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Looking to the Future: Key Points for Sustainable Management of Northern Great Plains Grasslands

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The grasslands of the northern Great Plains (NGP) region of North America are considered endangered ecosystems and priority conservation areas yet have great ecological and economic importance. Grasslands in the NGP are no longer self-regulating adaptive systems. The challenges to these grasslands are widespread and serious (e.g. climate change, invasive species, fragmentation, altered disturbance regimes, and anthropogenic chemical loads). Because the challenges facing the region are dynamic, complex, and persistent, a paradigm shift in how we approach restoration and management of the grasslands in the NGP is imperative. The goal of this article is to highlight four key points for land managers and restoration practitioners to consider when planning management or restoration actions. First, we discuss the appropriateness of using historical fidelity as a restoration or management target because of changing climate, widespread pervasiveness of invasive species, the high level of fragmentation, and altered disturbance regimes. Second, we highlight ecosystem resilience and long-term population persistence as alternative targets. Third, because the NGP is so heavily impacted with anthropogenic chemical loading, we discuss the risks of ecological traps and extinction debt. Finally, we highlight the importance of using adaptive management and having patience during restoration and management. Consideration of these four points will help management and restoration of grasslands move toward a more successful and sustainable future. Although we specifically focus on the NGP of North America, these same issues and considerations apply to grasslands and many other ecosystems globally.

Key words: adaptive management, anthropogenic chemicals, fragmentation, invasion, prairie, restoration

Implications for Practice

- Like grasslands and other ecosystems around the world, the current and future conditions of the grasslands in the northern Great Plains (NGP) are very different from past conditions.
- Getting satisfactory results from the same old management or restoration techniques is happening less often.
- Because of changing climate, invasive species, fragmentation, altered disturbance regimes, and anthropogenic chemical loading, management and restoration targets and methods need to change.
- Land managers and restoration practitioners need to be aware of the potential to created ecological traps and of extinction debt.
- Adaptive management and patience are essential for sustainable restoration and management in the NGP.

Introduction

Mention the northern Great Plains (NGP) and the mind's eye conjures a bucolic "sea of grass." However, the reality of this large, complex, and ecologically and economically important region of North America is more complicated. The NGP encompasses areas of Nebraska, South Dakota, North Dakota, Wyoming, and Montana in the United States, and Saskatchewan and Alberta in Canada. This approximately 13 million ha (50,000 mile^2) region contains over 1,600 species of native plants, 220 butterfly species, and 95 mammal species including some of the most iconic North American mammals, the American bison (*Bison bison*) and pronghorn (*Antilocapra americana*). The NGP provides critical habitat for migrating birds and breeding waterfowl (Zimpfer et al. 2013). The NGP comprises the majority of the Missouri River Basin and therefore is important for the vitality of the Missouri River, the Mississippi River, and ultimately the Gulf of Mexico. The region contains 22% of the U.S. beef cow and 19% of the sheep populations, houses 37% of the honey bee colonies, and produces 46% of the honey in the United States (USDA-NASS 2017). Unfortunately, the NGP is also an endangered ecosystem (Samson et al. 2004) because of the extent of conversion of grasslands to crop production (e.g. Lark et al. 2015; Comer et al. 2018). This heightened vulnerability makes it a priority conservation area for the World Wildlife Fund (www.worldwildlife.org), the National Fish and

Wildlife Foundation (www.nfwf.org), and The Nature Conservancy (www.nature.org). Grasslands with similar precipitation and temperature to the NGP occur in eastern Europe and Asia as well as in the South American Pampas (Woodward et al. 2004).

This ecologically and economically important region is facing an uncertain future due to complex and widespread challenges such as climate change, invasive species, fragmentation, altered disturbance regimes, and anthropogenic chemical loading. To help move restoration and management into this uncertain future, we discuss four key points for land managers and restoration practitioners in the NGP to consider.

