Chapter 5
Heterogeneity as the Basis for Rangeland Management

Samuel D. Fuhlendorf, Richard W.S. Fynn, Devan Allen McGranahan, and Dirac Twidwell

> *Most people view averages as basic reality and variation as a device for calculating a meaningful measure of central tendency ……. **Central tendency is a harmful abstraction and variation stands out as the only meaningful reality***
>
> —Stephen Jay Gould- Full House: The Spread of Excellence from Plato to Darwin

Abstract Rangeland management, like most disciplines of natural resource management, has been characterized by human efforts to reduce variability and increase predictability in natural systems (steady-state management often applied through a command-and-control paradigm). Examples of applications of traditional command and control in natural resource management include wildfire suppression, fences to control large ungulate movements, predator elimination programs, and watershed engineering for flood control and irrigation. Recently, a robust theoretical foundation has been developed that focuses on our understanding of the importance of variability in nature. This understanding is built upon the concept of heterogeneity, which originated from influential calls to consider spatial and temporal scaling in ecological research. Understanding rangeland ecosystems from a resilience perspective where we recognize that these systems are highly variable in space and time cannot be achieved without a focus on heterogeneity across multiple scales.

S.D. Fuhlendorf (✉)
Natural Resource Ecology & Management, Oklahoma State University, Stillwater, OK 74078, USA
e-mail: sam.fuhlendorf@okstate.edu

R.W.S. Fynn
Okavango Research Institute, University of Botswana, PVT Bag 285, Maun, Botswana

D.A. McGranahan
Range Science Program, North Dakota State University, Fargo, ND, USA

D. Twidwell
Agronomy & Horticulture, University of Nebraska-Lincoln, Lincoln, NE 68583, USA

We highlight the broad importance of heterogeneity to rangelands and focus more specifically on (1) animal populations and production, (2) fire behavior and management, and (3) biodiversity and ecosystem function. Rangelands are complex, dynamic, and depend on the variability that humans often attempt to control to ensure long-term productivity and ecosystem health. We present an ecological perspective that targets variation in rangeland properties—including multiple ecosystem services—as an alternative to the myopic focus on maximizing agricultural output, which may expose managers to greater risk. Globally, rangeland science indicates that heterogeneity and diversity increase stability in ecosystem properties from fine to broad spatial scales and through time.

Keywords Scale • Landscape ecology • Hierarchy • Pattern • Disturbance • Resilience

5.1   Introduction

The modern era of natural resource management has been characterized by human efforts to reduce variability and increase predictability in natural systems. This command-and-control paradigm is an extension of societal attempts to identify problems and design and apply solutions to control or mitigate those problems (Holling and Meffe 1996). Examples of command and control in natural resource management include wildfire suppression, fences to control large ungulate movements, weed control for herbaceous native forbs, predator elimination programs, and watershed engineering for flood control and irrigation, including dams, terraces, and subsurface tile drainage. Each of these practices employs human technology to attempt to modulate and regulate the spatial and temporal distribution of resources and complexity of ecological processes. As a result of these attempts (and others), modern natural resource management has created more simple and homogeneous landscapes, which have been considered to be more economically productive due to their perceived increase in predictability. Alongside resource homogenization, land subdivision, fences, transport networks, growing human populations, and other forms of development are increasingly fragmenting ecosystems into smaller management units (Hobbs et al. 2008).

Paralleling command-and-control management is a scientific paradigm that likewise seeks to control or even eliminate variation. Generations of scientists have been trained to design experiments that control all variations except for that which is expected to drive the hypothesized differences. Extreme examples are greenhouse studies and small plot studies that attempt to control for weather and spatial variation, even though we are studying systems that are often described as non-equilibrial and interconnected with other systems. Data from such experiments have most often been subjected to Fisherian statistics, which describe differences between groups in terms of variation around mean values. These models have tra-

ditionally considered variation only as a nuisance parameter that is only useful to calculate an accurate mean, rather than a critical parameter in itself. These factors have contributed to a scientific discipline that has tendencies to reduce variation and study small plots, rather than embracing variation and studying complex landscapes at multiple scales.

Yet natural systems are subject to a host of biotic and abiotic processes that shape these landscapes ranging from broad-scale, long-term changes in climate to more localized, short-term events such as droughts, floods, and fires (Fig. 5.1). Over time these factors have created complex systems in nature with a high degree of spatio-temporal variability associated with topography, soils, climate, weather, and disturbance regimes overlain with a diversity of plant and animal communities. Consequently, management seeking to maintain homogeneity presents a major quandary, and often comes at substantial cost, because it is attempting to override the inherent heterogeneity of rangelands and the behavior of disturbances. Considerable money and energy are spent attempting to minimize heterogeneity. Rangeland managers have long sought to override variability in nature with management infrastructure (e.g., fencing, water provisioning) and by controlling disturbances (e.g., channeling or damming water courses and suppressing fires). Despite these efforts, disturbances such as fire, flooding, and drought continue to create variation in systems managed for equilibrium, although the variability is structured differently. This has led to a prevailing view that such disturbances are destructive threats to production systems.

Fig. 5.1 The complexity of rangeland landscapes is a consequence of varying topo-edaphic characteristics and disturbance patterns, including land use. Photo by Sam Fuhlendorf

A robust theoretical foundation now underlies our understanding of the importance of variability in nature. This understanding is built upon the concept of heterogeneity, which originated from influential calls to consider spatial and temporal scaling in ecological research (Wiens 1989; Levin 1992), that resulted in the field of landscape ecology (Urban et al. 1987; Turner 1989; 2005). As a consequence, heterogeneity has become a familiar concept in the study and management of landscapes. But heterogeneity has only recently become appreciated as a component of ecological systems, and adopting it as a guiding principle for ecosystem management has been slow. Obstacles to heterogeneity-based management and policy stem from problems associated with understanding the concept, inconsistent definitions and measurement, as well as a general affinity for homogeneity of landscapes associated with command-and-control management to optimize efficiency.

The intentional simplification and fragmentation of landscapes have contributed to a limited understanding of variability and complexity. In this chapter, we synthesize the current status of rangeland science and management demonstrating the importance of heterogeneity in rangeland ecosystems and the limitations of homogeneity-based management approaches. This chapter is organized into the following sections. First, we discuss how heterogeneity is defined and measured. Second, we use case examples from rangeland research in North American and sub-Saharan Africa to address the following questions: (1) How does heterogeneity support faunal diversity and abundance? (2) How is heterogeneity critical to ecosystem function? (3) How is heterogeneity featured in policy and management? We end by offering suggestions as to how heterogeneity may represent the cornerstone to rangeland management, which should support a large degree of spatial and temporal variability.

5.2 Heterogeneity and Scale: Concepts Linking Pattern and Process

Because heterogeneity is largely associated with spatial and temporal variation of pattern–process relationships, heterogeneity depends on the scale of measurement or observation. Thus, heterogeneity cannot be operationalized without explicit consideration of scale—both in time and space. A widely accepted approach is to measure and evaluate heterogeneity across several scales (Senft et al. 1985; Fuhlendorf and Smeins 1999). Still, studies that have actually evaluated hierarchical relationships between the scale of heterogeneity and the structure and function of rangeland ecosystems are very limited. In this section, we discuss (1) the different types of heterogeneity and (2) the sources of heterogeneity contributing to variation in rangeland ecosystems.

