

Small-scale patch structure in North American and South African grasslands responds differently to fire and grazing

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Abstract Fire and grazing significantly impact small-scale patch structure and dynamics in savanna grasslands. We assessed small-scale grass-forb associations in long-term fire and grazing experiments in North America (NA) and Southern Africa (SA). Transects of 128 0.25 m² contiguous quadrats were sampled in areas with different combinations of grazing (ungrazed, single grazer, or multiple grazers) and fire frequency (unburned or annually burned). We predicted that (1) the patch structure of each of the dominant grasses in NA and SA would respond similarly to fire and grazing, and (2) that forb richness would be correlated to grass patch structure. Semi-variance analysis was used to determine patch structure of dominant grasses and forb cover. Community structure responded similarly in NA and SA to fire, grazing, and fire-grazing interactions. Species richness, diversity, and community heterogeneity were significantly higher in unburned-grazed sites. Grazing significantly increased forb cover and decreased cover of the dominant grasses, and the effects of fire on community structure depended on the grazing regime.

Contrary to our prediction, we found that small-scale patch structure of the dominant grass species in NA and SA responded differently to grazing and fire. We found strong grass patch structure in unburned-ungrazed grasslands in both sites; however, grazing and fire reduced patch structure in NA but not SA, and in no instance did grass patch structure influence forb community structure. We conclude that fire and grazing have larger impacts on small-scale patch structure in NA than they do in SA even though overall community structure responded similarly on both continents.

Keywords Dominance-diversity · Grass-forb interaction · Heterogeneity · Konza Prairie · Kruger National Park · Semi-variance

Introduction

Savanna grasslands, defined by a continuous layer of grasses with widely scattered shrubs and trees (Scholes and Archer 1997; Knapp et al. 2004), cover approximately one-third of the terrestrial surface (Sala 2001) and provide economically important services such as grazing lands, tourism, and carbon sequestration (Fuhlendorf and Engle 2001; Gibson 2009). Grazing and fire control the dynamics of savanna grasslands (Scholes and Walker 1993; Knapp et al. 1998b; du Toit et al. 2003), yet the direction and magnitude of responses varies with site and location. The majority

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of fire and grazing studies are site specific, small scale, or short-term (Knapp et al. 2004; Lehmann et al. 2009) limiting the potential to generalize grassland responses across systems. Studying the effect of long-term fire and grazing regimes across sites is an important step towards understanding how these drivers control function in different savanna grasslands.

Globally, grasslands exhibit hierarchical patch structure due to the combined effects of grazing and fire (Collins and Barber 1985; Wu and Loucks 1995), and this patch structure occurs over a range of spatial scales (Forman and Gordon 1986; Wu and Loucks 1995). A patch is defined as a region in an environment where the abundance of something (organism or resource) is high (Roughgarden 1977). On larger scales, a patch can be a watershed burned by fire or a grazing lawn created by bison (Wu and Loucks 1995). On smaller scales in plant communities, patches are expressed as distinct groupings of species (Forman and Gordon 1986). Three main characteristics—strength of patch formation (the degree to which patches are differentiated from the surrounding area by their distinct, within-patch homogeneity), patch size, and patch repeatability across a landscape—are commonly used to describe patch structure of vegetation.

Grazing and fire maintain and control patch structure by differentially influencing community dominance, diversity, and resource heterogeneity (Steinauer and Collins 1995; Blair 1997; Bond and Keeley 2005). Large herbivores generally increase diversity in light to moderately grazed mesic grasslands by altering plant community structure (Collins 1987; Hartnett et al. 1996) through selective grazing and increased resource heterogeneity through soil disturbances (trampling, wallowing) and nutrient deposition (Steinauer and Collins 1995). Conversely fire is a large-scale generalist “herbivore” (Bond and Keeley 2005) that homogenizes resources (Blair 1997) by uniformly removing aboveground biomass (Knapp and Seastedt 1986), and homogenizes community composition by promoting the growth of fire-tolerant C_4 grasses (Collins 1992). When considered independently, fire and grazing have opposite effects on community composition and resource heterogeneity, but together grazing and fire interact to further increase heterogeneity in savanna grasslands on multiple scales (Fuhlendorf and Engle 2004; Archibald et al. 2005; Collins and Smith 2006).

In North American tallgrass prairie, a small number of dominant grasses make up the majority of plant biomass while richness is largely a function of the number of forb species. At large and small scales, richness is negatively correlated with grass cover across a range of grazing and fire treatments implying that abundance of the dominant grasses impacts local species diversity (Baer et al. 2004; Collins and Calabrese 2012). Although it is widely acknowledged that grazing and fire contribute to the maintenance of grassland patch structure, the interactive effects of grazing and fire on the strength, size, and repeatability of small-scale patch structure is poorly understood.

Here, we examined the effects of grazing and fire on the small-scale patch structure and dynamics of herbaceous vegetation in mesic savanna grasslands in North America and South Africa to address three main questions. (1) How do grazing and fire independently and interactively affect community structure including richness, diversity, and grass and forb abundance? (2) How do fire and grazing affect small-scale patch structure of dominant grasses? And (3) is the patch structure of dominant grasses a driver of forb distribution and abundance and therefore species diversity in moderately grazed mesic grasslands?

