A Hierarchical Analysis of Species' Abundance Patterns in Grassland Vegetation

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A HIERARCHICAL ANALYSIS OF SPECIES' ABUNDANCE PATTERNS IN GRASSLAND VEGETATION

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Numerous factors affect the number of species in a community, as well as the dynamic relationship between the distribution and abundance of species within and between communities (Whittaker 1965; Shmida and Wilson 1985). Several models that incorporate varying degrees of habitat heterogeneity have been proposed to explain the relationship between local and regional patterns in the distribution and abundance of species (Magurran 1988). Often, these models assume that the abundance of a species at a site is a function of its abundance within the surrounding region (Hanski 1982a; Brown 1984; Ricklefs 1987; Kolasa 1989). These models indicate, in general, that most species are both locally and regionally sparse, and few species occur throughout the region (Levins 1969).

Hanski (1982a), in particular, proposed an alternative dynamic model of species' distributional patterns among similar habitats within a region. Hanski's model incorporated stochastic variation in immigration and extinction rates, where the latter are inversely proportional to distribution, from which he derived the core-satellite hypothesis. This hypothesis states that, within a region, a large number of sparse, or "satellite," species occur at only a few sites, and a distinct mode of dominant, or "core," species occurs throughout the region.

The purposes of our study were to determine, first, if the distribution of plant species in grasslands conforms to the regionally based predictions of the core-satellite hypothesis and, second, whether patterns in the relationships of richness and distribution are similar for data sets ranging from regional spatial scales (>1 km^2) to local assemblages of species (<100 m^2). To do so, we examined the patterns of distribution and abundance on three spatial scales from different grassland study areas.

Recently, Gotelli and Simberloff (1987) attempted to determine whether field data from the Konza Prairie Research Natural Area supported the bimodal core-satellite hypothesis (Hanski 1982a) or the alternative, unimodal model proposed by Levins (1969). Using data from a number of 10-m^2 quadrats in seven different soil types, Gotelli and Simberloff found a positive correlation between the distri-

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bution and abundance of grassland species among soil types. For samples within each soil type, they concluded that their data supported the core-satellite hypothesis. Gotelli and Simberloff were unable to test regional patterns because of the drastically unequal sample sizes (15–119 quadrats) from the different soil types. The core-satellite hypothesis as proposed by Hanski (1982a–c), however, is based on a *regional* distribution of species within similar habitat types. Because Gotelli and Simberloff were analyzing species data from within a soil type based on an unknown sampling distribution, they were actually addressing within-community, not regional, patterns.

The fact that Gotelli and Simberloff (1987) did conclude that their community-level data supported the core-satellite hypothesis, however, is of interest because it implies that the predictions of Hanski's (1982a) model are not unique to regional-level phenomena. If this is true, it does not negate the validity of the core-satellite hypothesis, but it does imply that factors affecting species' distributions and patterns of community structure on a large spatial scale may be the same as, or constrained by, those factors operating on smaller scales, and vice versa. That is, community structure may exhibit self-similarity (Milne 1988), which would provide a common linkage among levels in a hierarchical analysis of community structure (Allen et al. 1984; Pickett et al. 1989).

METHODS

To test the core-satellite hypothesis, Hanski (1982a) stressed that samples must come from areas of similar habitat to allow for the possibility that all species could be present in any sample area. We met this criterion by analyzing vegetational data from prairie communities in Oklahoma and Kansas.

The basic hierarchical data set was derived from vegetational samples on three spatially distinct scales in the Konza Prairie Research Natural Area, a 3487-ha tallgrass prairie in northeastern Kansas. Although this is the same study area used by Gotelli and Simberloff (1987), we did not use the same data set. The spatial scales for our data set included an analysis of regional species' distributions among watersheds, community-level analysis of species' distributions among samples within watersheds, and small-scale analysis of species' distributions among samples in 100-m² blocks within a watershed. In the following, we use *site frequency* (the number of sites occupied) as a measure of distribution in a region; at the community-wide and small-scale levels, we use *frequency* (the proportion of samples in which a species occurs) as a measure of distribution (Hanski 1982a). On all scales, average cover is used as a measure of *abundance* (Gotelli and Simberloff 1987), and *richness* is defined as the number of species in a specific distribution class, ranging from sparse to widespread.

Species cover was estimated three times during the growing season, using 20 10-m² quadrats located along four transect lines in 18 different watersheds in the Konza. The watersheds in our study differ in burning history and soil type (upland, Florence soils and lowland, Tulley soils), which affect species' richness and abundance within a watershed (Gibson and Hulbert 1987; Gibson 1988; Collins and Gibson 1990). Nevertheless, all study sites are characterized as

tallgrass prairie. Burning treatments (number of watersheds) include unburned (3), annually burned (6), burned every other year (2), and burned every 4 yr (7). The number of species per quadrat ranged from 16.1 to 23.5. The total number of species per watershed ranged from 47 to 90, and the total number of species among all watersheds was 144. See Gibson and Hulbert (1987) for a detailed description of study sites and sampling methodology.

