

## Opinion piece



**Cite this article:** Fuhlendorf SD, Davis CA, Elmore RD, Goodman LE, Hamilton RG. 2018 Perspectives on grassland conservation efforts: should we rewild to the past or conserve for the future? *Phil. Trans. R. Soc. B* **373**: 20170438.  
<http://dx.doi.org/10.1098/rstb.2017.0438>

Accepted: 12 September 2018

One contribution of 16 to a theme issue 'Trophic rewilding: consequences for ecosystems under global change'.

**Subject Areas:**  
ecology

**Keywords:**  
conservation, bison, grazing, biodiversity, fire, Pleistocene rewilding

**Author for correspondence:**  
Samuel D. Fuhlendorf  
e-mail: [sam.fuhlendorf@okstate.edu](mailto:sam.fuhlendorf@okstate.edu)

# Perspectives on grassland conservation efforts: should we rewild to the past or conserve for the future?

Samuel D. Fuhlendorf<sup>1</sup>, Craig A. Davis<sup>1</sup>, R. Dwayne Elmore<sup>1</sup>,  
Laura E. Goodman<sup>1</sup> and Robert G. Hamilton<sup>2</sup>

<sup>1</sup>Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078, USA

<sup>2</sup>Tallgrass Prairie Preserve, The Nature Conservancy, Pawhuska, OK 74056, USA

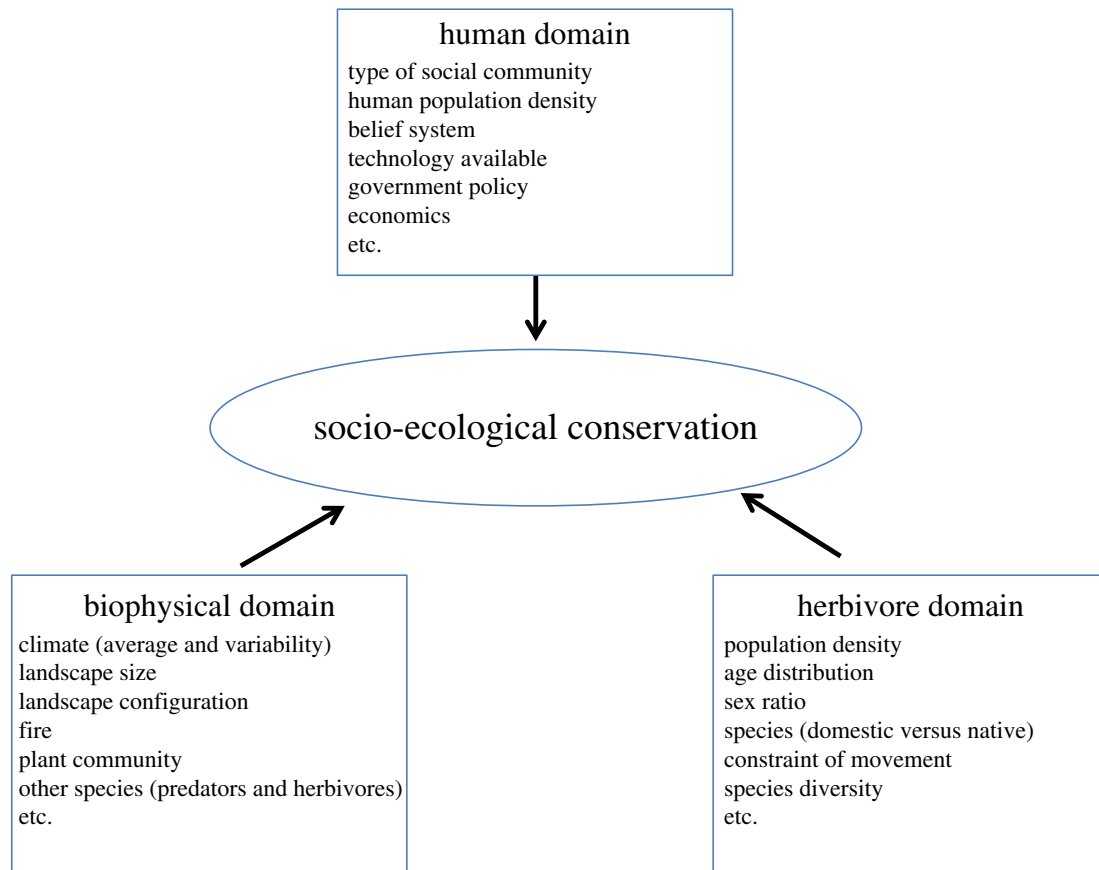
SDF, 0000-0002-8726-9402

Grasslands are among the most imperilled biomes of the world. Identifying the most appropriate framework for restoring grasslands is dependent on the objectives of restoration, which is inherently determined by human priorities. Debates over the appropriate conservation model for grasslands have often focused on which species of herbivores should be the focus of restoration efforts. Here we discuss three perspectives of herbivore-based conservation in North American grasslands. First, the Pleistocene rewilding perspective is based upon the idea that early humans contributed to the demise of megafauna that were important to the evolution and development of many of North America's grasslands; therefore, their aim of restoration is rewilding of landscapes to pre-human times. Second, the bison rewilding perspective considers American bison a keystone herbivore that is culturally and ecologically important to North American grasslands. A third perspective focuses on restoring the pattern and processes of herbivory on grasslands and is less concerned about which herbivore is introduced to the landscape. We evaluate each of these three conservation perspectives in terms of a framework that includes a human domain, an herbivore domain and a biophysical domain. While all conservation perspectives partly address the three domains, they all fall short in key areas. Specifically, they fail to recognize that past, current and future humans are intimately linked to grassland patterns and processes and will continue to play a role in structuring grasslands. Furthermore, these perspectives seem to only superficially consider the role of fragmentation and climate change in influencing grassland patterns and processes. As such, we argue that future grassland conservation efforts must depend on the development of a model that better integrates societal, economic and policy objectives and recognizes climate change, fragmentation and humans as an integral part of these ecosystems.

This article is part of the theme issue 'Trophic rewilding: consequences for ecosystems under global change'.