To address these questions we sampled small-scale patch structure in mesic savanna grasslands at Konza Prairie Biological Station, Kansas, USA (Konza) and Kruger National Park, South Africa (Kruger) (Table 1; Figure S1). Both sites are dominated by long-lived, clonal C_4 grasses with scattered woody vegetation and have a diverse forb flora, and both contain long-term experiments (+30 year) that manipulate the individual and combined effects of grazing and fire. Although these sites differ in evolutionary history, we selected these sites for comparison because they are subjected to common drivers of plant community structure: grazing by mega herbivores, frequent fire, and similar growing season climatic regimes (Knapp et al. 2004; Knapp et al. 2006). These similarities provide an excellent opportunity to compare community responses to fire and grazing in savanna grasslands. Because large, clonal C_4 grasses dominate both systems, we predicted that community properties and small-scale patch structure and dynamics would respond similarly to grazing and fire in both Konza and Kruger.

Table 1 Comparisons of multiple attributes between North American (NA) and South African (SA) savanna grasslands

Attribute	NA	SA
Age (rise of biome)	5–7 mya	40–60 mya
Age of extant community	8–10,000 years	4–6 million years
Historic mega herbivore richness (1)	49 species	45 species
Current mega herbivore richness (2)	2 species	33 species
Plant diversity (3)	Low	High
Soil nutrients (3)	High	Low
Climate	Temperature	Sub-tropical
Growing season precipitation (4)	609(±183) mm	456(±176) mm
Dormant season	Low temperatures	Drought
Dominant herbaceous vegetation	C ₄ grasses	C ₄ grasses

(1) Data on all megafauna of NA and SA come from Martin (1984). (2) Data from SA is specific to Kruger National Park and in NA to Konza Prairie (Kaufman et al. 1998). (3) From Scholes et al. 2003a, b. (4) From Knapp et al. (2006) and Buis et al. (2009)

Methods

Study site

Small-scale patch composition and structure were measured in long-term fire and grazing experiments at the Konza Prairie Biological Station (Konza) in Kansas, USA, and in the south-central Satara region of Kruger National Park (Kruger), South Africa (Table 1; Figure S1). Konza Prairie is one of the last remaining large remnants (3,487 ha) of native unplowed tallgrass prairie in North America. The system is dominated by a small number of C₄ grasses, such as *Andropogon gerardii*, *Panicum virgatum*, *Schizachyrium scoparium* and *Sorghastrum nutans*, which account for the majority of herbaceous primary productivity (Knapp et al. 1998a), while species richness is generally a function of a large variety of forb species (Collins and Glenn 1991). Over 70 % of the species found on Konza are perennial (Freeman 1998). Common forbs include *Ambrosia psilostachya*, *Aster ericoides*, *Salvia azurea*, *Solidago missouriensis* and *S. canadensis*, and common woody species include *Cornus drummondii*, *Rhus glabra*, and

Juniperus virginiana. The climate is temperate (July mean temperature = 27 °C), and precipitation averages 835 mm/year with approximately 70 % (585 mm) falling as rain during the April to September growing season. During our study, growing season precipitation was 889 mm. Soils are fine textured udic argiustolls underlain by cherty limestone and shales (Melzer et al. 2010).

Konza includes fully replicated watershed-level fire and fire/grazing treatments, established in 1977 and 1987, respectively. Replicate watersheds (mean size ~60 ha) are burned at 1-, 2-, 4-, and 20-year intervals, mainly in the spring, to encompass a range of natural fire frequencies and management practices (Knapp et al. 1998b). To address the role of native grazers and fire/grazing interactions (Hobbs et al. 1991; Johnson and Matchett 2001), bison (*Bos bison*) were reintroduced in a 1000 ha fenced area that includes 10 replicate watersheds burned at the same frequencies as the ungrazed areas. The overall grazing intensity is considered moderate with a bison density of approximately 0.2 animals/ha (Knapp et al. 1998b; Knapp et al. 1999). Based on movable exclosures, grazing intensity at this site was 41 % of aboveground net primary production (ANPP) (Knapp et al. 2012).

Kruger National Park is a 2 million ha protected area of savanna grassland located in northeast South Africa. The vegetation is characterized by the coexistence of dominant perennial C₄ grasses, such as *Bothriochloa radicans*, *Digitaria eriantha*, *Panicum coloratum*, and *Themeda triandra*, and woody species, including *Acacia nigrescens* and *Sclerocarya birrea*. Common perennial forbs include *Becium obovatum*, *Heliotropium steudneri*, *Hibiscus micranthus*, *Ipomoea obscura*, and *Solanum panduriforme*. Due to the large size of the park, climatic gradients are substantial, but our research was conducted in the south-central region of Kruger where rainfall is approximately 544 mm/year (Venter et al. 2003), an amount similar to growing season rainfall at Konza (Buis et al. 2009). Growing season rainfall during our study was 481 mm. The climate is tropical with a mild, dry, and frost free dormant season and a warm summer with mean monthly maximum air temperature in January of 29 °C. Soils are fine-textured, rhodic nitisols, haplic luvisols, and leptic phaeozems underlain by basalt (Melzer et al. 2010).

The Experimental Burn Plots (EBP) were established in Kruger in 1954 to determine the importance

of fire seasonality and frequency in this savanna grassland ecosystem (Trollope 1982; Biggs and Potgieter 1999). Similar to Konza, experimental burns occur at 1-, 2- and 3-year intervals, along with unburned control plots (Biggs et al. 2003). The EBPs are one of the longest running fire ecology experiments in Africa. This research focused on the Satara EBP where precipitation, soil type, and the mix of herbaceous and woody plants are similar to Konza. The abundance and grazing intensity of herbivores in Kruger is considered moderate for regional savanna grasslands, and 12–14 mega herbivores (e.g. elephant, rhinoceros, wildebeest, zebra) are commonly seen on the Satara EBPs. Grazing intensity was 48 % of ANPP (Knapp et al. 2012). Adjacent to the Satara EBPs is the Cape buffalo enclosure, erected in 2002 for veterinary purposes. The 900 ha permanent enclosure contains 50–80 Cape buffalo (*Syncerus caffer*), a relatively non-selective grazer of grass (Hofmann 1973). The enclosure is divided into six blocks. One block was burned annually for the duration of the project, and another was left unburned. Also, a 9 ha unburned area within the enclosure was fenced to prevent grazing. The grazing intensity in the Cape buffalo enclosure is comparable to the moderate levels imposed throughout Kruger. Grazing intensity was 43 % of ANPP (Knapp et al. 2012). Thus, Kruger offers sites with a gradient of known long-term fire history and mega herbivore diversity (0, 1, and 12–14 species) all located on the same soil type with similar grazing intensities within a 1 km² area.

