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Assessing the Potential for Transitions from Tallgrass Prairie to Woodlands: Are We Operating Beyond Critical Fire Thresholds?

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ABSTRACT

A growing body of evidence suggests humans are pushing ecosystems near or beyond key ecological thresholds, resulting in transitions to new, sometimes undesirable phases or states that are costly to reverse. We used remotely sensed fire data to assess if the Flint Hills—a landscape of tallgrass prairie in the Central Great Plains, United States—is operating beyond fire frequency thresholds. Long-term fire experiments and observational evidence suggests that applying prescribed fire at return intervals > 3 yr can lead to transitions from grassland to shrubland. Fire return intervals > 10 yr and complete fire suppression, in particular, can result in transitions to woodlands over 30 − 50 yr. Once shrublands and woodlands are established, restoration back to grassland is difficult with prescribed fires. We applied these fire frequency cutoffs to remotely sensed fire data from 2000 to 2010 in the Flint Hills, identifying the extent of tallgrass prairie susceptible to shrub and tree expansion. We found that 56% (15 620 km^2) of grasslands in this region are burned less than every 3 yr and are therefore susceptible to conversion to shrub or tree dominance. The potential effects of this large-scale shift are greater risk for evergreen *(Juniperus virginiana)* woodland fires, reduced grazing potential, and increased abundance of woodland adapted species at the expense of the native grassland biota. Of the 12 127-km^2 area likely to remain grassland, 43% is burned approximately annually, contributing to vegetative homogenization and potential air-quality issues. While this synthesis forecasts a precarious future for tallgrass prairie conservation and their ecosystem services, increases in shrub or tree dominances are usually reversible until fire frequency has been reduced for more than 20 yr. This delay leaves a small window of opportunity to return fire to the landscape and avoid large-scale transformation of tallgrass prairie.

Introduction

A major challenge in rangeland stewardship is managing in the face of uncertainty and multiple trade-offs (Westoby et al., 1989; Chapin et al., 2011; Collins et al., 2011). Two core challenges are avoiding ecological thresholds or "tipping points" (Walker and Salt 2006; Briske et al., 2008; Rockström et al., 2009, Barnosky et al., 2012) and maintaining the social and ecological diversity that confers adaptive potential to unknown challenges in the future (Chapin et al., 2011; Carpenter et al., 2012). In this synthesis, we focus on fire management in tallgrass prairie, which, along with grazing, is one of the most widely manipulated ecological processes in grasslands, savannas, and related rangelands (Bowman et al., 2009; Archibald et al., 2012; Ellis et al., 2013).

The tallgrass prairie grasslands of the Central Great Plains play an important societal role in this region. The geology over much of the Flint Hills landscape—our study region—precluded conversion to tillage agriculture but was conducive to cattle ranching (Smith and Owensby 1978), which remains a prominent source of agricultural livelihoods throughout much of the landscape (Middendorf et al., 2009). Intact tallgrass prairie provides a suite of other ecosystem services, such as freshwater, resistance to soil erosion, wildlife habitat, and mitigation of nutrient deposition (Kaufman et al., 1990; Fuhlendorf et al., 2009; McLauchlan et al., 2014; Matlack et al., 2008). Tallgrass prairie also has an important conservation role. In North America, tallgrass prairie has been reduced to ~4% of its historical extent (Sampson and Knopf, 1994), making it one of the most altered ecosystems in North America

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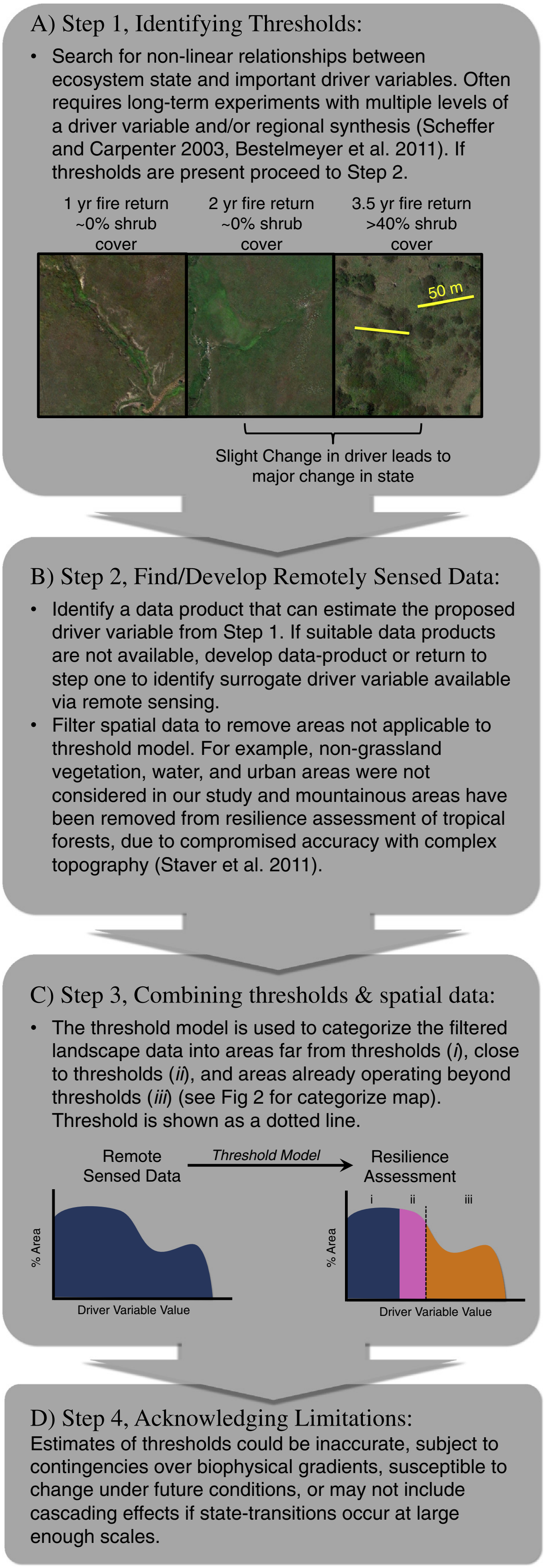

Fig. 1. A schematic of the process used in this study to combine an ecological threshold framework with remotely sensed data. Satellite images in "Step 1" are from Google Earth imagery in the year 2012 in lowlands of watersheds 1D, 2A, and 4B at Konza Prairie Biological Station and LTER (located in Riley County, KS). Note that the darker green vegetation in the 3.5-yr fire return interval are large shrub species capable of overtopping and excluding grasses (primarily Roughleaf Dogwood, *Cornus drummondii*). No shrubs are present in the aerial photographs shown for 1- and 2-yr fire return intervals.

(Hoekstra et al., 2005). Loss of this landscape contributes to the decline of grassland bird populations, one of the fastest diminishing avifauna in North America (Sauer and Link 2011). The Flint Hills landscape is the largest remaining tract of intact tallgrass prairie landscape (Samson and Knopf 1994). For this reason, loss of grasslands within this region has a major impact on tallgrass prairie conservation.