## 1. Introduction

Conservation of North American grasslands, including restoring natural disturbance regimes and rewilding landscapes with mega-herbivores or their surrogates, has been a popular topic in ecology [1,2]. As conservation has developed as its own discipline, specific approaches, objectives and targets have also evolved. Conceptual conservation models range in perspectives from those that are integrated with current conditions to perspectives that are naive to current landscapes and based on retrospective target conditions that are uncertain at best. Much of the discussion around the most appropriate approach has focused on the importance of large herbivores, as well as other disturbances in the evolution and development of flora and fauna on these landscapes [3,4]. A primary practical question of the conservation community has been: which herbivore is



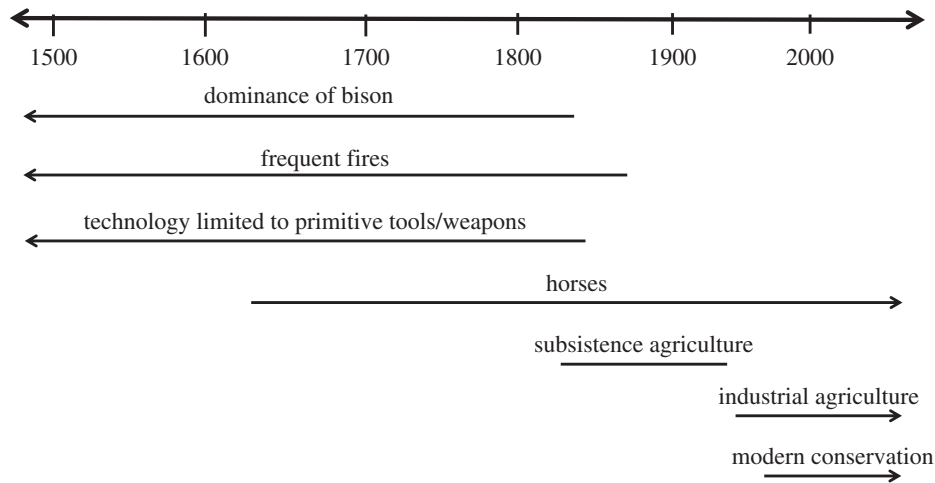
**Figure 1.** A simplistic organizational framework to evaluate the socio-ecological conservation of North American grasslands. (Online version in colour.)

best for restoration? Prior to approximately 15 000 years ago, mega-herbivores were dominant on these landscapes until early humans contributed to their extinctions leading to their replacement by the modern American bison (*Bison bison*, hereafter bison) [5]. Until the near extirpation of bison in the late 1800s, they were keystone herbivores within the Great Plains, sharing complex landscapes with other herbivores, predators and humans for nearly 10 000 years [4,6,7]. The vast and complex landscapes that contained diverse herbivores have in most places been replaced by fragmented agricultural lands where domestic cattle are the dominant grazers on remnant grasslands. Simultaneously, many obligate grassland species declined such that now they are considered imperilled. As North American grasslands continue to decline in cover and many remnants become degraded, it is increasingly important that we evaluate conservation models through a conceptual framework that guides our conservation practices. In particular, conservation of not only grasslands, but all ecosystems, requires a perspective that recognizes that these environments are highly variable in space and time such that the complexity of the system can overwhelm our understanding of the important drivers of patterns and processes in these ecosystems [1,8]. This is even more of a challenge for conservation of grasslands that are commonly being used for agricultural and energy production. Consequently, it is a challenge for conservation to achieve the vision necessary to restore and/or maintain grassland ecosystems, but also remain practical with modern society and the requirements of agricultural and energy production.

As evidenced by the degradation that included the loss of large native herbivores and replacement with domestic livestock, a focus on restoring an appropriate herbivore for a

restoration context is important for both the conservation of the herbivore species as well as their recognized role in conserving biodiversity broadly. Unfortunately, many other changes were concomitant with the replacement of native with domestic herbivores (e.g. landscape fragmentation, woody plant encroachment, alteration of fire regimes, cultural demand on natural resources). For this paper, we focus on describing three primary perspectives of herbivore-based conservation of North American grasslands that have been proposed and discuss the challenges of incorporating these perspectives in future grassland conservation efforts. First, we consider the Pleistocene rewilding perspective that suggests early humans contributed to the demise of megafauna that were important to the evolution and development of many of the grasslands in North America [9,10]. Second, we focus on a dominant perspective in North America of bison restoration and rewilding that considers American bison a keystone herbivore that is culturally and ecologically important to North American grasslands [6,11]. Lastly, we discuss a perspective that is less focused on the question of which herbivore to include, but more focused on restoring the pattern and processes of herbivory on grassland landscapes [12,13].

Conservation is clearly a human endeavour that is critically dependent on cultural values, policy, economics and other aspects of social sciences. A fundamental objective of our focus on the three ecological perspectives of grassland conservation is to highlight the need of a more integrated socio-ecological approach for restoration and conservation of grasslands that includes clearly stated objectives and includes the human, biophysical and herbivore domains (figure 1). We do not intend to develop a comprehensive socio-ecological framework for conservation of grasslands and we



**Figure 2.** Timeline of the numerous changes that have occurred on the socio-ecological landscape of the North American Great Plains.

question whether a single framework is even appropriate. Before discussing the conservation perspectives, we briefly describe the types of changes that have occurred in the three domains (human, biophysical and herbivore) over the past 15 000 years in North American grasslands to highlight the challenges of restoring/rewilding these landscapes. By evaluating the dynamics within these domains, we stress the importance of explicitly stating conservation objectives and targets. Then, we discuss the conservation perspectives in relation to the changes that have occurred in the domains. Finally, we propose some critical considerations for future conservation efforts of North American grasslands and include some examples of perspectives that have been applied. We hope to highlight that critical questions must be addressed prior to developing a conservation model that include the following. Should rewilding focus on dominant herbivores or plant communities or ecological processes? Is the conservation objective focused on biodiversity, maintaining ecosystem functions or providing societal goods and services? How important is selecting the 'proper' herbivore or 'proper' target date of our conservation efforts? What is the role of humans in the model system that is our conservation target? Is there one model that is most appropriate? Are there models that are not appropriate? It is only through answering each of these questions that we can develop specific and explicit conservation objectives that will lead to successful conservation strategies for North American grasslands.

## 2. Human domain

Conservation, rewilding, restoration and degradation of ecosystems are all human endeavours and any model or perspective that insufficiently addresses this reality will face insurmountable challenges. Most conservationists recognized the role of humans in the past century or two in contributing to the loss and degradation of grasslands but there is less recognition of the importance of humans in the management of these landscapes prior to European settlement. In fact, humans have played a significant role in the development, maintenance and degradation of North American grasslands for over 10 000 years (figure 2). Human culture in the North American Great Plains has been variable in space and time but generally transitioned from mostly hunter-gatherers to European settlers who were largely focused on subsistence

agriculture. This European dominance eventually transitioned to industrial agricultural landscapes where grasslands were small remnants of their historical vastness.