Vegetation sampling

Transects were established to measure grassland patch structure at multiple sites at Konza and Kruger. At Konza transects were established in a subset of the long-term experimental grazing and fire watersheds: (1) ungrazed, unburned; (2) ungrazed, annually burned; (3) single grazer (bison), unburned; (4) single grazer (bison), annually burned. At Kruger transects were established in three grazing treatments and two burn treatments: (1) ungrazed, unburned; (2) single grazer (Cape buffalo), unburned; (3) single grazer (Cape buffalo), annually burned; (4) grazed by multiple herbivores, unburned; (5) grazed by multiple herbivores, annually burned. The ungrazed, annually burned treatment does not occur at Satara. We established a single 64 m transect of 0.25 m²

contiguous quadrats at each site for a total of 128 quadrats per transect. Transects were oriented from north to south, on nearly level ground avoiding areas with high woody cover. We targeted areas that represented the typical vegetation of that particular treatment combination. The time required to sample transects at each site (3 weeks) made transect replication impossible. However, as part of a larger comparative project utilizing the same treatment blocks as this study as well as 2 more of each treatment type, we found no significant differences in plant community structure between the treatment replicates at each site (Eby et al. unpublished data; Koerner et al. unpublished data). Thus, we believe the patterns we measured adequately reflect the response of small-scale patch structure to fire and grazing.

Cover of each plant species rooted in each quadrat was visually estimated near the beginning and end of the growing season of 2008 in Konza and 2009 in Kruger. Each study site was effectively uniform in topography, moisture, and vegetation structure. Cover data for each species on the 1 m² scale were used to compute standard metrics of community structure, including grass, forb, and total species richness (S), Shannon–Weiner diversity (H'), evenness (H'/S), and the relative cover of each species. Community heterogeneity (dissimilarity) at the 1 m² scale was calculated using Jaccard dissimilarity coefficient (SAS Institute V.9.3; Cary, N.C.). All metrics were calculated using the maximum average cover values of each species for the entire growing season and then averaged for four adjacent 0.25-m² plots.

Statistical analyses

We tested for differences among treatments for each community structure metric using mixed model analysis of variance (ANOVA) with grazing and fire treatments as fixed effects (SAS Institute V.9.3; Cary, N.C.). We used semi-variance analysis (GS + v7.0, Gamma Design 2007) to quantify spatial variation and small-scale patch structure of the dominant grasses in each treatment (Keane et al. 2012; Vasques et al. 2012; Wang et al. 2012). Semi-variograms show the average variance found in comparisons of samples taken at increasing distances. Four common semi-variogram models can be used in the analysis of spatial structure—linear, exponential, spherical, and gaussian. We ran all four models on each of the structural

variables examined and reported results from the best-fit model in each instance. When not normally distributed, data were log-transformed. The active lag was 31.75 m, and the lag class distance interval was 0.5 m in each model.

If spatial dependence exists among sample units then semi-variance increases with distance until leveling off at a more or less constant value (sill) where spatial dependence no longer exists (Figure S2) (Legendre and Fortin 1989; Steinauer and Collins 2001). Parameters derived from the best-fit model quantified three main aspects of spatial structure. First, the strength of the patch or the proportion of sample variance explained by patchiness at the scales examined (i.e. the degree to which patches were differentiated from the surrounding area by their distinct, within-patch homogeneity) is reflected in the ratio between the sill (asymptote) and the nugget (y-intercept) of the variogram. The strength of the patch has three levels, strong (>0.666), moderate (between 0.333 and 0.666), and weak (< 0.333) (Cambardella et al. 1994). Second, size or mean diameter of those patches is estimated by the range, or separation distance at which the variogram reaches an asymptote. And third, patch repeatability or the arrangement of patches across the area is reflected by the presence of significant fluctuations in semi-variance at spatial scales beyond the first peak. Such fluctuations indicated that patches were aggregated whereas a lack of fluctuation would mean that the patches were arranged at random.

Results

North America

At Konza, total richness per transect ranged from 30 to 80 species, and mean species richness per 1 m² ranged from 16 to 32 (Table 2). Grazing significantly increased total species richness ($F = 424.3$; $P < 0.0001$) while fire had the opposite effect, decreasing total species richness ($F = 2116.0$; $P < 0.0001$). The magnitude of the fire effect (a decrease of 1.5 species m⁻²) was significantly less than the effect of grazing (increase of 15 species m⁻²), and there was no interactive effect of grazing and fire (Table 2). Similar patterns were seen in species diversity. Grazing significantly increased forb cover ($F = 436.8$; $P < 0.0001$), and fire significantly reduced forb cover ($F = 13.4$; $P = 0.0004$). The

interaction of grazing and fire ($F = 53.1$; $P < 0.0001$) increased forb cover significantly more than grazing alone, while fire in the absence of grazing decreased forb cover and richness (Table 2). Forb abundance and richness were not related to grass cover in any treatment. Community heterogeneity was significantly different between each treatment ($F = 479.1$; $P < 0.0001$) with unburned-grazed plots being the most dissimilar or having the highest heterogeneity while the annually burned ungrazed plots had the lowest heterogeneity (highest mean similarity) (Table 2). Based on species accumulation curves (Fig. 1a) small-scale differences in richness were largely driven by grazing. As scale increased, grazing was still the primary determinant of richness, but in ungrazed plots richness also decreased with fire.

