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A Hierarchical Perspective to Woody Plant Encroachment for Conservation of Prairie-Chickens

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ABSTRACT

Encroachment of Great Plains grasslands by fire-sensitive woody plants is a large-scale, regional process that fragments grassland landscapes. Using prairie grouse (*Tympanuchus* spp.) of conservation concern, we apply hierarchy theory to demonstrate how regional processes constrain lower-level processes and reduce the success of local management. For example, fire and grazing management may be locally important to conservation, but the application of fire and grazing disturbances rarely cause irreversible fragmentation of grasslands in the Great Plains. These disturbance processes cause short-term alterations in vegetation conditions that can be positive or negative, but from a long-term perspective fire maintains large tracts of continuous rangelands by limiting woody plant encroachment. Conservation efforts for prairie grouse should be focused on landscape processes that contribute to landscape fragmentation, such as increased dominance of trees or conversion to other land uses. In fact, reliance on local management (e.g., maintaining vegetation structure) to alter prairie grouse vital rates is less important to grouse population persistence given contemporary landscape level changes. Changing grass height, litter depth, or increasing the cover of forbs may impact a few remaining prairie-chickens, but it will not create useable space at a scale relevant to the historic conditions that existed before land conversion and fire suppression.

Introduction

Many factors contribute to the fragmentation of rangelands, which is a primary cause of population declines in species endemic to these landscapes (Herkert 1994; Helzer and Jelinski 1999). Fragmentation describes the active conversion or separation of large tracts of a vegetation type or state into small isolated fragments that may have limited value for certain species (Pietz et al. 2009). Separation of habitat into smaller, more isolated units can lead to local extinction or regional declines because of limited dispersal among habitat patches (Herkert 1994). For populations of species such as grouse that rely on expansive landscapes, fragmentation can have dire consequences. Population declines of Lesser Prairie-Chicken *(Tympanuchus pallidicinctus)* and Greater Prairie-Chicken *(Tympanuchus cupido)* have been attributed to fragmentation from alteration of disturbance regimes (primarily fire) and the associated woody plant encroachment (Merrill et al. 1999; Wu et al. 2001; Fuhlendorf et al. 2002a; McNew et al. 2012).

One of the major challenges for conservation efforts of a myriad of species occurring on public and private lands is that the conditions that are critical for the support and restoration of a population often occur at many spatial scales that may or may not correspond to management scales (Wiens 1989; Fuhlendorf and Smeins 1996). For example, many grouse species have specific life history requirements that are proximally required and variable for different activities such as nesting, brood rearing, lekking, or roosting (Fig. 1). This local heterogeneity may be critical to maintain populations, but from a broader spatial and temporal perspective, large suitable landscapes that are connected to other populations may be more important for species persistence (Fuhlendorf et al. 2002a; Johnson et al. 2003). In fact, the size of the landscapes necessary for even a given population to persist often can exceed parcel size, making local management largely irrelevant if the landscape matrix is not suitable for the species of concern. Further, conservation practices at the more local scale (e.g., for a given parcel or landholding) can be quite different from those focused on broader scales and either population or species persistence. For example, local conservation practices may focus on conditions related to successful nesting or brood rearing while broader scale perspectives may focus on landscape composition and pattern that prioritize connectivity between local populations. While reproduction and survival at the local scale are obviously necessary for population persistence, they are inherently constrained by higher-order processes and are therefore a secondary concern to landscape-scale conservation efforts. As resources for conservation are always limited, it is critical that we prioritize conservation actions that

