Patch structure in tallgrass prairies: dynamics of satellite species

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Space in tallgrass prairie communities is dominated by a few core species. A large number of less abundant, satellite species occupy the remaining space. These satellite species define vegetation patches that vary within and between growing seasons. In order to determine if patch structure was random we established five permanent 100-m^2 blocks in undisturbed tallgrass prairie in Oklahoma and Kansas. Presence of core and satellite species in each m^2 was sampled over one or two growing seasons. Patch types were defined by cluster analysis. Characteristics of patch structure included number of patch types, patch type diversity, patch composition, number of spatial groups, group size, and fractal dimension of the spatial groups. We generated simulated data sets with random species associations, in which we quantified patch structure. Actual patch structure, defined mainly by satellite species, was not significantly different from simulated patch structure, except that simulated patches were more fragmented. Therefore, processes that affect species associations may not be important controls of patch structure of satellite species within the spatial and temporal scale of this analysis. Because there was some degree of spatial autocorrelation in patch structure, dispersal processes may have significant effects on patch structure at this scale. In order to understand grassland community dynamics, we propose that satellite species should be modelled using stochastic models constrained by core species dynamics. This approach may be applicable to any community with major components operating at different hierarchical levels.

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Introduction

Space in tallgrass prairie communities is dominated by a few species of perennial grasses with a large number of satellite species in the remaining space (Gotelli and Simberloff 1987). The ubiquitous species across a study area, known as core species, and the infrequent or satellite species, are often found in greater numbers than species that are intermediate in distribution (Hanski 1982). This type of community structure is most obvious at regional and local scales in tallgrass prairie (Collins and Glenn 1990). Satellite species may be annuals or perennials and are spatially and temporally dynamic (Hanski 1982, Collins and Glenn 1990). The combined effects of disturbance and edaphic variability result in prairies being patchy (Collins and Barber 1985,

Gibson and Hulbert 1987). Within a community, patches are delineated as distinct assemblages of species, potentially repeatable over space (Forman and Godron 1986). Tallgrass prairie vegetation generally exhibits an undivided heterogeneous patch structure (sensu Addicott et al. 1987). Over time, composition and spatial structure of patches may change (Grubb 1988) and processes causing these changes may operate over different temporal and spatial scales (Collins and Glenn 1988).

Recent analyses of community patch dynamics have focused primarily on small- or large-scale succession following disturbance (Sousa 1979, Pickett and White 1985). Although Watt's (1947) description of plant community change acknowledged the importance of endogenous patch dynamics, studies of community patch

dynamics independent of disturbance are still uncommon (Grubb 1988).

In undisturbed tallgrass prairie, the dynamics of core species are likely to be slower than those of satellite species because many core species are long-lived perennials with large populations (Collins and Glenn 1990). Little is known about the spatial distribution and patch dynamics of satellite species. Therefore, this study was designed to measure small-scale patch structure and dynamics in two tallgrass prairie communities and to determine if patch structure and dynamics were random.

Methods

Field methods

We measured small-scale patch structure in 10 by 10 m² permanent blocks in tallgrass praries in Oklahoma and Kansas. We established three blocks at the USDA Livestock and Forage Research Station at El Reno, Oklahoma in May 1986. This grassland had been burned infrequently, with the last fire in April 1984. A 25 by 50 m² exclosure was erected in May, 1986 to eliminate cattle from the study area. Similarly, we established two permanent blocks in June 1987 in tallgrass prairie at the Konza Prairie Research Natural Area, near Manhattan, Kansas. This site had been ungrazed since 1971 and was last burned in 1981. The presence of living above ground parts of each species in 100 contiguous quadrats (1 m²) in each block was recorded periodically in Oklahoma in 1986 and 1987 and in Kansas in 1987.