Cover of the dominant C₄ grass in each treatment at Konza exhibited strong small-scale spatial pattern (mean proportion = 0.757) (Table 3; Fig. 2a). Grazing decreased and fire increased the strength of small-scale grass patch structure. The combined effects of grazing and fire decreased patch structure further than grazing alone (Fig. 2a). The patch size of the dominant grass depended on the fire-grazing treatment (mean size = 25 m) (Table 3; Fig. 2c). Grazing increased patch size while fire decreased patch size. Grazing and fire combined increased patch size more than grazing alone (Fig. 2c). The unburned-ungrazed grasslands at Konza exhibited significant fluctuations in semi-variance at spatial scales beyond the first peak while the other three treatments did not (Fig. 3a).

Forb richness in each treatment exhibited moderate small-scale patch structure (mean proportion = 0.582) (Table 4). Both grazing and fire decreased patch structure of forbs. The combined effects of grazing and fire decreased patch structure though not as strongly as either grazing or fire individually (Table 4). Patch size of forb richness was random in response to either fire or grazing, but the largest patch size of forb richness occurred in unburned-ungrazed sites (Table 4). Forb richness did not show significant fluctuations in semi-variance at spatial scales beyond the first peak in any of the treatments (Fig. 3c).

Total cover of forbs in each treatment exhibited moderate patch structure (mean proportion = 0.674) (Table 4). Individually, grazing increased and fire decreased small-scale patch structure of forb cover, whereas the combined effects of grazing and fire increased patch structure of forb cover (Table 4).

Table 2 Herbaceous vegetation characteristics for study sites

Site	Treatment	Total species richness (\pm SE)	Diversity (\pm SE)	Heterogeneity (\pm SE)	Grass species richness (\pm SE)	Cover of dominant grass (\pm SE)	Forb species richness (\pm SE)	Forb cover (\pm SE)
NA	Unburned-ungrazed	17 (0.5)	2.05 (0.05)	0.40 (0.01) ^a	7 (0.3) ^a	58 (4.4)	10 (0.4) ^a	39 (2.9) ^a
	Unburned-grazed	32 (0.9)	2.71 (0.04)	0.63 (0.01) ^b	14 (0.3) ^b	24 (4.3)	18 (0.7) ^b	73 (2.7) ^b
	Annual burn-ungrazed	16 (0.5)	1.85 (0.03)	0.17 (< 0.01) ^c	10 (0.3) ^c	56 (2.0)	6 (0.4) ^c	12 (1.3) ^c
	Annual burn-grazed	31 (1.0)	2.61 (0.04)	0.49 (0.01) ^d	14 (0.4) ^b	28 (3.8)	17 (0.6) ^b	82 (2.7) ^d
SA	Unburned-ungrazed	8 (0.3) ^a	1.09 (0.06) ^a	0.65 (0.01) ^a	4 (0.2) ^a	32 (4.2)	5 (0.3) ^a	11 (1.2) ^a
	Unburned-single grazer	12 (0.4) ^b	1.56 (0.04) ^{bc}	0.56 (0.01) ^b	5 (0.1) ^b	29 (2.4)	7 (0.4) ^b	15 (1.5) ^b
	Unburned-multiple grazers	18 (0.4) ^c	2.06 (0.04) ^d	0.62 (0.01) ^a	7 (0.2) ^c	28 (2.34)	10 (0.4) ^c	23 (1.2) ^c
	Annual burn-single grazer	13 (0.4) ^d	1.68 (0.05) ^b	0.64 (0.01) ^a	6 (0.2) ^b	25 (2.83)	8 (0.4) ^b	14 (1.2) ^{ab}
	Annual burn-multiple grazers	10 (0.3) ^c	1.47 (0.03) ^c	0.50 (0.01) ^c	5 (0.2) ^b	35 (2.99)	4 (0.2) ^a	18 (1.7) ^b

Means and standard error (\pm SE) were calculated for richness, Shannon–Weiner diversity, community heterogeneity (Jaccard dissimilarity coefficient), grass species richness and the cover of the dominant grass species in each treatment, and forb species richness and forb cover for both NA and SA. Means were calculated at the 1 m² scale along transects in each treatment. The main effects of fire and grazing were significant ($P < 0.05$) for all variables at both sites. Letters denote significant ($P < 0.05$) grazing fire interactions within a site

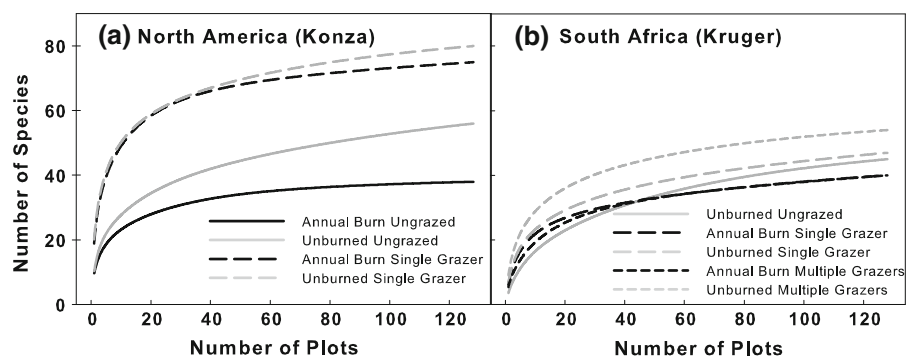


Fig. 1 Species accumulation curves for grasslands in North America (a) and South Africa (b). In NA there were four treatments: (1) ungrazed, unburned, (2) ungrazed, annually burned, (3) single grazer (bison), unburned, (4) single grazer (bison), annually burned. In SA there were five treatments: (1)

ungrazed, unburned, (2) single grazer (Cape buffalo), unburned, (3) single grazer (Cape buffalo), annually burned, (4) grazed by multiple herbivores, unburned, (5) grazed by multiple herbivores, annually burned

Patch size of the forb cover was highly variable, but in general patch size increased with grazing and decreased with fire. Patch size also decreased under

a combination of fire and grazing (Table 4). No significant fluctuations in semi-variance at spatial scales beyond the first peak occurred (Figure S3).

