# Effect of local and regional processes on plant species richness in tallgrass prairie

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Historically, diversity in a community was often believed to result primarily from local processes, but recent evidence suggests that regional diversity may strongly influence local diversity as well. We used experimental and observational vegetation data from Konza Prairie, Kansas, USA, to determine if: (1) there is a relationship between local and regional richness in tallgrass prairie vegetation; (2) local dominance reduces local species richness; and (3) reducing local dominance increases local and regional species richness. We found a positive relationship between regional and local richness; however, this relationship varied with grazing, topography and fire frequency. The decline in variance explained in the grazed vegetation, in particular, suggested that local processes associated with grazing pressure on the dominant grasses strongly influenced local species richness. Experimental removal of one of the dominant grasses, *Andropogon scoparius*, from replicate plots resulted in a significant increase in local species richness compared to adjacent reference plots. Overall all sites, species richness was higher in grazed (192 spp.) compared to ungrazed (158 spp.) areas. Across the Konza Prairie landscape, however, there were no significant differences in the frequency distribution of species occurrences, or in the relationship between the number of sites occupied and average abundance in grazed compared to ungrazed areas. Thus, local processes strongly influenced local richness in this tallgrass prairie, but local processes did not produce different landscape-scale patterns in species distribution and abundance. Because richness was enhanced at all spatial scales by reducing the abundance of dominant species, we suggest that species richness in tallgrass prairie results from feedbacks between, and interactions among, processes operating at multiple scales in space and time.

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Current theory proposes that local species richness may be highly dependent on regional richness (Ricklefs 1987, Cornell and Lawton 1992, Ricklefs and Schluter 1993, Pärtel et al. 1996, 2000, Loreau and Mouquet 1999, Cornell 1999, Liira and Zobel 2000). Formerly, species richness in a community was considered primarily to be the product of local processes that occurred under the influence of multiple, interacting environmental factors (Connell 1978, Huston 1979, Ricklefs 1987, Grace 1999). Local processes include competition, dis-

turbance, and predation, whereas speciation, extinction, dispersal, and fluctuation in range distribution are regional processes. The relative roles of local and regional processes may depend, in part, on whether or not local communities are strongly interactive, and local richness is at or near saturation (Cornell and Lawton 1992, Huston 1999, Smith and Willig 2001).

Most tests of local–regional relationships are based primarily on linear and non-linear regression analyses. Linear relationships may imply that the local commu-

nity is not saturated, whereas non-linear relationships indicate saturation and control by local processes. Yet, it is difficult to infer process from such patterns (Srivastava 1999, Loreau 2000, Shurin et al. 2000, Schoolmaster 2001). In addition, many studies span very large spatial scales that may be discordant with the mechanisms proposed to drive the relationship (Huston 1999). Indeed, the range of scales at which the local–regional relationship holds is unknown, but analyses should occur at scales that reflect processes driving the local–regional interactions (Huston 1999, Loreau 2000, Shurin et al. 2000, Findley and Findley 2001, Karlson and Cornell 1998, 2002). If the local–regional relationship applies over a broad range of scales, including relatively small, homogeneous "regions," then mechanistic studies at small scales coupled with regression analyses may identify the relative influence of local processes, as well as other factors affecting patterns of species distribution and abundance.

In this study, we used observational and experimental data from tallgrass prairie vegetation to address several hypotheses on the relative roles of local and regional processes on local and regional species richness. First, we determined if there was a relationship between local and regional richness in tallgrass prairie vegetation. In our study, the local scale was a 10 $m^2$ plot of tallgrass prairie, the regional scale was the surrounding watershed (12 to 136 ha), and the landscape is the Konza Prairie Biological Station (36 $km^2$) where this study occurred. Assuming that the mechanisms linking local and regional richness apply at a range of spatial scales, we argue that analyses at smaller scales can serve as surrogates for understanding pattern and process at larger spatial scales. Smaller-scale studies are valuable because sample heterogeneity is lower at this scale, and because experiments can be performed to assess mechanisms underpinning the strength of the local–regional relationship.

