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SPECIAL FEATURE – ESSAY REVIEW

GRASS–WOODLAND TRANSITIONS

Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the Central Great Plains of North America

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Summary

1. This review synthesizes evidence that altered fire frequency drives discontinuous ecosystem transitions from mesic grasslands to shrublands or woodlands in the Central Great Plains, USA.

2. Long-term fire manipulations reveal that grassland to shrubland transitions are triggered when fire-free intervals increase from 1–3 years to ≥ 3–8 years, and longer fire returns (~10 years or more) result in transitions to woodlands. Grazing and soil properties alter these fire thresholds.

3. Grassland to shrubland transitions are abrupt and exhibit nonlinear relationships between driver and state variables. Transitions to shrublands and woodlands exhibit hysteresis, where reintroducing frequent fires does not reverse transitions in management-relevant time-scales (decades).

4. Nonlinear transitions and hysteresis emerge because grasses generate positive feedbacks with fire that create strong demographic barriers for shrub and tree establishment. Fire-free intervals allow shrubs and trees to reach a size sufficient to survive fire, reproduce and disrupt the fire feedback loop through competition.

5. *Synthesis*. Mesic grasslands, shrublands and woodlands constitute self-reinforcing states (alternative attractors) separated by critical fire frequency thresholds. Even without major shifts in climate, altered fire frequency can produce dramatic state changes, highlighting the importance of fire for predicting future ecosystem states. Local management should focus on prevention of unwanted transitions rather than *post hoc* restoration.

Key-words: alternative stable states, bi-stability, bush encroachment, critical transitions, plant population and community dynamics, positive feedbacks, resilience, restoration, stability, tallgrass prairie, tipping points, woody encroachment

Introduction

Woody encroachment – the increasing extent and dominance of woody plants in grass-dominated systems – is occurring across most North American grassland ecosystems (Archer *et al.* 1988; Briggs *et al.* 2005; Van Auken & McKinley 2008; Barger *et al.* 2011; Ratajczak, Nippert & Collins 2012) and in many other grasslands globally (Eldridge *et al.* 2011). This recent widespread increase in shrub and tree cover in grasslands and savannas can lead to states of co-dominance by shrubs and grasses or complete conversions of grasslands to shrublands or tree-dominated woodlands, often referred to as an ecosystem transition.

The ramifications of these ecosystem transitions are multifarious, with impacts on community composition and vegetation structure (Eldridge *et al.* 2011; Ratajczak, Nippert & Collins 2012), ecosystem function (Barger *et al.* 2011), ecohydrology (Huxman *et al.* 2005; Brunsell, Nippert & Buck 2014) and long-term conservation of biodiversity (Gray & Bond 2013). Woody encroachment into mesic grassland can impact regional economies by reducing forage for large grazers (Hoch, Briggs & Johnson 2002; Briggs *et al.* 2005; Limb *et al.* 2010), hindering economically important livestock production (Limb *et al.* 2011).

Woody encroachment into grasslands has been attributed to a variety of drivers operating at global (increased CO_2, climate change; Bond & Midgley 2012; Kulmatiski & Beard 2013), regional (nitrogen deposition, fragmentation; Köchy & Wilson 2001; Briggs *et al.* 2005) and local scales (over-grazing, fire; Walker *et al.* 1981; Roques, O'Connor & Watkinson 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

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have been implicated as important proximate drivers of transitions from grasslands to shrublands and woodlands (Briggs *et al.* 2005; Bond 2008; Fuhlendorf *et al.* 2008; Gibson 2009; Twidwell *et al.* 2013a).

As with many grasslands and savannas globally (Archibald, Staver & Levin 2012), fire frequency in the North American Central Great Plains (CGP) is largely controlled by the number of ignition events, which occur via lightning strikes or by humans (Allen & Palmer 2011; Stambaugh, Guyette & Marschall 2013; Twidwell *et al.* 2013b). The best estimates of pre-settlement fire regimes in CGP grasslands suggest that fire-free intervals generally ranged from 3 to 5 years (Wright & Bailey 1982; Desantis, Hallgren & Stahle 2010; Allen & Palmer 2011; Stambaugh, Guyette & Marschall 2013). Fire frequency now varies across the region (Mohler & Goodin 2012) from annual or biennial 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 sub-urban development (Hoch, Briggs & Johnson 2002; Briggs *et al.* 2005; Mohler & Goodin 2012). A critical question is whether and how this landscape will respond to changes in fire frequency.

This review synthesizes and expands upon recent research on fire as a driver of woody encroachment in mesic grasslands (i.e. tallgrass prairies) of the North American CGP. For this review, we define the CGP as the 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). The focus on temperate mesic grassland transitions is timely, given the need for increased conservation of this grassland (Hoekstra *et al.* 2005) and widespread manipulation of fire in grasslands (Mohler & Goodin 2012; Twidwell *et al.* 2013b). We review the mechanistic and experimental evidence for whether fire frequency creates tipping points that separate grasslands, shrublands and woodlands as alternative attractors. We build on > 30 years of extensive research manipulating fire frequency and grazing 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.

Conceptual framework

Woody encroachment of grasslands has been described using many different conceptual frameworks, including succession (Archer *et al.* 1988), gradual linear dynamics (Roques, O'Connor & Watkinson 2001), state and transition models (Westoby, Walker & Noy-Meir 1989; Briske, Fuhlendrof & Smeins 2005; Briske, Fuhlendorf & Smeins 2006), alternative attractors (or alternative stable states) (Walker *et al.* 1981; Frehlich & Reich 1999; Anderies, Janssen & Walker 2002; Folke *et al.* 2004; Bestelmeyer *et al.* 2011), demographic models (Higgins & Scheiter 2012), rapid changes in ecosystem drivers (Bestelmeyer *et al.* 2013), physiological thresholds (Hoffmann *et al.* 2012; Twidwell *et al.* 2013a) and others (Scholes & Archer 1997; Briggs *et al.* 2005; Bond 2008). Here, we focus on comparing linear and alternative attractor models, because ecosystems with alternative attractors are susceptible to rapid and difficult-to-foresee regime shifts (Holling 2001; Folke *et al.* 2004; Walker & Salt 2006; Scheffer 2009) and knowledge of potential alternative attractors is also key for successful ecosystem restoration (see Briske *et al.* 2008; Suding & Hobbs 2009).

