IMPORTANCE OF SPATIAL AND TEMPORAL DYNAMICS IN SPECIES REGIONAL ABUNDANCE AND DISTRIBUTION[1]

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Abstract. Several recent models have been proposed to explain the pattern of species distribution within a region. Brown's niche-based model, Levins' stochastic immigration–extinction model, and Hanski's core–satellite hypothesis (a modification of Levins' model) differ in relative spatial scales, and degree of stochastic variation in species distribution over time. To test the predictions of these models, we analyzed the regional distribution and temporal dynamics of plant species across 19 sites in tallgrass prairie over an 8-yr period. Spatial patterns of species regional distribution were bimodal each year, a pattern in accord with the core–satellite hypothesis. In addition, temporal patterns of species distribution within a site were also bimodal. The dynamics of the core–satellite hypothesis are driven by patterns of immigration and extinction. Extinction was positively related to richness, however, in contrast to the theory of island biogeography, immigration was not related to species richness. In addition, the variances in the differences in species frequencies from one year to the next were greater than three times the mean, a condition necessary for bimodality in the core–satellite model, for 88 of 135 (65.1%) species. These results provide strong support in favor of the core-satellite hypothesis and imply that stochastic factors may be the primary determinant of plant species dynamics and plant community structure in grasslands at the scale of several kilometres. Evidence from prairie communities at much larger spatial scales supported the patterns predicted by Brown's niche-based model. Thus, these apparently competing models are, in fact, compatible when viewed at the appropriate spatial scale.

Key words: community structure; core–satellite hypothesis; extinction; immigration; Kansas; Konza Prairie; Long-Term Ecological Research site; species richness; stochastic factors; temporal distribution pattern.

INTRODUCTION

Historically, ecologists have dealt primarily with intracommunity patterns whereas regional factors were the realm of the biogeographer. It is becoming increasingly evident, however, that regional phenomena govern, to some extent, local community structure (Hanski 1982a, Brown 1984, Bock 1987, Ricklefs 1987). Such results can be expected from hierarchy theory, which predicts that phenomena at a given focal level are a function of processes and constraints operating at higher and lower organizational levels (Allen et al. 1984, O'Neill 1989). For example, community richness is a function of dispersal from large-scale regional source pools of species countered by the small-scale competitive interactions among neighboring species within a community (Clements 1916, Gleason 1926).

Several models have been developed to describe and predict the distribution and abundance of species among similar communities in a region (Levins 1969, Hanski 1982a, Brown 1984). In this paper, richness will refer to the number of species in a community (=site), abun-

dance is defined as the importance of a species in a community, and distribution is a measure of the number of sites in a region in which a species occurs. These large-scale models of distribution and abundance represent a logical extension of intracommunity analyses, such as the log-series model (Williams 1950), to the regional scale. One common and well-documented assumption of the regional models is that a positive correlation exists between the average abundance of a species in a community and the distribution of that species within the region (McNaughton and Wolf 1970, Hanski 1982a, Bock and Ricklefs 1983, Brown 1984, Bock 1987). That is, regionally common species have higher average abundances in a community than regionally rare species. Brown's (1984) niche-based model builds on this theme. This model assumes that the abundance of a species along a gradient, such as elevation (e.g., Whittaker 1956, 1960), is Gaussian. Essentially, the niche-based model is a regional extension of the Gaussian theme in that abundance generally decreases from the center to the edge of a species range (Hengeveld and Haeck 1982). This is predicted on the logical notion that species are adapted to a certain range of habitat, that habitat factors vary independently, and therefore habitat suitability decreases from the center to the edge of a range. Thus, a normal distribution of species abundance should occur along a transect across the
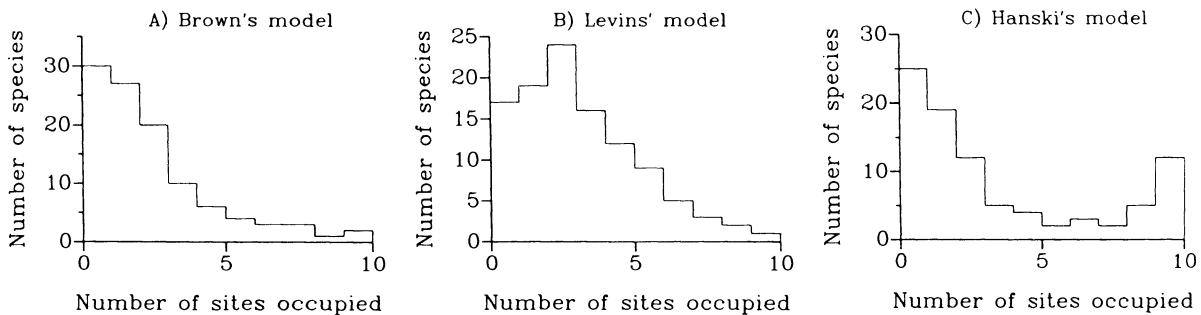
FIG. 1. Schematic representation of the predictions of the regional distribution models of Brown (1984), Levins (1969), and Hanski (1982a).

range of a species (Burgman 1989). From this model Brown (1984) predicts that species will be abundant only in communities near the center of the range and will decrease in importance in communities located near the edge of the range. That is, few species will be found in all samples across a region (Fig. 1A) because as more communities are sampled, more habitat variation will be incorporated in the samples. Because species are adapted to only a certain combination of environmental variables, they can only occur in a subset of the samples. Species with broad niches will occur in a larger subset of samples than species with narrow niches. Because Brown's model deals with variation across the range of a species, his model addresses patterns of species abundance over potentially very large geographic areas ($>10^3$ km) and predicts unimodal regional distributions of species (Fig. 1A).

