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Essay

Pyric Herbivory: Rewilding Landscapes through the Recoupling of Fire and Grazing

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Abstract: *Our understanding of fire and grazing is largely based on small-scale experimental studies in which treatments are uniformly applied to experimental units that are considered homogenous. Any discussion of an interaction between fire and grazing is usually based on a statistical approach that ignores the spatial and temporal interactions on complex landscapes. We propose a new focus on the ecological interaction of fire and grazing in which each disturbance is spatially and temporally dependent on the other and results in a landscape where disturbance is best described as a shifting mosaic (a landscape with patches that vary with time since disturbance) that is critical to ecological structure and function of many ecosystems. We call this spatiotemporal interaction* pyric herbivory *(literal interpretation means grazing driven by fire). Pyric herbivory is the spatial and temporal interaction of fire and grazing, where positive and negative feedbacks promote a shifting pattern of disturbance across the landscape. We present data we collected from the Tallgrass Prairie Preserve in the southern Great Plains of North America that demonstrates that the interaction between free-roaming bison (*Bison bison*) and random fires promotes heterogeneity and provides the foundation for biological diversity and ecosystem function of North American and African grasslands. This study is different from other studies of fire and grazing because the fires we examined were random and grazing animals were free to roam and select from burned and unburned patches. For ecosystems across the globe with a long history of fire and grazing, pyric herbivory with any grazing herbivore is likely more effective at restoring evolutionary disturbance patterns than a focus on restoring any large vertebrate while ignoring the interaction with fire and other disturbances.*

Keywords: biodiversity, bison, disturbance ecology, fire, grasslands, grazing, herbivory, heterogeneity

Herbivoría Pírica: Restablecimiento de Paisajes Silvestres Mediante la Combinación de Fuego y Pastoreo

Resumen: *Nuestro entendimiento del fuego y del pastoreo se basa principalmente en estudios experimentales de pequeña escala en los que se aplican tratamientos uniformes a las unidades experimentales que son consideradas homogéneas. Cualquier discusión sobre una interacción entre fuego y pastoreo generalmente se basa en un método estadístico que ignora las interacciones espaciales y temporales de los paisajes complejos. Proponemos un nuevo enfoque de la interacción ecológica de fuego y pastoreo en el que cada perturbación es dependiente espacial y temporalmente de la otra y resulta en un paisaje en el que la perturbación es mejor descrita como un mosaico cambiante (un paisaje con parches que varían con el tiempo desde la perturbación) que es crítico para la estructura y función ecológica de muchos ecosistemas. Denominamos* herbivoría pírica *a esta interacción espaciotemporal (la interpretación literal significa pastoreo dirigido por fuego). La herbivoría pírica es la interacción espacial y temporal del fuego y el pastoreo, donde la retroalimentación negativa y positiva promueve un cambio del patrón de perturbación en el paisaje. Presentamos datos que recolectamos en la Reserva Tallgrass Prairie en las Grandes Planicies de Norte América que demuestran que la interacción entre los bisontes (*Bison bison*) libres y los incendios ocasionales promueve la heterogeneidad y proporciona el fundamento para la diversidad biológica y el funcionamiento del ecosistema de los pastizales de Norte América y de África. Este estudio es diferente de otros estudios de fuego y pastoreo porque los incendios que*

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examinamos fueron aleatorios y los animales estaban libres y podían seleccionar entre parches quemados y no quemados. Para ecosistemas con una larga historia de fuego y pastoreo en todo el mundo, es probable que la herbivoría pírica de cualquier herbívoro sea más efectiva para la restauración de los patrones de perturbación que enfocar la restauración de un vertebrado mayor ignorando la interacción con el fuego y otras perturbaciones.

Palabras Clave: biodiversidad, bisonte, ecología de la perturbación, fuego, herbivoría, heterogeneidad, pastizales, pastoreo

Introduction

Proposals to conserve grazed ecosystems and landscapes often focus on the appropriateness of reintroducing native herbivores or surrogates of extinct herbivores that were important to the development of grassland and savanna ecosystems (Donlan et al. 2005; Sanderson et al. 2008). This species-centric focus on restoring grazed ecosystems effectively conserves certain herbivores but inadequately represents disturbance processes within complex landscapes that are important for biodiversity. For example, introduction of African megafauna (i.e., rewilding) was recently proposed as an ecological solution to conservation issues on North American grasslands (Donlan et al. 2005). Response and rebuttal to this proposal was predictably swift and direct (Caro 2007). Two criticisms are negative impacts on native biodiversity and incompatibility with human community structures (Shay 2005; Smith 2005). Others argue the measure is unnecessary because native megafaunal recovery and reintroduction in North America (i.e., bison [*Bison bison*]) is succeeding and restoring wild ecosystems (Dinerstein & Irvin 2005; Schlapher 2005). We argue that a major oversight in the rewilding proposal, as well as other approaches focused on restoring native herbivores, is neglecting to address historic disturbance regimes important to the evolution of flora and fauna in many grassland and savanna ecosystems.