Use "Historical Fidelity" as a Target Sparingly, If at All

Historically, climate and disturbance regimes (fire and grazing) created and were the dominant forces maintaining the grasslands; we acknowledge that it is instructive to examine how these functioned in the past. However, the future of the NGP grasslands will be fundamentally different from the past due to changing climate, invasive species, fragmentation, and altered disturbance regimes. Managing for historical fidelity, or as if historical conditions and processes still are the dominant forces on the landscape (or could be replicated), is ill-considered and not likely to be successful. Yet, managing in ignorance of historical conditions is also unwise. We propose that understanding historical conditions alongside current and future conditions will provide insight that will improve restoration and management outcomes.

The NGP is historically and currently a climatically variable system in regard to both temperature and precipitation; however, models predict a departure from the historical range of variability by 2080 (Dobrowski et al. 2013; IPCC 2014). Models for the NGP consistently predict an increase in average annual temperature by 2–3°C by 2050 and maximum temperatures are expected to increase 4–6°C by 2085 (Derner et al. 2018). In general, warming is expected to be greater in winter and spring than during summer and fall, and the frost-free period is projected to increase by 30–40 days by 2100 (Wienhold et al. 2018). Predictions about precipitation are less consistent. Unlike more southern grasslands, precipitation in the NGP is predicted to increase slightly, but frequency and intensity of precipitation events are expected to change more significantly (Derner et al. 2018). These changes have the potential to increase productivity but change the species composition and disturbance regimes of grasslands (Jonas et al. 2015). Furthermore, changing climate has the potential to shift species phenologies so that key interactions (e.g. plant–pollinator relationships or grazer-forage availability) may be lost (Dunnell & Travers 2011).

Invasive species' arrival in the NGP coincided with European settlement. NGP grasslands are among the most severely invaded areas in the Great Plains. The first published report of invasive species occurred in 1893 when 30,000 acres (12,140 ha) in South Dakota were infested with *Salsola kali* (Dewey 1893). *Poa pratensis* was reported in the vegetation of the region in 1908 (Harvey) and in 1930 (Steiger). Invasive plants in the region include trees (e.g. *Elaeagnus angustifolia*,

Espeland et al. 2017), forbs (e.g. *Euphorbia esula*, *Cirsium arvensis*, and *Melilotus* spp., Larson et al. 2001), and grasses. Cool-season grasses (e.g. *P. pratensis* and both perennial and annual *Bromus* spp.) are among the most threatening invasive plants in the region, accounting for more than 80% of the annual production in some areas (DeKeyser et al. 2015; Ashton et al. 2016). The implications of these invasions vary from trivial to severe in NGP grasslands. Invasive species have the potential to decrease native species diversity (Bennett et al. 2014), alter pollinator networks (Larson et al. 2016), and impact wildlife habitat (reviewed in Ellis-Felege et al. 2013). Although invasive species often increase with disturbance and fragmentation (Perkins & Nowak 2013), they also are present in undisturbed and relatively unfragmented areas in the NGP (reviewed in DeKeyser et al. 2013).

Fragmentation, including grassland loss and loss of connectivity between grassland patches, is severe in the NGP. By 2004, the NGP had experienced at least a 40% loss of grassland (Samson et al. 2004), and the losses have only continued as the U.S. Corn Belt expands west into the NGP with annual rates ranging from 1 to 5.4% (Wright & Wimberly 2013; Gage et al. 2016). Recent estimates of loss suggest at least another 10% of the grasslands in the NGP have been converted to crop production (Comer et al. 2018). This expansion often occurs in remnant (previously unplowed) grasslands and other areas previously thought to have marginal value for crop production (Lark et al. 2015). Approximately 283,280 ha (700,000 acres) of NGP grassland were converted to row-crop agriculture in 2016 alone (Gage et al. 2016; World Wildlife Fund 2017). The extent and rate of conversion of grassland to cropland is an ongoing and longstanding issue (Weaver & Fitzpatrick 1934).

