9 January 1970, Volume 167, Number 3915 SCIENCE

Dominance and the Niche in Ecological Systems

Dominance is an expression of ecological inequalities arising out of different exploitation strategies.

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The concept of dominance, that is, the idea that certain species so pervade the ecosystem that they exert a powerful control on the occurrence of other species, is one of the oldest concepts in ecology. But, while the concept is universally employed in early texts and continues to be widespread (*1*), many recent texts have omitted it (*2*). The concept, in fact, seems to have fallen somewhat into disrepute because of its ambiguity (*3*), and some population biologists have suggested that the term is not biologically meaningful (*4*).

Current disenchantment with the idea of dominance undoubtedly arises out of an absence of rigorous proof of its occurrence together with general omission of the idea from recent theories of community diversity (*5*). The idea of dominance, however, is closely tied to species diversity and, as Whittaker has pointed out (*6*), many widely employed indices of "diversity" are actually measures of the concentration of dominance in the community. Dominance, relative abundance of species in communities, and species diversity of communities are intricately interrelated in the conceptual framework of ecology, and, while diversity and relative abundance problems have been concisely explored, their relationship to the earlier idea of dominance has not been carefully developed. It is obvious that the abundances of species in a local area vary, and that the diversities of communities are often distinct. What is not obvious is how these differences relate to the organization of communities.

The conceptual difficulty is confounded by a frequent failure to distinguish between absolute and relative abundances of a species. Since ecological interactions must be most frequent among proximal organisms, an examination of absolute abundances in a localized area, or of relative abundances if several localized areas are combined in analysis, will provide us with insight into the nature of those interactions. However, an examination of absolute abundances over a large area, although it may provide substantial insight into the overall organization of the biosphere, is unlikely to provide information about the most rigorous ecological interactions, those among species that occur together.

We propose an examination of the distribution of relative abundances in several communities to test the validity of the concept of dominance and to test the relationship of the relative abundance of species to techniques of exploiting environmental gradients, both in space and time. We are primarily interested in the relationship between relative abundance or degree of dominance in a particular community and the degree of specialization or generalization of the particular species. We propose to measure the degree of specialization as the ability of a species to exploit an environmental range, either in space or time, and hence, as the ability of a species to maintain populations in differing types of environments. Generalist and specialist species are defined relative to one another, with the former being able to maintain themselves over a broader environmental range than the latter. We are dealing with composite environments as encountered by species in nature and have made no attempt to subdivide the niche parameters of the species. Since we are using data that were used to document species composition of communities along either time or space gradients, it was impossible to separate the parameters. It is hoped that we will stimulate tests of the relevance of the model proposed to such carefully defined niches.

We assume that dominance is the appropriation of potential niche space of certain subordinate species by other dominant species and so can be manifested most clearly only within a trophic level; that is, a producer cannot dominate a decomposer or predator because the immediate sources of their energy and inorganic nutrients are not overlapping. This does not mean that these types may not be mutually limited by resources since it is obvious that what is incorporated in support structure for predators is not available for producers. We also assume that communities tend toward saturation of the environment with biotypes so that many species have overlapping niche spaces. One distinction we make is between dominant and essential species. Certain species are essential because of their important function in mineral cycling or energy flow (*7*) and, at the same time, may not be dominant in the sense of occupying niche space potentially occupied by other species in the system.

In the initial tests of dominance and the formulation of the dominance

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model, we have utilized data on plant communities from (i) Chadwick and Dalke's (*8*) data on a 100-year successional sequence on sand dunes in Nevada, (ii) McNaughton's (*9*) study of the effects of soil type and exposure on California grasslands, and (iii) Whittaker's (*10*) data on the tree species at low elevations on gabbro-derived soils in the Siskiyou Mountains of Oregon. We used these data because they provided roughly equal numbers of species occurrences including a variety of vegetation types, methods of community analysis, and environmental situations. Chadwick and Dalke analyzed shrub communities of different ages using coverage to estimate importance. McNaughton examined grasslands along a moisture gradient, including an abrupt discontinuity between sandstone and serpentine soils, and used biomass to estimate species importance. Whittaker analyzed forests along an intuitive exposure gradient with no abrupt discontinuities and used density to assess species importance.

Relative abundance of the *t*th species in the community is measured as

$$I_t = 100\,(y_t/Y) \qquad (1)$$

where y_t is the abundance of species t, Y is the sum of all abundances in the stand, and I_t is the relative abundance of t as a percentage of total abundance.

Distribution of Abundances in Communities

The most satisfactory general theory of the distribution of absolute species abundance in nature is Preston's (*11*) canonical system. As Whittaker (*6*) has pointed out, however, the distribution of sets of species in communities may depart from the lognormal distribution of Preston in which

$$n_R = n_0 e^{-(aR)^2} \qquad (2)$$

where n_R is the number of species in the Rth octave from the modal octave, n_0 is the number of species in the modal octave, and a is a constant such that

$$a = n_0(\pi)^{\frac{1}{2}}/\Sigma n \qquad (3)$$

Our first test is an examination of the absolute abundances of species in the three plant systems to test for fit to the Preston model. The data were combined as six octaves of abundance from least- to most-abundant species (*12*). A chi-square test of fit to Preston's model indicates that the distribution of absolute abundances of the species in these systems agrees with the predictions of the model (Fig. 1). What we ask now, from Whittaker's observation that species in the same community may not fit this model, is how the distribution of relative abundances departs from the lognormal distribution.