Table 3 Semi-variance model parameters for the dominant grass species in each treatment in NA and SA

Site	Treatment	Dominant grass species	Model type	R ²	Nugget variance (C _o)	Structural variance sill (C _o + C)	Range (A _o)	Proportion (C/ C _o + C)	Class of structural dependence
NA	Unburned- ungrazed	<i>Andropogon gerardii</i>	Spherical	0.44	208.0	1159	5.0	0.82	Strong
	Unburned- grazed	<i>Andropogon gerardii</i>	Exponential	0.95	286.0	1010.0	35.6	0.72	Strong
	Annual burn- ungrazed	<i>Schizachrium scoparius</i>	Exponential	0.06	51.0	407.0	1.1	0.88	Strong
	Annual burn- grazed	<i>Andropogon gerardii</i>	Gaussian	0.89	1.5	4.0	58.6	0.62	Moderate
SA	Unburned- ungrazed	<i>Digitaria eriantha</i>	Spherical	0.58	0.4	3.2	3.7	0.89	Strong
	Unburned- single grazer	<i>Panicum coloratum</i>	Exponential	0.66	314.0	784.3	7.4	0.60	Moderate
	Unburned- multiple grazers	<i>Bothriocloa radicans</i>	Spherical	0.43	311.0	699.1	4.7	0.55	Moderate
	Annual burn- single grazer	<i>Themeda triandra</i>	Spherical	0.43	336.0	847.0	5.1	0.60	Moderate
	Annual burn- multiple grazers	<i>Bothriocloa radicans</i>	Exponential	0.52	1.1	2.5	8.9	0.56	Moderate

Parameters reported are derived from the best-fit model

South Africa

At Kruger, total richness per transect ranged from 37 to 55 species, and mean species richness per 1 m² ranged from 8 to 18 (Table 2). Total species richness per 1 m² increased as number of grazers increased (F = 94.8; P < 0.0001) while fire had the opposite effect, decreasing total species richness (F = 76.9; P < 0.0001). The magnitude of the fire effect (a decrease of 0.5 species m⁻²) was significantly less than the effect of grazing (increase of 4.5 and 6.0 species m⁻² with a single grazer and multiple grazers, respectively). We found a significant fire by grazing interaction (F = 142.3; P < 0.0001). In the absence of fire, grazing increased total richness, while in annually burned sites multiple grazers decreased richness (Table 2). Similar patterns were seen in the diversity response. Forb cover increased as number of grazers increased (F = 21.4; P < 0.0001). Fire had no main effect on forb cover; however, we found a significant fire by grazing interaction (F = 4.1; P = 0.0451) with forb cover being highest in unburned-multiple grazer sites and lowest in unburned-ungrazed sites (Table 2). Forb cover and

richness were not related to grass cover in any treatment. We found a significant fire by grazing interaction on community heterogeneity (F = 56.2; P < 0.0001); however, no clear trend was apparent. The highest level of homogeneity occurred in the annual burn-multiple grazer treatment while high heterogeneity was found in the unburned-ungrazed, unburned-multiple grazers, and annual burn-single grazer treatments (Table 2). Species accumulation curves (Fig. 1b) indicated that on larger scales, annual burning decreased richness with grazing levels having no effect. In unburned grasslands as grazing intensity increased species richness increased. On smaller scales, no clear patterns emerged with fire or grazing.

Unburned-ungrazed grasslands exhibited the strongest small-scale patch structure while the four other treatments showed moderate patch structure. Grazing decreased patch structure, and fire had no effect on patch structure (Table 3; Fig. 2b). The patch size of the dominant grass changed little among treatments with a mean of 6-m (Table 3; Fig. 2d). Ungrazed-unburned grasslands had the smallest patch size of 3.7-m. Grazing increased patch size, and fire decreased patch size in the presence of a single grazer but

