

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

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*Submitted October 1, 1984; Revised August 8, 1985, and July 24, 1986;
Accepted November 4, 1986*

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 1982a). Hanski (1982a) pointed out that distribution and abundance are often studied separately, the former by biogeographers and the latter by ecologists. The separa-

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 ($0 \leq p \leq 1$):

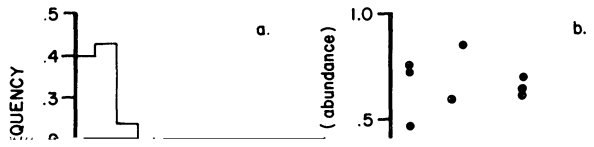
$$dp/dt = ip(1 - p) - ep. \quad (1)$$

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 (1998) showed that the Levins (1969) model predicts a unimodal distribution of

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.



FRACTION OF PLOTS
OCCUPIED

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OCCUPIED

LEVINS' MODEL

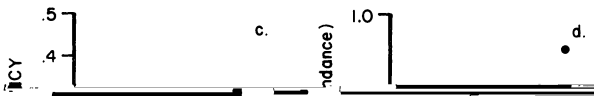


TABLE 1
ABUNDANCE CLASSES USED IN QUADRAT CENSUSES
OF PRAIRIE PLANT COMMUNITIES

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 calculate 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
		ridgetops	brown silt-clay loam			
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