To determine if distributional patterns in the real data are similar to those expected if species were randomly distributed, we constructed a null model, which assumes that each species has a probability of occurrence within a region based on average frequencies among watersheds. This null model was constructed as

$$F_a = \sum_{i=1}^{18} f_i \Big/ 18,$$

where F_a is average frequency of species a among watersheds and f_i is the species frequency in watershed i. Species were then randomly assigned to watersheds based on this average frequency, from which we constructed a null richness-distribution histogram. Real and null frequency distributions were compared by a Kolmogorov-Smirnov two-sample test (Siegel 1956).

The second level of analysis addressed community-level relationships within a watershed in the Konza. Here, we plotted the number of species occurring in 1%–10%, 11%–20%, . . . , 91%–100% of the quadrats within a watershed. In this case, species with frequency values greater than 90% are considered core species within a watershed. This is the type of analysis Gotelli and Simberloff (1987) used to address the core-satellite hypothesis; however, it is not a measure of regional distribution. Instead, such an analysis provides an assessment of within-community distributional patterns for each of the 18 watersheds.

Small-scale patterns of distribution and abundance were determined in two square blocks (10 m × 10 m) located at one of the watersheds in Konza Prairie. In each block, vegetation was sampled three times during the growing season by estimating the cover of all species occurring in contiguous 1-m^2 quadrats. As in the community-level analyses, frequency histograms were constructed on the basis of the number of species occurring in 1%–10%, 11%–20%, . . . , 91%–100% of the quadrats. Again, species with frequency values greater than 90% within a block are considered core species. This provides a highly localized measure of species' distribution in grassland vegetation.

An additional assumption of many models relating abundance and distribution is that the average abundance of a species is positively correlated with its distribution (Hanski 1982a; Brown 1984; Ricklefs 1987). To determine if our data conformed to this prediction, correlations between frequency and average cover were calculated for samples at each hierarchical level. Zero values were not included when calculating average cover.

A second data set from two grassland regions in Oklahoma was used to determine if the patterns derived from the Konza data were also evident in other grassland vegetation. Regional and community-level analyses were based on species-cover data from 100 randomly located 0.5-m^2 quadrats within a 0.5-ha area

at each of seven study sites in the Wichita Mountains Wildlife Refuge, a 24,000-ha region of oak forest and mixed-grass prairie in southwestern Oklahoma (Crockett 1964; Dooley and Collins 1984). The sites sampled were all within a radius of 2 km and differed primarily in disturbance history. The disturbance regimes included grasslands that were (1) undisturbed, (2) grazed by ungulates, (3) grazed and marked by buffalo wallows, (4) burned, (5) burned and grazed, (6) burned, grazed, and marked by buffalo wallows, and (7) heavily grazed by a colony of prairie dogs. These disturbances affect richness, dominance, and diversity at each site (Collins and Barber 1985). The average number of species per quadrat ranged from 6.7 in the prairie dog colony to 12.6 at the grazed, burned, wallowed site. The total number of species at each site ranged from 33 to 64, and the total number of species among all sites was 122. (For a more detailed description of the study area and methodology, see Collins and Barber 1985.)

Small-scale patterns of distribution and abundance were determined during 1986 in three blocks (10 m × 10 m) in a tallgrass prairie at the USDA Forage and Livestock Research Station in El Reno, Oklahoma. This area was grazed by cattle during the growing season until May 1986 and was last burned in April 1984. (For a more complete site description, see Glenn and Collins 1990.) The Oklahoma data were analyzed as described for the regional, community, and small-scale levels of analysis of the Konza data sets.

RESULTS AND DISCUSSION

Regional Distributions

Data from both the Konza Prairie and the Wichita Mountains are in accord with the predictions of the core-satellite hypothesis (fig. 1). The frequency histograms clearly show that, at both sites, the majority of species are sparse. There is, however, a second peak of core species at both sites. In Kansas, the core species occur in the highest frequency class (18 of 18 sites), whereas, in the Wichita Mountains, the peak occurs at the second-highest class (6 of 7 sites). Based on the Kolmogorov-Smirnov two-sample tests, both distributions are significantly different ($P < 0.01$) from the null models (figs. 1A,C) constructed from average frequency values; thus, these patterns are not the result of a random distribution of species.

