Effects of scale and disturbance on rates of immigration and extinction of species in prairies

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Relationships between local annual immigration and extinction rates of plant species and total species richness were determined from long-term data in permanent plots in tallgrass and shortgrass prairies in Kansas. Combining plots resulted in higher equilibrium numbers of species as predicted from immigration and extinction rates. Immigration and extinction rates also increased with scale. Extinction rates are higher because the regional scale supports more rare species which, in turn, have high probabilities of extinction. We also tested the hypotheses that extinction rates would be higher on burned versus unburned grasslands, and that immigration rates would be higher on grazed versus ungrazed grasslands. Extinction rates were positively correlated with the number of species at a site, and this relationship was not altered by burning or grazing. Immigration rates were variable, but were sometimes positively correlated with growing season precipitation. Immigration rates decreased in years sites were burned. Therefore, after fire, the number of species going locally extinct was still dependent on earlier species richness, but the number of species added to the site was reduced. Variances in immigration and extinction rates were high, therefore, confident predictions regarding the effects of burning or grazing regimes on species richness could not be made. Variance in rates of immigration and extinction results in a range of values within which the equlibrium number of species fluctuates randomly.

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Dynamics within a community may be modelled by immigration and extinction of populations. This approach has been extensively pursued in research on island communities (MacArthur and Wilson 1967) and on isolated communities in disjunct habitats (Janzen 1968, Brown 1978, Leck 1979, McCoy 1982, Wright and Hubbell 1983). Even within continuous expanses of communities, local species immigration and extinction are often used to explain community responses to disturbance and succession. Dispersal to a site is a fundamental cause of successional change following disturbance and species turnover is one of the basic tenets of plant succession (Pickett et al. 1987). Even in the absence of disturbances, however, herbaceous plant communities may be spatially and temporally dynamic (Hol-

land 1978, Collins and Glenn 1990, Glenn and Collins 1990). These dynamics involve local extinctions and immigrations among patches within continuous communities. Individual fluctuations of local populations may result in small-scale patterns of species associations (Collins et al. 1987, Glenn and Collins 1990) and differences in composition between communities may result from local extinctions (Collins et al. 1987). Stochastic local immigration has often been incorporated into models of community dynamics and diversity (Levins 1969, Hanski 1982, Shmida and Wilson 1985).

Moderate disturbances, such as fire or light grazing in grasslands, may alter composition without initiating succession per se. Grazing of prairie may promote immigration of grazing tolerant species and local extinc-

tion of species that do not tolerate grazing (Collins 1987, Facelli et al. 1989). Burning may directly eliminate fire intolerant species as well as enhance the growth of perennial grasses, resulting in local extinctions from shifts in competitive interactions (Collins 1987, Biondini et al. 1989). Therefore, disturbances and combinations of disturbances alter local immigration and extinction processes and result in changes in community composition (Belsky 1986, Collins 1987, Collins and Glenn 1988).

Local immigration and extinction rates may be scale dependent. MacArthur and Wilson (1967) modelled extinction rates on islands as decreasing with area because population size increases with area and larger populations have reduced probabilities of extinction. Extinction rates were negatively related to area in island systems (Simberloff 1976), but not in fragmented herbaceous communities on mainlands (Robinson and Quinn 1988). In contiguous tallgrass prairies it has been previously unknown if community dynamics resulting from local immigration and extinction are scale dependent, or if scale dependence is equivalent to area effects.

Hanski (1982) used scale-dependent models of population extinction and immigration to predict species distribution patterns across a series of habitat islands. This model's assumptions predict that immigration and extinction patterns in a series of plots scattered across the landscape will vary depending on the resolution of the analysis. Hanski's model incorporated MacArthur and Wilson's (1967) hypothesis that extinction probability decreases when a population occupies more sites, with the assumption that population size is positively correlated with the number of sites occupied. Immigration rates increase with scale (Hanski 1982) or area (MacArthur and Wilson 1967) because of the availability of a larger regional species pool able to colonize a larger target. Increasing immigration and decreasing extinction rates with increasing scale of analysis would yield an increase in the number of species as scale increases, a result commonly accepted in sampling theory (Kershaw 1973).