Levins (1969) was one of the first to develop a dynamic, regional model of distribution and abundance based on patterns of immigration and extinction according to the theory of island biogeography (MacArthur and Wilson 1967). In a version of Levins' model in which immigration and extinction rates varied stochastically over time, the model produced a unimodal distribution of species with the mode at $0 \leq p_y \leq 1$, where p_y is the proportion of sites occupied by species y (Fig. 1B). Hanski (1982a) demonstrated, however, that extinction was negatively correlated with the number of sites occupied, so Hanski modified Levins' model by including a term that made extinction a function of the number of sites occupied. In the stochastic version of Hanski's (1982a) model, the combined distribution of all species among sites in a region is bimodal (Fig. 1C). From this model Hanski derived the "core–satellite hypothesis," which states that within a region there are two primary groups of species: core species, which are abundant within sites and occur at >90% of all sites, and satellite species, which are sparse within sites and occur at <10% of all sites (Hanski 1982a). This model predicts that species will fluctuate randomly between the core and satellite modes, and the most rapid dynamics are shown by those species with intermediate regional distributions (e.g., occupy 50% of

the sites). Year-to-year fluctuations occur in response to variation in local environmental conditions. In any one year, bimodal distributions occur because some species are regionally abundant whereas others are regionally rare. This would differ from Brown's (1984) model in which temporal fluctuations in species abundance are dampened, at least for species with broad niches because the response to environmental variation is incorporated within the species niche. Because Levins' and Hanski's models are based on the dynamics of colonization and extinction, these models are scaled to dispersal distances that may be relatively small for many plant species (0.10–10 km).

The models of Levins (1969) and Brown (1984) produce patterns over large spatial scales that mimic those of intracommunity patterns. That is, most species are locally distributed (regionally rare), and only a few species will be found at all sites. The model of Hanski (1982a, b, c) is clearly distinct from the others in that the stochastic version of the model predicts a bimodal distribution of species frequencies within a region, species tend to be either very rare or very common. Like the model of Levins, Hanski's is a dynamic regional model that assumes species populations fluctuate stochastically over time in response to stochastic environmental fluctuation and interspecific interactions. Thus far, however, the only tests of these models have been to determine if data from spatially distinct sites are uni- or bimodal (Hanski 1982a, b, c, Gotelli and Simberloff 1987, Collins and Glenn 1990).

The Long-Term Ecological Research (LTER) site at Konza Prairie Research Natural Area (KPRNA) provides an excellent opportunity to test these regional distribution–abundance models. Abundance data have been collected in permanent plots at KPRNA since 1981 for ≈250 plant species scattered across 19 sites in 12 watersheds. All sites are close together to allow species potentially to colonize adjacent sites (Fig. 2). The advantage of this database is the small scale and rapid community dynamics in grasslands (Collins 1987, 1989, Glenn and Collins 1990). Thus, the general goal of this study was to determine if both spatial and temporal data from plant communities at KPRNA are
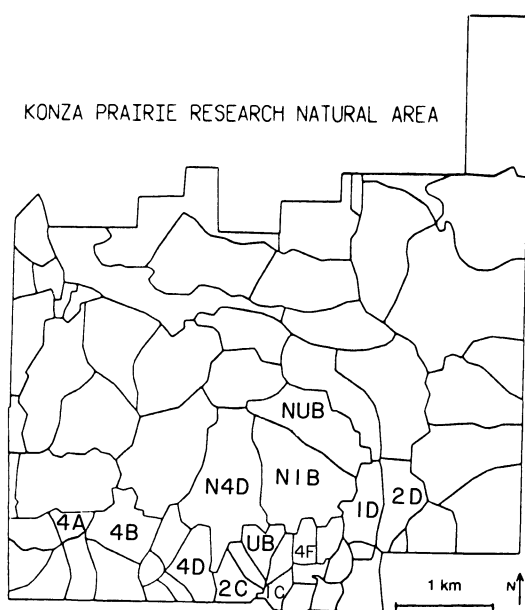
KONZA PRAIRIE RESEARCH NATURAL AREA

FIG. 2. Map of the study area showing watershed boundaries and burning treatments at Konza Prairie Research Natural Area. Watershed codes: N=native grazer (not yet on site; treatments will be separated by electric fencing; A, B, C, D, F=watershed replicate; U=unburned; 1, 2, 4=fire frequency (no. years between burns). Only the watersheds used in this analysis are labeled.

consistent with assumptions and predictions of the models of Hanski (1982a), Levins (1969), or Brown (1984). To do so, we measured the dynamics and variability of plant species' immigration and extinction rates among the 19 sample sites at Konza Prairie over an 8-yr time period.