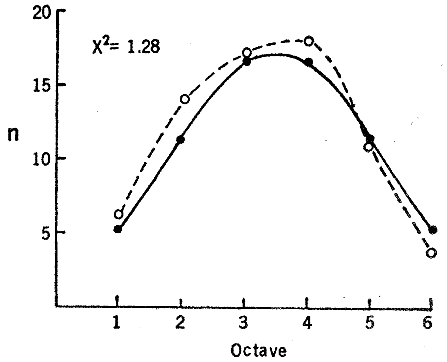

Fig. 1. Observed (O) frequencies of species absolute abundances in 26 plant communities compared with the frequencies predicted (●) by Preston's lognormal equation; *n*, number of species; *Octave*, octave of absolute abundance.

An octave plot of relative abundances (Fig. 2) is truncated on the right by the upper limit of 100 upon the relative abundance of species, compared to absolute abundances which have no independently definable upper limit. What we are most interested in, however, is the distribution of relative abundances around the mode. If they are symmetrical about the mode, in fit to Preston's lognormal distribution, we may assume that there are no species interactions in a community which do not occur in a universe. That is, fit of relative abundances to the lognormal would disprove the overlapping niche assumption stated earlier. However, if there is niche overlap among species in a common area, and species are not equally efficient in the exploitation of overlap zones, then dominance will occur, and relative abundances will be impoverished in classes above the mode and enriched in classes below the mode. We test for dominance by testing for fit to Eq. 2. Data from the three studies of vegetation confirm the occurrence of dominance (Fig. 2) with frequencies greater than predicted in the abundance classes below the mode and less than expected in the abundance classes above the mode.

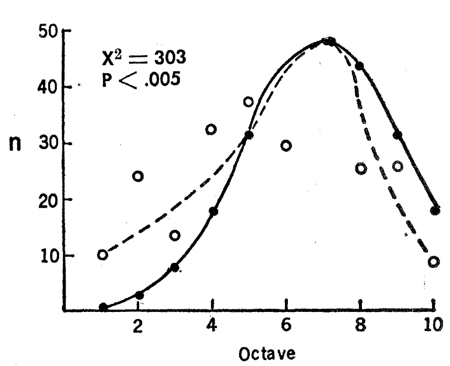

Fig. 2. Observed (O) frequencies of species relative abundances in 26 plant communities compared with the frequencies predicted (●) by Preston's lognormal equation; *n*, number of species occurrences; *Octave*, octave of relative abundance.

We can test more thoroughly for the nature of the departure from the lognormal by the regression of n/n_R on the upper limit of the relative abundance octave where n is observed frequency. We find (Fig. 3) that

$$\log n/n_R = 0.481 - 0.471 \log I_u$$

where I_u is the upper limit of the octave. From this equation, $I_u = 10.5$ percent when $n = n_R$, which suggests that species with abundances greater than this will be less frequent than we would predict if communities were universes, while species with relative abundances below 5.25 percent will be more frequent than we would predict from the universe. It seems likely that species for which $I > 10.5$ percent are probably occupying niche space of species for which $I < 5.25$ percent.

Dominance and the Niche in Species

If we consider the environment as a single dimension, we can plot I against the environment and expect, from Whittaker (*6*), to get a series of bell-shaped curves. One of the more interesting questions in ecology is the relationship between the form of these curves and $I_{\max}$ for a species. The form of these curves relates to the problem of niche width. We propose to measure niche width as

$$W = \left[\frac{\Sigma(y_p \cdot p)^2 - (\Sigma y_p \cdot p)^2/\Sigma y}{\Sigma y}\right]^{\frac{1}{2}} \qquad (4)$$

where p is the position of the community in the environmental ordering (from 1 to 10), y_p is the importance of the species in that community, Σy is the total importance of the species for all of its occurrences, and W is niche width of the species. Another assessment of niche width, pointed out by

Levins (*13*), is the derivation from information theory with

$$H = -\Sigma r_p \log r_p \tag{5}$$

where r_p is the proportion of the species' abundance occurring in position p, and e^H gives the number of sites on which the species would occur if it were equally distributed among all positions. This measure is closely related to W (Fig. 4) with

$$e^H = 0.873 + 2.179\ W$$

The principal differences between the two definitions is that e^H assumes that there is no information in the environmental ordering while W weights the importances for their positions in the environmental gradient. More formally, we may say that W measures constancy of relative abundance over a range of environments.

An examination of the relationship between niche width of a species and the dominance of that species as defined by its maximum contribution to community structure (Fig. 5) shows that

$$W = 0.659 + 0.025\ I_{\max}$$

This indicates that those species which are most dominant, in the community where they make the maximum contribution, have the broadest niche. Species which have a high relative abundance in the community of their maximum development, also have the broadest niches. This is a somewhat different observation than Levins' (*13*) that the most abundant Puerto Rican *Drosophila* species have the broadest niches since he refers to absolute abundance rather than ecological efficiency under optimum conditions, which $I_{\max}$ estimates.

The idea of the niche was first proposed as a description of the dissimilar ecological requirements of different bird species (*14*) but was first generalized precisely by Hutchinson (*15*). The fundamental proposition of niche theory, arising out of competition experiments by Gause (*16*), is the competitive exclusion principle which states that species with identical niches cannot coexist. Most of modern niche theory (*17*) derives from efforts to relate the competitive exclusion principle to Hutchinson's n-dimensional niche. Niche theory provides two alternative explanations of the greater niche width of more dominant species. Either dominant species are generalists with adaptations to many more dimensions in their niches and, as a result, less frequently encounter a limiting dimension, or they are specialists that have evolved adaptations to a single dimension which is most likely to be limiting in the current environmental array. If the dominants are generalists, all of the species in a trophic level have a certain similarity of ecological requirements, with the relative efficiences in exploiting these requirements reflected in the species' relative abundances. The subordinate species, then, can coexist only by occupying portions of niche dimensions where the dominants are inefficent. In this explanation, the dominants are generalists while subordinate species are specialists less through genetic requirements than through being excluded, by the greater efficiency of the dominants, from some environmental dimensions they would occupy in the absence of the dominants. In the alternative explanation, all species are specialists, and the relative abundances reflect the abundances of the speciality. That is, there are a variety of environmental factors on each site likely to be limiting and the species can exploit only one of them efficiently. For instance, if a plant develops adaptations to exploit low soil nitrogen levels, it may not simultaneously exploit low potassium levels. In a site where nitrogen was generally low and potassium was infrequently low, this species would be dominant and a species specialized for the exploitation of low soil potassium would be a subordinate species restricted to spots where nitrogen was high and potassium was low.