Dominant disturbance regimes (fire and grazing) across the entire Great Plains and specifically in the NGP are fundamentally different now than at any time in the past. Historically, wildfire was widespread but did not have a predictable return interval, instead being much more prevalent in wetter periods that supported more plant biomass production (Brown et al. 2005) and less prevalent during drier periods (Clark et al. 2002). Additionally, anthropogenic fire occurred on the landscape long before European settlement (Higgins 1986). Today, wildfire has essentially been eliminated from the landscape and anthropogenic fire occurs in the system mainly through prescribed burning during the spring season. Historically, the keystone grazers impacting vegetation of the NGP were American bison and prairie dogs (Knapp et al. 1999; Antolin et al. 2002; Knowles et al. 2002; Augustine & Baker 2013). Grazing by American bison created a detectable impact on vegetation in the NGP only within the last 1,000 years (Grimm et al. 2011). During European settlement, perceived competition with domestic livestock resulted in widespread eradication of prairie dog colonies and a shift in the grazing regime from free-ranging bison to managed and fenced cattle (*Bos taurus*) herds. Bison, at equal stocking rates, may be ecologically equivalent to cattle (reviewed by Knapp et al. 1999 but see Allred et al. 2011). Even if the change in the species of grazing animals did not alter the effects of grazing on vegetation, the change in grazing regimes (free-roaming to managed and fenced) would. Both

fire and grazing have been removed from much of the landscape entirely and where they still occur, the scale is much smaller. Grazing cattle on an allotment or using prescribed burning on a management unit is a much smaller-scale disturbance than the free-ranging bison or uncontrolled wildfires that occurred in the past.

Using prescribed fire and managed grazing to create a site with historical fidelity have often been the default methods for managing and restoring grasslands in the NGP. However, dramatic changes in the scale of how disturbances are able to be used and potential interactions with invasive species and shifting climate may make achieving historical targets challenging. For example, conducting prescribed fire in the spring is already getting more challenging due to changing climate (Yurkonis et al. 2019), and although forage quantity may increase as climate changes, changing temporal availability and quality of forage along with increasing prevalence of invasive species may change how grazing can occur across the landscape (Derner et al. 2018). Therefore, instead of implementing traditional or historic disturbance regimes, land managers and restoration practitioners must decide if applying prescribed fire or managed grazing as tools are going to achieve their desired goals. For example, if prescribed fire or managed grazing creates conditions favorable for invasive species, are we working at cross purposes when we use these tools to manage or restore grasslands? If this is the case, and if lack of management will still lead to woody dominance (Ratajczak et al. 2016), prescribed fire or managed grazing applied as tools must be accompanied by additional actions to minimize their negative effects (i.e. to thwart invasive species that benefit from these disturbances) or perhaps the timing or intensity of these tools needs to be adjusted to favor native diversity. Restoration practitioners and land managers will need to use the knowledge of how historical disturbance processes worked on the landscape in the past coupled with current conditions and processes to develop new strategies that address contemporary realities in the NGP.

Embrace Resilience as a Target and Aim for Long-Term Persistence of Populations

Because historical fidelity may be an unrealistic or unattainable target, land managers and restoration practitioners may want to focus on ecosystem resilience and the long-term persistence of populations as alternative targets. A resilient system has the capacity to retain essentially the same function, structure, and feedbacks during and after perturbation (reviewed in Bestelmeyer & Briske 2012). Resilience is an emergent property of an ecosystem (Falk 2017) and arises from biodiversity and heterogeneity. Restoration and management for resilience should emphasize the creation or conservation of a range of site characteristics (i.e. niches or heterogeneity) that support high biodiversity at the landscape scale.

It is important to realize that biodiversity, not necessarily species identity, plays a critical role in ecosystem resilience (Folke et al. 2004). The identity and dominance of plant species at any given site in the NGP shift over time. At times over the

last 1,000 years, and specifically in the last 100 years, forbs were more prominent on the landscape (and in the pollen record) than grasses (Weaver & Albertson 1936; Grimm et al. 2011). Even when grasses were the most prominent vegetation on the landscape, shifts between C3 and C4 grass dominance have occurred (Clark et al. 2002). In this context, moving attention from the presence or absence of specific species to nontarget effects of management that might reduce overall native species richness and diversity is especially important.