In the grasslands of North America, herbivores were a strong driving factor on these landscapes, but over at least the past 10,000–15,000 years the effects of herbivore activity were largely controlled by an interaction between fire and grazing, hereafter termed *pyric herbivory* (i.e., herbivory shaped by fire). These same processes have been dominant in other parts of the world for much longer (e.g., Africa). Grazing and fire may best be viewed as a single disturbance process in ecosystems that evolved with fire and grazing, and this interaction has created a shifting mosaic of disturbance patches across a complex landscape (e.g., Fuhlendorf & Engle 2001; Salvatori et al. 2001; Hassan et al. 2008). Our goals for this paper were to describe pyric herbivory within ecosystems that have a long history of fire and grazing as dominant evolutionary processes and to summarize results from studies to illustrate the importance of a spatially and temporally variable interaction of fire and grazing as an alternative to focusing on charismatic herbivore species independent of fire (e.g., Sanderson et al. 2008).

Conventional Fire and Herbivory Research

Fire and grazing are critical disturbances in the development of grassland ecosystems and the evolution of species within these environments. Considerable research has focused on their effects as independent forces that alter landscapes throughout the world. Much knowledge of fire and grazing has been gained through experimental studies designed for Fisherian statistics in which treatments are uniformly applied to small, homogenous experimental units to minimize variance other than that associated with the grazing or fire treatments (Table 1). These conventional experimental studies are similar to agronomic studies that treat fire and grazing as independent factors of a factorial experiment in which treatments are often limited to binary (yes or no) levels (Fig. 1a), and treatments are applied uniformly or removed from the entire treatment unit. This approach has created a vast body of literature that defines the effects of homogeneous application of fire or grazing and, less commonly, to homogeneous concomitant application of fire and grazing (Table 1). In our view this unnaturally decouples fire and grazing, which are dynamic processes that interact with each other and with spatial and temporal variability across complex landscapes.

A shifting-mosaic landscape, which is critical for biodiversity, is the result of grazing animals freely selecting from burned and unburned portions of the landscape, and the dependence of fire occurrence on the removal of fuel by herbivores (e.g., Norton-Griffiths 1979; Fuhlendorf & Engle 2001). The result is anything but uniform applied treatments. The ecological interaction between fire, grazing, and other disturbances occurs at multiple scales that often include much broader scales than the experimental scale of most studies (Fuhlendorf & Engle 2001; Archibald et al. 2005; Waldram et al. 2007), so a simplified understanding of the independent effects of fire and grazing is not surprising. Perhaps a holdover of the grossly outdated view that disturbance in ecosystems

Table 1. Examples of the conventional approach (applying fire and grazing as single and as combined treatments as a statistical interaction) to the study of fire and grazing in fire- and grazing-maintained grassland and savanna compared with an approach in which fire and grazing are viewed as a dynamic, ecological interaction (pyric herbivory, herbivory shaped by fire).

Experimental treatments	*Spatial scale*	*Temporal scale*	*Comparison treatment*	*Ecosystem and location*	*Reference*
Conventional approach					
fire only (grazing excluded)					
fire season	applied to entire plot (10 × 20 m)	burn applied from 1 to 3 years	not burned	tallgrass prairie; North America (Oklahoma, USA)	Engle et al. 1998
fire season	applied to entire plot (10 × 20 m)	annual; 56-year data set	not burned	tallgrass prairie; North America (Kansas, USA)	Towne & Owensby 1984
fire frequency and season; fire exclusion	applied to entire plot (7 ha)	50-year data set, frequency 1-, 2-, and 3-year fire-return interval and season	burning compared with fire exclusion	Savanna; Africa (South Africa and Mozambique)	Higgens et al. 2007
grazing only (fire excluded)					
rotational grazing	grazing and burning applied to entire pasture (24 ha)	16-year study; no burning years 1–13 and annual burning years 14–16	continuous grazing; no burning years 1–13 and annual burning years 14–16	tallgrass prairie; North America (Kansas, USA)	Owensby et al. 1973
stocking rate	grazing at 4 stocking rates applied to entire pastures (13 head of cattle stocked in pastures varying from 16 to 65 ha)	33-year study	comparison among stocking rate treatments; each grazed pasture compared with a grazing exclosure within the pasture	rough fescue grassland; North America (Alberta, Canada)	Wilms et al. 1985
fire and grazing as a statistical interaction applied as whole-plot treatments					
fire and grazing	fire applied to entire plots (10 × 10 m); half of plots placed in a grazed pasture and half in a grazing exclosure	burned 3 times in 8 years	no burning, no grazing	desert shrub-steppe; North America (Arizona, USA)	Valone 2003
fire and grazing	fire applied to 1 of 2 18.2-ha plots; grazing excluded in 0.1-ha subplots	annual burning.	no burning, no grazing	tallgrass prairie; North American (Oklahoma, USA)	Collins 1987
fire and grazing	fire applied to 10 watersheds at different frequencies (spatially fixed by watershed) within a 1012-ha area in which bison had free access to all watersheds in grazed area	1-, 4-, and 20-year intervals (Knapp et al. 1999*a*)	burning without grazing; grazing without burning; no burning and no grazing	tallgrass prairie; North America (Kansas, USA)	Collins et al. 1998