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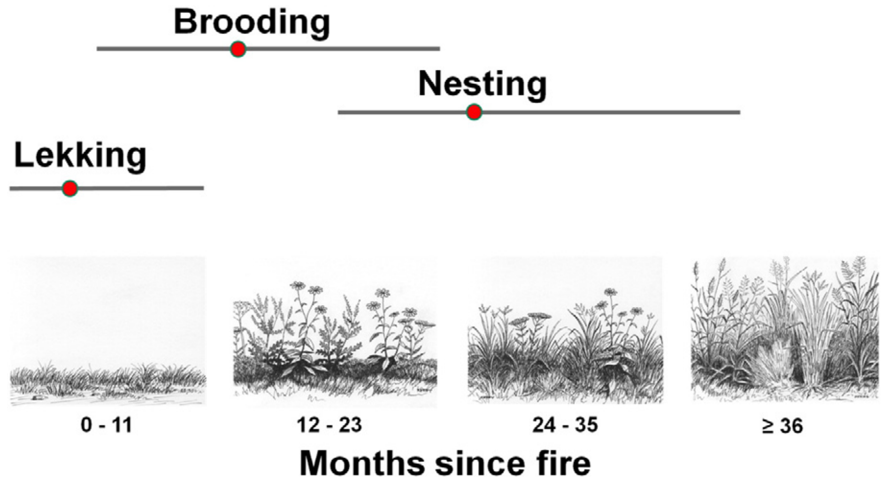

Figure 1. Median (red dot) and first and third quartile (lines) of sites selected by Greater Prairie-Chickens *(Tympanuchus cupido)* for lekking, nesting, and brood rearing, illustrating how different life history needs are met by various vegetation conditions. Data were collected at The Nature Conservancy's Tallgrass Prairie Preserve, OK, USA, 2010-2013. (Artwork courtesy of Gary Kirby.)

are most likely to be successful. It is the goal of this paper to provide a generalized framework to prioritize conservation from a landscape perspective for prairie grouse in the Great Plains.

How to Prioritize Conservation Practices on Rangelands

The range management discipline has focused traditionally on managing vegetation to sustain production of forage for the livestock industry (Holechek et al. 2004). Recently, an alternative approach that is based on conservation of pattern and processes on rangelands has been proposed (Fuhlendorf et al. 2012). This approach suggested the following principles: 1) maintain large continuous tracts of rangeland, 2) understand the importance of stocking rate while recognizing that no single rate is appropriate, 3) promote uneven distribution and understand heterogeneity, 4) promote shifting mosaics where disturbance patterns are variable in space and time, 5) recognize that all species are important to conservation, and 6) emphasize the importance of restoring disturbance regimes on large landscapes. In addition to the need for a new approach focused on conservation of rangelands, many other practices and actions on rangelands influence the ability of a landscape or region to support species of conservation concern.

A primary approach for prioritizing conservation is to use hierarchy theory, viewing habitat as a hierarchically nested organization of conditions and resources required by an organism, where all units are composed of subunits within larger subunits (Kolasa and Waltho 1998; Fuhlendorf et al. 2002a). This pattern results in a situation where broad-scale patterns constrain fine-scale processes and suggests that broad-scale conditions must be suitable before success (e.g., increased nest survival) can occur from finer-scale management actions. Through this framework, there is no justification for conducting local management if populations are constrained by higher-level fragmentation as the objectives will not be achievable until higher-order patterns and conditions are addressed relevant to the species of interest. Therefore, in fragmented landscapes, the major conservation focus should be on limiting additional fragmentation and attempting to identify the best places to reverse previous fragmentation. A first step in this process is to determine what constitutes fragmentation for the species of conservation concern.

When prioritizing factors that contribute to fragmentation, it would be most effective to first focus on factors that are at risk of crossing a threshold where reversal is unlikely (Fahrig 2001). This aims to limit additional and irreversible damage to landscapes and the species that require broad-scale continuity. For example, land cover/land use changes contribute to fragmentation, but if change is due to development from suburban conversion or cultivation, reversal of those changes is unlikely. Avoiding these kinds of nonreversible changes should be the initial goal of conservation, particularly when they occur at large spatial scales (Fig. 2). Once the landscape is largely converted, then the priority should be addressing the most at-risk and easily restored landscape elements that will provide the greatest connectivity. When landscape connectivity is maintained and large rangeland landscapes are intact, finer-scaled and reversible management focused on factors that influence proximal vegetation structure suitable for certain life history activities have a reasonable expectation of success (Fitzgerald and Tanner, 1992).