Different fire frequencies could generate nonlinear transitions that are difficult to reverse (i.e. tipping points, critical thresholds). Nonlinear responses occur when an ecosystem state is initially resistant to external forcing, but has a point(s) where gradual forcing precipitates nonlinear changes in state (threshold systems) (Fig. 1, Noy-Meir 1975; May 1977; Holling 2001; Walker *et al.* 1981, Folke 2006; Briske *et al.* 2008; Scheffer 2009; Bestelmeyer *et al.* 2011). In more extreme cases, threshold transitions also exhibit hysteresis, where eliminating the external forcing or returning driving variables to their pre-transition levels is insufficient to reverse the state transition (Noy-Meir 1975; May 1977; Walker *et al.* 1981). When a system exhibits threshold transitions and hysteresis, we refer to the potential states as alternative attractors (similar to the concept of alternative stable states and critical transitions), 'critical thresholds' refer to non-reversible thresholds, and 'regime shifts' refer to transitions from one alternative attractor to another (Scheffer 2009).

Determining whether systems have alternative attractors requires multiple lines of inference, including but not limited to mechanistic studies and studies relating salient driver variables to ecosystem state (Scheffer & Carpenter 2003; Schröder, Persson & De Roos 2005; Bestelmeyer *et al.* 2011; D'Odorico, Okin & Bestelmeyer 2012). Mechanistic studies of ecological thresholds typically focus on demography and feedback processes (Archer *et al.* 1988; Roff & Mumby 2012; Higgins & Scheiter 2012), because ecological thresholds occur primarily in systems with demographic barriers and/or strong feedback mechanisms (De Roos & Persson 2002; Walker & Salt 2006; D'Odorico, Okin & Bestelmeyer 2012; Higgins & Schieter 2013, Huss *et al.* 2013). Demographic bottlenecks are establishment barriers or low population growth rates for a life stage (Huss *et al.* 2013), resulting from evolved life-history traits and/or ecological constraints (Grime 1979). Demographic bottlenecks can suppress a potentially dominant functional group through priority effects and other mechanisms (De Roos & Persson 2002; Higgins & Scheiter 2012; Huss *et al.* 2013). Distinguishing between feedbacks and demographic bottlenecks can be difficult because feedbacks by one group or species can create demographic bottlenecks for one or more other species. However, feedbacks generally refer to interactions that amplify (positive feedbacks) or dampen (negative feedbacks) pressures (Walker & Salt 2006; D'Odorico, Okin & Bestelmeyer 2012). Experimental and observational approaches can identify thresholds by determining whether a system exhibits linear or threshold relationships between driver and state (Scheffer & Carpenter 2003; Bestelmeyer *et al.* 2011). Reversing the change in drivers that precipitated a threshold transition can identify hysteresis (Fig. 1). For transitions from grasslands to shrublands and woodlands, we first review the mechanistic evidence for feedbacks and demographic barriers, followed by evidence for fire frequency thresholds, abrupt ecological shifts and hysteresis.

GRASSLAND TO SHRUBLAND TRANSITIONS

Mechanistic background

Historically, much of the CGP was tallgrass prairie, an herbaceous plant community dominated by rhizomatous C_4 (i.e. warm-season) grasses with a diverse subdominant community of C_3 grasses, forbs and legumes (Collins & Adams 1983; Gibson & Hulbert 1987; Collins & Calabrese 2012). In this region, the balance between precipitation and evapotranspiration can support woody vegetation (Borchert 1950; Hayden 1998), and yet woody plant cover was historically low, except along riparian corridors and certain other landscape features (e.g. outcrops, seeps, etc.) (Weaver 1954; Wells 1970; Abrams 1985; Axelrod 1985). The dominant grasses of this region are well adapted to fire and drought, but poorly adapted to light limitation (Knapp 1993; Scholes & Archer 1997; Bond 2008; Nippert *et al.* 2011; Scheiter *et al.* 2012), and they generate self-reinforcing feedbacks that promote these conditions and demographic barriers that inhibit other plant growth forms by: (i) leaving little open space for colonization by other species, even in post-fire windows (Weaver 1954; Briggs & Knapp 2001; Benson & Hartnett 2006); (ii) producing large concentrations of fibrous roots in the upper 30 cm (Jackson *et al.* 1996; Nippert & Knapp 2007; Nippert *et al.* 2012) that can rapidly utilize water and nutrients at this soil depth (Knapp 1993; Epstein *et al.* 1997; Knapp, Briggs & Koelliker 2001; Bredenkamp, Spada & Kazmierczak 2002; Ocheltree, Nippert & Prasad 2013, 2014); and (iii) generating large amounts of herbaceous biomass that facilitates frequent and intense fires, resulting in direct mortality of unprotected meristems (Gibson, Hartnett & Merrill 1990; *sensu* Van Wilgen *et al.* 2002; Bond 2008; Scheiter *et al.* 2012). As a result, the establishment of shrub seedlings in frequently burned grasslands is rare (Benson & Hartnett 2006; Ratajczak *et al.* 2011).

However, once shrubs establish in grasslands, the competitive dynamics between grasses and shrubs change dramatically. Initially, shrub seedlings recruit as single-stemmed ramets that are highly susceptible to top-kill by fire. Given sufficient time and resource availability, encroaching shrub species in CGP tallgrass prairie, such as *Cornus drummundii* and *Rhus glabra*, form clonal multistem clusters in the grassland matrix ('shrub islands') that increase in both height and radial extent over time (Petranka & McPherson 1979; Collins & Adams 1983; Anderson, Schwegman & Anderson 2000; Harrell, Fuhlendorf & Bidwell 2001; McCarron & Knapp 2003; Brudvig *et al.* 2007; Ratajczak, Nippert & Ocheltree 2014). Increasing shrub cover leads to light limitation for grasses, along with concomitant decreases in grass cover, grass biomass and the fine fuels that carry fire (Heisler *et al.* 2004; Lett & Knapp 2005). While the reductions in grass biomass are greatest at the centre of shrub clusters, even the cluster edges have significantly lower fine fuels, allowing new clonal recruits to benefit from shrub-mediated fire suppression (Ratajczak *et al.* 2011). If fire kills the above-ground portion of large shrubs, they typically resprout and reach their former height in as little as 1 or 2 years (Heisler *et al.* 2004; Hajny, Hartnett & Wilson 2011). In the even rarer instances where fire kills shrubs completely, the potential for C_4 grasses to recover their pre-transition productivity in short time frames (2 years or less) has usually eroded (Lett & Knapp 2005), leaving windows of opportunity for shrub seedlings to establish in a low-competition environment. Thus, while frequent prescribed fires might inhibit shrub establishment, they may no longer be a viable filter for prohibiting shrub expansion once shrub establishment is initiated.

