Disturbance Frequency and Community Stability in Native Tallgrass Prairie

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ABSTRACT: Ecological communities are spatially and temporally variable in response to a variety of biotic and abiotic forces. It is not always clear, however, if spatial and temporal variability leads to instability in communities. Instability may result from strong biotic interactions or from stochastic processes acting on small populations. I used 10–15 yr of annual data from the Konza Prairie Long-Term Ecological Research site to examine whether plant, breeding bird, grasshopper, and small mammal communities in tallgrass prairie exhibit stability or directional change in response to different experimentally induced fire frequencies. Based on ordination and ANOVA, plant and grasshopper communities on annually burned sites differed significantly from plant and grasshopper communities on less frequently burned sites. Breeding birds and small mammals differed among sites as well, but these differences were not clearly related to disturbance frequency. A modified time series analysis indicated that plant communities were undergoing directional change (unstable) on all watersheds, regardless of fire frequency. Contrary to expectations, directional change was greatest on the annually burned sites and lowest on the infrequently burned sites. Unlike the plant communities, breeding bird, grasshopper, and small mammal communities were temporally stable, despite high-compositional variability from 1 yr to the next. Stability among the consumer communities within these dynamic plant communities occurs because three-dimensional vegetation structure does not change over time, despite changes in plant species composition. Evidence suggests that instability in the plant community results from strong biotic interactions among temporally persistent core species and stochastic dynamics among infrequent satellite species. Overall, community stability cannot be assessed if the pattern of temporal dynamics is unknown. Long-term empirical studies of different taxa under different disturbance regimes are needed to determine over what time frames and spatial scales communities may be stable. Such studies are essential for the development of generalities regarding the rela-

tionship between disturbance frequency and community stability in terrestrial and aquatic systems.

It is almost axiomatic that ecological communities vary in space and time (Clements 1916; Curtis 1959; Knapp 1974; Whittaker 1975). This variation results from the interplay of biotic and abiotic processes operating at a variety of spatial and temporal scales (Hastings et al. 1993; Wu and Loucks 1995). These interactive processes may produce "instabilities" that lead to directional change in a community over ecological time (DeAngelis and Waterhouse 1987). Instabilities can be "local," in response to a single small disturbance, or "global," reflecting an overall response to a large disturbance (Lewontin 1969) or perhaps a change in the disturbance regime. Alternatively, temporal variation in communities may occur within what DeAngelis et al. (1985) referred to as a loose equilibrium. That is, despite high year-to-year fluctuation in composition and abundance, community structure remains stable, on average, over long time frames or large spatial scales (Whittaker and Levin 1977; Bormann and Likens 1979). Based on these notions, I consider a community to be globally stable if it does not exhibit a statistically defined directional change in composition and abundance over an ecological time frame in response to disturbance. From this perspective, a community can be both highly variable from 1 yr to the next, yet remain stable (a loose equilibrium) in terms of its average trajectory over time.

Quantifying temporal variability empirically has been difficult, however, because of the relatively short duration of many field studies (Tilman 1989). Indeed, investigations of community stability have been limited primarily to theoretical evaluations rather than to empirical field studies (Connell and Sousa 1983; DeAngelis and Waterhouse 1987; Ives 1995). Determining long-term patterns of temporal variation and factors that cause them are key research needs in community ecology. Quantifying such patterns would further our understanding of the controversial re-

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lationship between diversity and stability (e.g., Tilman et al. 1997; Wardle et al. 1997) as well as increase our ability to predict the response of communities to both natural and anthropogenic environmental change.

Grassland communities, in particular, provide an appropriate system for the analysis of community stability. Grasslands are highly variable in space and time (Rotenberry and Wiens 1980b; Evans 1988; Collins and Glenn 1991, 1997a; Kaufman et al. 1998). Grassland ecosystems contain a complex disturbance regime composed of frequent large- and small-scale disturbances that interact with interannual climate variation to affect spatial and temporal dynamics (Collins 1987; Coffin and Lauenroth 1988; Day and Detling 1990; Jaramillo and Detling 1992; Milchunas and Lauenroth 1993; Bragg 1995; Steinauer and Collins 1995; Frank et al. 1998; Knapp and Seastedt 1998; Knapp et al. 1999). Indeed, the evolution of the North American grassland biome and the regional persistence of grassland ecosystems have been attributed, in part, to this complex disturbance regime (Axelrod 1985). It is unclear, however, whether grassland community variation over ecological time frames reflects a loose equilibrium or a directional change in response to different rates of natural disturbance.

I used long-term data from the Konza Prairie Long-Term Ecological Research (LTER) site to examine whether grassland communities exhibit global stability or directional change in response to different experimentally induced disturbance frequencies. I examined the dynamics of not only the vascular plant community, but also the breeding bird, grasshopper, and small mammal communities. I used information on these four groups of organisms to test the similarity of responses among groups to different frequencies of experimental burning.

Fire is widely recognized as a critical component of the natural disturbance regime in tallgrass prairie ecosystems (Anderson 1990; Bragg 1995). The estimated point return interval of fire in mesic tallgrass prairie is once every 3–5 yr (Wright and Bailey 1982). Because fire enhances dominance of C_4 grasses and deters establishment of woody plants (Gibson and Hulbert 1987; Anderson 1990), it is presumed to stabilize tallgrass prairie communities (Anderson and Brown 1986). This leads to an apparent contradiction with the traditional view that disturbance is a destabilizing force on communities (Connell 1978; White 1979; Pickett and White 1985; Collins and Glenn 1997b).

Although no community is stable over extended time periods (Pimm 1991), my basic hypothesis is that the grassland plant community on Konza Prairie will be stable over a 10–20-yr time period under the historical fire frequency for the region, which is hypothesized to be once every 3–5 yr (Wright and Bailey 1982). Stability will decrease as fire frequency increases or decreases relative to

the historical average fire return interval (Anderson and Brown 1986). Given that consumer species exist within a matrix of grassland plants that serve as food and habitat, I also tested the hypothesis that community dynamics of consumer species (breeding birds, grasshoppers, and small mammals) mirrored the dynamics of the plant community (Milchunas et al. 1998). That is, temporal stability of breeding bird, grasshopper, and small mammal communities will occur under historical burning regimes, and stability will decrease at higher or lower fire frequencies.

