

SCALE-DEPENDENT INTERACTION OF FIRE AND GRAZING ON COMMUNITY HETEROGENEITY IN TALLGRASS PRAIRIE

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Abstract. Natural disturbances affect spatial and temporal heterogeneity in plant communities, but effects vary depending on type of disturbance and scale of analysis. In this study, we examined the effects of fire frequency (1-, 4-, and 20-yr intervals) and grazing by bison on spatial and temporal heterogeneity in species composition in tallgrass prairie plant communities. Compositional heterogeneity was estimated at 10-, 50-, and 200-m² scales. For each measurement scale, we used the average Euclidean Distance (ED) between samples within a year (2000) to measure spatial heterogeneity and between all time steps (1993–2000) for each sample to measure temporal heterogeneity. The main effects of fire and grazing were scale independent. Spatial and temporal heterogeneity were lowest on annually burned sites and highest on infrequently burned (20-yr) sites at all scales. Grazing reduced spatial heterogeneity and increased temporal heterogeneity at all scales. The rate of community change over time decreased as fire frequency increased at all scales, whereas grazing had no effect on rate of community change over time at any spatial scale. The interactive effects of fire and grazing on spatial and temporal heterogeneity differed with scale. At the 10-m² scale, grazing increased spatial heterogeneity in annually burned grassland but decreased heterogeneity in less frequently burned areas. At the 50-m² scale, grazing decreased spatial heterogeneity on 4-yr burns but had no effect at other fire frequencies. At the 10-m² scale, grazing increased temporal heterogeneity only on 1- and 20-yr burn sites. Our results show that the individual effects of fire and grazing on spatial and temporal heterogeneity in mesic prairie are scale independent, but the interactive effects of these disturbances on community heterogeneity change with scale of measurement. These patterns reflect the homogenizing impact of fire at all spatial scales, and the different frequency, intensity, and scale of patch grazing by bison in frequently burned vs. infrequently burned areas.

Key words: bison; burning; fire disturbance; grassland; grazing; Kansas (USA); scale; spatial heterogeneity; tallgrass prairie; temporal heterogeneity.

INTRODUCTION

All communities and ecosystems exhibit some degree of spatial and temporal heterogeneity (Legendre and Fortin 1989, Kotliar and Wiens 1990, Wu and Loucks 1995, Micheli et al. 1999, Cottingham et al. 2001, Huxman et al. 2004). Heterogeneity, the point-to-point dissimilarity in environmental conditions, species composition, or process rates in space and/or time (e.g., Inouye et al. 1987, Adler and Lauenroth 2000, Collins 2000), varies in response to the interaction of multiple biotic and abiotic factors operating at different spatial and temporal scales (Kolasa and Rollo 1991). Theoretical and empirical studies have shown that spatial and temporal heterogeneity affect species diversity, coexistence, and ecological thresholds in communities (Levins 1979, Grover 1988, Chesson and Huntley 1997, Tilman 1999, Peters et al. 2004). Therefore, as human activities continue to simplify ecosystems (Cha-

pin et al. 1997, Aber et al. 2001), it is vital to understand the causes and consequences of heterogeneity in order to maintain species diversity and ecological processes in ecosystems that are increasingly dominated by humans.

A primary cause of heterogeneity is disturbance (Levin 1992, White and Jensch 2001, Roxburgh et al. 2004). Although disturbances vary in type, size, frequency, and intensity (Miller 1982, Mackey and Currie 2000, McCabe and Gotelli 2000), many disturbances reduce the abundance of dominant species, increase resource availability, and create colonization opportunities for less competitive species (Huston 1979, Pickett and White 1985, Petraitis et al. 1989). In other cases, low rates of disturbance may accumulate over time to equal effects of one severe disturbance (Flecker and Taylor 2004). Disturbed patches often support a species assemblage that is initially different from, but may gradually converge upon, a composition similar to predisturbance conditions (Sousa 1984, Gelwick and Matthews 1997, Benedetti-Cecchi 2000). As a consequence, disturbances create a mosaic of patch types in different stages of succession that result in high point-to-point variation in resource availability, species compo-

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sition, vegetation structure, and ecosystem processes within a region (Milchunas and Lauenroth 1993, White and Jensch 2001).

North American grasslands are highly variable in space and time in response to a suite of disturbances that occur at different spatial and temporal scales, all within a variable environmental template (Collins and Glenn 1991, Burke et al. 1999). Broad-scale disturbances, such as climate variability, fire, grazing, and numerous small-scale soil disturbances produce a complex mosaic of patch types in grasslands (Coffin and Lauenroth 1988, Umbanhower 1992, Collins and Glenn 1997, Milchunas et al. 1998, Knapp et al. 1999). These disturbances may interact to alter heterogeneity in ways that might differ from the individual effects of each disturbance type (Collins 1987, Hartnett et al. 1996, Steinauer and Collins 2001). In tallgrass prairie, for example, frequent fires reduce diversity, whereas grazing increases diversity even in frequently burned grassland (Collins 1992, Collins et al. 1998). Therefore, the interactive effects of disturbances within a complex disturbance regime may be a significant source of spatial and temporal heterogeneity in grassland ecosystems. It is not known, however, if the individual and interactive effects of these and other disturbances on heterogeneity are scale dependent.