The effects of resource competition and availability also change as shrubs reach larger size-classes. Mature clonal shrubs are deep-rooted and obtain a larger percentage of their water from deeper soils (> 50 cm depth), reducing competition for water with the dominant grasses, which rely primarily on shallow soil water (McCarron & Knapp 2001; Nippert & Knapp 2007; Ratajczak *et al.* 2011). Use of deeper water

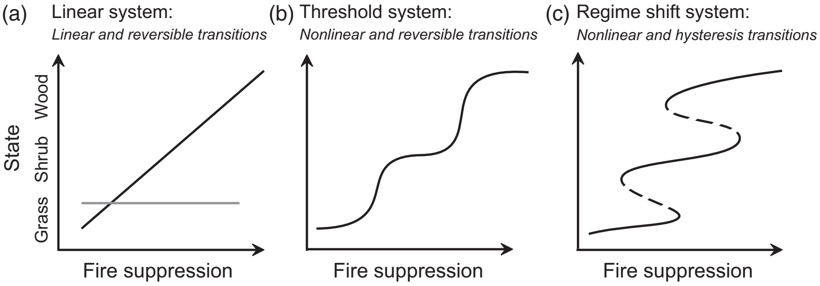

Fig. 1. A depiction of potential internal ecosystem dynamics in response to fire. For all panels, solid lines denote stable equilibria, and in c) dotted lines delineate unstable repellors. (a) Shows the null hypothesis where fire does not result in ecosystem transitions (grey line) and a scenario where 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 attractors (c), shifts between states show threshold behaviour as in (b). However, returning drivers to their pre-transition values does not reverse the transition. 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).

sources by shrubs mitigates susceptibility to summer drought and climate variability (Nippert *et al.* 2013). Crucially, deep-rooted parent stems can also 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). The clonal growth form and rooting properties of these shrubs, combined with their effects on fire suppression, create a positive feedback loop with low fire intensity and alter the demographic bottleneck related to shrub recruitment, both of which facilitate shrub cluster survival and expansion (Petranka & McPherson 1979; Yao *et al.* 1999; Ratajczak *et al.* 2011; similar to De Roos & Persson 2002; D'Odorico, Okin & Bestelmeyer 2012; Huss *et al.* 2013), but only if shrubs are allowed to increase in size by fire-free intervals.

Experimental and observational evidence for fire thresholds

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 suggests that this transition may be nonlinear and capable of hysteresis (Walker & Salt 2006). Synthesis of fire frequency studies (Figs 4–5) shows that fire return intervals ≤ 2 years prevent shrub expansion in CGP grasslands (Bragg & Hulbert 1976; Briggs & Gibson 1992; Kettle *et al.* 2000, Bowles & Jones 2013; Ratajczak, Nippert & Ocheltree 2014; Fig. 2), 3-year fire returns sometimes maintain grasslands, but can also allow transitions to shrublands, and fire returns > 3 years consistently result in rapid shrub expansion (Brudvig *et al.* 2007; Bowles & Jones 2013, Ratajczak, Nippert & Ocheltree 2014). This nonlinear relationship between fire and shrubland formation is consistent with alternative attractor theory. Moreover, the transition from grassland to shrubland has the hallmarks of a threshold transition (e.g. Scheffer & Carpenter 2003; Bestelmeyer *et al.* 2011): abrupt shifts in shrub cover over time, spatiotemporal bi-modality of system state and nonlinear correlations between state and driver variables (Fig. 2; Ratajczak, Nippert & Ocheltree 2014). The transition to shrub–grass co-dominance typically takes 20 years, with gradual increases in shrub cover at first and rapid rates of clonal expansion later in the process, as illustrated by long-term measurements at KPBS (Fig. 2b; Collins & Adams 1983; Ratajczak, Nippert & Ocheltree 2014). Analysis of 28 years of plant composition at KPBS and elsewhere indicates that abrupt shifts in shrub cover are not related to abrupt shifts in climate or fire (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; Ratajczak, Nippert & Ocheltree 2014). This suggests that the abrupt transition from grassland to shrubland represents the crossing of a threshold, rather than a response to abrupt changes in salient driver variables (Bestelmeyer *et al.* 2011). Demographic rates, in particular the high survival and rapid rate of clonal expansion, might also contribute to the abruptness of grassland to shrubland transitions. The importance of demographic bottlenecks (e.g. Huss *et al.* 2013) is further evidenced by the 8-fold faster expansion rates by clonal shrubs, compared with non-clonal wood plants (Fig. 2a–c).

For grasslands and shrublands to be alternative attractors, they must also show hysteresis with respect to fire frequency and grass dominance (Fig. 1c). The clonal shrub *Rhus glabra* has the capacity to withstand annual fires once established (Hajny, Hartnett & Wilson 2011), and although exposing clonal oak shrublands to biennial fires initially lowers cover, it returns to previous levels within 2 years and shrubs that survive increase in size, reducing long-term fire susceptibility (Harrell, Fuhlendorf & Bidwell 2001; Boyd & Bidwell 2002). Data from KPBS also show hysteresis. Directly after a transition to shrubland, ungrazed grasslands were burned twice in 4 years, but failed to return a grassland state (Ratajczak, Nippert & Ocheltree 2014). We attribute these examples of hysteresis to the ability of shrubs to suppress grasses, resist fire, and resprout when top-killed.