Material and Methods

Study Sites

Data for the following analyses come from the Konza Prairie LTER site near Manhattan, Kansas. The Konza Prairie Research Natural Area is a 3,487-ha native grassland in the Flint Hills region of northeastern Kansas. Watersheds at Konza Prairie have been experimentally subjected to 1-, 4-, and 20-yr intervals of fire since 1972 (Knapp et al. 1998). Before that time, sites were burned every 2–3 yr, on average, and grazed by cattle. Sampling was initiated 5–9 yr after cessation of grazing and the start of the experimental burning treatment to allow the system to adjust to this change in the disturbance regime.

Konza Prairie occurs on topographic gradients that vary in elevation from 320 to 444 m above sea level. Konza Prairie is divided into replicated watershed units, some of which have been burned at 1-, 4-, and 20-yr intervals since 1972 and others that have been burned at these same intervals since 1981. Konza Prairie contains continuous grassland vegetation with occasional gallery forest along the larger streams. The vegetation is dominated by perennial C_4 grasses, especially *Andropogon gerardii*, *Andropogon scoparius*, *Panicum virgatum*, *Sorghastrum nutans*, *Sporobolus asper*, and *Sporobolus heterolepis* (nomenclature follows Great Plains Flora Association 1986). Perennial forbs, such as *Aster* spp., *Ambrosia psilostachya*, *Artemisia ludoviciana*, *Solidago* spp., *Kuhnia eupatoroides*, *Salvia azurea*, and *Vernonia baldwinii*, are common throughout the vegetation. Gallery forests along drainages are dominated by *Quercus* spp. The surrounding region contains frequently burned, unplowed prairie grazed by domestic cattle. Knapp et al. (1998) provide a detailed description of the physical and biotic features of this tallgrass ecosystem.

Field Methods

Plants. Permanent vegetation sampling plots were established in 1981, 1983, and 1984 on watersheds subjected to different fire frequencies at Konza Prairie. Upland veg-

etation has been sampled on each watershed in the spring and fall of each year from the time each site was established. Upland vegetation is sampled in five permanently marked 10-m^2 circular quadrats located along each of four 50-m transects. Cover of each species in each quadrat was visually estimated with the Daubenmire cover scale: $1 \leq$ 1% cover (e.g., present), $2 = 2\%$–5%, $3 = 6\%$–25%, $4 = 26\%$–50%, $5 = 51\%$–75%, $6 = 76\%$–95%, and $7 \geq 95\%$. 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. See Gibson and Hulbert (1987) for details on sampling methods and Freeman (1998) for descriptions of plant communities on Konza Prairie.

Breeding birds. Breeding bird species were sampled while walking along approximately 1 km of permanently located transects in watersheds subjected to different fire frequencies during June of each year from 1981 to 1995. At 15–20-m intervals along each transect, all individuals seen or heard were counted during a 3–5-min sampling period. Abundance of each species is the total number of individuals counted along a transect. Wide-ranging species, such as the red-tailed hawk (*Buteo jamaicensis*) or the turkey vulture (*Cathartes aura*), were not included in the analyses because multiple watersheds were potentially encompassed within the territory of a single pair. See Zimmerman (1993) for further details of the bird communities at Konza Prairie.

Grasshoppers. Grasshopper populations were sampled each year from 1982 or 1984 through 1991 on different watersheds at Konza Prairie. Samples were taken by sweeping with standard 38-cm canvas nets during the midsummer of each year. In 1982, 200 sweeps (10 sets of 20 sweeps) were taken at each site, 400 sweeps were used in subsequent years (20 sets of 20 sweeps). Sweeps were taken along parallel 10-m transects. A sweep was taken at each step by traversing an arc of 180° with the net through the top layer of vegetation. After 20 sweeps, the contents of the net were emptied into a bag and returned to the laboratory for identification. Abundance of each species is the total number of individuals counted at each site. Further details of this sampling technique, its biases, and grasshopper communities at Konza Prairie are given in Evans (1984, 1988).

Small mammals. Small mammals were sampled from 1981 or 1982 through 1995 along permanently located trap lines in different watersheds on Konza Prairie. Each trap line contained 20 stations; stations were located at 15-m intervals and consisted of two large Sherman live traps (7.6 cm × 8.9 cm × 22.9 cm). Traps were baited with peanut butter and oatmeal on 4 consecutive nights in spring and fall of each year. Captured animals were identified, toe-clipped, and released at the site of capture.

Abundance was measured as the average of the spring and fall counts of total number of individuals of each species at each site. Additional details of small mammal communities at Konza Prairie are given in Kaufman et al. (1998).

Data Analyses

In the following analyses, the focal data set comes from three ungrazed watersheds: an annually burned watershed, a watershed burned once every 4 yr, and a watershed burned once every 20 yr (table 1). Plants, breeding birds, grasshoppers, and small mammals have all been sampled annually on these three watersheds for 10 or more years. For some analyses, data from replicate watersheds were used when available, although in some cases these data sets were too short in duration to analyze patterns of temporal variability (table 1).

Ordination analysis provides a mechanism to summarize general patterns of similarities and differences among samples on the different experimental treatments. I used detrended correspondence analysis (DCA) ordinations to determine whether species assemblages differed on watersheds burned at different fire frequencies. Preliminary analyses with different ordination techniques (reciprocal averaging, principal components analysis, nonmetric multidimensional scaling) showed that DCA, in this case, was least affected by often inexplicable outlier samples. Separate data matrices were constructed for each taxon group. Each species × site × year data matrix contained annual abundance values; cover for plants; and number of individuals for breeding birds, grasshoppers, and small mammals. Ordinations were performed on two replicates of each fire treatment for each taxon set, except for grasshoppers, where data were available for only one annually burned site. For plants and small mammals, data from replicate watersheds were available for only a relatively small number of years compared to data from focal watersheds (table 1).

DCA scores integrate composition and abundance data from yearly samples of vegetation, breeding bird, grasshopper, or small mammal communities at each site. In these ordinations, samples that are separated along the primary axes differ in composition and abundance among the constituent species. ANOVA and Bonferroni tests were used to determine whether the DCA axis 1 and 2 scores were significantly different between burning treatments for each taxon set. Although the scores for a site within an ordination are not truly independent, this analysis tests the hypothesis that, over time, the community structure of each taxon group differs significantly among watersheds based on fire frequency.

