THE DISTRIBUTION AND ABUNDANCE OF TALLGRASS PRAIRIE PLANTS: A TEST OF THE CORE-SATELLITE HYPOTHESIS

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The relationship between abundance and geographical distribution is central to modern population ecology (Andrewartha and Birch 1954; Krebs 1985). *Distribution* here refers to the number of population sites occupied by a species, whereas *abundance* is a measure of plant or animal numbers within a site (Hanski 1982*a*). Hanski (1982*a*) pointed out that distribution and abundance are often studied separately, the former by biogeographers and the latter by ecologists. The separation is artificial, however, because small, local populations are often found at the periphery of a species' range (Andrewartha and Birch 1954; Hengeveld and Haeck 1982); in other words, local abundances set the limits of distribution (Hengeveld and Haeck 1981, 1982).

We recognize two kinds of models that relate distribution and abundance: static and dynamic. In a static model, the distribution and abundance of a species do not vary through time, barring major climatic or habitat changes (Rapoport 1982). Whittaker (1967) proposed that environmental gradients cause abundance to decline near the edge of a species' range. Brown (1984) recently expanded Whittaker's concept to two spatial dimensions as an explanation for peak abundances near the center of a species' geographic range. Both hypotheses are consistent with Grinnell's idea of the niche as "the range of values of environmental factors that are necessary and sufficient to allow a species to carry out its life history" (James et al. 1984). The decline in abundance near the edge of the range may be caused by a variety of factors, both physical and biological (Andrewartha and Birch 1954; Terborgh 1973).

Other static models do not predict a gradual decline in abundance toward the periphery of the range, and many mechanisms can lead to abrupt distributional limits. For example, MacArthur (1972) discussed how behavioral interactions can cause abundances of two species to decline sharply at a zone of contact. Terborgh (1971) presented a model incorporating both environmental gradients and competitive effects to explain the vertical distribution of bird species on an elevational

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gradient in the eastern Andes of Peru. Climatic changes and historical effects may also be responsible for range discontinuities of Andean birds (Graves 1985).

In contrast to these static models, dynamic models of distribution and abundance posit that both a species' geographic range and its local abundance vary through time. For example, species may pass through a taxon cycle (Wilson 1959; Ricklefs and Cox 1972), in which a widespread species differentiates, its range fragments, and it is finally reduced to a few isolated populations that are driven to extinction by interspecific competition. In contrast to the taxon cycle, Willis' (1922) "age and area" model proposes that endemic distributions are caused by a failure to disperse, usually because of insufficient time, and are not relictual ranges of previously widespread species. Rapoport (1982) discussed several related models of species' range expansion and contraction, but only the taxon model is explicit about concurrent changes in local abundance.

Levins (1969) derived a mathematical model of regional distribution that is dynamic. It considers changes in p, the fraction of habitable sites occupied by a species ($0 \leq p \leq 1$):

$$dp/dt = ip(1 - p) - ep.$$ (1)

Here the first term, $ip(1 - p)$, is the rate at which empty sites are colonized, and the second term, ep, is the rate of local extinctions (Levins 1969). Levins (1970) allowed e to vary stochastically and found that the new model predicts a single internal equilibrium value for p. Thus, a frequency histogram of the number of sites occupied by one species at different times should be unimodal. Hanski (1982a) pointed out, following Kimura (1964), that an equally valid interpretation of the result of the stochastic model is that a frequency histogram for different species at one time should also be unimodal for a community of "similar" species.

Levins (1969, 1970) emphasized that regional extinction ($p = 0$) occurs when e exceeds i. He did not explicitly consider the relationship of the probability of local extinction (e) and regional occurrence (p). For three data sets, Hanski (1982a) showed that the more sites a species occupied, the lower its probability of becoming extinct at any one site. Thus, there is a negative relationship between distribution and the probability of local extinction. On this assumption, Hanski's model is

$$dp/dt = ip(1 - p) - e'p(1 - p).$$ (2)

In this case, however, the stochastic version does not predict a single internal equilibrium point. The distribution is either bimodal or else all sites are occupied, depending on the relationship between $i - e'$ and the variance of $i - e'$ (Hanski 1982a). If the extinction probability varies stochastically, a species should tend toward omnipresence ($p = 1$) or regional extinction ($p = 0$). Again, the result can also be interpreted for a community of similar species at one time as predicting a bimodal distribution: many species present in few sites, many species present in many sites, and few species with an intermediate distribution (Hanski 1982a,b). Even though the species have different immigration and extinction parameters, no species is likely to stay for a long time with intermediate values of p (Hanski 1982b). Numerical analyses (Hanski 1982b) show that the prediction of bimodality

for the stochastic version of model (2) versus unimodality for the stochastic version of model (1) holds despite mathematical errors in Levins' initial treatment (Boorman and Levitt 1973).

Hanski's model thus predicts a dichotomy within a group of similar species, between a set of abundant, widely distributed core species and a set of rare, patchily distributed satellite species. The existence of this dichotomy is the *core-satellite hypothesis*.

