Saving imperiled grassland biomes by recoupling fire and grazing: a case study from the Great Plains

Bradford P Wilcox[1*], Samuel D Fuhlendorf[2], John W Walker[3], Dirac Twidwell[4], X Ben Wu[1], Laura E Goodman[2], Morgan Treadwell[3], and Andrew Birt[5]

Woody plant encroachment – the conversion of open grasslands and savannas to woodlands – represents one of the gravest threats to grassland biomes worldwide. This is especially true for the Great Plains of the US. We contend that the widespread adoption of pyric herbivory (the synergistic application of fire and grazing) and mixed-species grazing (cattle [*Bos taurus*] and goats [*Capra* spp]) would not only make grasslands and savannas more resilient to woody plant encroachment but would also enhance the profitability and resiliency of livestock production systems. These management strategies control woody plants, increase biodiversity, improve grassland ecosystem function, and favor livestock production. Although this management paradigm holds tremendous potential by mimicking original grassland disturbance regimes, it has not been widely adopted because of cultural constraints. Saving the remaining natural grasslands in the Great Plains and elsewhere will require a widespread shift in cultural norms – facilitated by targeted government incentives and a coordinated program of regional research, extension, and education that involves farmers and ranchers as key stakeholders.

Grasslands and savannas are found throughout the tropical and temperate regions of the world. Prior to the advent of mechanized agriculture, grasslands and savannas accounted for nearly 40% of Earth's surface; today, the remaining intact grasslands and savannas cover only a little over 20% (Mishra and Young 2020). They are hotspots of wildlife biodiversity,

In a nutshell:

- Woody plant encroachment has greatly altered grassland biomes across the world and poses a continuing threat to the grasslands that remain
- Animal production systems that depend on grassland biomes are increasingly threatened by environmental change, including woody plant encroachment, a warmer and drier climate, and catastrophic wildfires
- Adoption of pyric herbivory and mixed-species grazing holds the potential to increase livestock production, reduce woody cover, and mitigate the adverse effects of climate change and wildfire
- Widespread adoption of these management practices is feasible through integrated research and extension programs with a focus on participatory and multistakeholder partnerships

[1]Department of Ecology and Conservation Biology, Texas A&M University, College Station, TX *(bwilcox@tamu.edu); [2]Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK; [3]Texas A&M AgriLife Research and Extension, San Angelo, TX; [4]Department of Agronomy and Horticulture, University of Nebraska, Lincoln, NB; [5]Texas Transportation Institute, Texas A&M University, College Station, TX

including iconic megafauna and endemic birds; enormous repositories of soil carbon; and source areas for clean and abundant water. In addition, they support most of the world's livestock production (Yahdjian *et al*. 2015; Mishra and Young 2020). The affinity we have for these biomes is assuredly linked to the fact that they are widely considered as the birthplace of humanity (Archibald *et al*. 2020).

The distinction between a grassland and a savanna biome is blurry. In the strictest sense, grasslands lack trees and shrubs, whereas savannas may consist of 10–80% woody vegetation. At present, many ecosystems classified as grasslands have a substantial woody component (Archer *et al*. 2001; Mishra and Young 2020). While some ecologists argue that savannas are confined to tropical climates with bimodal annual precipitation patterns (Hutley and Setterfield 2008), others consider temperate wooded grasslands to be savannas as well (McPherson 1997). In the absence of a consensus definition of savannas, it has become common practice to simply lump grasslands and savannas under the catchall term of "grassland biome" (Bond and Parr 2010).

Grassland biomes, then, are broadly defined as ecosystems having a more-or-less continuous herbaceous layer of grasses and forbs, with trees – if present – being discontinuous (Bond and Parr 2010; Veldman *et al*. 2015). These landscapes have co-evolved with disturbance, including droughts, fire, and mammalian grazing (Parr *et al*. 2014), and indeed frequent fire and herbivory are required for their persistence (Veldman *et al*. 2015).

In spite of their importance, grassland biomes are imperiled worldwide. Up to half of the world's grassland biomes have been converted to croplands or altered by afforestation (Anderson 2006; Parr *et al*. 2014), while those that remain have been degraded by other factors, including invasive species,

overgrazing, altered fire regimes, and elevated carbon dioxide (CO_2) (Parr *et al.* 2014; Veldman *et al.* 2015).

Woody plant encroachment is a major threat to grassland biomes

Woody plant encroachment (WPE) is a major threat to grassland biomes (Sala and Maestre 2014; Veldman *et al.* 2015). The proliferation of trees and shrubs on rangelands is one of the most striking land-cover changes of the past 100–200 years. Overgrazing, especially during the late 1800s, played a key role in disrupting longstanding fire regimes, which set the stage for the expansion of woody plants (Wilcox *et al.* 2018). As noted by Archer *et al.* (2017), "the arrival of livestock with Anglo-European settlers in the Americas, Australia and Southern Africa coincided with dramatic and swift changes in woody abundance in grasslands and savannas". Of course, other factors may also contribute to WPE, including the dissemination of woody plant seeds by livestock, eradication of native browsers, increased atmospheric CO_2 concentrations, a warming climate, and in some cases extreme drought, but these are secondary to changes in fire regime (Archer *et al.* 2017).