Many challenges exist to maintain economic productivity and biodiversity in tallgrass prairies, including the Flint Hills. One is the transition of tallgrass prairie to shrublands and woodlands, often referred to as "woody encroachment" (Briggs et al., 2005; Fig. 1). Woody encroachment alters ecosystem structure and function of temperate grasslands, resulting in a loss of biodiversity and grazing productivity (Coppedge et al., 2001; Engle et al., 2008; Fuhlendorf et al., 2008; Eldridge et al., 2011; Ratajczak et al., 2012; Anadon et al., 2014). Transitions to woodlands near urban and suburban areas may also pose a danger to humans, as woodlands can sustain large crown fires with flames up to 15 m in height, with the potential to cast embers into settled areas (Twidwell et al., 2013a, 2013b).

Transitions to shrubland and woodland in temperate climates are largely attributed to changes in fire management (Briggs et al., 2005; Peterson et al., 2007, Bond 2008; see discussion for other factors). In the Flint Hills, humans are a major determinant of where and when fires occur (Stambaugh et al., 2013; Twidwell et al., 2013b). In tallgrass prairie, reoccurring fire intervals of > 3 yr between fires can potentially result in transitions to shrublands or woodlands (Ratajczak et al., 2014a and see methods). While 1- to 2-yr fire intervals are common in some portions of tallgrass prairie, the geographic extent of tallgrass prairie burned infrequently enough to foster transitions from grassland to shrubland and woodland is still debated (Engle et al., 2008; Twidwell et al., 2013a, b), but empirical assessments are lacking. Current and projected increases in grazing pressure (Fuhlendorf et al., 2008), winter precipitation (Nippert et al., 2013), and atmospheric CO_2 (Bond and Midgley 2012) should further increase the probability of transitions to shrubland/woodland.

Woody encroachment is not the only fire-related management concern in the Central Great Plains. Many cattle ranching operations employ frequent spring burns to remove dead litter and enhance palatability, leading to greater and more consistent weight gain in cattle (Smith and Owensby 1978; Vermeire and Bidwell 1998). While annual spring burning is beneficial in curtailing woody encroachment, it also can homogenize plant and avian communities (Kaufman et al., 1990; Collins et al., 1998; Reinking 2005; Matlack et al., 2008; Fuhlendorf et al., 2009; Collins and Calabrese 2012; McNew et al., 2015). More recently, smoke from prescribed burns has been implicated in urban air-quality problems, stimulating the discussion and adoption of various smoke management options (see http://www.ksfire.org/ for more details).

The transformative and often intransigent nature of ecosystem transitions to shrubland and woodland (Briggs et al., 2005; Twidwell et al., 2013a) make it critical to forecast the potential for shrub and tree expansion. Similarly, relying primarily on annual burning at a large scale could reduce the adaptive potential to unforeseen challenges (Carpenter et al., 2012), in addition to its noted potential impacts on air quality. Combining satellite estimates of fire frequency (Mohler and Goodin, 2011) with the recently developed fire threshold framework for the Central Great Plains (Ratajczak et al., 2014a), we assess the susceptibility of the Flint Hills to shrubland and woodland transitions. This study area is a landscape of tallgrass prairie and multiple human uses and settlement types, with ~28,000 km^2 of grassland (Fig. 2). For

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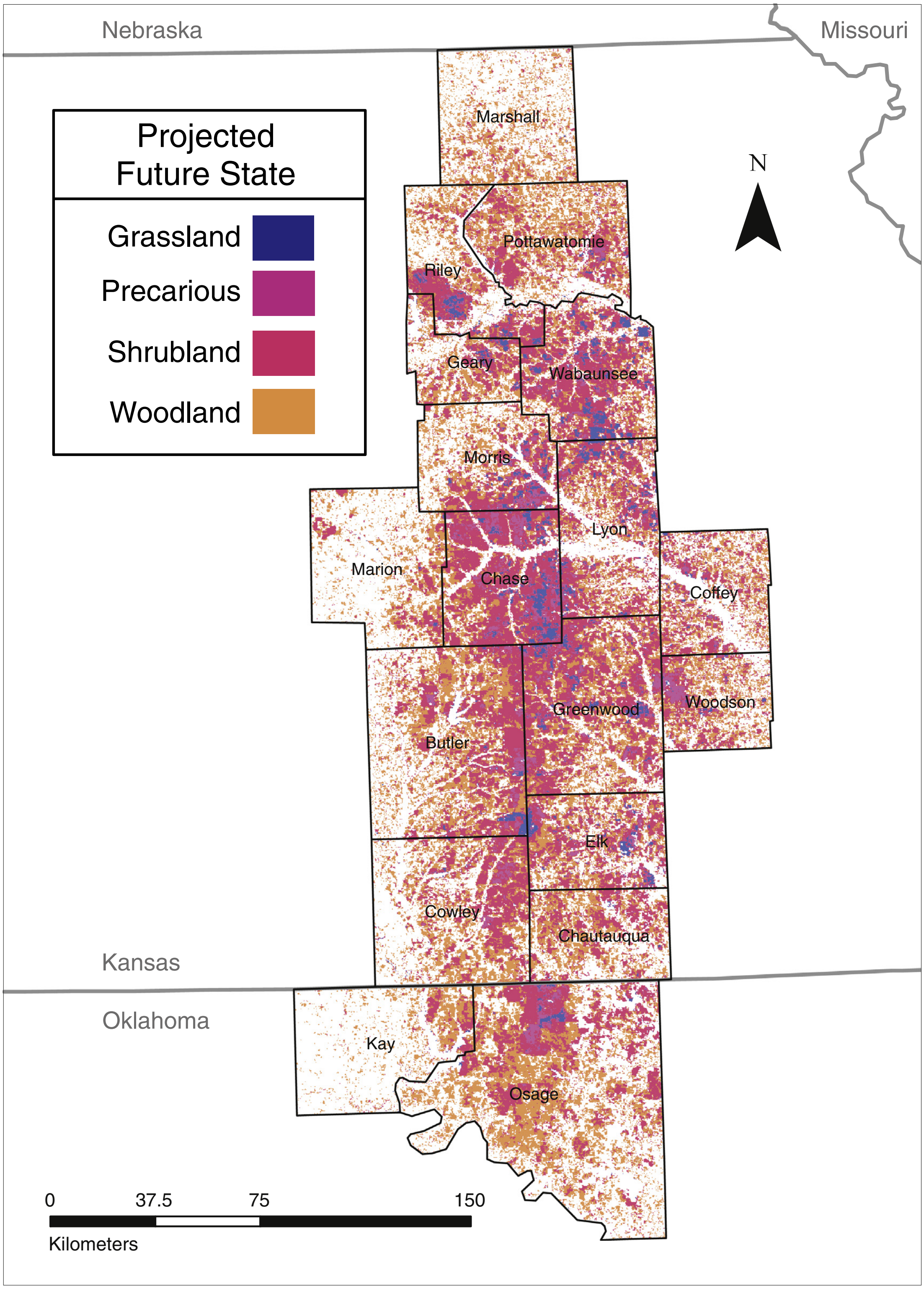

Fig. 2. Spatial distribution of predicted future ecosystem states for tallgrass prairie in the Flint Hills ecoregion, United States. Areas not classified as "grassland" are depicted as white. Grassland areas are colored relative to their potential future state: grassland (blue; mean fire return interval [MFI] 1 — 2.2), precarious (purple; MFI 2.8), shrubland (red; MFI 3.7 and 5.5), and woodland (orange; MFI 11 and unburned). See Fig. 3 for further details of future state classification and note that upland and lowland sites within an area will differ in their potential for transitions.

areas burned often enough to resist woody encroachment, we quantify the range of fire frequencies employed. Our mapping of fire thresholds is set against a backdrop of economic and social trade-offs, but for this synthesis we address predicted changes in ecosystem structure and leave most discussion of social dynamics for future work. Nevertheless, this assessment comes at a time when conservation planning and burning regulation are under public debate in the Flint Hills and nationally (www.ksfire.org).