When we can model the potential range of variability in the NGP, we can then identify refugia that provide heterogeneity on the landscape and allow persistence of unique or specialized populations and communities that can later expand during climate fluctuations. For example, wet areas formed by seeps or springs that can persist during a prolonged drought would provide a reservoir of species that can expand and provide resilience during wetter times. These refugia could be targets for protection (e.g. Anderson et al. 2014) as they preserve the raw ingredients for adaptation in the larger ecosystem. An effort is underway by The Nature Conservancy to map site resilience across the continental United States using geophysical characteristics and local connectivity (Anderson et al. 2014). The goal of this work is to identify representative sites across the different types of geophysical characteristics in each ecoregion that have the potential to support biodiversity long-term because of high niche diversity (e.g. high variability in topography or moisture gradients) and local connectivity that will allow species to move as climate and conditions change. This approach can inspire land managers to identify and protect areas that still have high biodiversity and resilience (Anderson et al. 2015).

Long-term persistence of populations requires genetic variability. Genetic variability can be promoted by maintaining or reestablishing connectivity among grassland patches to allow gene flow or if this is not possible, by augmenting gene flow. Connectivity among patches is important for populations to maintain the genetic variability that will allow them to adapt to changing conditions, shift geographic distributions (Frankham 1996; Booy et al. 2000), and adapt in natural systems (Heller & Zavaleta 2009). The extreme fragmentation of the NGP (discussed above) has decreased connectivity for numerous species of mammals and birds (Beckmann et al. 2012; Thompson et al. 2015). For species with short dispersal distances, such as many pollinators, even small decreases in connectivity may have dramatic impacts (e.g. Wimberly et al. 2018). We acknowledge that improving connectivity, as with all management actions, can have negative consequences (e.g. when corridors increase predation or invasion; Åström & Pärt 2013, Haddad et al. 2014), but in the context of the level of fragmentation in the NGP, benefits almost certainly outweigh risks.

In highly fragmented landscapes where creating connectivity may no longer be possible, augmenting gene flow may be necessary to maintain or recover genetic variability. Populations in small, isolated grassland patches are likely to experience drift and a decrease in genetic variability over time (Frankham 1995), and augmenting gene flow could help increase fitness and evolutionary potential. Restoration and management efforts augment gene flow by adding individuals to either extant, but

depauperate, populations or to areas where a species has been extirpated. In the case of vegetation, augmentation is most often achieved by adding seed. Often land managers and restoration practitioners try to use locally sourced seed assuming these will be locally adapted (e.g. Wilkinson 2001), but this assumption is not always valid (Galloway & Fenster 2000). Furthermore, given the already changing climate (discussed above), local adaptation to current conditions may not be optimal in the near future (Dunnell & Travers 2011; Mckenna et al. 2017). Current literature recommends the use of seed mixes from multiple sources in restorations, and some suggest climate matching of seed sources or increasing the size of seed zones as a strategy for restoration (McKay et al. 2005; Galatowitsch et al. 2009). Caution must be taken and managers or restorationists should seek to understand the system before automatically adding seed from diverse sources. However, increasing the pool of genetic diversity for native species used in restorations by mixing source populations provides a wider gene pool for natural selection (e.g. Carter & Blair 2013) and enhances the potential for climate adaptation (Etterson 2004).

Beware of Ecological Traps and Extinction Debt

Ecological traps, areas which are attractive to wildlife but cannot sustain populations (Battin 2004), may inadvertently be created during management or restoration of NGP grasslands. Restoration and management actions often fail to produce satisfactory results for wildlife, not only by failing to attract desired animals but more seriously, by attracting wildlife they cannot support (Hale & Swearer 2017). Ecological traps are especially problematic for wildlife with low population sizes and can cause rapid local extirpation or even extinction (Schlaepfer et al. 2002). A restored or managed fragment of grassland in a landscape otherwise dominated by agriculture may be an ecological trap due to anthropogenic chemicals, increased rates of predation (Phillips et al. 2003), and high levels of invasive species (reviewed by Ellis-Felege et al. 2013, discussed above).