The separate and interactive effects of disturbances, such as fire and grazing, on heterogeneity are likely a function of spatial scale and temporal extent. Fires, when they occur, generally have relatively consistent impacts over fairly large areas, although fire intensity may vary within burned areas (Vogl 1974, Gibson et al. 1990). As a result, frequent fires in mesic grasslands tend to reduce the spatial variation of grassland vegetation by enhancing the abundance of a few common C_4 grasses (Collins 1992, Collins et al. 1995). This increase in grass dominance enhances ecosystem functioning by stabilizing aboveground production (Smith and Knapp 2003). Grazing, on the other hand, is spatially variable. Grazers make foraging decisions along a hierarchy from landscape elements to bite locations based on the quality and quantity of forage (Senft et al. 1987, WallisDeVries and Schipper 1994, WallisDeVries et al. 1999). When given the choice, grazers generally prefer to forage in recently burned grasslands where the quality and quantity of forage is greatest (Briggs et al. 1998, Coppedge and Shaw 1998, Knapp et al. 1999, Trager et al. 2004). In addition, grazers create small-scale disturbances through deposition of urine and feces (Steinauer and Collins 2001). Bison (*Bos bison*), a formerly abundant native grazer in North America (England and DeVos 1969), have additional behaviors that cause disturbances at intermediate scales, such as wallowing and the formation of grazing lawns (Knapp et al. 1999), both of which could contribute to high spatial heterogeneity (Brown and Allen 1989, Fuhlendorf and Smeins 1999). Collectively, these disturbances can enhance community heterogeneity at relatively small scales (Knapp et al.

1999), but larger scales of observation are likely to include both disturbed and undisturbed patches, thus reducing heterogeneity. As a consequence, the interactive effects of fire and grazing on community heterogeneity likely vary with spatial scale (e.g., Gross et al. 2000, Scheiner et al. 2000, Chalcraft et al. 2004).

A previous analysis (Collins 2000) found that community heterogeneity and rates of change over time differed depending on fire frequency. However, that analysis occurred at only one spatial scale and did not include sites grazed by bison. Here we use data from the Konza Prairie Long-term Ecological Research site to determine the individual and interactive effects of two natural disturbances, fire and grazing by bison, on spatial and temporal heterogeneity across three scales or foci (i.e., scales in which measurement grains or units are aggregated; Scheiner et al. 2000) over eight years. The small (10 m^2) and intermediate (50 m^2) spatial scales in our study represent the scale in which bison make foraging decisions and create small- and intermediate-scale disturbances. The largest scale (200 m^2) was selected to capture variation in fire effects and grazing across the landscape. We tested the following hypotheses: (1) frequent burning reduces spatial heterogeneity at all scales of observation; (2) grazing increases spatial and temporal heterogeneity at small, but not large spatial scales; (3) fire and grazing will interact to maximize spatial and temporal heterogeneity at all scales with decreased effects at larger scales; and (4) grazing increases the rate of community change over time, independent of fire frequency, with decreased effects at larger scales.

METHODS

Study area

This study was conducted at the Konza Prairie Biological Station (KPBS; information *available online*)⁴ in northeastern Kansas, USA. KPBS is a 36-km^2 topographically diverse area of native tallgrass prairie that has been divided along watershed boundaries into 64 management units ranging in size from 12 to 136 ha. Replicate management units are burned at 1-, 4-, and 20-yr intervals (Knapp and Seastedt 1998). Some burning treatments have been in effect since 1972; others were started in 1981. Cattle were removed from KPBS in 1971. In 1987, 30 bison (*Bos bison*) were reintroduced to a portion of the area. Herd size increased over time and was maintained during our study period at approximately 200 individuals that have unrestricted access to a 1012-ha portion of the landscape containing 10 management units subjected to 1-, 4-, and 20-yr fire frequencies. This herd size was selected so that $\sim 25\%$ of net primary production (ANPP) is consumed annually (Towne 1999). Although lowlands are generally more productive than uplands, long-term observations at KPBS indicate

⁴ (<http://climate.konza.ksu.edu>)

that bison do not appear to prefer one topographic position to the other (B. L. Brock, G. A. Hoch, and L. C. Johnson, *unpublished manuscript*).