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Methods

This study required two pieces of information: estimates of how fire frequency relates to vegetation change and large-scale assessments of fire frequency. Fig. 1 shows our scheme for combining long-term experiment and remotely sensing data to generate large-scale assessments of ecosystem management relative to ecosystem thresholds.

Fire Frequency Thresholds

Thresholds are points where small changes in external drivers or ecosystem state can lead the ecosystem to reorganize around a new set of self-reinforcing processes, resulting in an ecological shift that is both dramatic and difficult to reverse (Holling 1973; Folke et al., 2004; Walker and Salt 2006; Briske et al., 2008; Bestelmeyer et al., 2011). In this synthesis, thresholds are considered as points where a small change in fire frequency leads to a greater proportional response in the ecosystem state (see Fig. 1A; Groffmann et al., 2006; see Scheffer and Carpenter 2003 and Bestelmeyer et al., 2011 for general methods used to detect thresholds). As an example of fire thresholds, we show photographs from the Konza Prairie Biological station. After more than 30 yr of observation, lowland areas of the station with 1- and 2-yr fire intervals are essentially devoid of large shrubs. In contrast, a small increase in the mean fire-free interval to 3.5 yr in a nearby watershed has resulted in an increase to > 40% shrub cover and >100 shrubs per hectare (see Fig. 1A; Briggs et al., 2005, Ratajczak et al., 2014b). In this case, a small change in fire frequency has led to a large change in vegetation.

The framework used in this synthesis (see Ratajczak et al., 2014a) applied the previously described approach to a wide set of studies ranging from Northern Oklahoma to North Kansas, including tallgrass prairie remnants in nearby states (e.g., Bowles and Jones 2013). The framework derived the relationship between fire frequency and vegetation change by comparing the initial state (grassland, shrubland, or woodland); fire frequency; information about soil characteristics; and the trajectory of the ecosystem state over time. We separate tallgrass prairie into two ecological sites: 1) lowlands, which are typified by deep soil profiles, greater water holding capacity, and low aspect (e.g., the Tully series), and 2) uplands, which are typified by thinner soils and lower water holding capacity (e.g., the Florence series).

Evidence from this synthesis suggests that the transition from tallgrass prairie to shrubland or woodland follows threshold or threshold-like behavior (Briggs et al., 2005; Twidwell et al., 2013a, b; Ratajczak et al., 2014a, b). For lowland areas: 1) annual to biennial fires consistently maintained tallgrass prairie in a grass-dominated state (Owensby et al., 1973; Bragg and Hulbert 1976; Briggs and Gibson 1992; Kettle et al., 2000; Briggs et al., 2002; Bowles and Jones 2013; Ratajczak et al., 2014b), 2) 3-yr fire return intervals may or may not maintain tallgrass prairie (Bowles and Jones, 2013; Fuhlendorf et al., 2009) depending on the juxtaposition of woody seed sources and other factors, 3) fire return intervals >3 yr typically lead to transitions to shrubland (Briggs and Gibson 1992; Briggs et al., 2002; Bowles and Jones 2013; Ratajczak et al., 2014b), 4) fire-free intervals > 10 yr can potentially lead to the formation of woodlands, and 5) areas not burned for 30 − 50 yr almost always transition to woodland given enough time (Bragg and Hulbert 1976; Kettle et al., 2000; Hoch et al., 2002). Upland areas follow a slightly different scheme. In uplands, shrubs are less prevalent and the shrubland state is either nonexistent or more likely to be a phase between the grassland and woodland (Ratajczak et al., 2014a). This occurs because shrubs rely on avoiding competition with grasses by developing deep roots (Ratajczak et al., 2011), which is not possible in a shallow soil profile.

Transitions to shrubland and woodland may eventually become difficult to reverse, but only if fire frequency is changed for a substantial duration. As shrubs and trees expand and mature, they become more resistant to fire and decrease grass biomass that would fuel subsequent fires (Boyd and Bidwell 2002; Heisler et al., 2004; Peterson et al., 2007; Fuhlendorf et al., 2008; Burton et al., 2010; Eldridge et al., 2011; Hajny et al., 2011; Harrell et al., 2001; Ratajczak et al., 2014b; Twidwell et al., 2013a). In extreme cases the entire aboveground grass layers can be lost (Hoch et al., 2002; Heisler et al., 2004; Fuhlendorf et al., 2008), causing ground fire temperatures to drop sharply and woody plant mortality rates to decrease (Vanderweide and Hartnett, 2011; Twidwell et al., 2013a). At this point, a state transition has probably occurred and typical prescribed burns are largely ineffective at restoring grassland. In the case of transitions to shrubland, it appears that it takes at least 15 − 20 yr before some shrubs reach a size sufficient to resist resumption of frequent burning (Ratajczak et al., 2011). For woodland trees in lowland sites, it takes 10 − 20 yr before some trees are fire resistant and up to 40 yr before large-scale irreversibility is achieved (depending on how abundant seeds are, among other factors) (Hoch et al., 2002; Fuhlendorf et al., 2008). Upland sites take much longer for trees to expand, due mostly to shallower soils (Bragg and Hulbert 1976). We stress that the length of time needed to trigger state transitions is currently an estimate that requires significant refinement. In the meantime, a good indicator of reaching a shrubland or woodland state is the near-complete loss of grass cover and grass meristems (although grass seed banks or seed rain can enable transitions back to grassland, albeit slowly). Once shrub and tree dominance reaches this point, mechanical removal, chemical treatments, or extreme, dry-season fires are needed to reverse the transition quickly (Owensby et al., 1973; Twidwell et al., 2013a; Wonkka et al., in press). In addition to the duration of changes in fire frequency, certain factors can alter relationships between fire frequency and woody plant expansion at a given place and time. We address these factors in the discussion section.

Remotely Sensed Fire Frequency

We combined information on thresholds with burned area maps that were created specifically for the Flint Hills from Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data, for the years 2000 − 2010 (Mohler and Goodin, 2011; Mohler and Goodin 2012). Recently burned tallgrass prairie has very different spectral properties than unburned prairie, including a significantly lower reflectance of red light (Mohler and Goodin 2013), which can be leveraged to generate statistical procedures that identify burned areas using remotely sensed satellite data. The fire frequency data were created by performing a supervised classification on the two MODIS bands (red, 620 − 670 nm; near-infrared [NIR], 841 − 876 nm) that are available at 250-m spatial resolution (all other bands have resolution ≥ 500 m). Fire frequency was determined on a pixel-by-pixel basis at this 250-m scale, for multiple satellite passes per year (~20 per spring/early summer). Following Mohler and Goodin (2012), a mask was used to block nongrassland areas from being considered as burned or unburned areas. This constricted our analyses to only grasslands (similar to the approach by Staver et al., 2011) and limited false positives that are common with land cover types such as water and wet cropland soils, which resemble burned areas in the red and NIR parts of the spectrum. For the 2 yr of calibration, the accuracy of the maps was approximately 90% when burns are < 2 wk old, and accuracy decreases past that time due to fading of the burn signature (Mohler and Goodin 2013). For the 2 yr of calibration, this customized method produced better accuracy than the existing MODIS burned area products, which use general algorithms in order to map burned areas globally across a wide variety of biomes (Mohler 2011). This data product allows us to determine if fire suppression is sufficient to promote woodland regime shifts. Data are presented as mean fire return intervals (MFIs):

$$\text{MFI} = \text{years of observation/number of fires detected (years/fire)} \quad \textbf{[1]}$$

If zero fires were detected for an area, it was classified as "unburned."