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 sizes and

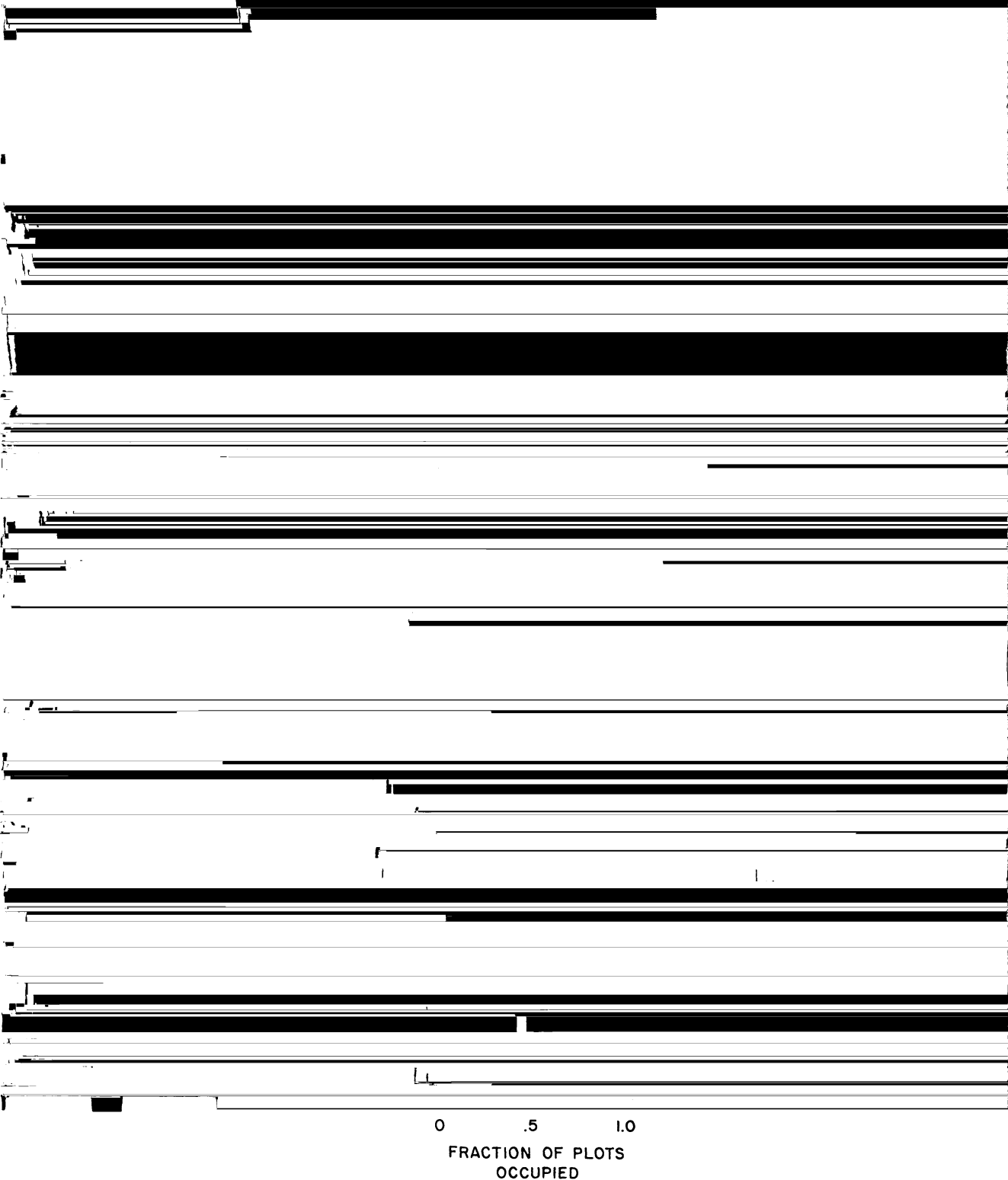


FIG. 3.—The distribution of 170 species of prairie plants on 433 quadrats in the Konza Prairie. Compare with figures 1a and 1c.

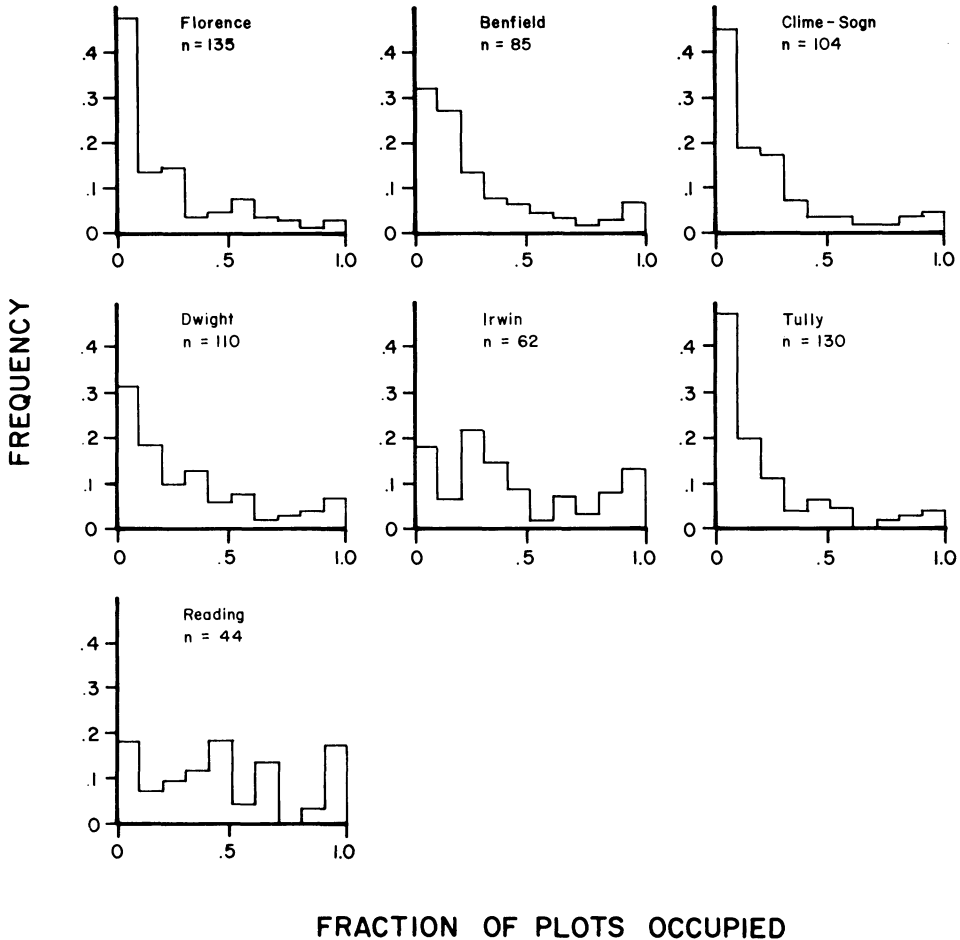


FIG. 5.—The distribution of species across seven soil series. Sample sizes are the number of species on that soil series. Compare with figure 3, a plot of the aggregate data.