Huston (1999) proposed that the impact of regional diversity would be strongest on sites with intermediate productivity. At high productivity in the absence of disturbance, local processes dominate and local richness declines regardless of regional diversity. If disturbance reduces competitive dominance, only then can regional richness affect local richness. We tested this hypothesis by comparing the strength of the local–regional relationship in grassland plots with similar productivity potential, but with different disturbance regimes (grazing and fire). Given that grassland productivity is higher and species richness lower under high fire frequency and on deep, lowland soils (Briggs and Knapp 1995, Collins et al. 1995), we predicted that grazing would reduce dominance and enhance the local–regional relationship in frequently burned compared to unburned grassland and in lowland compared to upland soils.

The abundance–occupancy relationship predicts that locally abundant species are widespread regionally, whereas locally rare species have restricted regional distributions (Gaston 1996, Hanski and Gyllenberg 1997). This relationship is also the product of interactions between local and regional processes. Consequently, the interaction of local and regional processes may not only affect species richness, but also quantitative patterns of species distribution and abundance across the landscape. Reducing abundance of dominants may therefore allow subordinate species to increase local abundance and regional distribution. We tested this hypothesis by comparing the abundance–site occupancy relationships in grazed compared to ungrazed areas to determine if disturbance would reduce dominance and enhance the spatial distribution of species across the landscape.

## Methods

### Study area

Most of this study was conducted at the Konza Prairie Biological Station (KPBS) in northeastern Kansas, USA. KPBS is a 36 $km^2$ area of native tallgrass prairie that has been divided into a series of replicated watersheds. The area is essentially continuous grassland habitat along moderate topographic relief, with scattered gallery forest along large streams. Watersheds, which range in size from 12 to 136 hectares, are subjected to burning regimes of 1-, 2-, 4-, 10-, and 20-yr intervals (Knapp and Seastedt 1998). For a number of watersheds, burning treatments have been in effect since 1972, others were started in 1981. The influence of burning on net primary production varies with fire history and topography, but in general, fire increases productivity in the year burning occurs (Briggs and Knapp 1995). Cattle have been excluded from this site since 1971. In 1987, 30 bison (*Bos bison*) were re-introduced to a portion of the area. Herd size is currently maintained at approximately 200 individuals that have unrestricted access to a 1012 ha portion of the landscape. Although lowlands are generally more productive than uplands, bison do not appear to prefer one topographic position to the other.

A portion of this research was also conducted at the USDA Livestock and Forage Research Station in El Reno, Oklahoma, USA. In 1986, a 30 m by 50 m fenced exclosure was constructed around the study area prior to the beginning of this research to prevent cattle from grazing the experimental area. The site was burned in 1984. Both KPBS and the USDA Livestock and Forage Research Station support tallgrass prairie vegetation dominated by $C_4$ grasses, such as *Andropogon scoparius*, *A. gerardii*, *Sorghastrum nutans* and *Panicum virgatum* (nomenclature follows Great Plains

Flora Association 1986). In addition, both sites contain a large variety of native herbaceous dicots, including *Solidago* spp., *Artemisia ludoviciana*, *Aster* spp., and *Ambrosia psilostachya*.

## Local–regional richness relationships

### Field methods

In 1997, we selected 40 sites at KPBS within different watersheds subjected to different burning histories, 20 sites in the grazed area and 20 in the ungrazed area. Most watersheds had multiple sample sites, one in upland and one in lowland areas. At each of the 40 sites, we measured vegetation in five 10 m² quadrats that were evenly spaced along each of four randomly located 50 m long transects (total of 20 10 m² quadrats per site). We visually estimated cover of each species in each quadrat using the Daubenmire cover scale: 1 = <1% cover (e.g. present), 2 = 2–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–95%, and 7 = >95%. Abundance of each species at each site was determined by converting the Daubenmire scale to the midpoint of the cover range and averaging across the 20 quadrats at a site.