A hierarchical approach requires recognition of factors that alter conservation by constraining the success of local management. Broadly, we can categorize these into constraining and fine-scaled (proximal) management factors. The argument through hierarchy theory is that conservation should first focus on limiting constraining factors and then focus on the fine-scaled management. This process of classification

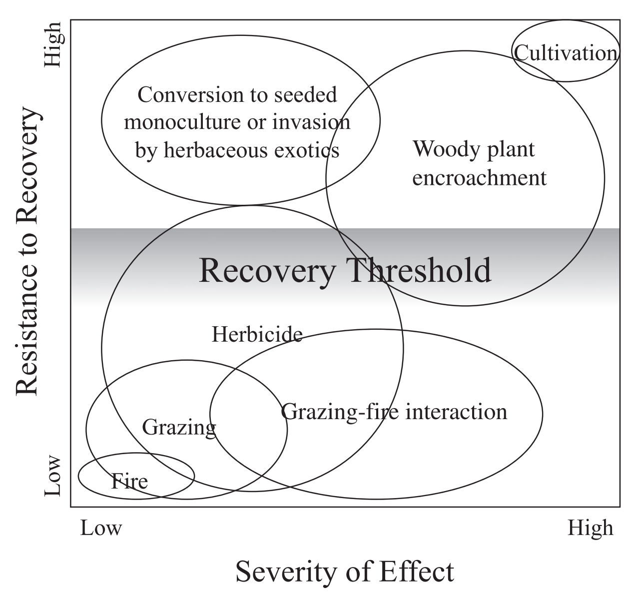

Figure 2. Descriptive matrix of categories of practices grouped by resistance to recovery and by severity of change. Size and shape of a sphere denote the relative severity of the change and influence of the disturbance practice on the resulting patch's resistance to recovery. The horizontal line marks a recovery threshold beyond which rangeland will not likely recover from the change. Rangelands subjected to change above the recovery threshold constrain the influence of local management practices.

will differ among species and regions, so it is important to develop specific case studies. For this paper, we focus on Lesser and Greater Prairie-Chickens in the Southern Great Plains, although the implications could be more broadly applied to many conservation issues on rangelands.

Fragmentation—The Constraining Factor for Grouse

Grouse species require large, relatively unfragmented landscapes that include local heterogeneity (Johnsgard 2002). Specifically, Greater Prairie-Chickens and Lesser Prairie-Chickens require expansive landscapes that resemble native vegetation and include local needs for activities such as nesting and brood rearing but also encompass year-round needs such as wintering, roosting, and lekking locations (Hovick et al., 2014a, 2014b; McNew et al. 2015). These patterns are not unique among prairie chickens. For example, similar findings have been reported for the Greater Sage-grouse *(Centrocercus urophasianus)* on rangelands of the western United States (Coates et al., 2015; Dahlgren et al. 2016). To promote the conservation of these grouse species, landscape-level models may be required to identify specific geographical areas with high potential to serve as core areas, while local-level models may be best for evaluating effects of site-specific management (i.e., local disturbances) within the landscape context (Coates et al., 2015). A key component for nesting ecology is fine-scale concealment at nest locations (Coates and Delehanty, 2010; Hovick et al. 2015a; McNew et al. 2015; Dinkins et al. 2016), but as we emphasize in this paper, filters at higher scales such as woody encroachment and land conversion need to be considered for population persistence (Fuhlendorf et al., 2002a, 2002b; Doherty et al., 2010). For purposes of this review, we keep our main focus on the Great Plains and the prairie grouse that occupy this region, but most of these principles apply to grouse found throughout rangelands, including sage grouse.

Historically, conversion of rangeland to cropland has caused the greatest alteration to the Great Plains (Samson and Knopf 1994). The widespread cultivation of grasslands is frequently cited as having permanently altered the Great Plains. This alteration represents the single greatest threat to sustainability of Great Plains grassland ecosystems and their fauna (e.g., Samson and Knopf 1994). Cultivation in particular has long-term consequences including soil erosion, increased decomposition, depletion of soil organic matter, and reduced site fertility (Tieszen et al. 1982; Aguilar et al. 1988; Burke et al. 1989). Because of these effects, recovery of native grasslands after cultivation, even with reseeding, is either slow or nonexistent in shortgrass prairie (Coffin et al. 1996; Hyder et al. 1971), mixed prairie (Fuhlendorf et al. 2002b), and tallgrass prairie (Collins and Adams 1983). Ecosystem processes, such as nutrient cycling, are irreversibly altered and nutrient status is reduced and cannot be restored even 50 + years after restoration seeding (Burke et al. 1989; Lauenroth et al. 1994; Fuhlendorf et al. 2002b).