Community-Level Distributions

At the community level, peaks in abundance at the highest frequency classes are less obvious in the Konza data set (fig. 2). The mode is small in the most-abundant frequency class in 13 of 18 communities. If the frequency distribution were to fluctuate randomly between adjacent classes, we would expect an increase in the number of species in the highest frequency class over the preceding class to occur in 9 of 18 cases. The difference between the observed number of sites with a mode in the highest frequency class and random expectation is significant ($P = 0.05$), based on the G statistic. Therefore, there are significantly more modes in the highest frequency class than expected by chance, and random
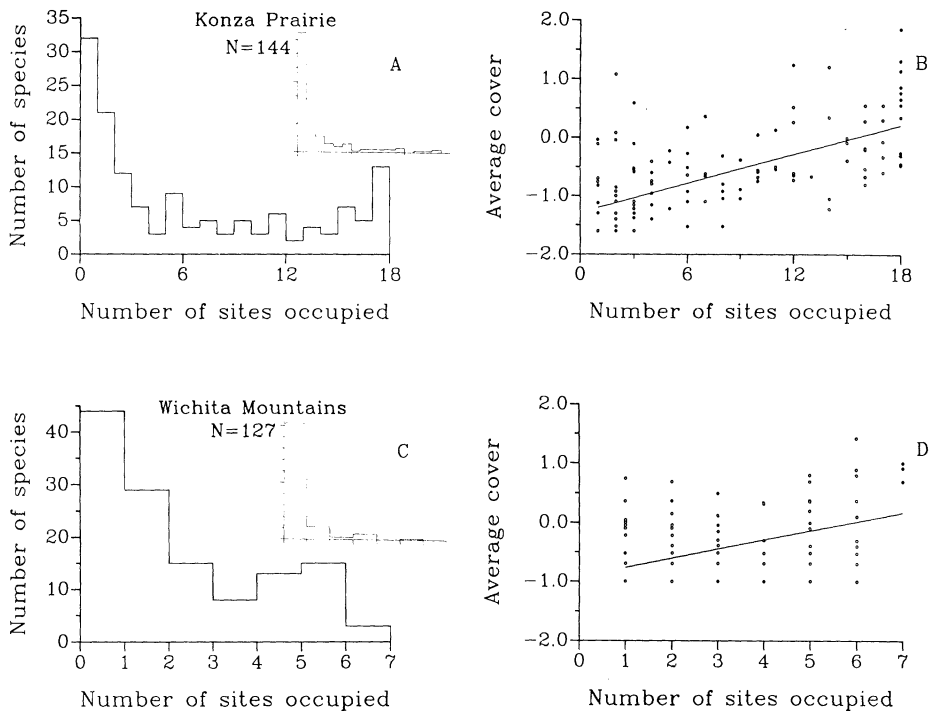
Fig. 1.—The distribution of species abundances for two regions: A, the 18 watersheds in the Konza Prairie Research Natural Area, Kansas; C, the seven study sites in the Wichita Mountains Wildlife Refuge, Oklahoma. N is the total number of species. There is a significant positive relationship between the number of sites a species occupies and the average cover (log-transformed) from that species; B, Konza Prairie (r^2 = 0.66, P < 0.001) and D, the Wichita Mountains (r^2 = 0.50, P < 0.001). Insets, Null distribution of species based on the average frequency of species across all watersheds in Konza and across all in the Wichita Mountains (see the Methods section).

fluctuations cannot explain the number of communities with a mode in this frequency class.

