonized. Therefore, both of these groups are probably representative of encroached conditions.

4. Foster and Shaff 2003: Though this study includes older forests, we used values from ~80 yrs ago when forest development can be readily attributed to human activity. Data from "managed" and "un-managed" forests are included in this study. We only used data from "unmanaged" because they had not been subject to selective forest clearing.

5. Dye et al. 1995: In this study, richness was reported near the base of trees, in the middle of the tree canopy and at the canopy edge. We averaged values for the base of trees and the middle of the canopy, because edge habitat should disappear with time and this type of averaging was more consistent with methods used for other sites.

6. Collins et al. 1983: For this study we compared how diversity changed over time in the plots at the one site where encroachment occurred.

7. Miller et al. 2000: we excluded data from the encroachment of low-sagebrush, because encroachment appeared to just beginning at this site (only 24% tree cover compared to 40-60 in others), which could affect results since they used a macro-plot design (i.e. that covered the whole site, not just under trees). Unfortunately, data were not available from several of the most encroached sites used in this analysis. Therefore, any data from this study should be considered an under-estimate of the impact of encroachment in this location.

8. Tausch and Nowak 1999: This study presented the present cover of encroaching species and species richness at 17 sites. We regressed richness with tree cover, which resulted in a quadratic relationship ($r^2 = 0.52$). We compared changes in diversity between the top of this curve to the bottom of the curve, since some tree dominance is probably the natural state for this ecosystem (see Peterson and Reich 2008 for similar dynamics).

9. Leach and Givinish 1999, Peterson and Reich 2008: the relationship between tree cover and richness is quadratic in oak savannas. Like Tausch and Nowak 1999, we compared richness from the peak of the richness curve to the bottom, since some woody dominance is probably the reference state for this ecosystem as well.

10. Crawford and Young 1997: We averaged the response ratio of "mid-island" and "back-island" encroachment, which denote dune grasslands of different ages (younger and older, respectively).

Appendix B—Appendix for Chapter 5

Appendix B.1: History of Data-sets and Analyses of Temporally Limited Data-Sets

In addition to the core data-set used in the main text (hereafter the "core data-set"), another long-term data-set exists for Konza started by Gene Towne in 1991 to 1993 (hereafter the "Towne Data-set") within grazed 1 (N1A), 4 (N4A), and 20 yr (N20A), and 4 yr ungrazed watersheds (4A). These data are in separate catchment basins than the core data-set, but similar to the core data-set, this data-set was started in herbaceous-dominated plots. This data-set adds lowland and slope replicates to the grazed 4 and 20 yr fire treatments, and a lowland replicate to the grazed 1 yr fire and ungrazed 4 yr fire treatments. Table A1 shows the watersheds used in both data-sets, their spatial coverage, and their fire histories.

The preliminary results from the Towne data-set provide similar trends as the core-data-set. In the grazed 4 yr and 20 yr treatments there has been a gradual decrease in dominant C_4 grass cover, linear or peak-like behavior in *Solidago* spp., stochastic fluctuations in sub-dominant C_4 grasses, and just recently, a potential non-linear shift in shrub cover within half of grazed treatments (Fig A1). C_4 grasses in the 4 yr ungrazed treatment are also starting to show the same cyclic behavior as C_4 grasses in the core-data-set. The non-linear shifts in shrub cover have occurred just as these treatments have reached the same shrub-cover thresholds identified in the core data-set (~5% cover for the 4 yr treatment and ~10 for the 20 yr treatment). The 4 yr ungrazed treatment is getting close to grass and shrub cover thresholds identified in the core data-set (Fig A2). Considered with the core data-set, the Towne data-set reinforces the importance of long-term data for identifying the potential for regime shifts in terrestrial ecosystems.

References:

Towne, E.G., D.C. Hartnett, and R.C. Cochran. 2005. Vegetation trends in tallgrass prairie from

bison and cattle grazing. Ecological Applications 15: 1550-1559.

Table A1. Meta-data for data used in core and Towne data-sets.