Konza Prairie experiences a midcontinental climate with average monthly temperatures ranging from -2.7°C in January to 26.6°C in July. Average annual precipitation is 834 mm with most falling during the growing season (April–September). The vegetation and biomass are dominated by perennial C_4 grasses (*Andropogon gerardii*, *A. scoparius*, *Panicum virgatum*, *Sorghastrum nutans*, *Sporobolus asper*, *S. heterolepis*; nomenclature follows Great Plains Flora Association 1986). A diverse array of perennial forbs (i.e., *Aster* spp., *Ambrosia psilostachya*, *Artemisia ludoviciana*, *Solidago* spp., *Kuhnia eupatorioides*, *Salvia azurea*, *Vernonia baldwinii*) are common throughout the vegetation (Collins and Glenn 1991, Smith and Knapp 2003).

Field methods

Vegetation was sampled in five permanently marked 10-m^2 circular quadrats evenly spaced along each of four 50-m transects located in similar upland (20 plots) and lowland sites (20 plots) within each management unit (total of 40 plots per management unit). Cover of each species in each quadrat was visually estimated twice (May, September) each year using a modified Daubenmire percent cover scale: 1, $<1\%$ (e.g., present); 2, 2–5%; 3, 6–25%; 4, 26–50%; 5, 51–75%; 6, 76–95%; and 7, $>95\%$. Cover of each species was determined by converting the Daubenmire scale to the midpoint of the cover range. Species maximum annual cover values were used in all analyses. See Gibson and Hulbert (1987) for details on sampling methods and Freeman (1998) for descriptions of plant communities on Konza Prairie.

For this study, we focused our analyses on plant species composition data collected from 1993 to 2000 in replicate ($N=2$) management units burned at 1-, 4-, and 20-yr intervals in areas with (grazed) and without (ungrazed) bison (a total of 12 management units). This was the longest time interval during which all plots in each management unit were sampled annually. During the study period, the 4-yr fire interval treatments were burned two or three times (Ungrazed: Rep A, 1994, 1999; Rep B, 1994, 1998, 2000; Grazed: Rep A, 1994, 2000; Rep B, 1993, 1999). One of the 20-yr grazed watersheds burned during the study period due to a wildfire in 1996.

Data analyses

Spatial heterogeneity was calculated as the mean dissimilarity in species composition among different sample points in space, and temporal heterogeneity was calculated as the mean dissimilarity in species composition for the same sample points over time (Inouye et al. 1987). For the spatial analysis, we used data from 2000 to capture the long-term cumulative effects of fire and grazing. For temporal heterogeneity we used data collected annually from 1993 until 2000. We used

Euclidean distance (ED) as our quantitative measure of heterogeneity (Collins et al. 2000). Heterogeneity, as measured by ED, increases as the degree of difference in composition among sample units increases. We used ED rather than percent similarity (PS), because ED is less affected by species richness and therefore more accurately measures community heterogeneity than PS (Collins et al. 2000).

To determine if community heterogeneity in space or time was scale dependent, we calculated heterogeneity at three focal scales (aggregations of the 10-m^2 measurement units): 10 m^2 , 50 m^2 , and 200 m^2 . We treated each 10-m^2 plot as an independent sample because community composition has been found to be independent between plots at this scale (Bartha et al. 1995). The distance (mean \pm SD) between transects in upland sites is $311.1 \pm 241.8\text{ m}$ ($N=72$; range, 13.0–1087.8 m) and in lowland sites is $191.7 \pm 209.38\text{ m}$ ($N=72$; range, 15.5–851.1 m). The average distance between upland and lowland sites within a management unit, however, is much greater ($538.8 \pm 381.5\text{ m}$, $N=192$; range, 87.2–1653.6 m). For spatial heterogeneity, we minimized the distances between comparisons by constraining contrasts at the 10-m^2 and 50-m^2 scales to upland and lowland sites within a management unit, and at the largest scale to the 200-m^2 sampled areas in upland and lowland sites within a management unit. Thus for the smallest scale, we calculated the average ED of each pairwise comparison ($N=380$) of the twenty 10-m^2 plots within an upland or lowland site. For spatial heterogeneity at the 50-m^2 scale, we averaged species abundances among the five 10-m^2 plots on each of the four transects within an upland or lowland area, and calculated the average ED of each pairwise comparison ($N=12$) of the four 50-m^2 sampled areas within an upland or lowland site in each management unit. For spatial heterogeneity at the 200-m^2 scale we averaged species abundances among the four transects in each upland or lowland site and calculated ED between the 200-m^2 upland and lowland sites within each management unit. Although statistical power is limited at the largest scale ($N=1$ comparison per management unit, $N=6$ total), we included results at this level for comparative purposes. For temporal heterogeneity, we calculated the average ED for each 10-m^2 plot within an upland or lowland site over time ($N=7$ in all cases), for each 50-m^2 area within an upland or lowland site over time using average abundances of species among the five plots on each transect, and for each 200-m^2 upland or lowland site within a management unit over time using average abundances of species among the four upland or lowland transects (see Appendix).