Although ordination analyses can be used to assess gen-

Table 1: Watershed size and fire history, species sampled, and years species were sampled

Watershed	Size (ha)	Fire history	Species	Duration of samples
Focal:				
1D	41.6	Annually since 1978	Plants	1981, 1983–1995
			Breeding birds	1981–1995
			Grasshoppers	1982–1991
			Small mammals	1981–1995
4B	54.5	1979, 1983, 1987, 1991, 1994	Plants	1981, 1983–1995
			Breeding birds	1981–1995
			Grasshoppers	1982–1991
			Small mammals	1981–1995
20B	23.8	1973, 1991	Plants	1981, 1983–1995
			Breeding birds	1981–1995
			Grasshoppers	1982–1991
			Small mammals	1981–1995
Replicate:				
1A	26.3	Annually since 1972	Birds	1981–1995
			Small mammals	1985–1988
1C	12.3	Annually since 1972	Plants	1983–1990, 1993–1995
4A	19.0	1973, 1980, 1984, 1988, 1992, 1994	Plants	1984–1995
			Breeding birds	1981–1995
4F	16.4		Grasshoppers	1984–1991
			Small mammals	1981–1995
10D	15.6	1973, 1986, 1991	Grasshoppers	1985–1987, 1990–1991
20D	36.4		Birds	1981–1995

Note: Watersheds 1D (annually burned), 4B (burned once every 4 yr), and 20B (burned once every 20 yr) are focal watersheds on which all four taxa were sampled. Replicate watersheds were used in some analyses to increase sample size.

eral patterns of temporal change in community data (Austin 1977), ordinations do not provide statistical inferences as to whether or not compositional change is truly directional (Wildi 1988). To determine whether directional change had occurred since sampling began, I calculated a Euclidean distance (ED) resemblance matrix for the species × site × time data matrix for each taxon group. I then plotted the ED values at each time lag from 1 to n time lags for each taxon group on each watershed. By using all time lags, the analysis produces a measure of global stability regardless of the timing of individual disturbance events under different disturbance regimes. For example, a data set for bird abundances on an annually burned watershed with continuous sampling from 1981 to 1995 would have 15 sample points in time, with 14 1-yr ED time lags (1981 vs. 1982, 1982 vs. 1983,...1994 vs. 1995) and 13 2-yr ED time lags (1982 vs. 1984, 1983 vs. 1985, etc.) through 1 14-yr ED time lag (1981 vs. 1995), a total of 105 time lags over the entire period. I then calculated a linear regression on the square root of the time lag (independent variable) versus Euclidean distance (dependent variable) for each time series. The square root transformation reduces the probability that the smaller number of points at larger time lags will bias the analysis.

This analytical approach can produce several theoretical patterns with time series data. If the regression line is significant, positive, and linear, then it implies that the assemblage in question is unstable because it is undergoing directional change. If the regression line is not significant or the slope is not significantly different from 0, it implies the community is stable. That is, the community exhibits fluctuation or stochastic variation over time. If the slope of the line is significant, negative, and linear, it again implies the community is unstable. In this case, the instability is a form of convergence, where interannual variation is high, but species composition is converging on a community-type characteristic of one of the early sample periods. Other patterns could also be possible. For example, cyclical succession (van der Maarel 1988) could produce significant nonlinear patterns, yet no long-term directional trends. Whereas directional change, cyclical succession, and stochastic variation might be common in community time series data, convergence is the least plausible of the theoretical patterns. Such a result would produce high variance at short time lags and low variance at longer time lags. The slope of the line indicates the rate and direction of change, and the regression coefficient is a measure of signal versus noise. For example, a significant

positive relationship ($P < .01$) with an $r^2 = 0.10$ suggests that directional change is occurring but that change is slow and stochastic variation is high. A larger r^2 value would indicate a stronger signal of directional change and less noise.

One mechanism that produces temporal variability in communities is species turnover. Turnover is a measure of change in species occurrences from 1 yr to the next. I calculated annual turnover for each taxon at a site as the sum of the appearance and disappearance of species on each site from 1 yr to the next. "Appearance" was calculated as the number of species that were absent in year X but were present in year $X + 1$; "disappearance" equals the number of species that were present in year X but were absent in year $X + 1$. Two replicate time series data sets were used for each taxon on each fire frequency treatment when available.

In addition to turnover, the distribution of species occurrences over time was plotted for each taxon on focal watersheds. Essentially, this is a temporal version of a spatial metapopulation analysis (Collins and Glenn 1991, 1997a). In this case, the independent variable is the number of years in which a species occurred over a 10–15-yr time frame, rather than the number of sites occupied over some spatial scale, as in most metapopulation studies (Hanski 1991). Core species in time are those species that occur in >90% of the years sampled. Satellite species are those that occur in <10% of the years sampled. I also tested the hypotheses that species that were persistent over time had higher average abundance (measured as cover for plants or number of individuals for animals) than species that occurred less frequently at a site over time. A large proportion of core species and a positive relationship between temporal persistence and average abundance would indicate that core species lend some degree of stability to a community over time.

Results

The DCA ordination of plant community dynamics on watersheds subjected to 1-, 4-, and 20-yr fire frequencies clearly revealed the effect of fire frequency on plant community composition (fig. 1). Composition of annually burned watersheds is distinct from composition of watersheds burned at 4- and 20-yr intervals throughout the 15-yr time period. In addition, there is some separation of vegetation under 4- and 20-yr fire frequencies. DCA axis 1 scores for the annually burned sites are significantly different from the scores for the 4- and 20-yr sites (table 2). In addition, the two annually burned sites were also significantly different along DCA axis 2 (fig. 1; table 2). The differences along the first DCA axis reflect a higher abundance of the C_4 grasses and a lower forb diversity on

the annually burned sites than on the less frequently burned sites. Also, the C_3 grass *Poa pratensis* is common on the infrequently burned sites, whereas this grass is virtually absent from the annually burned watersheds. The two annually burned sites differ in total cover of forbs (32.6% vs. 19.2% cover; $F = 6.19$, $P = .0001$, $N = 11$ and 14, respectively) and total species richness (84 vs. 102 species 200 m^{-2}). Thus, despite dissimilarity among the two annually burned sites, consistent differences in composition were observed for plant communities under different fire frequencies.

Animal communities were also dissimilar under different burning regimes (fig. 1), but these differences did not parallel those found in the plant communities. As in the plant communities, the community of grasshoppers on annually burned grassland was distinct from communities on sites burned at 4- and 20-yr intervals (table 2). However, differences between breeding bird and small mammal communities on sites with different fire frequencies are less distinct. Although there are significant differences in DCA axis 1 and 2 scores for breeding bird and small mammal communities on different watersheds, these differences are not completely related to fire frequency. Rather, they reflect individualistic differences in species composition among watersheds. For birds, one of the annually burned sites was significantly different from all other communities. For small mammals, on the other hand, one of the sites burned every 20 yr was distinct from all the others. Thus, breeding bird, grasshopper, and small mammal communities differed from one watershed to the next, but these differences only partially matched the patterns found in the response of plant communities to fire frequency.