Combining Fire Frequency Thresholds and Fire Frequency Data

We used the inference of fire frequency thresholds to categorize areas into likely to remain grassland (MFI < 3), precarious (MFI ~3),

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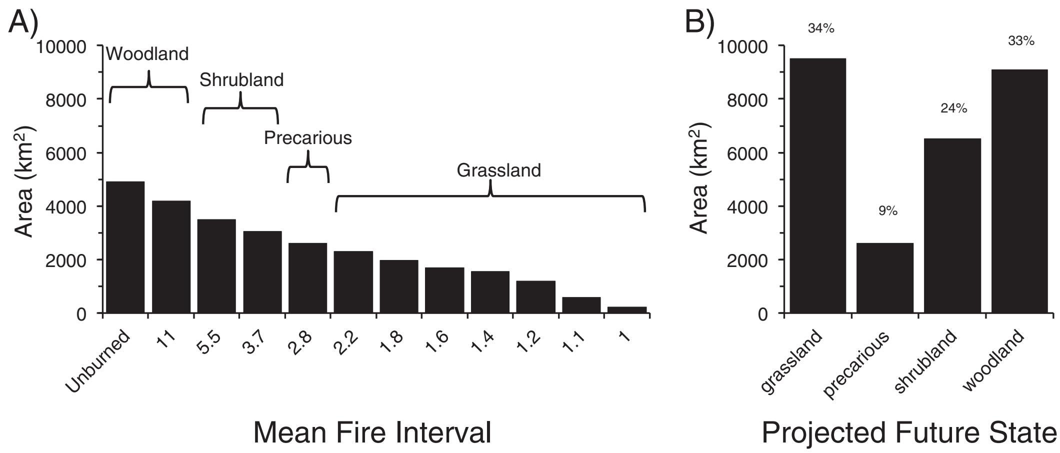

Fig. 3. A, Detailed view of fire return intervals in grasslands across the Flint Hills grassland area. **B,** Total area categorized as likely to remain grassland, precarious, susceptible to shrubland transitions, and susceptible to woodlands transitions. Labels of each bar in **(A)** give the mean fire return interval. Brackets above data in **(A)** show threshold values used to categorize fire frequencies in **(B).** Note that upland and lowland sites will differ in their potential for transitions.

susceptible to shrubland transitions (10 < MFI > 3), or susceptible to woodland transitions (MFI > 10 or unburned). This approach has three main assumptions: MFI is an appropriate measurement of fire frequency, fires occur primarily in the spring, and fire frequency data are available at an appropriate scale.

In some rangelands, woody plant growth rates are so high that they can reach an "escape height" in < 10 yr or less (Hoffmann et al., 2012). In these areas, the longest length between fires can be more important than the average fire interval. For example, consider an instance where a woody plant can grow fast enough to escape a fire trap in 6 yr. If a 12-yr interval had 6 yr in a row with fire, but then 6 yr without fire, the area would become woodland even though the MFI = 2. In tallgrass prairie, transitions to shrubland and woodland are a multifaceted process that require decades of reoccurring changes in fire to trigger state transitions (Collins and Adams 1983; Twidwell et al., 2013a, b; Ratajczak et al., 2014b). These delays are due to the long persistence of grass meristems as a source for grassland recovery (Weaver, 1954) and the slower rate of shrub and tree growth in more water-limited ecosystems. Due to the slow nature of change in the system and its dependence on long-term fire frequency, we consider MFI to be a useful predictor of shrubland and woodland transitions but recommend that other fire frequency statistics (median, longest fire-free interval) might be appropriate for ecosystems where grasses can decline faster or woody plants have higher maximum growth rates.

The second assumption is that fires occur primarily in the spring because our fire frequency threshold was derived from studies where fires were conducted in the spring, typically before grass green-up. To date, most fires were recorded between late March and the middle of April (Mohler and Goodin 2012), even though images used extended into late April to early May.

Finally, gauging ecosystem proximity to thresholds requires that the grain of the satellite data match the scale of bistability in the system. For instance, large-scale, positive feedbacks between rainfall and vegetation cover are thought to be an important stabilizing force of alternative stable states in the Sahara (Claussen et al., 1999). In this instance or when connectivity is particularly high, average vegetation cover across a large scale is probably a better predictor of a single patch's future state (Peters et al., 2004; Van Nes and Scheffer, 2005; Okin et al., 2015). For this study, landscape scale averages are less important because the patch size of grass (Koerner and Collins, 2013), shrub (Briggs et al., 2002; Heisler et al., 2004), and tree patches is on the order of $20-100$ m^2 or smaller. Yet the resolution of the data is a fine enough grain to catch changes in management decisions, which typically apply to parcels of land ≥ 1.6 × 1.6 km (1 × 1 mile).

Results

The remotely sensed assessment of fire frequency reveals that about 43% (12 127 km^2) of the Flint Hills is burned every 1 to 3 yr (see Figs. 2 and 3; Mohler and Goodin 2012), which is probably frequent enough to prevent woody encroachment in these locations (Briggs et al., 2005; Fuhlendorf et al., 2009; Ratajczak et al., 2014a, but see "Discussion" later). However, ~9% of grasslands are burned at an MFI of 2.75 yr, which is often enough to maintain grasslands now but could become susceptible to shrub expansion with minor decreases in fire frequency, especially where there are nearby woody seed sources or grazing reduces fuel loads (see Fig. 1A). Approximately 5 245 km^2 of the Flint Hills grasslands, 43% of the area likely to remain grassland, have an almost annual burn frequency (MFI < 1.6 yr).

Outside of the pockets of frequent burning, fire is much less common. About 24% of grasslands (6 526 km^2) have an MFI of 3.7 or 6.5 yr (see Fig. 3; Mohler and Goodin 2012) and are, therefore, at risk of shrub expansion. Approximately 33% of the grasslands (9 097 km^2) have an MFI of 11 or are unburned, which should allow tree establishment if this management is continued. Thus, these results suggest that ~15 600 km^2 (~56%) of the Flint Hills may be susceptible to shrubland or woodland transitions in the coming decades. As of 2011, there was no indication that the average amount of burned area was increasing or decreasing over time (Mohler and Goodin 2012).

Discussion

The predominance of high (~1 MFI) and low burn frequencies (>6 MFI) across the landscape represents a major divergence from historic fire frequency in the Flint Hills, which could have implications for ecology and people of the region (see Fig. 3). Knowledge of pre-European fire frequencies is far from complete, but most studies estimate that fire return intervals typically ranged from 2 to 10 yr, with an average return interval of ~$2.5-4$ yr (Desantis et al., 2010; Allen and Palmer 2011; Stambaugh et al., 2013). Now, only 27% of the landscape is burned at more intermediate frequencies (see Fig. 3; MFI = $2.2-3.7$ yr).