### Data analyses

In many studies of local and regional richness, estimating richness at different scales is challenging (Grace 2001a). To obtain relatively unbiased estimates of local (number of species per 10 m²) and regional (number of species in the regional pool) richness, we randomly sub-sampled (without replacement) five of the 20 quadrats at a site, and then calculated an average richness for these five quadrats. This average was used as a measure of local richness. Regional richness was determined based on the remaining 15 quadrats at each site. We repeated this procedure for each site 1000 times using Poptools Version 2.3.7 (http://www.dwe.csiro.au/vbc/poptools/). In this way, independent data are used to calculate local and regional richness. We then averaged the 1000 subsamples of local and regional richness for each site and used these averages in a linear regression to determine if local richness was dependent on regional species richness. This approach increases the statistical independence of measurements of local and regional richness (Srivastava 1999), and also has the advantage of maintaining equal sample numbers and sample areas across all sites. Statistical independence and unequal sample sizes are problems that may plague efforts to determine local–regional relationships (Caley and Schluter 1997, Srivastava 1999, Winkler and Kampichler 2000, Karlson and Cornell 2002).

We used these data to determine if the form of the relationship (slope, variance accounted for) between local and regional richness differed in grazed and un-

grazed vegetation. We also used linear regression to determine if maximum and minimum local richness (per 10 m²) were related to regional richness. We predicted that maximum plot richness would be related to regional richness reflecting regional processes, but that minimum richness would not because minimum richness reflects local processes that tend to reduce local richness. Finally, we used linear regression to test the hypothesis that grazing would increase the strength of the local–regional relationship at sites with high, but not low, productivities (Huston 1999). To do so, we compared local–regional relationships under high and low fire frequencies, and on lowland and upland sites.

## Reduction of *A. scoparius*

### Field methods

The impact of dominance on local richness in tallgrass prairies was experimentally evaluated at sites in Kansas and Oklahoma. At each site, two randomly located 10 × 10 m experimental plots were established. The watershed used at KPBS has been burned at 10 year intervals starting in 1981. The prairie site in Oklahoma was also burned infrequently, with the last fire in 1984. In February 1989, individual clones of *Andropogon scoparius* were mapped in each 10 × 10 m experimental plot, and all clones were removed from a randomly selected half (5 × 10 m area) of each of the four experimental plots. A shovel was used to cut across the base of the meristems to remove the aboveground parts of the plant. At the time of removals, the ground was frozen; therefore, disturbance to the soil was minimized. Large, conspicuous clumps were removed, whereas small clumps were left because removing them would potentially disrupt too many neighboring plants. Limited regrowth of *A. scoparius* occurred during the 1989 growing season, and the treatments significantly reduced cover of this grass by 17–54% relative to reference plots and prior years (Glenn and Collins 1993). Presence and cover of all plants rooted in each of the 100 1-m² quadrats in each of the four 10 × 10 m experimental plots were estimated three times per year in 1988, before removal or *A. scoparius*, and again during the 1989 growing season after removal of *A. scoparius*.

### Data analyses

We determined the number of core and satellite species that occurred in each of the treatment and reference halves of each 10 × 10 m plot before and after removal of *A. scoparius*. Following Hanski (1982), core species were defined as species that occurred in >90% and satellite species were those that occurred in ≤10% of the quadrats (N = 50) in either the removal or reference halves, respectively. We then used a Kruskal–Wallis one-way analysis of variance (KW-ANOVA) to deter-

mine if the change in the number of core and satellite species in removal plots (N = 4) was significantly different from change in reference plots measured before and after the removal of *A. scoparius*. We focus on the core and satellite categories in this analysis because, unlike other categories of distribution, these have historical precedence and can be defined objectively (Hanski 1982).