The core-satellite hypothesis could be correct even if Hanski's model (eq. 2) were not. That is, one might conceive of reasons other than stochastic immigration-extinction dynamics why a group of similar species should be dichotomously distributed over a group of similar sites. In our Discussion, we explicitly consider some alternative explanations for bimodality.

Equation (2) embodies the negative correlation between the probability of local extinction and the number of sites occupied. The underlying assumption of the equilibrium theory of island biogeography (MacArthur and Wilson 1967) extended to more recent treatments of extinction (Diamond 1984) is that population extinction probabilities decrease with increasing population size. If this assumption is correct, then there should be a positive relationship between distribution and abundance: the more sites a species occupies, the greater the average abundance at those sites (Bock and Ricklefs 1983).

Thus, if Hanski's model is correct and if, in addition, extinction probability increases with decreasing population size, distribution and abundance should be positively correlated. Hanski (1982a) found such a correlation for examples from four invertebrate taxa. Levins' model predicts no such relationship between distribution and abundance. Figure 1c suggests a pattern that one might look for to test the core-satellite hypothesis against the hypothesis of unimodality that Levins' model suggests (fig. 1a). Figure 1d depicts the relationship between distribution and abundance predicted by Hanski's model, and figure 1b shows the alternative predicted by Levins' model.

Of course, there are alternatives to the core-satellite hypothesis other than unimodality and there are models other than Hanski's that predict a bimodality of species at sites. Similarly, the relationships between abundance and distribution depicted in figures 1b and 1d are not exhaustive (for other treatments, see Armstrong 1976; Levin 1978; Yodzis 1978; DeAngelis et al. 1979). Our main goal in this paper is modest: to bring some data to bear on the core-satellite hypothesis and one model leading to it. The data could falsify the hypothesis, the model, or both, but, whether they do or not, they would not indicate a unique interpretation of the relationship between distribution and abundance.

MATERIALS AND METHODS

In this paper we compare the patterns in figure 1 with an extensive data set on plant distributions in a tallgrass prairie in Kansas. The data, generously provided by the late L. C. Hulbert, are visual estimates of the percent canopy cover of 170 species of plants in 433 circular quadrats of 10 m^2 each. The censuses were taken in 1978 and 1979 in the Konza Prairie Research Natural Area, 3487 ha of protected
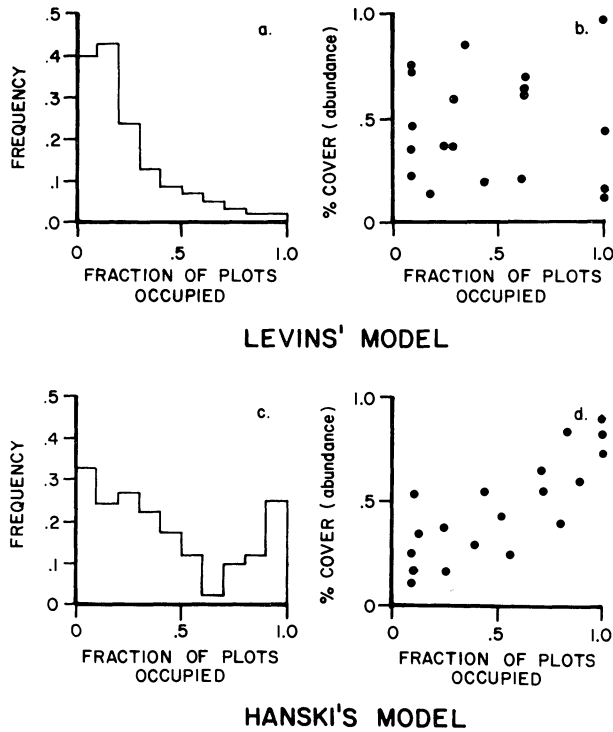
FIG. 1.—Predicted patterns of distribution and abundance from the models of Levins (1970) and Hanski (1982). Predictions of Levins' model: *a*, a unimodal distribution of species at sites; *b*, no relationship between distribution and abundance. Predictions of Hanski's model: *c*, a bimodal distribution; *d*, a positive correlation between distribution and abundance.

tallgrass prairie in the Flint Hills, Riley and Geary counties. Table 1 gives the abundance classes; we used the midpoint of each abundance class to calculate the average percent cover for each species. The 433 quadrats were located on seven different soil series (table 2). The sites had been unburned since 1977 and ungrazed by large herbivores since 1971. The numbers of individual plants (genets) per quadrat is unknown, but must have been quite large. The mean number of stems per 10 m^2 for similar quadrats taken from the same prairie was ca. 20,000 (Dokken and Hulbert 1978), and the mean number of species per quadrat for these 433 quadrats was 27.65, with a minimum of 13. All this is to say that the quadrats are not so small that a statistical pattern would be likely to arise as an artifact, as might have been the case if, for example, many quadrats had only 1–10 individuals. However, some obvious limitations of this data set are the problems (discussed below) in establishing whether sites are sufficiently similar.