The relationship between distribution and abundance is positive and significant for each of the 18 communities (r^2's averaged 0.44; range, 0.22–0.56). Thus, at the level of communities, species with large cover values tend to be widespread. This relationship is similar to that at the regional level (fig. 1). Therefore, general distributional patterns within communities also conform to the patterns of the core-satellite model. The individual core species within a watershed, however, tend to differ among watersheds, which is in agreement with the immigration and extinction dynamics of the core-satellite model. For example, 21 species were classified as core species in the community-level analyses for the Konza. Only 11 of these were also core species in the regional analysis, whereas 2 regional core species were not widely distributed at the community level. Only big bluestem, *Andropogon gerardii*, was a core species at all sites, whereas 9 of 21 species were core species in only one or two communities. The differences in core species
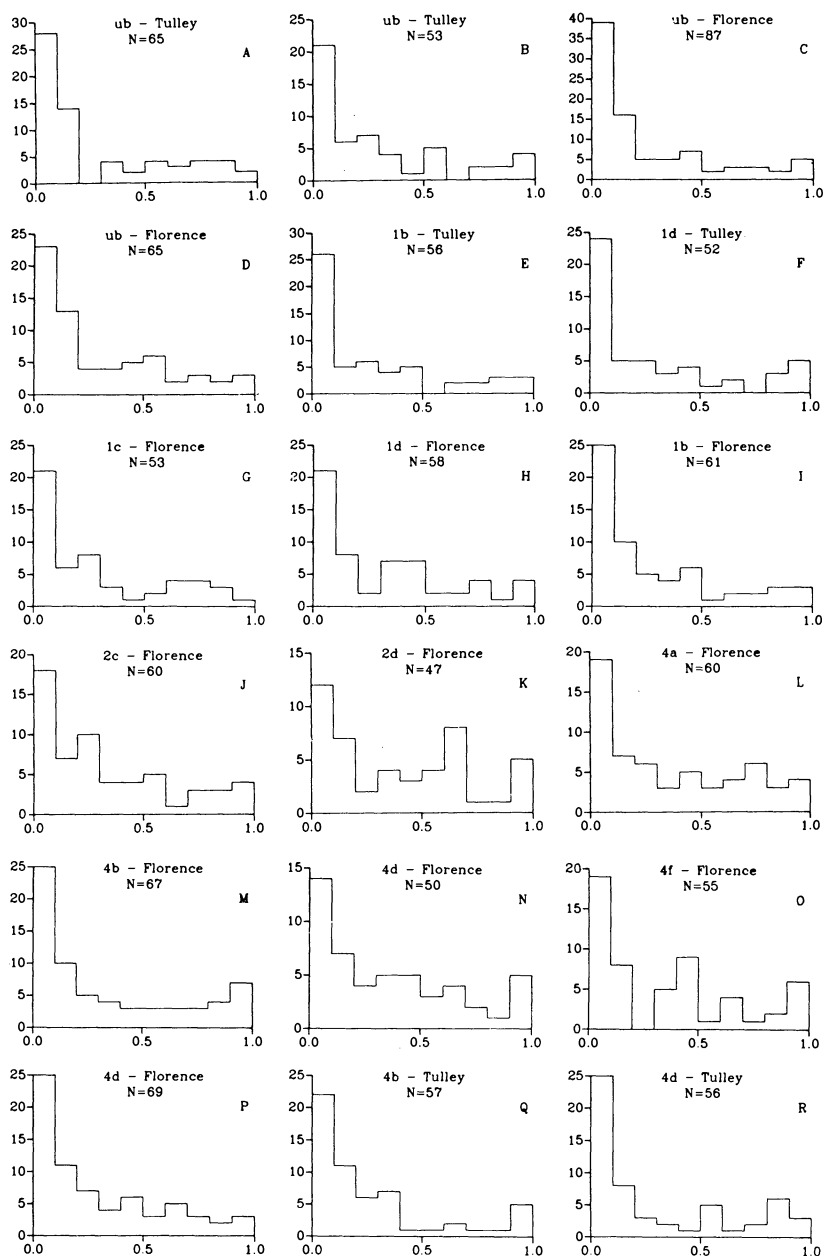
FIG. 2.—Richness-distribution histograms for species within tallgrass-prairie communities in the Konza Prairie, Kansas. In each histogram, the abscissa represents the proportion of 20 quadrats in which a species occurs. Each community is subjected to a different fire frequency: *A–D*, never (unburned, ub); *E–I*, annually; *J, K*, every 2 yr; *L–R*, every 4 yr. In each panel, the letters a, b, c, d, and f refer to watershed replicates; Tulley and Florence are soil types; and *N* is the number of species in each watershed.

among watersheds are in accord with the dynamic view of the core-satellite hypothesis, which predicts that dominance patterns in a community change over time and space.

The richness-frequency histograms for the Wichita Mountains data provide a less obvious pattern of bimodality. Four of the seven sites (figs. 3C,D,E,G) show bimodality, but only two sites have a mode at the highest frequency class (figs. 3C,E), which is significantly less than expected on the basis of random fluctuation between adjacent classes (G statistic, $P < 0.05$). As in the Konza, the relationship between distribution and abundance is significant and positive at all seven sites for the Wichita Mountains data set (r^2's averaged 0.77; range, 0.67–0.85). Nine species were classified as core species at the community level in the Wichita Mountains. Three of the nine were also regional core species. Thus, six species were locally, but not regionally, abundant. The most common core species was the weedy perennial *Ambrosia psilostachya*. In both the Konza and the Wichita Mountains, the high degree of variability among core species at the community level probably reflects the impacts of the different disturbance regimes (burning in the Konza; burning, grazing, and wallowing in the Wichita Mountains) in each study area, as well as variation in edaphic and microenvironmental conditions.

Small-Scale Analyses

The frequency histograms from the five different 10-m × 10-m blocks all depict a mode of core species (fig. 4). For the June samples in each block, the correlations between distribution and abundance are positive and significant (r^2's averaged 0.64; range, 0.52–0.73). Thus, the small-scale patterns are similar to the regional analyses and conform to the patterns predicted by the core-satellite hypothesis. In the Konza, the core species in the two blocks were also core species on the larger scales. *Andropogon gerardii*, *Schizachyrium scoparium*, and *Poa pratensis* were core species in both blocks, with the addition of *Ambrosia psilostachya* as a core species in block 2. At El Reno, *A. gerardii*, *S. scoparium*, *A. psilostachya*, *Dicanthelium scribnerianum*, and *Conyza canadensis* were the core species in each block. Thus, little variation occurred among the core components on the smallest scale of analysis. Samples taken the following year at El Reno, however, indicate that *C. canadensis* was no longer a core species, which again provides evidence in favor of the dynamic nature of the core-satellite hypothesis.