## Landscape-scale reduction of dominance

Linear regression was used to determine if a positive relationship existed between number of sites occupied across the landscape and average abundance (calculated for occupied sites only (Hanski 1982)) in either the grazed or ungrazed areas. Bison preferentially graze the dominant $C_4$ grasses, which reduces their abundance locally (Vinton and Hartnett 1992). We used a t-test to determine if the slope of the abundance–occupancy regression differed in the grazed compared to the ungrazed data. Next, to assess the patterns in regional distributions of species we plotted the number of species occurring in 10%, 20%, 30%, ..., 100% of sample sites in either the grazed or ungrazed landscapes (Collins and Glenn 1990, 1991). We then tested the hypothesis that the pattern of distribution would be significantly different between grazed and ungrazed areas using a goodness of fit test. If local abundance reduces richness then lowering dominance by grazing should allow more species to occur at more sites in the landscape. Thus, we predicted that landscape species richness would be higher, and that the proportion of widely distributed species would be higher in grazed compared to ungrazed landscapes.

## Results

### Regional–local relationships

There was no relationship between species richness and watershed area: ungrazed $r^2 = 0.02$, F = 0.36, N = 20, P = 0.56; grazed $r^2 = 0.12$, F = 2.34, P = 0.14. There was, however, a significant, positive relationship between regional and local richness in ungrazed (adjusted $r^2 = 0.72$, F = 49.46, N = 20, P < 0.0001) and grazed (adjusted $r^2 = 0.39$, F = 13.39, N = 20, P = 0.002) vegetation (Fig. 1). The slopes of these lines were not significantly different (slope = 0.24 and 0.22 for ungrazed and grazed areas, respectively, t = 0.99, P = 0.33). Regional richness was highly correlated with local maximum plot richness in ungrazed ($r^2 = 0.77$, F = 61.47, N = 20, P < 0.0001) and grazed areas ($r^2 = 0.45$, F = 14.99, N = 20, P = 0.001). Regional richness was correlated with local minimum plot richness only in ungrazed areas ($r^2 = 0.41$, F = 12.33, N = 20, P =

0.003). Local richness was highly related to regional richness in ungrazed lowland ($r^2 = 0.95$, F = 80.7, N = 6, P = 0.0008) but not in grazed lowland ($r^2 = 0.17$, F = 1.21, N = 8, P = 0.314). The opposite was true in uplands (ungrazed upland $r^2 = 0.23$, F = 1.8, N = 8, P = 0.23; grazed upland $r^2 = 0.49$, F = 4.74, N = 7, P = 0.08). There was a significant positive relationship between local and regional richness under high fire frequency in grazed ($r^2 = 0.72$, F = 13.05, N = 7, P = 0.015) and ungrazed areas ($r^2 = 0.91$, F = 58.3, N = 8, P = 0.0003). There was a weak relationship between local and regional richness in ungrazed, infrequently burned areas ($r^2 = 0.37$, F = 5.87, N = 12, P = 0.035) but not in grazed, infrequently burned areas ($r^2 = 0.18$, F = 2.86, N = 13, P = 0.153). Together, these results indicate that regional processes influence local species richness more in ungrazed than in grazed watersheds, which is counter to our original hypothesis that the local–regional relationship would be strongest under conditions that reduced local dominance.

### Reduction of *A. scoparius*

There was no difference in the change in number of core species on treatment versus reference plots after the removal of *A. scoparium* (Table 1, Kruskal Wallis one-way analysis of variance, KW = 0.02, NS). Satellite species, on the other hand, increased significantly on the removal plots compared to reference plots (KW = 4.74, P = 0.03). On average there was an increase of 3.3 satellite species on the removal plots compared to a decrease of 2.3 satellite species on the adjacent reference plots. This demonstrates that dominance by core spe-
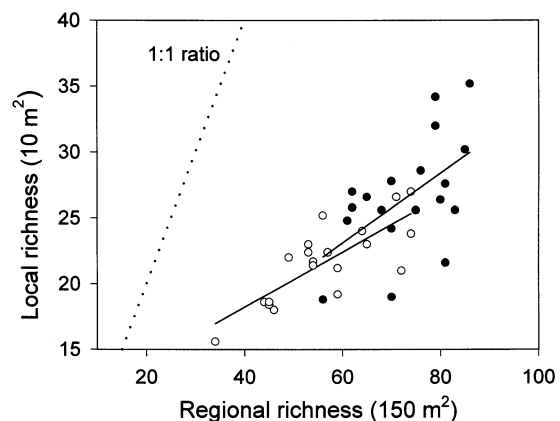