Similar to other alternative attractors (Staver, Archibald & Levin 2011; Roff & Mumby 2012), critical 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 (Fuhlendorf *et al.* 2008; Twidwell *et al.* 2013a) and *vice versa* (Ratajczak, Nippert & Ocheltree 2014). 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 uplands with thin soils are rarely colonized by shrubs, even with long-term fire suppression (Fig. 2d, Bragg & Hulber 1976; Ratajczak *et al.* 2011; Bowles & Jones 2013). This is surprising, because upland fires are less intense (Gibson, Hartnett & Merrill 1990). The inability of shrubs to reach a fire-resistant size in uplands is most likely due to greater run-off, coarser soils and shallower soil depth, which collectively results in lower available soil moisture (Nippert *et al.* 2011) and forces shrubs to compete directly with grasses in upper soil layers (Nippert & Knapp 2007; Ratajczak *et al.* 2011).

Herbivory alters grass–shrub competition in many ecosystems (Holdo *et al.* 2013). Browsing in CGP grasslands does not appear to play a major role in shrubland transitions, considering that the species most preferred by browsers have increased the most in cover (van der Hoek *et al.* 2002 vs. Heisler, Briggs & Knapp 2003; Ratajczak *et al.* 2011). However, introducing more diverse or larger browsers could potentially have an effect, as seen in similar systems on other continents (Staver *et al.* 2012). In many grasslands globally, grazing has shifted grassland–shrubland thresholds in favour of shrubs by reducing grass dominance (Walker *et al.* 1981; Scholes & Archer 1997; Fuhlendorf *et al.* 2008). Recent research in the CGP does not support this paradigm. If anything, grazing appears to suppress dominant shrub establishment (Kettle *et al.* 2000; Brudvig *et al.* 2007; Ratajczak, Nippert & Ocheltree 2014), perhaps because native grazers

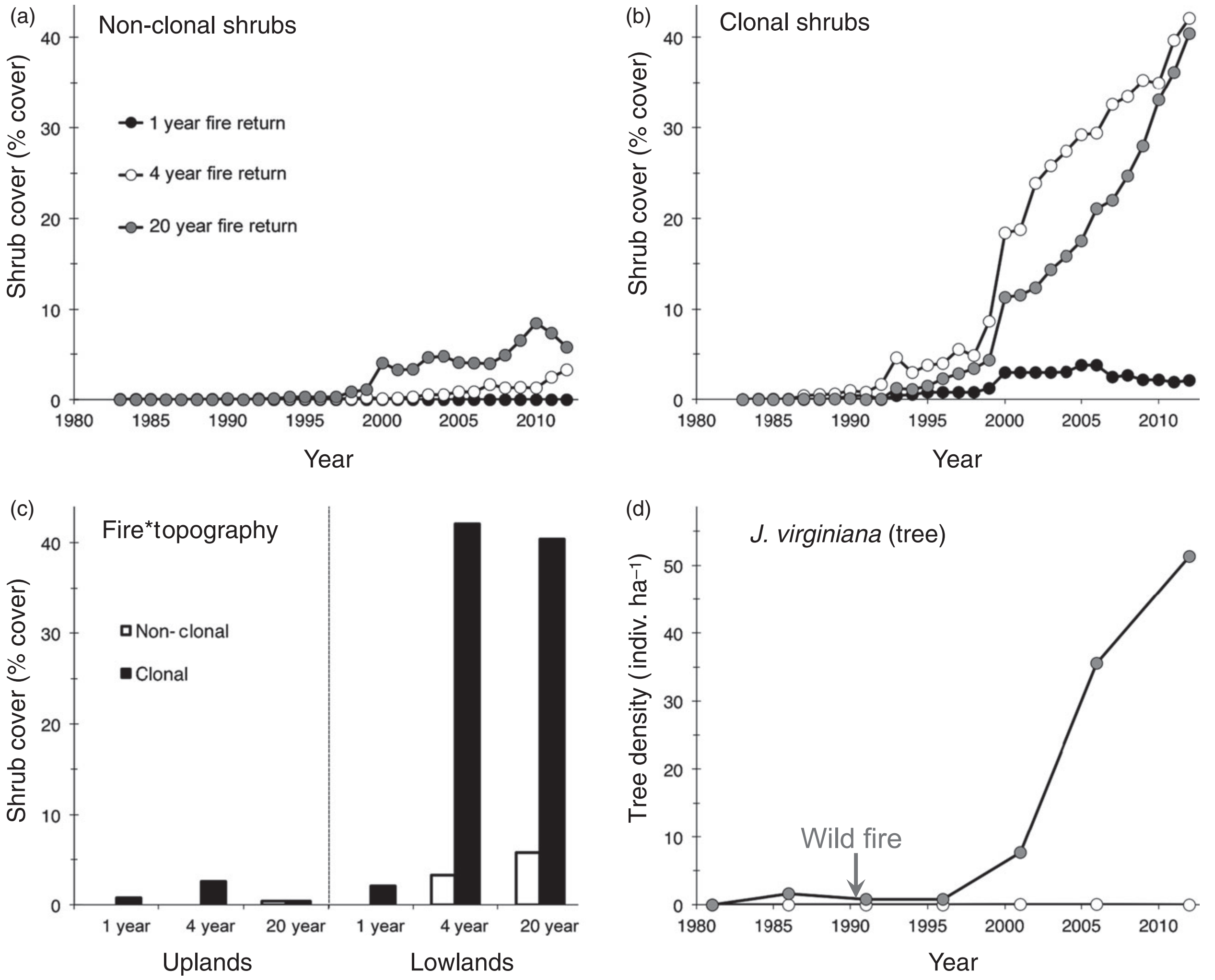

Fig. 2. Measurements of shrub and tree dynamics in treatments of Konza Prairie exposed to different prescribed frequencies starting in the late 1970s. 'Clonal shrubs' refer to *Cornus drummondii*, *Rhus glabra* and *Prunus americana* cover, and 'non-clonal shrubs' include all other shrub species with a canopy that extends above the grass layer. (a) and (b) Depict changes in shrub cover within lowland topographies for non-clonal (a) and clonal (b) functional groups. Fire-free intervals vary from 1 year (black fill), 4 years (white fill) and 20 years (grey fill). (c) Depicts the factorial cross of fire frequency and topography (uplands and lowlands) with respect to shrub cover, for non-clonal (white) and clonal shrubs (black) after 30 years of fire frequency manipulation (i.e. the level of shrub cover circa 2012). All shrub cover estimates are averaged across grazed and ungrazed treatments (n = 40, 10 m^2 plots per combination of fire and topography, derived equally from grazed and ungrazed areas). (d) Shows changes in *J. virginiana* tree density for ungrazed areas with a fire-free interval of 4 years (white fill) and 20 years (grey fill). These data come from detailed mapping of catchment basins (see Fig. 3 and Briggs, Knapp & Brock 2002). The arrow in (d) indicates the timing of a wildfire that affected the 20-year fire treatment.