METHODS

Konza Prairie Research Natural Area is located in Riley and Geary counties, northeastern Kansas, USA. KPRNA contains 3487 ha of tallgrass prairie subjected to a research management plan established in 1978, which includes maintaining different watersheds under burning treatments at 1-, 2-, 4-, 10-, and 20-yr intervals (Hulbert 1985; Fig. 2). For a number of watersheds the experimental burning treatments have been in effect since 1972. The annual, 2-yr, and unburned (20-yr) treatments, at least, should by now be in a steady-state relative to fire frequency (Gibson and Hulbert 1987). Vegetation on these grasslands is dominated by *Andropogon gerardii, Sorghastrum nutans, Sporobolus asper, Carex heliophylla, Poa pratensis, Artemisia ludoviciana, Dicanthelium oligosanthes, Solidago missouriensis, Ambrosia psilostachya,* and *Aster* spp. (Gibson and Hulbert 1987).

As part of the LTER protocol, species composition is recorded at 19 sites on 12 experimental watersheds. In 1981, permanent vegetation plots were established in upland Florence (FL) and lowland Tully (TU) soils

in four watersheds, UB (unburned), 1D (annually burned), and N4D and 4B (both burned once every 4 yr). Six more sample sites were initiated in 1983 (NUBFL, NUBTU, N1BFL, N1BTU, 1CFL, and 1CTU), and five more sites were added in 1984 (2CFL, 2DFL, 4AFL, 4DFL, and 4FFL). Vegetation on each soil type in each watershed is sampled in 20 permanently marked 10-m^2 circular quadrats located along four 50 m long transects. Vegetation samples were collected in May, July, and September. Cover was estimated by eye using the Daubenmire cover scale: 1 = <1% cover (e.g., present), 2 = 1–5%, 3 = 5–25%, 4 = 25–50%, 5 = 50–75%, 6 = 75–95%, and 7 = >95%. Average cover was determined for each species by converting the Daubenmire scale value to the midpoint of the cover range and averaging across the 20 quadrats at a site. In this study, summary data for a sample site were based on the maximum frequency or cover for each species observed during the growing season. Thus, each of the 19 sites represents a "community" in the KPRNA "region."

For some reason, the original eight plots were not sampled throughout the year in 1982, but they were sampled in 1981 and all sites have been continuously sampled since 1984. To measure the pattern of regional distribution, we plotted the number of species occurring in 1, 2, 3 . . . , *n* sample sites for each year (1981, *n* = 8; 1983, *n* = 14; 1984–1988, *n* = 19). Temporal patterns in distribution were determined by plotting the number of species that occurred in 1, 2, 3 . . . , *n* years (*n* ranges among sample sites from 5 to 7 yr) within a site. Data from site NUBFL were not used in this temporal analysis of distribution because one of the four transects of permanent plots was moved in 1986.

Immigration rates were determined by counting the number of new species at a sample site compared to the previous year. Extinction rates were measured by counting the number of species that disappeared from one year to the next in each site. Because data were not collected in 1982, only data from years of continuous sampling (1983–1988) were used to estimate rates of immigration and extinction. Because the models of Hanski and Levins are scaled to immigration and extinction dynamics as in the equilibrium theory of island biogeography, regressions were used to determine the relationships between immigration and extinction vs. species richness for all sites.