Fig. 1. The relationship between regional species richness and local species richness in ungrazed (open circles) and grazed (filled circles) vegetation at Konza Prairie Biological Station. Vegetation at each site was sampled in 20 permanently located 10 m$^2$ quadrats. Regional richness is the average of 1000 subsamples of the cumulative number of species found in 15 quadrats at a site, local richness is the average of 1000 subsamples of the average number of species occurring in remaining five 10 m$^2$ quadrats at a site.

Table 1. Change in the number of core (C) and satellite (S) species before and after removal of a dominant grass, *Andropogon scoparius*, from $5 \times 10$ m areas in tallgrass prairie. Core species occur in $> 90\%$ of the 1 m² sample plots (N = 50), satellite species occur in $\leq 10\%$ of the plots (N = 50). Average changes with different superscripts are significantly different. (Kruskal–Wallis one-way analysis of variance: KW = 4.74, P = 0.03, N = 4).

| Treatment | Control | | Removal | |
|---|---|---|---|---|
| | C | S | C | S |
| *Replicate 1* | | | | |
| Before | 3 | 7 | 4 | 10 |
| After | 4 | 8 | 6 | 16 |
| Change | +1 | +1 | +2 | +6 |
| *Replicate 2* | | | | |
| Before | 4 | 17 | 3 | 8 |
| After | 4 | 12 | 3 | 9 |
| Change | 0 | −5 | 0 | +1 |
| *Replicate 3* | | | | |
| Before | 2 | 18 | 3 | 15 |
| After | 4 | 15 | 4 | 19 |
| Change | +2 | −3 | +1 | +4 |
| *Replicate 4* | | | | |
| Before | 2 | 13 | 2 | 12 |
| After | 5 | 11 | 6 | 14 |
| Change | +3 | −2 | +4 | +2 |
| Average change | +1.5[a] | −2.2[b] | +1.8[a] | +3.2[c] |

cies, such as *A. scoparius*, reduced the abundance of satellite species at small spatial scales in this tallgrass prairie.

### Landscape-scale reduction of dominance

At the landscape scale, we recorded a total of 192 and 158 species in the grazed and ungrazed areas, respectively. Richness of $C_4$ grasses, forbs, woody plants, annuals, and perennials were all significantly higher in the grazed compared to ungrazed areas (Table 2). Surprisingly, few comparisons of the abundance of functional groups were significantly different between grazed and ungrazed vegetation. Only cover of forbs was significantly lower and cover of annuals was significantly higher in grazed compared to ungrazed areas (Table 2). Grazing by bison did not significantly reduce dominance by the core $C_4$ grasses cross the entire landscape. However, bison preferentially graze in recently burned areas. As a result, cover of $C_4$ grasses on frequently burned, grazed areas was significantly lower than that in frequently burned, ungrazed areas (66.9 vs 91.5 percent on grazed and ungrazed areas, respectively, based on analysis of variance ($F_{1,13} = 10.53$, P = 0.006)). Thus, grazing significantly reduced the abundance of perennial grasses only in frequently burned portions of the landscape.

A highly significant and positive relationship existed between number of sites occupied and average abun-

dance of species in both the grazed and ungrazed areas (Fig. 2). Although the slope of the regression for grazed vegetation (slope = 1.43) was lower than that for ungrazed vegetation (slope = 1.54), these slopes were not significantly different (t = 0.56, NS). This similarity between abundance–distribution relationships in grazed and ungrazed areas was also reflected in the frequency distribution of species among sites across the landscape. There was no difference between the frequency distribution of species occurrences in grazed and ungrazed areas (goodness of fit test, G = 12.60, N = 10, P = 0.18). Although more species occurred in the grazed area, at the landscape scale, patterns of dominance and distribution were indistinguishable in grazed and ungrazed prairie.