Fire	Grazing	Watershed ID	Data-Set ID	Topography	Beginning of Data Collection	# Transects	Years With Fire
1 yr	grazed	N1B	Core	Lowland	1983	4	Every year since 88
1 yr	ungrazed	1D	Core	Lowland	1983	4	Every year except 96
4 yr	grazed	N4D	Core	Slope	1993	4	88, 91, 94, 98, 01, 05, 09
4 yr	grazed	N4D	Core	Lowland	1983	4	88, 91, 94, 98, 01, 05, 10
4 yr	ungrazed	4B	Core	Lowland	1983	4	83, 87, 91, 94, 98, 00, 03, 05, 09
20 yr	grazed	N20B	Core	Slope	1993	4	91, 96
20 yr	grazed	N20B	Core	Lowland	1983	4	91, 96
20 yr	ungrazed	20D	Core	Lowland	1983	4	91
1 yr	grazed	N1A	Towne	Lowland	1993	4	Every year except 1987,
4 yr	grazed	N4A	Towne	Slope	1991	4	84, 88, 92, 94, 00, 02, 04, 08, 12
4 yr	grazed	N4A	Towne	Lowland	1991	4	84, 88, 92, 94, 00, 02, 04, 08, 12
4yr	ungrazed	4A	Towne	Lowland	1992	4	84, 88, 92, 94, 99, 02, 06, 10
20 yr	grazed	N20A	Towne	Slope	1993	4	89, 90, 91, 92, 12
20 yr	grazed	N20A	Towne	Lowland	1993	4	89, 90, 91, 92, 12

Figure Legends:

Fig A1. Patterns of shrub cover (a), dominant C_4 grass cover (b), *Solidago* spp. cover (c), and subdominant grass cover (d) in grazed treatments of the Towne data-set. 20 yr fire treatments appear as black circles, 4 yr fire treatments as grey circles, and 1 yr fire treatments as open circles. The histograms next to panel A show the frequency of different cover classes, derived from the core data-set. There are included to compare the Towne data-set to thresholds derived in the core data-set.