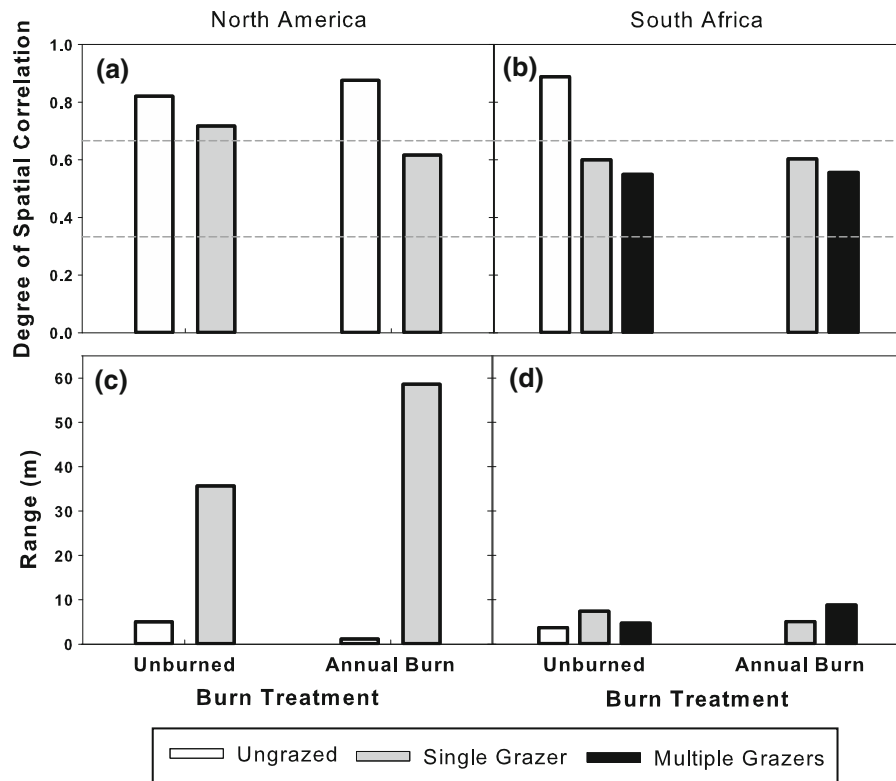


Fig. 2 The strength of patch structure or the degree of spatial autocorrelation for North America (a) and South Africa (b) and the patch size of the dominant grasses in North America (c) and South Africa (d). Values were calculated based upon best-fit models for each treatment. Dotted lines in a and b represent the strong, moderate, and weak classes of spatial dependence. In NA there were four treatments: (1) ungrazed, unburned, (2) ungrazed, annually burned, (3) single grazer (bison), unburned,

(4) single grazer (bison), annually burned. In SA there were five treatments: (1) ungrazed, unburned, (2) single grazer (Cape buffalo), unburned, (3) single grazer (Cape buffalo), annually burned, (4) grazed by multiple herbivores, unburned, (5) grazed by multiple herbivores, annually burned. Patch structure is moderate to strong in all treatments. Grazing increases patch size in NA, and fire effects depend upon the grazing regime. However, neither grazing nor fire affect patch size in SA

increased patch size in the presence of multiple grazers (Fig. 2d). All five treatments exhibited significant fluctuations in semi-variance at spatial scales beyond the first peak (Fig. 3b).

Forb richness in each treatment in Kruger exhibited moderate patch structure (mean proportion = 0.433) (Table 4). Grazing decreased and fire increased patch structure (Table 4). Patch size of forb richness varied with no clear trend in response to grazing or fire but the largest patch size occurred in unburned-ungrazed sites (Table 4). No significant fluctuations in semi-variance at spatial scales beyond the first peak were found in any treatment for forb richness (Fig. 3d).

Forb cover in each treatment in Kruger exhibited moderate patch structure (mean proportion = 0.522) (Table 4). Grazing and fire both increased patch structure (Table 4). Patch size of forb cover varied,

but in general, grazing and fire both decreased patch size (Table 4). No significant fluctuations in semi-variance at spatial scales beyond the first peak were found in any treatment (Figure S3).

Discussion

As predicted, aspects of plant community structure responded similarly at Konza and Kruger to fire, grazing, and fire-grazing interactions. Species richness, diversity, and community heterogeneity were highest in unburned-grazed areas in both sites. Grazing increased the cover of forbs and decreased the cover of the dominant grasses, and the effects of fire on community structure were dependent upon the grazing regime. Despite these similarities, we found that small-