GENERAL DISCUSSION

Patterns of Distribution

The analyses of species' distribution and abundance at the regional, community-wide, and local assemblage levels all generally conform to the predictions from the core-satellite hypothesis (Hanski 1982a). Species' patterns were distinctly bimodal on the largest and smallest scales, and at least for grasslands in the Konza, the number of species in the 91%–100% frequency class increased, compared with the 81%–90% class in the majority of community-level analyses. The lack of distinct bimodality at the community level is a function of several factors,
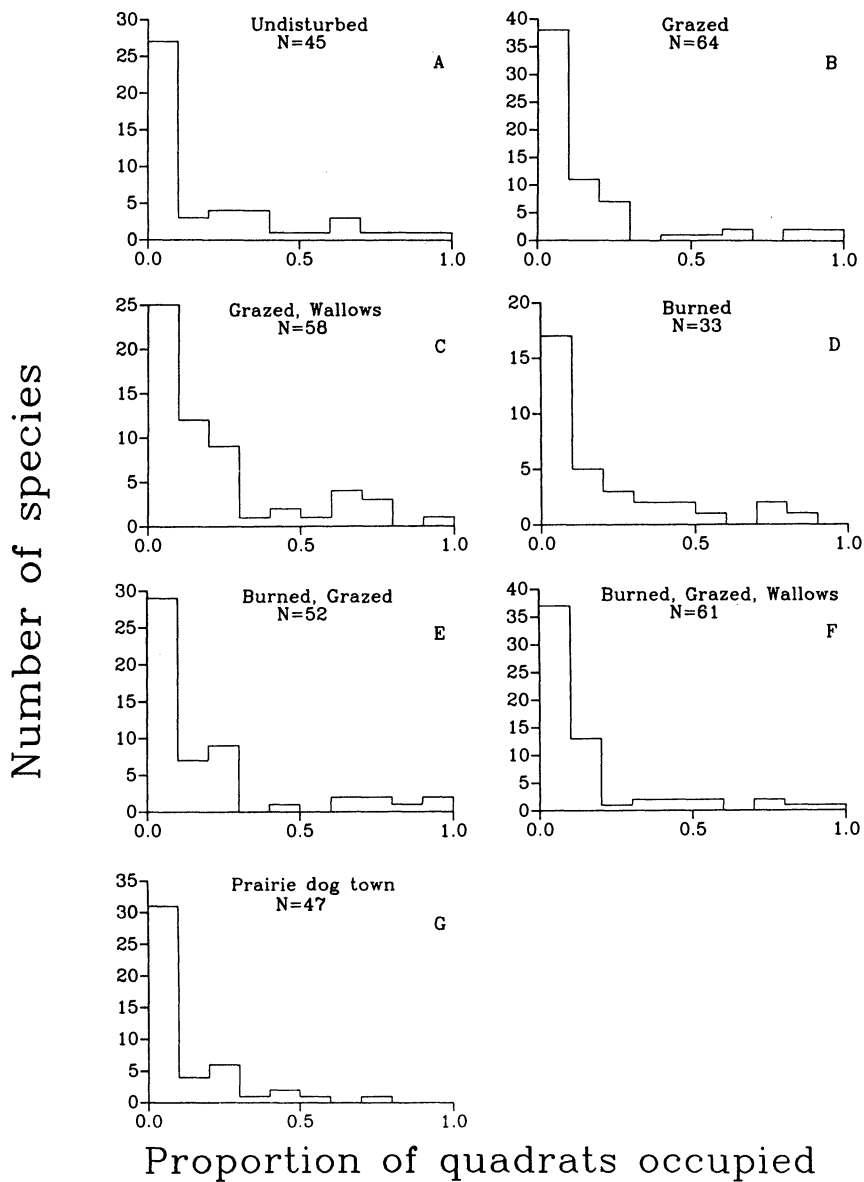
FIG. 3.—Richness-distribution histograms for species within mixed-grass prairie communities in the Wichita Mountains Wildlife Refuge, Oklahoma. In each histogram, the abscissa represents the proportion of 100 quadrats in which a species occurs. Each community was subjected to a different disturbance regime (see the Methods section). N is the number of species at each site.
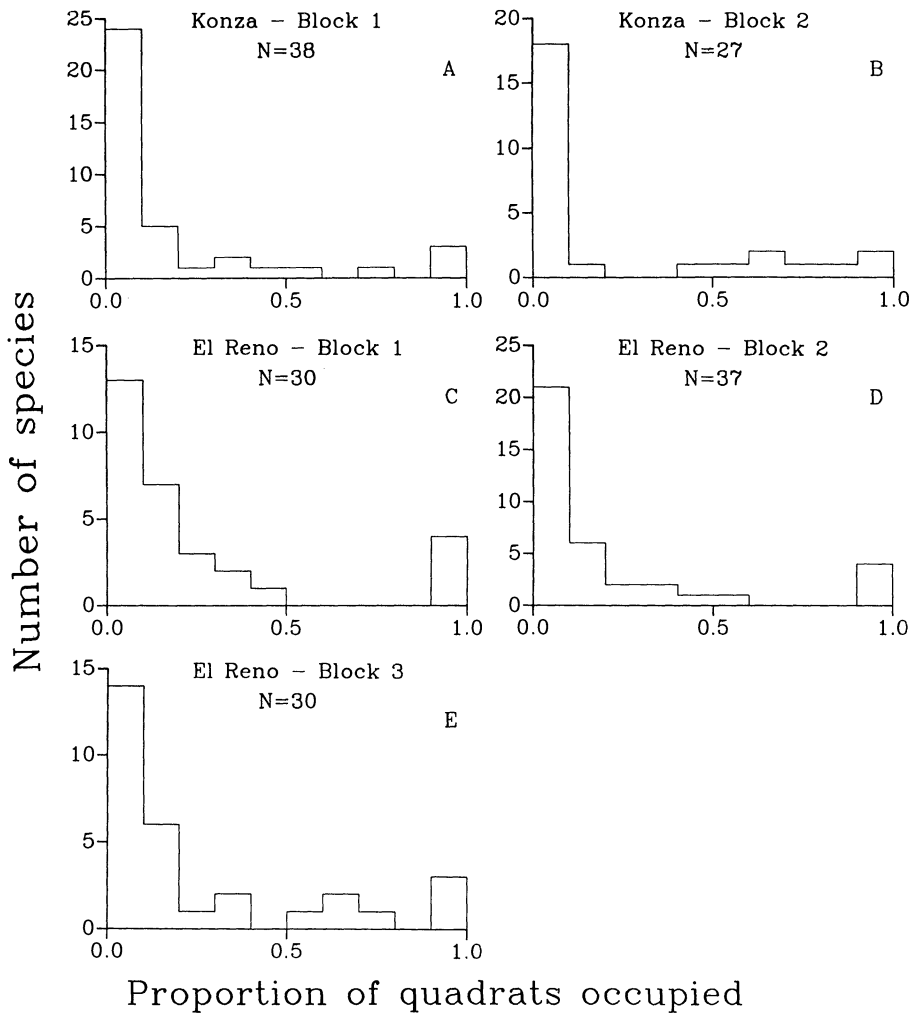
FIG. 4.—Small-scale richness-distribution relationships within a local assemblage of species in tallgrass prairie: A, B, Konza Prairie, Kansas; C, D, E, El Reno, Oklahoma. In each histogram, the abscissa represents the proportion of 100 quadrats in which a species occurred within a square block 10 m × 10 m. N is the number of species within each block.