### Discussion

We have demonstrated that (1) local richness is related to regional richness particularly in the absence of grazing (Fig. 1), but that this relationship was contingent upon soil type, grazing and fire frequency, (2) contrary to our hypothesis, reducing dominance did not increase the influence of regional richness on local richness in most cases, and (3) these grassland communities are strongly interactive because removing a locally dominant, widespread species increased local species richness (Table 1). The strong positive relationship between regional and local richness in ungrazed vegetation yields compelling evidence that regional processes impart significant influence on local species richness in the

Table 2. Cover and species richness of functional groups on grazed and ungrazed watersheds on Konza Prairie Biological Station. Values are mean ± S.E. Superscripts within a functional group indicate significant difference in cover or richness between grazed (N = 20) and ungrazed (N = 20) sites based on analysis of variance.

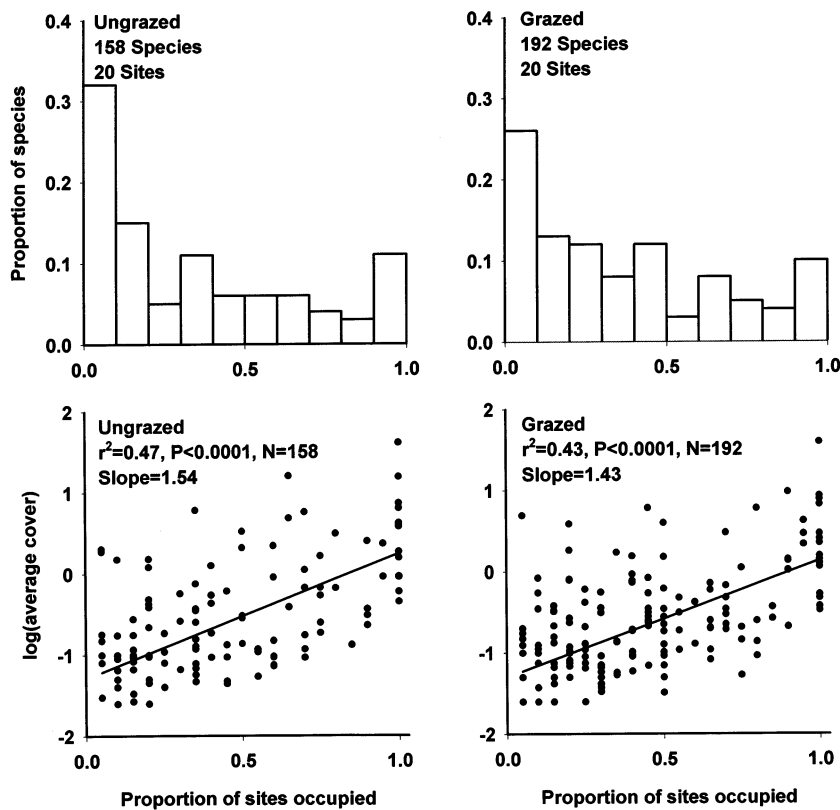| Functional group | Richness | Cover |
|---|---|---|
| *C₃ grasses* | | |
| Grazed | 9.4 ± 0.7 | 18.1 ± 3.5 |
| Ungrazed | 7.8 ± 0.5 | 15.4 ± 2.6 |
| *C₄ grasses* | | |
| Grazed | 9.8 ± 0.4[a] | 68.5 ± 1.9 |
| Ungrazed | 8.3 ± 0.2[b] | 74.3 ± 4.3 |
| *Forbs* | | |
| Grazed | 51.8 ± 1.8[a] | 26.9 ± 1.7[a] |
| Ungrazed | 39.2 ± 2.1[b] | 35.3 ± 3.5[b] |
| *Woody plants* | | |
| Grazed | 6.3 ± 0.4[a] | 14.5 ± 2.7 |
| Ungrazed | 4.8 ± 0.6[b] | 12.1 ± 2.4 |
| *Annuals* | | |
| Grazed | 13.2 ± 6.1[a] | 4.7 ± 8.6[a] |
| Ungrazed | 5.6 ± 4.1[b] | 0.6 ± 0.8[b] |
| *Perennials* | | |
| Grazed | 57.8 ± 5.2[a] | 108.9 ± 18.6[a] |
| Ungrazed | 49.6 ± 7.2[b] | 124.3 ± 20.6[b] |