Heterogeneity is a measure of variation, but not a measure of the *rate* of change (Collins 2000). We used time lag analysis to determine the effects of fire, grazing, and their interaction on the rate of community change over time (see Collins et al. 2000). To do so, we created an ED resemblance matrix for the species \times time data

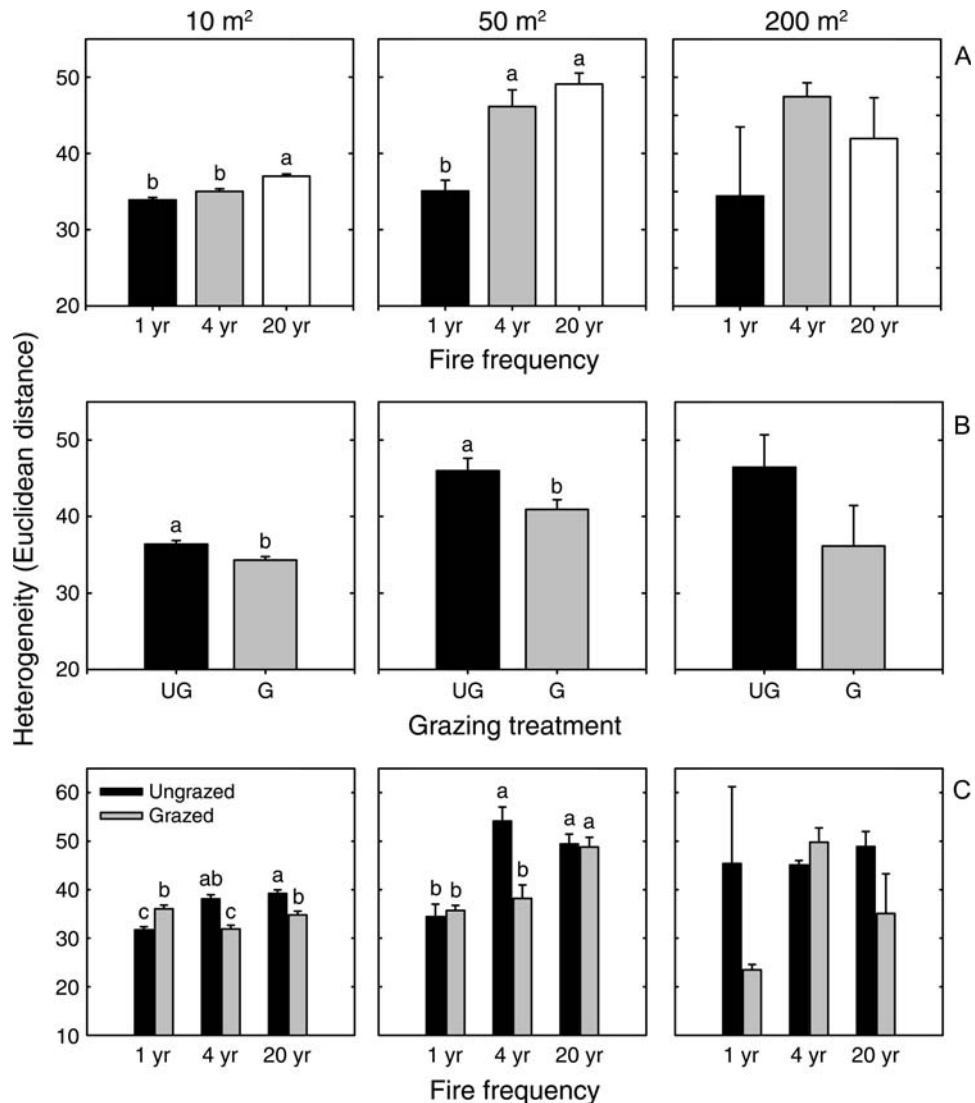


FIG. 1. Effects of (A) fire frequency, (B) grazing, and (C) fire–grazing interaction on spatial heterogeneity at three different scales (10, 50, and 200 m²; see *Methods*) in a native tallgrass prairie. Fire frequency ranged from annual burning (1-yr interval) to long-term unburned (20-yr interval); grazing treatments are grazed (G) and ungrazed (UG). Bars show means + SE. Letters above bars within each panel indicate significant differences ($P \leq 0.05$). Statistical power was low at the largest scale of analysis ($N = 6$), but results are presented to show trends across multiple scales.

matrix for each quadrat within a site (10 m²), each transect within a site (50 m²), and each upland or lowland site within a management unit (200 m²). We plotted ED values at each time lag from 1993 to 2000 at each spatial scale. This analysis produced a measure of the relative rate of community change for each spatial scale of analysis regardless of the timing of individual disturbance events under different disturbance regimes. For each time series, the slope of the linear regression of the square root of the time lag vs. ED was used as our measure of rate of community change. If the slope of the regression is significant, positive, and linear, then it implies that the assemblage in question is undergoing some degree of directional change (Collins et al. 2000).