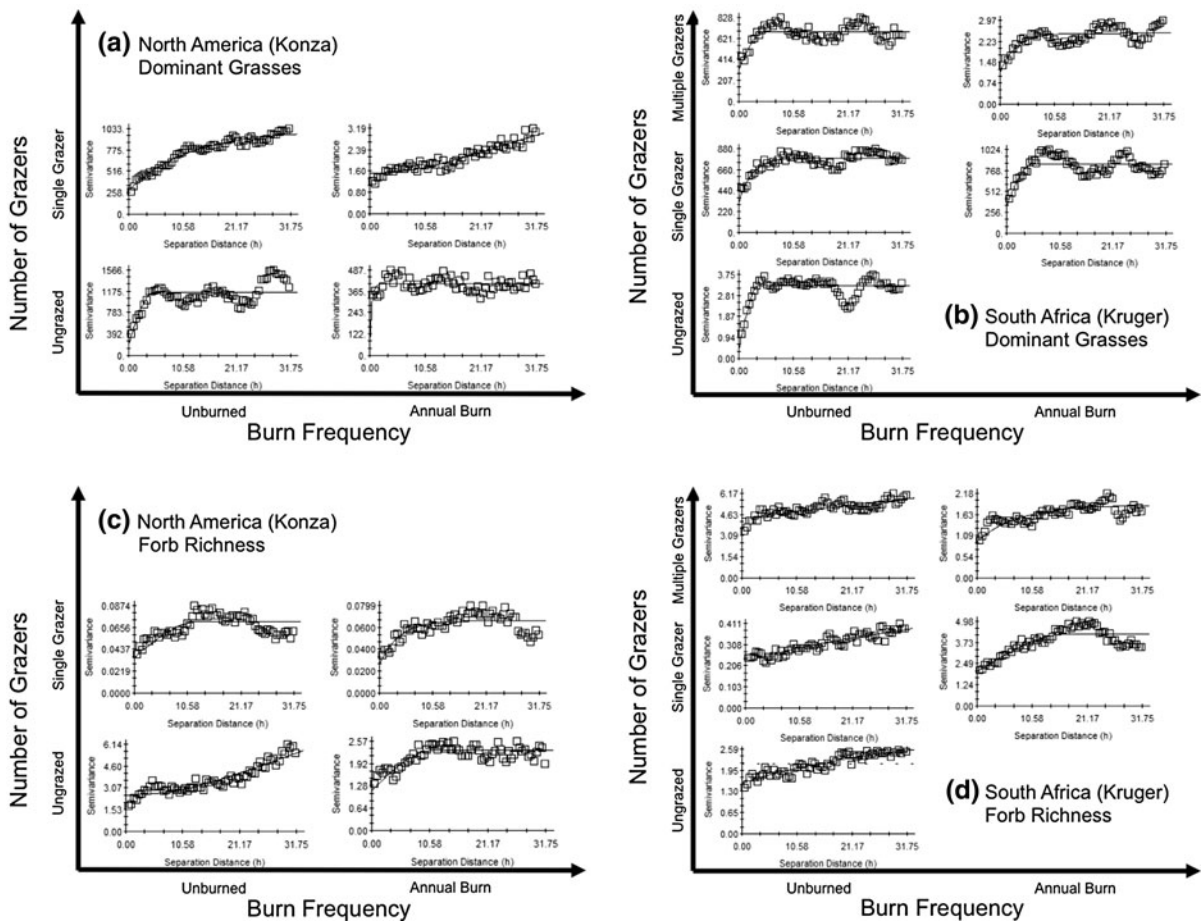


Fig. 3 Semi-variograms of the dominant grasses in North America (a) and South Africa (b) and for forb richness in North America (c) and South Africa (d) for each of the treatments. In NA there were four treatments: (1) ungrazed, unburned, (2) ungrazed, annually burned, (3) single grazer (bison), unburned, (4) single grazer (bison), annually burned. In SA there were five treatments: (1) ungrazed, unburned, (2) single grazer (Cape buffalo), unburned, (3) single grazer (Cape buffalo), annually

burned, (4) grazed by multiple herbivores, unburned, (5) grazed by multiple herbivores, annually burned. The multiple peaks seen in the dominant grass semi-variograms in each of the SA treatments and in NA unburned-ungrazed signifies repeatability of patches across a landscape or a non-random distribution in those disturbance regimes. The lack of repeated peaks in each of the forb richness semi-variograms signifies the lack of repeatability of patches across a landscape

scale patch structure at Konza and Kruger responded differently to grazing and fire. We found strong patch structure of the dominant grasses in undisturbed sites at both Konza and Kruger; however, grazing and fire affected patch structure at Konza but not at Kruger, and in no instance did grass patch structure control forb community structure or diversity.

At Konza, grazing increased species richness, diversity, and forb cover, and fire decreased richness and diversity. These results are consistent with previous studies in a variety of grasslands ecosystems (Collins 1987; Collins et al. 1995; Frank 2005). Forb abundance and richness are generally negatively

correlated with grass cover (Hartnett and Fay 1998; Baer et al. 2004; Collins and Calabrese 2012; Koerner et al. 2013). Therefore, forb abundance and richness increase as grazing decreases the abundance of dominant grasses. As in Konza, grazing also increased richness, diversity, and forb cover in Kruger; however, fire effects on richness, diversity, and forb cover varied depending on the number of grazer species. The inconsistent effects of fire on community structure in grazed areas could indicate that although South African grasses are directly affected by fire, forbs are not, as found in other grasslands with grazers (Lunt and Morgan 2002; Uys et al. 2004). Many South

Table 4 Semi-variance model parameters for forb richness and forb cover in each treatment in NA and SA

Site	Treatment	Metric	Model type	R ²	Nugget variance (C _o)	Structural variance sill (C _o + C)	Range (A _o)	Proportion (C/C _o + C)	Class of structural dependence	
NA	Unburned- ungrazed	Forb Richness	Gaussian	0.87	2.6	9.1	70.7	0.72	Strong	
		Forb cover	Gaussian	0.96	167.0	744.9	59.6	0.78	Strong	
	Unburned- single grazer	Forb richness	Exponential	0.42	0.0	0.1	10.7	0.50	Moderate	
		Forb Cover	Exponential	0.69	383.0	766.1	74.4	0.50	Moderate	
	Annual burn- ungrazed	Forb Richness	Spherical	0.62	1.2	2.3	11.0	0.50	Moderate	
		Forb cover	Exponential	0.39	0.5	1.0	12.6	0.50	Moderate	
	Annual burn- Single grazer	Forb richness	Exponential	0.54	0.0	0.1	11.6	0.61	Moderate	
		Forb cover	Exponential	0.09	0.0	0.1	1.0	0.92	Strong	
	SA	Unburned- ungrazed	Forb Richness	Exponential	0.85	1.6	3.1	93.1	0.50	Moderate
			Forb cover	Exponential	0.87	1.1	2.3	89.1	0.51	Moderate
Unburned- single grazer		Forb richness	Linear	0.85	0.2	0.4	31.5	0.40	Moderate	
		Forb cover	Exponential	0.81	0.8	1.7	96.7	0.52	Moderate	
Unburned- multiple grazers		Forb Richness	Linear	0.61	4.4	5.8	31.5	0.24	Weak	
		Forb cover	Exponential	0.56	0.4	0.8	7.0	0.50	Moderate	
Annual burn- single grazer		Forb richness	Spherical	0.72	2.0	4.2	17.3	0.53	Moderate	
		Forb cover	Spherical	0.72	0.6	1.3	18.0	0.50	Moderate	
Annual burn- multiple grazers		Forb richness	Exponential	0.61	0.9	1.9	23.0	0.50	Moderate	
		Forb cover	Exponential	0.40	0.3	1.1	3.3	0.74	Strong	

Parameters reported are derived from the best-fit model

African forbs are highly resilient to fire, and many forb species like *H. steudneri* tolerate a wide range of seasonality and fire frequency (Uys et al. 2004). Local site conditions can have more influence than fire on forbs (Uys et al. 2004), and large herbivore grazing patterns strongly affect local site conditions, as recently burned grasslands generally attract grazers. The single herbivore site was limited to Cape buffalo, a grass specialist, whereas the multiple grazers site included species with diverse grazing strategies. Diverse grazers likely lead to lower diversity because both grasses and forbs are consumed (Burns et al. 2009).