(continted)

Table 1. continued

Experimental treatments	Spatial scale	Temporal scale	Comparison treatment	Ecosystem and location	Reference
disturbance (tillage and fire) applied to plots either grazed or not grazed	tillage and fire applied to 1 × 2 m plots within a main plot (13 × 17 m) either grazed or ungrazed	5-year study with burned plots burned in the 2nd and 3rd year; grazed main plot was grazed each year of the study	no burning, no grazing, no soil disturbance	shortgrass, midgrass, and tallgrass sites; Serengeti National Park, Tanzania	Belsky 1992
fire or clipping; fire and clipping	applied to entire plot (0.6 × 0.9 m)	annual to 2 in 3 years		mixed prairie; North America (Texas, USA)	Ansley & Castellano 2007
fire and grazing	grazed pastures of unspecified area with treatment plots (20 × 20 m)	3-year study with 3 to >20 fire events preceding and during the study years	grazing only, burning only, and grazing plus burning compared with no grazing no burning	low-elevation basalt grassland; Yahudia Nature Reserve, Israel	Noy-Meir 1995
	grazed, incidentally burned areas of unspecified area with treatment plots (20 × 20 m)				
Pyric herbivory approach					
controlled, manipulative studies					
burning and grazing interaction	burned one-third of grazed pastures (230–239 ha)	one-third of pasture burned annually	none	pine-bluestem savanna; North American (Louisiana)	Duvall & Whitaker 1964
burning and grazing interaction	burned one-sixth of grazed pasture (45–65 ha)	one-third of pasture burned annually (one-sixth burned in each of 2 seasons)		tallgrass prairie; North America (Oklahoma)	Fuhlendorf & Engle 2004
mowing with fire and grazing interaction	20-m circular, mowed plot within 90,000 ha; average annual area burned 26% and average area of individual fires 9.1 km^2	3.8 years mean fire-return interval	mowed plot compared with a paired plot not mowed (response of both treatments influenced by burned patches within the landscape)	South Africa	Archibald et al. 2005
descriptive studies					
burning with grazing	20% of 2900-ha area burned annually	3 seasons of burning each year with a mean 5-year fire-return interval	none	tallgrass prairie; North America (Oklahoma)	Coppedge et al. 1998
burning with grazing	variable extent, depending on fuel load and fire management policy	variable fire-return interval, with a mean of 3.8 years and a median of 1.3 years	none	mesic savanna; northern Kwa-Zulu Natal, South Africa	Balfour & Howison 2002

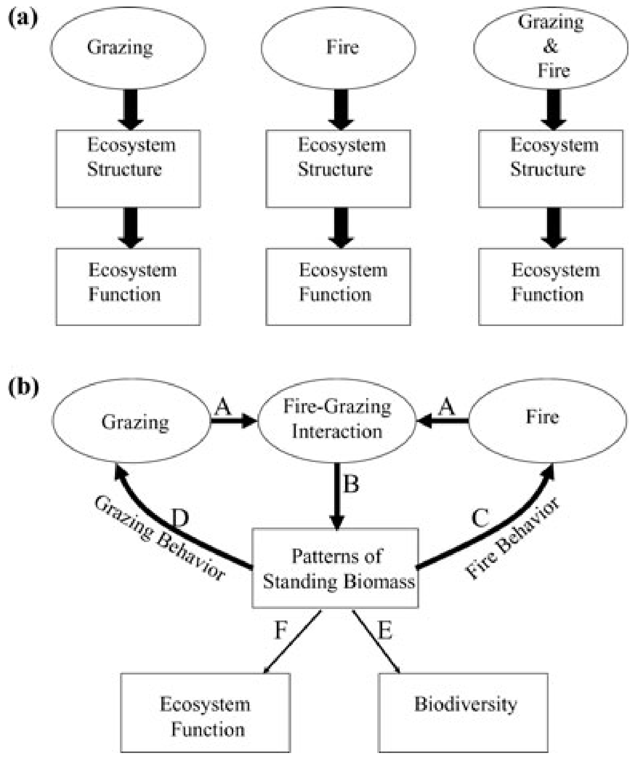

Figure 1. Conceptual models of approaches to studying fire, grazing, and their interactions: (a) conventional factorial approach used to study the separate effects of fire and grazing and their statistical interaction and (b) model of a dynamic landscape approach used to study effects of the ecological interaction of grazing and fire that forms a shifting mosaic of disturbance patches across the landscape that in turn influences ecosystem function and biodiversity (A, B, C, D, E, and F represent components of the model that could be specific topics of study).