We used ANOVA (SAS Institute 2005) to determine if spatial or temporal heterogeneity varied with either fire frequency or grazing, or fire–grazing interaction at each spatial scale. We also used ANOVA to determine if the rate of community change varied among the different grazing or burning treatments at each scale.

RESULTS

Spatial heterogeneity

Spatial heterogeneity was lower on annually burned sites than on sites burned every 4 or 20 years, regardless of focal scale or grazing treatments (Fig. 1A). This effect of annual burning was significant at the 10- and 50-m²

scales but not the 200-m² scale, in part because we lacked sufficient replication at this scale. Spatial heterogeneity changed little with increasing scale in annually burned areas, whereas heterogeneity generally increased with scale in infrequently burned grassland. With grazing, spatial heterogeneity was lower in grazed compared to ungrazed areas at all scales, although, this pattern was only significant at the 10- and 50-m² scales (Fig. 1B). Overall, it appears that the separate effects of fire and grazing on spatial heterogeneity are scale independent (i.e., similar patterns, though not always significant, were observed across scales).

There was a significant fire–grazing interaction on spatial heterogeneity at both the 10- and 50-m² scales (Fig. 1C). At 10 m², heterogeneity increased with grazing on annually burned sites, whereas grazing decreased heterogeneity under lower fire frequencies. At the 50-m² scale, grazing significantly reduced heterogeneity under intermediate fire frequencies, but had no effect on either annually burned or unburned areas. Although not significant, at the 200-m² scale in annually burned sites, heterogeneity was 50% lower in grazed compared to ungrazed areas. Together these results suggest that the interactive effects of fire and grazing on community heterogeneity vary with spatial scale, especially in annually burned grassland.

Temporal heterogeneity

Temporal heterogeneity was significantly lower on annually burned sites compared to 4- and 20-yr burn frequencies across grazing treatments (Fig. 2A), whereas temporal heterogeneity was higher in grazed compared to ungrazed areas at all scales (Fig. 2B). Again, the impact of grazing on temporal heterogeneity tended to decrease with increasing scale. As with spatial heterogeneity, there was a significant fire–grazing interaction on temporal heterogeneity at the smallest scale (Fig. 2C). Grazing significantly increased temporal heterogeneity in annually burned and 20-yr burn areas but had no effect on heterogeneity in 4-yr burns. Overall, temporal heterogeneity was lowest in annually burned areas with or without grazing. Together these results indicate that the effects of fire and grazing alone are scale independent, but that fire–grazing interactions on temporal heterogeneity vary with scale.

Rate of change over time

At the 10-m² scale, the rate of community change over time was highest on grasslands burned once every 20 years compared to those burned annually or every 4 years (Fig. 3A). This pattern changed slightly at the 50-m² scale in which rate of change on 4-yr burn sites was intermediate between annually burned and 20-yr burn sites. The same trend occurred at the largest scale. Grazing had no significant effects on rate of change at any scale, and there were no fire–grazing interactions on the rate of community change over time.

DISCUSSION

Overall, our results show that fire and grazing have differential effects on spatial and temporal heterogeneity in mesic grassland, and that the independent effects of each disturbance are generally scale independent (i.e., the pattern of response is consistent across scales). Spatial heterogeneity in annually burned grassland was significantly lower than heterogeneity in less frequently burned areas (Fig. 1). Grazing also decreased spatial heterogeneity at all scales. Patterns of temporal heterogeneity and rate of community change over time were also scale invariant (Figs. 2 and 3). Over each scale, frequent burning decreased temporal heterogeneity whereas grazing increased temporal heterogeneity. In contrast, the interactive effects of fire and grazing on spatial and temporal heterogeneity were scale dependent. At the smallest scale, grazing increased spatial heterogeneity in annually burned grassland but decreased heterogeneity in less frequently burned areas. A similar pattern occurred at the smallest scale with temporal heterogeneity; grazing increased heterogeneity in annually burned grassland but either decreased or had little effect on heterogeneity with infrequent fire. However, at the 50-m² scale, grazing had no effect on spatial heterogeneity in annually burned or unburned areas, but significantly reduced heterogeneity at intermediate burn frequencies.