In the plant community, temporal variability and community stability also differed among fire frequencies, but results differed from the expectation that communities would be most stable under a 4-yr fire frequency (fig. 2). Vegetation on the 4-yr fire treatments was clearly undergoing directional change over time. In addition, vegetation on the annually burned watersheds showed low temporal variation and stronger directional change than the 4- or 20-yr burn sites (fig. 2). That is, as fire frequency decreased, the plant communities showed increasing year-to-year variability and less clear patterns of directional change. Indeed, the regression line for the watershed burned once every 20 yr had the lowest slope and a low r^2, indicating that the infrequently burned site was more stable than the more frequently burned sites.

Temporal variation in animal communities did not mimic the patterns in the plant communities. Only one of 15 time lag regressions for birds, grasshoppers, and small mammals was significant. In the one case where the time lag regression was significant and positive (small mammals on one 20-yr burn site: $r = 0.28$, $F = 9.24$, $P = .003$, $N =$
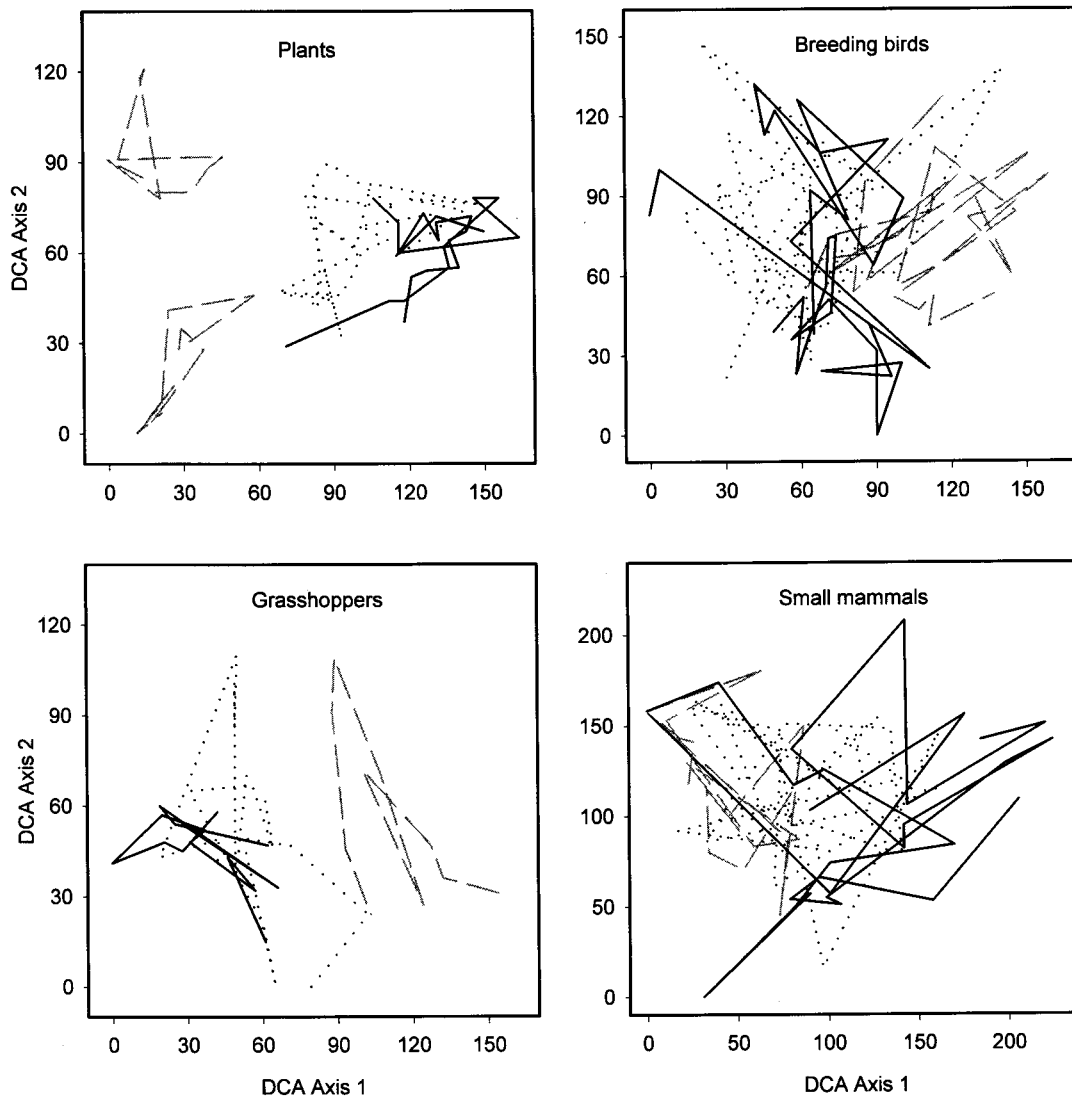
Figure 1: Detrended correspondence analysis (DCA) ordinations of annual samples of plants, breeding birds, grasshoppers, and small mammals on watersheds subjected to 1- (*dashed lines*), 4- (*dotted lines*), and 20-yr (*solid lines*) fire intervals. In all cases (except for grasshoppers on 1-yr burns), there are two replicate watersheds for each taxon set. In some cases, replicates differ in length of the time series. Traces in each ordination track compositional change through time on a particular watershed.

105), the regression accounted for only 8.0% of the variance. This implies that some weak directional change may be occurring in this local community but that variability at most time lags is quite high, and this variation swamps any clear temporal pattern of change in this local community.