5.2.1   Types of Heterogeneity

5.2.1.1   Measured vs. Functional

Measured Heterogeneity. This is a measure of the variability of an ecological property or process without explicit relations to variability in animal behavior or ecological function (Li and Reynolds 1995). Measured heterogeneity is the product of the perspective of the observer and dependent on sampling protocols and arbitrary decisions of experimental design. For example, a study conducted with meter square sampling plots uniformly or randomly distributed that calculates the variation among this arbitrary plot size and arrangement should be described as measured heterogeneity. Studies that considered multiple levels of arbitrary or measured heterogeneity have demonstrated considerable differences in the measured response of an ecological property or process across multiple scales of studies (Wiens 1989; Fuhlendorf and Smeins 1999). These measures can be useful for understanding how important patterns and processes change with scale. However, measured heterogeneity can only be used to infer ecological function since relationships are arbitrarily established and may, in fact, have little relevance to the ecological questions of interest. Also, if the range of scales measured does not include the appropriate scale to describe the relationship, we can erroneously conclude an inappropriate value of heterogeneity in describing the process.

 Functional Heterogeneity. This is variability at a scale that influences the function of a specific ecological property or process (Li and Reynolds 1995). Because the ecosystem properties that are important to a beetle are not the same as those that are important to a fox or an elk, the scale of heterogeneity relevant to their behavior differs among species. Also, patterns driven by climate fluctuations occur at differing scales than topo-edaphic features or local pathogen outbreaks. Functional heterogeneity assumes that scale of variability is determined by the ecological entity of interest, and is based on the perspective of the participating ecological entities, not the perspective of the ecologist.

 The functional heterogeneity concept suggests that rather than asking if a species or process responds to heterogeneity, the more relevant question is what types, patterns, and scales of heterogeneity are important to a species or process of interest (Kolasa and Rollo 1991). Experiments demonstrate that functional heterogeneity has greater potential to explain variability in the relationship between pattern and process than measured heterogeneity (Gómez et al. 2004; Twidwell et al. 2009). But functional heterogeneity requires greater knowledge of pattern–process relationships and often demands more sampling effort. In the face of such limitations, measured heterogeneity and establishment of arbitrary sampling points across multiple spatial or temporal scales have the potential to identify likely scales of interaction between pattern and process. Measured heterogeneity can therefore be a useful step toward understanding the spatiotemporal scales at which functional heterogeneity emerges (Twidwell et al. 2009).

Linking pattern and process through a lens of functional heterogeneity is extraordinarily rare in rangeland research and monitoring. Random sampling points are used to satisfy assumptions of independence for commonly used statistical analyses (e.g., analysis of variance, ANOVA). But heterogeneity occurring within the study area can lead to misinterpretations from arbitrary sampling approaches and produce erroneous results. This occurs because a fundamental assumption of many sampling procedures and statistical analyses is that heterogeneity within experimental units is not present or unimportant and the ecological property or process of interest operates uniformly across experimental units. While small homogeneous plots can have some value, it is important to recognize that ecological processes rarely operate in this way.

5.2.1.2   Spatial vs. Temporal

Landscapes consist of variable patterns and processes that are dynamic in space and time and lead to complexity that is an essential characteristic of rangelands. *Spatial heterogeneity* refers to how an ecosystem property—nutrients, vegetation type, or amount of cover—varies among points within the landscape. *Temporal heterogeneity* is similar but refers to variability at one point in space over time. When we consider heterogeneity we often consider spatial and temporal heterogeneity separately for statistical and logistical reasons, but in nature they are largely inseparable. For example, if temporal heterogeneity differs between two locations, the locations are also spatially heterogeneous (Kolasa and Rollo 1991). Furthermore, when patch types change positions within the landscape—which often occurs at some spatial and temporal scale in nature because ecosystems are not static—then heterogeneity is changing over both space and time.

A third scenario is the shifting mosaic, in which a specific set of patch types shift across space over time, such that the same *type* of patch occurs in each time step but never in the same *space* in consecutive time steps. In such cases, spatial heterogeneity within the landscape is conserved over time. Although the pattern of bison following burned areas of the pre-European North American Great Plains has become a model for the shifting mosaic, the phenomenon has been repeatedly shown to drive the conservation of pattern–process relationships and the functioning of rangeland ecosystems (Fuhlendorf et al. 2012). Experimental and statistical norms limit our ability to understand landscapes that are highly dynamic in space and time and overcoming these norms is an important challenge to producing usable science on rangelands.

5.2.2   Sources of Heterogeneity

Heterogeneity in rangeland landscapes arises from two main sources. *Inherent heterogeneity* is variability driven by abiotic factors such as geology and topo-edaphic variation influenced by factors such as soil depth, soil fertility, and soil water

availability that ultimately contribute to patterns of vegetation composition, productivity, and nutrient content (McNaughton and Banyikwa 1995; Fynn et al. 2014). *Disturbance-driven heterogeneity* is variability influenced by processes such as fire and grazing. These effects can be temporary or persistent and are strongly interactive. On rangelands, a heterogeneous patchwork of vegetation conditions can result from differential timing of disturbances and corresponding out-of-phase succession among patches (Fuhlendorf and Engle 2004); spatial heterogeneity of resources associated with rainfall (Sala et al. 1988; Hopcraft et al. 2010); topo-edaphic patterns (Acres et al. 1985; Scoones 1995); or competitive interactions among plant species (Fuhlendorf and Smeins 1998).

5.2.2.1 Inherent Heterogeneity

Rangelands are inherently heterogeneous in that community composition, productivity, and diversity can vary across scales ranging from centimeters to continents (Fuhlendorf and Smeins 1999; Fuhlendorf et al. 2009). Several environmental factors drive spatial heterogeneity in plant community composition (through competition or tolerance), which can in turn create functional heterogeneity. For example, soil fertility, as influenced by geology and landscape position, plays an important role in determining nutrient concentrations in grasses. In some cases higher clay fertility soils derived from weathered, mineral-rich rock (e.g., dolerite or basalt) promote higher concentrations of protein and minerals in grass tissue than sandy, leached soils derived from sandstone and granite (Hopcraft et al. 2010). High soil salinity can inhibit growth while providing an excess of minerals for uptake by grasses (e.g., McNaughton and Banyikwa 1995; Murray 1995; Grant and Scholes 2006). Another, illustrative example is that patterns in soil depth that can occur at fine or broad spatial scales can lead to differences in species composition that may be as important as and interactive with disturbance processes (Fuhlendorf and Smeins 1998).