is unnatural, the comparison treatment (i.e., the control) in empirical studies is often undisturbed (i.e., neither burned or grazed), which is an even more unnatural and rare condition within ecosystems that are subject to grazing and fire than the homogeneous treatments they are compared with (Axelrod 1985; Milchunas et al. 1998; Collins 2000) (Table 1). This suggests that understanding of fire and grazing is simplified and distorted within a long-term evolutionary perspective.

In their native habitats, large herbivores in North America and Africa interact with and respond to patterns of fire across unfragmented landscapes (e.g., Fuhlendorf & Engle 2001; Archibald & Bond 2004; Archibald et al. 2005; Klop & Goethem 2008). Herbivores preferentially select nutritious and available forages provided in recently burned areas and avoid unburned areas (Duvall & Whitaker 1964; Gureja & Owen-Smith 2002; Tomor & Owen-Smith 2002; Fuhlendorf & Engle 2004), and grazing patterns strongly interact with the movement patterns of large carnivores (Ripple & Beschta 2006). Grazing pressure may be moderate across the landscape, but local areas that have burned recently would be heavily grazed, whereas other areas that did not burn would not be grazed because they were not burned over the past few years. Recently burned areas that attract heavy grazing pressure would not have an accumulation of fine fuel, reducing the likelihood and intensity of fires in environments where fine fuel can be limited (Fuhlendorf et al. 2008).

Limiting the interaction between fire and grazing to a statistical interaction of fire and grazing treatments applied in a spatially uniform manner (Fig. 1a), although statistically sound, fails to encompass the dynamic spatial and temporal interactions characteristic of fire and grazing on complex landscapes (Fig. 1b). It also ignores the spatially variable habitat within which native grazers, such as bison, evolved. We do not imply that grazing by native herbivores was unimportant in these grasslands (Knapp et al. 1999) or that fire alone was not a formative driver in the development of grasslands (Anderson 1990); rather, we contend that grazing and fire do not operate independently and in many cases their interaction is more important than the independent effects would predict. Pyric herbivory, the ecological interaction of fire and grazing, recognizes that the spatial pattern of grazing depends on fire and the pattern of grazing influences future patterns of fire. This interaction cannot be studied from the traditional factorial experimental design of fire and grazing because these treatments are typically uniformly applied. Furthermore, we propose that natural fire-grazing interactions be considered heterogeneous and that their restoration be made the first conservation priority for native ecosystems with a long history of fire and grazing.

Promotion of Homogeneous, Moderate Disturbance

Although an herbivore-based focus on restoration of grazed ecosystems is simplistic at best, traditional land conservation and management is no better. Land management on the basis of a statistically constrained approach to understanding fire and grazing has led to wholesale application of management toward a single ecological state that minimizes the importance of spatiotemporal patterns of dynamic disturbance processes (Fuhlendorf & Engle 2001; Briske et al. 2003). This is often justified on the basis of the intermediate-disturbance hypothesis (described by Collins et al. 1995) and a socioeconomic goal of organization within ecosystems. The importance of spatial and temporal heterogeneity to conservation is now widely recognized, but it is rarely incorporated into applications of ecological theory or conservation of wildlands.

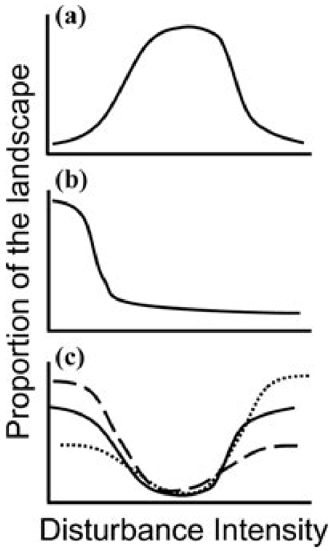

Figure 2. Conceptual models of the proportion of the landscape receiving different disturbance intensities. In grassland ecosystems, (a) represents the agricultural land-management model and the intermediate-disturbance hypothesis in which the majority of the landscape is moderately disturbed, (b) represents a protectionist model in which disturbance is minimized across the entire landscape, and (c) represents the landscape disturbance pattern expected from a fire and grazing interaction that creates a shifting-mosaic landscape.