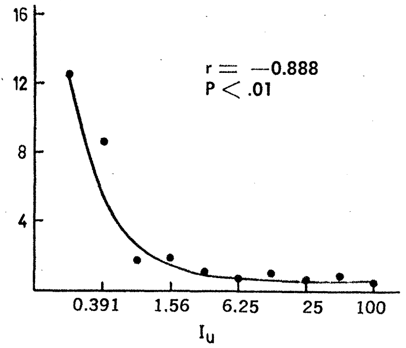

Fig. 3. Relation between observed (n) and predicted (n_R) frequencies in a relative abundance octave and the upper limit of that abundance octave (I_u).

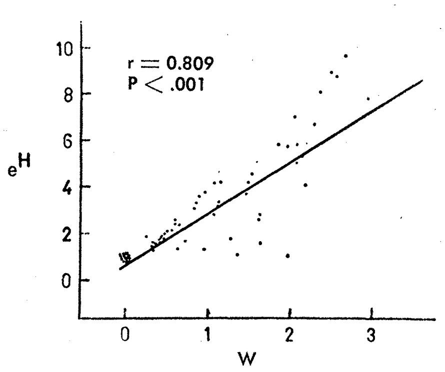

Fig. 4. Relation between the niche-width estimator proposed by Levins (e^H) and the measure proposed in this paper (W).

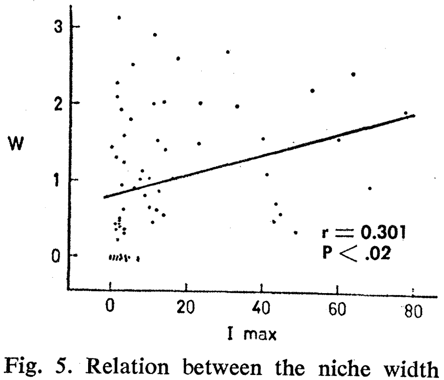

Fig. 5. Relation between the niche width of a species (W) and the contribution of the species in the community where it attains its greatest relative abundance ($I_{\max}$).

There is some evidence to support the hypothesis that all species are specialists and that the most abundant species have specialized on a widely distributed environmental parameter which forces other species into peripheral specializations. Connell (*18*) has shown that the most abundant barnacle in marine communities of the Scottish coast is specialized for occupation of space below the high tide line. Above the high tide line it is replaced by another species capable of living under periodic desiccation. The interesting point is that the desiccation-adapted, and less abundant, barnacle, which would have a narrower realized niche, is actually capable of occupying inundated sites if the other species is removed. But the most abundant and widely distributed species cannot occupy sites above the tide line, even if competition is eliminated. Similar evidence is available from the marsh plants, cattails. The broad-leaved cattail is a widely distributed species which, except in areas with a high frequency of saline sites, is much more abundant than another species, the narrow-leaved cattail, which is generally restricted to saline habitats (*19*). From this, we would conclude that the narrow-leaved cattail is a saline habitat specialist. Experiments on salt tolerance controvert this (*20*) by indicating that whereas narrow-leaved cattail, the presumed specialist, can occupy both high and low salt conditions, the broad-leaved cattail can occupy only freshwater sites. Ecological specialization, then, arises out of physiological generalization. The narrow-leaved cattail is an ecological specialist on high salt sites because it has not physiologically specialized, as the broad-leaved cattail has, for effective competition in freshwater sites. The narrow-leaved cattail becomes an ecological specialist out of inability to compete under freshwater conditions, rather than out of inability to grow at these conditions. The broad-leaved cattail, by physiological specialization on the most widely distributed type of habitat, becomes an ecological generalist.

Dominance and the Niche in Communities

A related problem in community ecology is the relationship between dominance in the community and position of the community on a habitat gradient. To gain insight into this problem, we have examined McNaughton's (*21*) community dominance index

$$\mathrm{DI} = 100\ (y_{1,2}/Y) \tag{6}$$

where $y_{1,\,2}$ is the abundance of the two top species on the dominance-diversity curve (*6*), in relation to the environmental ordering of mesic, mesic-sandstone, and old stands to xeric, xeric-sandstone, and young stands in the three vegetation studies. We discover that

$$\mathrm{DI} = 58.34 + 1.91\,B$$

where B is environmental position from "equitable" (*1*) to "harsh" (*10*) sites, but there is substantial scatter around the line ($r = 0.345$ for $0.1 > P > .05$ with d.f. $= 24$). It seems likely, however, that the environmental orderings, although internally consistent, allowing us to use them in defining niche width earlier, are not consistent with one another and thereby create scatter in this analysis. In addition, none of these orderings contain moist sites, which should be included for a conclusive analysis of community dominance properties in relation to environmental gradients.