including, perhaps, differences in site quality and disturbance regimes among these grasslands, which alter species' relative dominance and distributions.

The abundance and sparseness of species are due to many factors (Rabinowitz 1981), including dispersal, competition, stress, and disturbance (Grime 1979). In communities dominated by large sessile species that compete for space, such as the intertidal zone (Sousa 1985) or tallgrass prairies (Collins 1987), dominance increases and richness decreases in the absence of disturbance. In grasslands, this pattern is especially altered by disturbance, however, because the dominant species appear often to be most sensitive to disturbance.

In grasslands, the two most common types of large-scale disturbance are grazing and fire (Anderson 1982; Collins and Glenn 1988; Milchunas et al. 1988). The disturbance regime in the Wichita Mountains is more complex than that in the Konza Prairie (Collins and Barber 1985; Collins and Gibson 1990). In the Wichita Mountains, high rates of disturbances, including fire, grazing, trampling, and wallowing, interact to reduce dominance and increase spatial heterogeneity (Collins and Barber 1985). This results in high species' richness but low dominance and few core species. The only large-scale disturbance in the Konza is fire. Fire enhances dominance of the large clonal grasses (Hulbert 1988; Seastedt and Ramundo 1990), but periodic fires may also increase richness, especially of satellite species (Collins 1987; Gibson 1988; Collins and Gibson 1990). In the absence of fire, clonal species remain dominant, but a deep litter layer reduces richness (Knapp and Seastedt 1986). Therefore, disturbances such as fire and grazing alter the extinction rates of species in a community. Because of differences in disturbance regime, extinction rates of species in the grasslands of the Wichita Mountains are higher than those in the Konza Prairie. This then shifts the peak of widely distributed species for the Wichita Mountains to the left, into a lower frequency class than in the Konza (figs. 1A,C), as predicted by Hanski's (1982a) model.