For example, conservation and management of grasslands for agricultural production focus on minimizing intense disturbance and the amount of undisturbed land (e.g., everything intermediately or moderately disturbed; management to the middle) (Fig. 2a).

To some conservationists ecosystem preservation implies removing disturbance or protection from disturbance. In certain landscape contexts or on small refuges this approach can be appropriate, but in general, disturbance protection lowers coarse-scale heterogeneity on large grassland landscapes, resulting in dominance of undisturbed ecosystems with minimal area moderately or intensely disturbed (Fig. 2b). We suggest heterogeneity has been driven by an interaction of fire and grazing that has resulted in intense disturbance in some areas and no disturbance over much of the landscape within a given year, with time since disturbance varying throughout (Fig. 2c) (Dublin 1995; Fuhlendorf & Engle 2001). Some local sites may have had chronic intense disturbance (e.g., prairie dog [*Cynomys* spp.] towns) and other sites may have been protected from fire and grazing, but areas with repeated, moderate disturbance (e.g., moderate grazing without fire) would have been rare. Yet the average disturbance across the landscape may have been moderate.

Moderate disturbance is rare in fire- and grazing-dependent landscapes because of operative disturbance feedback mechanisms associated with fire and grazing at broad spatial scales (Fuhlendorf & Engle 2004). Positive disturbance feedback, in which grazing animals select recently burned areas, and negative disturbance feedback, which reduces the probability of fire on recently grazed areas, ensures differential disturbance intensity across the grassland landscape. The result is a spatial pattern of differential aboveground biomass, which demonstrates that understanding heterogeneity is critical for conservation of these ecosystems (Fig. 2c). Fire and grazing can have species-dependent positive, negative, or no effect on native species of flora and fauna, so restoration of diverse communities requires a highly variable landscape sculpted by restoration of ecologically interacting disturbance processes to a landscape. With a mosaic of out-of-sequence responses to disturbances driven by the interaction of fire and grazing, disturbance-dependent and disturbance-sensitive species can coexist within a heterogeneous landscape (Knopf 1996; Fuhlendorf et al. 2006).

Figure 3 is a conceptual model of the fire-grazing interaction that illustrates the dynamics of an individual patch. Fire increases the likelihood a patch will be grazed, which changes the plant community structure and thereby reduces the likelihood of fire. Because grazing animals preferentially forage within patches that have burned recently, previously burned and grazed patches receive correspondingly less disturbance. The result is a shifting mosaic of habitat patches at the landscape level that is critical for conservation of native flora and fauna.

Pyric Herbivory in Practice: Conservation of North American Prairies

In 1989 The Nature Conservancy purchased a 14,000-ha tract of remnant tallgrass prairie in the Great Plains of North America and designated this area as the Tallgrass Prairie Preserve. A prescribed burning program was initiated in September 1993, and bison were introduced to a 2000-ha portion (the bison unit) of the preserve in October 1993 with the objective of restoring the interaction of fire and grazing to a complex landscape. Prescribed burning for the preserve consisted of 80% dormant-season (40% fall and 40% late spring) burns and 20% growing-season burns conducted randomly in a regime designed to mimic pre–European settlement burn frequency and season. Internal fences were removed and the bison unit is now over 9000 ha. Burns within the bison unit have been conducted on patches of varying area (100–600 ha) under a variety of fuel and weather conditions, and the average fire-return interval has been about 3–5 years (Fuhlendorf & Engle 2001; Fuhlendorf et al. 2006).