In terms of local plant productivity, the effect of geology depends on landscape position. In some cases, deep moist and fertile soils in bottomland positions promote the growth of taller, more productive grasses (Briggs and Knapp 1995; McNaughton and Banyikwa 1995). On shallow but fertile soils in some uplands there may be strong moisture limitation of growth (McNaughton and Banyikwa 1995). From a herbivore perspective, short, leafy grasses often provide higher forage quality (digestibility and nutrient concentrations) than taller grasses (O'Reagain and Owen-Smith 1996; Coetsee et al. 2011), but taller grasses in wetter sites can provide an important source of biomass during the resource-limited dry season. Consequently, functional heterogeneity for herbivores is distributed along forage productivity gradients with high-quality forage needed to satisfy the high-resource demands of herbivores during calving, lactation, and growth occurring in less productive sites but forage to sustain livestock maintenance during the dry season occurring in more productive sites (Maddock 1979; Hopcraft et al. 2010; Fynn et al. 2014).

Inherent heterogeneity at the scale of variable ecological sites dominates discussions of heterogeneity within rangeland landscapes. These patterns of sites are characterized by differences in plant communities and different responses to disturbances such as fire and grazing. Ecologists and soil scientists working with these sites recognize that patterns exist within sites and at broader scales, but this resolution was based on the ability to map soils and other features. The spatial scale of mapping sites is arbitrary indicating that this is measured heterogeneity, rather than functional heterogeneity, which makes its relevance to management and society dubious.

5.2.2.2   Disturbance-Driven Heterogeneity

Ecologists understand that rangeland ecosystems evolved with disturbances, including fire and grazing, but the spatial patterns and heterogeneity of these disturbances were not recognized until recently (Fig. 5.2). Research on spatial and temporal heterogeneity in rangelands has been motivated by loss of habitat for species of conservation concern, as well as the recognition that animals need to be able to respond to extreme climate events through behavior (Allred et al. 2011). Many of the wildlife species that are declining on rangelands today likely evolved with conditions that are best described as heterogeneous across many spatiotemporal scales and are largely driven by disturbance.

Disturbances like fire or prairie dog colonization create feedbacks in which heterogeneity influences subsequent disturbance—the effect or condition of a patch in

Fig. 5.2 Fire interacts with topography and other disturbances to produce a shifting mosaic that is variable in fire severity and time since fire. This landscape in British Columbia was modified by prescribed fire. Photo by Sam Fuhlendorf

one spatial context at a given time not only depends upon the nature of other patches in previous times, but also influences patches at future times. Patterns created by feedbacks are either shifting continuously or relatively stable, and can even vary between the two at different scales. For example, the shifting mosaic created by fire-grazing interaction in tallgrass prairie induces great contrast between patches within a single season, but little permanent change in plant community composition at broad spatial scales through time (Fuhlendorf and Engle 2004; Fuhlendorf et al. 2009). Alternatively, if grazing is sustained in sufficient intensity on certain portions of the landscape or uniformly across the entire landscapes, shifts in plant communities—such as compositional changes from tall grass species to short grass species—are either permanent or at least persist through the duration of the disturbance and may require decades to change to their former composition (Knapp et al. 1999; Archibald et al. 2005). Examples include the white rhinoceros-moderated grazing lawns in South Africa's Hluhluwe-iMfolozi Park (Coetsee et al. 2011) as well as within spatially discrete bison patch grazing in tallgrass prairie (Knapp et al. 1999). With domestic herbivores, long-term changes in composition and structure are often the result of constant grazing distribution from water distribution patterns or promotion of more uniform grazing through cross-fencing.

5.3 Heterogeneity and Rangeland Function: Three Major Cases

In this section, three major cases are presented to demonstrate the importance of heterogeneity. These are just a few examples but understanding heterogeneity is essential for most major rangeland functions. These cases are (1) herbivore population productivity and stability, (2) fire and rangeland ecosystems, and (3) biodiversity and ecosystem function.

5.3.1 Heterogeneity and Herbivore Populations

Herbivores must be able to move across a landscape to deal with stressors associated with availability of resources (water and forage) as well as thermal stress or predation (Allred et al. 2011). Simplification or fragmentation can result in smaller units that will limit an animal's ability to use its behavior to deal with stress that can be cyclic and predictable or stochastic. Smaller pastures or land fragments result in less inherent variation within each pasture and potentially more inherent variability among pastures (Wiens 1989). This shift in variability results in a fundamental change in management required to sustain and match primary and secondary productivity. Small management units suggest a need for greater knowledge and management control of animal requirements and

availability of forage quality and quantity, as well as refugia from thermal stress or predation. Consequently, smaller management units will often require greater economic and management inputs—supplementary feeding, licks, and controlled movement—to compensate for limited adaptive foraging options available to herbivores on large landscapes. Larger management units enhance an animal's ability and freedom to respond to variable requirements and the changing environment without management interference (Hobbs et al. 2008). Wild and domestic herbivores, whether grazers or browsers, must cope with elevated requirements for protein, energy, and minerals during certain life stages (Murray 1995; Parker et al. 2009) that may not match resource patterns due to weather and plant phenology, especially when landscapes are small and compartmentalized (Ellis and Swift 1988; Owen-Smith 2004). It is critical that we understand that periods of limited forage biomass and quality may be most important to herbivore populations, rather than average conditions across space and time (Hempson et al. 2015).

Landscape or regional-level variability in plant community composition and productivity—inherent and/or disturbance driven—is important on many rangelands. For example, on African rangelands high-quality short grass sites provide excellent wet-season grazing, but they generally provide little growth and forage during dry periods (McNaughton and Banyikwa 1995; Fynn et al. 2014). By contrast, greater soil moisture availability for dry-season forage production is found in low-lying, poorly drained positions in the landscape such as various wetland types and floodplains (Vesey-FitzGerald 1960; Pamo 1998), as well as in high-rainfall regions receiving significant rainfall during the dry season (Breman and de Wit 1983; McNaughton and Banyikwa 1995). Shallow water tables of wetland sites enable perennial grasses to regrow after fire in the dry season, thereby providing quality regrowth for herbivores (Vesey-FitzGerald 1960; Fynn et al. 2014). Access to green regrowth after fire in the dry season may greatly increase dry-season protein intake for herbivores (Parrini and Owen-Smith 2010). In the absence of fire, taller coarser grasses may be left uneaten, thereby forming a drought-refuge resource for herbivores if rains fail. Such uneaten resources of productive perennial grasses can buffer herbivore populations against the effects of drought, despite their low quality, and have been referred to as buffer resources (Owen-Smith 2002) or key resources (Illius and O'Connor 2000). Loss of access to these key resource areas can result in herbivore population crashes during droughts (Fynn and Bonyongo 2011). Soil texture also plays an important role in facilitating moisture available for growth during the dry season with sandy soils generally supporting growth later into the dry season than clay soils (Sala et al. 1988; McNaughton and Banyikwa 1995). Heterogeneity in clay and sandy soils across landscapes contributes to variation in soil water availability and habitat productivity on strongly developed catenas. When these inherent patterns interact with disturbances such as fire, functional heterogeneity and adaptive foraging options for herbivores are maximized allowing animals to deal with environmental stress. It is important to note that pastoralists of West Africa and wild herbivores that share landscapes follow similar

seasonal patterns across large regions indicating that both may have converged on key ecological indicators reflecting seasonal functionality of habitats along various ecological gradients and importance of broad-scale spatial patterns to herbivore-dominated landscapes (Vesey-FitzGerald 1960; Jarman 1972; Pamo 1998; Bartlam-Brooks et al. 2011).