It is important to note that WPE is not necessarily synonymous with landscape degradation (Eldridge *et al.* 2011). In many cases soil degradation will not occur. This is especially true for savannas in subhumid or relatively wet semiarid climates, in which vegetation cover in both the canopy and intercanopy remain high (Basant *et al.* 2020). Nevertheless, WPE does generally diminish forage production on rangelands and can jeopardize the provision of ecosystem services inherent to grassland systems (Archer *et al.* 2011). For more arid climates, WPE leads to degradation by dramatically increasing the amount of intercanopy bare ground, which facilitates erosion.

The challenge of managing woody plants on rangelands

The expansion of woody plants on rangelands has long been a global concern. Since the 1940s, the range management community has aggressively worked to reverse woody proliferation, relying heavily on mechanical and chemical brush control, with the primary goal of increasing forage production for livestock. In the US, enormous amounts of time, money, and effort have been expended on attempts to reverse WPE (Briske *et al.* 2016), but to date the results have generally been transitory (5–10 years) and only marginally effective (Archer *et al.* 2017; Ding *et al.* 2020). In addition, these traditional methodologies have become increasingly unaffordable, especially in the absence of government subsidies (Van Liew *et al.* 2012).

Many of the grasslands remaining today have clearly persisted in areas where it is explicitly recognized that some semblance of the fire regimes under which these landscapes

evolved is critical for maintaining their structure and function (Lehmann and Parr 2016). But despite this recognition, widespread adoption of fire for its potential ecological benefits – whether by using prescribed burning or letting wildfires burn unchecked – is hampered by multiple concerns related to fuel loads, smoke hazards, climatic conditions, and risk to infrastructure and life. Landowners are often reluctant to use prescribed fire because of lack of labor, fear of liability, and legal impediments (Kreuter *et al.* 2019).

Case study: the US Great Plains

The Great Plains region of North America is among the most imperiled grassland biomes in the world. Stretching from southern Texas to across the Canadian border, this region at one time encompassed a continuous cover of grass, making it a paradise for biodiversity, including many iconic megafauna. The dozens of plant assemblages identified across the region may be classified under the broad descriptors of tall, mixed, and short grasses, and the locations of the prairie zones defined by each type are dictated by rainfall regimes. Over the past century, large-scale agriculture has dramatically altered the Great Plains – more than half of the area is now under cultivation; almost all of the original tallgrass prairie has disappeared; and the remaining grassland biomes are threatened by fragmentation, invasive species, and altered disturbance regimes (Perkins *et al.* 2019).

Barger *et al.* (2011) estimated that woody plants are expanding faster in the Great Plains than any other region of the US. In the southern Great Plains, for example, the South Texas Plains, the Edwards Plateau, the Rolling Plains, and the Southwestern Tablelands ecoregions are now largely woodlands despite enormous amounts of time, money, and labor that have been spent trying to reverse encroachment. To the east and north, woody plants – primarily mesquite (*Prosopis* spp) and eastern red cedar (*Juniperus virginiana*) – are expanding rapidly in the Central Great Plains and Cross Timbers ecoregions (Figure 1). Even in the Flint Hills of Kansas, where burning is an accepted and common land use practice, woody plants are invading what remains of the tallgrass prairie (Briggs *et al.* 2005).

The Great Plains region is the epicenter of US livestock production (Klemm *et al.* 2020). For this reason, WPE represents a threat not only to grassland biomes but also to the farmers and ranchers who depend on them. At the same time, other environmental changes – although not necessarily a direct threat to grassland biomes – are stressing livestock producers in the region. These include a warmer and drier climate and an increased frequency of catastrophic wildfires.

A warmer and drier climate

We can expect that the already extreme and variable climate of the Great Plains will become even more so in the future, putting additional pressure on livestock producers and rural

communities. Average annual temperatures in the southern Great Plains are projected to rise 2–3°C by mid-century, with excessive heat becoming more common (Kloesel *et al.* 2018).

Uncertainty and variability in weather is one of the greatest challenges to livestock and other agricultural enterprises, and large year-to-year changes in precipitation can have severe socioeconomic consequences. For example, a warming climate brings periodic droughts that diminish both the quality and quantity of forage, often forcing producers to reduce the number of breeding stock (Fuhlendorf *et al.* 2001). From 1994 to 2015, warmer climate conditions resulted in a 10% reduction in the protein content of cattle [*Bos taurus*] diets (Craine *et al.* 2017). Warming conditions also facilitate the proliferation of insect pests and crop diseases, shifts in species composition, and increased risk of wildfires. In addition, more frequent prolonged heat waves with higher nighttime temperatures will exacerbate animal stress, particularly among those kept in confinement (Hatfield *et al.* 2008).