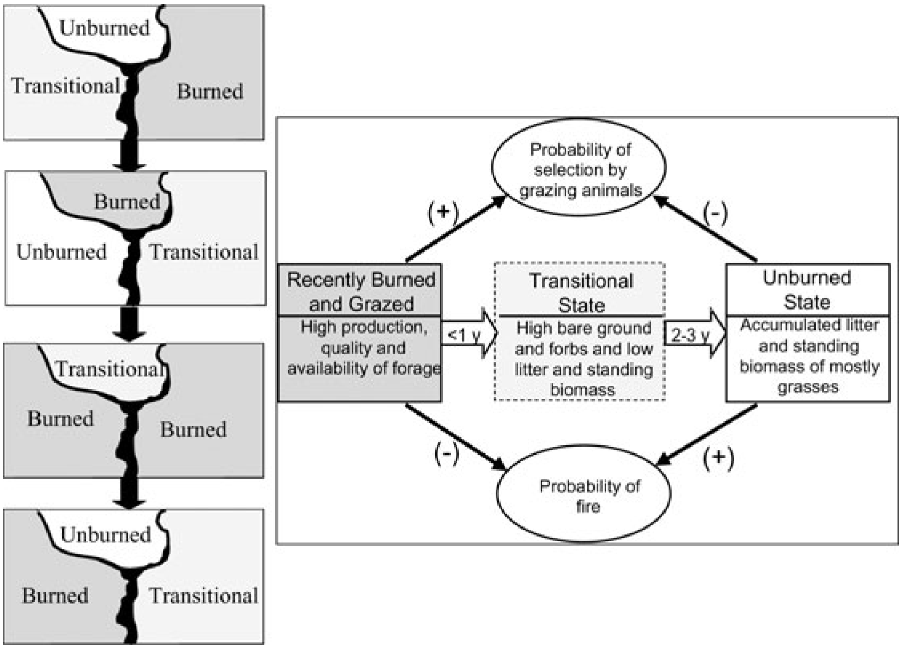

Figure 3. A conceptual model of pyric herbivory illustrating the dynamics of an individual patch. The 3 small boxes within the large box on the right represent the characteristics of the individual patch as a function of time since intense disturbance. Boxes on the left illustrate the dynamics across a landscape composed of multiple patches that differ by time since intense disturbance (Fuhlendorf & Engle 2004).

In keeping with the model of pyric herbivory, bison movement and selective grazing have been unrestricted. The randomly located burn patches within the landscape at the Tallgrass Prairie Preserve have created a shifting patchwork of areas grazed at different intensity and frequency by the free-ranging bison herd. This shifting mosaic created by randomly locating burns and free-roaming animals is unique in the fire and grazing literature. We established permanent sampling points on the basis of time since fire and season of fire. The random spatial application of fire continued over time so each year some sites were burned and some were not, and for each sample all points were variable in time since focal disturbance (fire and grazing). At each sampling point, 25 randomly located 0.1-m^2 plots were sampled for composition of plant functional groups, habitat structure, and aboveground plant biomass. Functional groups of plant species were based on previous studies in tallgrass prairie (Fuhlendorf & Engle 2004; Fuhlendorf et al. 2006) and included tallgrasses (*Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, *Schizachyrium scoparium*), other perennial grasses, annual grasses, sedges and rushes, legume forbs, nonlegume annual forbs, nonlegume perennial forbs, *Lespedeza cuneata* (an invasive exotic plant), woody plants, bare ground, and litter. We estimated cover of each functional group in each plot.

Our sampling data indicated that an average 3-year fire-return interval followed by intense herbivory across a tallgrass prairie landscape created a mosaic of patches in which patches varied in time since focal disturbance (Fig. 4). The result was a fully functioning, resilient tallgrass prairie landscape that provides habitat for a variety of grassland obligate species that occur in the area but have very different habitat requirements. Overall functional group composition, measured by a detrended correspondence analysis (DCA), revealed that composition of functional groups differed most between plant communities that had been burned and grazed in the past year and those that have not been burned or grazed in the past 3 or more years. Beyond 2–3 years since focal disturbance, there was no additional change in the composition of functional groups, which indicates plant communities that were 2–3 years since focal disturbance by fire and grazing had fully recovered in terms of composition. End-of-season standing biomass followed a similar pattern of recovery of about 3 years (Fig. 4). Burning increases

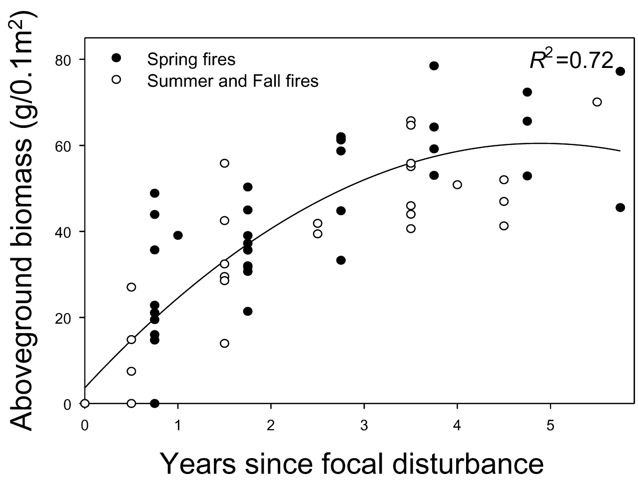

Figure 4. Plant biomass at the end of the growing season over years since focal disturbance by fire and grazing across differentially disturbed patches within the bison unit at the Tallgrass Prairie Preserve during 2002 and 2003.

biomass production (Blair 1997), so the reduced standing biomass on recently disturbed areas primarily results from focal grazing associated with increased site selection by herbivores following fire. Analyses of season of burn (growing season vs. dormant season) showed no difference in biomass, functional group composition, or vegetation structure. Season of fire was not critical to plant community structure, but did provide forage diversity for herbivores and may be important to native fauna. Summer burning is not typically conducted in the area, but it provides critical foraging sites during late summer and fall when nutritious forage is typically limited. The landscape-level result is a corresponding out-of-phase succession among patches just as the pyric-herbivory model predicts (Coppedge & Shaw 1998; Coppedge et al. 1998; Fuhlendorf & Smeins 1998). Even though grazing intensity for the entire bison enclosure is moderate (6–7 ha/female bison) (Coppedge et al. 1998), forage use by bison of recently burned patches is heavy, whereas forage use of unburned areas is light or absent (Coppedge & Shaw 1998).