Similar patterns in grassland productivity-driven heterogeneity are seen in North American prairies on landscape-scale soil depth gradients (Briggs and Knapp 1995) and regional-scale rainfall gradients. Elevation and the associated temperature gradients provide another key source of functional heterogeneity by prolonging the length of time during which herbivores have access to forage at peak nutritional quality (Hobbs and Gordon 2010). Warmer conditions and less snow accumulation at lower elevations result in forage growing earlier in spring than at higher altitudes but also maturing and losing quality earlier such that the highest quality forage will move in a "green wave" up the altitudinal gradient over summer as the snowline recedes (Frank et al. 1998; Hobbs and Gordon 2010). Livestock in transhumance systems as well as wildlife such as bison, elk, and bighorn sheep track this high-quality green wave upslope into higher altitude regions during the growing season (Festa-Bianchet 1988; Albon and Langvatn 1992; Frank et al. 1998; Omer et al. 2006; Hebblewhite and Merrill 2007). If forage across the available landscape all matured at the same time then herbivores would have a much shorter period of access to optimal quality forage over the growing season (Hobbs and Gordon 2010). The ability of herbivores to migrate and track the early phenology peak-quality forage in relation to increasing altitude and variation of aspect has been demonstrated to result in increased body size of red deer compared to nonmigratory individuals (Albon and Langvatn 1992; Mysterud et al. 2001).

In the absence of disturbance-driven patches of high-quality forage patches, large regional- and landscape-level movements may be required for a foraging animal to be able to access alternate forage resources and sustain year-around diet quality and quantity. The spatial scale at which heterogeneity is distributed determines the distance that herbivores need to move to forage adaptively over the annual cycle. Disturbance can further enhance heterogeneity at community, landscape, and regional scales by modifying grassland structure and forage quality (Fuhlendorf and Engle 2004). As landscapes are made smaller from fragmentation and compartmentalization, promoting highly variable disturbance patterns to provide greater heterogeneity becomes even more important.

In conclusion, heterogeneity associated with large and complex landscapes enables herbivores to optimize energy and nutrient intake rates during key growth periods of pregnancy, lactation, and body growth while minimizing losses of gains in body mass or population size during resource-limited periods such as the dry season, hot summers, or extreme winters. In addition to diet, herbivores must simultaneously moderate thermal stress and maintain access to water, which is a function of the interaction between the type of animal and its grazing environment (Fig. 5.3; Allred et al. 2011). Similarly, empirical studies have demonstrated much lower mortality of wildlife and livestock during drought years if they have greater access
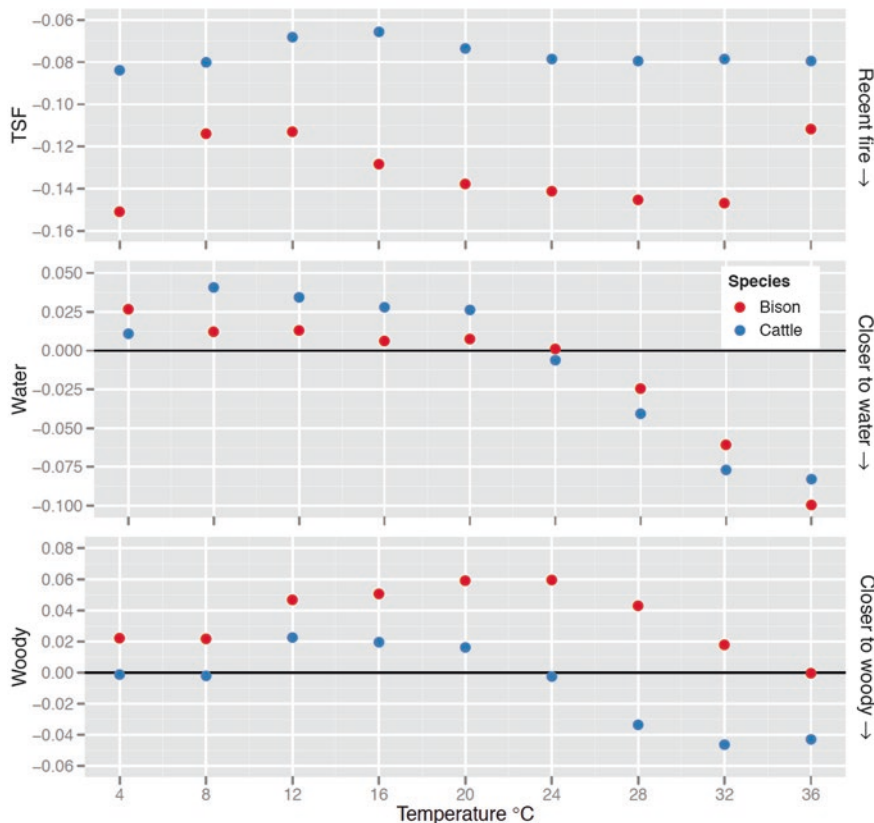
Fig. 5.3 Resource selection coefficients at varying air temperatures for bison and domestic cattle at the Tallgrass Prairie Preserve, USA. Environmental factors include time since fire (TSF), distance to water (Water), and distance to woody vegetation (Woody). Bison and cattle most strongly select for areas that minimize time since fire, but begin selecting sites nearer woody vegetation and water as the temperature increases. Domestic cattle-grazing behavior changes sooner and more dramatically than does bison behavior. Modified from Allred et al. (2013)

to functional heterogeneity (Walker et al. 1987; Scoones 1993). In addition, access to greater functional heterogeneity in rangelands with increasing spatial scale results in a decrease in the strength of density dependence in the relationship between stocking rate and animal growth rate (Hobbs et al. 2008) and also increases body size (Albon and Langvatn 1992; Mysterud et al. 2001). These conclusions are in direct contrast to management prescriptions that reduce functional heterogeneity by reducing the management scale and simplifying the landscape suggesting that greater managerial certainty is expected by a command-and-control perspective on management. Rangeland management should be designed to specifically acknowledge and address uncertainty and variability and we advocate that it should consider the importance of maintaining or enhancing heterogeneity at multiple scales and allow animals to effectively interact with their environment.