To obviate these problems, we utilized Dix and Smeins' (*22*) analysis of marsh, meadow, and prairie vegetation in North Dakota. The moisture gradient sampled ranged from "permanently incomplete" to "excessive" drainage. In accordance with the above analysis, dominance within the community increases from mesic to dry sites. However, this analysis also indicates that dominance increases from mesic to wet sites so that the curve is antimodal and the best fit line is a second degree polynominal (Fig. 6) with

$$\mathrm{DI} = 28.1 - 7.75\,B + 0.842\,B^2$$

where B is the position of the community in the ordering from 1 (dry) to 10 (wet). There is very little scatter around this line, indicating that the scatter above probably does arise out of environmental orderings which are not cross-consistent.

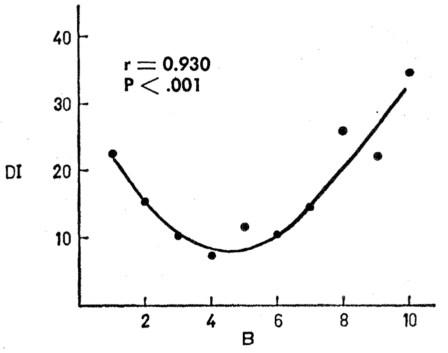

Fig. 6. Relation between the degree of dominance in a community (*DI*) and the position of that community on a habitat gradient from dry (1) to wet (10).

The analysis of North Dakota vegetation allows us to test the relationship between dominance and diversity. An inverse relationship between these two community properties has been proposed (*23*). Some authors (*24*) have argued that the documentation of this relationship elsewhere (*21*) is a mathematical artifact arising out of interdependence of definitions. Although the argument has been answered (*25*), an additional examination is allowed by the data of Dix and Smeins, in which we define diversity as its simplest component, R, of the diversity equation

$$d = (R - 1)/\ln N \tag{7}$$

where d is diversity in bits per individual, R is number of species in the community, and N is the number of individuals in the community (*26*). That is, we compare diversity as its simplest case, floristic richness of the community, with DI. The relationship between these two properties in the North Dakota communities is linear and negative, with

$$R = 71.380 - 2.024\,\mathrm{DI}$$

and $r = -0.890$ for $P < .001$ with $N = 10$, in accord with previous studies of terrestrial systems (*9*) and with the model (*23*).

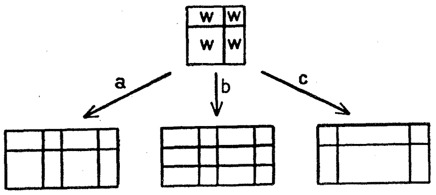

Fig. 7. Diagrammatic representation of methods by which species may be added to the community, assuming that species addition is accompanied by an increase in carrying capacity of the system (*K*) where *W* is niche width of a species (represented here as an area) and *K* is envisioned as an approximation to the sum of the niche structures of the species. That is, the model assumes a close approach to saturation of the available resources with exploitive biotypes. In alternative *a*, species are added to the system in direct proportion to *K* increase. In *b*, species are added more rapidly than *K* increases, so niches are "squeezed." And, in *c*, species are added less rapidly than *K* increases so that niches expand with increasing richness.

The intriguing observation here, however, is that at this point modern ecosystem ecology of Margalef and others converges with the classical community ecology of Clements (*27*). For the stands with minimum dominance and maximum richness, that is, climax by modern theory, are midprairies dominated by *Andropogon scoparius, Stipa spartea,* and *Sporobolus heterolepis* which occupy "by far the largest acreage of ungrazed prairie" in the area (*22*), that is, climax by classical theory. The increase in dominance and decrease in richness on both sides of this type of community on the habitat gradient suggest that the community best organized to cope with site contingencies may be objectively defined as the community on the landscape with minimum dominance. Although the argument at this point becomes circular, the conclusion generated from the North Dakota communities is in accord with early intuitive ecological theory (*27*), more recent empirically derived theory (*23*), and mathematically generated theory (*28*).

The richness property of communities brings us to one of the fundamental questions of ecology for which, through niche-width analysis, we may now propose an answer. That is, how are species added to communities? We, with Hutchinson (*15*), conceive of the niche as an *n*-dimensional hypervolume, with *n* defined by the variety of physiological requirements of the population and with the integrated volume a function of the range and efficiency of dimensional exploitation. The community also has a niche hypervolume, defined by the hypervolumes of its constituent species. For visualization, however, we simplify the model to a planar system (Fig. 7), and ask what happens during community development as species are added to the system. We assume, as the model indicates, that communities are near the innate carrying capacity of the environment, *K*, so that $\Sigma W = K$. Our question is how species fill the *K*-area as more species are added to the system. Species may be added to the system at the same rate at which *K* expands (alternative *a*), in which case niche width and richness are unrelated, or (alternative *b*) species may be added to the system more rapidly than *K* expands, generating a negative relationship between richness and mean niche width of the community constituents. To be logically consistent, although the argument is not biologically compelling, we may assume (alternative *c*) that species are added to the community less rapidly than *K* expands, with an increase in mean niche width as richness increases. These arguments are essentially an expansion of a previous dominance-diversity model in which *K* was treated as a constant (*25*). We find that alternative *b* is supported by the data, with a decrease in niche width as richness increases (Fig. 8). But the nature of the relationship is different for the forest communities of the Siskiyou Mountains and the grasslands and shrubs in California and Nevada. For the trees

$$\overline{W} = 2.789 - 0.063\,R$$

and for the shrub and grass systems

$$\overline{W} = 1.759 - 0.063\,R$$

where $\overline{W}$ is mean niche width of the community and *R* is the number of species in the community. The average niche width is somewhat greater in the forests, but the rate of decrease in niche width as species are added is similar in all of the systems. This indicates that niches are being "squeezed" as species are added to the system, and we interpret this to mean that diversification generates increased competition. Although we draw the niches discretely in Fig. 7, we believe that the discreteness arises out of competitive exclusion rather than out of totally distinct physiological requirements. We can also analyze mean niche width in relation to community dominance and find that for the trees

