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of certainty might be considered in combinations which would yield conclusions carrying differing confidence estimates. For any of this to happen, private, subjective experience must be made objective.

But success may still be elusive, for subtle reasons related to the investigator's capacity for delineating the sought events. The selection of characteristics can be too closely tied to cultural or personal prejudices—for example, a prejudice favoring symmetry or another favoring uniformity. This, we believe, is what Warren, the experimentalist, expressed when he wrote (6): "If we knew nothing of the matter, and were shown a perfect crystal of a diamond and rough piece of broken brick, I think we should imagine that there was more evidence of human design in the crystal with its perfect regularity of form and its polished facets, than there was in the brick." History provides cautionary examples, such as the case of the 18th-century microscopists who saw miniature human beings in spermatozoa because they expected them to be there, and the contrasting behavior of those who, in peering through the first telescopes, lacked the imagination to grasp what they beheld.

Summary

Recognition of early human industries takes on significance with the realization that commitment to tools is the novel adaptive design accounting for the emergence of man. The most abundant evidence for the emergence of man consists of the stones that he refashioned. But recognizing these objects is a problem, as they are both rare and similar to the stones of the environments in which they occur. Because the validity of a procedural, or course-of-action, approach to the problem of recognition can be demonstrated, such an approach is preferable to the intuitive and heuristic approaches that have dominated attempts to deal with the possible traces of early man.

We have modified a course of action proposed 25 years ago and have explored its potentialities by applying it to a case where an industry had already been identified by subjective means. Although the problem of recognition is found in many fields, it is most difficult where characterization of the sought events is itself a task, as it is in this case and in other investigations where threshold phenomena are the object of the inquiry.

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Dominance and Diversity in Land Plant Communities

Numerical relations of species express the importance of competition in community function and evolution.

R. H. Whittaker

Natural communities are mixtures of species which are unequally successful. In a given community one or a few species, the dominants, overshadow all others in their mass and biological activity and may strongly affect conditions of environment for other species. The community also includes other species which are of intermediate abundance or rare, and it is the number of these less conspicuously successful species which primarily determines the community's diversity—its richness in species. When species are arranged in a sequence from most to least important, they form a continuous progression from dominants through intermediates to rare species. This article is an inquiry into the form and meaning of these progressions in plant communities on land, based on field data from Great Smoky Mountains National Park. A number of "laws," interpretations, and models to fit such progressions have been offered (1–10); curves expressing four major hypotheses are shown in Fig. 1. Much of the discussion that follows concerns the fact that the relations are less lawful, orderly, and consistent than ecologists might wish. They are no less significant for all that, in relation to both ecology and evolution.

Two approaches to measurement need to be distinguished, although they are often closely related. (i) Species-diversity may be measured on the basis of numbers of species in sample units large enough to include some minor species. In terrestrial communities relations of species numbers to sample areas are complex; but, within limits, numbers of species increase approxi-

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mately as the logarithm of sample area (11). It is not feasible in most cases to obtain all the species from the community, and comparing numbers of species in sample quadrats of equal area is the most convenient way to compare diversities in different communities. Measurements which are based on relations of numbers of species to numbers of individuals have been suggested by Fisher, Corbet, and Williams (4), who propose the relationship

$$S = \alpha \ln(1 + N/\alpha),$$

and Margalef (9), who proposes

$$d = (S - 1)/\ln N.$$

(In these equations S is the total number of species in the sample, α and d are diversity measurements, and N is the sum of the "importance values" for all species in the sample.) (ii) Other measurements, based on quantitative relations of species, include Simpson's (12) index,

$$c = \Sigma (y/N)^2;$$

the slope of the geometric progression (13),

$$y = Ac^{(x-1)};$$

and the measurement used by MacArthur (14; see 9),

$$c = -\Sigma (y/N) \log (y/N).$$

[Here c is a measurement of concentration of dominance (in the last equation c decreases with increasing concentration of dominance); y is the "importance" of a given species (number of individuals, biomass, productivity, coverage, and so on); A is the importance value for the most important species; and x is the number of a species in the sequence from most important to least important.] Although measurements of the group ii type have been used as diversity measurements, their magnitudes are determined primarily by the extent to which importance values are concentrated in one or a few major species; they express concentration of dominance.