First, suppose the histories of the quadrats had been identical. Are quadrats of the same soil series similar enough that one would expect to find the predicted patterns within soil series if the core-satellite hypothesis were true? The sort of autecological research that would answer this question has not been done on these

TABLE 1

ABUNDANCE CLASSES USED IN QUADRAT CENSUSES
OF PRAIRIE PLANT COMMUNITIES

Class Number	Midpoint	Class Range
0	.00	.00
1	.005	.00–.01
2	.030	.01–.05
3	.150	.05–.25
4	.375	.25–.50
5	.625	.50–.75
6	.850	.75–.95
7	.975	.95–1.00

NOTE.—Values are expressed as fraction of total canopy
cover (0 to 1). The midpoint of each class was used to calcu-
late average percent cover.

TABLE 2

SOIL SERIES AND DESCRIPTIONS OF KONZA PRAIRIE

Soil Series	Slope	Habitat	Surface Layer	Depth	Drainage	No. of 10-m^2 Quadrats Surveyed
Florence	level	uplands	very dark cherty silt or silt-clay loam	25 cm	good	119
Benfield	level	uplands	dark gray silt-clay loam	15 cm	good	45
Clime-Sogn	5%–20%	uplands	light silt-clay loam	23 cm	excessive	45
Dwight	level	uplands	dark gray silt loam	10 cm	moderate	75
Irwin	4%–8%	upland ridgetops	dark gray, grayish-brown silt-clay loam	28 cm	good	15
Tully	4%–8%	foot slopes	very dark gray silt-clay loam	25 cm	good	119
Reading	0.1%	stream ter-races, foot slopes	dark grayish-brown silt loam	28 cm	good	15

species. Certainly, there is more to habitat for these plants than just soil character-
istics. Nevertheless, soil characteristics can play a predominant role in determin-
ing microgeographic distributions of at least some plants (Daubenmire 1959;
Chikishev 1965; van den Bergh 1969). Hulbert (pers. comm.) contended that ex-
perienced prairie ecologists can correctly identify at least the soil series of a plot
from only a list of associated species. This sort of identification can often be made
on the basis of particular indicator species (Chikishev 1965); thus, we cannot
claim that all 170 species have highly specific associations with particular soils,
only that soil must be a key determinant of distribution for many species.

These soil series differ in a variety of factors, including drainage, erosion, depth, topography, slope, and clay content. Any or all of these factors are likely to influence the distribution and abundance of any particular species (Daubenmire 1959). Although the Konza soils are derived from various admixtures of shale and limestone, Hulbert (pers. comm.) suggested that it is reasonable to view them as a catena, a sequence of soils with similar geological and climatic histories that differ in relief and drainage. If the soil series were ordered along gradients of relief or drainage, perhaps meaningful correlations would emerge with the distribution and abundance of particular species (Whittaker 1967). Our goal, however, is not to elucidate causal mechanisms on a case-by-case basis. Rather, we are interested in community patterns, especially patterns in the entire data set compared with those for each soil series.

A second limitation of the data set is that these sites have different grazing and burning histories, some of which are unknown, and effects of these treatments can be persistent (Hulbert 1969; Platt 1975; Hover and Bragg 1981). Finally, there is likely to be variation in microhabitat within a single soil series. Such variation may obscure emergent community patterns. Without empirical data on the micro-habitats, physical and chemical composition, and past history of each quadrat, these issues are difficult to address. Nevertheless, from the perspective of the resident species, we can at least say that the soil series do represent quite distinct environments. A separate χ^2 analysis showed that 76% of the species display significant positive or negative associations with one or more soil series (Simberloff and Gotelli 1983). This finding supports our contention that differences within soil series are, on the average, much less than those between soil series.

In spite of a generous sample size, we also face a statistical problem: bimodality is often in the eye of the beholder. Hanski's plots (1982b) are unequivocal, but ours are not. The only published test for bimodality we are aware of is by Giacomelli et al. (1971). This test is inappropriate for our purposes because the alternative hypothesis is a uniform distribution. We concocted a pair of statistics for measuring degree of bimodality when modes are expected to be at the ends of the range of the independent variable (in this case, fraction of quadrats occupied). These statistics are LT, the fraction of the distribution in the left-hand tail, and RT, the fraction in the right-hand tail. That is, for LT, we first determined how many consecutive bars were in the frequency histogram, beginning on the left, such that the height of each bar was less than or equal to the height of the preceding bar. For RT, we made the analogous calculation beginning on the right.