Modern Native Americans are descendants of Siberians who crossed the Bering Land Bridge at least approximately 14 600 years ago [14]. Early Clovis hunters are most often associated with the extirpation of 35 genera of large mammals in North America at approximately 11 000 years ago [15,16]. The demise of these large mammals occurred simultaneously with changes in climate that resulted in a complex interaction that ultimately resulted in the dominance of smaller herbivores in North America [5]. The dominance of American bison coincided with an increase in human populations and increased use of fire, which was the primary landscape management tool for many indigenous people [17,18]. Though there was a high degree of variability in the effects of Native Americans on North American grasslands, it is clear that the descendants of Siberian explorers and their use of fire and early agriculture had a large influence on North American landscapes for over 10 000 years and influenced the structure and function of grassland ecosystems that were first encountered by early European settlers [19]. Therefore, any discussion of rewilding that does not fully account for the role of humans, including hunting and fire, in shaping plant and animal assemblages is grossly incomplete and naive.

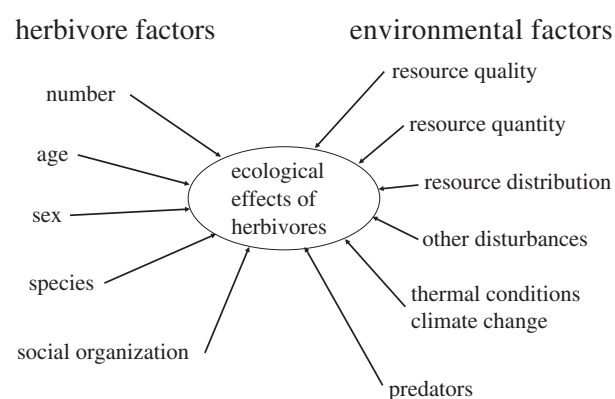
Over the past 500 years, it is difficult to disentangle the biophysical changes in North America from the cultural changes (figure 2). Generalizations are challenging because the social changes were complex and heterogeneous in space and time, but the most significant changes started when Europeans began exploring and eventually settling North America resulting in a blend of cultural contact and colonialism [20]. Initially, the arrival of the first Europeans brought horses and novel diseases which greatly altered the indigenous human population and their use of the landscape. Early accounts of explorers lead to contentious debates but in general it is likely that Native Americans had a substantial influence on the distribution and abundance of herbivores throughout much of North America even when human population densities were relatively low [21,22]. With the eventual settlement of most of the United States, all that was considered 'wild' was not tolerated and agriculture would forever alter these grassland landscapes and the species that occurred on them. Initially, much of agriculture was subsistence-based but in the first half of the 1900s,

industrial agriculture developed. Eventually, agricultural intensification occurred and large areas were settled and many of the grasslands were cultivated. Environmental events, such as the Dust Bowl of the 1930s, and social policies influencing agricultural economics and production resulted in land use and population dynamics that included land abandonment and declining human populations in some regions that were formerly dominated by grasslands. More recently, agricultural policy has promoted the conversion of marginal cropland back to grassland, but these landscapes remain highly fragmented [23] and the vast majority of many of these grasslands, such as the Great Plains, remain privately owned and managed for agriculture and energy development.

In response to many of the agricultural and land use changes, the human endeavour of conservation started in the mid-1900s with a utilitarian perspective prevalent through much of the 1900s [1,13]. Many of the early conservation efforts on grasslands were focused on reducing intense grazing and creating more moderate and uniform grasslands. Remnant grasslands were often managed homogeneously to promote the dominant forage species and maintain long-term agricultural production. The important attention to conservation of biodiversity, pattern and processes of ecosystems, and rewilding landscapes did not appear until recent decades. Early and current efforts focused on managing all grasslands for moderate grazing to minimize intense disturbance has had a negative effect on agricultural production and biodiversity [10,24]. Studies of management that promotes heterogeneity indicate that grazing of bison or domestic livestock can be managed for restoring and enhancing biodiversity while maintaining profitable levels of animal production [12,25,26]. Our recent understanding of the effects of land management suggests that herbivores can be used to create heterogeneity and that biodiversity of these landscapes is highly dependent on spatial patterns that include areas that have been heavily grazed and areas with little or no grazing. This suggests that humans, and their variable application of different management practices, may be the most important variable in predicting the impacts of herbivores on contemporary grasslands, which we will expand upon in subsequent sections.

### 3. Herbivore domain

A major focus of the conservation community has been on the importance of selecting the appropriate dominant herbivore species [2,27]. Short of a fairly recent proposal to reintroduce surrogates to mega-herbivores and the Pleistocene rewilding, the majority of the discussion is focused on the debate about the importance of bison versus domestic cattle on conservation landscapes. This debate includes natural history perspectives as well as the potential of whether cattle can be used as a surrogate species. Clear differences in the life history of these species suggest that differences could be expected. A recent survey of literature (2009) identified 87 papers that compared bison with cattle, yet only nine focused on the comparison in an ecological context and only two attempted to control other socio-ecological factors [27–29]. As late as 2009, there were no peer-reviewed studies that directly compared bison and cattle on large complex landscapes (greater than 300 ha). Since then, several studies



**Figure 3.** A conceptual model illustrating the complexity of variables that can modify the effects of any herbivore population. Humans can be considered within this model or they can be involved through making management decisions that modify both herbivore and environmental factors.

have attempted the comparison with variable levels of control in terms of the socio-ecological context [2,30,31]. Conclusions from these studies in the context of conservation and rewilding are difficult and often infused with dogma and casual observations. It is difficult from the research literature to draw many consistent conclusions, but in general there are subtle differences in diets and feeding behaviour and some substantial differences in the use of complex landscapes associated with thermal heterogeneity [32]. It is unclear how relevant these differences would be from a broad conservation perspective, but when restricted to small landscapes, reported differences in the scientific literature are minimal. Further, lack of clear objectives and outcomes from the conservation community make the limited evidence of differences between these herbivores all but irrelevant for predictive purposes.