Hanski's (1982a) core-satellite model is essentially a spatial extension of community-level models to the regional scale, with the restriction that sites sampled within that region have comparable environmental conditions. One common link among many of the recent models of species' abundance patterns within communities is the positive relationship between distribution and abundance (Sugihara 1980; Brown 1984; Ricklefs 1987; Kolasa and Strayer 1988). That is, these models are based on niche relationships, predicting that species with broad niches will often be more abundant within a community than are species with narrow, specialized niches. This assumption appears valid for tallgrass-prairie vegetation. The tallgrass-prairie region of North America, which extends from Canada to Texas, is dominated by a small number of species with broad niches, such as *Andropogon gerardii*, *Schizachyrium scoparium*, and *Sorghastrum nutans* (Bazzaz and Parrish 1982). Differences in community composition along this north-south gradient are basically due to restricted distributions of numerous subordinate taxa and a shift in dominance among the common tallgrass species (Diamond and Smeins 1988). Thus, on a geographical scale, the dominant species have broader niches than the subordinate species. Within our study area, we detect patterns of species' distribution-abundance relationships that reflect these geographical patterns and concur with predictions of the core-satellite hypothesis.

The bimodal pattern in site frequency has often been reported and criticized (Raunkiaer 1934; Williams 1950; McIntosh 1962; Noy-Meir and van der Maarel 1987). Raunkiaer's law of frequencies, for example, predicts a bimodal distribution similar to that of the core-satellite hypothesis. However, Williams (1950) demonstrated that the bimodal form of Raunkiaer's (1934) law of frequencies could be a function of inefficient sampling. This criticism concerning sampling efficiency does not apply to our data sets. Study sites in the Konza and the Wichita

Mountains were intensively sampled, and the 10-m × 10-m blocks in Oklahoma and Kansas represent a complete sample of plant species.

Frequency, as a measure of distribution, is more influenced by arbitrary sampling decisions than most other measures of vegetation. For example, unlike frequency, density does not depend on quadrat size, is not truncated at some upper value (i.e., 100% frequency), and can express sparseness as a large number of values rather than as one value, as does the lowest frequency class. Allen (pers. comm.) suggested that bimodality may be a function of this characteristic of frequency, in that the index is saturated at the extremes. That is, a species cannot be more frequent than 100% or less frequent than 0%. This is somewhat analogous to the curvilinearity problems in ordinations induced by the limitations of measures of dissimilarity (Allen 1987; Wartenberg et al. 1987). Thus, the mode of core species in our analyses may be an artifact of frequency. As noted by Williams (1950), a species' frequency will change when the size or number of samples is changed. Again, we feel that this argument would be most relevant to our community-level analysis because it is at this level that inefficient sampling yields only core species. However, it is at this level that bimodality was least obvious. At the regional level, our analysis is based on presence or absence, not frequency. On the local scale, our resolution is limited by quadrat size. Increasing sample size by merging quadrats would enhance the core component; however, at our smallest scale of resolution, 1 m^2, bimodality is still apparent. Thus, although frequency may provide a biased measure of distribution, we do not believe that this problem can account for the hierarchical patterns of species' distribution evident in our data set.

Patterns of Abundance

At both sites, a positive relationship exists between abundance and the distribution of species among sites (figs. 1B,D), indicating that, in general, core species have higher importance values than satellite species within a region. The high degree of scatter in figures 1B and 1D results, in part, from using cover as a measure of abundance. Unfortunately, this problem is unavoidable with nondestructive sampling of vegetation in permanent plots in grasslands. The weak relationship occurs because of enormous differences in maximum size among species. Some grassland species are both widely distributed and large (e.g., *Andropogon gerardii*), whereas others are widely distributed and small (e.g., *Oxalis stricta*). Nevertheless, for the regional analysis, frequency histograms and the correlation of distribution and abundance are in accord with the core-satellite hypothesis.

The weak positive relationship between distribution and abundance conforms to empirical observations of both Hanski (1982a) and Brown (1984). Mitchley and Grubb (1986) and Mitchley (1988) provided experimental evidence supporting the notion that abundant species are widely distributed. They determined that larger species are better competitors in herbaceous communities under light grazing pressure and that these superior competitors are widespread in chalk grassland. They concluded, however, that this pattern would be altered at more-intensive levels of grazing, in which dominance and frequency are reduced and richness is increased.