physically damage woody species (Coppedge & Shaw 1997) and create more bare ground, which increases sensible heat and reduces surface soil moisture (Walker *et al.* 1981; Nippert *et al.* 2013). More research is needed on how grazing affects grass–shrub interactions, considering the predominance of grazing in the CGP and mesic grasslands globally.

TRANSITIONS TO WOODLANDS

Mechanistic background

The final state of woody plant expansion that we consider is conversion to woodlands. We focus primarily on *Juniperus virginiana* (eastern red cedar) woodlands (subsequently referred to as Juniper woodlands) rather than deciduous woodlands, because Juniper woodlands exhibit the greatest expansion in the CGP (Twidwell *et al.* 2013b).

As with shrubs, the pyrogenic traits of C_4 grasslands impose limits on Juniper trees. In fact, Juniper woodland expansion should be acutely constrained by fire because unlike grasses and shrubs, *J. virginiana* does not resprout when top-killed and *J. virginiana* develops bark slowly, leaving it poorly insulated against fires until older ages (VanderWeide & Hartnett 2011). Correspondingly, smaller *J. virginiana* (< 2 m tall) suffer high mortality rates during fires (Hoch, Briggs & Johnson 2002; Fuhlendorf *et al.* 2008; VanderWeide & Hartnett 2011). For these reasons, greater fire suppression should be needed for Juniper woodland formation, compared to shrublands.

Once *J. virginiana* reaches a larger size, its response to fire may exhibit hysteresis. *J. virginiana* suppresses grass growth with dense canopies that intercept the majority of sunlight (Hoch, Briggs & Johnson 2002; McKinley *et al.* 2008; Myster 2009; Limb *et al.* 2010; Van Els *et al.* 2010). With time, this disruption of fuel continuity decreases fire transmission (Abades, Gaxiola & Marquet 2014; this issue), creating a positive feedback between *J. virginiana* and fire suppression. With long-term fire suppression, *J. virginiana* can also overtop and replace shrubs, as shown in long-term vegetation surveys and the inability of shrubs seedlings to regenerate under older *J. virginiana* canopies (Myster 2009, Van Els *et al.* 2010). Thus, while the fires typical of grasslands and shrublands might prohibit tree establishment, exposing mature woodland trees to fires should have little effect.

Unlike transitions to shrubland, low water availability and thin soils are less important constraints for *J. virginiana* expansion (Volder, Tjoelker & Briske 2010; Volder, Briske & Tjoelker 2013). Evergreen trees are at least, if not more, drought resistant than grasses under most drought scenarios (Awada *et al.* 2012). As a result, *J. virginiana* seedlings in fire-free locations have high survivorship in both high-diversity and grass-dominated patches (Ganguli *et al.* 2008), shallow soils and through droughts (Yao *et al.* 1999; Eggemeyer *et al.* 2006; Engle, Bodine & Stritzke 2006; Volder, Tjoelker & Briske 2010; Volder, Briske & Tjoelker 2013) – conditions that typically exclude trees and most invasive species (Bond 2008; Seabloom *et al.* 2013).

Experimental and observational evidence for fire thresholds

Statistical indications of regime shifts (e.g. abrupt shifts, state bi-modality) require experiments and observational data sets with frequent sampling events and replicates that are scaled with the life span and spatial footprint of organisms involved (van Nes & Scheffer 2005; Bestelmeyer *et al.* 2011). Given the long generation time of *J. virginiana*, observing a threshold transition to woodland would require an experiment that increases fire returns slowly, allowing tree species to equilibrate with their changing carrying capacity until a potential threshold is crossed. Instead, most observations of woodland transitions have large gaps between samples (~a decade, Fig. 4, 5- references therein), which are not suitable for tests of abrupt shifts between states. Moreover, most examples of woodland transitions take place when fire frequency is altered from frequent fires (1–3 years) to complete fire suppression. This effectively pushes the driver variable (fire) far past any potential thresholds. The ecological response to this change in driver variables should be loss of grasses and a pattern of logistic growth by trees and shrubs as they reach their new carrying capacity (May 1977; Hughes *et al.* 2012); this result is evident over 30- to 50-year observations in areas with fire suppression (Figs 2 and 3) (Anderson, Schwegman & Anderson 2000; Hoch, Briggs & Johnson 2002; Peterson, Reich & Wrage 2007; Limb *et al.* 2010; Van Els *et al.* 2010, Twidwell *et al.* 2013a,b; Ratajczak, Nippert & Ocheltree 2014).