Pyric herbivory, the spatially and temporally variable ecological interaction, provides greater botanical and vegetation structural diversity across the landscape than when the same amount of grazing and fire is uniformly applied, as is done on most rangelands that are commonly managed for livestock production (Fuhlendorf & Engle 2004). Analyses of grassland birds, insects, and small mammals suggest that some species of these groups depend on recent disturbances, whereas other species depend on habitat indicative of several years without disturbance (Fig. 5) (Fuhlendorf et al. 2006; Engle et al 2008). For example, Henslow's Sparrows (*Ammodramus henslowii*) were absent from locations where fire and grazing were uniformly applied across the comparison treatment each year because these locations lacked accumulated plant litter. Under pyric herbivory, this regionally rare bird was a codominant in patches that had not been burned or grazed in 2 or more years. Upland Sandpipers (*Bartramia longicauda*) and Killdeer (*Charadrius vociferous*) were abundant in patches at the other end of the disturbance gradient (i.e., areas with minimal litter and abundant bare ground) owing to recent application of fire and resulting focal grazing.

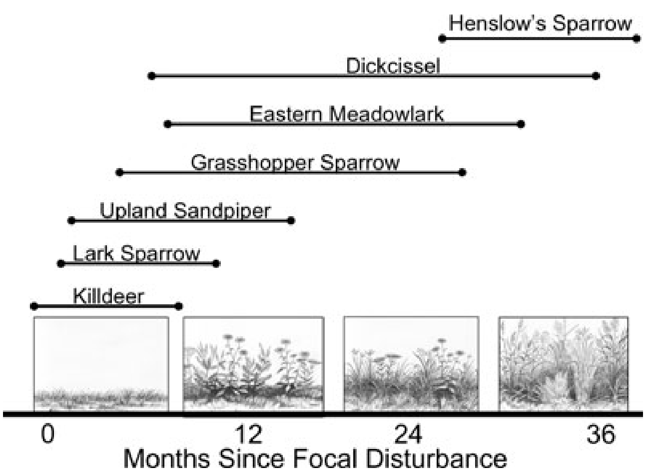

Figure 5. Response of grassland birds to time since focal disturbance by fire and grazing at the Tallgrass Prairie Preserve from 2001 to 2003. Art work in the figure courtesy of Gary Kerby.

Wildlife populations in African grasslands and savannas are also responsive to pyric herbivory (Salvatori et al. 2001; Yarnell et al. 2007). The interaction concomitantly provides, within close proximity, habitat for species that require vegetation structure associated with undisturbed habitats and species that require vegetation structure associated with intensely disturbed habitats. Many endangered or threatened species require the ends of the disturbance gradient (i.e., undisturbed or heavily disturbed), whereas some, such as Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) and Greater Prairie-Chicken (*Tympanuchus cupido*), require the entire disturbance gradient within their home range.

In addition to habitat structure required by grassland-obligate wildlife, pyric herbivory uniquely influences ecosystem function compared with fire or grazing without the interaction. Fire produces patterns of focal grazing. These concentrations of animals produce episodic "grazing lawns," where heavy grazing pressure results in higher nitrogen available to plants in situations where both wild grazers and domestic grazers occur (McNaughton 1984; Anderson et al. 2006). Nitrogen is typically a limiting resource in mesic grasslands, so greater availability could enhance production and diet quality. It has even been suggested that focal grazing may be an adaptation of herbivores to low-nitrogen environments (McNaughton 1984; McNaughton et al. 1997). In contrast, traditional management of domestic livestock minimizes grazing lawns and often requires high levels of supplemental feeding largely because of nitrogen limitations on many of these same landscapes. Conservation of African savannas and grasslands considers the interaction of fire, grazing, and rainfall as the essential determinant of grazing lawns (Archibald 2008). From an herbivore perspective, pyric herbivory may contribute to greater diet stability because it moderates seasonal limitations of high-quality, high-nitrogen-content forage in response to the seasonal variability of fires and the consistent presence of recently burned areas on the landscape.