Numerical methods

Patch types were determined using an unweighted pair group clustering algorithm on a quadrat similarity matrix based on Jaccard's coefficient (Romesburg and Marshall 1984). At a similarity level of 0.633, the resulting dendrograms were divided into discrete clusters with few single quadrat groups. Using this similarity level, we classified quadrats into patch types.

The number of patch types was determined for each block at each sampling date. Patch type diversity (Romme and Knight 1982) was measured using the Shannon-Weaver index,

$$H' = -\Sigma p_i \ln p_i,$$

where p_i is the proportion of quadrats in each patch type. Discriminant functions analysis (DFA) was used to determine which species were important in defining patch types. The correlation between each species and the discriminant function was used as an indicator of the importance of each species in defining the model which best discriminated between patch types.

The number of spatial groups is greater than the number of patch types because a single patch type may be fragmented into small groups. Patch types were mapped over the 100 quadrats to assess spatial patterns of patches. From these maps we calculated average group size and number of groups regardless of patch type. Fractal dimension has been used as an index of shape and pattern complexity (Mandelbrot 1977, Burrough 1981, Morse et al. 1985, Krummel et al. 1987, Milne 1988). Fractal dimension (D) was calculated as,

$$D = \frac{\log (A)}{\log (P/4)},$$

where A is area of the patch type and P is the total perimeter of the patch type (Burrough 1981, Gardner et al. 1987, Milne 1988). D is a similarity dimension of a fractal set and decreases as perimeters become more complex (Milne 1988). Therefore D is scaled from one for highly fragmented linear patterns, to two for compact, two-dimensional shapes (Morse et al. 1985, Krummel et al. 1987). D was calculated for each patch type and averaged over a block. Small patches (1–3 m²) were not included because their shape is constrained by the number of quadrats.

To determine if the patch structure differed from random, we developed simulations of communities in which species associations were random. To create simulated data sets, relative frequencies were calculated for every species, and used to represent the probability of species i (p_i) occurring in a quadrat. A species was assigned to a quadrat if r < p_i, where r was a random number between zero and one chosen for each species for each quadrat. For species with p_i = 1.0 all random numbers chosen would be less than p_i, and the species would be present in all quadrats. Similarly, species with low p_i values would be assigned to fewer quadrats. Since this method assigned species to quadrats independently, species associations were random. A total of 81 simulated data sets of 100 quadrats each were created.

For each simulated data set, we analyzed patch structure using the same techniques as for original data sets. We calculated number of patch types, patch type diversity, and the importance of each species in defining patches based on a DFA. In addition, number of spatial groups, average group size, and fractal dimension were calculated. For all measures at each sample date, we used three simulations to determine confidence limits of ± 2 standard deviations around the mean for comparison to real data for each block. DFA results were tested with a pair-wise t-test comparing the squared correlation coefficient of each species in the real data to the mean coefficient for each species in the simulated data. The magnitude of these calculations prevented us from increasing the number of simulated data sets.

Tab. 1. Total numbers of satellite species found at any sampling time in three blocks in Oklahoma and two blocks in Kansas.

Species characteristics		Oklahoma	Kansas
Grasses:	Perennial C-3	1	3
	Annual C-3	1	1
	Perennial C-4	7	5
	Annual C-4	1	0
Sedges:	Annual C-3	2	1
Forbs:	Perennial C-3	23	30
	Annual C-3	6	4
Total satellite species:		41	44

Nomenclature follows Gould (1975) for grasses and Waterfall (1972) for other vascular plants.