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

TABLE 3
 PROPORTION OF SPECIES OCCURRING IN THE LARGEST (0.9-1.0)

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

TABLE 4
 SIMULATION RESULTS OF A TEST FOR BIMODALITY OF SPECIES OCCURRENCE ON PLOTS

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

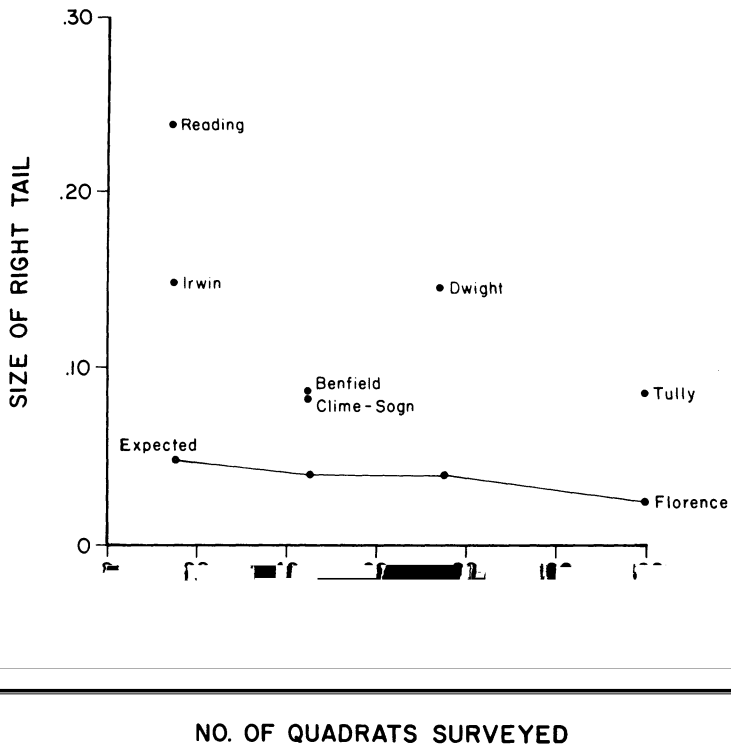


FIG. 6.—Sample-size dependence of bimodality. Expected and observed right tail sizes.

TABLE 6
THE DISTRIBUTION OF CORE SPECIES ACROSS SEVEN SOIL SERIES

SPECIES	F	B	C	D	I	T	R
<i>Andropogon gerardi</i>	+	+	+	+	+	+	+
<i>Andropogon scoparius</i>		+	+	+	+	+	
<i>Bouteloua curtipendula</i>	+	+	+		+		
<i>Panicum oligosanthes</i> var. <i>schrubnerianum</i>				+			
<i>Sorghastrum avenaceum</i> (<i>S. nutans</i>)			+	+	+	+	+
<i>Ambrosia psilostachya</i>	+	+		+		+	+
<i>Aster ericoides</i>	+	+		+		+	+
<i>Kuhnia eupatorioides</i>		+					
<i>Oxalis stricta</i>		-	-		+		+
<i>Vernonia baldwini</i> var. <i>interior</i>					+		
<i>Psoralea tenuiflora</i> (<i>P. floribunda</i>)		-		+	+		+
<i>Tripsacum dactyloides</i>	-	-		-	-	-	+

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

incorrect. Rabinowitz (1981a) 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