Previous research shows that tallgrass prairie plant communities in Kansas experience rapid dynamics. Local (200 m²) annual rates of immigration and extinction averaged 9.4 and 9.7 species per year, respectively (Collins and Glenn 1991). Patterns of immigration and extinction at other scales have not been previously examined nor have effects of different types of disturbances on species immigration and extinction been measured. Understanding patterns of immigration and extinction in response to disturbance may help explain differences in species composition among grasslands within a region. Therefore, we tested the following hypotheses using long-term data from two different grassland communities in eastern and western Kansas:

1) Relationships between local immigration or local extinction and number of plant species in tallgrass prai-

rie are affected by scale. Population models predict lower extinction rates and higher immigration rates with increasing scale or area (Hanski 1982, MacArthur and Wilson 1967).

2) Extinction rates in grasslands will increase with burning. Community models predict lower species richness in tallgrass prairie following burning because the dominant grasses grow rapidly and occupy much of the space (Collins 1987).

3) Immigration rates will be higher on grazed grasslands than on ungrazed grasslands because grazing reduces the biomass of dominant grasses and opens space for colonization (Collins 1987).

4) Immigration rates will be positively correlated with precipitation because increased available water will aid in establishing local immigrants in the semi-arid environment of tallgrass prairies (Collins and Glenn 1991).

Methods

Field methods

Vegetation was sampled from 1983 to 1990 on Konza Prairie Research Natural Area (KPRNA), a 3487-ha tallgrass prairie in northeastern Kansas. This prairie is dominated by *Andropogon gerardii, Schizachyrium scoparium, Sorghastrum nutans,* and *Panicum virgatum.* The vascular flora of KPRNA includes 441 reported species, though some of these are limited to non-grassland habitats (Freeman and Hulbert 1985). KPRNA is divided into topographically defined management units, and the burning regime of each management site has been experimentally controlled since 1972. Nineteen ungrazed sites in these management units were used in this study. At each site, four 50 m transect lines each with five evenly spaced permanent 10 m² circular plots were sampled. The transects are scattered across management units of approximately 9 to 50 ha. At each plot, a species list was compiled each year based on samples collected in May, July, and September as part of the Konza Prairie Long-term Ecological Research Program. Data sheets from previous years were used in the field to aid in searching for all species recorded in the preceding sample.

Defining immigration and extinction is a problem for all studies in species turnover (MacArthur and Wilson 1967, Simberloff 1976, McCoy 1982), therefore, we adopted an ecological definition as opposed to a floristic definition. The recorded presence of a species was assumed to indicate a measurable ecological contribution of the species to the system. This sampling approach would miss seedlings that appeared between sample times but did not successfully establish. Winter annual species were not included in these analyses if they completed their life cycle between the September and May samples. Species present in a dormant form, such as

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Table 1. Species richness (S), local immigrations (I) and local extinctions (E) occurring over the next year on 13 sites and on these sites combined on Konza. Burning events are indicated (+) in the year of the burn.

Year	S	I	E	S	I	E	S	I	E	S	I	E	S	I	E	S	I	E	S	I	E
1983	59	10	11	55	08	12	+46	11	08	+56	08	09	+32	12	04	+47	10	03	+55	15	09
1984	57	05	08	51	08	08	+49	02	10	+55	05	08	+40	02	08	+54	03	07	61	07	11
1985	54	17	05	51	11	08	+41	10	02	+52	13	08	+34	02	03	+50	08	06	57	07	07
1986	66	07	08	54	12	10	+49	06	09	+57	08	06	+33	05	03	+52	05	08	57	09	08
1987	65	05	14	56	04	12	+47	07	07	+59	01	12	+35	07	02	+49	03	06	+58	11	13
1988	56	12	09	48	08	06	+47	06	04	+48	05	03	+40	02	06	+46	04	00	56	07	08
1989	59	16	08	50	12	03	+49	10	08	+50	09	04	+36	08	03	+50	09	04	55	09	05
1990	67			61			+51			+55			+41			+55			59		

Year	S	I	E	S	I	E	S	I	E	S	I	E	S	I	E	All sites combined		
																S	I	E
1983	+63	18	12	70	17	18	60	09	10	65	08	16	61	14	14	63	14	10	131	23	14
1984	69	08	12	69	09	16	59	09	09	57	03	12	61	09	13	67	09	11	140	10	30
1985	65	11	09	62	13	12	59	08	07	48	16	08	57	13	15	65	11	09	120	29	17
1986	67	08	11	63	12	07	60	10	11	56	07	07	55	14	10	67	09	08	132	24	22
1987	+64	10	16	68	05	22	59	12	11	56	12	12	59	08	15	68	04	16	134	21	27
1988	58	10	07	51	17	00	+60	07	06	+56	18	08	+52	24	09	+56	17	05	128	29	14
1989	61	18	05	68	19	12	+61	09	08	+66	08	18	67	19	18	68	15	13	138	32	20
1990	74			75			+62			+56			68			70			150		

seeds, were not included in these analyses because they were not ecologically active. Seed bank and seed rain were not measured as immigration events; colonization without successful visible establishment was not measured as immigration. Therefore, immigration refers to the appearance of living aboveground vegetation, and extinction refers to the local disappearance of living aboveground vegetation of a particular species. This sampling technique included a large number of relatively rare species that were highly variable in abundance and distribution from year to year (Collins and Glenn 1990, 1991).