Fig. 2. Plant species distribution patterns, and the relationship between number of sites occupied and average abundance of species in grazed (N = 20) and ungrazed prairie (N = 20) at Konza Prairie Biological Station.

absence of grazing by bison. The decrease in variance explained between the grazed and ungrazed areas suggests that the regional influence on local species richness declines as grazing reduces grass dominance. This is contrary to our hypothesis that regional richness would have a greater influence on local richness as dominance declines. Thus, local dispersal and colonization may impart more influence on local richness in grazed compared to ungrazed vegetation.

To scale-up our field experiment, we tested the hypothesis that light to moderate grazing at the landscape-scale was a mechanism that would decrease dominance of highly competitive $C_4$ perennial grasses and increase the overall species richness. With reduced dominance, we expected higher local abundances, which would ultimately result in larger populations with wider spatial distributions, thus reducing the likelihood of local extinction (Johnson 1998). Results were equivocal. Although the *A. scoparius* removal experiment supported our first hypothesis that dominance by a regionally widespread, $C_4$ grass reduced local species richness (Table 1), at the landscape-scale, reducing local dominance of core grasses by grazing did not alter the frequency distribution patterns of species (Fig. 2). On the one hand, regional diversity was higher in grazed areas, but pattern of species distribution across the landscape, and the relationship between site occupancy

and abundance, were similar in grazed and ungrazed grasslands.

The short time since bison were reintroduced on Konza Prairie and the differential response times of local and regional processes contribute to these contrasting patterns in richness at local and regional scales. Bison were reintroduced on Konza Prairie only 13 years ago and it took several years for the herd to reach a herd size that can be managed to consume about 25–30% of the average annual aboveground production (Knapp et al. 1999). However, this level of grazing is not consistent across the landscape (Briggs et al. 1998). Bison concentrate their foraging in recently burned areas throughout much of the growing season (Coppedge and Shaw 1998, Briggs et al. 1998). Because grazing is not a uniform process across the landscape, grazing effects may only scale-up within a watershed, but not necessarily across watersheds (Steinauer and Collins 2001). Indeed, grazing reduced cover of $C_4$ grasses on frequently burned but not on infrequently burned watersheds. As a result, grazing reduced dominance and generated higher diversity primarily in frequently burned watersheds, whereas diversity was generally high to begin with in infrequently burned watersheds with or without grazing (Gibson and Hulbert 1987, Collins et al. 1995, 1998, Smith and Knapp 1999). In combination, these patterns of diversity re-

sulted in many locally, intermediate and widely distributed species across the landscape.

It is clear that local processes, in particular interspecific competition, affect local patterns of species richness (Table 1) even though all regressions of regional and local species richness were linear (Fig. 1). Traditionally, a linear relationship would imply that these communities were not saturated, and consequently, local structure results primarily from the regional species pool rather than local interactions (Ricklefs 1987, Cornell and Lawton 1992). Increasingly, there is evidence that linear relationships occur even when local richness may be saturated (Loreau 2000, Shurin and Allen 2001). Thus, the linear relationships that we found are not inconsistent with strong local interactions.