RESULTS

In all years, the distribution of species across sites is strongly bimodal (Fig. 3). Thus, most species are regionally rare, but there are consistently 10–15 species that occur at every site and 17–20 species that occur in >90% of sites. A third peak often appears at an intermediate abundance category, as well (Fig. 3). Thus, the spatial data conform to the predicted patterns of the core–satellite hypothesis. It is possible that the per-
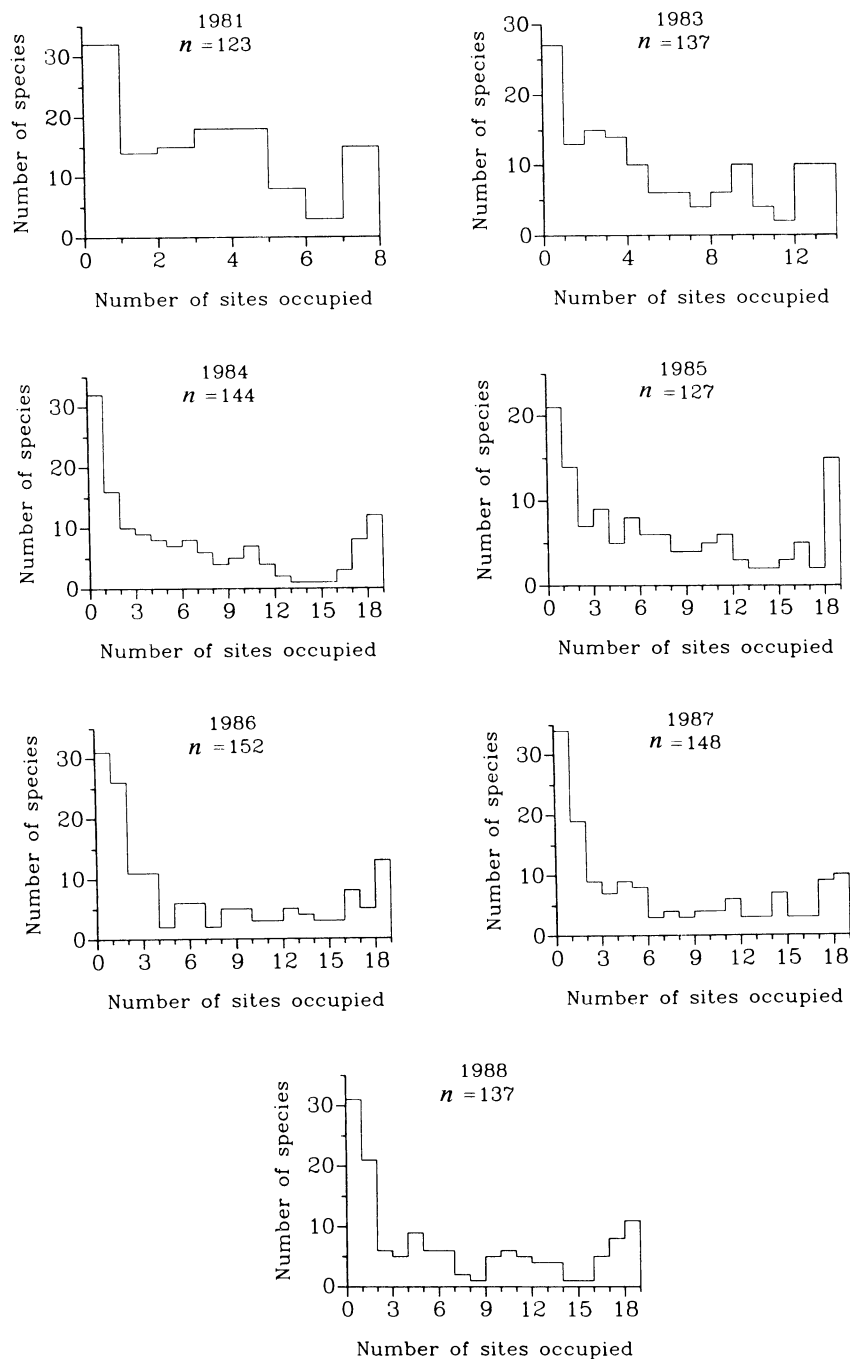
FIG. 3.　Species distribution patterns among sample areas at Konza Prairie Research Natural Area over an 8-yr period. Eight sites were sampled in 1981, 14 sites were sampled in 1983, and 19 sites were sampled from 1984 to 1988. n=the total number of species among all sites. (Data for 1986 modified from Collins and Glenn 1990.)

ceived bimodality is simply a function of a small number of samples within the region. However, the number of core species (defined as species occurring in all sites) is remarkably stable even with the addition of 11 sites by 1984. That is, the 137% increase in the number of sites did not decrease the number of regional core species.

A total of 19 species were core species during the 7 yr of this study, of which only five were core species every year (Table 1). All are native perennial true prairie species except for the annual forb *Oxalis stricta*. Core species represented 7.3–12.2% of the total number of species each year. There is a wide range in average cover values among the core species, which re-

TABLE 1. Core species across sites, number of years they were in the core category, life form of each species (A = annual, P = perennial, G = graminoid, F = forb), average cover over all years, average change (S) and variance (S_{var}) in frequency from year to year. Core species are defined as those occurring in all sites in a given year.

Species	Number of times core	Life form	Average cover (%)	S	S_{var}
Ambrosia psilostachya	7	PF	5.9	0.0	0.0
Andropogon gerardii	7	PG	73.0	0.0	0.0
A. scoparius	7	PG	16.7	0.0	0.0
Dicanthelium oligosanthes	7	PG	0.6	0.0	0.0
Panicum virgatum	7	PG	4.3	0.0	0.0
Physalis pumila	6	PF	0.3	0.0	0.42
Aster ericoides	6	PF	5.7	0.0	0.39
Ruellia humilis	6	PF	0.5	0.0	0.42
Sorghastrum nutans	6	PG	16.4	0.0	0.37
Vernonia baldwinii	6	PF	1.5	0.0	0.37
Bouteloua curtipendula	4	PG	1.5	0.30	2.38
Artemisia ludoviciana	4	PF	5.0	0.10	1.42
Asclepias viridis	3	PF	0.2	0.58	3.93
Sporobolus asper	3	PG	3.0	1.32	8.75
Amorpha canescens	2	PF	2.8	0.00	0.43
Carex heliophylla	2	PG	0.2	1.96	11.83
Dalea purpurea	1	PF	0.2	0.16	2.22
Kuhnia eupatoroides	1	PF	0.5	0.40	1.78
Oxalis stricta	1	AF	0.1	1.04	12.12

flects the large differences in maximum size among the species.