To assess grazing effects on immigration and extinction rates, shortgrass prairies in western Kansas (Morton County) were sampled annually in June from 1962 to 1980. These sites were dominated by *Bouteloua gracilis*, *Buchloe dactyloides*, *Sporobolus cryptandrus* and *Artemesia filifolia*. At each site, presence of species was recorded in 25 permanent 1000 cm² quadrats along a transect. Two sites were grazed, one site was ungrazed, and one site was grazed for the first 11 years. Fire was recorded in two of the sites in 1963.

Numerical methods

The 13 sites on KPRNA with complete species lists from 1983 to 1990 (Table 1) were analyzed at three spatial scales; transect, site (management unit), and Konza (all sites combined) levels. At the transect level, species lists from the five plots were combined and the total number of species counted (species richness) for each year within the total 50 m² area. At the site level, lists from

four transects across the site were combined and totaled (200 m² area), and at the Konza level, lists from all 13 sites were combined and totaled (3600 m² area). At each scale, species lists were compared between years, and local immigration (I) was defined as the number of new species found, and local extinction (E) was defined as the number of species disappearing between years. Average species richness, average numbers of immigrations per year, and average numbers of extinctions per year and their standard deviations (sd) were compared between scales using t-tests which incorporate sample size differences. If species only move between transects or sites, immigration and extinction rates would decrease as scale increases. If immigration or extinction rates do not change with scale, then the functions are scale independent. If increasing scale incorporates more dynamic species then immigration or extinction rates would increase.

Product-moment correlation coefficients and least square regression lines were calculated for the relationships between immigration and species richness, and between extinction and species richness at each spatial scale. In these analyses, species richness already at the plot was used as the independent variable. Correlations and regressions were also calculated for the relationships between immigration or extinction and growing season precipitation (April through September at the Manhattan, Kansas weather station). Growing season precipitation used in all analyses was measured in the year the immigrations and extinction were counted.

At each scale, least square regression lines were calculated for the relationship between species richness and the net change in species richness (I-E) over the

Table 2. Sample size (n), species richness, immigrations, and local extinctions with standard deviation (sd) over 8 years for 13 sites (see Table 1) combined (Konza), separately (sites), and at the transect level. Measures are also shown over 8 years for 76 transects in burned versus unburned years on Konza, and over 19 years for 4 grazed and ungrazed sites in western Kansas. Statistical differences between scales or treatments were analyzed with t-tests (*** $p < 0.001$, ** $p < 0.01$, ns $p > 0.05$).

	n	Species richness		Immigrations		Extinctions	
		Mean	sd	Mean	sd	Mean	sd
13 sites							
Konza	7	131.7	6.64	24.0	6.64	20.6	6.21
Sites	91	55.7	7.30***	9.57	4.57**	8.92	4.25**
Transects	364	35.1	6.67***	6.83	3.26***	6.40	3.02***
Konza transects							
Unburned	314	37.1	6.15	7.92	3.55	6.84	3.17***
Burned yrs	197	32.9	6.53***	6.23	2.79***	5.68	2.81
Western Kansas sites							
Grazed	46	14.5	5.10	5.41	4.37	5.20	3.15
Ungrazed	25	17.0	4.87^{ns}	5.08	3.03^{ns}	5.04	2.75^{ns}

previous year. The equilibrium number of species expected (S*) on a plot and variance in this number were calculated at the y-intercept of these regressions because this represents the point of no change in the number of species (I-E = 0).

Analyses of burning treatments were done at the transect level for all nineteen sites. To determine if there were burning effects in the year of a fire, immigration and extinction transect data were divided into burned years and unburned years. A transect was moved on one of the unburned sites in 1985, therefore immigration and extinction data from this transect between 1985 and 1986 were not included in the analyses. Average species richness, average numbers of immigrations per year, and average numbers of extinctions per

year were compared between burned and unburned transects using t-tests. Product-moment correlation coefficients and least square regression lines were calculated for the relationships between immigration and species richness, and between extinction and species richness for unburned and burned transects. Correlations were also calculated for relationships between immigration or extinction and growing season precipitation. Equilibrium numbers of species were calculated for burned and unburned transects using the same method as in the scale analyses.