The change in fire frequency probably stems primarily from changes in management. Before European arrival, some fires were the result of lightning strikes, but Native Americans almost undoubtedly increased the number of fire ignitions, through accidental ignitions and by purposely using fires to increase forage quality in order to attract wildlife such as bison *(Bos bison)* (Sherow 2007; Stambaugh et al., 2013). The increase in areas burning almost annually is likely attributable to intensive early stocking for yearling cattle, which has been adopted by many ranchers (Smith and Owensby 1978; Vermeire and Bidwell 1998). The

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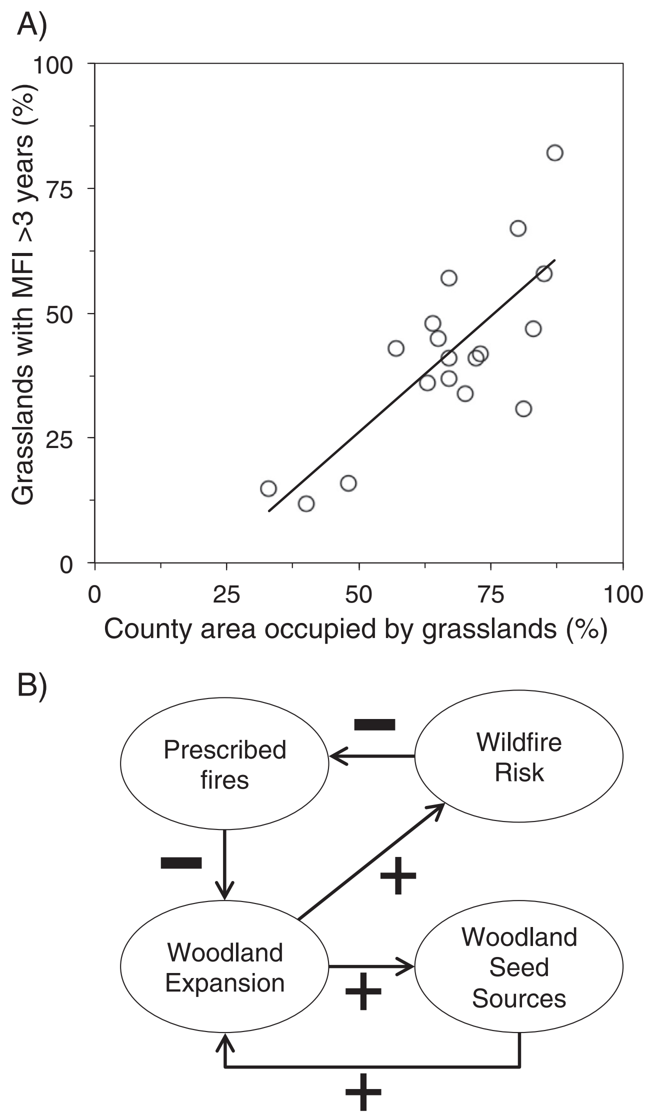

Fig. 4. A, The relationship between % area of a county classified as grassland (x-axis) and the % of grasslands burned frequently enough to avoid transitions to shrubland or grassland (y-axis; mean fire return interval < 3.6). **B,** Potential set of feedbacks that might partially account for how and why prescribed burns decline and woodlands expand as the area of grasslands decreases. *Arrows* accompanied by a "+" sign are positive effects and "−" are negative effects. The feedback with seed availability is a biophysical feedback, while the feedback with wildfire risk is a coupled social-biophysical feedback that results from woodlands expanding near human settlements.

causes behind the expansion of land with a > 3.5-yr MFI are more difficult to pinpoint, but one factor is a lack of fuel to sustain burns in heavily grazed areas. Prescribed burning is also restricted by proximity to highways and human settlements. Both of these landscape features are increasing components within the Flint Hills (i.e., exurban development embedded in the tallgrass prairie matrix) that increase human-health and safety risks associated with prescribed fires. Even when ignitions are present, the possibility of fire propagation has decreased. Before the 18th and 19th centuries, the only barriers to fire spreading were rivers, areas with low grass biomass due to recent fires and/or grazing, and other natural features. Today roads, croplands, and multiple settlement types now impede fire transmission from one patch to another, which should lead to a decreased potential for large fires (Archibald et al., 2012).

Looking forward, our analyses suggest that within 20 − 60 yr the Flint Hills could undergo a dramatic transformation. If current burning practices continue, we should expect that a large percentage of tallgrass prairie will transition to shrub thickets and woodlands. This would constitute a major landscape transition, relative to the open grasslands that covered the Central Great Plains shortly before and after European arrival (Wells 1970; Cordova et al., 2011). Our results mirror predictions by Engle et al., (2008) that a "Green Glacier" of shrublands and woodlands is poised to transform the Central Great Plains under current management schemes. In fact, it is likely that this large-scale transition to shrubland or woodland is under way in many locations (Hoch et al., 2002; Twidwell et al., 2013b). Predicted increases in winter precipitation and elevated atmospheric CO_2 could reduce water stress in shrubs and trees, resulting in even greater loss of grasslands (Bond and Midgley 2012; Nippert et al., 2013; Volder et al., 2013; Brunsell et al., 2014).

Certain local factors can alter the exact projections of what areas are likely to remain grassland or see woody plant expansion. Areas farther from shrub and tree seed sources should remain grass dominated longer initially, requiring longer interfire intervals to result in transitions to shrubland and woodland (Briggs et al., 2005). If woody plants continue to expand across the landscape, these areas currently isolated from woody seeds will eventually become more susceptible to woody encroachment (Briggs et al., 2005; Engle et al., 2008; Fig. 4**B**). Rates of woody expansion and the degree of irreversibility also depend on the identity of shrub and tree recruits. *Juniperus virginiana* (eastern red cedar) is a common encroaching species in the Flint Hills, but some resprouting species, such as *Maclura pomifera* (Osage orange), *Gleditsia triacanthos* (Honey Locust), and other deciduous trees may be more problematic in the central and southern Flint Hills (personal observations, B. Obermeyer). The ability to resprout should allow these species to establish with shorter reoccurring interfire intervals (Bond 2008) or perhaps persist as a phase between a grassland and woodland state. Large browsers and use of herbicides can further constrain woody encroachment, allowing grassland to persist at longer interfire intervals (Engle et al., 2006).

Grazing is one of the most widespread management factors with the potential to alter the shrubland and woodland transitions. Grazers are generally thought to increase the probability of transitioning to shrubland or woodland because their selective grazing reduces grass biomass (Walker et al., 1981; Fuhlendorf et al., 2008). This reduction in grass biomass can reduce fire fuel loads, allowing shrubs and trees to survive prescribed burns (Fuhlendorf et al., 2008). However, certain grazers might also cause physical damage to trees (Coppedge and Shaw 1997), and with very high stocking rates, the ensuing soil erosion and compaction can limit shrub and tree establishment (Walker et al., 1981). Without an experimental consensus on the impact of grazers on shrubland and woodland transitions, we recommend that individual stakeholders rely on local knowledge and adaptive management to assess local grazing impacts on woody plant expansion.