Fire has been shown to both increase and decrease spatial and temporal heterogeneity in grasslands depending on fire season, frequency, and/or scale of measurement (Biondini et al. 1989, Collins 1992, 2000, Glenn et al. 1992, Howe 1994, Harrison et al. 2003, Towne 2003). Anderson and Brown (1986) proposed that fire was a stabilizing force in grasslands because of its critical role in the evolution and maintenance of the grassland biome (Axelrod 1985). At ecological time scales, however, fire effects may vary based on differences in fire seasonality, land use history, or time since the previous burn (Howe 1995, Turner et al. 1997). In our study, fire treatments have been consistently applied to these experimental management units for >30 yr in some cases. Therefore, in this mesic grassland we conclude that annual spring burning consistently homogenizes community structure, as well as other ecosystem processes (Hobbs et al. 1991, Blair 1997, Johnson and Matchett 2001), across several scales of resolution.

Like fire, grazing has been shown to both increase and decrease spatial and temporal variation in mesic grasslands depending on grazing intensity and history, and scale of measurement (Bakker et al. 1983, McNaughton 1983, Glenn et al. 1992, Stohlgren et al. 1999, Adler and Lauenroth 2000, Fuhlendorf and Engle 2001, 2004, Harrison et al. 2003). Grazing also has a long evolutionary history in the central Great Plains of North America (Axelrod 1985, Milchunas et al. 1988). Unlike fire, grazing intensity varies greatly in space and time as a function of resource distribution patterns, hierarchical

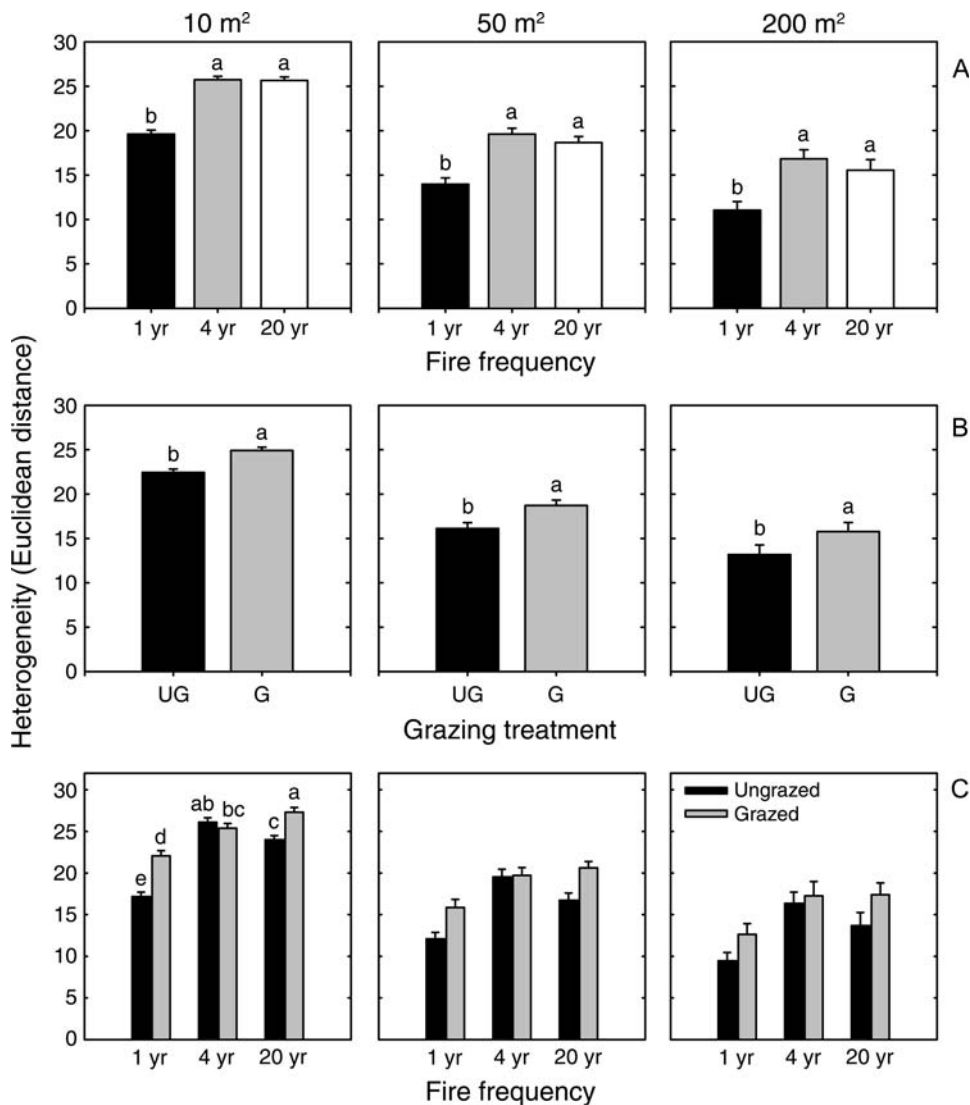


FIG. 2. Effects of (A) fire frequency, (B) grazing, and (C) fire-grazing interaction on temporal heterogeneity (1993–2000) at three different scales (10, 50, and 200 m²; see *Methods*) in a native tallgrass prairie. Fire frequency ranged from annually burned (1-yr interval) to long-term unburned (20-yr interval); grazing treatments are grazed (G) and ungrazed (UG). Bars show means + SE. Letters above bars within each panel indicate significant differences ($P \leq 0.05$). Statistical power was low at the largest scale of analysis ($N = 6$), but results are presented to show trends across multiple scales.