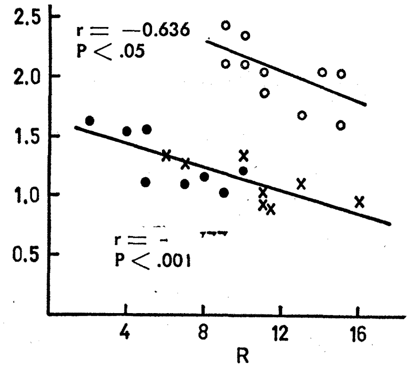

Fig. 8. Relation between mean niche width ($\overline{W}$) of the system and number of species (*R*) contributing to the system. Communities are shrubs (●), grasslands (X), or forests (O).

$$\overline{W} = 1.18 + 0.014\,\text{DI}$$

with $r = 0.787$ for $P < .01$ with $N = 10$, and for the shrub and grass communities

$$\overline{W} = 0.579 + 0.009\,\text{DI}$$

with $r = 0.734$ for $P < .01$ with $N = 16$.

Although the niche characteristics of the species are similar in relation to the maximum relative abundance of the species whether the plant is a shrub, an herb, or a tree, the forest communities are organized somewhat differently than the shrub and grass systems. The niche widths are larger in the forest for a given diversity or dominance, but the change in niche width with changes in dominance-diversity relations are similar in all of the systems. The similarities of the slopes indicate generally comparable responses to the addition of species although the "starting points" are somewhat different in tree than in the shrub and grass communities.

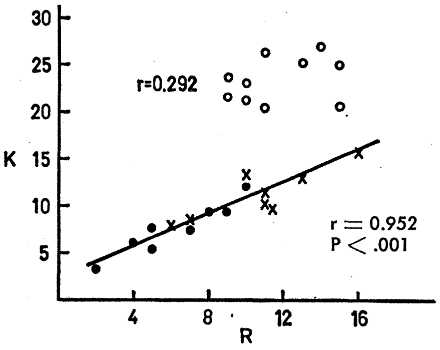

Fig. 9. Relation between carrying capacity of the system (*K*) and number of species (*R*) contributing to the system. Communities are shrubs (•), grasslands (X), or forests (O).

Finally, we ask whether *K* does increase, as we suppose, with increasing species diversity. We make no judgment on the relationship between the two, whether an increase in richness is a response to, or the generator of, *K*. That is, increasing *K* may allow more species to occupy the site by allowing more overlap of niches, or increasing richness may generate a larger *K* through more efficient utilization of total site resources. In fact, there may be no cause and effect relation definable between *K* and richness. We define *K* as ΣW, from Fig. 7, and ask whether *K* is related to *R*. For the shrub and grass systems, there is a significant relation (Fig. 9) such that

$$K = 3.11 + 0.778\,R$$

but for the forests the association is not significant even though the slope of the line,

$$K = 19.79 + 0.319\,R$$

is in the same direction. This suggests that *K* changes much less consistently, and less rapidly, in the forests than it does in the shrub and grassland systems (*29*). Overall, the plant systems fit alternative *b* of the model although the rate of *K* expansion is somewhat less in the trees than in the grass or shrub systems.

Tests of the Dominance Model

With theoretically derived models, errors are most likely to arise from the premises from which the model obtains, and the validity of these premises can be tested only on real systems. With empirically derived models, such as the present one, errors are most likely to arise from the peculiarities of the data used to generate the model. The test for validity here also is reliability of the conclusions in application to other real systems. To make this test, we have compiled data from two additional sources. One is a series of bird communities in the southeastern United States which vary along a successional sequence (*30*), and the other is a series of shrub-grass communities in the northwestern United States which vary along a broad climatic gradient with sampling stabilized for substrate and exposure (*31*).

In all systems, the trends are in the same direction (Table 1). There tend to be fewer species than expected with high relative abundance and more spe-

Table 1. Components of the dominance model tested on shrub-grass and bird communities.