Anthropogenic chemicals (including herbicides, insecticides, fungicides, and fertilizers) are abundant and diverse in the NGP. Although these chemicals are applied to crop fields, their presence in streams and windblown particles suggest that they are being transported outside crop fields and can move into grasslands, wetlands, aquifers, and, ultimately, the food chain (Mazak et al. 1997; Clay et al. 2000; Hallmann et al. 2014; Mahler et al. 2017). Sampling of streams in the Midwest United States detected 94 different pesticides (Van Metre et al. 2016; Nowell et al. 2018). Between 2013 and 2015, grasslands in the NGP received as much as 10–15 kg/ha annual total nitrogen deposition (wet and dry, National Atmospheric Deposition Program 2019). The western portions of the NGP generally receive less nitrogen deposition than the eastern portions; however, areas immediately adjacent to fertilized crops may receive substantially more nitrogen through soil erosion and water run-off from fields (DeSutter et al. 1998). Although these amounts of N are less than the recommended application rate for growing corn (Clark 2019), it is equivalent to an unwanted annual fertilization regime that is sufficient to elicit a response from grasslands.

The effects of this nitrogen deposition include: changes in plant community composition (Smart et al. 2013) favoring invasive species (Mattingly & Reynolds 2014); alteration of the structure and function of the soil microbial community (Ramirez et al. 2012) with a decrease in species that serve as mutualists to native plants (Van Diepen et al. 2010); and decreased root growth, which makes vegetation more vulnerable to drought (Valliere et al. 2017). Further, these anthropogenic chemicals are nearly always found in mixtures (e.g. 1,196 of 1,197 stream samples contained more than one pesticide; Nowell et al. 2018). Unfortunately, most ecotoxicity research is done with single chemicals, even though combinations of chemicals can produce synergistic effects on target organisms (Rizzati et al. 2016). Therefore, it may be wise for land managers and restoration practitioners in the NGP to monitor anthropogenic chemicals to ensure that lands they manage are truly providing benefit and not creating ecological traps.

Given the significant challenges in the NGP, grasslands are almost certainly accruing extinction debts (Kuussaari et al. 2009; Jackson & Sax 2010). Extinction debt refers to the time lag for a species to go locally extinct after conditions are no longer suitable to sustain the population (Tilman et al. 1994). Evidence for a large extinction debt in the NGP is mounting. Grassland songbirds as a guild have been declining for decades (Sauer & Link 2011), and the number of grassland species listed under the Endangered Species Act is increasing (e.g. Poweshiek skipperling [*Oarisma poweshiek*], Dakota skipper [*Hesperia dacotae*], and rusty patched bumble bee [*Bombus affinis*]). The longer-lived a species is, the less likely managers will be able to discern population shifts that signal extinction debt because individuals are still observed. Even harder to detect is the increased tendency for populations in grassland fragments to have low genetic diversity which will contribute to eventual extinction debt (Takkis et al. 2013). Therefore, managers and restoration practitioners need to constantly be mindful of the potential for extinction debt.

Employ Active Adaptive Management and Have Patience

Active adaptive management is seen by many as the gold standard for learning from restoration and management actions (Allison 2012). Adaptive management encourages land managers and restoration practitioners to change their focus from simply repeating the "tried-and-true" methods that are increasingly producing unsatisfactory results to analyzing the root cause of ecosystem changes and addressing them with carefully considered actions. Active adaptive management (Williams 2011) in the NGP requires models that test hypothesized mechanisms that create desired ecosystem changes. Ultimately, adaptive management sets up the potential for a thoughtful discussion about the balance among social, economic, and environmental values, the three pillars of sustainability. The vegetative community, in this context, is no longer simply an environmental component of sustainability, but rather a desired social norm that may be difficult to abandon, but that ultimately becomes economically impractical to sustain.

In the current dynamic system with no expectation of equilibrium, a further challenge is to impose conditions, via well-considered restoration and management actions, that allow a well-adapted, resilient native plant community to thrive and out-compete invasive species. Importantly, this community may not necessarily mimic historical communities at the site. Therefore, adaptive management is especially relevant and is, in fact, beginning to yield promising results (Moore et al. 2019). When many system parameters are changing simultaneously, beginning decision analysis with equally weighted models allows evidence to dictate model weights over time. This process, although slow, will begin to illuminate patterns of success that may be impossible to detect without a systematic monitoring and modeling approach. The process can be accelerated by simultaneously applying the models in many locations, as is being done in the Native Prairie Adaptive Management program in the Dakotas (Moore et al. 2013) and by the Grassland Monitoring Team in Minnesota (Ahlering et al. unpublished data).