The left and right tails were compared to an appropriate null distribution, which we produced by randomizing the 433 quadrats, then assigning to each of seven imaginary soil series a number of quadrats corresponding exactly to the number of quadrats for a real soil series. In other words, we assigned each quadrat to an imaginary soil series independent of its real soil series. Our reasoning was that if soil series were really a sufficiently important aspect of the habitat for many plant species, and if the core-satellite hypothesis were correct, the frequency histogram for each soil series should yield extreme values of the bimodality statistic relative to the randomized data sets.
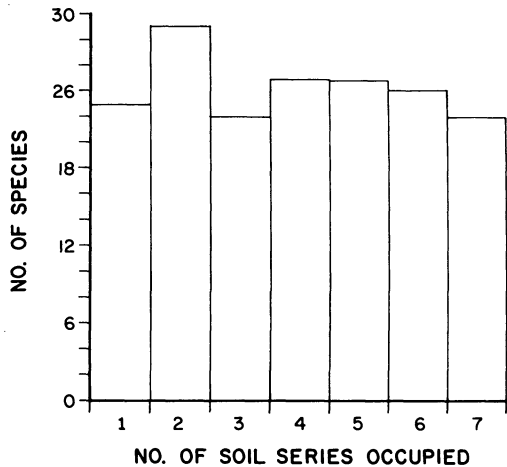
FIG. 2.—The distribution of species across the seven soil series. A species is considered present on a soil series if it occurred in at least one quadrat.

RESULTS

We begin by disregarding soil series and considering the frequency of occurrence of all species on the 433 quadrats. Lumping the soil-series data would be inappropriate if each series contained a unique set of species, since this would mean that, for each species, not all sites are habitable, as required by the models. Figure 2 shows that this is not the case. Most species occur on at least four different soil series, and 27% occur on six or seven soils. Even if every species could occupy all the series, we would not expect to detect them all because of sampling variation. In particular, since the Irwin and Reading series are represented by only 15 quadrats each, at least some species that regularly occur in these series were probably missed. In spite of significant associations with certain soil series, most species appear capable of inhabiting most soils. Tentatively, then, we can disregard soil series and examine the distributions for the entire prairie plant assemblage.

Figure 3 gives the distribution of p, the fraction of (habitable) sites occupied by each species. We see little evidence of bimodality here. Most species occur on fewer than 10% of the plots; very few occur on more than 90% of them. There is a small increase in the last two histogram intervals, but this is trivial compared with the rest of the histogram. This distribution seems indistinguishable from a log series (Fisher et al. 1943), in which each successive interval contains fewer species than the one before it. After Williams (1964, table 146), we fit a log-series distribution to the data in figure 3 and found good agreement between observed and expected frequencies ($\chi^2 = 7.90$, df = 6, $P > 0.20$; successive intervals with small expectations (<5.0) were pooled).

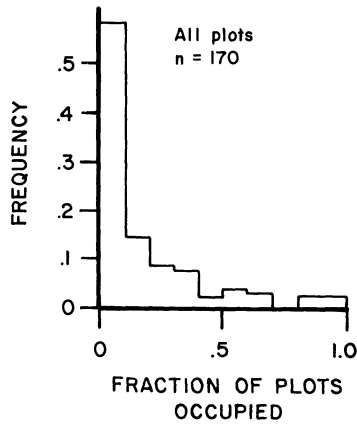This unimodal plot is consistent with the prediction of Levins' model. How-

FIG. 3.—The distribution of 170 species of prairie plants on 433 quadrats in the Konza Prairie. Compare with figures 1a and 1c.
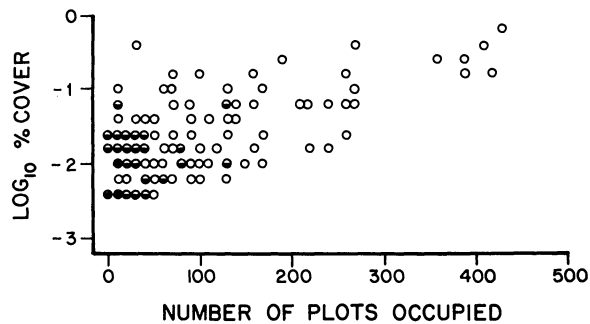

FIG. 4.—A plot of the average proportion of cover (abundance) versus the number of quadrats occupied by each species. *Open circles*, single points; *half circles*, 2 to 9 points; *solid circles*, 10 or more points. Compare with figures 1b and 1d.

ever, Levins' model does not predict a relationship between abundance and frequency of occurrence. In fact, the correlation between average abundance and frequency of occurrence is significant and positive ($r^2 = 0.44$, $P < 0.001$; fig. 4). The more quadrats a species occupies, the greater its average percent cover in those quadrats.

For plants of the Konza Prairie, patterns of distribution and abundance seem to have conflicting implications. The frequency distribution of species at sites is unimodal, as Levins' model but not the core-satellite hypothesis predicts (fig. 1a); yet the correlation between distribution and abundance is significant and positive, as might be expected under Hanski's model (fig. 1d).