While differences and similarities between bison and cattle may exist (or for any other species as well), the focus on these differences could be a distraction from a conservation perspective if we fail to evaluate the ecological effects of the two species. Any differences between these species, or potentially other species, may be overwhelmed by differences in management styles that often accompany them and are associated with the human domain (figure 3) [27,29]. For example, cattle herds are typically associated with ranches that are managed for optimum commodity production. This type of operation commonly relies on herds where animals are separated for most of the year on the basis of sex and age (e.g. cow-calf, stocker steers) and the sex ratio is often highly skewed depending on the objective. Additionally, cattle ranches often use general animal husbandry practices (e.g. supplemental feeding and minerals) and land management practices that homogenize the landscape. These landscapes are often heavily cross-fenced with extensive water development and potentially managed to increase the dominance of a few key forage species [13]. Bison may be managed as production herds as well, but are also managed as conservation-focused herds on preserves or refuges. Production/commodity systems with bison are often managed in a way similar to cattle systems, allowing for effective comparison in that simplified environment. Preserves focused on conservation may manage their bison herds as wildlife or livestock, but typically much less intensively than production systems. Cattle are rarely, if ever,



managed as wildlife or with a conservation focus; consequently, many comparisons between bison and cattle are inevitably confounded by differing land management approaches or, alternatively, focus on comparing two similar production systems (i.e. small pastures intensively managed). In other words, many of the observed differences between species may in fact be largely due to varying management plans (e.g. the human domain) rather than ecology of the species. In order for bison to be substantially different from domestic livestock, they need to interact with large landscapes where they can respond to heterogeneity associated with topographic conditions, complex patterns of fire and other important species like prairie dogs [2,27]. However, few places exist where these conditions are present at scales relevant to any semblance of ecosystem restoration. Therefore, rewilding plans that hinge almost exclusively on changing the herbivore within the modern landscape context are unlikely to produce intended outcomes without substantial management plans.

This is not to say that which herbivore species are included on a landscape is not an important decision in conservation planning of grasslands. If the focus is specifically conservation for an individual species (e.g. bison) then this decision is simplified considerably. However, if the focus is on conservation of a landscape and other grassland-associated taxa, such as plants, birds and arthropods, the dominant species of herbivore may be less important. Unfortunately, the debate of the introduction of native versus domestic herbivores becomes constrained by cultural and logistical perspectives based on an incomplete understanding of the factors that influence the effects of grazing (figure 3). Conservation groups, agencies and private land-owners have biases towards native or domestic herbivores despite the fact that studies have demonstrated that similar responses in biodiversity can be achieved by cattle and bison as long as both species are allowed to interact with heterogeneous fire patterns [12,33].

A focus on a dominant herbivore may also ignore the importance of secondary herbivores that may have much different impacts on landscapes because of differing foraging behaviours. Diverse herbivores can alter the impacts on woody plant encroachment and plant diversity because of diverse foraging behaviour [34]. Species that have more of a selective foraging behaviour that focuses on woody plants can be very important to grassland conservation by altering woody plant encroachment and diversity even if they are not dominant [34]. In some cases in the North American Great Plains, prairie dogs may be keystone species that influence large herbivore distribution, plant species composition and biodiversity. In fact, the widespread changes in the distribution and abundance of small herbivores have probably led to more significant plant community change than have changes in large herbivores. For example, the elimination of the black-tailed prairie dog (*Cynomys ludovicianus*) in some parts of its distribution can contribute to increased woody cover and shifts in the herbaceous plant community [35–38]. Black-tailed prairie dog populations are now estimated to be at only 2% of their historic levels and may have historically had an equivalent landscape-level impact to large herbivores and fire [39,40]. The effects of other species of small mammals are not as well studied, but have probably had major effects on grassland landscapes. In summary, to suggest that adding one species of herbivore (or a selected suite of species) will result in a return to some previous landscape condition is at best simplistic.

## 4. Biophysical domain

Since the arrival of humans on the North American continent, the biophysical environment has changed from near-peak glaciation approximately 20 000 years ago to our current climate with considerable variation in between. The climate fluctuated substantially over the past 10 000 years including warm and cool periods with a general trend of warming that has been accelerated over the past 100 years from anthropogenic climate change [19,41]. When humans first arrived, much of the Northern Great Plains would have been heavily influenced by glaciers. Also, many Southern Great Plains grasslands that are now dominated by C4 grasses were dominated by C3 grasses approximately 11 000 years ago [19]. Shifts from C3 to C4 grass dominance would have a substantial influence of altering critical features associated with forage quality and quantity. Since Glacial Maximum, vegetation and climate have been dynamic, suggesting that contemporary ecosystems are not good indicators of past conditions [42,43].

While grasslands and fires occurred prior to human arrival, the arrival of humans is clearly associated with an increase in fires from anthropogenic burning [19,44]. Sometime after human arrival, grassland landscapes changed dramatically as human use of fire became important, the climate warmed, and many species of dominant large herbivores were lost [17]. The American bison became a dominant large herbivore because of a complex interaction with fire (pyric herbivory), humans, predators, other herbivores and the regionally variable climate (figure 3) [12,19]. This interaction occurred on large and continuous grassland landscapes where disturbance patterns were highly dynamic in space and time. Many of the grassland species in the region are well suited to live in these large and heterogeneous landscapes that are often referred to as a shifting mosaic [12]. Multiple species contributed to these complex patterns that occurred across large areas that were very heterogeneous in soils, topography and climate.

European settlement fragmented large landscapes, introduced cultivation and domestic livestock and concomitantly reduced fires. Management of these landscapes transitioned from hunter–gatherers to subsistence farming and eventually industrial agriculture. Natural and semi-natural grasslands were integrated into agricultural regimes and grazing animals became intensively managed with a goal of promoting homogeneous vegetation that was often inaccurately perceived to be superior for livestock production [24,45]. Fire was no longer used and fire suppression became a dominant culture that further led to fragmentation of continuous grasslands through woody plant encroachment [26]. Conservation efforts have worked locally on restoring previously cultivated lands [23] and restoring fire regimes [46], but across the entire Great Plains, grassland fragmentation has continued through increases in energy development and woody plant encroachment and remains the primary limitation in conservation or rewilding of grasslands [26,47].

## 5. Current and future conservation landscape

Grasslands are declining worldwide and many of the grassland obligate species that remain are declining [48–50]. Conservation of remaining landscapes is critical to global biodiversity and will be dependent on multiple models that range from the attempt to restore wilderness to conservation-based

management on privately owned landscapes that are agriculturally based. Many conservation models have been suggested and we present three that have been proposed for conservation of North American grasslands: (i) Pleistocene rewilding [10], (ii) bison restoration [11] and (iii) conservation of pattern and process [12]. These models have similarities and differences and none are complete on their own, but we have chosen them for comparison to describe the complexities and challenges of grassland conservation on contemporary landscapes.