Fig A2. Patterns of shrub cover (a), dominant C_4 grass cover (b), *Solidago* spp. cover (c), and subdominant grass cover (d) in the 4 yr ungrazed treatment of the Towne data-set. The histograms next to panel A show the frequency of different cover classes, derived from the core data-set. There are included to compare the Towne data-set to thresholds derived in the core data-set.
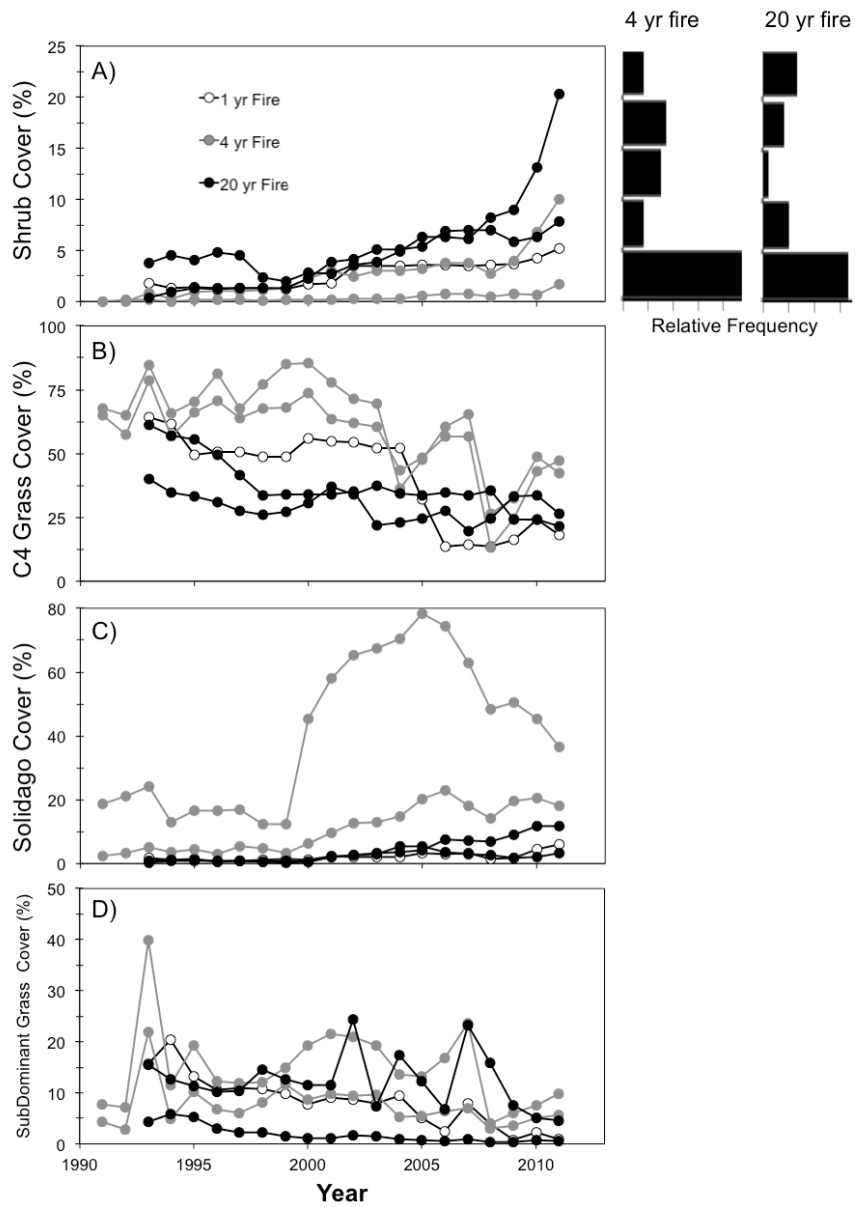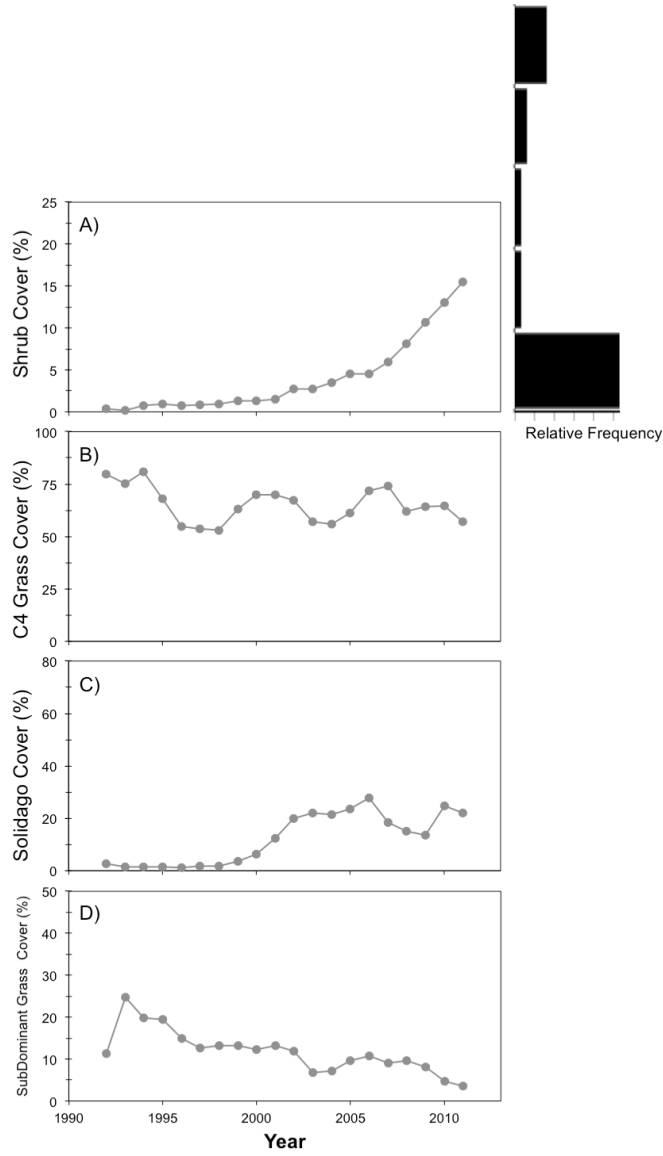
Fig A1.

Fig 2.

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Appendix B.2: Temporal dynamics and modality of non-target functional groups and climate.

Table B1. Temporal Dynamics of Solidago *spp.*

Treatment	Single Line (r^2/AIC)	Logistic (r^2/AIC)	Split Line: ind. intercepts (r^2/AIC)	Split Line: ind. Slopes (r^2/AIC)	Split Line: ind. slopes & intercepts (r^2/AIC)	Quadratic (r^2/AIC)	Lorentian Peak (r^2/AIC)
1 yr grazed	0.72/209	0.98/141	0.72/209	0.72/209	0.72/209	0.93/172	0.99/125
1 yr ungrazed	0.15/110	110/0.18	0.16/110	0.16/110	0.16/110	0.18/112	0.41/102
4 yr grazed	0.07/334	334/0.8	0.07/337	0.1/335	0.1/338	0.1/335	0.089/335
4 yr ungrazed	0.27/247	247/0.37	0.45/241	0.42/243	0.66/230	0.41/0.244	0.8/211
20 yr grazed	0.46/295	295/0.57	0.56/288	0.46/297	0.56/290	0.46/297	0.6/283
20 yr ungrazed	0.43/249	249/0.56	0.6/241	0.58/243	0.82/221	0.55/245	0.92/193

Table B2. Temporal Dynamics of Subdominant C4 Grasses.