The conflict may be partially resolved by analyzing individual soil series. For those species that occur on each soil series, we have plotted frequency histograms
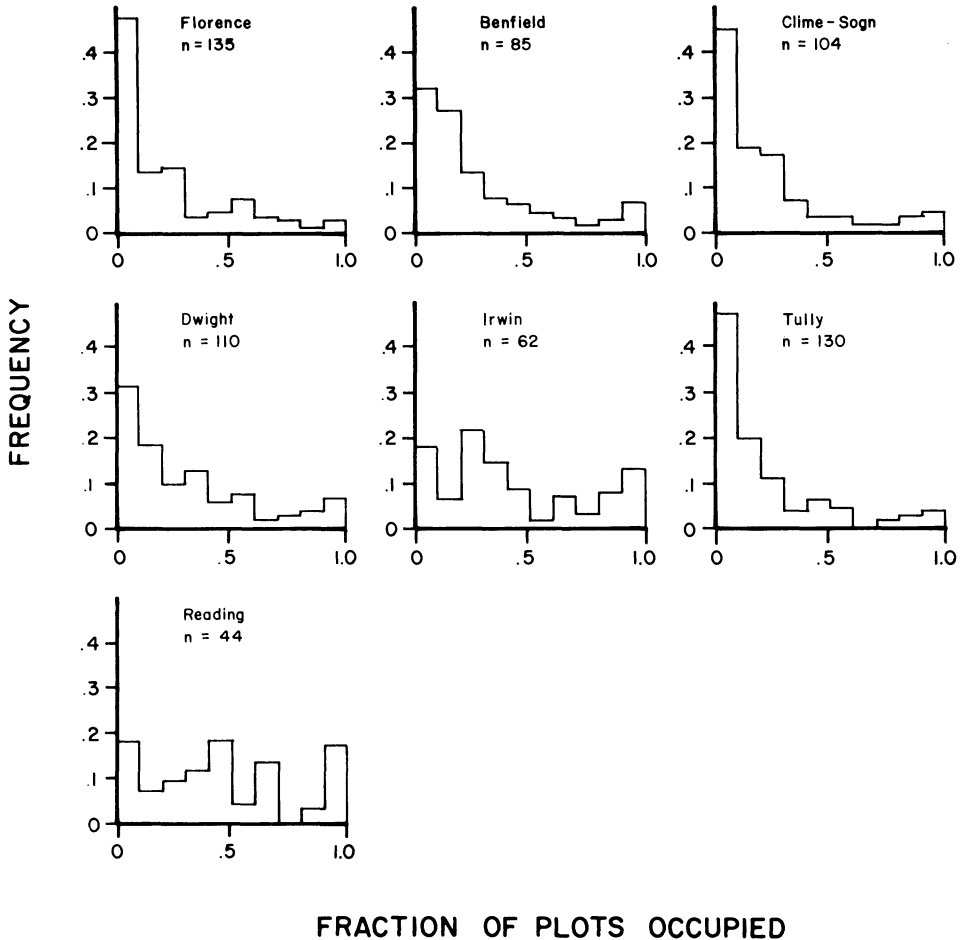
FRACTION OF PLOTS OCCUPIED

FIG. 5.—The distribution of species across seven soil series. Sample sizes are the number of species on that soil series. Compare with figure 3, a plot of the aggregate data.

of p, the fraction of sites occupied (fig. 5). Table 3 is derived from figure 5 and shows that there is a smaller fraction of rare species ($p < 0.10$) and a larger fraction of common species ($p > 0.10$) for all soil series than for the overall distribution.

The results of the simulation confirm that these histograms are unexpectedly bimodal (table 4). The statistic LT, which represents the satellite species (found in few quadrats), is significantly smaller than expected for four of the seven soil series. However, there is no doubt from figure 4 that all soil series, except possibly Reading, have a satellite mode of rare species. For our purposes, the critical statistic is RT, representing core species. For all soil series except Florence, RT is significantly larger than expected.

TABLE 3

PROPORTION OF SPECIES OCCURRING IN THE LARGEST (0.9–1.0)
AND SMALLEST (0–0.10) FREQUENCY INTERVALS

Soil Series	Proportion of Species Occurring on < 10% of the Plots	Proportion of Species Occurring on > 90% of the Plots
Florence	.474	.030
Benfield	.318	.071
Clime-Sogn	.442	.038
Dwight	.318	.064
Irwin	.177	.129
Tully	.469	.038
Reading	.182	.159
All quadrats	.582	.018

NOTE.—Values are taken from figure 3 (all quadrats) and figure 5
(different soil series).

TABLE 4

SIMULATION RESULTS OF A TEST FOR BIMODALITY OF SPECIES OCCURRENCE ON PLOTS

Soil Series	Observed Tail	Expected Tail	Observed < Simulated	Observed > Simulated
		LEFT TAIL (SATELLITE SPECIES)		
Florence	.607	.879	99	1
Benfield	.859	.787	54	46
Clime-Sogn	.933	.803	22	78
Dwight	.600	.868	95	5
Irwin	.242	.442	96	4
Tully	.815	.877	85	15
Reading	.250	.464	97	3
		RIGHT TAIL (CORE SPECIES)		
Florence	.037	.037	86	14
Benfield	.082	.040	0	100
Clime-Sogn	.086	.041	0	100
Dwight	.145	.039	0	100
Irwin	.290	.048	0	100
Tully	.085	.037	0	100
Reading	.182	.053	0	100

NOTE.—The expected values are averages of 100 randomly generated soil series. The table shows
the number of times the simulated tail size was less than the observed tail size. Observed values are
taken from figure 5. Results are presented for the left tail (rare species) and the right tail (common
species).