Early calls for Pleistocene rewilding made grandiose suggestions of reintroducing mega-herbivores (or their surrogates) that went extinct not long after human arrival in North America. They originally claimed that their goals and ideas of restoring the original anthropogenic extirpations were 'justified on ecological, evolutionary, economic, aesthetic and ethical grounds' [9]. While these ideas are engaging to many and stimulate excitement, they are usually based on a romantic objective of restoring something long lost and probably impossible to restore. This approach to conservation may loosely recognize that landscapes are spatially and temporally dynamic and largely dependent upon people, but they generally fall short of incorporating these concepts into any semblance of a workable plan [10]. The intent is to restore conditions back to a time prior to human influence on the fauna of North America. Most of the remaining grasslands of North America are privately owned and there is limited consideration in the Pleistocene rewilding approach of the ownership of these lands in the model. The complexity of land ownership and management of the lands appears to be left to fate with some limited discussions of national parks and their associated economic opportunities and challenges. Additionally, there is little recognition of landscape complexity or dynamics. Wild herbivores that are unmanaged require heterogeneity to persist and as parcel size gets smaller this heterogeneity becomes more important [26,51,52]. In order for these landscapes to be wild and support herds of mega-herbivores and their predators, they would have to exist on large and unfragmented grasslands that are rare or even absent. It is uncertain how herd size and structure would be regulated and how introduced species would interact with existing native species. Similarly, climate projections, as well as land use changes, suggest that these landscapes will become more different from their pre-historical conditions over the next century. Recent and future climate change, increasing human population and land fragmentation suggest that this model is largely an academic discussion that has limited practical value. Suggesting that we restore large herbivores or their surrogates (while ignoring small herbivores) into a novel plant community, a novel climate and a novel human population has extremely limited application potential.

The second model is focused on restoring American bison to grasslands and includes a full array of bison managers with objectives ranging from food production to variable versions of rewilding [11]. A variant of this perspective was first suggested through discussions of the 'Buffalo Commons' or the 'Big Open' [53,54]. Much of the original justification was not merely based on conservation of bison, but largely on the economic and social upheavals that have occurred on North American grasslands since the Dust Bowl of the 1930s. The current bison restoration approach is to consider regional socio-economics and restore bison to as much of its

historical distribution as is culturally, socially and ecologically possible [11]. While this approach acknowledges the social and cultural domain, like most other approaches it does not suggest specific policies or land management concerns that would be required to rewild large landscapes with free-roaming herds of bison. Additionally, this approach does not adequately address the tremendous human implications (e.g. shifting populations and food production) of such a model. There are examples where variations of this approach are being applied, such as the American Prairie Reserve (APR) in Montana, USA, where a vision of restoring a very large landscape and allowing bison to roam freely is a conservation goal. The approach of the APR is very bison centric but they do acknowledge the importance of restoring ecological processes and patterns on large and continuous landscapes [55]. These bold visions have largely been unencumbered by conservationists who are practically constrained to the realism of concerns of how the land will ultimately be managed in the future. In the case of APR, they recognized the importance of bison to Native American tribes and have attempted to engage Native American tribes. Additionally, they have recognized the importance of engaging the local community in their vision, but their perceptions and acceptance remain a challenge. For APR, bison is a primary focus of their conservation vision but they recognize the importance of restoring heterogeneity with fire and other disturbances, such as prairie dogs. However, in the case of fire, it largely remains an objective for the future. Interestingly, APR views these large landscapes inhabited by free-roaming bison as a potential economic benefit to the local economy through tourism. Humans are, therefore, part of the plan and APR provides an example of a tentatively successful restoration of bison to large but limited areas. Despite APR's success, bison conservation and in some cases rewilding have not always acknowledged the complexity of rewilding landscapes and the types of management that may be required to achieve conservation objectives.

The third model, called conservation of pattern and process, lacks the grandiose vision of the previous models, and instead is focused on pragmatically restoring pattern and processes of grasslands through heterogeneity-based management of contemporary landscapes [13]. The conservation approach was developed through studying bison and other herbivore interactions with fire and the resulting heterogeneity in structure that influences biodiversity [12]. The model developed from large native herbivores (originally bison, but later other herbivores) was then transferred to domestic livestock within a rangeland setting [25,33]. This approach is less focused on the specific herbivore (e.g. bison versus cattle) and more focused on developing management approaches that can maintain agricultural production and simultaneously enhance biodiversity. Specifically, by creating variable spatial patterns in vegetation structure that shift throughout the landscape and create uneven animal distribution and fire patterns that interact, livestock production may be enhanced by improved forage quality on burned areas while different wildlife species will use different vegetation structures thereby increasing biodiversity [50,56]. A similar approach has been proposed that is focused on the food web and considers the mosaic associated with herbivores and fire the central goal of conservation without limiting the attention to a specific herbivore or suite of

herbivores [57]. Conservation of pattern and process was developed in a rangeland management context to integrate conservation objectives into our current land use and cultural networks but it lacks the objective of restoring the Great Plains to historic time periods. Rather, the intent is to maintain as much biodiversity as possible by restoring disturbance processes and patterns in ways that allow humans to meet current and future needs from the landscape.

These three perspectives vary from an unencumbered vision to a more practical perspective that attempts to integrate regional societal objectives (table 1). In the past, the first two perspectives have been described as unlikely approaches to grassland conservation, but the progress of APR suggests that some visionary ideas may be locally important because cultural limitations change and there is considerable uncertainty in the future. The more practical approach of conservation of pattern and process seems more likely to achieve conservation goals across many fragmented landscapes in the near term because it is compatible with the current human culture of livestock and agriculture. However, it is still limited from a socio-ecological perspective. Research in the Great Plains indicates that some segments of the public have a strong aversion to fundamental aspects of biodiversity, such as heterogeneity and diversity of plants [58]. Many land owners have learned to manage against many of the goals that conservationists find important even when those goals may be compatible with their land management objectives. These cultural barriers are fundamental to conservation goals regardless of perspectives or conservation models.