To determine the effects of grazing on immigration and extinction rates, species lists from each western Kansas site (2.5 m^2 area sampled) were compared between years. Immigration rates, extinction rates, spe-
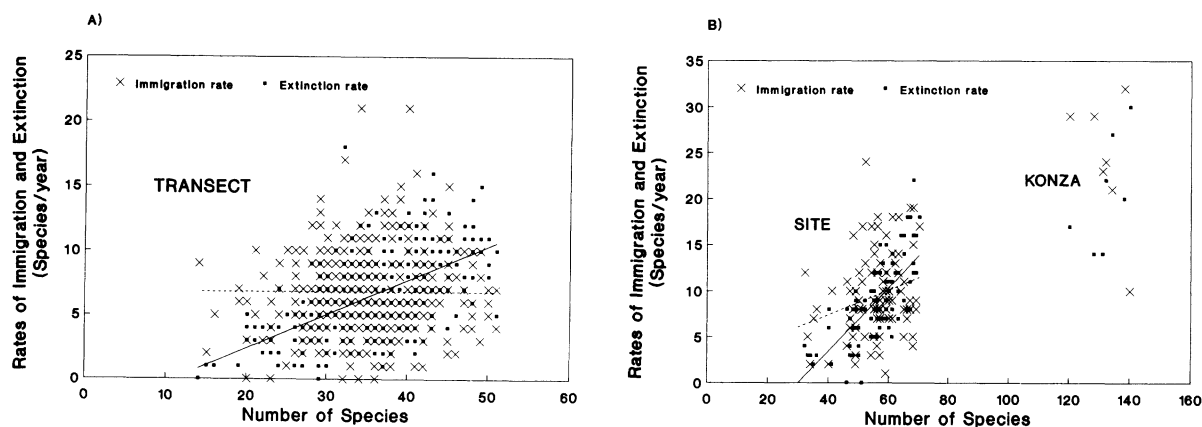

Fig. 1. Rates of local immigration (x) and local extinction (.) at the transect, site, and all Konza scales on Konza Prairie, Kansas. A) At the transect level coefficient of determination (r^2) between species richness and immigration was 0.010 (p = 0.062) (dashed line is average immigration rate). Coefficient of determination (r^2) between species richness and extinction was 0.342 (p = <0.001) (solid regression line). B) Coefficients of determination (r^2) between species richness and immigration were 0.262 (p = 0.24) for all Konza and 0.067 (p = 0.01) for individual sites (dashed regression line). Coefficients of determination (r^2) between species richness and extinction were 0.420 (p = 0.12) for all Konza and 0.507 (p<0.001) for sites. Significant regressions between extinction and species richness are shown using solid lines.
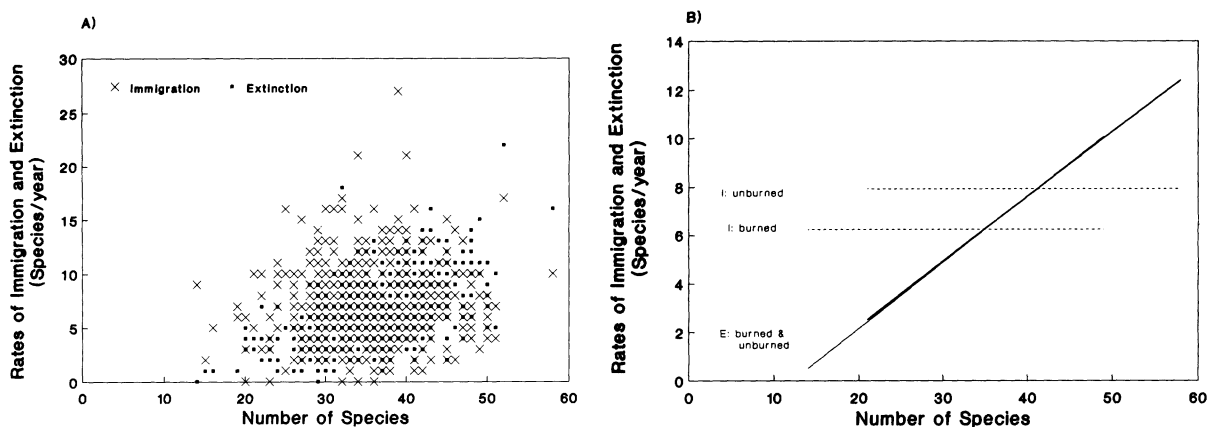
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Fig. 2. A) Rates of local immigration and local extinction for transects on Konza Prairie, Kansas. B) Regression of rates of local immigration (I) and local extinction (E) versus species richness on 76 transects on Konza Prairie in burned and unburned years. Coefficients of determination (r^2) between species richness and immigration were 0.000 (p = 0.973) and 0.000 (p = 0.846) for unburned and burned years respectively, therefore, average number of immigrations per transect are shown (dashed lines). Coefficients of determination (r^2) between species richness and extinction were 0.270 (p<0.001) and 0.401 (p<0.001) for unburned and burned years respectively (solid lines).