	Fit of relative abundances to lognormal distribution		
Model	$X^2 = 303.2$	for $P < .005$ with $N = 10$	$a = 0.338$
Shrub-grass	$X^2 = 33.94$	for $P < .005$ with $N = 9$	$a = 0.335$
Birds	$X^2 = 12.98$	for $P < .1$ with $N = 9$	$a = 0.341$
	Actual and predicted frequency (n/n_r) *and abundance class* (I_u)		
Model	$\log n/n_r = 0.481 - 0.471 \log I_u$	$r = -0.888$ for $P < .01$ with $N = 10$	
Shrub-grass	$\log n/n_r = 0.266 - 0.258 \log I_u$	$r = -0.799$ for $P < .05$ with $N = 9$	
Birds	$\log n/n_r = 0.065 - 0.098 \log I_u$	$r = -0.530$ for $P > .1$ with $N = 9$	
	Niche width (W) *and dominance* (I_{max})		
Model	$W = 0.659 + 0.024\ I_{max}$	$r = 0.301$ for $P < .02$ with $N = 67$	
Shrub-grass	$W = 1.13 + 0.048\ I_{max}$	$r = 0.571$ for $P < .001$ with $N = 34$	
Birds	$W = 0.531 + 0.011\ I_{max}$	$r = 0.333$ for $P < .05$ with $N = 35$	
	Community dominance (*DI*) and *harshness* (B)		
Model	$\mathrm{DI} = 58.34 + 1.91B$	$r = 0.345$ for $P < .1$ with $N = 26$	
Shrub-grass	$\mathrm{DI} = 55.17 + 1.19B$	$r = 0.547$ for $P < .02$ with $N = 20$	
Birds	$\mathrm{DI} = 9.30 + 9.08B$	$r = 0.811$ for $P < .01$ with $N = 9$	
	Niche width (W) *and community richness* (R)		
Trees	$\overline{W} = 2.79 - 0.063R$	$r = -0.636$ for $P < .05$ with $N = 10$	
Grass and shrubs	$\overline{W} = 1.76 - 0.063R$	$r = -0.777$ for $P < .001$ with $N = 16$	
Shrub-grass	$\overline{W} = 4.15 - 0.127R$	$r = -0.838$ for $P < .001$ with $N = 20$	
Birds	$\overline{W} = 0.924 - 0.005R$	$r = -0.304$ for $P > .1$ with $N = 9$	
	Carrying capacity ($\Sigma W = K$) *and richness* (R)		
Trees	$K = 19.79 + 0.319R$	$r = 0.291$ for $P > .1$ with $N = 10$	
Grass and shrubs	$K = 3.11 + 0.778R$	$r = 0.952$ for $P < .001$ with $N = 16$	
Shrub-grass	$K = 18.21 + 0.562R$	$r = 0.460$ for $P < .05$ with $N = 20$	
Birds	$K = 1.066 + 0.745R$	$r = 0.972$ for $P < .001$ with $N = 9$	

cies than expected with low relative abundance, as compared to the distribution of abundances predicted by the lognormal distribution. Dominance, then, seems to be a real characteristic of the organization of communities inasmuch as high measures of importance in communities are concentrated in fewer species than in universes. However, dominance seems to be less important in the bird communities than in the plant communities. This suggests that bird species are either specialists on resources that are less abundant or they are more able to subdivide the resources.

The decrease in average niche width in a community as the number of species increases is present in all cases. However, for the plants the average niche width is greater as the number of species approaches zero than it is for the birds. This suggests that the birds are more specialized when there are few species and that species which are added are only slightly greater specialists than the ones already present. Throughout the range of communities, in this case along a successional gradient, the bird species are about equally specialized at each stage. For the plants there is a significant decrease in average niche width, suggesting that the species which are added are in fact more narrow in niche hypervolume than species occurring in less rich communities. On the model, then, the birds fit alternative *a* and the plants fit alternative *b*.

Dominant species tend to have broader niches than less dominant or subordinate species. The similarity in the *Y* intercepts for the plant data are striking. Compared to birds, species of plants which contribute very little to community production are more broadly distributed on an environmental gradient. The major difficulty with all these comparisons of niche width is that *W* is in part a function of the number of stages or sites on which a species occurs and will be larger for environmental series that are more finely divided. However, it must be remembered that in one collection of data from which the model was derived, the ordering was eight stages over a period of 1000 years, far more gross than the bird divisions. The birds generally have narrower niches for the same maximum contribution than the plants. This may arise from the types of resources which the two groups utilize and the distribution of these resources.

Overall, the model of niche structure in relation to species dominance and community structure is a powerful description. It encompasses diverse systems and types of data. The signs are the same for every equation generated. The marginal confidence intervals in certain cases with the birds probably arise more out of the small size of samples available rather than out of striking functional differences. We hope that more data on other animal systems will become available for tests of the dominance and niche models at different trophic levels.

Evolution of the Niche:

The Meaning of Dominance

In the systems which we have examined, we find that: (i) dominance is a characteristic of the most abundant species, (ii) dominant species have broader niches than subordinate species, (iii) species are added to the system by compression of niches or expansion of *K*, or both, and (iv) community dominance is minimum on the most equitable sites.

The observation that there tend to be few abundant species and many rare species in communities has been made frequently in the past (*32*). What we offer that is new is evidence that this phenomenon is a manifestation of species interactions that do not occur in a universe. The argument, rephrased, is: the distribution of absolute abundances of species in nature is best described by Eq. 2; if relative abundances of species in the same community (localized area) are distributed according to this equation, we may assume that there are no species interactions in a localized area that do not occur in a universe. In testing this null hypothesis, we find that all systems analyzed fail to fit the lognormal distribution. We test for the direction of departure by the regression of n/n_R on I_u and find that the slope is negative in all cases, which supports the theory of dominance and, in contradiction of Ehrlich and Holm (*4*), demonstrates that dominance is a biologically meaningful concept.

Preston (*11*) points out that the constant *a* approaches 0.2 in canonical arrangements of absolute species abundances in universes. For the arrangements of relative abundances here, the value of *a* approaches 0.34 with the 95 percent limit, by Student's *t*-test, being 0.331 to 0.345, clearly far from 0.2. The higher value of this constant indicates that the distribution of relative abundances falls off more rapidly from the modal class than the distribution of absolute abundances. Or, more formally, the larger *a* indicates increased leptokurtosis and a general depauperization of communities relative to floras and faunas. The number of species occurrences based on an *a* of 0.34 is 59 percent of the number that would be predicted from an *a* of 0.2. The reason progressively smaller samples show progressively poorer fit to Preston's model is that such samples increasingly reflect the interactions among populations. MacArthur (*33*) has recently disavowed his broken-stick model (*34*) of community organization, and it seems unlikely that models such as this which are based on randomness will provide a satisfactory description of communities because communities are grounded in order. Ecologically, our argument is quite straightforward. Individuals react primarily with their neighbors. Populations react primarily, through their individuals, with intermixed or adjacent populations. Unequal efficiency at these interactions generates dominance, thereby distorting the lognormal in a regular and predictable way.