5.3.2 Fire and Rangeland Ecosystems

5.3.2.1 Heterogeneity and the Shifting Mosaic

Grasslands, shrublands, and savannas are often described by their dependence on herbivores and fire. Most studies have focused on these factors independent of each other and based on studies of relatively small experimental units that could be well replicated (Fuhlendorf et al. 2009; Fuhlendorf et al. 2012). Recently studies have investigated the landscape-level interaction of fire and herbivores across many continents and various herbivores Fuhlendorf and Engle 2004; Archibald et al. 2005; Allred et al. 2011). These large-scale patterns are best described as a shifting mosaic where fire and grazing interact through a series of feedback mechanisms. As herbivores select recently burned areas for foraging sites, unburned areas are subject to less grazing activity and accumulate fuel. When additional areas burn, grazing animals switch to the more recently burned areas and previously burned areas recover through a transitional stage eventually reaching a state that has accumulated its maximum fuel load. This fire-grazing interaction, or pyric herbivory (grazing driven by fire), results in a shifting mosaic across the landscape allowing herbivores to select from high-quality, recently burned sites and sites that have high biomass accumulation. Herbivores in rangelands of North America spend as much as 70 % of their time on recently burned areas and for domestic herbivores it can increase livestock gains (Limb et al. 2011) and stabilize productivity through drought years when compared to areas managed homogenously (Allred et al. 2014) (Fig. 5.4). For bison of North America, access to burned and unburned areas leads to increased selection of burned areas and higher reproductive rates compared to herds that do not have variable fire patterns (Fuhlendorf and Engle 2001; Fuhlendorf et al. 2009).

The effect of patch fires on forage available for herbivores is best described as a shifting mosaic with patches that vary in forage quantity and quality (Figs. 5.3 and 5.5). Averaged across pastures or experimental units, biomass may be similar between the shifting mosaic and a pasture more traditionally managed. But, the variability is much greater in terms of forage quality and quantity when the shifting mosaic is maintained. Recently burned patches produce forage of high quality and digestibility. Alternatively, biomass accumulation is higher on areas that have greater time since fires, resulting in an overall increase in heterogeneity of forage resources. Animals may respond to this variability differently depending on age, sex, and conditions pre- and postfire. In dry years unburned areas can serve as forage, albeit low quality, through the dry season. Following rain, rapid growth occurs in burned patches and herbivores, particularly females, can select high-quality diets. Heterogeneous landscapes that have been created by patch fires have greater functional heterogeneity as indicated by the high degree of deviation around the mean (Fig. 5.6, Panel B), than landscapes without fire or that are homogeneously managed (Fig. 5.6, Panel C). Smaller landscapes where animal movements are
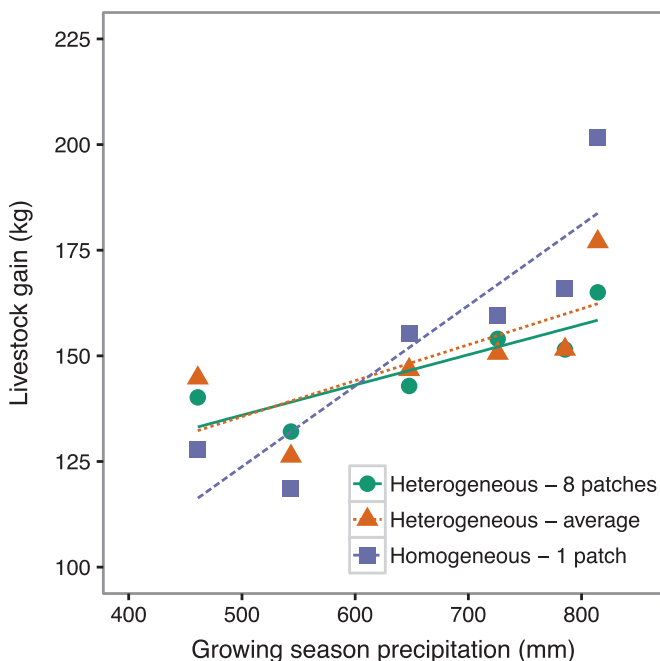
Fig. 5.4 Livestock gain (kg/head) in relation to growing season precipitation within pastures that varied in heterogeneity in tallgrass prairie of North America. Heterogeneous pastures had 2–8 patches that had been burned in a fire-grazing interaction while the homogeneous pasture was uniformly burned annually. The heterogeneous—eight patches—treatment had two patches burned annually (one in spring and one in summer) over 4 years and was the most heterogeneous treatment. Pastures that were managed to promote heterogeneity had more consistent livestock production and were less influenced by low-rainfall years. Modified from Allred et al. (2014)

Fig. 5.5 Bison are able to forage in different patches to meet their differing forage requirement. This photo is from the Tallgrass Prairie Preserve in Oklahoma and illustrates the increased heterogeneity in forage quality and quantity. Photo by Steve Winter
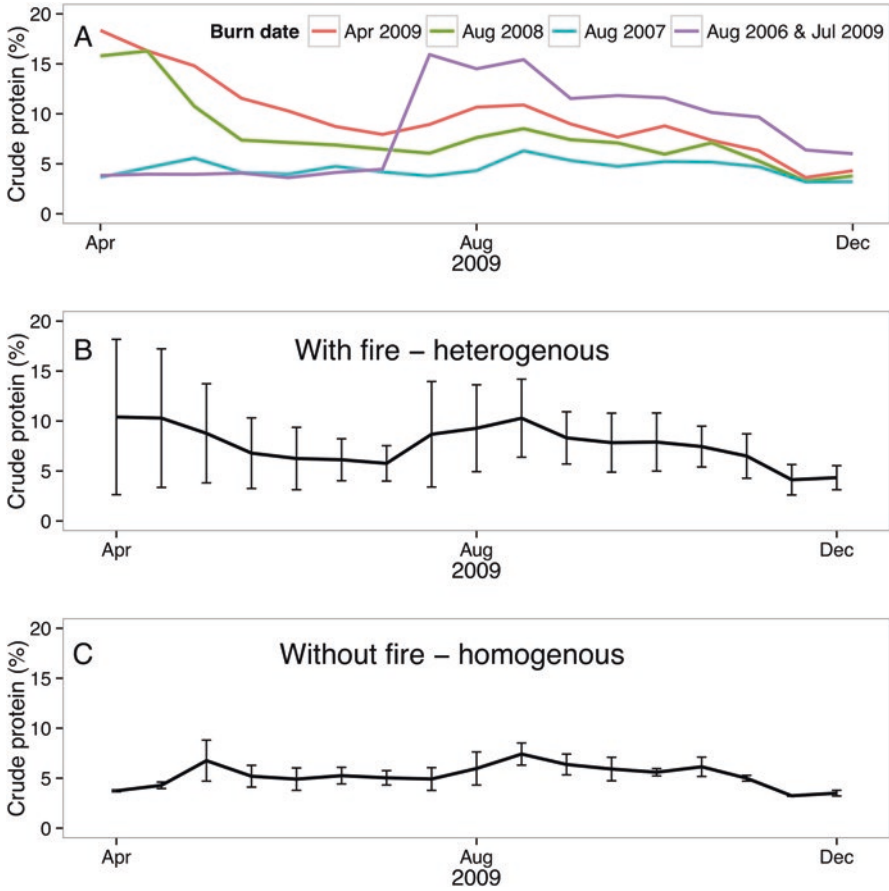
Fig. 5.6 Forage crude protein (%) as influenced by fire-grazing interactions in tallgrass prairie. (**a**) Forage quality of patches that vary in time since fire. Recently burned areas have much higher forage quality than unburned areas and remain high throughout the season as animals graze thereon. (**b**) Error bars reflect the heterogeneity in forage quality available to herbivores. Due to the high variation in forage resources when heterogeneous fires are applied to the landscape, animal choice is unrestricted so animals can seek out desired forage based on dietary needs and preferences. (**c**) Elimination of fire (mean of unburned patches) results in low forage quality through time and low patch variability. This low variation homogenizes available forage resources to restrict livestock choice

strongly limited by fences may require more application of alternative disturbances than large landscapes with free-roaming herds. It has been demonstrated that grazing operations on small pastures characteristic of many compartmentalized rangelands also benefit from the creation of fire-driven heterogeneity promoted by small burned patches that are rotated over several years (Limb et al. 2011; Allred et al. 2014).