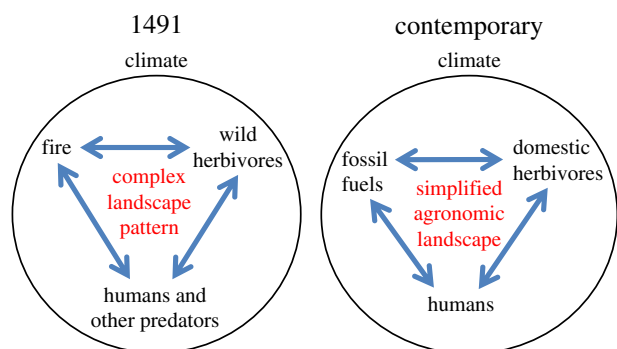
## 6. Conclusion

One of the greatest challenges of rewilding and grassland conservation is accounting for and incorporating the complexity that occurs in socio-ecological systems. A grossly simplistic model that is limited to a comparison between two time periods (Pre-European settlement – 1491 compared with contemporary) illustrates the magnitude of the conversion that has occurred across most grasslands of North America since European settlement (figure 4). As stated in Holling [8], any conservation framework should be (i) as simple as possible, but not too simple; (ii) dynamic and prescriptive, not static and descriptive; and (iii) able to embrace uncertainty and unpredictability. Any discussions and conservation strategies that focus solely on dominant large herbivores of the past and downplay the importance of the human domain or the broader biophysical domain (not to mention other less charismatic herbivores) are violating all of these suggestions.

Rewilding, like restoration, has long struggled with the importance of identifying target conditions that are desirable and monitoring approaches that can verify progress towards their goals. There are limited examples of conservation groups that have at least identified specific goals and developed monitoring methods to evaluate progress towards their goal [55]. A few government programmes exist that promote conservation of patterns and processes on privately owned grasslands for specific conservation objectives and, in some cases, these are monitored and evaluated towards those objectives (e.g. Lesser Prairie Chicken Initiative through United States Department of Agriculture-Natural Resource Conservation Service). Some conservation approaches have focused on

**Table 1.** Summary of differences and similarities between three conservation perspectives in terms of important aspects of the socio-ecological framework.

	restoration target date	herbivore	consideration of other animal parameters (e.g. densities/grazing intensity)	climate considerations	fire	role of humans
Pleistocene rewilding	~13 000 years ago	Pleistocene megafauna or surrogates	not specified	target existed under much cooler climate	not acknowledged	removing all humans
bison rewilding/restoration	~10 000 years ago – 1492	America bison—others secondary	limited discussion	target was cooler but bison are tolerant of extremes	not acknowledged	post-European as a target but limited acknowledgement of the role of Native Americans
conservation of pattern and processes	contemporary	objective based	critical	contemporary	critical	contemporary with variable land-owners and objectives



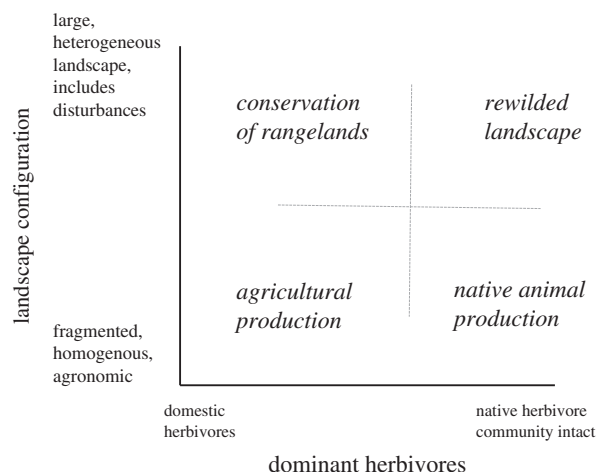
**Figure 4.** Simplified conceptual model for North American grasslands indicating the major changes to socio-ecological structure of grassland ecosystems at different times. (Online version in colour.)

combining components from several of these perspectives. The Nature Conservancy's Tallgrass Prairie Preserve of Oklahoma, USA, combines the bison rewilding with the conservation of pattern and process. They have restored free-roaming bison and random anthropogenic fires on a large landscape, but are also encouraging research and outreach on developing conservation approaches for surrounding ranchers to promote a similar heterogeneous landscape with domestic livestock [12]. These success stories suggest that bison rewilding and conservation of pattern and process perspectives can be integrated to develop a socio-ecological approach that can be achieved across fairly large areas. In all cases, a primary goal is putting together the broken pieces of a previously fragmented landscape and, without this first step, other efforts will have limited benefits for conservation of grasslands [26]. Local management or herbivore modifications will have minimal influences on highly fragmented landscapes, while on large landscapes these factors can be important.

There is no single conservation model that successfully argues for a specific herbivore that is most appropriate for all objectives that are associated with rewilding or conserving grassland ecosystems. All models can be evaluated for their contribution to biodiversity and other goods and services in a matrix that is variable with different land use objectives (figure 5). The three perspectives we present all have differing objectives. The most appropriate model is dependent on the human priority of (i) restoring a certain herbivore or group of herbivores, (ii) the processes and patterns that are critical to biodiversity of all remnant grassland species and (iii) the ecological processes that provide goods and services. There are several critical factors that are absent or limited by all of these perspectives and will probably limit their success. None of the models adequately consider the human dimensions of conservation and will probably struggle with policy, economics, threats and opportunities in the future. These models give but passive recognition that the greatest resistance to any form of conservation is social and is associated with land use, land ownership and large-scale

## References

1. Weddell BJ. 2002 *Conserving living natural resources: in the context of a changing world*, 426 pp. Cambridge, UK: Cambridge University Press.
2. Allred BW, Fuhlendorf SD, Hamilton RG. 2011 The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle behavior. *Ecosphere* **2**, 1–17. (doi:10.1890/ES10-00152.1)
3. Axelrod DI. 1985 Rise of the grassland biome, central North America. *Bot. Rev.* **51**, 163–201. (doi:10.1007/BF02861083)



**Figure 5.** A matrix illustrating the complex conditions that can exist with all contributing to ecosystem functions and biodiversity on grasslands.

fragmentation. Small conservation areas can provide local refugia for biodiversity but they are incapable of restoring pattern and processes that are critical to conservation at relevant scales. The conservation of pattern and process perspective lists maintaining large tracts of land as the first principle but does little to discuss how this can be accomplished [13]. Additionally, the current and impending threat of major shifts in climate is a primary limitation to most models that are focused on using the past for target conditions. Integrating the support for these and other perspectives into a comprehensive, forward-looking socio-ecological framework that is capable of preparing for climate change should be the goal of all conservationists.