Because of the long-term impacts of cultivation, conservation in the Great Plains must consider historical and current patterns of land conversion. In fact, the historical cultivation of native grasslands and shrublands is considered the primary factor in the decline of many sensitive conservation species within the Great Plains during the first century of European settlement. As an example, declines in prairie-chicken populations primarily occurred during this period as cropland exceeded thresholds suitable for maintaining natural cover necessary for nesting and brood-rearing (Crawford and Bolen 1976; Taylor and Guthery 1980; Johnsgard 2002). Establishing perennial grass and forb cover on former croplands has clearly benefited grassland passerines and prairie-chickens (Reynolds et al. 1994; Coppedge et al. 2001a; Matthews et al. 2013), but restoration of cultivated landscapes remains costly and socially constrained, suggesting that focusing on restoration of cropland may be less efficient (i.e., lower benefit-to-cost ratio) than other conservation activities (see Fig. 2) (Fuhlendorf et al. 2002a; Hellerstein and Malcolm 2011; Sohl et al. 2012; Feng et al. 2013). Identifying areas of high biological value that are at risk of conversion to cropland can help prioritize regional conservation efforts (Stephens et al. 2008).

From Texas to the eastern deciduous forest that borders the Great Plains, woody plants have encroached northward and westward because of changes in climatic conditions and widespread fire suppression (Briggs et al. 2005). This gradual and insidious encroachment has been described as a “green glacier” (Engle et al. 2008) and has converted grasslands and shrublands to woodlands, altering livestock production, ecological processes, and wildlife habitat (Coppedge et al. 2001a; Fuhlendorf et al. 2008). Conversion of grasslands to woodlands began more than 100 years ago and continues today on rangelands throughout North America and beyond (Twidwell et al. 2013). This increase has had profound impacts on grassland birds and prairie grouse in particular (Coppedge et al. 2001a). Specifically, landscapes with declining populations of Lesser Prairie-Chickens experience more large-scale fragmentation from factors like woody plant encroachment than landscapes with sustained populations (Fuhlendorf et al. 2002a). Similarly, Greater and Lesser Prairie-Chickens tend to maximize distance from trees when selecting nesting sites (Hovick et al. 2015a). So, while cultivation may have been the early contributor to fragmentation and may continue in some local areas, from a prairie-chicken perspective in the southern half of the Great Plains, the majority of active fragmentation is due to woody plant encroachment.

Multiple types of fragmentation exist throughout the Great Plains, and many of them are increasing (Engle et al. 2008; Fargoine et al. 2009). Woody encroachment throughout much of the Central and Southern Great Plains is approaching a threshold that will prevent the reintroduction of fire for effective management, thereby reducing the capacity for these areas to function as habitat for grassland obligate species (Fuhlendorf et al. 1996; Coppedge et al. 2001a; Fuhlendorf et al. 2008). Additionally, other sources of fragmentation exist as a result of landowner choice and federal programs where much of the cultivated land has been converted to monocultures of exotic perennial grasses (Laycock 1988; Leathers and Harrington 2010). Moreover, land use such as cultivated crops, biofuels production, energy development, and urban expansion are projected to dominate the Great Plains, which could further reduce native plant cover up to 36% by 2100 (Sohl et al. 2012). Large tracts of prairie will likely be restricted to land parcels where fire is a landscape management practice and where cultivation is not feasible or desirable. These changes have the potential to further reduce populations of obligate grassland fauna of the Great Plains and as a consequence reduce the effectiveness of local