5.3.3   Heterogeneity of Fuel and Fire Effects

Improving our understanding of the variability of fire effects on rangelands requires that researchers account for heterogeneity. Contradictory findings are evident throughout fire effects research and little information elucidates why inconsistencies among studies exist. Disparate findings are likely due to a lack of recognition of the role of heterogeneity in fire effects and limited studies at sufficient spatial scale to capture real-world fire behavior (Fuhlendorf et al. 2011). As an example, a fire experiment was established to link variability in fuels, fire behavior, and crown scorch (the portion of the crown of a tree that is killed by heat) (Fig. 5.7) and mortality of *Juniperus ashei* for fires conducted in wet and dry periods of the growing season (refer to Twidwell et al. 2009 for complete methodology). During a wet period of the study, when herbaceous fuel moisture content was near its maximum level, the pattern of area burned was a function of fine-scale patch dynamics. Of the parameters measured, the type of fuel patch and its size were the two factors most important in determining discontinuities in the propagation of fire across the landscape. Discontinuities in the fuel bed create fuel gaps—patches without herbaceous fuels that occurred within a continuous bed of grassland fuels—drove this relationship (Fig. 5.8).

Studying fire on rangelands requires an understanding of functional heterogeneity of fire and pattern of area burned on the landscape, which is ultimately a function of the spatial arrangement of these different patch types. But functional heterogeneity is dynamic and therefore should not be measured or characterized at a single scale of measurement. Understanding functional heterogeneity improves understanding of

Fig. 5.7 Variability in height of tree scorch on two adjacent Ashe juniper (*Juniperus ashei*) trees indicates that heterogeneity of fuel load and tree size may be critical in understanding fire effects on rangelands. Photo by Dirac Twidwell
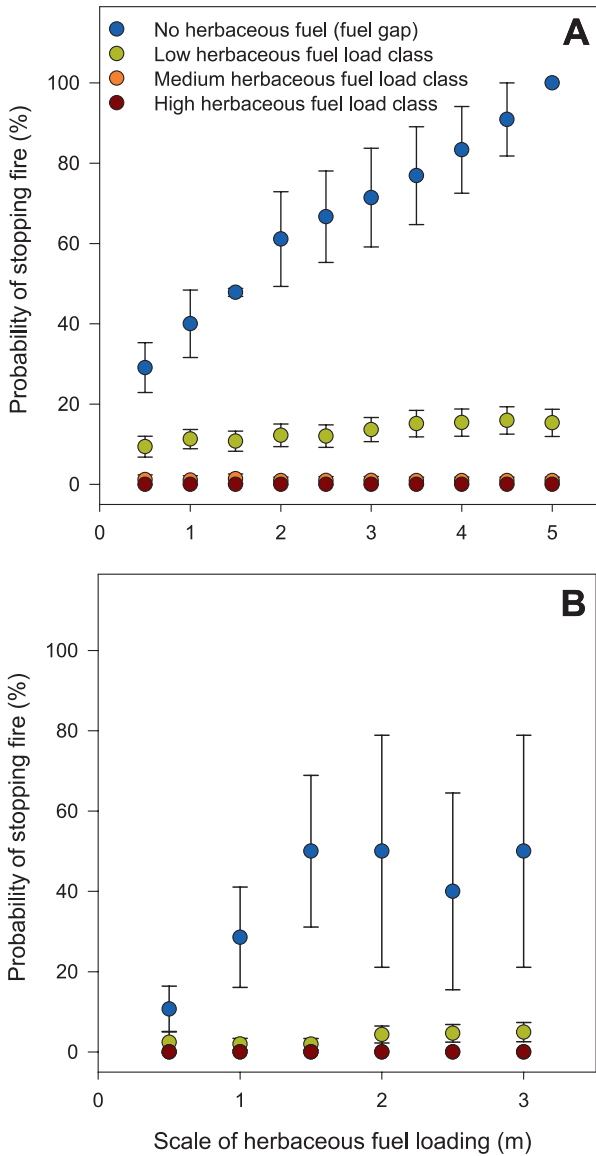
Fig. 5.8 Fine-scale determinants of area burned, shown here as the relationships between the amount of herbaceous fuel loading occurring at multiple spatial scales and the probability of stopping fire spread for fires conducted in two different fuel moisture conditions (**A**, high fine fuel moisture; **B**, low fine fuel moisture). Increasing gaps in herbaceous fuels increase the probability of stopping fire, but the relationship is less predictable in fuel conditions promoting more erratic fire behavior (e.g., in low fuel moisture conditions)

second-order fire effects that are also the result of discontinuities in fire spread and variability in fire behavior. Discontinuities in fire spread allow some juniper trees to escape damage from fire, whereas others directly adjacent to them are completely scorched and killed (Fig. 5.7). In other cases, trees are partially scorched, indicating that the heat applied was below the threshold required for mortality.

Understanding functional heterogeneity resulting from interactions between variability in fuels, fire behavior, and fire effects requires a sampling procedure that differs from traditional approaches. Most often, herbaceous fuel load is randomly sampled across a landscape and in the interspaces between trees, followed by random sampling of flame length (if done at all), and then random sampling of physical damage caused by the fire. In contrast, sampling in this experiment was stratified to account for the influence of the tree on the fuels beneath it, which subsequently influenced the fire intensity occurring beneath the specific tree of interest, and in turn influenced crown scorch and mortality. Importantly, no single spatial scale was used to characterize this relationship, but instead individual trees were of different sizes and influenced interrelationships between fuels, fire intensity, and crown scorch differentially. The contribution of functional heterogeneity to fire effects was best described by establishing a variable scale that accounted for differences in the size of each tree. Using this approach, a clear relationship of functional heterogeneity emerged that enabled the empirical detection and quantification of the fire intensity threshold required for juniper mortality (Twidwell et al. 2013a, b). This threshold could not be detected using simple random sampling that assumes homogeneity around the average in fuel load and fire behavior (Twidwell et al. 2009), which has been the most common procedure used to attempt to understand how fuels drive fire effects in rangelands.

5.3.4   Biodiversity and Ecosystem Function

Meeting variable forage demands and analyzing fire effects are just a couple of examples of enhanced functionality created by heterogeneity in rangelands. Heterogeneity can also increase habitat availability for different plant, insect, bird, and mammal species. Research worldwide describes how different species within major taxonomic groups have variable habitat requirements, and managing for spatially heterogeneous landscapes creates multiple habitat types simultaneously (Tews et al. 2004; Fuhlendorf et al. 2006; McGranahan et al. 2013a, b). Furthermore, plant biomass production varies less across seasons in spatially heterogeneous landscapes (McGranahan et al. 2016).