DISCUSSION

The data presented thus far are consistent with the predictions of both Hanski's
model and the core-satellite hypothesis: the distribution of species on plots of
similar habitat is more bimodal than on all plots together, and distribution and
abundance correlate significantly. Each soil series (except Florence) is character-
ized by a small set of widespread, locally abundant "core" species and another,

TABLE 5

ANALYSIS OF COVARIANCE OF LOG (PROPORTION COVER) ON FREQUENCY OF OCCURRENCE
OF SPECIES ON SEVEN SOIL SERIES

Source of Variance	df	Sum of Squares	Mean Square	F Value	P
Equality of slopes	6	1.27	.21	1.55	0.16
Error	656	89.82	.14		
Zero slope	1	92.90	92.90	675.13	<0.0001
Equality of adjusted means	6	9.39	1.57	11.38	<0.0001
Error	662	91.10	.14		

NOTE.—The test for zero slope shows that the correlation between distribution and abundance is significant for each soil series.

larger set of patchily distributed, locally rare "satellite" species. Relatively few species show an intermediate distribution. The bimodality results appear to support Hanski's model over the alternative Levins' model, but an explicit test of equation (2) is impossible without direct data on local extinction and colonization, which we do not have. Hanski's model could be falsified if one could show that alternative explanations better account for the patterns we have described. Here, we consider some explicit alternative hypotheses for the correlation between distribution and abundance and for the bimodal distribution of species at sites.

Alternative Explanations for the Relationship between Distribution and Abundance

A spurious correlation between distribution and abundance may arise if an arbitrary geographic location is sampled (Bock and Ricklefs 1983; cf. Ricklefs 1972), and the peak abundance of each species occurs at the center of its geographic range (Hengeveld and Haeck 1982). In this scenario, species that by chance have their geographic ranges centered in the study area are counted as widespread and abundant, whereas species that have peak abundances in different locations (because of presumed spatial variation in habitat) are counted as rare and uncommon. This explanation could account for the relationship in figure 4, but only if the widespread species happen to have their geographic ranges centered in the Konza Prairie. This is not likely. More importantly, this scenario would not account for the significant relationship between distribution and abundance for each soil series (table 5). Repeated samples from relatively homogeneous habitat would not generate the spurious correlation. Whether the relationship between distribution and abundance reflects the underlying dynamics of equation (2) is unknown, although the pattern has been described for many communities of plants and animals (Hanski 1982a,b; Brown 1984; other references in Bock and Ricklefs 1983).

Alternative Explanations for the Bimodality of Species at Sites

Hanski's model is by no means the first description of bimodality in species-occurrence data. The "law of distribution of frequencies" (summarized, with
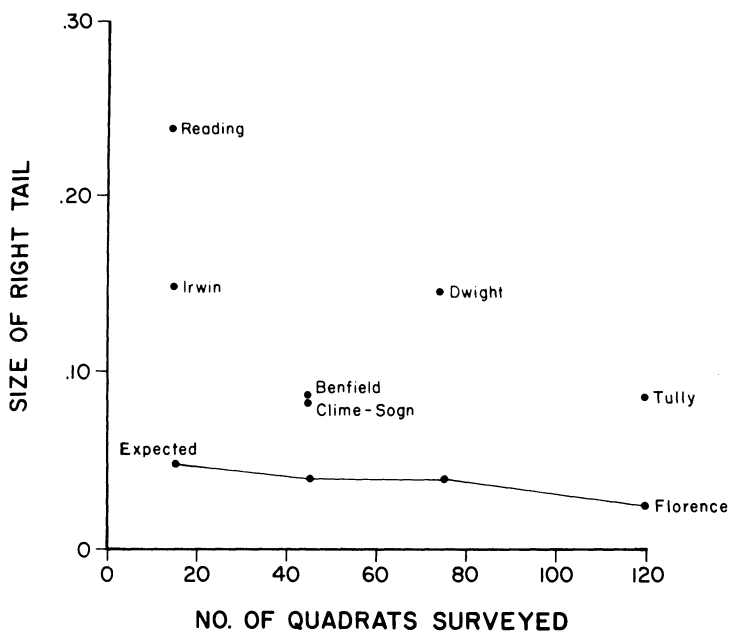
FIG. 6.—Sample-size dependence of bimodality. Expected and observed right-tail sizes versus the number of quadrats sampled of each soil series. The solid line connects the expected values, which were generated by computer simulation (see table 4).

earlier citations, in Raunkiaer 1934) is one of the most widely cited (references in Hanski 1982a) and lambasted (e.g., McIntosh 1962) empirical laws of plant ecology. It treats a group of plant species distributed among a set of quadrats, with five classes for the fraction of quadrats occupied: A = 1%–20%, B = 21%–40%, C = 41%–60%, D = 61%–80%, E = 81%–100%. The law states that the heights of the histogram bars will have the relation A > B > C $\leqq$ or = D < E. That is, there is typically a bimodal distribution with rare species A and ubiquitous species E comprising modes. A and E correspond to the satellite and core modes, respectively, in Hanski's treatment.