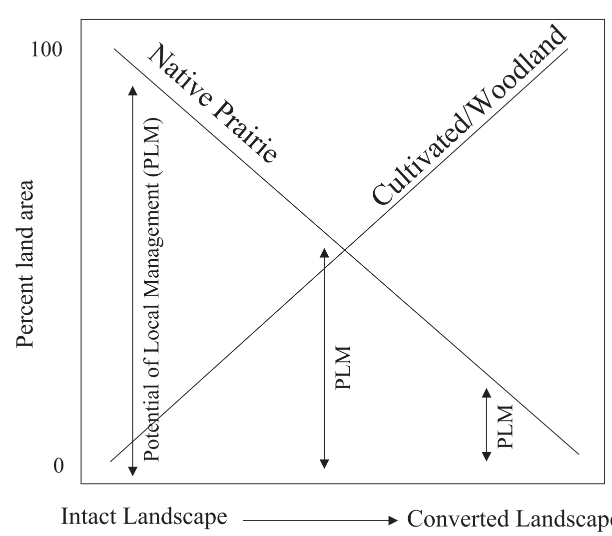

Figure 3. A model illustrating the application of hierarchy theory in which large-scale, regional factors (cultivation of grasslands or tree encroachment into grasslands) constrain the influence of local factors (management practices such as grazing or prescribed burning).

management practices applied for conservation purposes (Fig. 3). The cumulative sum of these changes to rangelands across the Great Plains has led to the endangered status of the Attwater's Prairie-Chicken *(Tympanuchus cupido attwateri),* which is a subspecies of the Greater Prairie-Chicken; formerly threatened status of the Lesser Prairie-Chicken; and reduced distribution and many statewide listings as a species of conservation concern for the Greater Prairie-Chicken (Robel 2004; USFWS, 2014).

An emerging and expanding constraint on prairie grouse inhabiting the Great Plains is the industrialization of rangelands through energy development. High levels of energy development are contributing to additional fragmentation for prairie-chickens, but additional data are needed to determine how and under what circumstances energy development constitutes fragmentation for these species. Existing data have reported mixed impacts of energy development on Greater Prairie-Chickens depending on the sex, life history stage, and other factors (Winder et al., 2013, 2014, 2015a, 2015b, but globally, energy development appears to have consistent, negative influence on grouse survival and behavior (Hovick et al., 2014a, 2014b). Moreover, it is apparent that a large amount of net primary production (i.e., biomass that functions as cover and food for prairie grouse) is lost to oil and gas development specifically, and this undoubtedly has direct effects on native flora and fauna as a result of direct habitat loss (Allred et al. 2015).

Proximal Management

Proximal management is focused on local objectives that could be based on the premise of improving livestock production or other local goals without consideration for effects at broader scales. These practices include most of the local management activities conducted by managers on rangelands, and while they can be locally successful for some objectives such as changing forage yield for livestock production, their success for other objectives is largely dependent on the constraining effect of landscape context. This is particularly true when considering prairie-chicken populations and the immediate effects of local landscape management interacting with short-term weather variables across landscapes with variable capacities to buffer these fine-scale effects (Hovick et al. 2015a; Winder et al., 2015a, 2015b; Hagen & Elmore, 2016).

When considering the potential effects of proximal management and the constraining effect of higher-order landscape features, it is necessary to understand the dominant historic disturbances within the Great Plains, which were fire (anthropogenic and lightning caused), climatic fluctuation, and grazing by mammalian herbivores (Anderson 2006). Additionally, the interaction between grazing animals and fire led to a feedback that resulted in heterogeneous landscapes that included burned and heavily grazed plant communities and ungrazed, unburned plant communities interspersed among many patches in variable successional stages (Fuhlendorf et al. 2009; Fuhlendorf and Engle 2001). This disturbance regime resulted in some level of local heterogeneity in terms of variable vegetation structure and composition, while limiting coarser fragmentation of grasslands by restricting most trees and fire-intolerant plants to drainages and rocky outcrops where fine fuels limited fire frequency. Great Plains landscapes were therefore dominated by grasslands that were a shifting mosaic of patches of various structure and composition following fire and grazing (Fuhlendorf and Engle 2001). For grassland birds, some species were best adapted to particular patches resulting from various time post disturbance while others with broader niche breadth occurred in all or most patch types (Knopf 1996a). The heterogeneity of vegetation types was critical to maintaining floral and faunal diversity across Great Plains landscapes. Some wildlife species such as prairie-chickens (see Fig. 1) and upland sandpipers (Sandercock et al. 2015) require multiple vegetation structure types to complete the annual stages of their life history. This shifting mosaic provided the vegetation structure required for the entire suite of breeding and nonbreeding birds that occupy grasslands in a particular region (Fuhlendorf et al. 2006; Hovick et al., 2014a, 2014b).