Results

In all blocks, the C-4 perennial grasses *Andropogon gerardii* and *Schizachyrium scoparium* were present in over 90% of the quadrats. *Poa pratensis*, a C-3 perennial grass, was also a core species in one block in Kansas. In Oklahoma, *Ambrosia psilostachya*, a C-3 perennial forb, and *Dicanthelium oligosanthes* (formerly *Panicum oligosanthes*) var. *scribnerianum*, a C-3 perennial grass, were core species in two blocks in 1986 and in all three blocks in 1987. *Conyza canadensis*, a C-3 annual forb, was a core species in two blocks in Oklahoma in 1986. We refer to all non-core species with a frequency of less than 90% in a block as satellite species. This includes species normally considered intermediate between core and satellite, but these species are likely to have rapid dynamics (Hanski 1982) and account for a small proportion of total species (Collins and Glenn 1990). The number of satellite species varied with time. In Oklahoma, the maximum number of satellite species per block were 25, 29, and 28 in 1986, and 26, 33, and 27 in 1987. In Kansas, there were 35 and 25 satellite species in the two blocks in 1987. The satellite species were predominantly perennial C-3 forbs (Tab. 1).

The number of patch types in both grasslands was correlated with species richness (r = 0.713, p < 0.01) and both number of patch types and species richness generally decreased over the growing season (Fig. 1). The mapping of patch types showed that the number of spatial groups also decreased over the growing season (Fig. 1), partly in response to the decrease in the number of patch types (r = 0.797, p < 0.01). Few satellite species were present late in the growing season, thus limiting the number of patch types and spatial groups. Patch type diversity was highly correlated with number of patch types (r = 0.927, p < 0.01), therefore patch type diversity provided little additional information. Average group size was correlated with number of spatial groups (r = −0.849, p < 0.01) which is to be

expected because increasing the number of spatial groups must decrease group size when it is constrained by a 100 m² area.

The trends over time were not as clear in the Oklahoma site for the first growing season because this site was recovering from grazing. This was especially evident in Block A, which was heavily trampled in May 1986. However, the trends in Oklahoma in the second growing season were similar to those in Kansas prairie, which had been ungrazed by ungulates and unburned for many years. Therefore, the Oklahoma site rapidly recovered patch dynamics characteristic of tallgrass prairie without these large-scale disturbances.

The partial r² values of each species in discriminant functions separating patch types reflect the importance of the species in explaining variance between groups. Core species that were in 100% of the quadrats were not important in defining patches (partial r² = 0.0). Therefore, highest partial r²'s were generally found in satellite species, though the values were highly variable over time.

Fractal dimensions were generally between 1.0 and 1.2 (Fig. 2), indicating that patches were linear and highly fragmented. This is likely a result of constraints imposed by core species such as *S. scoparium*. Where this perennial bunchgrass is abundant, only small, fragmented spaces are available for establishment of satellite species (Fig. 3).

In general, number of patch types and patch type diversity in the real data sets were not significantly different from those found in the simulated data sets (Fig. 1). Patch types in real and simulated data sets were not defined by different species (Tab. 2). The number of groups in the real data was less than that found in simulations and the average group size was greater, therefore the simulations had a more fragmented spatial pattern, with more small patches. This is supported by higher fractal dimensions, implying more compact shapes in the real data than in the simulations (Fig. 2).

Discussion

The number and diversity of patch types found in Oklahoma and Kansas grasslands were the same as those in data sets generated by our simulation model that incorporated random species associations. Satellite species were important in defining patch types in both real and simulated data, because core species were found in all patch types. The number of patch types and number of spatial groups decreased over the growing season, as a result of fewer satellite species.