While we lack the data to identify ‘abrupt shifts’ during woodland transitions, we can identify management thresholds by asking: is there a fire frequency threshold that prohibits transitions from shrubland to woodland? And if so, does increasing fire frequency in woodlands reverse the transition or does the ecosystem show hysteresis? Detailed mapping of tree establishment and analyses of shrub cover at KPBS shows that 30 years of prescribed fire at 3- to 4-year frequencies allows establishment of shrubs, but not trees (Fig. 2). The lack of tree establishment over a 30-year period with 3- to 4-year fire intervals and the prevalence of clonal shrublands throughout the region (Petranka & McPherson 1979; Collins & Adams 1983; Anderson, Schwegman & Anderson 2000; Harrell, Fuhlendorf & Bidwell 2001; Brudvig *et al.* 2007; Ratajczak *et al.* 2011) suggests that shrublands are a separate alternative attractor from woodlands and that longer fire-free intervals are needed to precipitate a transition to woodland. Less frequent burning (~20-year fire returns) or complete fire suppression allows tree establishment (Fig. 3) and eventual formation of closed-canopy woodland (Bragg & Hulber 1976; Kettle *et al.* 2000; Norris *et al.* 2001; Hoch, Briggs & Johnson 2002; Engle, Bodine & Stritzke 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). To resist typical grassland fires, *J. virginiana* must reach a height of ~2.5 m and diameter of 17.5 cm at breast height (1.4 m) (Owensby *et al.* 1973; Hoch, Briggs & Johnson 2002; Vanderweide & Hartnett 2011). Connecting these physiological thresholds to reported *J. virginiana* growth rates (Owensby *et al.* 1973; Engle & Kulberth 1992; Schmidt & Wardle 2002), we estimate that fire-free intervals of 15–20 years would allow consistent tree establishment, although this interval may be as short as 6–10 years for locations with abundant tree seed sources and heavy grazing (Owensby *et al.* 1973; Hoch, Briggs & Johnson 2002; Fuhlendorf *et al.* 2008). These estimates closely match modelling by Fuhlendorf *et al.* (2008), as well as historical observations that *J. virginiana* is more common in pyrrhic woodlands with a fire frequency > 5 years (Batek *et al.* 1999; Stambaugh, Guyette & Marschall 2013; Desantis, Hallgren & Stahle 2011). Similarly, a fire following 15 years of fire suppression at KPBS killed approximately three-fourths of Juniper trees, but did not stop the transition to woodland when it was followed by further fire suppression (Fig. 2c). This indicates that transitions to Juniper woodland are possible at 15-year fire return intervals. However, the rate of transition will be significantly suppressed with more frequent fires (Fig. 2c).

Expansion of *J. virginiana* can decrease fire intensity, which could create hysteresis in response to fire. In mixed deciduous/Juniper woodlands, reintroduction of 3-year fire returns and aerial chemical controls allows *J. virginiana* to maintain ~20% cover (Engle, Bodine & Stritzke 2006). In both the southern and northern CGP, reintroducing fire returns of ~2–3 years for a duration of 20–30 years had only marginal effects on tree cover and increased grass cover to only

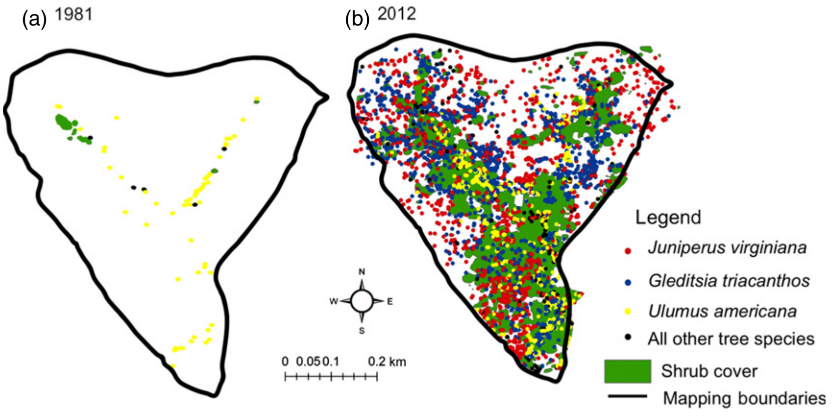

Fig. 3. Changes in woody species occurrence on an ungrazed catchment basin at Konza Prairie in (a) 1981 and (b) 2012, with only one fire since 1983. In both 1981 and 2012, coordinates of all tree stems and shrubs above the grass canopy were recorded. Trees were mapped as points and shrubs as polygons (see Briggs, Knapp and Brock 2002 for more details). For symbols, *Juniperus virginiana* = red dots, *Gleditsia triacanthos* = blue dots, *Ulmus americana* = yellow dots, all other tree species = black dots, and shrub cover = green polygon. Note that the watershed boundaries changed between 1981 and 2012; therefore, the original mapping boundaries are delimited with a black line.