The fire–grazing interaction is especially important in the North American Great Plains, where more distinct habitat types are created in rangeland managed with pyric herbivory than in rangeland managed with fire or grazing alone (Fuhlendorf et al. 2009). This breadth of habitat types is essential for the conservation of grassland-obligate fauna, such as the Henslow's Sparrow (*Ammodramus henslowii*), which requires dense, moribund grass material for nesting, and the regal fritillary

Fig. 5.9 Greater prairie chickens require short vegetation for their breeding displays, but females build their nests in nearby dense vegetation that has not been burned or grazed for 1 year or more. Brood rearing requires open vegetation with high plant and insect diversity and structural heterogeneity required for protection from temperature extremes and ease of movement. Photo by Torre Hovick

(*Speyeria idalia*), a fire-dependent but grazing-sensitive butterfly, which might depend on spatial heterogeneity to persist in working rangeland landscapes that are managed specifically for grazing (Fuhlendorf et al. 2006; Moranz et al. 2014).

Perhaps the most illustrative example of a species that requires the full breadth of habitat types available under heterogeneity-based fire and grazing management is the greater prairie chicken (*Tympanuchus cupido*) (Fig. 5.9, Hovick et al. 2014). These grassland-obligate birds begin the breeding season on leks, areas of extremely short vegetation where males gather and display to attract females. Upon mating, females seek dense vegetation to hide their nests during incubation, and between hatching and fledging, prairie chicken broods benefit from transitional patches following focal disturbance from pyric herbivory, as these areas provide aerial plant cover with limited obstruction from litter and other vegetative debris. Importantly, prairie chickens require each of these habitat types to be accessible within relatively short distances. Greater prairie chickens select nesting sites at coarse scales to be near leks (frequently on burned sites) and far from trees and at very fine scales for specific sites best suited to moderate temperature extremes (Hovick et al. 2014).

Likewise, several African antelope species require patches of short grassland for grazing and adjacent taller grass patches for resting and concealing young (Everett et al. 1991). Short-grass grazers such as wildebeest and Thomson's gazelle occur in higher densities in the heavily grazed livestock areas outside the Masai-Mara Game Reserve in East Africa, whereas tall-grass grazers such as Cape buffalo (*Syncerus caffer*) are restricted to within the less heavily grazed taller grass areas within the game reserve (Bhola et al. 2012). Similarly, diverse communities of African herbivores require heterogeneity due to topo-edaphic patterns as well as disturbance.
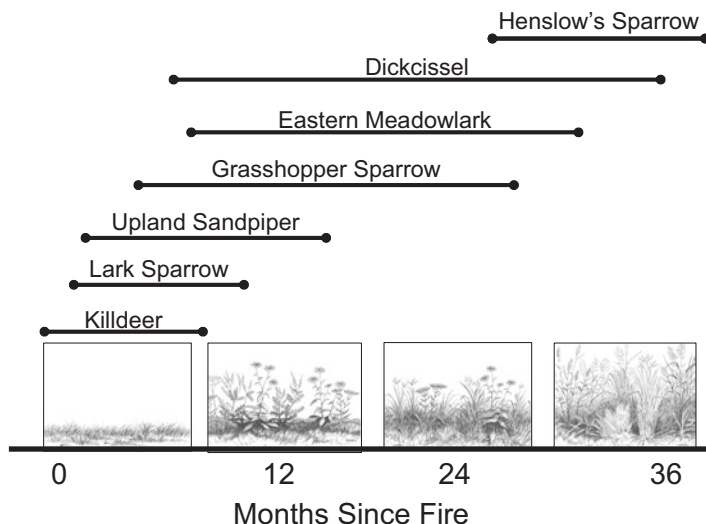
Fig. 5.10 Response of grassland birds to time since disturbance by fire and grazing at the Tallgrass Prairie Preserve, Oklahoma, from 2001 to 2003. Some birds native to the area require recently burned patches that are heavily grazed while others require habitats that are undisturbed for several years (Fuhlendorf et al. 2006)

Similar patterns of plant, insect, and bird compositional responses to burning and grazing frequency effects on grassland structural heterogeneity have been observed in both North American and African rangelands. On both continents, the interactive effects of fire and grazing on grassland structure and plant composition translated into differences in invertebrate communities (Chambers and Samways 1998; Engle et al. 2008; Dosso et al. 2010; Doxon et al. 2011). The community composition of several bird taxa—especially passerines—also varies with grassland structure in both continents (Fig. 5.10) (Fuhlendorf et al. 2006; Bouwman and Hoffman 2007; Krook et al. 2007; Gregory et al. 2010; Chalmandrier et al. 2013). Exceptions, however, do exist, and the community composition of some taxa is not associated with spatially heterogeneous disturbance patterns especially when those patterns are limited in spatial extent and largely based on measured rather than functional heterogeneity estimates (Pillsbury et al. 2011; Davies et al. 2012; Moranz et al. 2012; McGranahan et al. 2013a, b).

Beyond maximizing habitat heterogeneity across a landscape within a given season, maintaining a spatial mosaic of patches across several seasons increases stability of important ecosystem functions like aboveground biomass production and habitat. Ecologists have long recognized that biological diversity—often measured as plant species richness or functional types—can stabilize community composition and ecosystem function (McNaughton 1977; Tilman and Downing 1994; Tilman et al. 2006; Zimmerman et al. 2010; Isbell et al. 2011). Experiments now demonstrate that ecological diversity—measured as differences among patches within heterogeneous landscapes—can stabilize avian community composition, as well as

both plant biomass and livestock production, over time (McGranahan et al. 2016; Allred et al. 2014; Hovick et al. 2014). This suggests that spatially heterogeneous disturbance regimes that reduce temporal variability in primary production might represent a land-use paradigm that enhances landscape-level diversity to promote rangeland conservation and resilience in a changing world (Fuhlendorf et al. 2012). So, we would argue that at broad scales, functioning rangelands should have variable disturbance patterns that interact with inherent topo-edaphic variability and are central to many aspects of landscape and population stability. This relationship among disturbance, pattern, diversity, heterogeneity, and stability is more realistic at broad scale than the more simplistic focus on diversity as a driver of stability as predicted by small-plot agronomic experiments.

Increasing spatial heterogeneity might buffer ecosystem function against climate change, which is consistent with the predictions of diversity-stability theory (Mori et al. 2013). In many rangelands, variation in primary production can destabilize ecosystem structure and function. Such variability is expected to increase under many climate change scenarios, which might make ecosystems more vulnerable to degradation of ecosystem function (Walker et al. 2004; Mori et al. 2013). Because rangeland management often depends upon a degree of dynamic equilibrium (Briske et al. 2003; Mori 2011), enhancing a spatial pattern of heterogeneity that buffers against temporal variability can enhance response to global change much in the way of portfolio effects of diversity-stability studies (Turner 2010).