Wildfire

The fire history of the Great Plains is inextricably linked to human activities. Prior to European settlement of the region, fires were common – occurring on average every 1–12 years (Stambaugh *et al.* 2014) – and usually ignited by Indigenous peoples (Pyne 2017). After settlement, the frequency of fires declined dramatically across the region due to active fire suppression, plowing of grasslands, and overgrazing (Pyne 2017). Currently, consistent with global and national trends, unintended and uncontained fires in the Great Plains are increasing in extent and frequency (Donovan *et al.* 2020). A recent analysis by Donovan *et al.* (2017) indicated that the total area burned by large (>400 ha) wildfires has quadrupled over the past 30 years. Considering that wildfire was relatively uncommon in the Great Plains 50 years ago, this change is quite remarkable and can be attributed partly to a warming climate (with longer dry spells) and partly to increases in flammable fuels, including woody plants (Stambaugh *et al.* 2017). Wildfires in this region are likely to become more frequent in the future, which will have enormous social and economic consequences – for both rural and urban areas.

Although the rise in wildfires does not represent a threat to grassland biomes, it does represent an economic threat to many livestock producers in terms of losses of forage, infrastructure, and even animals (Healy 2017). In 2017 alone, wildfire-caused losses to livestock producers in Oklahoma and Kansas amounted to almost $100 million (Morrison 2017).
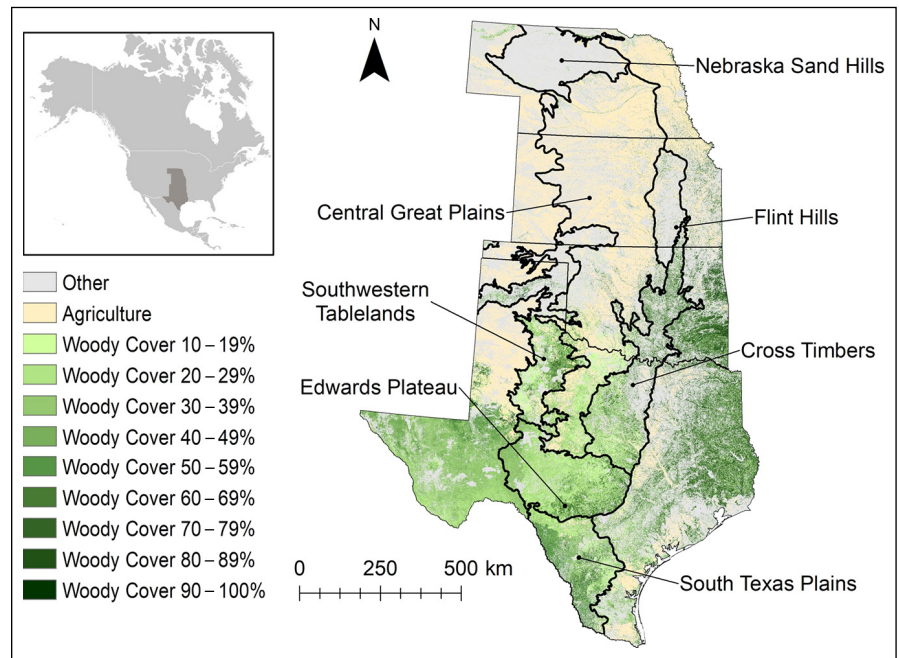

Figure 1. Major ecoregions and extent of woody plant cover over the Great Plains states of Texas, Oklahoma, Kansas, and Nebraska. Much of the present-day woody plant cover within this region has developed over the past 100 years.

Livestock production systems in the Great Plains will likely be faced with the following environmental challenges: (1) woody plants will continue to expand into grasslands and savannas – in much of Oklahoma, Kansas, and Nebraska, expansion is in its early stages and will likely accelerate, whereas in Texas, WPE has been ongoing and is already complete in some portions (Figure 1; Archer *et al.* 2017); (2) the climate will be warmer than in the past and rainfall intensities will continue to increase, even though the total amount of precipitation may be highly variable and remain within historical norms; and (3) the extent and intensity of wildfires will continue to increase, with concomitant economic consequences (Donovan *et al.* 2017).

■ The need for an alternative management paradigm

The threats of WPE, climate extremes, and wildfire bring with them a rise in risk factors for landowners and livestock producers. Effectively responding to these threats will require a different management paradigm – one that mimics the disturbance regimes under which grasslands and savannas have evolved. The evolutionary history of most grassland/savanna landscapes, especially those in North America and Africa, is one of strong linkages between herbivory (including both grazing and browsing) and fire disturbances (Fuhlendorf *et al.* 2018). In fact, these two processes are so tightly interconnected that they should be considered a single disturbance regime. Changes in both processes (the loss of browsers along with altered fire patterns) have contributed to WPE (O'Connor *et al.* 2019). In Africa, for example, Venter *et al.* (2018), on

the basis of a comprehensive evaluation of both the rates and drivers of WPE across the continent, concluded that although global and regional drivers – such as increases in CO_2, temperature, and rainfall – facilitate the expansion of woody plants, these large-scale drivers can be largely mitigated by managing fire and herbivory at the local scale.

Emerging research has identified some management strategies that are extremely promising, not only for maintaining livestock production across the Great Plains but also for increasing it (Fuhlendorf *et al.* 2017). Examples include pyric herbivory and mixed-species grazing. Both strategies, especially if used in combination, limit WPE: pyric herbivory enhances forage quality and increases heterogeneity through the synergistic application of prescribed fire and managed grazing, while mixed-species grazing, by incorporating more browsers, increases animal production potential through the diversification of herbivore functional guilds. In addition, both strategies buffer livestock producers from the effects of climate variability and climate extremes. Pyric herbivory leads to higher spatial heterogeneity of vegetation, which lessens the effects of rainfall variability over time, and has also been shown to reduce fuel loads on rangelands, leading to greater resilience to wildfire (Starns *et al.* 2019). Mixed-species grazing (specifically, the addition of goats [*Capra* spp]) lessens the vulnerability of animal production systems to climate extremes (Klemm *et al.* 2020).