Over the past century, the rangeland profession has encouraged managing these landscapes with uniform grazing, and in some cases fire and herbicides, to promote homogenous plant communities dominated by a few key forage plant species (Fuhlendorf and Engle 2001; Fuhlendorf et al. 2012). On rangelands of the Great Plains, grazing and fire effects are largely reversible unless grazing intensity and duration are sufficient to promote erosion (Milchunas et al. 1988; Milchunas and Lauenroth 1993; Milchunas et al. 1994; Fuhlendorf and Smeins 1997; Fuhlendorf and Engle 2001; Fuhlendorf et al. 2009). On most grasslands, the dominant effect of grazing is altering the structure of vegetation that may be important for some wildlife species (Lauenroth et al. 1994; Knopf 1996b).

Herbicide applications for weed and brush control is another form of proximal disturbance that is widely recommended and frequently adopted to reduce species that are perceived as undesirable for maximizing cattle production (Vallentine 1989; Hanselka et al. 1990; New 1997). Herbicides used on woody plants in the Great Plains are often used to reduce the inherent structural complexity of the vegetation (Vinton and Collins 1997), which in some cases has been altered from historic conditions due to changes in both fire and grazing regimes (Fuhlendorf and Engle 2001). Changes in the woody plant structure and composition can change the availability of food and cover for some wildlife including prairie-chickens (Koerth 1996). As mentioned earlier, limiting woody plants can maintain connectivity of grasslands, and in the case of some species like mesquite (*Prosopis glandulosa* Torr.), herbicides are an important option for management. For other plants, such as juniper species in the Great Plains, herbicides are largely ineffective and fire may be more appropriate. Other species that may be targeted by herbicides include edaphically limited native shrubs such as shinnery oak (*Quercus havardii* Rydb.) and sand sagebrush (*Artemisia filifolia* Torr.), which are critical to conservation of some populations of prairie chickens in the Central and Southern Great Plains (Lauenroth and Milchunas 1991; Boyd and Bidwell 2001; Harrell et al. 2001; Patten et al. 2005; Thacker et al. 2012). Beyond application of herbicides for woody plants, herbicide is often targeted toward herbaceous dicot species (Fuhlendorf et al. 2009). Unfortunately, many of these targeted dicot species provide food both directly and indirectly to prairie-chickens, as well as provide important cover for broods. Herbicide application can produce variable-edge contrasts and have variable resistance to recovery depending on the specific action and the conditions at time of application. Therefore, it may constitute either low or moderate severity of disturbance, but in some cases these vegetation types can cross a recovery threshold that will take decades to change (Thacker et al. 2012).

All of these proximal management practices have variable effects on conservation of landscapes, and some are more useful depending on conservation and other societal objectives. In general, these traditional management actions are usually applied for local management objectives rather than focused on promoting connectivity of the landscape. There are various reasons that local management is often the focus, including parcel size, additional objectives such as livestock grazing, and cost-share programmatic structure. Nevertheless, it is critical to recognize that grazing and vegetation management that is focused on conservation will have limited positive influence when broader-scale patterns have not been considered.

Conservation Priorities and Management Implications

For long-term sustainability of rangeland endemic fauna, conservation strategy must shift from focusing primarily on locally recommended management to a regional focus on preventing high-severity change that contributes to nearly irreversible fragmentation of the Great Plains. Application of hierarchy theory suggests that regional processes will constrain lower-level processes and reduce the success of proximal or local management (see Fig. 3). Because fragmentation is a regional process, local management focused on prescribed grazing and grassland condition will fail to maintain populations of rangeland endemic wildlife when higher-level processes such as tree encroachment and land conversion are fragmenting large landscapes (Hovick et al. 2015a).