Small-scale grass patch structure responded differently at Konza and Kruger in response to grazing and fire. Overall, the dominant grass at each site showed strong spatial autocorrelation. Disturbances often impart spatial patterns on grassland plant communities at varying scales by increasing soil moisture heterogeneity, increasing nutrient availability, and reducing the abundance of dominant species (Schimel et al. 1985; Collins 1992; Glenn et al. 1992; Frank et al. 1994; Knapp et al. 1999; Steinauer and Collins

2001). At Konza, small-scale patch structure of the dominant grasses fluctuated widely depending on the grazing and fire treatment, while in Kruger patch structure of the dominant grasses remained constant regardless of the grazing or fire treatment. In Kruger, patchiness was moderate to strong, patch size was approximately 6-m, and patches were repeatable across space. The only treatment at Konza that exhibited similar grass structure to Kruger was unburned-ungrazed. Therefore, when undisturbed, small-scale patch structure at Konza was similar to that in Kruger. However, disturbances altered grass patch structure at Konza, while grass patch structure in Kruger remained stable regardless of grazing or fire treatment.

The different response of patch structure to grazing and fire in North American and South African savanna grasslands may result from differences in their evolutionary histories. North American savanna grasslands are young with the extant community only arising 8–10,000 years ago while South African savanna grasslands are 4–6 million years old (Axelrod 1985; Bond et al. 2003). Stability in the face of

different disturbance regimes could be a manifestation of the longer evolutionary history of grazing and fire in South African savanna grasslands allowing species to adapt to a wide range of disturbance regimes. For example, functional redundancy is greater in South African savanna grasslands, with multiple grass species exhibiting similar patch structure and each dominating a different disturbance regime (Burns et al. 2009). In Kruger as grazing reduces the abundance of palatable grasses, an unpalatable grass species increases (e.g. *Bothriochloa radicans*), altering dominance but maintaining patch structure. In the younger savanna grasslands of North America one species dominates most disturbance regimes, and when grazed, patch structure is altered.

Another factor impacting the responses to grazing and fire is the architectural difference in the dominant grasses between these two sites. Although both sites are dominated by tall C₄ grasses, Konza is dominated by *A. gerardii*, a rhizomatous grass, whereas Kruger is dominated by bunch grasses including *B. radicans*, *T. triandra*, and *D. eriantha*. Grass form influences plant canopy and basal cover. In Kruger canopy cover tends to be patchy with large spaces of bare soil between individual grass clumps, while in Konza, canopy and basal cover are continuous. Patchiness in cover can influence soil nutrient patterns in drier grasslands (Vinton and Burke 1995). Additionally, in Kruger the plant interspaces are likely to have lower root biomass (Hook et al. 1994) as compared to the more continuous root layer in Konza soils (Reed et al. 2005). These architectural differences impose different patterns of heterogeneity at small scales. The homogeneous cover and root layer associated with *A. gerardii* in Konza creates little small-scale variation (Derner and Briske 2001), whereas in Kruger, the heterogeneous basal cover, in particular, associated with bunch grasses creates small-scale variation in resource availability. In addition under similar environmental conditions, bunch grasses tend to concentrate nutrients in their rhizosphere (Hook et al. 1991; Burke et al. 1998; Burke et al. 1999), whereas rhizomatous grasses do not (Vinton and Burke 1995). Bunch grasses may create a positive feedback, and once a patch pattern is formed, grazing and fire are unable to overcome the small-scale patch structure imposed by soil nutrient heterogeneity created by the grasses themselves.

In both sites, forb community structure was not related to small-scale grass patch structure. If forb

patch structure were related to grass structure, we would predict similar semi-variograms and a negative correlation between grass and forb abundance. Instead, we found no correlation between grass and forb abundance and the semi-variograms showed that the spatial structure of grasses was unrelated to that of forbs (Fig. 3c, d; Figure S3; Table 3). Therefore, grass patch structure did not control patterns of forb community structure. Forbs expressed a moderate degree of spatial autocorrelation; however, patch size and repeatability across space were not similar to the dominant grasses. This suggests different drivers for grass and forb patch structure. Spatial structure is just one of many factors that contribute to the maintenance of species diversity.

Fire and grazing are considered to be major factors influencing plant community structure and dynamics in mesic savanna grasslands worldwide. These drivers generally alter the availability and spatial heterogeneity of limiting resources, which affect community heterogeneity. The inherent small-scale patchiness in these savanna grasslands due to the dominant long-lived clonal grasses can be altered by fire and grazing. In general, moderate levels of grazing by native herbivores reduced dominance by C₄ grasses and increased plant species diversity across burning regimes. In addition, unburned, ungrazed areas in North America and South Africa showed moderate to strong small-scale patch structure. However, patch structure in South Africa was unaffected by disturbance, while fire and grazing reduced small-scale patch structure in North American grassland. In South Africa, the ability to maintain consistent patch structure in different fire and grazing regimes is likely a reflection of the architecture of the dominant grasses and the longer evolutionary history with grazing and fire. Thus, fire and grazing have larger impacts on savanna grasslands in North America than they do in South Africa. As a consequence findings from one site cannot be generalized across multiple sites with different evolutionary histories and different architectures of dominant plants.

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