Ephemeral patches may be found where disturbances are common and the vegetation is composed of many patches in different stages of secondary succession. The response of the community depends on the frequency, size, and magnitude of the disturbance (White and Pickett 1985). In some communities, the number of patch types may remain constant, though patch positions
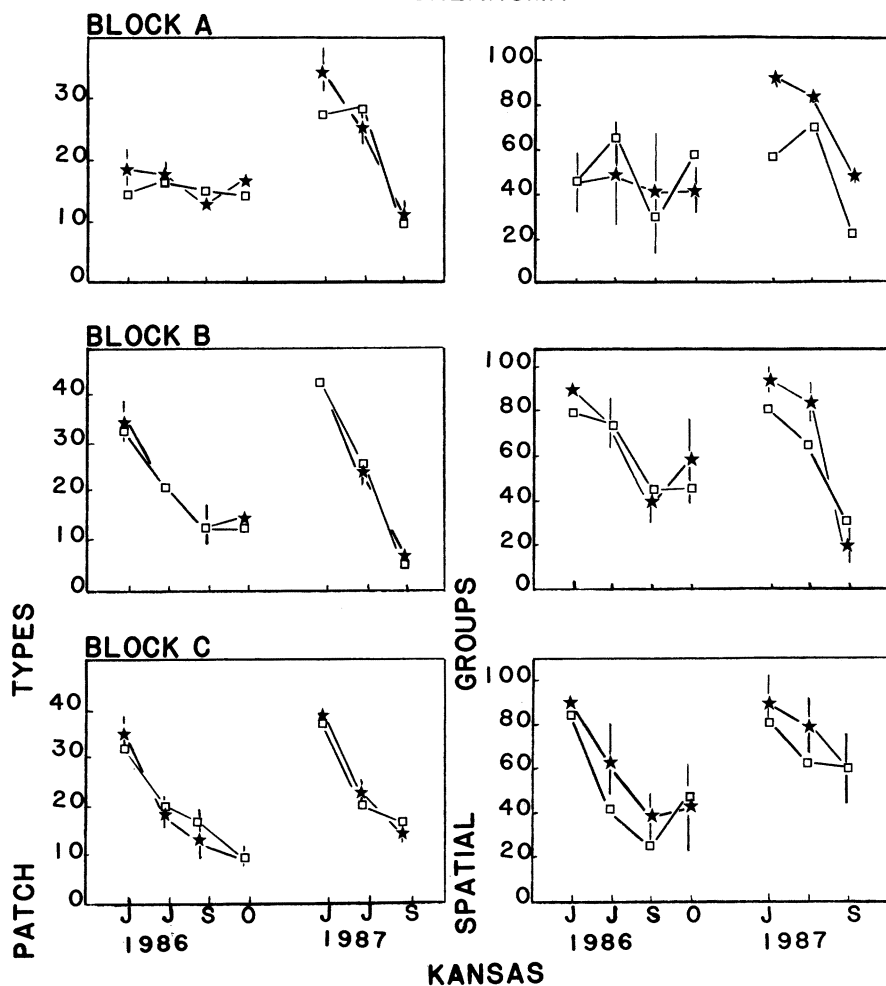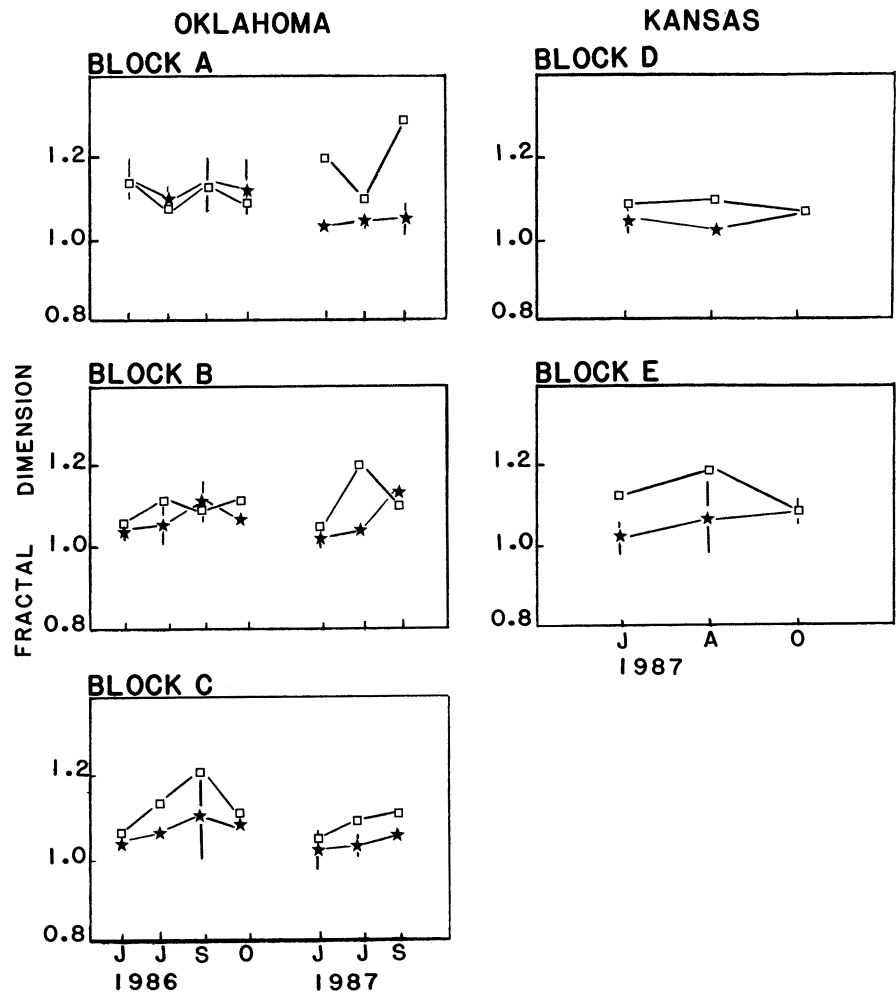
Fig. 1. Number of different types of patches and number of spatial groups in tallgrass prairie through time (squares). Stars represent mean number of patch types and spatial groups ($\pm$ 2 standard deviations) in three simulated data sets for each sample date.