Rewilding, in its purest sense, is a naive idea that can never be fully achieved on fragmented landscapes in our modern world, but it may be a useful concept to illustrate the importance of conservation goals and objectives and could be integrated into a comprehensive conservation approach on grasslands of North America and beyond. We do believe that it is time to acknowledge humans as a central part of ecosystems that can lead to conservation or degradation of grassland and other systems. Conservation efforts should develop specific objectives within a socio-ecological framework that can include monitoring and adaptive management based on targets. The future of conservation is dependent on the development of many forward-focused conservation models that better integrate societal, economic and policy objectives and recognize that humans are an integral part of ecosystems that are highly dynamic in space and time with a changing climate.

**Data accessibility.** This article has no additional data.

**Competing interests.** We declare we have no competing interests.

**Funding.** We received no funding for this study.



4. Anderson RC. 2006 Evolution and origin of the Central Grassland of North America: climate, fire, and mammalian grazers. *J. Torrey Bot. Soc.* **133**, 626–647. (doi:10.3159/1095-5674(2006)133[626:EA00TC]2.0.CO;2)
5. Hill Jr ME, Hill MG, Widga CC. 2008 Late Quaternary bison diminution on the Great Plains of North America: evaluating the role of human hunting versus climate change. *Quat. Sci. Rev.* **27**, 1752–1771 (doi:10.1016/j.quascirev.2008.07.002)
6. Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, Towne EG. 1999 The keystone role of bison in North American tallgrass prairie. *Bioscience* **49**, 39–50. (doi:10.2307/1313492)
7. Kolipinski M, Borish S, Scott A, Kozlowski K, Ghosh S. 2014 Bison: yesterday, today, and tomorrow. *Nat. Areas J.* **34**, 365–375. (doi:10.3375/043.034.0312)
8. Holling CS. 2001 Understanding the complexity of economic, ecological, and social systems. *Ecosystems* **4**, 390–405. (doi:10.1007/s10021-001-0101-5)
9. Donlan J. 2005 Re-wilding North America. *Nature* **436**, 913–914. (doi:10.1038/436913a)
10. Donlan CJ *et al.* 2006 Pleistocene rewilding: an optimistic agenda for 21st century conservation. *Am. Nat.* **168**, 660–681. (doi:10.2307/3873461)
11. Sanderson EW *et al.* 2008 The ecological future of the North American bison: conceiving long-term large-scale conservation of wildlife. *Conserv. Biol.* **22**, 252–266. (doi:10.1111/j.1523-1739.2008.00899.x)
12. Fuhlendorf SD, Engle DM, Kerby J, Hamilton R. 2009 Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conserv. Biol.* **23**, 588–598. (doi:10.1111/j.1523-1739.2008.01139.x)
13. Fuhlendorf SD, Engle DM, Elmore RD, Limb RF, Bidwell TG. 2012 Conservation of pattern and process: developing an alternative paradigm for rangeland management. *Range. Ecol. Manage.* **65**, 579–589. (doi:10.2111/REM-D-11-00109.1)
14. Raghavan M *et al.* 2015 Genomic evidence for the Pleistocene and recent population history of Native Americans. *Science* **349**, aab3884. (doi:10.1126/science.aab3884)
15. Stuart AJ. 1991 Mammalian extinctions in the late Pleistocene of Northern Eurasia and North America. *Biol. Rev.* **66**, 453–562.
16. Grayson DK, Meltzer DJ. 2003 A requiem for North American overkill. *J. Archaeol. Sci.* **30**, 585–593. (doi:10.1016/S0305-4403(02)00205-4)
17. Pyne SJ. 1982 *Fire in America: a cultural history of wildland and rural fire*. Princeton, NJ: Princeton University Press.
18. Keeley JE, Rundel PW. 2005 Fire and the Miocene expansion of C4 grasslands. *Ecol. Lett.* **8**, 683–690. (doi:10.1111/j.1461-0248.2005.00767.x)
19. Cordova CE, Johnson WC, Mandel RD, Palmer MW. 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. (doi:10.1016/j.catena.2010.08.015)
20. Silliman SW. 2005 Culture contact or colonialism? Challenges in the archaeology of native North America. *Am. Antiq.* **70**, 55–74. (doi:10.2307/40035268)
21. Kay CE. 1998 Are ecosystems structured from the top-down or bottom-up? A new look at an old debate. *Wildl. Soc. Bull.* **26**, 484–498.
22. Laliberte A, Ripple WJ. 2003 Wildlife encounters by Lewis and Clark: a spatial analysis of interactions between native Americans and wildlife. *Bioscience* **53**, 994–1003. (doi:10.1641/0006-3568(2003)053[0994:WEBLAC]2.0.CO;2)
23. Tanner ET, Fuhlendorf SD. 2018 Impact of an agr-environmental scheme on landscape patterns. *Ecol. Indic.* **85**, 956–965. (doi:10.1016/j.ecolind.2017.11.043)
24. Briske DD, Derner JD, Brown JR, Fuhlendorf SD, Teague WR, Havstad KM, Gillen RL, Ash AJ, Wilms WD. 2008 Rotational grazing on rangelands: reconciliation of perception and experimental evidence. *Range. Ecol. Manage.* **61**, 3–17. (doi:10.2111/06-159R.1)
25. Fuhlendorf SD, Engle DM. 2004 Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *J. Appl. Ecol.* **41**, 604–614. (doi:10.1111/j.0021-8901.2004.00937.x)
26. Fuhlendorf SD, Hovick TJ, Elmore RD, Tanner AM, Engle DM, Davis CA. 2017 A hierarchical perspective to woody plant encroachment for conservation of prairie chickens. *Range. Ecol. Manage.* **70**, 9–14. (doi:10.1016/j.rama.2016.08.010)
27. Fuhlendorf SD, Allred BW, Hamilton RG. 2010 Bison as keystone herbivores on the Great Plains: can cattle serve as proxy for evolutionary grazing patterns? ABS Working Paper No. 4.
28. Plumb GE, Dodd JL. 1993 Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. *Ecol. Appl.* **3**, 631–643. (doi:10.2307/1942096)
29. Towne EG, Hartnett DC, Cochran RC. 2005 Vegetation trends in tallgrass prairie from bison and cattle grazing. *Ecol. Appl.* **15**, 1550–1559. (doi:10.1890/04-1958)
30. Allred BW, Fuhlendorf SD, Engle DM, Elmore RD. 2011 Ungulate preference for burned patches reveals strength of fire-grazing interaction. *Ecol. Evol.* **1**, 132–144. (doi:10.1002/ece3.12)
31. Kohl MT, Kohl PR, Kunkel K, Williams DM. 2013 Bison versus cattle: are they ecologically synonymous? *Range. Ecol. Manage.* **66**, 721–731. (doi:10.2111/REM-D-12-00113.1)
32. Allred BW, Fuhlendorf SD, Hovick TJ, Dwayne Elmore R, Engle DM, Joern A. 2013 Conservation implications of native and introduced ungulates in a changing climate. *Glob. Change Biol.* **19**, 1875–1883. (doi:10.1111/gcb.12183)
33. Fuhlendorf SD, Harrell WC, Engle DM, Hamilton RG, Davis CA, Leslie Jr DM. 2006 Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecol. Appl.* **16**, 1706–1716 (doi:10.1890/1051-0761(2006)016[1706:SHBTBF]2.0.CO;2)
34. Allred BW, Fuhlendorf SD, Smeins FE, Taylor CA. 2012 Herbivore species and grazing intensity regulate community composition and an encroaching woody plant in semi-arid rangeland. *Basic Appl. Ecol.* **13**, 149–158. (doi:10.1016/j.baae.2012.02.007)
35. Weltzin JF, Archer S, Heitschmidt RK. 1997 Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology* **78**, 751–763. (doi:10.1890/0012-9658(1997)078[0751:SMROVS]2.0.CO;2)
36. Coppock DL, Detling JK, Ellis JE, Dyer MI. 1983 Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia* **56**, 1–9. (doi:10.1007/BF00378210)
37. Winter SL, Cully Jr JF, Pontius JS. 2002 Vegetation of prairie dog colonies and non-colonized shortgrass prairie. *J. Range Manage.* **55**, 502–508. (doi:10.2307/4003230)
38. Miller SD, Cully Jr JF. 2001 Conservation of black-tailed prairie dogs (*Cynomys ludovicianus*). *J. Mammal.* **82**, 889–893. (doi:10.1644/1545-1542(2001)082<0889:COBTPD>2.0.CO;2)
39. Wuerthner G. 1997 Viewpoint: the black-tailed prairie dog – headed for extinction? *J. Range Manage.* **50**, 459–466. (doi:10.2307/4003699)
40. Hoogland JL. 1995 *The black-tailed prairie dog: social life of a burrowing mammal*. Chicago, IL: University of Chicago Press.
41. Nordt L, von Fischer J, Tieszen L. 2007 Late Quaternary temperature record from buried soils of the North American Great Plains. *Geology* **35**, 159–162. (doi:10.1130/G23345A.1)
42. Nordt LC, Boutton TW, Hallmark CT, Waters MR. 1994 Late Quaternary vegetation and climate change in Central Texas based on the isotopic composition of organic carbon. *Quat. Res.* **41**, 109–120. (doi:10.1006/qres.1994.1012)
43. Hall SA, Valastro S. 1995 Grassland vegetation in the southern Great Plains during the last glacial maximum. *Quat. Res.* **44**, 237–245. (doi:10.1006/qres.1995.1068)
44. Power MJ *et al.* 2008 Changes in fire regimes since the Last Glacial Maximum: an assessment based on a global synthesis and analysis of charcoal data. *Clim. Dyn.* **30**, 887–907. (doi:10.1007/s00382-007-0334-x)
45. Limb RF, Fuhlendorf SD, Engle DM, Weir JR, Elmore RD, Bidwell TG. 2011 Pyric-herbivory and cattle performance in grassland ecosystems. *Range. Ecol. Manage.* **64**, 659–663. (doi:10.2111/REM-D-10-00192.1)
46. Twidwell D, West AS, Hiatt WB, Ramirez AL, Winter JT, Engle DM, Fuhlendorf SD, Carlson JD. 2015 Plant invasions or fire policy: which has altered fire behavior more in tallgrass prairie? *Ecosystems* **19**, 356–368. (doi:10.1007/s10021-015-9937-y)
47. Allred BW, Smith WK, Twidwell D, Haggerty JH, Running SW, Naugle DE, Fuhlendorf SD. 2015 Ecosystem services lost to oil and gas in North America. *Science* **34**, 401–402. (doi:10.1126/science.aaa4785)