It is difficult to apply some of these measures to plant communities because it is uncertain what constitutes a plant individual in some vegetation (15). It also seems inappropriate to compare on the same scale individuals as disparate in size as trees and herbs. Terrestrial plant species are best ranked by scales —of productivity, biomass, or coverage—which are independent of the con-

cept of "individual" and more directly expressive of importance than are numbers of individuals. "Success" and "importance," words derived from human affairs, must be given meaning by the ecologist if they are to be used in discussing species in natural communities. Probably the best single measure of the species' importance in the community is its productivity (dry weight of organic matter produced or energy bound per unit area per unit time), which both expresses the species' biological activity and indicates the share of the community's environmental resources that it utilizes.

Table 1 gives the numbers of species in quadrats and the Simpson indexes (12) of dominance concentration for plant communities in the Great Smoky Mountains. The species numbers are numbers of tree and shrub species in a 0.1-hectare (20 × 50 m) quadrat and numbers of herb species within, and outside, 20 randomly selected quadrats, of 1 square meter each, within the 0.1-hectare quadrats. The Simpson indexes are computed from measurements (16) which indicate relative net annual primary production (dry weight of organic matter produced by green plants, after respiration by these plants, per unit area per year) of species (17).

Ranges of Dominance and Diversity Values

Species-diversities in the Great Smoky Mountains show a wide range of values. The "quadrat totals" (of tree and shrub species in the 0.1-hectare quadrats plus herbs in the 20 1-square-meter quadrats) may be compared with data for the Siskiyou Mountains of Oregon (18) and the Santa Catalina Mountains of Arizona (19). The poorest communities are high-elevation heath balds with 2 to 4 vascular plant species. (Some stands consist of a single vascular plant species, but several lichen and moss species are also present.) Floristically poor forests, including many high-elevation stands of spruce and fir in all three mountain ranges and western yellow pine (Pinus ponderosa) forest in the Santa Catalinas, have quadrat totals of 5 to 15 species. The creosote-bush (Larrea divaricata) desert below the Santa Catalina Mountains has an average quadrat total of 9.3 species, exclusive of winter herbs. Many plant communities have quadrat totals of 15 to 35; these communities include a wide range of forests and
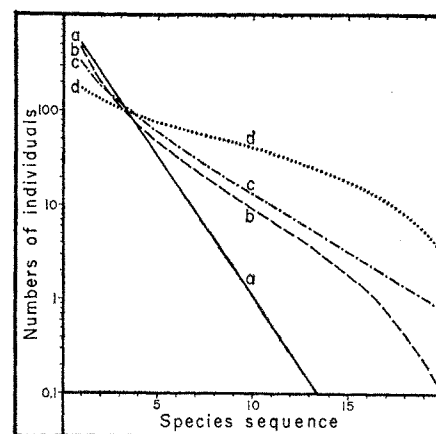

Fig. 1. Curves to fit dominance-diversity relations—four major hypotheses: (curve a) geometric series of Motomura (1), $c = 0.5$; (curve b) lognormal distribution of Preston (6), $a = 0.2$, $n_0 = 2.26$; (curve c) logarithmic series of Fisher, Corbet, and Williams (4), $\alpha = 3.542$; (curve d) random niche hypothesis of MacArthur (10). Numbers of individuals in the species, on the ordinate, are plotted against species number in the sequence of species from most to least abundant, on the abscissa. The curves are all computed for a hypothetical sample of 1000 individuals in 20 species.

woodlands in all three ranges, as well as desert grasslands and most types of desert in the Santa Catalina Mountains. The richest communities have quadrat totals of 40 or more; these are the deciduous cove forests, or mixed mesophytic forests, and one oak forest in the Great Smoky Mountains, certain rich grasslands and open woodlands in the Santa Catalina Mountains, and the north-slope, shrub-phase Sonoran desert of mountain slopes in the Santa Catalina Mountains. The species-diversity of vascular plants in this desert actually exceeds that of the rich cove forests if the many winter annual herbs of the desert, excluded from its quadrat total of 43 species, are considered (19). Diversities of varied communities in Norway (20) and Wisconsin (21), though not directly comparable because they are based on samples of different sizes, show similar wide ranges.