OKLAHOMA

KANSAS

BLOCK A

BLOCK D

BLOCK B

BLOCK E

BLOCK C

vary, resulting in a shifting mosaic of vegetation (Whittaker and Levin 1977, Bormann and Likens 1979, Pickett 1980). Where many types of disturbances occur, the community may reflect interactions of different successional processes (Collins 1987, Pickett et al. 1987). Disturbances and edaphic factors may also interact, and such a combination has been invoked to explain a two-phase mosaic in the Serengeti (Belsky 1986). The effect of vegetation on its environment, and vice versa, may also be responsible for changes in patch structure over an initially homogeneous environment (Roberts 1987).

The tallgrass prairies observed have not been extensively disturbed recently (burned, grazed by ungulates, or plowed), yet over the extent of this study, patch structure varied unpredictably. Patch structure was defined by a large number of satellite species and few patches remained consistent within or between growing seasons (Collins and Glenn 1988). Such changes may result in stable random species associations that Aarssen and Turkington (1985) described for early successional pastures. However, there was no evidence for this type of equilibrium because patch composition was

not consistent between years. Also, ephemeral patch structure was observed in both Oklahoma and Kansas and is therefore not simply a result of the Oklahoma grassland recovering from grazing. It is also unlikely that climatic (Neilson 1987) or edaphic controls on population dynamics (Zedler and Zedler 1969, Hanawalt and Whittaker 1977, Tilman 1982, Belsky 1983, Andrew 1986) could account for these rapid changes in community patch structure. This unpredictability is characteristic of middle number systems because neither statistical nor mathematical approaches adequately characterize the system (Allen and Starr 1982). The patterns observed may be the result of large-scale constraints of climate and soil interacting with small-scale processes of immigration and competition.