site selection processes by herbivores, and previous within-season grazing patterns (Senft et al. 1987, Coppedge and Shaw 1998, Pastor et al. 1999, WallisDeVries et al. 1999). Because of this inherent variability, we predicted that grazing would result in high small-scale spatial heterogeneity, but differences in heterogeneity between grazed and ungrazed areas would decrease at larger scales because sample plots in grazed areas would include both grazed and ungrazed patches. Instead, we found that grazing decreased spatial heterogeneity and increased temporal heterogeneity across all scales (Figs. 1–3). The decrease in spatial heterogeneity reflects a more even distribution of dominance and a general increase in forb abundance

with grazing (Vinton et al. 1993). High temporal heterogeneity results from changes in the spatial location between grazed and ungrazed patches over time (Fuhlendorf and Engle 2004). Our smallest scale of measurement (10 m²), however, is larger than a typical grazing patch or feeding station (Wallace et al. 1995, WallisDeVries et al. 1999, Steinauer and Collins 2001). Thus even at the smallest scale in our study, most sample plots could include both grazed and ungrazed patches. Indeed, at very small measurement scales (0.25 m²), grazing increased community heterogeneity in both frequently and infrequently burned grasslands (G. F. Veen, J. M. Blair, M. D. Smith, and S. L. Collins, *unpublished manuscript*).

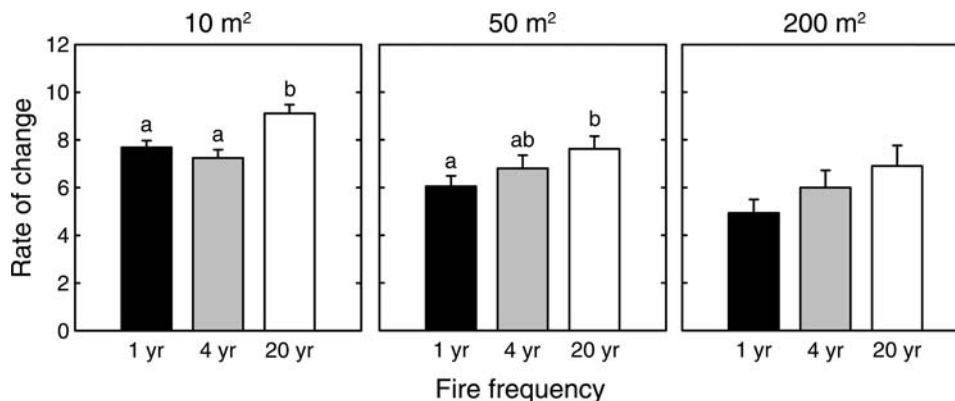


FIG. 3. Effects of fire on rate of community change over time at three scales in a native tallgrass prairie. Fire frequency ranged from annual burning (1-yr interval) to long-term unburned (20-yr interval). Bars are means \pm SE. Letters above bars within each panel indicate significant differences ($P \leq 0.05$). Grazing had no effect on rate of change over time, and there were no fire–grazing interactions. Statistical power was low at the largest scale of analysis ($N = 6$), but results are presented to show trends across multiple scales.

Fire and grazing interact to increase species diversity in tallgrass prairie plant communities (Collins 1987, Collins et al. 1998), yet the interactive effects of fire and grazing on spatial and temporal heterogeneity are less well understood. Given that frequent fire homogenizes vegetation (Collins 1992, Collins et al. 1995) and increases dominance of palatable C_4 grasses (Fuhlendorf and Engle 2004) in mesic grassland, we predicted that fire and grazing would interact to maximize heterogeneity, because grazers would target sites dominated by the palatable C_4 grasses and graze these more intensely the year in which they were burned, thus reducing their probability of burning the following year (Fuhlendorf and Engle 2004). However, we predicted that the interactive effects of fire and grazing would decline with spatial scale, as larger samples would include grazed and ungrazed patches. At the smallest focal scale, grazing increased both spatial and temporal heterogeneity in annually burned vegetation, whereas grazing significantly decreased spatial heterogeneity in infrequently burned grassland and either increased or equalized temporal heterogeneity (Figs. 1 and 2). At the intermediate scale the patterns were similar, although the reduction in spatial heterogeneity in sites burned once every four years was greater ($\sim 50\%$ compared to $\sim 10\%$ at the 10-m^2 scale). Thus fire and grazing interact to affect heterogeneity in grasslands, but these effects are contingent upon fire frequency and spatial scale.