The most important question raised by our analysis is: What determines niche width? The alternatives, restated, are (i) relative efficiencies at exploiting critical limiting factors, or (ii) frequency and carrying capacity of the exploitation specialty. We believe that the available data provide much more support for the latter proposition. However, as MacArthur points out (*35*), the statement "two species with identical niches cannot coexist" is true, but trivial, when applied to Hutchinson's *n*-dimensional niche since it is probable that no two individuals, much less species, have identical niches. There are numerous documentations of niche divergence among coexisting species, including birds (*36*), grazing ungulates (*37*), and plants (*38*). The important point, however, is that although niches diverge, they do not become distinct. These studies indicate that substantial overlap is preserved even though the centers of exploitation are nonidentical. Root's (*39*) analysis of the foliage-gleaning guild in California oak woodlands provides particularly compelling evidence of the tight packing of the exploitation volume through divergent, but overlapping, food size preferences and foraging behavior.

What, then, determines niche width? We believe it is genetic diversity. And it seems likely that the greater niche width of more abundant species would, in fact, be driven by their greater abundance (*40*). There are two major competitive interfaces in communities, the interface between individuals of the same species, and the interface between individuals of different species. Competition must arise, in part, out of contact frequency. Dispersal mechanisms will tend to maintain a somewhat higher contact frequency among individuals of the same species than among individuals of other species. This will tend to generate genetic divergence among individuals of the same species. If we assume that two species are occupying, initially, the same niche dimension, the species whose abundance is larger will, through the increased frequency of competition with members of its own species, be driven toward genetic differentiation of individuals, while the species with a slightly smaller initial abundance will be driven, by competition with members of the other species, toward increasing genetic uniformity. The latter species eventually becomes subordinate, perpetuated in the system only through specialization on another niche dimension.

To pose a reasonable test of this idea, we must have three pieces of information about a single niche dimension. We must know the rates of exploitation of the dimension by different species, the distribution of resources along the dimension, and the distribution of species exploitations along the dimension. Root's (*39*) studies of the foliage-gleaning guild provide us with these measures. He presents measurements of frequency of observation in this niche during the breeding season, as well as estimates of the distribution of the size classes of prey present in the habitat and prey sizes taken by each of the species. The dominant species should be driven, by intraspecific competition, toward diversification to the limits of the niche resources. That is, for the major exploiter of the dimension, there should be a close correlation between the distribution of prey size classes in the dimension and size classes taken. As species become less abundant along the dimension, the correlation between their preference and availability should decrease or become negative. Of the five species observed by Root, only the most abundant gleaner, the blue-grey gnatcatcher, shows a significant positive correlation ($r = 0.722$ for $P < .01$ with $N = 16$) between percentage of food taken and percentage available in the canopy with

$$P_t = 1.360 + 0.877\, P_a$$

where P_t is the percentage of the prey taken in a certain size class and P_a is the percentage of the prey available in a certain size class. It is interesting, also, that one of the least frequent utilizers of this dimension, the warbling vireo, showed a significant negative correlation ($r = -0.554$ for $P < .05$ with $N = 16$) between food taken and food available. In fact, the correlation between the slope of diet on niche resources and abundance in the niche shows a close, though not significant, association ($r = 0.849$ with $N = 6$) in support of the argument that, within the niche dimension, the most abundant species will diversify to the limits of the dimension while the less abundant species will be crowded into increasingly peripheral portions of the dimension, resulting, finally, in certain dimensionally rare species, like the warbling vireo, showing what appears to be inability to exploit the dimension.

The species which show poor association with this dimension should each show a strong correlation between food class taken and available within another dimension. The niche dimensions represent exploitation zones and each species in a community will specialize on a different zone so that community richness becomes a measure of the number of exploitation zones or, stated in other terms, the number of niche dimensions available in the system. We do not argue that all potential dimensions are occupied. Explosive evolution, of course, arises from the opening of a potential dimension through a new adaptive event. Neither do we argue that there may not be more efficient exploiters of the dimension than those currently present. Successful invasions that displace native species, like the rabbit invasion of Australia, indicate that more efficient occupants may occur in remote ecosystems.

In the species, there is a change in genetic structure from one end to another of the niche dimension exploited. The blue-grey gnatcatchers with longer bills exploit generally larger food classes, we assume, just as the warbling vireo population exploits larger food than the gnatcatcher population. The evolution of ecotypes (*41*) is a particularly easily examined case of genetic differentiation along functionally definable niche dimensions. This, of course, raises the question of temporal gradients, and we ask whether there are changes in the genetic structure of populations along successional gradients. Dobzhansky's (*42*) documentation of seasonally associated changes in *Drosophila* chromosomal inversions suggests that the answer is affirmative. This suggests that life is so wasteful of itself because of the inability of individuals to store sufficient information to deal with the information content of the environment.

There are two mechanisms for the storage of biological information. In the individual, information may be stored as heterozygosity. In the population, alleles may be stored both as heterozygosity and as heterogeneity. Small neighborhood size (*43*), self-fertilization, and strong selection (*41*) will tend to generate heterogeneous populations with a large degree of homozygosity. Large neighborhood size, outcrossing, and weak selection will tend to generate population homogeneity and individual heterozygosity. Heterozygosity generates phenotypic plasticity, physiological generalization, and ecological specialization. The species with a high degree of heterozygosity would be, like the barnacle that lives above the tide line (*18*), capable of living in a broad zone but forced, by competition, to live in a more narrow zone. Homozygosity generates phenotypic rigidity, physiological specialization, and ecological generalization.