cies richness, and the predicted equilibrium number of species were determined as in the KPRNA data. T-tests were used to determine if grazing affected average species richness, average immigration rates or average extinction rates. Product-moment correlation coefficients and least square regression lines were calculated for the relationships between immigration and richness, and extinction and richness, and between richness and the net change in species richness to determine the equilibrium number of species.

For all analyses, it should be noted that data between different years at the same site were pooled, therefore the samples were not totally independent. This problem was slightly reduced by using species richness values

only from years prior to immigration and extinction events in comparisons.

Results

Scale effects

Average species richness was significantly different at each scale (p < 0.001), and increased from transect level to the Konza level (Table 2). The average number of immigrations and extinctions per year also increased significantly from the transect level to the Konza level (p < 0.01, Table 2).
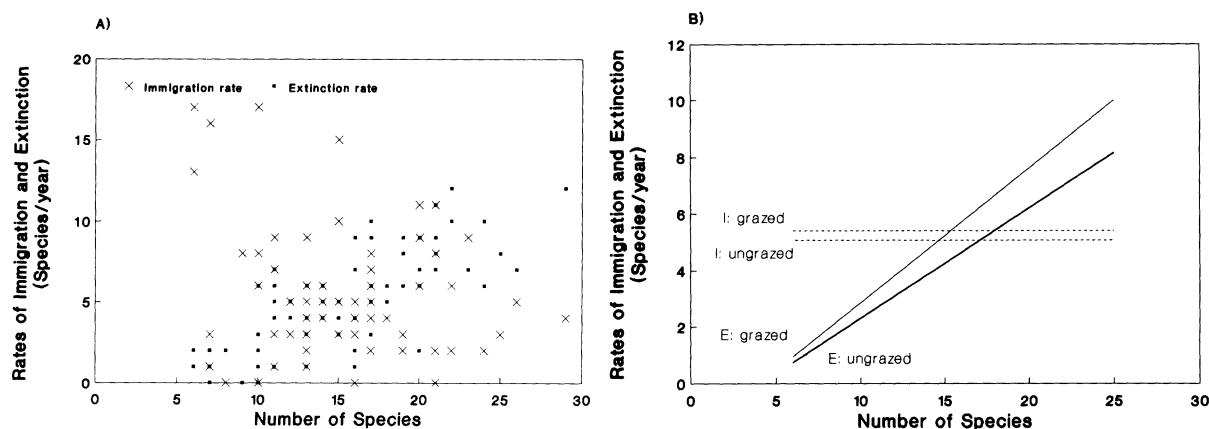

Fig. 3. A) Rates of local immigration and local extinction for sites in western Kansas. B) Regression of rates of local immigration (I) and local extinction (E) on grazed and ungrazed sites in western Kansas. Coefficients of determination (r^2) between immigration rates and species richness were 0.065 (p = 0.087) and 0.004 (p = 0.78) for grazed and ungrazed sites respectively, therefore, average number of immigrations per site are shown (dashed lines). Coefficients of variation (r^2) between extinction rates and species richness were 0.641 (p<0.001) and 0.479 (p<0.001) for grazed and ungrazed sites respectively (solid lines).
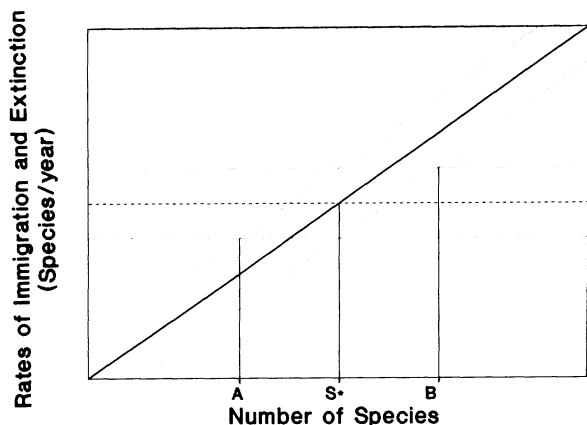
Fig. 4. Model of rates of local immigration (dashed line) and local extinction (solid line) with variance (dotted lines) as a function of species richness. If species richness is less than A, species richness will increase over time, and if species richness is greater than B, species richness will decrease over time. Between A and B, the number of species will fluctuate around the equilibrium number S^*.