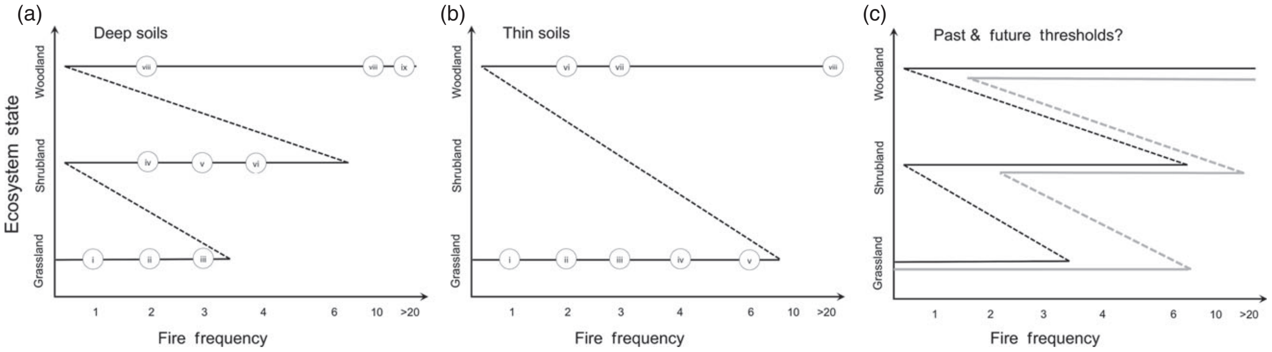

Fig. 4. The CGP tri-stability framework for alternative attractors of grasslands, shrublands and woodlands in (a) deep and (b) thin soils. Horizontal black lines denote alternative attractors, and dotted lines denote unstable states. Circles with roman numerals represent contrasting ecosystem states identified by experimental or observational studies showing that CGP ecosystem has existed at the respective state and fire frequencies indicated on the *x*- and *y*-axes. Following thresholds from Ratajczak, Nippert & Ocheltree (2014), grasslands were those ecosystems with < 10% shrub cover and C_4 grasses present, shrublands were 10–60% shrub cover, with minimal trees present, and woodlands were those ecosystems with many trees above 2.6 m tall, 17 cm diameter at breast height fire-mortality thresholds (Owensby *et al*. 1973, Hoch, Briggs & Johnson 2002; VanderWeide & Hartnett 2011). (c) depicts how thresholds may change (grey lines) relative to current thresholds (black lines), if shrub growth rate is increased more than grass growth rate (e.g. more grazing, increased CO_2). Factors that favour grass dominance would move the curve in the opposite direction. Note that shifts from grassland to shrubland were discrete (occurring in 2–5 years), whereas transitions are more gradual between grassland and woodland, and shrubland and woodland. Supporting citations: Bowles & Jones (2013): (a) i, ii, iii, v, (b) i, ii, iii, iv, v; Boyd & Bidwell (2002); (a) iv; Bragg & Hulber (1976): (a) ii, ix; Briggs & Gibson (1992); Briggs *et al.* (2002), Fig. 2 & 3 (this review): (a) i, ii, v, xi; (b) i, iii, viii; Fuhlendorf *et al.* 2008: (a) viii; Fuhlendorf *et al.* 2009: (a) iii; Harrell, Fuhlendorf & Bidwell (2001): (a) ii; Kettle *et al.* 2000: (a) ii, xi; Hoch, Briggs & Johnson 2002: (a) ix (b) viii; Owensby *et al.* 1973: (a) i, ii; Peterson, Reich & Wrage (2007): (a) vii, viii, ix; Process-based estimates (described in text): (a) viii; Ratajczak *et al.* 2011; Ratajczak, Nippert & Ocheltree 2014, Fig. 3: (a) i, iv, v, vi; (b) i, iv, viii; Engle, Bodine & Stritzke (2006): (b) vii, viii; Burton, Hallgren & Palmer 2010, 2011: (b) vi, viii.

10–20% (Peterson, Reich & Wrage 2007; Burton, Hallgren & Palmer 2010; Burton *et al.* 2011). In historical records (dendrochronology), Juniper woodlands persisted in areas with fire returns ranging from 2 to 6 years (Batek *et al.* 1999; Desantis, Hallgren & Stahle 2010; Stambaugh, Guyette & Marschall 2013). However, studies by Burton, Hallgren & Palmer (2010), (Burton *et al.* 2011) and Peterson, Reich & Wrage (2007) were performed in primarily deciduous woodlands, and results may not apply to Juniper woodlands.

A more rapid reversion of woodlands to grasslands typically requires physical or chemical removal of *J. virginiana* trees, combined with frequent burning to foster grass dominance and fire-promoting feedbacks (Engle, Bodine & Stritzke 2006; Pierce & Reich 2010; Alford *et al.* 2012). To achieve this, tree removal and reintroduction of fire should coincide, or the legacy effects of woodland dominance can facilitate a rapid return to the woodland state (Kettle *et al.* 2000). It also may be possible to achieve faster reversals to grasslands using novel burning techniques that stimulate high intensity (Twidwell *et al.* 2013a).

Woodland fire thresholds are context specific in ways that differ from thresholds differentiating grasslands and

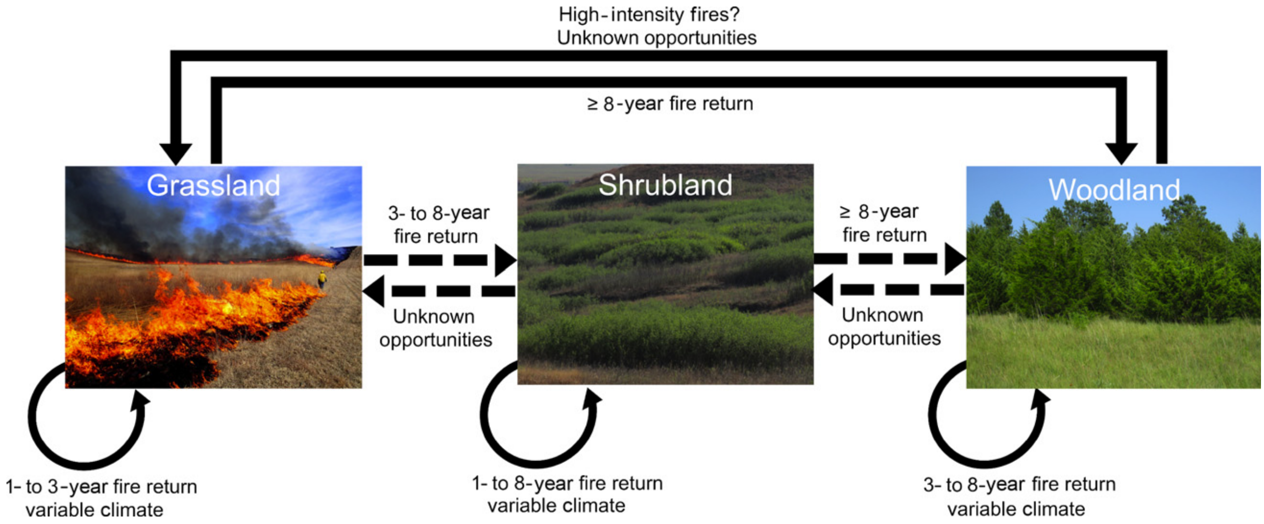

Fig. 5. State and transition model of grassland, shrubland and woodland states. Following Westoby, Walker & Noy-Meir (1989)and Briske, Fuhlendrof & Smeins (2005), squares represent states and arrows represent processes that may or may not elicit a transition to another state. Dashed arrows represent state trajectories that are only possible in lowland and mesic soils. Hysteresis is accounted for by the 'selfing' arrows for shrubland and woodland states, where conditions that used to maintain grasslands do not reverse shrubland and woodland transitions once they have occurred. There are few opportunities to reverse transitions to shrublands and woodlands with fire alone, but we have left an arrow labelled 'unknown opportunities' in anticipation that new techniques and adaptive management schemes will emerge to return CGP ecosystems to grasslands (Twidwell *et al.* 2013a,b). Photo Credits: (Grassland: Eva Horne, Shrubland: Zak Ratajczak, Woodland: John Blair).