5.4 Future Perspectives

Rangeland management has been slow to adopt a dynamic basis for ecosystem management that sustains multiple ecosystem services. Instead, livestock production systems continue to trump management for other rangeland services. For example, emergency haying programs in the USA permit the harvesting of grass biomass in grasslands prioritized for wildlife conservation when production is lower than optimal due to environmental stressors such as drought. The result is a strong reliance on command-and-control management approaches to rangeland management (e.g., attempting to minimize variation). To overcome natural rangeland variability, conventional grazing management relies upon a myopic focus on cross-fencing and controlled access to forage and water, seeking to minimize variability in disturbance intensity by promoting uniform, moderate grazing across the entire landscape. This attempt to override heterogeneity has been aptly described as management toward a uniform middle and has become the central theme to the discipline or rangeland management (Fuhlendorf and Engle 2001, 2004; Bailey and Brown 2011).

Mounting evidence suggests that heterogeneity enhances biodiversity in agricultural landscapes (Ricketts et al. 2001; Benton et al. 2003; Hobbs et al. 2008; Franklin and Lindenmayer 2009) where native biodiversity is threatened by the intensification and compartmentalization of land use (Reidsma et al. 2006; Flynn et al. 2009). But agricultural policy has been slow to respond. In the USA, no federal farm bill

program specifically targets farmland or rangeland heterogeneity, although limited heterogeneity-based management practices have been recently allowed for use in long-standing programs like the Conservation Reserve Program (NRCS 2004; Hart 2006), and such heterogeneity-based management has been shown to increase the quality of CRP projects for wildlife (Matthews et al. 2012). In Europe, where agricultural conservation policies tend to place greater emphasis on landscape-level objectives than in the USA (Baylis et al. 2008), agri-environmental schemes that can increase wildlife habitat heterogeneity remain an unstated objective and incidental outcome (Vickery et al. 2004).

Understanding heterogeneity has been an important limitation to the application and principles of science and management on rangelands. Globally, rangeland science indicates that heterogeneity and diversity increase stability in ecosystem properties from a broad spatial and temporal perspective. Management should no longer consider fine-scale spatial and temporal variability as a threat to ecosystem structure and function. It is logistically critical to the science of rangelands because of the importance of scale in experimental design and the point that traditional experimental design was largely based on Fisherian statistics where small experimental units were used to minimize variation within treatments (Fuhlendorf et al. 2009). Embracing heterogeneity requires academics, practitioners, and policy makers to realize the fallacy in building a profession that relies on statistical replications of small-scale plots to represent complex rangeland landscapes that are dynamic in space and time. This is a fundamental fallacy of our profession that is mostly a social construct of the profession rather than a reflection of a true need to simplify landscapes. Understanding that this simplified focus on homogeneity is cultural to the profession suggests that we can work to overcome these biases through academia and natural resource agencies. The greatest challenge and opportunity in contemporary rangeland science and management are overcoming our traditional focus on uniformity and developing policies and an understanding that promotes rangelands as heterogeneous natural resources that are complex and capable of achieving many objectives by operating at the nexus of working and wild landscapes.

5.5   Summary

Understanding rangelands as complex, dynamic ecosystems that are highly variable in space and time cannot be achieved without a focus on heterogeneity as a critical and multiscale characteristic. Comparisons between the state of our current scientific knowledge and the application of management have often identified scale and heterogeneity as limitations to making our science applicable to land management and policy (Bestelmeyer et al. 2011, Fuhlendorf et al. 2011). While we have theoretically understood rangelands as dynamic and variable in space there has been minimal effort focusing on the variability as a critical and inherent characteristic of rangelands. One very important exception to this has been the efforts to connect variation in soil, landform, and climate to ecological sites through USDA-NRCS

(Chapter 9, this volume). This is a critical first step, but still limits variability to mapping units that are primarily viewed as static in space and time. This is often still focused on a single state or phase existing within each site rather than a dynamic and shifting condition that is variable in space and time (Twidwell et al. 2013a, b). The limited use of non-equilibrial concepts and landscape ecological principles is surprising because rangelands are disturbance-driven ecosystems that are clearly dynamic in space and time.

Ultimately, the science and management of rangelands need to advance beyond a focus on average conditions and the current paradigm of uniform and moderate disturbance. This simplistic focus leads to debates, such as wildlife vs. livestock, fuel vs. forage, and forests vs. grassland. Understanding heterogeneity in space and time should be central to the framework for advancing our discipline and progressing to solve problems that arise with changes in societal desires on rangelands. Perhaps the greatest challenge for applying heterogeneity-based science in rangeland management is overcoming a century-old vision of rangelands as simple ecosystems that sustainably provide forage for domestic livestock. Below are general principles for our profession to begin thinking of rangelands as highly dynamic in space and time that provide many goods and services to society that include livestock production, wildlife habitat, biodiversity, and water quality and quantity (Fuhlendorf et al. 2012):

1. Large continuous tracts of rangelands are critical for conservation so that disturbance processes can interact with inherent heterogeneity to form multiscaled mosaics that are capable of providing multiple goods and services. Large landscapes will include more heterogeneity than small landscapes and this will buffer ecosystems and populations from unexpected and stochastic perturbations (Ash and Stafford-Smith 1996). Rangeland fragmentation that results in many small land units precludes sufficient patch size or number for long-term conservation and land management objectives. Conservancies and landowner associations can help coordinate heterogeneity-based management at broad spatial scales (Toombs et al. 2010; McGranahan 2011).

2. Professionals and the general public have largely learned to promote uniformity in disturbance processes and minimize the occurrence of both undistributed and severely disturbed areas. The first step in managing for heterogeneity and multiple objectives is to place value on these disturbance-driven attributes and to minimize efforts to manage for homogeneity or uniformity. This will require us to develop approaches that promote variability in disturbance frequency and intensity across complex and large landscapes, preferably by recognizing, maintaining, and restoring broad-scale processes.

3. Shifting mosaics of landscape patches are necessary for maintaining ecosystem structure and function and achieving multiple objectives such as improved productivity and stability of livestock production (Limb et al. 2011) and conservation objectives (Fuhlendorf et al. 2009). Managing for a single condition, state, phase, or successional stage is incapable of sustaining livestock production and is not capable of promoting biodiversity or multiple uses.

4. Inherent heterogeneity, associated with soils, topography, and temporal variability from climate, is a defining characteristic of rangelands. Additionally, disturbance regimes, such as fire and grazing, are as vital to ecosystem structure and function as climate and soils and are capable of driving landscape-level heterogeneity. These disturbances must be viewed as interactive processes that are critical to heterogeneity of rangelands rather than mere optional management tools.
5. As policy developers and implementers recognize the importance of multiple land uses and the full suite of ecosystem services, a focus must be placed on maintaining large landscapes, in spite of fragmented ownerships, and conserving the processes that drive heterogeneity at multiple scales. Developing policies that move beyond the traditional command-and-control paradigm/steady-state management model will be our greatest challenge in the next century.

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