Our analysis of niche structure of communities in relation to richness indicates that there are likely to be substantial changes in gene structures of populations through succession and in the types of species that occur in different stages. Successional species, in species-poor systems, should be heterogeneous, but their individuals should be more homozygous. Species occurring in climax communities should be less heterogeneous with the individuals more heterozygous.

What we are essentially arguing is adaptation versus acclimation as generators of niche structure. In climax species, we believe, there is more niche broadening through acclimation by the individual. In successional species, there is more niche broadening through diversification within the population. Kruckeberg (*44*) has observed that woody species occurring on both serpentine and more conventional edaphic substrates are rarely differentiated into ecotypes whereas earlier successional species commonly show striking differentiation into edaphic races. He points out the contradiction between this evidence and Baker's (*45*) observation that general-purpose genotypes are more likely to occur in early than in late successional species. The conflict arises out of Baker's failure to distinguish between the ability of the species and the ability of the individual to occupy diverse habitats. The successional species is likely to be capable of occupying a greater habitat range, while its individuals are likely to be organized for narrower portions of that range.

It is well known from studies of ecotypes that phenotypic homeostasis increases from north to south (*46*). It is well known from community ecology that diversity of communities increases from north to south (*47*). As a general conclusion, we state that niche structure of the species arises out of the conflicting demands for efficiency and adaptability, with diversification of the environment and interspecific competition driving evolution toward individual heterozygosity and population homogeneity, while uniformity of the environment and intraspecific competition drive evolution toward individual homozygosity and population heterogeneity.

A Cautionary Conclusion

We believe that our analyses of dominance structure and niche properties provide substantial insights into the organization of communities and species. We rely heavily, however, upon regression analysis and correlation, and we present the best-fit equations for what they are—initial approximations, rather than as final descriptions. In fact, the ranges of the intercepts and regression coefficients tend to be rather small, suggesting that we are close to general statements. There is no question from the close agreements of correlation analyses that we describe strongly associated variables, but the lack of identity among the regression terms indicates that we approach but do not reach descriptions of causality.

The extent to which our description departs from causality probably depends upon its distance from community analysis in energetic and entropic terms. Much has been made in ecology recently of the application of information theory to formulation of definitions, and our emphasis upon richness flies in the face of much of this application. If, however, we define information (*48*) as

$$T = k \log C \qquad (8)$$

where k is a positive constant and C is the number of possible cases from which one may be selected, then R becomes an approximation to C since it presumably describes the number of exploitation zones in a system. Wilson (*48*) has pointed out that T, rather than being negentropy as Brillouin supposed, is the same as entropy as defined in statistical mechanics. Our inability to distinguish niche broadening through heterozygosity and heterogeneity probably is the principal barrier between our analysis and regressions describing causality. A decrease in the scatter in our analysis probably depends upon true estimates of allelic frequencies in ecological systems. It would be interesting to compare allelic frequencies (*49*) in populations of a species which occur at different points along a successional gradient.

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Mission to an Asteroid

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Importance of Studying Asteroids

As long as the asteroids were regarded as fragments of a broken-up planet, interest in them was limited. There are now good reasons to believe that the asteroidal belt represents an intermediate stage in the formation of planets. This links the present conditions in the asteroidal region with the epoch in which the earth and the other planets were accreting from interplanetary grains. Hence, in order to understand how the solar system originated it may be essential to explore the asteroids.

We have already tangible samples of the earth and of the moon. Furthermore, meteorites have been carefully investigated. It is important to study also bodies intermediate in size between the moon and meteorites. The asteroids are such bodies. In this respect a study of an asteroid is more important than the study of Mars or Venus.

The Apollo 11 results suggest that the chemical composition of the moon may be significantly different from that of the terrestrial planets, the meteorites, and the sun. It is also possible that these differ from each other. It is therefore important to obtain samples of other bodies in order to establish the range of variation in elemental abundance in the solar system. There are indications that the chemical abundance in different bodies depends on their distance from the sun. An examination of samples from Mars and from one or several asteroids would clarify this. The data from asteroids would be easier to interpret than those from Mars since the asteroids are less likely to be differentiated.

Since a manned landing on Mars will not take place until after 1980, it is of interest to discuss whether a sample of an asteroid may be obtained in an easier way, at an earlier time, and as a technologically intermediate step.

A few asteroids have diameters of the order of 100 kilometers, but most of them have diameters as small as a few kilometers; probably there are also large numbers of microasteroids covering the entire range below the observed sizes.

A sample from an asteroid could in principle be obtained in two different ways:

1) A spacecraft could land on a large asteroid. This would be easier than a lunar landing because of the fact that the escape velocity of the asteroid is negligible. On the other hand, an asteroid mission is more difficult because of the distance to the asteroids and their large relative velocity with respect to the earth when some of them come into our neighborhood. An asteroid landing would be much easier than a landing on Mars.

2) A small asteroid could perhaps be captured and brought back to the earth, and either landed on the earth's surface or stored in orbit around the earth for later investigations. This would require that the asteroid be very small (mass less than 100 kilograms). The spacecraft need not necessarily be brought up to the full speed of the asteroid if some device could be constructed which catches and slows down the asteroid. A major problem is to detect objects that small and to compute their orbits.

Asteroids Close to the Earth

We shall confine ourselves to discussing missions—manned or unmanned—to asteroids in our close environment. There are a number of asteroids which at regular intervals come close to the earth. A landing on such an asteroid would be of special significance to the investigation of the early history of the solar system. Since such asteroids have acted as probes registering events in the neighborhood of the earth's orbit, an analysis of them could make possible a reconstruction of the essential features of the earth, the moon, and the earth-moon system as they were in the past. One could also derive clues to the history of the sun.

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