Treatment	Single Line (r^2/AIC)	Logistic (r^2/AIC)	Split Line: ind intercepts (r^2/AIC)	Split Line: ind. Slopes (r^2/AIC)	Split Line: ind. slopes & intercepts (r^2/AIC)	Quadratic (r^2/AIC)	Lorentian Peak (r^2/AIC)
1 yr grazed	0.23/130	0.27/131	0.23/130	0.23/130	0.23/130	0.24/132	0.23/133
1 yr ungrazed	0.37/225	225/0.4	0.37/225	0.37/225	0.37/225	0.4/227	0.4/226
4 yr grazed	0/339	339/0.04	0.01/341	0.02/340	0.03/342	0.01/341	0.01/340
4 yr ungrazed	0.02/152	152/0.03	0.15/151	0.08/153	0.24/150	0.06/154	0.09/153
20 yr grazed	0.04/285	285/0.05	0.09/285	0.05/287	0.09/287	0.05/287	0.05/287
20 yr ungrazed	0.05/136	136/0.16	0.11/137	0.37/126	0.48/123	0.35/127	0.41/124

Table B3. Distribution Modeling of *Solidago spp.*

Treatment	Uni-Modal (AIC)	Bi-Modal (AIC)	Johnson SI (AIC)
1 yr grazed	239	212	212
1yr ungrazed	112	100	90
4 yr grazed	336	315	309
4 yr ungrazed	254	240	234
20 yr grazed	318	295	297
20 yr ungrazed	264	253	257

Table B4. Distribution Modeling of Subdominant C4 Grasses.

Treatment	Uni-Modal (AIC)	Bi-Modal (AIC)	Johnson SI (AIC)
1 yr grazed	135	135	131
1yr ungrazed	337	245	336
4 yr grazed	337	298	306
4 yr ungrazed	151	154	149
20 yr grazed	285	280	263
20 yr ungrazed	135	136	136

Table B5. Temporal analyses of climate variables.

Climate Variable	Single Line (r2/AIC)	Logistic (r2/AIC)	Split Line: ind intercepts (r2/AIC)	Split Line: ind. Slopes (r2/AIC)	Split Line: ind slopes & intercepts (r2/AIC)	Quadratic (r2/AIC)	Lorentian Peak (r2/AIC)
Winter Temp	0.03/132	0.15/131	0.05/135	0.19/129	0.19/132	0.17/130	0.00/136
Spring Temp	0.12/115	0.14/117	0.13/117	0.12/118	0.15/119	0.13/117	0.13/117
Summer Temp	0.07/105	0.07/108	0.10/107	0.08/108	0.10/109	0.10/107	0.05/109
Fall Temp	0.14/95	0.14/98	0.15/97	0.13/98	0.15/100	0.14/98	0.14/98
Winter Precp	0.03/167	0.03/170	0.05/169	0.04/170	0.05/172	0.04/170	0.03/170
Spring Precip	0.00/248	0.00/251	0.04/250	0.00/250	0.04/253	0.00/251	0.00/251
Summer Precip	0.08/261	0.08/264	0.08/264	0.08/264	0.08/266	0.08/264	0.08/264
Fall Precip	0.04/227	0.04/230	0.05/229	0.05/229	0.06/231	0.05/230	0.04/230

Table B6. Modality analyses of climate variables.

Climate Variable	Uni-Modal (AIC)	Bi-Modal (AIC)	Johnson SI (AIC)
Winter Temp	131	134	134
Spring Temp	113	121	117
Summer Temp	105	112	107
Fall Temp	98	97	100
Winter Precip	166	171	166
Spring Precip	246	250	245
Summer Precip	261	268	259
Fall Precip	226	230	223

Figure Legends:

Fig A1. Histograms of the non-target functional groups (*Solidago* spp. and sub-dominant grasses), across different fire and grazing treatments.