Identifying the mechanistic models necessary for the practice of active adaptive management will be difficult, especially when mechanisms are in flux. A model that gains support initially may lose out to an alternative model several years hence, only to subsequently regain support, thus requiring a more dynamic form of adaptive management than most resource managers may be comfortable with (Williams & Brown 2016). Monitoring, always important for adaptive management, is even more crucial in this dynamic future. The goal is not only to learn how the target resource responds to management, but how that response changes with environmental variation which may be largely unpredictable. Appropriate management actions need to be taken at appropriate times: learning what *not* to do may be as important as learning what *to* do (Middleton et al. 2017).

Restoration and management efforts take time to produce results so patience is required. Recovery debt is the reduction of biodiversity and biogeochemical functions during the course of restoration (Moreno-Mateos et al. 2017). Grassland ecosystem components recover at vastly different rates: after 15 years, restored grasslands may only contain approximately 50% of the plant species abundance of reference sites (Moreno-Mateos et al. 2017) but carbon sequestration potentially requires more than 200 years to approach values found in native grasslands (Rosenzweig et al. 2016). Duck productivity may increase for 12 years after habitat restoration (Haffele et al. 2013) and native wild bee abundance and richness can reach levels comparable to remnant grasslands within 3 years after restoration (Griffin et al. 2017). New definitions of what full "recovery" looks like in the NGP will be important, both because the rate of recovery is slow and because the impacts of challenges are ongoing. A realistic assessment of the recovery of a grassland is needed to avoid overestimating status: restoration does not imply an immediate return to 100% function. Methods for assessing recovery over relevant spatial and temporal scales are key to informed management of the NGP.

Commitment to the long-term nature of the adaptive management process takes patience and persistence (Gannon et al. 2011). With long-lived perennial species and often 3–6-year prescribed fire return intervals, there are no quick fixes. The results of adaptive management may take many years to realize their potential. This can be challenging in the world of short-term budget cycles and frequent policy changes. With so little grassland left, land managers and restoration practitioners need to stay focused on long-term success by protecting the capacity for resilience where it still exists and using other strategies to help the system adapt where necessary.

Conclusion

Globally and specifically in the NGP, anthropogenic influence is ubiquitous and it is imperative that a paradigm shift in how we approach restoration and management occurs. Current alterations of ecosystems are immense and continuing at an unprecedented pace. The NGP, like many other ecosystems, is no longer a self-regulating adaptive system; it has been replaced by management units where we attempt to create the conditions and functions originally inherent in the ecosystem (Defries & Nagendra 2017). Alone any one of the challenges described above could cause the NGP to diverge from past ecological conditions, but we emphasize that the additive and likely synergistic effects from the numerous challenges facing the NGP will create a very different and dynamic future. To move confidently into this new future, we suggest land managers and restoration practitioners use historical conditions heuristically and embrace the goals of resilience and long-term population persistence. By adopting a broad perspective, managers and restoration practitioners can better achieve resilience with less likelihood of inadvertently constructing ecological traps or incurring extinction debts. Adaptive management that includes multiple stakeholders from the outset increases the likelihood of long-term sustainability. For the NGP to thrive into the future, all stakeholders need to embrace a philosophy of resilience, variability, and adaptive capacity. The focus needs to be on maintaining native diversity and function and its adaptive capacity at all scales. To maximize return on investment, the landscape must be the unit of consideration even if the management unit is much smaller and the goal must be to improve ecosystem function, native diversity, and connectivity. To achieve this result will require unprecedented cooperation among all stakeholders (e.g. Cong et al. 2014) and commitment to long-term vision and investments. Despite the numerous challenges facing the NGP, the naturally dynamic nature of this system will work in its favor as stakeholders strive to maintain the system's diversity and resilience.

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