The temporal analysis of occurrences within a site over time shows distinctly bimodal distributions for all but two sites (Fig. 4). That is, most species were present every year or present only one time regardless of burning frequency. The two sites that were not bimodal (1CFL and 2DFL) had a single mode of core species and low total species richness.

Colonization and extinction are the two processes that drive the core-satellite model. As noted above, this model is a dynamic regional model, which predicts that if the variance in the difference (S_{var}) in a species' frequency from year to year (related to immigration and extinction in Hanski's model) is at least three times as great as the mean ($\bar{S}$), then the regional pattern of distribution and abundance is bimodal. If $S_{var}=\bar{S}$, then a species tends to be maximally distributed (Hanski 1982a). According to Hanski (1982a, personal communication), S can be calculated for each species as:

$$S = (p_t - p_{t-1})/p_t(1 - p_t),$$

where p_t equals the proportion of sites occupied by a species at time t. From 7 yr of data, there are six values of S from which we can calculate $\bar{S}$ and S_{var}. For 88 of 135 species (65.1%), S_{var} was greater than three times the mean. This provides the most direct support for the core–satellite hypothesis and indicates that for many species there is a large degree of year-to-year stochastic variation in species abundance over time in this tall-grass prairie region. In the case of those species in the core category six or seven times, S_{var} often equals $\bar{S}$, indicating that the distribution of core species was generally stable (Table 1). The remaining species may not fit the model because of limited dispersal ability, subtle differences in site requirements, or response to disturbance. For example, Poa pratensis does not occur on sites that are burned annually, and Spartina pectinata is restricted to sites near drainage areas. Thus, the stochastic version of Hanski's model holds for most, but not all, species in these grassland communities.

Across all sites and years, extinction is positively correlated with species richness ($r = 0.76$, $P < .0001$), but the relationship between immigration and richness is not significant ($r = -0.03$, $P = .78$) (Fig. 5). Thus, the more species at a site the higher the probability that some will go extinct. In contrast to the equilibrium theory of island biogeography (MacArthur and Wilson 1967), however, immigration rates, although variable, are constant with respect to richness of a site. This is not surprising because each site contains only a fraction of the regional flora. These regression relationships suggest that the dynamics of species richness in these sites are driven by the rate of extinction, and predict an