Average annual turnover ranged from 11.0 to 19.2 plant species, a turnover rate of about 21%–32% of the average annual species richness (table 3). Average species richness and annual turnover were lowest on the annually burned

site and highest on the 4-yr burn sites. Average annual turnover of breeding bird species ranged from 4.5 to 6.6 species, a turnover rate of about 52%–60% of the species each year. Richness was lowest on the annually burned site, but overall differences among sites were relatively small. Small mammal richness was lowest and proportional turnover was highest on annually burned sites. Unlike the other taxon groups, grasshopper richness was lowest on the 20-yr burn; however, like small mammals, proportional turnover was highest on annually burned

Table 2: Average detrended correspondence analysis axis scores for ordinations of plants, breeding birds, grasshoppers, and small mammals on watersheds burned at 1-, 4-, or 20-yr intervals

	1 yr		4 yr		20 yr			
Species and axis	Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2	*F*	*P*
Plants:								
Axis 1	21.4[A]	24.8[A]	86.7[B]	108.5[C]	125.0[CD]	131.8[D]	96.8	<.0001
Axis 2	91.4[A]	17.5[B]	58.4[C]	65.6[C]	60.3[C]	61.9[C]	34.1	<.0001
Breeding birds:								
Axis 1	125.0[A]	94.5[B]	53.5[C]	63.4[C]	61.9[C]	74.2[BC]	17.5	<.0001
Axis 2	78.8[A]	69.5[A]	65.3[AB]	87.8[A]	90.3[A]	39.9[B]	8.0	<.0001
Grasshoppers:								
Axis 1	111.0[A]	…	54.0[B]	56.8[B]	34.3[B]	40.0[B]	22.9	<.0001
Axis 2	55.4	…	56.9	43.6	43.9	49.6	.6	.6822
Small mammals:								
Axis 1	17.0[A]	51.7[AB]	87.4[AB]	92.7[B]	88.8[AB]	148.3[C]	10.6	<.0001
Axis 2	140.0	109.5	115.1	116.0	105.3	95.4	1.0	.4478

Note: Values in each row with different superscripts are significantly different based on ANOVA and Bonferroni tests. Rep = replicate.

sites. Overall, temporal dynamics of local appearance and disappearance of species in response to fire frequency was not consistent among taxon groups.

The general pattern of species occurrences over time also differed among taxa and fire frequencies (fig. 3). In general, occurrence of plant species is bimodal, with peaks in the 0%–10% and 90%–100% occurrence classes under all three fire treatments. Occurrence of birds over time varied among fire frequencies. Indeed, nearly 30% of the species occurring on the annually burned sites were present in each of the 15 yr of sampling. This pattern differs dramatically from the 4- and 20-yr sites, where the highest mode is for species that occurred in less than 10% of the sample years. The opposite pattern occurs for grasshoppers (fig. 3). The highest mode in the annually burned site was for grasshopper species occurring in less than 10% of the sample years. For 4- and 20-yr burn sites, the highest mode was in the core category (>90%), although there were still many species of grasshoppers that occurred infrequently over time. Small mammal richness is relatively low on Konza Prairie. Only one core species occurred on Konza, *Peromyscus maniculatus*. Overall, populations of most species fluctuate in time, and the highest modes, where they are apparent, are for species that appeared in less than 30% of the annual samples.

In all cases for all four sets of taxa, there was a significant ($P < .05$), positive relationship between the number of years in which a species occurred and its average abundance in years of occurrence. Thus, temporally persistent species have higher abundances, in general, than temporally rare species. This relationship was weakest for grasshoppers (r^2s range from 0.21 to 0.28) and strongest for small mammals (r^2s range from 0.80 to 0.84) and breeding

birds (r^2s range from 0.73 to 0.80). The r^2 values for plants ranged from 0.46 to 0.56.

Discussion

Results from these analyses demonstrate, first, that plant communities on annually burned sites differed significantly from plant communities on less frequently burned sites; second, that animal communities did not show the same clear differentiation among fire treatments as did the plant communities; third, that plant communities on Konza Prairie were undergoing some degree of directional change on all watersheds regardless of fire frequency; and, finally, that unlike the plant communities, the animal communities exhibited little or no directional change under any fire frequency. For the plant communities, contrary to expectation, vegetation subjected to 4-yr burning regimes was undergoing directional change, and the rate of change on 4-yr burns was greater than that of 20-yr burn sites (fig. 2). Directional change was strongest under annual burning regimes, which was also unexpected given the historical role of fire in tallgrass ecosystems (Axelrod 1985; Anderson 1990; Bragg 1995) and the past burning history of Konza Prairie (Hulbert 1985).

The temporal change on the annually burned sites reflected shifts in the abundance of dominant species, lower spatial heterogeneity, and declines in species richness (Collins 1992; Collins et al. 1995; Collins and Glenn 1997*b*). In addition, cover of *Andropogon gerardii*, the most common C_4 grass on Konza, has decreased by 50% since 1983 on both annually burned sites, and cover of *A. scoparius* has increased by 25% on one of the annually burned sites. These compositional changes have occurred even though
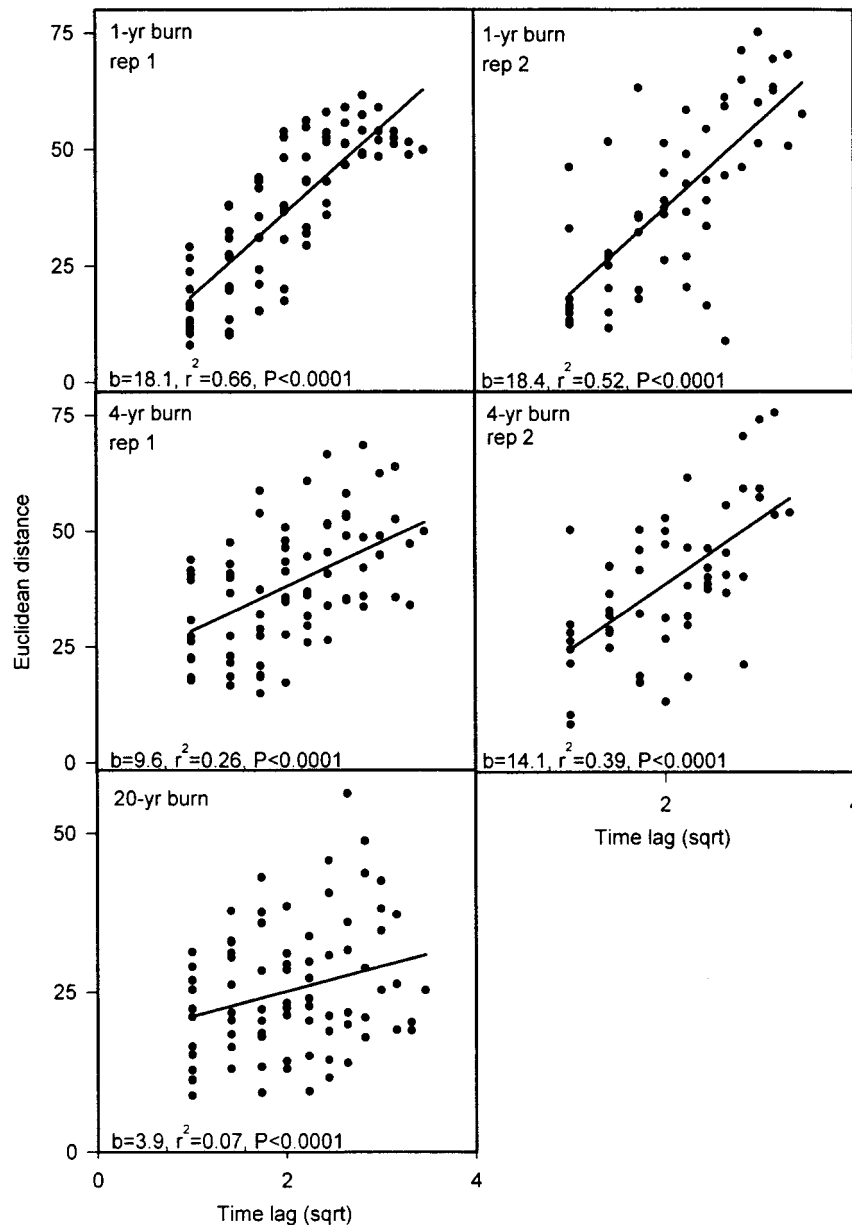
Figure 2: Time lag regression analysis of compositional change in plant communities on five watersheds subjected to different fire intervals. In all cases, regressions are significant and positive, indicating that vegetation is undergoing directional change over time. In general, rate of change (b = slope) decreases as fire frequency decreases.