shrublands. A unique attribute of woodland trees, relative to shrubs, is their ability to establish in more xeric and thin soils with sufficient fire suppression (Fig. 4b: Engle, Bodine & Stritzke 2006; Eggemeyer *et al.* 2006; Knapp *et al.* 2008; McKinley *et al.* 2008). Conventional cattle grazing generally favours greater tree establishment by reducing fuel loads, and thereby fire intensity (Hoch, Briggs & Johnson 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, native grazers such as bison (*Bos bison*) can significantly restrict woodland development. At moderate densities at KPBS, bison physically damage *J. virginiana* trees (personal observations), and these behavioural traits have been observed in *Bos bison* from other North American grasslands (Bork *et al.* 2013; but see Coppedge & Shaw 1997). At KPBS, this effect is so strong that *J. virginiana* is absent from *Bos bison*-grazed areas, and instead other trees are more prevalent, such as the thorned tree *Gleditsia triacanthos* (Z. Ratajczak, Unpubl. data). These observations further illustrate the importance of considering grazer impacts as a whole in grassland to woodland transitions, and not just their indirect effects on trees via grass abundance and soil characteristics.

Synthesis and opportunities

Based on the data presented here and our synthesis of results from other fire frequency studies (Fig. 4), we propose a conceptual framework of tri-stability for the CGP that treats grasslands, shrublands and woodlands as alternative attractors moderated by critical fire frequency thresholds. Based on experimental and observational studies of fire and ecosystem state, we have constructed complementary catastrophe fold (Fig. 4) and state and transition models that illustrate the positions of critical thresholds and the system's capacity for hysteresis (Fig. 5). In areas with lower water-holding capacity or thin soils that restrict access to deep soil moisture, shrubs cannot establish and grasslands and woodlands are the only viable alternative attractors. Starting with grasslands as the baseline state, fire return intervals of 3–8 years result in transitions to shrublands, and fire frequencies of 8–10 years lead to transitions to woodlands (Fig. 5). Once a shrubland or woodland state is established, self-reinforcing feedback mechanisms and altered demographic sensitivity to fire result in hysteresis, such that decreasing the fire return interval to pre-transition levels does not readily return the ecosystem to a grassland state.

The tri-stability framework presented here is novel on two fronts. First, evidence for alternative attractors with descriptive mechanisms *and* nonlinear transitions and hysteresis in response to changes in driver variables are rare in terrestrial ecosystems (Schröder, Persson & De Roos 2005). Identifying ecosystem thresholds, hysteresis and the mechanisms behind these processes are major challenges in adaptive management and governance (Walker & Salt 2006) and ecosystem and community ecology (Sutherland *et al.* 2013). Second, in a single region (CGP) and climate zone, we provide evidence for three distinct ecosystem states depending on human management of fire, soil type and to some extent, grazer identity and abundance. In the light of the growing control of fire by humans, we argue that predictions of future vegetation shifts cannot rely solely on climate and should incorporate fire frequency and social factors that determine fire management plans.

Our conceptual framework provides testable hypotheses that can be applied to other sites and in experimental settings. Spatial analyses of tree cover would provide evidence for whether transitions to woodland constitute a regime shift (using methods described in Hirota *et al.* 2011; Staver, Archibald & Levin 2011). Other avenues for future research include testing competition models (Chesson 2000), theoretically derived 'generic leading indicators' of impending thresholds (Scheffer *et al.* 2012) and demographic models that have advanced prediction in several ecological systems (De Roos & Persson 2002; Huss *et al.* 2013). Such research might also help identify opportunities for reversing transitions (Fig. 5; Holmgren & Scheffer 2001; Twidwell *et al.* 2013b).

In the CGP and similar systems, the tri-stability framework may serve as a valuable management tool, allowing landowners to employ fire frequency to avoid unwanted state changes. Given the economic and conservation priorities in the CGP (Hoekstra *et al.* 2005), 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 facilitate the transition back to a grassland state on management-relevant time-scales. Therefore, reversing unwanted transitions will probably require costly inputs, such as physical and chemical removal.

Combining theoretical predications and application, we agree with others who have cautioned that critical thresholds can vary over time (Bestelmeyer & Briske 2012). Conditions that facilitate grass growth, greater fire intensity, or reduce tree/shrub growth will favour the grassland state, requiring longer fire-free intervals to facilitate a transition to a shrubland or woodland (Fig. 4c, *sensu* Staver, Archibald & Levin 2011; Bond & Midgley 2012; Hoffmann *et al.* 2012; Roff & Mumby 2012). Initial evidence suggests that fire thresholds have already changed in the CGP; prior to European arrival, the estimated fire return interval for the CGP was ~4 years (Wright & Bailey 1982; Allen & Palmer 2011) and much of the region was devoid of shrublands and woodlands (Weaver 1954; Wells 1970; Axelrod 1985; Abrams 1985). Now, 3- to 4-year fire frequencies are often insufficient to prevent the transition to shrublands (Fig. 2). These observations suggest that fire thresholds have responded to global and/or regional pressures, such as increased CO_2 (Bond & Midgley 2012), loss of larger browsers and native grazers, and exurban expansions that have increased woody plant cover and enhanced woody plant seed sources (Briggs *et al.* 2005). Given this potential flexibility, continued monitoring of grasslands and adaptive management are critical (for examples, see Fuhlendorf *et al.* 2008; Bestelmeyer & Briske 2012; Twidwell *et al.* 2013b).

The CGP grasslands share many drivers, feedbacks and demographic traits for woody encroachment with other grasslands and savannas (Scholes & Archer 1997; Wu & Archer 2005; Bond 2008; Staver, Archibald & Levin 2011; D'Odorico, Okin & Bestelmeyer 2012; Higgins & Schieter 2013, Holdo *et al.* 2013), contributing fertile ground for cross-site syntheses and development of more sustainable grassland management. One major research opportunity is elucidating the role of grazers and browsers on woody encroachment in the CGP. Identifying system-specific roles of grazers and browsers on ecosystem transitions will improve our ability to identify patterns and generalize across ecosystems, resulting in better *a priori* detection of ecosystem thresholds and enhanced opportunities to avoid critical thresholds.

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