Implications

Fire management of the Flint Hills grasslands is an example of a coupled human-ecological system (or social-ecological system) where humans appears to be operating outside of key ecological thresholds (Rockström et al., 2009; Barnosky et al., 2012), with potential ramifications for the flow of ecosystem goods and services to humans (Collins et al., 2011). Even in areas where shrubland or woodland transitions prove easier to reverse, the temporary loss of forage for grazers and impacts on biodiversity has important consequences. The major challenges in addressing these issues will be balancing the needs of multiple stakeholders and increasing access to burning equipment and expertise (see Table 1 for further potential challenges). Land-managers and scientists can help expand the portfolio of tools to avoid unwanted transitions (Table 1). On the other hand, certain complications associated with prescribed burning are likely to grow due to the expansion of juniper woodlands in certain areas and their greater wildfire potential. These risks will be heightened where human settlements are embedded

Table 1
Emerging challenges and opportunities for adaptive management of ecosystem transitions in the Flint Hills, Central Great Plains.

Emerging Challenges	Description	Citation
Increased woodland fire risk	As woodlands become more common and interconnected, the risk for small and large woodland fires will grow, especially in juniper stands.	Twidwell et al. 2013b
Expansion of wildland-urban continuum	Intertwining of settled areas and woodlands will increase risk of damaging wildfires and exposure to ozone produced by fires.	Hoch et al. 2002, Middendorf et al. 2009
Uncertain climates	Increased winter precipitation will further favor deep-rooted shrub species. Warming climate might deter some shrub expansion but is unlikely to reverse past transitions.	Nippert et al. 2013, Volder et al. 2013
Elevated atmospheric CO_2	Increased atmospheric CO_2 can mitigate water stress in shrubs and trees because plants do not have to open their stomata as often to obtain the necessary CO_2 to meet their carbon needs.	Bond and Midgley 2012
Emerging Opportunities		
Expansion of burning cooperatives	Burning co-ops are increasing access to equipment and expertise for using prescribed burns. Also makes it easier to pool labor, employ more extreme fires, and navigate legislation, regulations, and liability concerns.	Twidwell et al. 2013b
Patch-burn grazing	A management technique that enhances the conservation value of grazed and burned areas; typically employs a fire return interval of 3 yr in tallgrass prairie.	Fuhlendorf et al. 2009, Allred et al. 2011
Better smoke management models	Coupled smoke and climate models are becoming more accurate and publically available, allowing land managers a tool to decide if burning on a certain day may impact downwind population areas.	e.g., www.ksfire.org/
New techniques for using fire to reverse transitions	New burning techniques may allow for safer burning during dry and/or high temperature conditions, which could make it possible to burn less often *and* prevent or even reverse transitions to shrubland and woodland.	Twidwell et al. 2013a
Burn outside traditional spring burn window	Burning outside the traditional burn window could alleviate air-quality issues associated with smoke from prescribed fires.	Towne and Owensby, 1984

in woodlands, potentially creating a positive feedback between loss of grasslands and interest in burning within remaining grasslands (see Fig. 4B). As Mohler and Goodin (2012) reported, counties with less grassland area tend to burn less often (Fig. 4A), suggesting that a loss of grassland area and declines in burning could be connected, accelerating the decline of prescribed burning if the contraction of grasslands begins.

In the past many regional-scale ecological changes in grasslands/rangelands occurred before potential warning signs were recognized (i.e., the Dust Bowl, overgrazing in the southwestern United States, and many global examples of woody plant expansion). Fortunately, transitions to shrublands and woodlands in mesic grasslands are not instantaneous, with at least a 10- to 20-yr buffer between the initiation of fire suppression and the point where shrub and woodland transitions become difficult to reverse. Therefore, reinstating frequent fires soon could limit shrub and tree expansion in grasslands currently burned at intervals > 3 yr. This may require alterations in grazing management to build fuel loads, especially in areas forecast to have increasing droughts due to climate change. Combined knowledge on the potential scale of grassland-woodland transitions and the expanding capacity to increase prescribed fire frequency could still facilitate the maintenance of Central Great Plains grasslands.

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References

Allen, M.S., Palmer, M.W., 2011. Fire history of a prairie/forest boundary: more than 250 years of frequent fire in a North American tallgrass prairie. J. Veg. Sci. 22, 436–444.
Allred, B.W., Fuhlendorf, S.D., Engle, D.M., Elmore, R.D., 2011. Ungulate preference for burned patches reveals strength of fire-grazing interaction. Ecol. Evol. 1, 132–144.
Anadon, J.D., Sala, O.E., Turner, B.L., Bennett, E.M., 2014. Effect of wood-plant encroachment on livestock production in North and South America. Proc. Natl. Acad. Sci. U. S. A. 111, 12948–12953.
Archibald, S., Staver, A.C., Levin, S.A., 2012. Evolution of human-driven fire regimes in Africa. Proc. Natl. Acad. Sci. U. S. A. 109, 847–852.
Barnosky, A.D., Hadley, E.A., Bascompte, J., Berlow, E.L., Brown, J.H., Fortelius, M., Getz, W.M., Harte, J., Hastings, A., Marquet, P.A., Martinez, N.D., Mooers, A., Roornarine, P., Vermeij, G., WIlliams, J.W., Gillespie, R., Itzes, J., Marshall, C., Matzke, N., Mindell, D.P., Revilla, E., Smith, A.B., 2012. Approaching a state shift in Earth's biosphere. Nature 486, 52–58.
Bestelmeyer, B.T., Ellison, A.M., Fraser, W.R., Gorman, K.B., Holbrook, S.J., Laney, C.M., Ohman, M.D., Peters, D.P.C., Pillsbury, F.C., Rassweiler, A., Schmitt, R.J., Sharma, S., 2011. Analysis of abrupt transitions in ecological systems. Ecosphere 2, 1–26.
Bond, W.J., 2008. What limits trees in C_4 grasslands and savannas. Annu. Rev. Ecol. Evol. Syst. 39, 641–659.
Bond, W.J., Midgley, G.F., 2012. Carbon dioxide and the uneasy interactions of trees and savannah grasses. Philos. Trans. R. Soc. 367, 601–612.
Bowles, M.L., Jones, M.D., 2013. Repeated burning of eastern tallgrass prairie increases richness and diversity, stabilizing late successional vegetation. Ecol. Appl. 23, 464–478.
Bowman, D.M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D'Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P., Johnston, F.H., Keeley, J.E., Krawchuk, M.A., Kull, C.A., Marston, J.B., Moritz, M.A., Prentice, I.C., Roos, C.I., Scott, A.C., Swetnam, T.W., van der Werf, G.R., Pyne, S.J., 2009. Fire in the Earth system. Science 324, 481–484.
Boyd, C.S., Bidwell, T.G., 2002. Effects of prescribed fire on shinnery oak *(Quercus havardii)* plant communities in Western Oklahoma. Soc. Ecol. Restoration 10, 324–333.
Bragg, T.B., Hulbert, L.C., 1976. Woody plant invasion of unburned Kansas bluestem prairie. Soc. Range Manag. 29, 19–24.
Briggs, J.M., Gibson, D.J., 1992. Effect of fire on tree spatial patterns in a tallgrass prairie landscape. Bull. Torrey Botanical Club 119, 300–307.
Briggs, J.M., Knapp, A.K., Blair, J.M., Heisler, J.L., Hoch, G.A., Lett, M.S., McCarron, J.K., 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. Bioscience 55, 243–254.
Briggs, J.M., Knapp, A.K., Brock, B.L., 2002. Expansion of woody plants in tallgrass prairie: a 15-year study of fire and fire-grazing interactions. Am. Midl. Nat. 147, 287–294.
Briske, D.D., Bestelmeyer, B.T., Stringham, T.K., Shaver, P.L., 2008. Recommendations for development of resilience-based state-and-transition models. Rangel. Ecol. Manag. 61, 359–367.
Brunsell, N.A., Nippert, J.B., Buck, T.L., 2014. Impacts of seasonality and surface heterogeneity on water-use efficiency in mesic grasslands. Ecohydrology 7, 1223–1233.
Burton, J.A., Hallgren, S.W., Palmer, M.W., 2010. Fire frequency affects structure and composition of xeric forests of eastern Oklahoma. Nat. Areas J. 30, 370–379.
Carpenter, S.R., Arrow, K.J., Barret, S., Biggs, R., Brock, W.A., Crepin, A., Engstrom, G., Folke, C., Hughes, T.P., Kautsky, N., Li, C., McCarney, G., Meng, K., Maler, K., Polasky, S., Scheffer, M., Shogren, H., Sterner, T., Vincent, J.R., Walker, B., Xepapadeas, A., Zeeuv, A., 2012. General resilience to cope with extreme events. Sustainability 4, 3248–3259.
Chapin, F.S., Powers, M.E., Pickett, S.T.A., Freitag, A., Reynolds, J.A., Jackson, R.B., Lodge, D.M., Duke, C., Collins, S.L., Power, A.G., Bartuska, A., 2011. Earth stewardship: science for action to sustain the human-earth system. Ecosphere 2, art89.
Claussen, M., Kubatzki, C., Brovkin, V., Ganopolski, A., 1999. Simulation of an abrupt change in Saharan vegetation in the mid-Holocene. Geophys. Res. Lett. 26, 2037–2040.
Collins, S.L., Carpenter, S.R., Swinton, S.M., Orenstein, D.E., Childers, D.L., Gragson, T.L., Grimm, N.B., Grave, J.M., Harlan, S.L., Kaye, J.P., Knapp, A.K., Kofinas, G.P., Magnuson, J.J., McDowell, W.H., Melack, J.M., Ogden, L.A., Robertson, G.P., Smith, M.D., Whitmer, A.C., 2011. An integrated conceptual framework for ong-term social-ecological research. Front. Ecol. Environ. 9, 351–357.
Collins, S.L., Adams, D.E., 1983. Succession in grasslands: thirty-two years of change in a central Oklahoma tallgrass prairie. Vegetatio 51, 181–190.
Collins, S.L., Calabrese, L.B., 2012. Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. J. Veg. Sci. 23, 563–575.
Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M., Steinauer, E.M., 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280, 745–747.