48. Sampson F, Knopf F. 1994 Prairie conservation in North America. *Bioscience* **44**, 418–421. (doi:10.2307/1312365)
49. Hoekstra JM, Boucher TM, Ricketts TH, Roberts C. 2005 Confronting a biome crisis: global disparities of habitat loss and protection. *Ecol. Lett.* **8**, 23–29. (doi:10.1111/j.1461-0248.2004.00686.x)
50. Fuhlendorf SD, Engle DM. 2001 Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *Bioscience* **51**, 625–632. (doi:10.1641/0006-3568(2001)051[0625:RHOREM]2.0.CO;2)
51. Owen-Smith N. 2002 A metaphysiological modelling approach to stability in herbivore–vegetation systems. *Ecol. Model.* **149**, 153–178. (doi:10.1016/S0304-3800(01)00521-X)
52. Owen-Smith N. 2004 Functional heterogeneity in resources within landscapes and herbivore population dynamics. *Landsc. Ecol.* **19**, 761–771. (doi:10.1007/s10980-005-0247-2)
53. Matthews A. 2002 *Where the buffalo roam: restoring America's Great Plains*. Chicago, IL: University of Chicago Press.
54. Popper DE, Popper FJ. 1999 The buffalo commons: metaphor as method. *Geogr. Rev.* **89**, 491–510. (doi:10.2307/216099)
55. Freese CH, Fuhlendorf SD, Kunkel K. 2014 A management framework for the transition from livestock production toward biodiversity conservation on Great Plains rangelands. *Ecol. Restor.* **32**, 358–368. (doi:10.3368/er.32.4.358)
56. Hovick TJ, Elmore RD, Fuhlendorf SD. 2014 Structural heterogeneity increases diversity of non-breeding grassland birds. *Ecosphere* **5**, art62. (doi:10.1890/ES14-00062.1)
57. Bowman DMJS, Perry GLW, Higgins SI, Johnson CN, Fuhlendorf SD, Murphy BP. 2017 Pyrodiversity is the coupling of biodiversity and fire regimes in food webs. *Phil. Trans. R. Soc. B* **371**, 20150169. (doi:10.1098/rstb.2015.0169)
58. Becerra TA, Engle DM, Fuhlendorf SD, Elmore RD. 2017 Preference for grassland heterogeneity: implications for biodiversity in the Great Plains. *Soc. Nat. Resour.* **30**, 601–612. (doi:10.1080/08941920.2016.1239293)