Variations in species-diversity do not simply parallel variations in community production. In the Great Smoky Mountains, production and diversity are not significantly correlated either in vegetation samples or in samples of foliage insects (22). The magnificent redwood forests of the California and Oregon coasts, probably among the most productive of temperate-zone climax forests (16), have low species-diversity (18). So far as the data can be

interpreted in relation to community development or succession (see *9, 23*) they suggest that diversities may both increase during successions and decrease during parts of successions [as from open to closed heaths (in Table 1, from sample 1 to sample 2 and from 5 to 6) and from some mixed heaths (samples 5 and 7) to climax spruce heath (sample 17)]. Diversity is as high in the disturbed, immature forests (samples 15, 19, 22) as in mature, stable forests of corresponding environments. Tree-stratum diversities increase from high elevations toward low (*24*). Diversities of herb and shrub species show no clear relation to elevation below 1400 meters in the Smokies. In both the Siskiyou and Santa Catalina Mountains herb diversities increase from low to middle elevations, and decrease from these to high elevations (Fig. 2) (*18, 19*). Along the moisture gradient in the Smokies, the highest tree diversities are in intermediate sites, the highest shrub diversities are in intermediate-to-dry sites, and the highest herb diversities are in moist sites. Diversities of the three strata are scarcely correlated (Table 1), and numbers of insect and bird species are not simply correlated with numbers of plant species (*14, 22*).

Simpson indexes of concentration of dominance in the tree stratum range from over 0.9 in forests with a single species strongly dominant, through values of 0.3 to 0.7 in a variety of other forests in which one species is less strongly dominant or in which two species share dominance, to values of 0.1 to 0.3 in stands with dominance shared among a number of important species. Stands of the last group include, from opposite ends of the moisture gradient, the moist deciduous cove forests and the dry oak heath and low-elevation pine forests. Those shrub and herb strata for which significant measurements can be obtained show similar ranges of values. No marked positive or inverse correlations among dominance concentrations for the three strata appear. An inverse relation be-

Table 1. Numbers of vascular plant species in quadrats, and dominance concentration values based on net production measurements, for communities in the Great Smoky Mountains.