Much of the alteration of grazing and fire under pyric herbivory is due to altered patterns of herbivore site selectivity (Cummings et al. 2007). Spatially discrete fires and free-roaming herbivores selecting between burned and unburned portions of the landscape alter the scale of selectivity by herbivores. Grazing animals make hierarchical decisions from the fine scale of the plant or plant part up to the regional scale. Patch fires reduce selective pressure on the most palatable species throughout the landscape and promote selection of a higher proportion of all species within the burned patch. This limits the increase in grazing-resistant plants (including invasive species) and favors the persistence of highly palatable, grazing-sensitive plants (Cummings et al. 2007).

Lessons from Pyric Herbivory for Ecology and Conservation

These studies of pyric herbivory exemplify several important emerging aspects of ecology and the conservation of biodiversity. First, understanding heterogeneity within and among ecosystems is important. It has been argued that heterogeneity should be the foundation of conservation and ecosystem management (Christensen 1997; Wiens 1997). The pyric-herbivory model illustrates that spatiotemporal patterns of grazing and fire are critical to nearly all aspects of structure and function of ecosystems with a long history of fire and grazing. Historically, fires and grazing with multiple herbivores interacted across vast regions with climate patterns and predators to create heterogeneity at multiple scales. Engineering these patterns and scale with historical accuracy is both overwhelming and impractical, but it does not diminish the importance of restoring these disturbance processes as an interactive part of the landscape and allowing the patterns that are critical for biodiversity to emerge from the interaction. Scaling limitations, societal issues, the existence of alternative disturbances on the landscape (e.g., cultivation) and lack of understanding of fire and grazing processes limit the widespread restoration of these processes. Nevertheless, our studies demonstrate that domestic herbivores or non-native proxies can be used as surrogates for native herbivores in the pyric-herbivory model and that agricultural production objectives can be achieved while biodiversity is enhanced on small private land holdings (Fuhlendorf & Engle 2004; Fuhlendorf et al. 2006). Seizing the opportunity to expand conservation beyond the boundaries of preserves to private land with significant human influence is an emerging movement in conservation biology (Knight 1999) and an attractive feature of the pyric-herbivory model.

Traditional single-factorial experiments have been valuable in describing basic mechanisms and fundamental relationships associated with homogenously applied grazing and fire. These traditionally designed studies were an important initial step toward understanding large-scale and complex relationships associated with the spatial and temporal interaction of fire and grazing. The pyric-herbivory model demonstrates limits to conventional experimental evaluations in ecology because treatments are usually imposed uniformly and typically to small experimental units rather than focusing on heterogeneity at the appropriate scale that matches conservation objectives. Overcoming limitations imposed through traditional experimental designs remains a critical challenge for conservation. Understanding complex interactions requires a broad perspective and some innovative statistical approaches that focus on spatial and temporal heterogeneity rather than static and homogeneous experimental units.

Although pyric herbivory is important, it is equally important to recognize that as the number of animals, duration of grazing, and the amount, season, size, and shape of fires change, the exact effects of the interaction will also change. A critical determining factor to the effects of pyric herbivory is the relationship of grazing pressure to the number of fires and the amount of area burned each year. If large areas are burned and grazing pressure is low, then the animals will create grazing lawns within the burned patch as the vegetation outgrows that animal's ability to forage throughout the entire burned area. If small areas are burned or grazing pressure is heavy, then the animals will uniformly consume most of the vegetation growing in the recently burned area and then return to areas burned in previous years. In addition, if fires are many and dispersed, they can contribute to the dispersal of herbivores, whereas if they are few and large they can lead to congregations of grazers (Archibald et al. 2005; Waldram et al. 2007). These considerations are further complicated by the fact that many conservation areas and preserves are small remnants within a fragmented landscape. In these situations creating variable patterns of heterogeneity may require special considerations and ecosystems will likely respond differently than large landscapes.

Conclusions

The focus of conservationists on species of herbivores has led to interesting debates such as the one on rewilding (Dolan et al. 2005) and the more long-standing debate on whether grassland conservation is best achieved through grazing of domestic herbivores or native species such as bison (Sanderson et al. 2008). Limited data that can be used to compare different herbivores have resulted in highly variable conclusions as to the importance of specific herbivores that are functionally similar. Obviously, herbivores that have highly divergent foraging behaviors (e.g., browser vs. grazer) will have different effects on the landscape, and multispecies grazing is often different from single-species grazing. Nevertheless, results of recent studies on managing herbivore species with similar foraging strategies (e.g., cattle vs. bison) show that effects can be similar and more dependent on management rather than species (Towne et al. 2005). We suggest that animal introductions, although important for conservation of the individual herbivore, may not restore landscape functions that are critical to many other currently imperiled grassland species. Pyric herbivory applied with any grazing herbivore, even domestic livestock, may more effectively restore evolutionary disturbance patterns than reintroduction programs for any large vertebrate that do not incorporate pyric herbivory.

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