Serious objections have been raised to the law (Gleason 1929; Williams 1950, 1964; McIntosh 1962; Greig-Smith 1964), but for our purposes, the most important criticism was that of Williams (1964, fig. 30), who found an effect of quadrat number on the shape of the curve: specifically, the more quadrats sampled, the greater the fraction of species in the satellite mode and the smaller the fraction in the core mode. We find (fig. 6) exactly this pattern for the size of the core mode: the more quadrats sampled in a soil series, the smaller the observed core mode (b = -2.216, r^2 = 0.644, P < 0.01); data were log-transformed in this and other analyses in this paragraph because the fit was far better. One would expect such a pattern simply as a sampling artifact, as Williams (1964) suggested. However, the slope of the regression of the expected size of the core mode (determined from the 100 randomizations described above) against the number of quadrats is more

TABLE 6

The Distribution of Core Species Across Seven Soil Series

	SOIL SERIES						
SPECIES	F	B	C	D	I	T	R
Andropogon gerardi	+	+	+	+	+	+	+
Andropogon scoparius		+	+	+	+	+	
Bouteloua curtipendula	+	+	+		+		
Panicum oligosanthes var. *schribnerianum*				+			
Sorghastrum avenaceum (*S. nutans*)			+	+	+	+	+
Ambrosia psilostachya	+	+		+		+	+
Aster ericoides	+	+		+		+	+
Kuhnia eupatorioides		+					
Oxalis stricta	−	−			+		+
Vernonia baldwini var. *interior*					+		
Psoralea tenuiflora (*P. floribunda*)		−		+	+		+
Tripsacum dactyloides	−	−		−	−	−	+

NOTE.—F, Florence; B, Benfield; C, Clime-Sogn; D, Dwight; I, Irwin; T, Tully; R, Reading. A plus sign indicates that the species occurs on more than 90% of the quadrats of the soil series; a minus sign indicates that the species is absent.

gradual ($b = -0.549$) than for the observed data. The difference in slopes is significant by an analysis of covariance ($F = 5.08$; df = 1, 10; $P < 0.05$); thus, the number of quadrats affects bimodality even more than one would have expected as a sampling effect. However, as is apparent from figure 6, and as we have already shown in table 4, the size of the core tail is much greater than expected for all but the Florence data. Therefore, the bimodal distribution of species at sites cannot be attributed solely to a random sampling process, as envisioned by Williams (1964).

Raunkiaer (1934) proposed another explanation for bimodality. He said, in essence, that the core species in any habitat are those adapted to that habitat, whereas the satellite species are relatively rare because they are adapted to and common in other habitats. This model, in contrast to Hanski's, is static. It predicts that, through time, the same species remain core (and satellite) species in quadrats of the same habitat. Raunkiaer's model also predicts that the core species in any one habitat will be satellite species in other habitats. Hanski's model makes no such prediction.

We have no data to test the first prediction, and these would be the best data of all. If one found, say a decade later, that the core species for each soil series had changed, this result would be strikingly consistent with Hanski's model. But we can test Raunkiaer's second prediction. That is, do core species for a soil series shift to lower frequency classes for other soil series? In most cases, no. Core species are generally widespread, and do not have exclusive distributions on one or two soil series (table 6). Thus, Raunkiaer's explanation for bimodality seems

incorrect. Rabinowitz (1981*a*) found that some plant species are rare in all habitats; the existence of such species that are satellites everywhere also argues against Raunkiaer's explanation.

Sampling Artifacts

Brown (1984) reviewed and synthesized many available data on distribution and abundance. He argued that spatial gradients of a few important environmental variables determine the major patterns of distribution and abundance of each species. He contended that the bimodal curves of the core-satellite hypothesis are artifacts of a failure to examine the entire geographic ranges of the species in the group of interest. By this line of reasoning, the core modes tend to disappear with expanded sampling because species that occupy most sites in a small region would not occupy most sites in a much larger region.

Expanding the sampling scale in this fashion will surely introduce more habitat heterogeneity among sites. But Hanski's model explicitly considers dynamics only among a set of identical sites. Thus, the disappearance of the core mode when the sampling scheme is expanded violates this assumption, but does not invalidate the model. On a much smaller spatial scale, we did find that bimodality disappeared when data from different habitats were combined (cf. figs. 3, 5). Note that Raunkiaer's model also predicts that bimodality will be lost when heterogeneous sites are aggregated.