there have been no net changes in total grass biomass over this time frame (Briggs and Knapp 1995). Together, loss of species richness and compensatory changes in abundance of dominant species lead to strong directional change in community structure under high fire frequency.

In tallgrass prairie, burning increases grass biomass at the expense of forbs and shrubs depending, in part, on fire frequency (Gibson and Hulbert 1987) and the season during which burning occurs (Howe 1994). Annual aboveground net primary production is generally higher on burned prairie than it is on unburned prairie (Briggs and Knapp 1995), whereas nitrogen availability decreases under frequent burning regimes (Blair 1997). This leads to a positive feedback loop as nitrogen is lost annually through volatilization by fire. With higher biomass, light levels may be reduced and competition for nitrogen in-

Table 3: Mean annual species richness, turnover, and proportional turnover for plants, breeding birds, grasshoppers, and small mammals on watersheds subjected to 1-, 4-, or 20-yr fire intervals

Taxon	1-yr burn	4-yr burn	20-yr burn
Plants:			
Average richness	52.3	60.8	58.9
Average turnover	11.0	19.2	16.2
Percentage turnover	21.0	31.6	27.5
Breeding birds:			
Average richness	8.7	11.0	10.2
Average turnover	4.5	6.6	5.8
Percentage turnover	51.7	60.0	56.9
Grasshoppers:			
Average richness	10.2	11.1	9.7
Average turnover	4.6	4.0	3.2
Percentage turnover	45.1	36.0	33.0
Small mammals:			
Average richness	3.7	4.9	4.5
Average turnover	2.7	3.4	2.9
Percentage turnover	72.9	69.4	64.4

Note: Plant data are from annual samples from 1983 to 1995, breeding birds from 1981 to 1995, grasshoppers from 1982 to 1991, and small mammals from 1981 to 1995. Values are per 200 m^2 for plants and per watershed for animals (see "Material and Methods"). $N = 2$ watersheds in all cases except plants and grasshoppers on 20-yr burns and small mammals and grasshoppers on 1-yr burns, where $N = 1$.

tensifies (Tilman 1987; Seastedt and Knapp 1993; Collins et al. 1995, 1998; Blair 1997; Turner et al. 1997). Decreased nitrogen availability increases competition for nitrogen, which may destabilize community structure by increasing dominance by C_4 grasses under an annual burning regime (Wilson and Tilman 1991; Wedin and Tilman 1993).

When fires are excluded for long periods of time in tallgrass prairie, litter accumulates, woody species invade, moisture and nutrient availability increase, and mesic grasslands eventually develop into shrubland and woodland vegetation (Bragg and Hulbert 1976; Petranka and McPherson 1979). These changes occur relatively slowly, however (fig. 2). Currently, cover of woody species is highest on the sites burned once every 20 yr (Gibson and Hulbert 1987), so development of woody vegetation is occurring on infrequently burned watersheds. However, invasion of these grasslands by woody species is patchy (Knight et al. 1994). As these patches grow and coalesce over time, this system will undergo a phase transition from grassland to shrubland vegetation. Thus, rate of change on unburned grasslands may eventually be nonlinear. Dominance by shrubs then facilitates further invasion of woody species (Petranka and McPherson 1979; Archer et al. 1988; Archer 1989) as succession continues in the absence of fire (Bragg and Hulbert 1976).

Factors other than fire have been shown to drive vegetation change in other grassland systems. In short-grass steppe vegetation, for example, Alward et al. (1999) found that abundance of the dominant C_4 grass *Bouteloua gracilis* decreased, while abundance of exotic and native C_3 forbs increased in response to increasingly warmer average annual minimum temperatures. Shrub cover increased in response to an extended period of above-average winter precipitation in a desert grassland (Brown et al. 1997). However, no such patterns in rainfall or temperature are apparent at Konza Prairie during the period of my study. Thus, compositional changes in vegetation at Konza Prairie most likely occurred in response to biotic instabilities driven by changes in resource availability and population structure as a function of fire return interval.

My analyses do not support the hypothesis that changes in animal communities mirror those of the plant community. Essentially, the breeding bird, grasshopper, and small mammal communities on Konza Prairie reflect a loose equilibrium (DeAngelis et al. 1985) and generally exhibit little directional change. In effect, they are temporally stable despite high year-to-year variability. Although the plant community often provides the structural context for animal communities, these relationships may be rather weak for many taxa (Wiens 1989). For example, Wiens et al. (1986) and Brown et al. (1986) noted that community-level responses by birds and small mammals, respectively, to habitat changes may be limited by time lags and philopatry. In addition, compositional changes in the plant communities may not always reflect physiognomic changes in these communities. In combination, these factors may cause dynamics of animal communities at Konza Prairie to occur at a rate that is not consistent with rates of change in the composition and structure of the plant communities.