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FIG. 4. Species distribution over time within 19 sample sites over 5-yr (1984–1988), 6-yr (1983–1988), or 7-yr (1981–1988) periods. No data were collected in 1982. Sample site names are based on watershed replicate (e.g., a, b, c), how often a watershed is burned (u = unburned, 1-, 2-, and 4-yr intervals between burns), and soil type (FL= upland Florence, TU=lowland Tully soils). n=total number of species occurring on the same area over time.
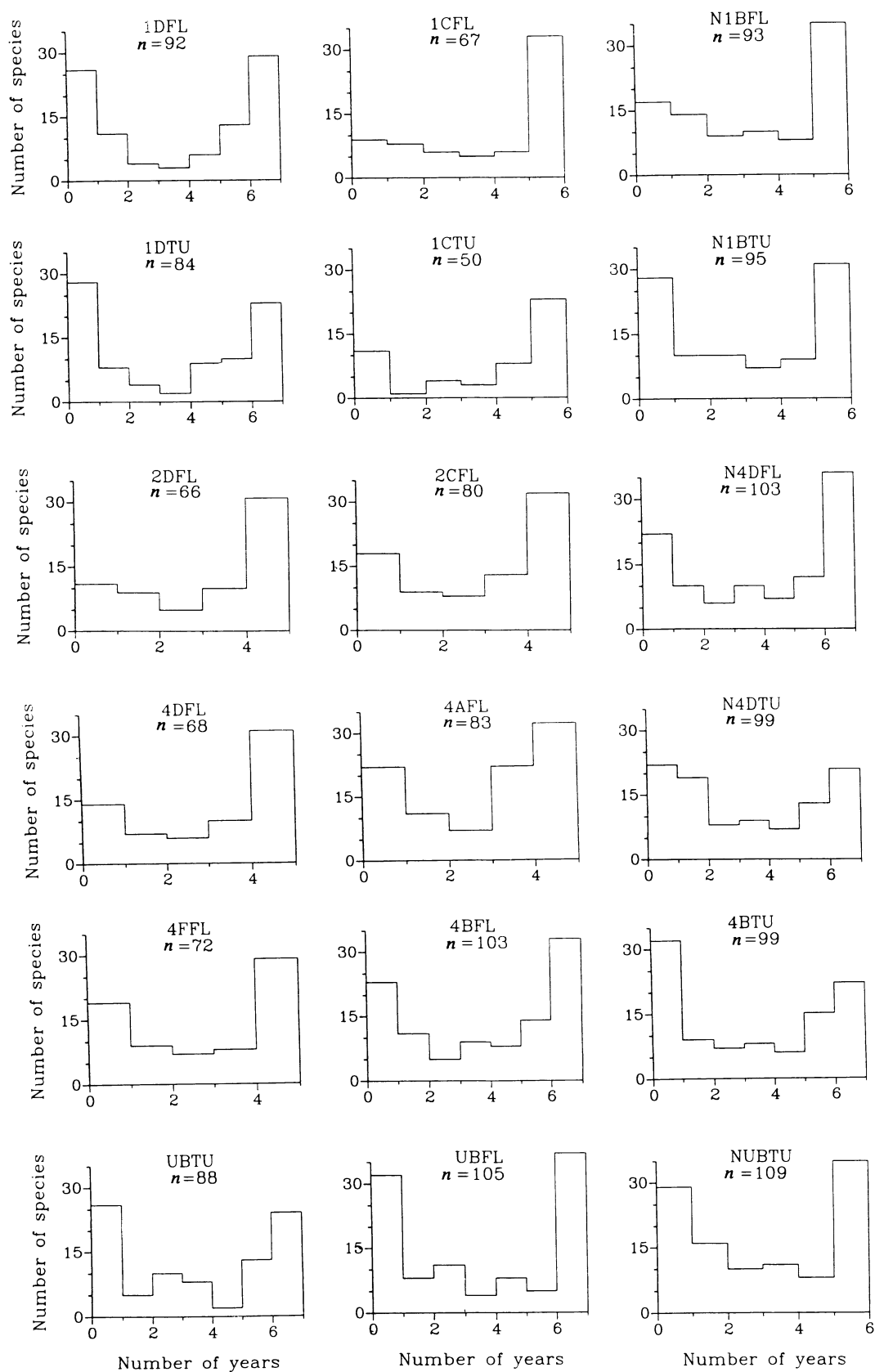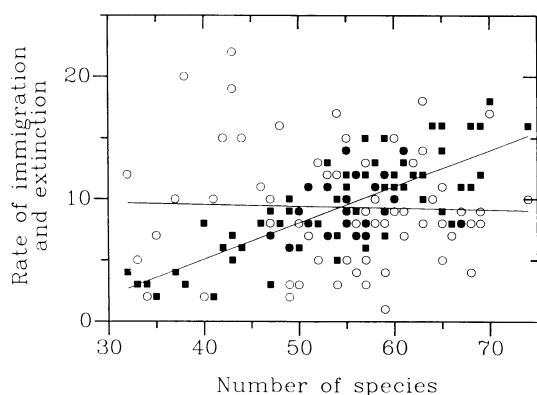
FIG. 5. Rates of immigration (O) and extinction (■) from year to year in relation to species richness (R) for each sample site. Immigration $= 10.1 - 0.014R$, $r^2 = 0.001$, $P=.78$; Extinction $= -6.85 + 0.298R$, $r^2 = 0.58$, $P < .0001$.

equilibrium number of 54.6 species per site. The average richness values per site range from 35.7 to 65.1 species with an overall mean of 53.9 species.

DISCUSSION

Bimodality

The evidence presented is generally in accord with the assumptions and predictions of the core–satellite model. The distribution of species was bimodal over space and time, although the measurement of bimodality is often difficult because there is only one statistical test available and the assumption of the test is a uniform distribution. This is obviously not a reasonable ecological null model. Thus, as Gotelli and Simberloff (1987) noted, bimodality is often in the eye of the beholder. It is clear, however, from the distributions in Figs. 3 and 4 that there are distinct modes in both the highest and lowest frequency classes.

Of greater concern is the controversial concept of bimodality. Raunkiaer's (1934) law of frequencies predicts bimodality for frequency (distribution) data, and distributional characteristics have been used as a measure of homogeneity for community analysis. Gleason (1929) and McIntosh (1962) have criticized this use as invalid because bimodality was simply a function of sample size. Williams (1950) also provided statistical documentation of these criticisms. Even though we increased the number of sites from 8 to 19, however, there was not a corresponding decrease in bimodality. Thus, although the measurement of bimodality may be scale dependent, bimodality is clearly evident at our scale of observation. Interestingly, DuRietz (in Noy-Meir and van der Maarel 1987) considered the bimodal distribution of Raunkiaer's (1934) "law" as an important measure of community homogeneity. However, Romell (1920) and Kylin (1926) (in Noy-Meir and van der Maarel 1987) suggested that such a distribution could be generated from simple assumptions associated with the random distributions of plants. This appears to fit well with the ideas proposed by Hanski (1982a).