Coppedge, B.R., Shaw, J.H., 1997. Effects of horning and rubbing behavior by bison *(Bison bison)* on woody vegetation in a tallgrass prairie landscape. Am. Midl. Nat. 138, 189–196.

Coppedge, B.R., Engle, D.M., Masters, R.E., Gregory, M.S., 2001. Avian response to landscape change in fragmented Southern Great Plains grasslands. Ecol. Appl. 11, 47–59.

Cordova, C.E., Johnson, W.C., Mandel, R.D., Palmer, M.W., 2011. Late quaternary environmental change inferred from phytoliths and other soil-related proxies: case studies from the central and southern Great Plains, USA. Catena 85, 87–108.

Desantis, R.D., Hallgren, S.W., Stahle, D.W., 2010. Historic fire regime of an upland oak forest in south-central North America. Fire Ecol. 6, 45–61.

Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G., 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecol. Lett. 14, 709–722.

Ellis, E.C., Kaplan, J.O., Fuller, D.Q., Vavrus, S., Goldewijk, K.K., Verburg, P.H., 2013. Used planet: a global history. Proc. Natl. Acad. Sci. U. S. A. 110, 7978–7985.

Engle, D.M., Bodine, T.N., Stritzke, J.F., 2006. Plant community in the cross timbers over two decades of brush treatments. Rangel. Ecol. Manag. 59, 153–162.

Engle, D.M., Coppedge, B.R., Fuhlendorf, S.D., 2008. From Dust Bowl to the Green Glacier: human activity and environmental change in the Great Plains Grasslands. In: Van Auken, O.W. (Ed.), Western North American *Juniperus* communities a dynamic vegetation type. Springer Press, San Antonio, TX, USA, pp. 253–266.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annu. Rev. Ecol. Evol. Syst. 35, 557–581.

Fuhlendorf, S.D., Archer, S.A., Smeins, F.E., Engle, D.M., Taylor, C.A., 2008. The combined influence of grazing, fire, and herbaceous productivity on tree-grass interactions. In: Van Auken, O.W. (Ed.), Western North American *Juniperus* communities: a dynamic vegetation type. Springer, New York, NY, USA, pp. 219–238.

Fuhlendorf, S.D., Engle, D.E., Kerby, J., Hamilton, R., 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. Conserv. Biol. 23, 588–598.

Groffmann, P.M., Baron, J.S., Blett, T., Gold, A.J., Goodman, I., Gunderson, L.H., Levinson, B.M., Palmer, M.A., Paerl, H.W., Peterson, G.D., Poff, N.L., Rejeski, D.W., Reynods, J.F., Turner, M.G., Weathers, K.C., Wiens, J., 2006. Ecological thresholds: the key to successful environmental management or an important concept no practical application. Ecosystems 9, 1–13.

Hajny, K.M., Hartnett, D.C., Wilson, G.W.T., 2011. Rhus glabra response to season and intensity of fire in tallgrass prairie. Int. J. Wildland Fire 20, 709–720.

Harrell, W.C., Fuhlendorf, S.D., Bidwell, T.G., 2001. Effects of prescribed fire on sand shinnery oak communities. Soc. Range Manag. 54, 685–690.

Heisler, J.L., Briggs, J.M., Knapp, A.K., Blair, J.M., Seery, A., 2004. Direct and indirect effects of fire on shrub density and above-ground diversity in a mesic grassland. Ecology 85, 2245–2257.

Hoch, G.A., Briggs, J.M., Johnson, L.C., 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 5, 578–586.

Hoekstra, J.M., Boucher, T.M., Ricketts, T.H., Roberts, C., 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecol. Lett. 8, 23–29.

Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L., Haridasan, M., Franco, A.C., 2012. Ecological thresholds at the savanna-forest boundary: how plant traits, resource and fire govern the distribution of tropical biomes. Ecol. Lett. 15, 759–768.

Holling, C.S., 1973. Resilience and Stability of Ecological Systems. Annu. Rev. Ecol. Syst. 4, 1–23.

Kaufman, D.W., Finck, E.J., Kaufman, G.A., 1990. Small mammals and grassland fires. In: Collins, S.L., Wallace, L.L. (Eds.), FIRE in the North American Tallgrass Prairies. University of Oklahoma Press, Norman, OK, USA.

Kettle, W.D., Rich, P.M., Kindscher, K., Pittman, G.L., Fu, P., 2000. Land-use history in ecosystem restoration: a 40-year study in the prairie-forest ecotone. Restor. Ecol. 8, 307–317.

Koerner, S.E., Collins, S.L., 2013. Small-scale patch structure in North American and South African grasslands responds differently to fire and grazing. Landsc. Ecol. 28, 1293–1306.

Matlack, R.S., Kaufman, D.W., Kaufman, G.A., 2008. Influence of woody vegetation on small mammals in tallgrass prairie. Am. Midl. Nat. 160, 7–19.