Regional Extinction

Brown noted another problematic aspect of Hanski's model: what prevents frequent regional extinction? Since the satellite mode is close to zero, stochastic extinction and colonization should occasionally cause regional extinction, just as genetic drift occasionally causes gene fixation (Wright 1931). Indeed, for species of narrow geographical distribution, regional extinction would be global extinction. Yet, regional extinction does not seem to occur often and, as Brown (1984) noted, many species seem to persist indefinitely at few sites. Thus, either the habitat specificity of these species is so narrow that they are really occupying most of the habitable sites, or forces not included in the model must prevent regional extinction. As Rabinowitz (1981*a*) pointed out, some species are found in apparently diverse habitats but are common in none of them. This observation suggests that subtle habitat specificity is not the solution to this problem: the solution is not that the few occupied sites are the core mode.

What forces not in the model, then, could prevent regional extinction? One might be colonization from outside the region. Brown viewed this solution as contrived and unrealistic, on the grounds that many of these colonists are unlikely to produce such propagules because they will also be uncommon in surrounding regions: they are species of low average abundance and narrow geographic range. However, Rabinowitz (1981*a*) classified rare plant species into seven types and found that only one type of rare species was nonexistent: a species of narrow geographic range and small population size that tolerates a wide variety of habitats (Rabinowitz et al. 1985). In other words, the number of occupied sites in a region could be small because (a) habitat specificity is narrow (the small number never-

theless represents the core mode), (b) the geographical distribution of the species is wide (the occasional arrival of propagules is not unlikely), or (c) the population size is not small (it is again not unlikely that propagules will be produced).

Further Tests

The distribution and abundance of tallgrass prairie plants confirm the core-satellite hypothesis and are at least consistent with the predictions of Hanski's model. Perhaps more important, alternative hypotheses proposed by Raunkiaer (1934), Williams (1964), Levins (1969), and Bock and Ricklefs (1983) could not account for these patterns.

However, a rigorous test of Hanski's model (eq. 2) requires long-term data from permanent plots (e.g., Goldberg and Turner 1986) and a measure of local extinction probabilities as a function of regional distribution (Hanski 1982a). If Hanski's model is correct, the identities of species in the core and satellite modes should change substantially through time. For example, Watt (1981a,b) documented three major changes in species dominance over a 37-yr period in a large grassland plot protected from grazing. Local extinction and regional distribution should also correlate negatively if Hanski's model is correct. For prairie plant communities, the presence of many long-lived perennial species (Werner 1978) and a viable seed bank (Rabinowitz 1981b) will complicate the analysis. Nevertheless, Hanski's model does a credible job of explaining static patterns of distribution and abundance. It remains to be seen whether temporal patterns can be accounted for as well.

SUMMARY

Levins (1969) and Hanski (1982a,b) presented dynamic models that describe the fraction of population sites occupied by species. Levins' model predicts a unimodal distribution of species at sites, whereas Hanski's model yields a bimodal distribution: a mode of widespread "core" species, and a mode of rare "satellite" species. The existence of this dichotomy is the core-satellite hypothesis. Hanski's model also predicts a positive correlation between the fraction of sites occupied by a species (distribution) and the average population size within occupied sites (abundance). Levins' model generates no such correlation between distribution and abundance.

We find that a large set of quadrat data on tallgrass prairie plants matches some of the predictions of Hanski's model: for plants of seven different soil series, distribution and abundance are positively correlated, and the distribution of species at sites is bimodal. The bimodality is obscured if distributions from the seven soil series are aggregated.

Two earlier hypotheses have been proposed to explain the core-satellite dichotomy. Williams (1964) showed that the degree of bimodality in species distributions depends on the number of quadrats examined: specifically, the smaller the sample, the larger the size of the core mode, and this is true even for randomly assembled communities of species. For our data, the size of the core mode correlates negatively with sample size, as Williams predicted. However, a com-

puter simulation showed that the observed core modes were significantly larger than would be expected by chance. Thus, Williams' sampling hypothesis does not entirely account for the bimodal distribution of prairie plant species.

Raunkiaer (1934, see "law of distribution of frequencies") argued that the core mode represented those species best adapted to a particular habitat. He also noted that when quadrats of dissimilar habitat were combined, the bimodality disappeared. The distributions of tallgrass prairie plants, however, do not conform to Raunkiaer's explanation: core species tend to be widespread across all soil series. If Raunkiaer's hypothesis were correct, each species would be widespread on only a few soil series, and each soil series would support a different assemblage of core species.

Although our analyses confirm the existence of the core-satellite dichotomy, they do not provide an explicit test of Hanski's model. The essence of the models by Hanski and Levins is that the distribution of each species is dynamic and fluctuates owing to stochastic variation in immigration and local extinction. The strongest test of Hanski's model would be to demonstrate that the distribution of each species varied through time and that the composition of the core and satellite modes was not constant. Long-term data about the distribution of species in a community are needed for such comparisons.

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