Extinction rates were significantly positively correlated with species richness at the transect and site levels (Fig. 1). Weak correlations between extinction rates and species richness at the Konza level may have resulted from small sample sizes at larger scales (Fig. 1). Immigration rates were significantly correlated with species richness only at the site level (Fig. 1). Extinction rates were not significantly correlated with growing season precipitation at any scale ($p > 0.05$). Immigration rates were only significantly correlated with precipitation at the transect level ($r^2 = 0.032$, $p = 0.0127$).

The equilibrium number of species (S^*), as defined when immigration equals extinction ($I-E = 0$), increased with spatial scale (Konza $S^* = 132.5$, sd = 6.30; Sites $S^* = 56.0$, sd = 8.39; Transects $S^* = 35.1$, sd = 6.35). There was a significant difference in the equilibrium number of species between scales ($p < 0.05$).

Burning effects

Transect data were divided into burned and unburned years to test for effects of burning on immigration and extinction rates. Average species richness, immigration rates, and extinction rates were significantly higher on unburned versus burned years ($p < 0.001$, Table 2). Extinction rates were significantly correlated with species richness and the regressions were not significantly different in burned versus unburned years (Fig. 2). Immigration rates were not significantly correlated with species richness (Fig. 3), possibly because the true relationship has a shallow slope (Fig. 2) (Neave and Worthington 1988). Equilibrium numbers of species were significantly greater on unburned versus burned transects (Unburned $S^* = 37.6$ sd = 5.95; Burned $S^* = 33.3$,

sd = 5.85). Extinction rates were not significantly correlated with growing season precipitation and immigration rates were significantly correlated with growing-season precipitation only on unburned transects ($r^2 = 0.030$, $p = 0.002$).

Grazing effects

On grazed sites in western Kansas, average species richness, immigration rates and extinction rates were not significantly different in grazed versus ungrazed sites (Table 2). Immigration rates were not significantly correlated with species richness in grazed or ungrazed sites, but extinction rates were significantly positively correlated with species richness (Fig. 3). The equilibrium number of species was not significantly different between grazed and ungrazed sites ($p > 0.05$).

Discussion

Tallgrass prairie plant communities at KPRNA exhibited rapid annual rates of species turnover compared to other more isolated systems (MacArthur and Wilson 1967). Immigrations and extinctions were measured on plots scattered across the prairie as opposed to a complete sample of the prairie vegetation. Up to 150 species were sampled in any year, which comprised a small portion (34%) of the total regional species pool, and there were no obvious barriers to dispersal. High species turnover is consistent with open systems where large regional species pools drive rapid community dynamics, as in islands situated close to a mainland species source (MacArthur and Wilson 1967) and especially on non-isolated mainland sites.

On average, immigration and extinction rates were equal (Table 2), a criterion necessary for a dynamic equilibrium in species richness. However, high variances in both immigration and extinction rates resulted in high variances in equilibrium numbers of species. This variance was acknowledged by MacArthur and Wilson (1967) in their probability model of immigration and extinction. Variability in species number may increase with variability in immigration and extinction rates (Diamond and Gilpin 1980). Because of this variability, a refinement of MacArthur and Wilson's (1967) model using a probabilistic approach may be more applicable to non-island systems (Fig. 4). Therefore, the equilibrium number of species (S^*) predicted when the immigration rate equals extinction rate will have an associated variance (Fig. 4). Disturbances may force a site far enough from equilibrium that directional changes in species number occur until limits of variance around equilibrium are reached. When the number of species is below a threshold (A), immigration rates are always greater than extinction rates and the number of

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species will increase (Fig. 4). Above an upper threshold (B), immigration rates are lower than extinction rates and species number will decrease (Fig. 4). Between these thresholds, species number will fluctuate around the equilibrium. Fluctuations may be stochastic and result from factors unrelated to richness. The slopes of the lines do not effect the general characteristics of this model. If an equilibrium exists, where immigration equals extinction, there will be variance regardless of the slopes. A variety of factors, including scale of analysis and disturbance regime, may affect variance around the equilibrium, and cause changes in the magnitude of stochastic fluctuations. Therefore, further research on immigration and extinction processes within communities should involve analyses of variance in immigration rates, extinction rates, and equilibrium numbers of species.