Time lag analysis of changes in the cover of grasses, forbs, and woody plants on the three focal watersheds illustrates this point and helps to explain the conflicting temporal patterns shown by plants and animals under some fire regimes. Habitat structure, like plant community composition, exhibited directional change under annual burning (fig. 4). Although cover of forbs has increased from about 2% to about 8% over this time frame, compositional change on annually burned sites is driven primarily by changes in abundances among the C_4 grasses. Such changes may not alter habitat structure as perceived by birds, grasshoppers, and small mammals. Habitat structure on the 4- and 20-yr burn sites, however, does not show directional change (fig. 4), even though directional change in composition is occurring on these watersheds. Thus, under all burning regimes, compositional change in the plant community is decoupled from structural change over this time frame.
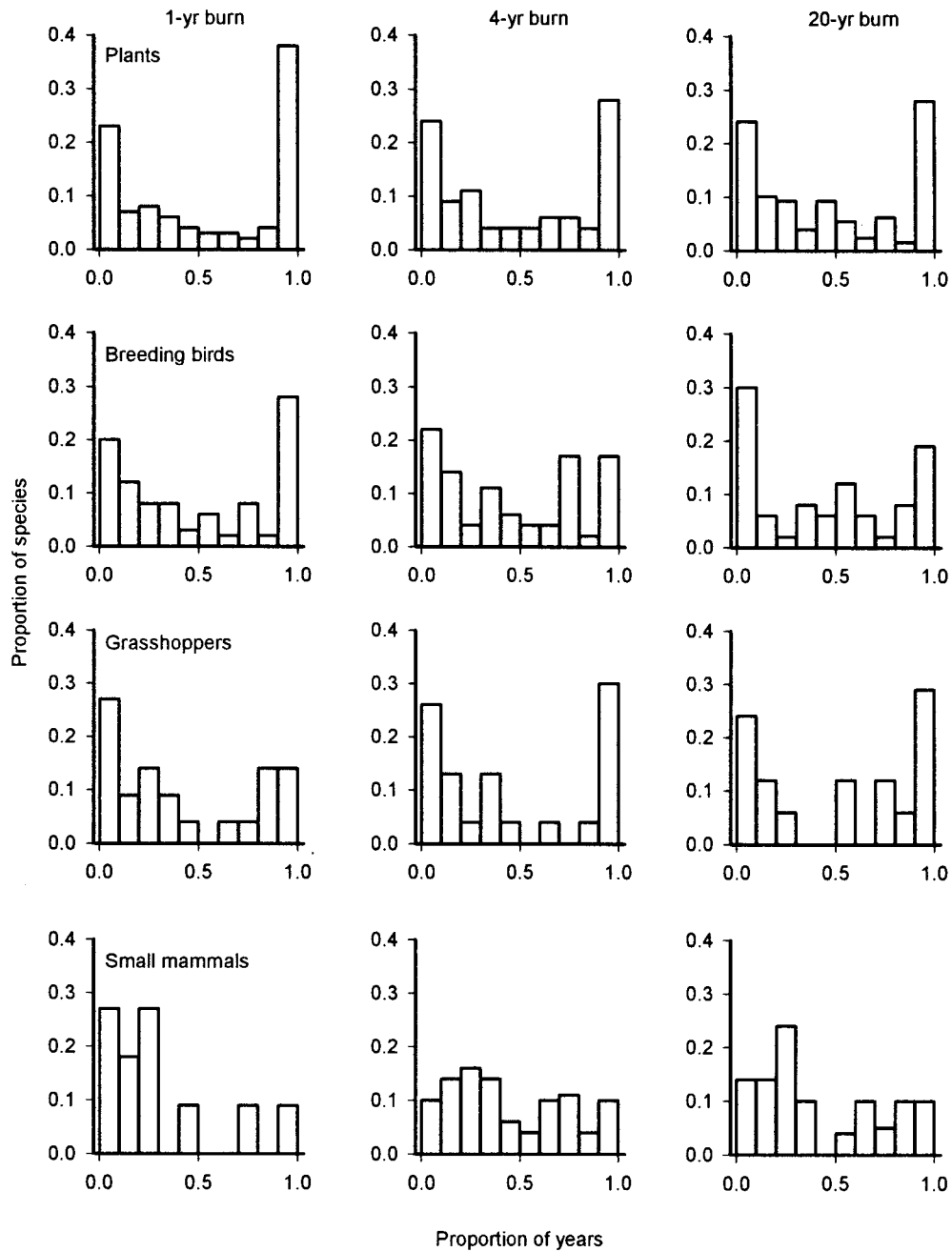
Figure 3: Distribution of plants (1981–1995), breeding birds (1981–1995), grasshoppers (1982–1991), and small mammals (1981–1995) over time on three focal watersheds where all four taxa were sampled. Core species are those that occur >90% of the time, and satellite species are those that occur ≤10% of the time. Values were converted to percentages in each case in order to standardize results across watersheds, taxa, and time.

Theoretical models suggest that the Konza Prairie plant communities should not be temporally stable. DeAngelis and Waterhouse (1987) note that highly interactive communities are susceptible to feedback instabilities, while weakly interactive communities are prone to stochastic extinctions. Feedback instabilities occur when biotic interactions in the absence of disturbance lead to competitive exclusion and temporal change. Weakly interactive systems suffer the vagaries of environmental stochasticities. The analysis of temporal core-satellite dynamics at Konza Prai-
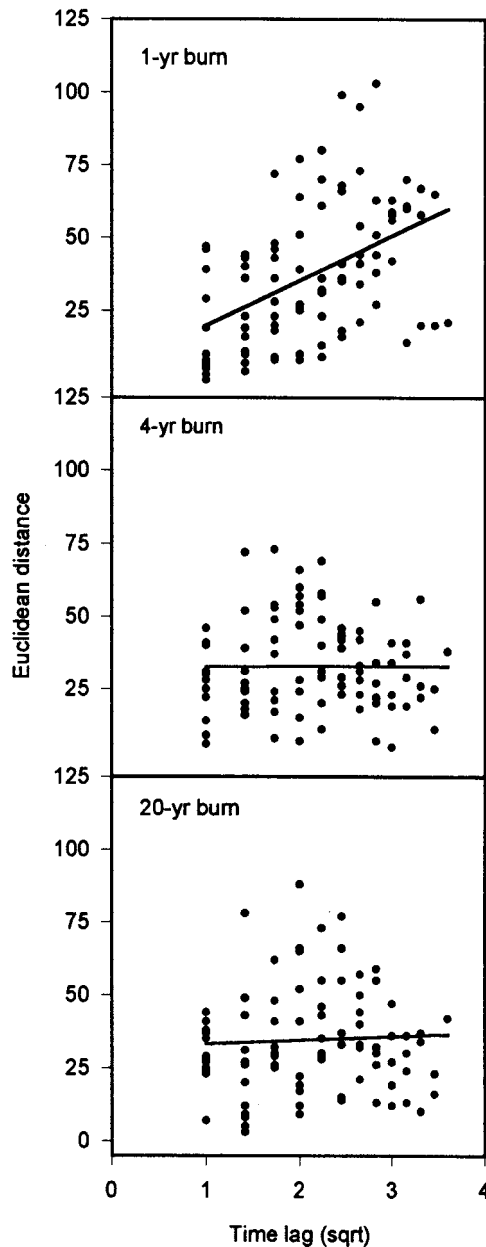
Figure 4: Time lag analysis of structural change on the three focal watersheds where plants, breeding birds, grasshoppers, and small mammals were sampled (see table 1). In this case, a Euclidean distance matrix was calculated based on average cover of grasses, forbs, and woody species at each site over time. Results show that habitat structure on annually burned sites is changing over time, whereas structure on 4- and 20-yr burn sites is stable.

rie (fig. 3) suggests that communities in these grasslands are susceptible to both forms of instability.