Pyric herbivory

The essence of pyric herbivory is grazing that is driven by fire (Figure 2). It is the synergistic combination of patch burning and grazing that creates a shifting mosaic of out-of-phase landscape patches (newly burned, recently burned with regrowth, and unburned areas), thereby increasing landscape heterogeneity (variability in vegetation structure at the patch scale) (Fuhlendorf *et al.* 2017). The underlying mechanism is that when herbivores are free to roam, the phenomena of fire and herbivory become spatially and temporally interdependent. Because grazing animals spend most of their time foraging in recently burned patches with regrowth (Figure 3) and largely ignore patches that have not been burned, fire and grazing disturbances can be localized, which allows for greater accumulation of herbaceous biomass in unburned patches than appears to be possible under traditional grazing practices.

A major benefit of pyric herbivory, and of regular fire occurrence in general, is that it maintains more open grasslands (Fuhlendorf *et al.* 1996; Fuhlendorf and Smeins 1997; Twidwell *et al.* 2013) and can even destroy more mature woody plants (Twidwell *et al.* 2012). The effectiveness of fire in controlling woody plants depends on myriad factors, including burn intensity and season, as well as the species, age, and density of woody plants (Ansley *et al.* 2008).
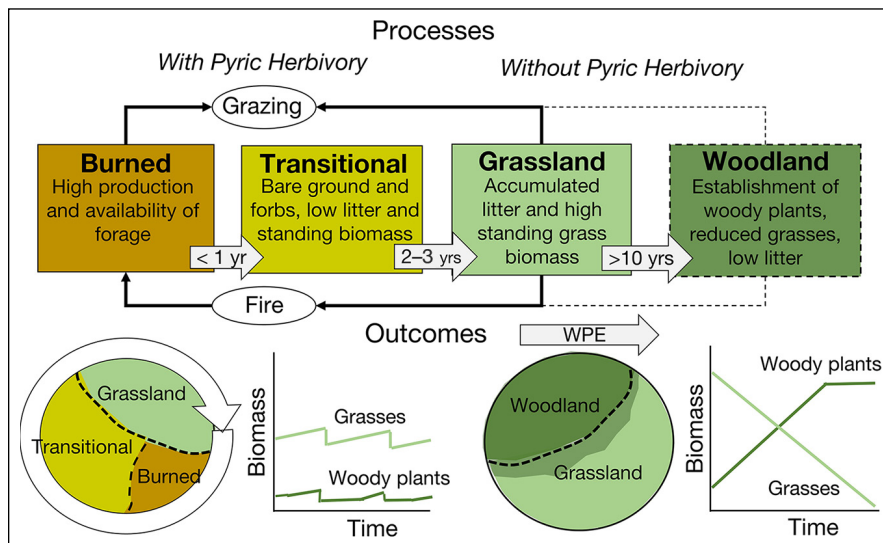
In addition, pyric herbivory promises to be an effective strategy for resolving the "fuel versus forage" paradox (that is, grass biomass can be one or the other but not both) brought about by the traditional management practice of treating fire and grazing as independent disturbances (Fuhlendorf *et al.* 2009; Allred *et al.* 2011). Pyric herbivory, by coupling fire and grazing, minimizes this paradox because grazing animals will prefer recently burned areas for the higher nutritive value of the forage (Hempson *et al.* 2015). Because burned areas are more heavily grazed, areas that are unburned, lightly grazed, or ungrazed are able to recover from past grazing and produce sufficient fuel for future fires that would keep woody plants in check. By reducing fuel loads, pyric herbivory also reduces the chances of catastrophic wildfires (Starns *et al.* 2019).

The net result is a fully functioning and resilient landscape that provides habitat for a wide variety of savanna-obligate species that have contrasting habitat requirements. Analysis of grassland birds, insects, and small mammals suggests that some species of these groups depend on recent

Figure 2. Conceptual model of rangeland vegetation processes and outcomes with and without pyric herbivory. With pyric herbivory (solid lines in top section), periodic fire limits the recruitment and establishment of woody plants. Herbivores preferentially graze in recently burned areas, enabling fine fuels necessary for fire to accumulate in less-grazed grassland patches. The outcome of this process is a landscape of vegetation in different stages of succession, which is driven by the spatial and temporal scale of past fire and grazing (pyric herbivory). Without pyric herbivory (dashed lines in top section), woody plants gradually but inexorably outcompete herbaceous vegetation. As woody plant abundance increases, grazing pressure on the remaining grass patches increases and the fine fuels necessary for fire no longer accumulate. As this transition occurs, the linkages between fire and grazing are broken, and become increasingly difficult to restore. WPE = woody plant encroachment.

disturbance, whereas other species depend on less disturbed habitat (Fuhlendorf and Engle 2004; Fuhlendorf *et al*. 2006), suggesting that pyric herbivory promotes and sustains biotic diversity.