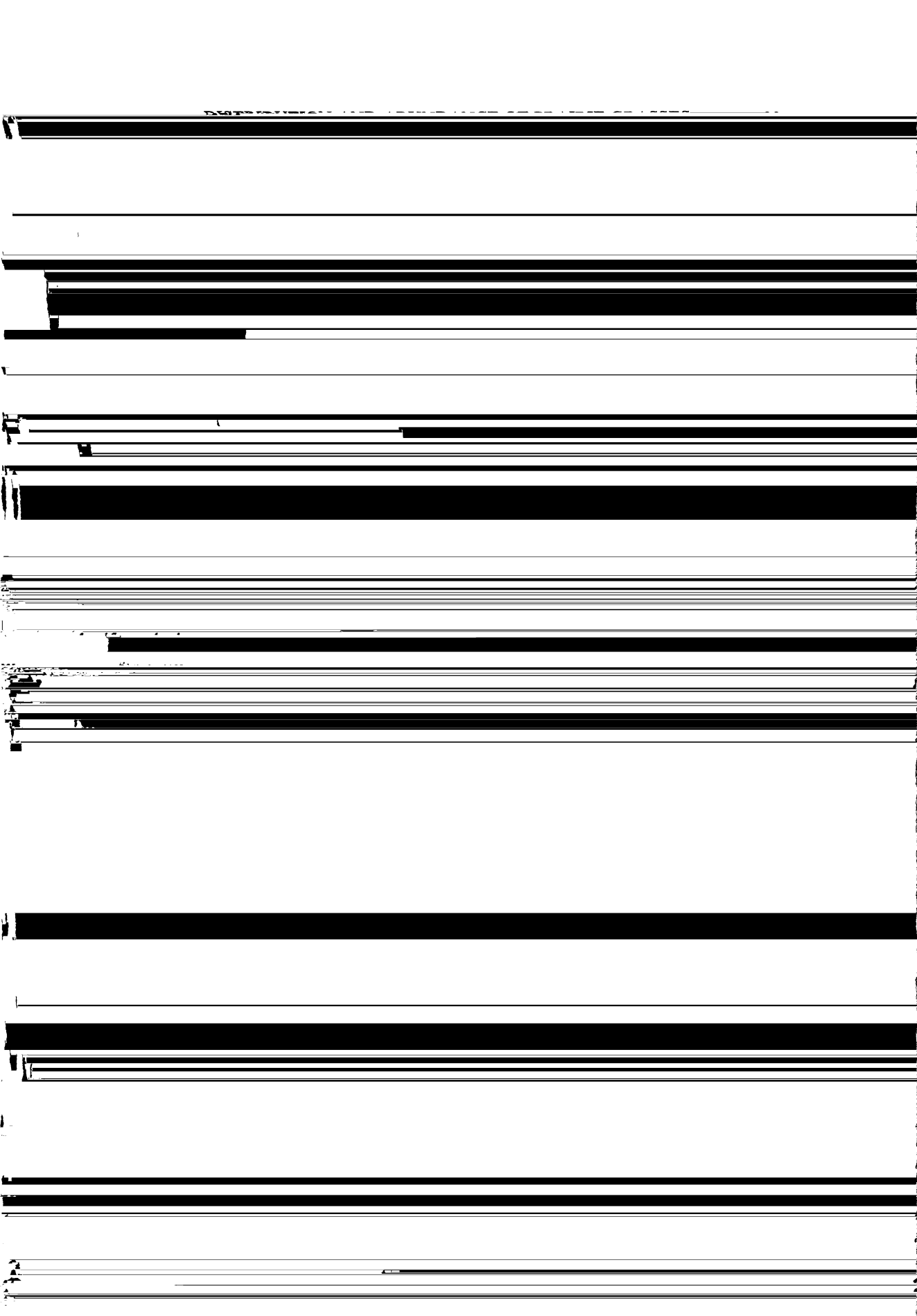
species. He contended that the bimodal curves of the core-satellite hypothesis are artifacts of a failure to examine the entire geographic ranges of the species in the group of interest. By this line of reasoning, the core modes tend to disappear with expanded sampling because species that occupy most 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 Hassel's model explicitly considers dynamic

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 Bounkier



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