Competitive interactions, leading to negative species associations may account for changes in patch structure. Comparison with our simulations in which species associations were random indicated that this could not account for the patch structure observed at this scale. Additionally, less than five percent of the correlations between species were significantly negative ($p < 0.05$).
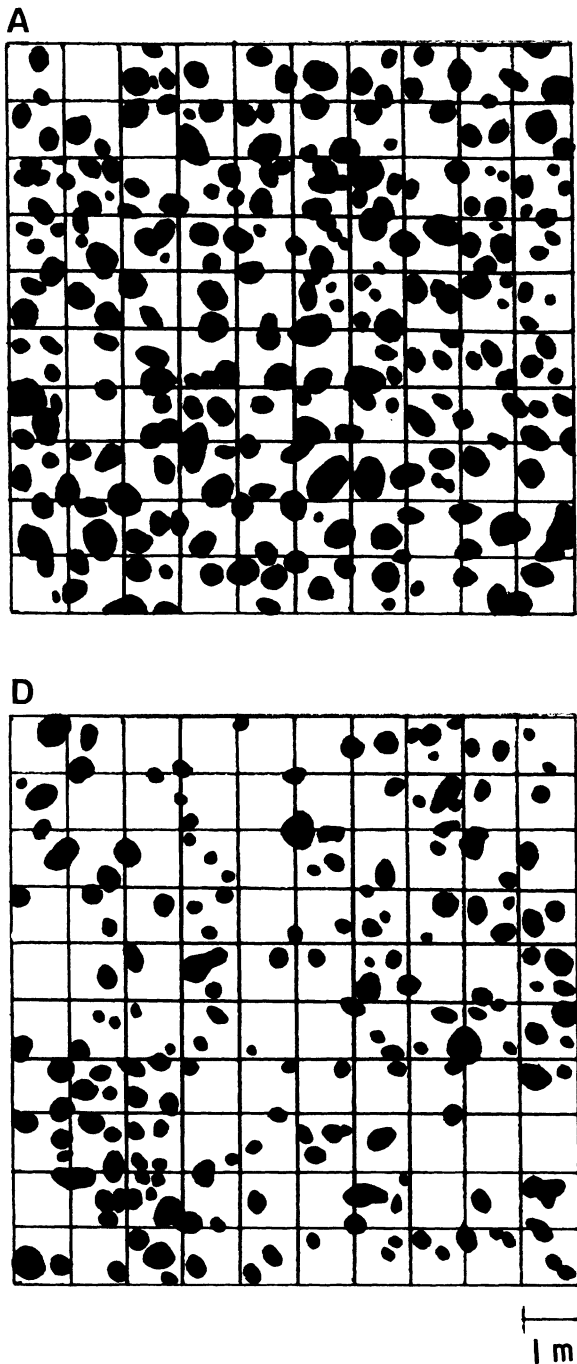
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Fig. 3. Maps of *Schizachyrium scoparium* for Block A in Oklahoma and Block D in Kansas. These maps were constructed by noting relative positions and sizes of bunches of *S. scoparium* in each 1 m² quadrat. The spaces between the bunchgrasses are highly fragmented, as reflected in low fractal dimensions of patches of satellite species.

Therefore, controls such as climate, soils, direct competition or even phenology did not regulate patch struc-

ture and dynamics in these grasslands. Phenology may not be predictable from year to year because of its dependence on changes in weather and local neighbourhood effects (Prins 1988).

Species frequency in a community is measured as the number of plots in which a species is found and is an indication of the probability of a species reaching a plot and surviving. Frequency, therefore, incorporates processes involved with dispersal and establishment. Because these may have been important in defining patch structure, we constructed a simulation model using average frequency of all species in a block as the probability of occurrence of each species. These simulations with altered species frequencies resulted in quadrats being highly dissimilar (100 quadrats fell into 100 patch types). Therefore, factors affecting frequency are important in defining patch structure at this scale.