Rabinowitz (1981) identified eight categories of abundance, seven of which are forms of sparseness. Based on our hierarchical analysis of the Konza data, we can identify species representing several forms of sparseness. Four of the eight categories can be eliminated because they involve distribution across a wide range of habitats, a factor that we have necessarily excluded in order to address the core-satellite hypothesis. The four categories left concern geographical distribution and local abundance within a habitat type. One form is represented by species that are widespread and dominant in a given habitat. The common prairie grass *Andropogon gerardii*, a core species on all spatial scales, fits this category. A second form of sparseness occurs when species are widely distributed at the regional level but not at the local level. Two species, *Artemisia viridis* and *Physalis pumila*, fit this category. A third group (*Salvia pitcherii*, *Carex heliophylla*, and *Panicum virgatum*) is composed of species that were common within one or a few watersheds but not common regionally. Those species that are locally abundant but regionally sparse, as well as those that are regionally widespread but locally sparse, also contribute to the scatter around the regressions in figures 1*B* and 1*D*. Finally, many of the species in our analyses were both locally and regionally sparse.

Rabinowitz et al. (1984) indicated that sparseness is not necessarily a function of poor competitive ability in grassland species. They argued that several factors, including herbivory, dispersal ability, and pathogens, interact to produce variation in the patterns of distribution and abundance of grassland species. We speculate that the dispersal ability of species, disturbance regimes, and competitive environments in grasslands have been dramatically altered by the elimination of large migratory ungulates, particularly bison (Collins and Uno 1985; Collins and Glenn 1988). Changes in these variously scaled factors would greatly influence present patterns of local and regional distribution and abundance.

Self-Similarity

As disturbances become less common, community structure becomes a function of interactions among individual plants. Thus, on the smallest spatial scale, patterns of distribution and abundance are a function of local interactions such as competition and dispersal. Competition is primarily a neighborhood phenomenon (Werner 1979); thus, as a mechanism of extinction (in the sense of Hanski 1982*a*), it operates on a small spatial scale. Dispersal, on the other hand, acts on both small and large scales (Howe and Smallwood 1982). That is, most dispersing seeds fall near the parent plant, creating a small-scale pattern (Rice et al. 1960; Rabinowitz and Rapp 1981), but seeds occasionally travel farther, providing a mechanism for colonizing similar habitats in different areas (in the sense of Hanski 1982*a*). Therefore, the combined effects of neighborhood processes on the scale of a local assemblage are transposed to pattern and process on larger spatial scales, and vice versa. That is, the patterns of community structure in grasslands are essentially fractal (West and Goldberger 1987; Milne 1988; Palmer 1988) because the structure of grassland vegetation exhibits self-similarity. By fractal, we mean that the larger unit is composed of numerous smaller units similar in structure to the larger unit. As a result, pattern and process on the scale of the local assem-

blage may impose constraints on structure at the community and regional levels, and regional-level factors may also constrain smaller-scale pattern and processes.

Because the data from Konza represent a truly nested spatial hierarchy, it is possible to measure whether or not self-similarity occurs in patterns of species' abundance. Correlations between the average cover of species in small blocks and the average cover of species at the regional level, using only species common to both levels, were used as a rough measure of self-similarity. For both blocks in the Konza, the correlation between average cover on these two spatial scales is significantly positive (block 1, $r^2 = 0.50$; block 2, $r^2 = 0.48$; $P < 0.05$). This indicates that abundance relationships at the smallest scale are similar in pattern to those at the regional level. Thus, the bimodal patterns in species' distribution and their correlation with species' average cover provide empirical evidence in support of the notion of self-similarity in grassland community structure.

The similar results from the analyses of regions, communities, and local assemblages of species in the Konza and the Wichita Mountains, despite different vegetational composition, history, and sampling protocols, implies that the observed patterns truly reflect the nature of community structure in grasslands. The fractal nature of these grasslands implies that the mechanisms associated with the core-satellite hypothesis at the regional level are an extension of interactions taking place at the level of local assemblages of species. This does not negate the validity of the core-satellite hypothesis. In fact, it appears that this simple dynamic model can explain patterns of community structure on several spatial scales. It also suggests, however, that small-scale studies of patch dynamics and community structure, at least in grasslands, may identify constraints on the patterns of structure and dynamics on larger spatial scales. In turn, studies of large-scale phenomena, such as geomorphological factors and disturbance regimes, may address constraints imposed on small-scale pattern and processes.

SUMMARY

The core-satellite hypothesis was proposed to explain regional patterns of species distribution. At the regional level, grassland data from sites in Oklahoma and Kansas conform to the general predictions of the core-satellite hypothesis. The patterns found on the scale of a local assemblage of species (m^2), however, were similar to those of the regional-level distributions (km^2). Factors affecting these distributions are competition and dispersal, which operate most commonly on small spatial scales, as well as disturbance, which is often a large-scale phenomenon in grasslands. Thus, grassland community structure exhibits self-similarity, in that the large-scale pattern is composed of numerous small-scale units of similar structure. We therefore conclude that grassland communities essentially exhibit small-scale patterns that are transposable to larger-scale patterns and vice versa. However, the patterns of distribution and abundance are dramatically affected by disturbance, and changes in these patterns are most obvious on an intermediate (community-level) scale of analysis.

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