Mixed-species grazing

Mixed-species grazing (two or more types of herbivores grazing together) is most efficient when combinations of grazers and browsers are used. Grazers primarily consume herbaceous plants, whereas browsers mainly consume shrubs and trees, thereby relieving grazing pressure on grasses; this relatively small overlap in diet ensures maximum niche separation (Fraser and Garcia 2018).

Grassy biomes with a woody component, which are highly heterogeneous in species composition and vegetation structure, are ideally suited for mixed-species grazing. A theoretical foundation for our understanding of the dynamics and benefits of mixed-species grazing comes from studies of African savannas, where a large number of diverse herbivores share a common resource (McNaughton 1985). Similarly, North American grasslands evolved under disturbance regimes that included both grazing and browsing by a rich suite of herbivores, including bison (*Bison bison*), elk (*Cervus canadensis*), deer (*Odocoileus* spp), and pronghorn antelope (*Antilocapra americana*). In recent times, however, most of the Great Plains has been grazed by a single type of livestock (cattle) and browsing has been dramatically curtailed (O'Connor *et al*. 2019). We contend that a large-scale return to mixed-species grazing – specifically, incorporating goats into cattle operations – would bring substantial economic as well as ecological benefits, including (1) improved animal performance, (2) increases in production and efficiency of grazing, (3) economic diversification, (4) increased resilience to climate extremes, and (5) biological control of woody plants (Allred *et al*. 2014; Fraser and Garcia 2018).

Some areas of the Great Plains, such as the Edwards Plateau and Trans Pecos ecoregions of Texas, have a long history of grazing cattle, sheep (*Ovis* spp), and goats (Wilcox *et al*. 2012). This grazing management practice originated and became popular for multiple reasons, including the ability of sheep and goats to better utilize the native vegetation in the more rugged terrain zones of these ecoregions, while also producing non-perishable commodities (wool and mohair) that can be transported from remote areas to markets. Mixed-species grazing was popular in these ecoregions from the time of European settlement until the 1960s, when a combination of low commodity prices, labor shortages, and increased predation led to a steady decline of sheep and goats in the mix and a concomitant increase in woody plant cover (Walker *et al*. 2005). Walker (1994) calculated that mixed-species grazing by cattle and goats could increase the carrying capacity of the land by 70% (because cattle and goats have less dietary overlap than cattle and sheep), and Fraser and Garcia (2018) estimated that this

Figure 3. Because animals will selectively graze recently burned patches, owing to their higher forage quality, pyric herbivory maximizes landscape heterogeneity, which can increase and stabilize livestock production.

grazing method can increase livestock production by at least 20% compared with single-species grazing.

In addition to improving carrying capacity and animal protein production, mixed-species grazing with goats can reduce WPE (Taylor 2008) and increase production of herbaceous forage (Figure 4), especially graminoids (Luginbuhl *et al*. 1998). Furthermore, combining goat browsing with fire can have a synergistic effect by controlling Ashe (blueberry) juniper (*Juniperus ashei*) and redberry juniper (*Juniperus pinchotii*) (Taylor 2008).

Although the advantages of mixed-species grazing have been recognized by both academic researchers and ranchers having a longstanding history of grazing goats, adoption of the practice has been slow for several reasons – including predation by coyotes (*Canis latrans*), traditional prejudices regarding small ruminants, lack of education, and commodity price fluctuations (Walker 1994). However, with commodity prices currently favoring small ruminants, the US importing more sheep and goat meat than it produces, and many rangelands being taken over by new landowners who may be more open to

Figure 4. Incorporating mixed species into rangeland-based animal production systems can help control woody plants and increase animal production.

Panel 1. Coupling of fire and grazing

Over the past century, the dominant rangeland management strategy has emphasized grazing by a single type of herbivore along with fire suppression (Figure 5, quadrant III). Adopting a mixed-species strategy that incorporates both grazers and browsers will slow the progression of woody plant encroachment (WPE; Figure 5, quadrant IV). Still greater conservation benefits are achievable by using fire synergistically with grazing (pyric herbivory; Fuhlendorf *et al.* 2009), and this is true even with a single type of herbivore (Figure 5, quadrant I). However, single-herbivore operations are less resilient to WPE than a mix of grazers and browsers (Twidwell *et al.* 2019). Before the introduction of modern grazing systems, grassland biomes featured a robust and diverse herbivore community that included bison (*Bison bison*), elk (*Cervus canadensis*), pronghorn antelope (*Antilocapra americana*), prairie dogs (*Cynomys* spp), and other animals, most of which selectively forage from recently burned areas (Figure 5, quadrant II). In the same way, management systems that strengthen feedbacks between fire and multiple herbivore types lead to higher conservation value, increased animal production, and improved grassland resilience to WPE (Fuhlendorf *et al.* 2012).

using goats (Duhigg 2012), it is an opportune time to promote these natural-disturbance-regime management practices.

For maximum benefit and effect, the two strategies of pyric herbivory and mixed-species grazing must be tightly coupled (see Panel 1). We maintain that if this combination of strategies were to be widely adopted, rangeland production systems in the Great Plains would be more profitable, productive, sustainable, and beneficial to society at large.