Previously, we hypothesized that a two-tiered competitive hierarchy in which the core species exerted strong control on local species diversity determined local community structure in mesic grassland (Collins and Glenn 1990, 1991). This control resulted from strong competitive interactions among core species, and strong asymmetric interactions between core and satellite species. The latter interaction lowers abundance of satellite species that compete for space within the matrix of the dominant core grasses. Relatively weak interactions exist among the satellite species, the presence and abundance of which fluctuate stochastically over time (Glenn and Collins 1990, 1993). The increase in richness of satellite species with removal of a core grass, and a negative relationship between $C_4$ grass abundance and forb richness at Konza Prairie (Collins and Glenn 1995), lend support to our hypothesized competitive hierarchy in tallgrass prairie.

Differential response times of local and regional processes also limit differences between grazed and ungrazed systems. Tallgrass prairie plant communities are highly dynamic locally both in response to large- and small-scale perturbations (Rabinowitz and Rapp 1985, Reichman and Smith 1985, Gibson and Hulbert 1987, Gibson 1989, Umbanhowar 1992, Collins 2000, Steinauer and Collins 2001), and in the absence of disturbances (Glenn and Collins 1990, 1993, Collins 2000). However, additional time may be required for small-scale processes to influence landscape-scale patterns of distribution and abundance (Wootton 2001). That is, dispersal and establishment are landscape-scale processes that require longer time frames than local population dynamics. Indeed, there is evidence that dispersal limitation may limit recruitment in herbaceous vegetation (Foster 2001, Franzén 2001, Levine 2001). Alternatively, patterns of local richness may not scale up over time. For example, Stohlgren et al. (1999) found that grazing enhanced local, but not regional diversity in Rocky Mountain grasslands. Glenn et al. (1992) found that patterns of heterogeneity in response to grazing in tallgrass prairie changed with increasing spatial scale. Because the grazed area at Konza Prairie had 34 more species than did the ungrazed area, the potential for local increases in species richness to translate to larger-scale patterns seems probable. Thus, we predict that changes in the abundance–occupancy relationship and in the frequency distribution of species across the landscape will occur as current grazing regimes continue on Konza Prairie.

Our findings that maximum plot richness was strongly positively related to regional richness but that minimum plot richness was only weakly related to regional richness supports the idea that local heterogeneity creates variability in the importance of local and regional processes (Shurin et al. 2000). The strong correlation with maximum plot richness implies that regional richness can influence maximum local richness under certain conditions, in this case in the absence of disturbance by grazing. The weaker relationship between regional and minimum richness shows that local interactions can reduce local richness despite the size of the regional species pool. For example, local richness is often strongly related to local productivity (Waide et al. 1999, Gross et al. 2000, Gough et al. 2000, Mittelbach et al. 2001). So, heterogeneity in productivity and disturbance creates variation in the strength of the relationship between local and regional richness under similar environmental conditions.

The relative role of local and regional processes may vary among communities and regions (Palmer et al. 1996, Grace 1999, Huston 1999). Understanding the mechanisms leading to local and regional patterns of species distribution and abundance remains challenging. Because no one mechanism is likely to explain distribution and abundance patterns at multiple scales, studies of the interactive effects of multiple mechanisms at multiple scales are needed (Grace 2001b). Given that local richness may be constrained by regional processes (Ricklefs 1987), disturbances may enhance local richness by increasing local heterogeneity. Local heterogeneity may then lead to a positive relationship between regional and local richness (Huston 1999). Changes in regional diversity in response to small-scale heterogeneity may develop, as well, but only over longer time frames. Even though local and regional processes may operate at different time scales, a positive feedback system may eventually develop between richness at local and regional scales. Thus, rather than viewing the flow of influence to be unidirectional, our results support the view that local species richness results from interactive processes, such as site history, disturbance, dominance, distribution, and dispersal, that occur over multiple scales in space and time (Pärtel et al. 1996, Cornell and Karlson 1996, Hanski and Gyllenberg 1997, Grace 1999, Sankaran and McNaughton 1999, Loreau and Mouquet 1999).

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