Some of the dynamics in tallgrass prairie plant communities were consistent with predictions made by MacArthur and Wilson (1967); extinction rates were positively correlated with species richness, and the equilibrium number of species increased with scale (Fig. 1) which is consistent with MacArthur and Wilson's area prediction. However, immigration rates were not negatively correlated with species richness as assumed by MacArthur and Wilson (1967). MacArthur and Wilson (1967) noted that immigration rates may not exhibit a depletion effect if the species pool is very large. This may occur more often in contiguous communities than in isolated communities. In a herbaceous grassland community, immigration rates on fragmented sites increased with species number (Robinson and Quinn 1988), and in that case the degree of fragmentation may not have been severe enough to affect immigration rates. Species dispersal by seed is patchy and unpredictable in grasslands, and is not highly correlated with recruitment (Goldberg 1987, Peart 1989). Dispersal and establishment may result in unpredictable community dynamics in tallgrass prairie (Glenn and Collins 1990). In unburned transects, immigration increased with growing season precipitation, but immigration was generally stochastic with regard to species richness.

MacArthur and Wilson (1967) assumed that extinction rates decreased with area of islands. Large areas would support larger populations with lower extinction probabilities. However, in this tallgrass prairie, these area effects were not equivalent to scale effects, and extinction and immigration rates increased with scale. The regional level was more likely to incorporate populations of rare species, especially in samples scattered across contiguous habitat. There are many rare species in prairies (Collins and Glenn 1990), and many are found in only one year on a site (Collins and Glenn 1991). Our results are consistent with diatom communities on slides (MacArthur and Wilson 1967), and annual grasslands (Robinson and Quinn 1988), where rare species tend to go extinct. This is an emergent property of communities that is not predictable from extinction

models of populations. Extinction rates increasing with area were predicted in Seagle and Shugart's (1985) model for small areas, in which the species pool was random, and species competed at a site. In their model, disturbances created successional patches, and larger areas had a greater number of patches experiencing high species turnover than small areas.

The effects of disturbances on relationships between immigration or extinction rates and species richness have not been previously examined. However, explanations of community responses to disturbances often imply the relative contribution of these processes. In this tallgrass prairie, burning treatments had little effect on extinction rates. At all scales of analysis, extinction rates were positively related to species richness, and these relationships were not changed by burning. Therefore, any differences in species richness after burning or in communities under different burning regimes is controlled by changes in immigration rates. The number of species becoming locally extinct would remain dependent on species richness, no matter what the burning regime, but the number of new immigrants decreased in the year the site was burned. However, large variances in immigration and extinction rates prevents making confident quantitative predictions regarding responses to disturbances.

Moisture appears to be one of the primary limiting variables in grassland communities (Dodd and Lauenroth 1979, Webb et al. 1983), however, only on unburned transects was immigration positively correlated with growing season precipitation. Precipitation was unrelated to extinction rates. Therefore, precipitation is not as limiting as other factors, some of which may also control water availability, such as soil temperature or litter buildup.

In western Kansas shortgrass prairie, immigration was unrelated to species richness in grazed or ungrazed sites (Fig. 3). No significant differences in average immigration rates or species richness were found (Table 2). Variability in immigration and extinction rates was greater than any changes in these rates resulting from grazing.

In conclusion, species richness and local extinction rates in tallgrass prairie plant communities increase from a local to regional scale. This is important in long-term community monitoring of tallgrass prairies, especially if changes in community composition are used as indicators of site quality. Changes in species numbers resulting from burning are the result of changes in immigration of new species to the sites, as opposed to changes in extinction rates. This does not imply that the community will respond to other disturbances in the same way, and other disturbances and combinations of disturbances need to be examined separately. High variability in immigration and extinction rates result in variability in the equilibrium number of species. Therefore, even at equilibrium, stochastic fluctuations will still occur within limits defined by this variability.

References

Belsky, A. J. 1986. Revegetation of artificial disturbances in grasslands of the Serengeti National Park, Tanzania. – J. Ecol. 74: 419–437.