■ The way forward

We recognize that changing the land use/management culture across an entire region is an enormous challenge. Rangeland managers in general are risk-averse and slow to embrace alternative management strategies, especially those that have not been widely adopted or endorsed. With respect to the use of prescribed fire, numerous impediments have been identified, including fear of liability, unfavorable government policies, lack of knowledge and equipment, and negative attitudes toward fire (Twidwell *et al.* 2019). However, we believe that these impediments are not insurmountable, especially if more enlightened and favorable government policies are enacted at local, regional, and national levels. Land-grant universities can also play a pivotal role, by fostering integrated research, extension, and education programs aimed at overcoming social barriers to the use of prescribed fire and mixed-species grazing.
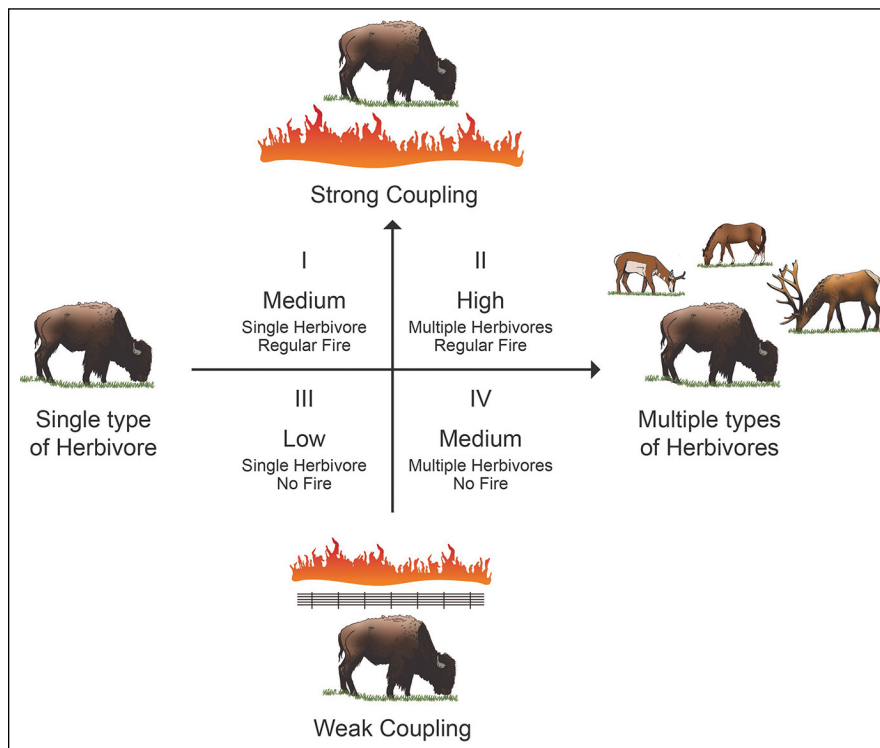
These targeted initiatives should creatively engage stakeholder groups across the region, including current and future land managers, natural resource professionals, producers, prescribed burn associations, conservation groups, state and local governments, and the general public in both rural and urban areas. The ultimate objective of such programs would be the improvement of rangeland condition by slowing and even reducing the coverage of woody plants, while at the same time helping rangeland-based production systems become more productive, profitable, and resilient to environmental stressors. Concomitantly, these changes would contribute to meeting many of the UN Sustainable Development Goals.

The reality remains, however, that if productive rangelands are to be maintained in the Great Plains region, fire as a management tool must be implemented on a regional scale and used synergistically with mixed-species grazing. As demonstrated by our collective responses to past environmental disasters in the Great Plains – such as the Dust Bowl in the 1930s and systemic overgrazing at the turn of the 20th century – we can reverse the current environmental degradation of this region through a combination of science-based

Figure 5. Rangeland management based on pyric herbivory can be viewed as a continuum that relates the number of herbivores to the strength of the fire–grazer coupling. The horizontal axis represents the extent to which multispecies herbivory occurs, and the vertical axis represents the extent to which fire occurs. High, Medium, and Low in the four quadrants indicate the level of conservation value (biodiversity, patch-scale heterogeneity, forage production and quality, and so forth).

management practices, public awareness, and enlightened agricultural policy.

Acknowledgements

References

Allred BW, Fuhlendorf SD, and Hamilton RG. 2011. The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle. *Ecosphere* **2**: 26.

Allred BW, Scasta JD, Hovick TJ, *et al*. 2014. Spatial heterogeneity stabilizes livestock productivity in a changing climate. *Agr Ecosyst Environ* **193**: 37–41.

Anderson RC. 2006. Evolution and origin of the Central Grassland of North America: climate, fire, and mammalian grazers. *J Torrey Bot Soc* **133**: 626–47.

Ansley RJ, Pinchak WE, and Jones DL. 2008. Mesquite, tobosagrass, and common broomweed responses to fire season and intensity. *Rangeland Ecol Manag* **61**: 588–97.

Archer SR, Anderson EM, Predick KI, *et al*. 2017. Woody plant encroachment: causes and consequences. In: Briske DD (Ed). Rangeland systems: processes, management and challenges. Cham, Switzerland: Springer.