Stochastic variation

There was a high degree of stochastic variation in the dynamics of colonization and extinction. Grassland environments are highly stochastic (Sims et al. 1978, Risser et al. 1981). For example, annual fluctuations in temperature and precipitation at KPRNA show a high degree of year-to-year variation with no apparent temporal trend (T. Seastedt, personal communication). These stochastic environmental fluctuations have been shown to affect the number of species that occur in grasslands from one year to the next (Gibson and Hulbert 1987, Collins and Gibson 1990). In fact, immigration is significantly correlated with growing season precipitation at Konza $(r = 0.9, P < .05)$. Thus, temporal fluctuations in precipitation and temperature, factors scaled differently than interactions within communities, impose stochastic variation on structure in grassland vegetation.

Our previous analyses have indicated that grassland patch dynamics are highly variable over several spatial scales (Collins and Glenn 1988, 1990, Glenn and Collins 1990). At a spatial scale of 10 × 10 m², satellite species defined patches that varied spatially within and between growing seasons (Collins and Glenn 1988). Actual patch structure was defined mainly by satellite species because the dominant grasses occurred in all patch types. That is, a few dominant core species were consistently widely distributed, whereas most other species fluctuated from year to year. More importantly, patch structure of the field data was not significantly different from patch structure in randomly simulated data sets (Glenn and Collins 1990). These results indicate that at small spatial scales there is a high degree of stochastic variation over time among satellite species within a stable matrix of core species (Glenn and Collins 1990). This variation is transposed to patterns at larger spatial scales (Collins and Glenn 1990). We recently analyzed the distribution and abundance of plant species at three spatial scales on KPRNA and two prairie communities in Oklahoma (Collins and Glenn 1990). At the regional level, species distributions were bimodal at both sites conforming to the predictions of the core–satellite hypothesis. The patterns found among the 100 quadrats within each of five 10 × 10 m² blocks were similar to those of the regional level distribution. That is, there were also core and satellite species distributed among the 100 quadrats. Thus, grassland community structure exhibits self-similarity because the large-scale pattern is composed of numerous small-scale units of similar structure (Collins and Glenn 1990). Again, this structure reflected stochastic variation in numerous satellite species within a matrix of stable competitive dominants.

Scaling

One of the explicit assumptions of Hanski's core–satellite model is that all sites must be of similar habitat so that all species could theoretically occupy every site. Brown considered this assumption to be restrictive because he documented that environmental variables change along gradients, and they become less suitable from the center to the edge of a species range. Thus, regional variation in habitat would not allow similar sites to exist. If one examines, however, the maps Brown (1984: Fig. 2) used to show abundance patterns within a species range, it is clear that the center of a species range may extend for hundreds of square kilometres. This is certainly true for a number of prairie species in the Central Great Plains (Diamond and Smeins 1988). Given the size of these regional centers of population abundance, the centers of many species ranges will overlap. Also, Brown's (1984) assumption that species are normally distributed along ecological gradients may not be valid. Westman (1980) and Austin (1980) determined that most field data from plant communities were not accurately described by a Gaussian curve. Instead, species distributions were highly skewed and often bimodal (Austin 1980). The fact that species distributions along environmental gradients are not always normal suggests that many species tolerate a wide range of habitat or that habitat variation is non-normal. Therefore, many species should be abundant within a large subset of their range and similar habitat must exist over a large region. Thus, the models of Brown and Hanski are essentially compatible in that Hanski's model is a spatially explicit subset of Brown's model. That is, in accord with Hanski's requirements, similar sites exist within a regional subset of a species' geographic range. Within these similar sites, the abundances of many species fluctuate stochastically over time. Thus, the models of Brown and Hanski are not competitive but complementary when properly scaled. In fact, many seemingly competitive models may actually be complementary when viewed at the appropriate scale of resolution (Allen and Starr 1982, Brown and Allen 1989).

Because Brown's model appears to apply to larger spatial scales than the model of Hanski, we have plotted data on the distribution of prairie plants from two surveys of regions much larger than KPRNA: vegetation on 29 prairie cemeteries on similar soils in northern Illinois and western Indiana (Betz and Lamp 1989), and vegetation on 77 remnant prairies in northeastern Oklahoma, southeastern Kansas, southwestern Missouri, and northwestern Arkansas (Eyster-Smith 1984). In both cases, the distribution of species is distinctly unimodal (Fig. 6) as would be predicted by Brown's larger scale model.

One major difference in the models lies in the validity of the stochastic variation in distribution over time proposed by Hanski (1982a) vs. the deterministic
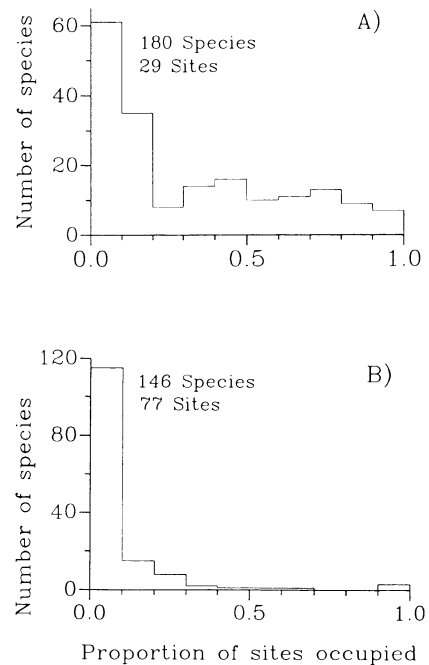