Resources are limited to support conservation and management. Therefore, we propose setting conservation priorities based primarily on a sites capacity to recover from changes that have occurred. Although severity of effects or landscape change is generally a local concern for land management, the overriding issue for regional conservation is the propensity for rangelands to recover from a particular event (see Fig. 2). Landscape change on sites that have the lowest likelihood of recovering should be given the lowest priority because without reversal, the impacts on Great Plains endemic fauna such as prairie-chickens may be nearly irreparable. Change that fragments rangelands such as conversion to cropland, increased dominance of trees, industrialization, some herbicide applications, seeding of invasive herbaceous monocultures, and increased dominance of exotic invaders are all examples of landscape-level change in the top-tier hierarchy that should be the primary conservation focus if prairie-chickens are an objective. Measurements of and management to change metrics such as stubble height, litter depth, bare ground, plant diversity, and percent cover by functional group are of secondary concern for prairie grouse. Conservation discussions, planning, and expenditure of resources should therefore follow in a logical hierarchal approach. Some changes, especially exotic plant invasions and native tree encroachment, contribute to habitat loss and the demise of many bird populations (Coppedge et al. 2001b; Fuhlendorf et al. 2002a), and others (fire and the fire-grazing interaction) contribute to habitat restoration and can increase diversity and stability in native communities (Hovick et al. 2015b; McGranahan et al. 2016). Fire and grazing management may be locally important to conservation, but these disturbances rarely cause irreversible fragmentation of grasslands (see Fig. 2). In fact, periodic fire and the fire-grazing interaction are processes critical to the maintenance of grassland dominance (Vinton and Collins 1997; Fuhlendorf and Engle 2001; Anderson 2006).

The most efficient approach to conserving the endemic biota of the Great Plains is to prevent changes that are long term and challenging to reverse for socioeconomic reasons. Restoring cultivated land and rangelands that have been invaded by exotic species or mature woody plants is expensive and is unlikely to meet the goal of complete restoration within a meaningful management timeframe (i.e., several decades). Cultivation has largely fragmented the Great Plains, yet over the past several decades, cultivated land has decreased in some regions because of government programs and many of the remnant prairies remain uncultivated because of topo-edaphic limitations. In contrast, invasive exotic species and encroaching trees have increased on remnant, native grasslands throughout the Great Plains (Briggs et al. 2002; Briggs et al. 2005; Engle et al. 2008). Thus, a top conservation priority for the long-term persistence of native Great Plains' biota, especially prairie-chickens, should be focused on limiting future cultivation of rangeland and encroachment by woody plants that would increase fragmentation of these landscapes.

A common logical error in reasoning that is relevant to developing conservation priorities is the survivorship bias, which focuses on people or things (i.e., stocks or companies) that have survived and inadvertently ignores those that have not persisted (Gazley and Guo 2015). In wildlife conservation, we often focus on studying species in landscapes where the species has persisted rather than trying to understand where it once existed but is no longer present. For example, the vast majority of the historical distribution of the Lesser Prairie-Chicken has experienced woody plant encroachment from fire suppression, and this encroachment has been a primary cause of decline in the species across its historical range (Fuhlendorf et al. 2002a). Changing grass height or litter depth or increasing the cover of forbs may impact a few remaining prairie-chickens, but it will not create useable space at a scale relevant to the historic conditions that existed before land conversion and fire suppression. Without a retrospective perspective, studies of a species response to changing landscapes will rarely be able to demonstrate the primary causes of the decline. For prairie-chickens, the factor that has driven landscape changes for the past 50 years (encroachment of woody plants) is also currently the dominant driver of fragmentation of the Southern Great Plains and when combined with historical patterns of cultivation encroachment of woody plants remains the dominant threat to rangelands of the region. In this context, the study of vital rates in response to proximal management that changes herbaceous vegetation structure is trivial when compared with conversion of millions of hectares of rangelands to nonhabitat for grouse. In summary, if prairie-chicken persistence is a conservation goal, a continuing focus on local conditions has a low probability of success but also diverts limited resources from addressing the driving sources of continued decline. While many in the conservation community have acknowledged that landscape factors are critical, it is time to act on these convictions if imperiled prairie grouse are to recover.

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