Archer SR, Boutton TW, Hibbard KA, *et al*. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Shulze E-D, Heimann M, Harrison S, *et al*. (Eds). Global biogeochemical cycles in the climate system. Cambridge, MA: Academic Press.

Archer SR, Davies KW, Fulbright TE, *et al*. 2011. Brush management as a rangeland conservation tool: a critical evaluation. In: Briske DD (Ed). Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps. Washington, DC: US Department of Agriculture.

Archibald S, Bond WJ, Hoffmann W, *et al*. 2020. Distribution and determinants of savannas. Chichester, UK: John Wiley & Sons.

Barger NN, Archer SR, Campbell JL, *et al*. 2011. Woody plant proliferation in North American drylands: a synthesis of impacts on ecosystem carbon balance. *J Geophys Res-Biogeo* **116**: G00K07.

Basant S, Wilcox BP, Leite PAM, and Morgan C. 2020. When savannas recover from overgrazing, ecohydrological connectivity collapses. *Environ Res Lett* **15**: 054001.

Bond WJ and Parr CL. 2010. Beyond the forest edge: ecology, diversity and conservation of the grassy biomes. *Biol Conserv* **143**: 2395–404.

Briggs JM, Knapp AK, Blair JM, *et al*. 2005. An ecosystem in transition. Causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* **55**: 243–54.

Briske DD, Bestelmeyer BT, Brown JR, *et al*. 2016. Assessment of USDA-NRCS rangeland conservation programs: recommendation

for an evidence-based conservation platform. *Ecol Appl* **27**: 94–104.

Craine JM, Elmore A, and Angerer JP. 2017. Long-term declines in dietary nutritional quality for North American cattle. *Environ Res Lett* **12**: 044019.

Ding JY, Travers SK, Delgado-Baquerizo M, and Eldridge DJ. 2020. Multiple trade-offs regulate the effects of woody plant removal on biodiversity and ecosystem functions in global rangelands. *Glob Change Biol* **26**: 709–20.

Donovan VM, Wonkka CL, and Twidwell D. 2017. Surging wildfire activity in a grassland biome. *Geophys Res Lett* **44**: 5986–93.

Donovan VM, Wonkka CL, Wedin DA, and Twidwell D. 2020. Land-use type as a driver of large wildfire occurrence in the US Great Plains. *Remote Sens-Basel* **12**: 1869.

Duhigg TS. 2012. The power of habit: why we do what we do in life and business. New York, NY: Random House.

Eldridge DJ, Bowker MA, Maestre FT, *et al*. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecol Lett* **14**: 709–22.

Fraser MD and Garcia RR. 2018. Mixed-species grazing management to improve sustainability and biodiversity. *Rev Sci Tech OIE* **37**: 247–57.

Fuhlendorf SD and Engle DM. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *J Appl Ecol* **41**: 604–14.

Fuhlendorf SD and Smeins FE. 1997. Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus-Quercus* savanna. *J Veg Sci* **8**: 819–28.

Fuhlendorf SD, Briske DD, and Smeins FE. 2001. Herbaceous vegetation change in variable rangeland environments: the relative contribution of grazing and climatic variability. *Appl Veg Sci* **4**: 177–88.

Fuhlendorf SD, Davis CA, Elmore RD, *et al*. 2018. Perspectives on grassland conservation efforts: should we rewild to the past or conserve for the future? *Philos T Roy Soc B* **373**: 20170438.

Fuhlendorf SD, Engle DM, Elmore RD, *et al*. 2012. Conservation of pattern and process: developing an alternative paradigm of rangeland management. *Rangeland Ecol Manag* **65**: 579–89.

Fuhlendorf SD, Engle DM, Kerby J, and Hamilton R. 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conserv Biol* **23**: 588–98.

Fuhlendorf SD, Fynn RWS, McGranahan DA, and Twidwell D. 2017. Heterogeneity as the basis for rangeland management. In: Briske DD (Ed). Rangeland systems: processes, management and challenges. Cham, Switzerland: Springer.

Fuhlendorf SD, Harrell WC, Engle DM, *et al*. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecol Appl* **16**: 1706–16.

Fuhlendorf SD, Smeins FE, and Grant WE. 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. *Ecol Model* **90**: 245–55.

Hatfield J, Boote K, Fay PA, *et al*. 2008. Agriculture. In: The effects of climate change on agriculture, land resources, water resources, and biodiversity. Washington, DC: US Climate Change Science Program and Subcommittee on Global Change Research.

Healy J. 2017. Burying their cattle, ranchers call wildfires 'Our Hurricane Katrina'. *New York Times*. March 20.

Hempson GP, Archibald S, Bond WJ, *et al.* 2015. Ecology of grazing lawns in Africa. *Biol Rev* **90**: 979–94.

Hutley LB and Setterfield SA. 2008. Savanna. In: Jorgensen SE (Ed). Ecosystem ecology. Amsterdam, the Netherlands: Elsevier.

Klemm T, Briske DD, and Reeves MC. 2020. Vulnerability of rangeland beef cattle production to climate-induced NPP fluctuations in the US Great Plains. *Glob Change Biol* **26**: 4841–53.