FIG. 6.   (A) Distribution of prairie plants on silt loam soils among 29 pioneer cemeteries located in northern Illinois and western Indiana (data from Betz and Lamp 1989). (B) Distribution of prairie plants among 77 remnant prairies in northeastern Oklahoma, southeastern Kansas, southwestern Missouri, and northwestern Arkansas (data from Eyster-Smith 1984).

and invariant niche-based mechanism suggested by Brown (1984). The dynamics in Hanski's (1982a) model are based on local and regional processes (Hanski 1983) such as competition and dispersal. If a species goes locally extinct it must recolonize from nearby populations. Brown (1984) argued that this assumption was unlikely because regionally rare species have small populations, therefore, they produce few propagules. Thus, Hanski's model predicts that species will change from one distribution category to another over time whereas Brown's model predicts that species will be relatively stable over time. In grasslands, the distribution and abundance of dominant core species are essentially at equilibrium, whereas many other species exhibit considerable year-to-year variation in distribution and abundance (Glenn and Collins 1990). Evidence presented thus far suggests that randomly varying processes in grasslands may in fact be important determinants of the distribution of many species at a regional scale, a phenomenon similar to that described for grassland bird communities (Wiens 1983). Brown's model, on the other hand, predicts few year-to-year changes in abundance at larger spatial scales because geographic constraints imposed by range limitations reduce fluctuations in local patterns of abundance (e.g., Brown and Maurer 1989).

In a sense, the random variation predicted by Hanski

is characteristic of the Gleasonian concept of the individualistic distribution of species among communities (Gleason 1926). In similar habitats, whether or not a species occurs at a site is initially a function of the stochastic process of dispersal. Based on a deterministic model, competitive interactions among species should result in divergent niches (Whittaker 1975). Plants that can survive and reproduce in similar habitats, however, are effectively similar in niche because plants require the same basic resources of light, nutrients, and water (Werner 1979, Hubbell and Foster 1985). Obviously, differences in resource requirements occur among species. Nevertheless, plant communities contain a large number of species with similar niche and habitat requirements (Mahdi et al. 1989).

Grassland plants may have functionally similar niches because they occupy similar habitats, thus differences in success within a community may result from a superior ability to exploit resources (Tilman 1989). However, Aarssen (1983) argued that the competitive ability of plants should increase and become more equal over evolutionary time because of selection to increase the efficiency of resource capture among plants. Similarly, Rabinowitz et al. (1984) demonstrated that rare prairie grasses were equal competitors to common grasses and that poor competitive ability could not explain rarity. Indeed, we found that many species with small average cover values were widely distributed at KPRNA (Collins and Glenn 1990).

Why then does the abundance of many species vary over time within these grasslands? Perhaps because there is a two-tiered competitive hierarchy in tallgrass prairie. Such two-tiered systems have been described in a variety of communities (Grubb 1986). The dominant perennial grasses compete for and occupy the largest amount of space in the community (Collins 1987, Tilman 1989). Highly competitive species with low average cover occur in most communities, as well. The numerous satellite species occupy small areas of soil between the large competitive grasses. The competitive dynamics of the satellite species may result from only a very small, stochastic difference between individuals, such as time of germination, to derive a site and time-specific competitive advantage (e.g., Ross and Harper 1972, Goldberg 1987). Thus, the determinants of competition may occur very early in the life of a plant. If these determinants are affected by stochastic factors, then Hanski's model may effectively describe the abundance patterns of many species in a region.

Our discussion of the similarity in plant niches and competitive ability contradicts the theory of limiting similarity set forth by May and MacArthur (1972). The concept of stochastic variation as a driving function in Hanski's model, however, provides a mechanism by which this contradiction can be resolved. Models incorporating random variation in environment or resource availability over space and time indicate that species with similar niches can coexist (Agren and Fagerstrom 1984, Schmida and Ellner 1984). As Yodzis (1989) noted, long-term field projects will be necessary to address experimentally the factors affecting limiting similarity and species richness in variable environments.

The results from these analyses are relevant to many questions concerning the distribution and abundance of species within and between communities. It does appear that a large component of community structure is determined by stochastic variation in patterns of immigration and extinction. These are generalized mechanisms that can be divided into specific biotic and abiotic interactions. Immigration, for instance, is a function of dispersal mechanisms, precipitation patterns, and availability of safe-sites, among other factors. Extinction incorporates the effects of fire, other types of disturbances, and interspecific interactions. These factors are relatively deterministic in that they depend on the species' ability to compete with its neighbors or withstand periodic disturbance. Rather than taking a bottom-up view of community structure, perhaps it will be necessary to discover pattern in species distribution and abundance, both regionally and within a community, and then work in a top-down fashion to determine underlying mechanisms (Cale et al. 1989). A hierarchical approach to regional patterns and mechanisms will provide the groundwork for further understanding the nature of interactions within and between communities.

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