Site selection and grazing intensity by herbivores varies over space and time. Within regions, herbivores, such as bison, select landscape units based on resource quality (Senft et al. 1987, Pastor et al. 1999). In our study area, observations of bison movement patterns over several years (B. L. Brock, G. A. Hoch, and L. C. Johnson, *unpublished manuscript*) indicate that bison select landscape units as a function of burning frequency, which drives interannual variation in landscape-scale resource quality (Johnson and Matchett 2001).

Generally bison prefer sites that are burned (Coppedge and Shaw 1998), but the time since fire is critical in determining the intensity of grazing and its variation over time. Within a growing season, bison select annually burned over unburned areas because palatable C_4 grasses are abundant, and resource quality is higher on annually burned sites (Blair 1997, Johnson and Matchett 2001). However, bison graze in periodically burned sites (4-yr fire frequency) in the year they are burned even more intensely than annually burned or unburned sites because of higher resource quality (Blair 1997, Knapp et al. 1999). We believe that this variation in site selection and grazing intensity over time leads to the scale dependence we observed in the interactive effects of fire and grazing on heterogeneity.

Variation in site selection at smaller scales may increase community heterogeneity. Complex decisions by herbivores go into selection of feeding areas and feeding stations within landscape units. These decisions may be tied to small-scale patterns of resource heterogeneity. Adler et al. (2001) hypothesized that community heterogeneity would (1) decrease when patch grazing reduced the contrast between patch types or (2) increase when patch grazing patterns were stronger than background patch structure. We believe both mechanisms operate in our study area but each occurs under different intervals of burning. Small-scale community heterogeneity is highest in grazed grasslands that are infrequently burned (Fig. 1). This heterogeneity reflects differences in the abundance of palatable grasses and unpalatable forbs. In these heterogeneous areas where feeding stations are discontinuous and variable, grazing by bison, particularly in the year of the fire, reduces grass cover in grazed patches and increases forb cover (Vinton et al. 1993). As a consequence, similarity between grazed and ungrazed patches increases, and community heterogeneity declines.

In contrast, long-term, annually burned, mesic grasslands are relatively homogeneous (Collins 1992, 2000) such that grazing creates identifiable patch structure that is superimposed on a relatively low amount of background variability. Small-scale movement patterns by bison and cattle are random within homogeneous feeding areas (Wallace et al. 1995, WallisDeVries et al. 1999), but patch grazing in such areas may be initiated by nonrandom foraging decisions that are based on otherwise random processes, such as location of nitrogen-rich urine patches (Steinauer and Collins 2001). Thus intensive within-season utilization of burned areas by bison creates a patch structure that is greater than background variability, which increases spatial heterogeneity, whereas patch grazing in the more heterogeneous, infrequently burned sites reduces the contrast between patch types and decreases spatial heterogeneity.

It is clear that community structure and dynamics vary in space and time (Micheli et al. 1999, Collins 2000, Cottingham et al. 2001, Knapp and Smith 2001) and that spatial and temporal variability are necessary to maintain local and regional diversity (Tilman 1999). What is needed, however, is a better understanding of the general drivers of community heterogeneity, their interactions, and how these drivers vary with scale. One of the key drivers of spatial and temporal heterogeneity in most ecosystems is disturbance (White and Jensch 2001), yet disturbances often differ in their spatial and temporal extents. This is certainly the case for North American grasslands, where fire, grazing, and numerous other disturbances occur at different spatial and temporal scales and interact in complex ways to create dynamic patch structure. As a consequence, community composition and patterns of species abundance and distribution are highly variable over multiple spatial and temporal scales. In mesic prairies, this variability effectively reduces stability (Collins 2000) while maintaining local and regional levels of species diversity (Collins et al. 2002). Here we have shown that while the independent effects of different disturbances may be predictable across scales, the effects of multiple disturbances change with scale because disturbances that vary in size, intensity, and frequency interact to generate complex patterns of heterogeneity in time and space. We believe these patterns are of general significance given that many ecosystems, e.g., streams (Flecker and Taylor 2004), intertidal communities (Benedetti-Cecchi et al. 2000), and forests (Platt et al. 2002), are subjected to a variety of natural and anthropogenic disturbances that span multiple spatial and temporal scales.

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APPENDIX

Schematic diagrams showing how plots are aggregated at increasing scales (*Ecological Archives* E087-128-A1).