Two processes, dispersal and establishment, will affect frequency, and hence patch structure. These factors are important aspects of immigration of both annual and perennial plants to quadrats. Perennial species may experience high turnover rates if they have difficulties becoming established or if they are short-lived. Establishment may be stochastic because of local factors such as microclimate, predation, competition, and facilitation. Seed dispersal is highly stochastic and could cause unpredictable changes in patch structure between seasons. Dispersal is considered important in maintaining a dynamic mosaic of patches (Whittaker and Levin 1977) and high species richness (Grubb 1986). The number of groups in real data sets was generally less and average

Tab. 2. Partial r² values of species defining a discriminant function separating patch types were compared between real data and simulations. Pair-wise t-tests were used to determine if partial r² values were significantly different at each sample date. T-statistics and probabilities of the differences being equal to zero (p) are given. Probabilities greater than 0.05 would indicate that the same species were important in defining patches in real and simulated data sets.

Date	Block A t(p)	Block B t(p)	Block C t(p)
Oklahoma			
1986			
Jun	−1.06 (0.299)	0.60 (0.554)	0.90 (0.377)
Jul	−0.72 (0.481)	−0.06 (0.953)	−0.24 (0.816)
Sep	0.26 (0.794)	0.24 (0.811)	−0.94 (0.356)
Oct	−0.20 (0.846)	0.27 (0.792)	0.67 (0.516)
1987			
Jun	1.45 (0.160)	0.03 (0.973)	−0.43 (0.670)
Jul	−0.99 (0.330)	−1.52 (0.139)	0.97 (0.346)
Sep	0.97 (0.346)	0.74 (0.468)	−0.57 (0.575)
	Block D	Block E	
Kansas			
1987			
Jun	−0.71 (0.484)	1.01 (0.320)	
Aug	−0.10 (0.924)	0.16 (0.871)	
Oct	0.04 (0.966)	1.43 (0.179)	

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group size was greater than found in simulated data sets, suggesting simulated data sets had smaller patches and more fragmented spatial patterns (Fig. 1). This observation is supported by higher fractal dimensions indicating more compact shapes in real data sets than in simulated data sets (Fig. 2). This may occur because the simulations did not incorporate spatial autocorrelation. The importance of spatial autocorrelation in the real data is consistent with the idea of dispersal being an important factor influencing patch structure, because seed dispersal and vegetative expansion are decreasing functions of distance from the parent plant (Sheldon and Burrows 1973, Howe and Smallwood 1982, Bigwood and Inouye 1988).

In modelling natural communities, concepts of equilibrium and non-equilibrium structure are often presented as conflicting hypotheses (Yodzis 1981, Chesson and Case 1985) though they represent differently scaled models of the same system (Allen and Starr 1982). Within a short time frame it is possible for communities to simultaneously exhibit characteristics of both. Patch structure in tallgrass prairie varied unpredictably in space within and between growing seasons, reflecting changes in abundance and distribution of satellite species. Therefore, patch dynamics reflect non-equilibrium variation of satellite species within a stable framework composed of a few dominant core species. Hanski (1982) suggested that distribution and abundance of core species such as the perennial grasses in tallgrass prairie reflected processes such as direct competition that are consistent with equilibrium models. However, even these competitive effects may be unpredictable because of disturbances (Sebens 1987), or masking by indirect effects (Yodzis 1988). Interactions between small- and large-scale processes, such as competition and disturbances, may also cause competitive effects to be unpredictable (Addicott et al. 1987, Hengeveld 1987, Allen 1987). Additionally, Yodzis (1981) reported that the structure of food webs was unlikely to have a stable equilibrium if there was a large proportion of species competing for the same resources. Briand (1983) reported similar results for food webs in a fluctuating environment. Because prairies incorporate equilibrium and non-equilibrium processes, it is necessary to develop deterministic models in a stochastic framework to understand patch dynamics in grasslands. This approach has been proposed by Den Boer (1981) for modelling population dynamics. Stochastic dynamics of satellite species can be constrained by different degrees of deterministic processes, such as dynamics of core species spreading in some areas and degenerating in others. An experimental approach may also be applied, such as assessing the effects of the removal of core species on the dynamics of satellite species. This approach will aid in understanding the spatial structure of complex and dynamic communities where different components operate at different hierarchical levels (Allen and Starr 1982).

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