McLauchlan, K.K., Craine, J.M., Nippert, J.B., Ocheltree, T.W., 2014. Lack of eutrophication in a tallgrass prairie ecosystem over 27 years. Ecology 95, 1225–1235.

McNew, L.B., Winder, V.L., Pitman, J.C., Sandercock, B.K., 2015. Alternative rangeland management strategies and the nesting ecology of Great Prairie-Chickens. Rangel. Ecol. Manag. 68, 298–304.

Middendorf, G., Becerra, T.A., Cline, D., 2009. Transition and resilience in the Kansas Flint Hills. Online J. Rural Res. Policy 4, 1–28.

Mohler, R.R.L., 2011. Multi-scale burned area mapping in tallgrass prairie using in situ spectrometry and satellite imagery (thesis) Kansas State University, Manhattan, KS, USA.

Mohler, R.R.L., Goodin, D., 2013. Temporal burn scar evolution in tallgrass prairie based on field spectroscopy. Int. J. Remote Sens. 34, 7199-7127.

Mohler, R.R.L., Goodin, D.G., 2011. Identifying a suitable combination of classification technique and bandwidth for burned area mapping in tallgrass prairie with MODIS imagery. Int. J. Appl. Earth Obs. Geoinf. 14, 103–111.

Mohler, R.R.L., Goodin, D.G., 2012. Mapping burned area in the Flint Hills of Kansas and Oklahoma, 2000–2010. Great Plains Res. 22, 15–25.

Nippert, J.B., Ocheltree, T.W., Orozco, G.L., Ratajczak, Z., Ling, B., Skibbe, A.M., 2013. Evidence of physiological decoupling from grassland ecosystem drivers by an encroaching woody shrub. PLoS One 8, 1–8.

Okin, G.S., las Heras, M.M., Saco, P.M., Throop, H.L., Vivoni, E.R., Parsons, A.J., Wainwright, J., Peters, D.P.C., 2015. Connectivity in dryland landscapes: shifting concepts of spatial interactions. Front. Ecol. Environ. 13, 20–27.

Owensby, C.E., Blan, K.R., Eaton, B.J., Russ, O.G., 1973. Evaluation of Eastern red cedar infestations in the Northern Kansas Flint Hills. J. Range Manag. 26, 256–260.

Peters, D.P.C., Pielke, R.A., Bestelmeyer, B.T., Allen, C.D., Munson-McGee, S., Havstad, K.M., 2004. Cross-scale interactions, nonlinearities, and forecasting catastrophic events. Proc. Natl. Acad. Sci. U. S. A. 101, 15130–15135.

Peterson, D.W., Reich, P.B., Wrage, K.J., 2007. Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands. J. Veg. Sci. 18, 3–12.

Ratajczak, Z., Nippert, J.B., Briggs, J.M., Blair, J.M., 2014a. Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the Central Great Plains of North America. J. Ecol. 102, 1374–1385.

Ratajczak, Z., Nippert, J.B., Collins, S.L., 2012. Woody encroachment decreases diversity across North American grasslands and savannas. Ecology 93, 697–703.

Ratajczak, Z., Nippert, J.B., Hartman, J.C., Ocheltree, T.W., 2011. Positive feedbacks amplify rates of woody encroachment in mesic tallgrass prairie. Ecosphere 2, 121.

Ratajczak, Z., Nippert, J.B., Ocheltree, T.W., 2014b. Abrupt transition of mesic grassland to shrubland: evidence for thresholds, alternative attractors, and regime shifts. Ecology 95, 2633–2645.

Reinking, D.L., 2005. Fire regimes and avian responses in the central tallgrass prairie. Stud. Avian Biol. 30, 116–126.

Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin III, F.S., Lambin, E.F., Lenton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J., Nykvist, B., de Wit, C.A., Hughes, T., van der Leeuw, S., Rodhe, H., Sörlin, S., Snyder, P.K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R.W., Fabry, V.J., Hansen, J., Walker, B., Liverman, D., Richardson, K., Crutzen, P., Foley, J.A., 2009. A safe operating space for humanity. Nature 461, 472–475.

Sampson, F., Knopf, F., 1994. Prairie conservation in North America. Bioscience 44, 418–421.

Sauer, J.R., Link, W.A., 2011. Analysis of the North American Breeding Survey using hierarchical models. Auk 128, 87–98.

Scheffer, M., Carpenter, S.R., 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol. Evol. 18, 648–656.

Sherow, J., 2007. The grasslands of the United States: an environmental history. Santa Barbara, CA, USA, ABC-CLIO, p. 341.

Smith, E.F., Owensby, C.E., 1978. Intensive-early stocking and season-long stocking of Kansas Flint Hills Range. J. Range Manag. 31, 14–17.

Stambaugh, M.C., Guyette, R.P., Marschall, J., 2013. Fire history in the Cherokee nation of Oklahoma. Hum. Ecol. 41, 749–758.

Staver, A.C., Archibald, S., Levin, S.A., 2011. The global extent and determinants of savanna and forest as alternative biome states. Science 334, 230–232.

Towne, G., Owensby, C., 1984. Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. J. Range Manag. 37, 392–397.

Twidwell, D., Fuhlendorf, S.D., Taylor, C.A., Rogers, W.E., 2013a. Refining thresholds in coupled fire-vegetation models to improve management of encroaching woody plants in grasslands. J. Appl. Ecol. 50, 603–613.

Twidwell, D., Rogers, W.E., Fuhlendorf, S.D., Wonkka, C.L., Engle, D.M., Weir, J.R., Kreuter, U.P., Taylor, T.A., 2013b. The rising Great Plains fire campaign: citizens' response to woody plant encroachment. Front. Ecol. Environ. 11, 64–71.

Vanderweide, B.L., Hartnett, D.C., 2011. Fire resistance of tree species explains historical gallery for community composition. For. Ecol. Manag. 261, 1530–1538.

Van Nes, E.H., Scheffer, M., 2005. Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. Ecology 86, 1797–1807.

Vermeire, L.T., Bidwell, T.G., 1998. Intensive early stocking. Oklahoma State University; Oklahoma Cooperative Extension Service, Stillwater, OK, USA Extension Facts No. 2875.

Volder, A., Briske, D.D., Tjoelker, M.G., 2013. Climate warming and precipitation redistribution modify tree-grass interactions and tree species establishment in a warm-temperate savanna. Glob. Chang. Biol. 19, 843–857.

Walker, B., Salt, D., 2006. Resilience thinking: sustaining ecosystems and people in a changing world. Islands Press, New York, NY, USA.

Walker, B.H., Ludwig, D., Holling, C.S., Peterman, R.M., 1981. Stability of semi-arid savanna grazing systems. J. Ecol. 69, 473–498.

Weaver, J.E., 1954. Papers of John E. Weaver (1884 — 1956). Johnsen Publishing Company, Lincoln, NE, USA.

Wells, P.V., 1970. Postglacial history of the Great Plains. Science 167, 1574–1582.

Westoby, M., Walker, B., Noy-Meir, I., 1989. Opportunistic management for rangelands not at equilibrium. J. Range Manag. 42, 266–274.

Wonkka, C. L., D. Twidwell, J. B. West, and W. E. Rogers. Shrubland resilience varies across soil types: implications for operationalizing resilience in ecological restoration. *Ecological Applications* (in press). doi: http://dx.doi.org/10.1890/15-0066.1

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