Biondini, M. E., Steuter, A. A. and Grygiel, C. E. 1989. Seasonal fire effects on the diversity patterns, spatial distribution and community structure of forbs in the Northern Mixed Prairie, USA. – Vegetatio 85: 21–31.

Brown, J. H. 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. – Great Basin Nat. Mem. 2: 209–227.

Collins, S. L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. – Ecology 68: 1243–1250.

– and Glenn, S. M. 1988. Disturbance and community structure in North American prairies. – In: During, H. J., Werger, M. J. A. and Willems, J. H. (eds), Diversity and pattern in plant communities. SPB Academic Publishing, The Hague, pp. 131–143.

– and Glenn, S. M. 1990. A hierarchical analysis of species' abundance patterns in grassland vegetation. – Am. Nat. 135: 633–648.

– and Glenn, S. M. 1991. Spatial and temporal dynamics in species regional abundance and distribution. – Ecology 72: 654–664.

– , Bradford, J. A. and Sims, P. L. 1987. Succession and fluctuation in *Artemesia* dominated grassland. – Vegetatio 73: 89–99.

Diamond, J. M. and Gilpin, M. E. 1980. Turnover noise: contribution to variance in species number and predictions from immigration and extinction curves. – Am. Nat. 115: 884–889.

Dodd, J.L. and Lauenroth, W.K. 1979. Analysis of the response of a grassland ecosystem to stress. – In: French N.R., (ed.), Perspectives in grassland ecology. Springer, New York, pp. 43–58.

Facelli, J. M., Leon, R. J. C. and Deregibus, V. A. 1989. Community structure in grazed and ungrazed grassland sites in the flooding pampa, Argentina. – Am. Midl. Nat. 121: 125–133.

Freeman, C.C. and Hulbert, L.C. 1985. An annotated list of the vascular flora of Konza Prairie Research Natural Area, Kansas. – Trans. Kans. Acad. Sci. 88: 84–115.

Glenn, S. M. and Collins, S. L. 1990. Patch structure in tallgrass prairies: dynamics of satellite species. – Oikos 57: 229–236.

Goldberg, D. E. 1987. Seedling colonization of experimental gaps in two old-field communities. – Bull. Torrey Bot. Club. 114: 139–148.

Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. – Oikos 38: 210–221.

Holland, P. G. 1978. Species turnover in deciduous forest vegetation. – Vegetatio 38: 113–118.

Janzen, D. H. 1968. Host plants as islands in evolutionary and contemporary time. – Am. Nat. 102: 592–595.

Kershaw, K.A. 1973. Quantitative and dynamic plant ecology. 2nd Edition. – Elsevier, New York.

Leck, C. F. 1979. Avian extinctions in an isolated tropical wet-forest preserve, Ecuador. – Auk 96: 343–352.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. – Bull. Entomol. Soc. Am. 15: 237–240.

MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. – Princeton Univ. Press, Princeton.

McCoy, E. D. 1982. The application of island-biogeographic theory to forest tracts: problems in determination of turnover rates. – Biol. Conserv. 22: 217–227.

Neave, H. R. and Worthington, P. L. 1988. Distribution-free tests. – Unwin Hyman, London.

Peart, D. R. 1989. Species interactions in a successional grassland. I. Seed rain and seedling recruitment. – J. Ecol. 77: 236–251.

Pickett, S. T. A., Collins, S. L. and Armesto, J. J. 1987. Models, mechanisms and pathways of succession. – Bot. Rev. 53: 335–371.

Robinson, G. R. and Quinn, J. F. 1988. Extinction, turnover, and species diversity in an experimentally fragmented California annual grassland. – Oecologia 76: 71–82.

Seagle, S. W. and Shugart, H. H. 1985. Faunal richness and turnover on dynamic landscapes: a simulation study. – J. Biogeogr. 12: 499–508.

Shmida, A. and Wilson, M. V. 1985. Biological determinants of species diversity. – J. Biogeogr. 12: 1–20.

Simberloff, D. 1976. Species turnover and equilibrium island biogeography. – Science 194: 572–578.

Webb, W. L., Lauenroth, W. K., Szarek, S. R. and Kinerson, R. S. 1983. Primary production and abiotic controls in forest, grassland, and desert ecosystems in the United States. – Ecology 64: 134–151.

Wright, S. J. and Hubbell, S. P. 1983. Stochastic extinction and reserve size: a focal species approach. – Oikos 41: 466–476.