Kloesel K, Bartush B, Banner JL, *et al.* 2018. Southern Great Plains. In: Reidmiller DR, Avery CW, Easterling DR, *et al.* (Eds). Impacts, risks, and adaptation in the United States: Fourth National Climate Assessment, vol II. Washington, DC: US Global Change Research Program.

Kreuter UP, Stroman DA, Wonkka CL, *et al.* 2019. Landowner perceptions of legal liability for using prescribed fire in the Southern Plains, United States. *Rangeland Ecol Manag* **72**: 959–67.

Lehmann CER and Parr CL. 2016. Tropical grassy biomes: linking ecology, human use and conservation. *Philos T Roy Soc B* **371**: 20160329.

Luginbuhl JM, Harvey TE, Green JT, *et al.* 1998. Use of goats as biological agents for the renovation of pastures in the Appalachian region of the United States. *Agroforest Syst* **44**: 241–52.

McNaughton SJ. 1985. Ecology of a grazing ecosystem – the Serengeti. *Ecol Monogr* **55**: 259–94.

McPherson GR. 1997. Ecology and management of North American savannas. Tucson, AZ: University of Arizona Press.

Mishra NB and Young KR. 2020. Savannas and grasslands. In: Wang Y (Ed). The handbook of natural resources: terrestrial ecosystems and biodiversity. Abingdon-on-Thames, UK: Taylor & Francis Group.

Morrison O. 2017. Damage from historic wildfires more than $80 million. *Wichita Eagle*. June 16.

O'Connor RC, Taylor JH, and Nippert JB. 2019. Browsing and fire decreases dominance of a resprouting shrub in woody encroached grassland. *Ecology* **101**: e02935.

Parr CL, Lehmann CER, Bond WJ, *et al.* 2014. Tropical grassy biomes: misunderstood, neglected, and under threat. *Trends Ecol Evol* **29**: 205–13.

Perkins LB, Ahlering M, and Larson DL. 2019. Looking to the future: key points for sustainable management of northern Great Plains grasslands. *Restor Ecol* **27**: 1212–19.

Pyne SJ. 2017. The Great Plains: a fire survey. Tucson, AZ: University of Arizona Press.

Sala OE and Maestre FT. 2014. Grass–woodland transitions: determinants and consequences for ecosystem functioning and provisioning of services. *J Ecol* **102**: 1357–62.

Stambaugh MC, Creacy G, Sparks J, and Rooney M. 2017. Three centuries of fire and forest vegetation transitions preceding Texas' most destructive wildfire: Lost Pines or lost oaks? *Forest Ecol Manag* **396**: 91–101.

Stambaugh MC, Sparks JC, and Abadir ER. 2014. Historical pyrogeography of Texas, USA. *Fire Ecol* **10**: 72–89.

Starns HD, Fuhlendorf SD, Elmore RD, *et al.* 2019. Recoupling fire and grazing reduces wildland fuel loads on rangelands. *Ecosphere* **10**: e02578.

Taylor CA. 2008. Ecological consequences of using prescribed fire and herbivory to manage *Juniperus* encroachment. In: Van Auken OW (Ed). Western North America *Juniperus* communities: a dynamic vegetation type. New York, NY: Springer-Verlag.

Twidwell D, Rogers WE, Fuhlendorf SD, *et al.* 2013. The rising Great Plains fire campaign: citizens' response to woody plant encroachment. *Front Ecol Environ* **11**: E64–71.

Twidwell D, Rogers WE, McMahon EA, *et al.* 2012. Prescribed extreme fire effects on richness and invasion in coastal prairie. *Invas Plant Sci Mana* **5**: 330–40.

Twidwell D, Wonkka CL, Wang HH, *et al.* 2019. Coerced resilience in fire management. *J Environ Manage* **240**: 368–73.

Van Liew D, Conner JR, Kreuter UP, and Teague R. 2012. An economic comparison of prescribed extreme fire and alternative methods for managing invasive brush species in Texas: a modeling approach. *Open Agriculture J* **6**: 17–26.

Veldman JW, Buisson E, Durigan G, *et al.* 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. *Front Ecol Environ* **13**: 154–62.

Venter ZS, Cramer MD, and Hawkins HJ. 2018. Drivers of woody plant encroachment over Africa. *Nat Commun* **9**: 7.

Walker JW. 1994. Multispecies grazing: the ecological advantage. *Sheep Res J* **Special Issue**: 52–54.

Walker JW, Johnson J, and Taylor CA. 2005. Challenges and opportunities for sustainable rangeland pastoral systems. In: Milne BT (Ed). Pastoral systems in marginal environments. Wageningen, the Netherlands: Wageningen Academic Publishers.

Wilcox BP, Birt A, Archer SR, *et al.* 2018. Viewing woody-plant encroachment through a social–ecological lens. *BioScience* **68**: 691–705.

Wilcox BP, Sorice MG, Angerer J, and Wright CL. 2012. Historical changes in stocking densities on Texas rangelands. *Rangeland Ecol Manag* **65**: 313–17.

Yahdjian L, Sala OE, and Havstad KM. 2015. Rangeland ecosystem services: shifting focus from supply to reconciling supply and demand. *Front Ecol Environ* **13**: 44–51.