Previously, we had postulated that mesic tallgrass prairie vegetation was structured by a two-tiered competitive hi-

erarchy in which a set of widely distributed core species (most of which are perennial C_4 grasses and C_3 forbs) was competitively superior to a large number of species with limited distributions and lower local abundances (Collins and Glenn 1990, 1991). Two lines of evidence support the existence of this competitive hierarchy and, as a consequence, the potential for biotic feedback instabilities. First, tallgrass prairie grazed by ungulates tends to have higher species richness than grasslands that are not grazed (Collins 1987; Hartnett et al. 1996; Collins et al. 1998). Ungulates, such as bison, selectively graze the dominant C_4 grasses, which reduces their competitive ability and increases local and regional species diversity (Knapp et al. 1999). Second, experimental removal of a core C_4 grass, *A. scoparius*, from replicated patches of grassland significantly increased the number of satellite species compared to adjacent patches of control vegetation where *A. scoparius* was not removed (Glenn and Collins 1993; S. M. Glenn and S. L. Collins, unpublished data). Both lines of evidence demonstrate that core species impart strong biotic feedback instabilities on local and regional patterns of satellite-species diversity.

The two-tiered competitive hierarchy was inferred from analysis of spatial distribution of species (Collins and Glenn 1990, 1991). However, this hierarchy also applies to the temporal patterns of species distribution and to the abundance observed in the current study. Indeed, within each site there is a core group of temporally common species and a larger number of species that appear and disappear at different rates over time (fig. 3). On average, the core species in time are strong competitors that have higher abundances than the temporally infrequent species. Many of the species common over time are also widely distributed spatially, but at many sites there are additional species that are locally distributed but temporally persistent. On the one hand, the presence and abundance of core species provides some element of temporal stability in community structure. That is, they place boundaries on community dynamics. On the other hand, the interaction of core species with each other and with satellite species leads to local extinctions and temporal instabilities. In addition, because many satellite species have small populations, they appear and disappear over time in response to numerous abiotic contingencies. Collectively, these environmental stochasticities lead to temporal instabilities in grassland plant communities.

Research on biotic interactions among grasshopper and breeding bird communities in grasslands suggests that biotic instabilities are less important than in plant communities. Evans (1992) found little evidence of interspecific competition among grasshopper species at Konza Prairie, even during a drought year. Rotenberry and Wiens (1980a) concluded that interspecific interactions in grass-

land breeding bird communities generally were weak during most years. At Konza Prairie, given that breeding birds, small mammals, and grasshoppers have a relatively large number of spatially and temporally rare species whose abundances are subjected to environmental stochasticities, year-to-year variation in these communities is likely to be high. Overall, these communities remain temporally stable, in part because of a lack of strong biotic interactions.

Conclusions

Fire is considered to be essential for the long-term maintenance of tallgrass prairie vegetation (Wright and Bailey 1982; Leach and Givnish 1996). Because of this role, Anderson and Brown (1986) suggested that fire was a stabilizing force in mesic prairie. The high rate of compositional change on annually burned watersheds and watersheds burned once every 4 yr at Konza Prairie contradicts the prediction that fire is a stabilizing force in this ecosystem. Moreover, this hypothesis contradicts the theory that disturbances are destabilizing because they modify community composition and initiate patch dynamics (Loucks 1970; White 1979; Wu and Loucks 1995). The validity of this hypothesis may be a function of scale (Fuhlendorf and Smeins 1996; Collins and Glenn 1997*b*). Small, frequent disturbances create local patch dynamics, whereas a dynamic steady state may develop at regional scales under a natural disturbance regime (e.g., Baker 1989). Again, because fires are frequent large-scale disturbances in tallgrass prairie, a dynamic steady state in this ecosystem may have occurred only at continental scales, if at all. Nevertheless, the spatial and temporal patchwork of fires across the Great Plains is clearly a causal factor in the evolution and maintenance of mesic grasslands throughout their history in North America (Axelrod 1985).

It is clear that fire frequency produces a patchwork of vegetation across the different watersheds on Konza Prairie (fig. 1). The different components of this vegetation patchwork are not stable over time regardless of the local frequency of disturbance by fire. In contrast, animal communities, although highly variable from 1 yr to the next, displayed little evidence of directional change. Thus, as was found for spatial patterns of distribution and abundance among these taxa (Collins and Glenn 1997*a*), temporal patterns of one taxon group cannot necessarily be extrapolated to other taxa. Overall, there is a surprising degree of directional change in vegetation (global instability) and temporal fluctuation (global stability) in animal communities over time under highly dissimilar frequencies of disturbance by fire (see also Milchunas et al. 1998).

In general, stability is a challenging property to define and measure in ecological communities (Connell and Sousa 1983; Ives 1995). The concept has received considerable theoretical and some empirical examination (May 1973; McNaughton 1977; DeAngelis and Waterhouse 1987; Tilman and Downing 1994; Tilman 1996). Measurement of stability is potentially relevant for conservation of biodiversity and its relationship to ecosystem functioning (Tilman 1996; Tilman et al. 1996; McGrady-Steed et al. 1997; Naeem and Li 1997), yet this topic remains controversial (Johnson et al. 1996; Hooper and Vitousek 1997; Huston 1997; Wardle et al. 1997). Community stability, and the related concepts of resistance and resilience, cannot be assessed, however, if the general temporal dynamics of the community in question are unknown. Our long-term data produced several unexpected patterns of animal community stability within dynamically unstable plant communities. Long-term empirical studies of different taxa under different disturbance regimes and in different ecosystems will be required to determine over what time frames and spatial scales communities may be stable. Such studies are essential for the development of generalities regarding the relationship between disturbance frequency and community stability in terrestrial and aquatic systems.

Acknowledgments

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