Sam-ple No.	Community	Eleva-tion (m)	Exposure (direction, inclination)	Trees, per 0.1 ha	Shrubs, per 0.1 ha	Herbs, per 20 m²	Additional herbs present*	Quadrat total	Tree	Shrub	Herb
				Numbers of species					Dominance concentration		
		Heath balds									
1	Rock succession	2110	SW, 30°		2	2	3	4		0.76	0.98
2	*Leiophyllum lyoni* mat	2110	SW, 20°		2			2		1.00	
3	*Rhododendron carolinianum*	2110	S, 32°		2			2		0.99	
4	*Rhododendron catawbiense*	2110	NE, 20°		4		1	4		.98	
5	Open mixed heath	1500	SE, 15°		7	5	1	12		.30	.48
6	Mixed heath, Peregrine Peak	1430	SW, 35°		5	2		7		.45	
7	Mixed heath, Brushy Mountain	1500	NE, 15°		7	3		10		.46	
8	Mixed heath, Rocky Spur	1560	SW, 20°		5			5		.54	
9	High mixed heath	1490	SE, 14°		8		1	8		.29	
		Forest Heaths									
10	Pine forest, Cades Cove	610	SW, 15°	12	10	5	2	27	0.24	.37	.51
11	Pine forest, Pittman Center	550	SW, 26°	13	7	12	10	32	.30	.40	.29
12	Pine heath, Brushy Mountain	1070	S, 30°	6	10	7	4	23	.92	.43	.58
13	Pine heath, Greenbrier Pinnacle	1340	SW, 22°	7	9	4	1	20	.51	.39	.75
14	Chestnut oak heath	970	W, 32°	9	9	5	2	23	.16	.24	.81
15	Hemlock-beech cove forest	430	Ravine	18	9	13	13	40	.21	.45	.15
16	Hemlock-rhododendron forest	1280	NNE, 30°	3	2		1	5	.74		
17	Spruce-rhododendron forest	1740	ESE, 40°	3	4			7	.69	.66	
		Forests									
18	Deciduous cove forest	730	NW, 17°	10	3	30	18	43	.18		.12
19	Cove forest transition	820	N, 17°	18	10	16	24	44	.12	.18	.23
20	Oak-hickory forest†	300	W, 8°	17	5	4	4	26	.40	.82	.56
21	Chestnut oak forest	820	ENE, 10°	13	8	6	1	27	.37	.84	.83
22	Successional tulip forest	760	NE, 10°	9	9	17	9	35	.73	.35	.15
23	Upper deciduous cove forest	1310	NNW, 25°	9	4	26	7	39	.26		.27
24	Hemlock mixed cove forest	870	N, 7°	8	3	20	5	31	.34		.38
25	Gray beech forest	1580	N, 25°	6	1	22	10	29	.65		.37
26	Gray beech forest	1580	S, 32°	4	3	14	7	21	.59		.22
27	Northern red oak forest	1450	E, 16°	9	5	27	4	41	.65		.27
28	Red oak, white oak forest	1390	SW, 15°	7	8	17	14	32	.36	.32	.23
29	Spruce-fir forest	1800	NE, 7°	4	3	10	2	17	.47		.41
30	Spruce-fir forest	1620	SW, 25°	5	5	4	7	14	.56		.46
31	Spruce-fir forest	1620	SW, 24°	4	1	9	8	14	.54		.29
32	Fraser fir forest	1920	NNW, 11°	3	5	6	2	14	.93		.52
33	Fraser fir forest	1900	SSW, 35°	3	2	1	2	6	.64		
43	Coast redwood forest‡	100	Flats	4	1	15	2	20	.99		.27
		Grassy balds									
34	Silers	1700			2	19	5	21			.79
35	Gregory	1670			1	9	6	10			.42
36	Thunderhead	1500			1	7	2	8			.97

* Additional herb species observed outside the 20-m² clipping quadrats, within the 0.1-hectare stand quadrat, which are excluded from the quadrat totals.
† From Oak Ridge National Laboratory, Oak Ridge, Tenn.   ‡ From Humboldt Redwoods State Park, Calif.

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tween dominance concentration and species-diversity can be observed, but it is weak. Results from measurements of both diversity and concentration of dominance reinforce previous observations (18, 22, 24) on the lack of simple pattern and lack of strong correlation in the relations of these community characteristics to environment and to each other.

Dominance-Diversity Curves

The data from the Great Smoky Mountains make it possible to rank most of the vascular plant species in a community by relative amounts of net annual production (16, 17). Dominance-diversity curves for a number of communities are shown in Fig. 3, with species arranged in sequence by estimated above-ground net annual production. A range of forms may be observed in these curves and in curves for other samples from the Smokies. The numbers in the following paragraph refer to production samples listed in Table 1 and tabulated elsewhere (16); the numbers are given to indicate the relative frequency of occurrence of different types of curves among the 37 samples.

Steeply oblique curves approximating geometric series occur in some communities of low species-diversity—in Fraser fir forest [No. 33 (illustrated in Fig. 3) and No. 32], hemlock forest (No. 16), California coast redwood forest (No. 43), and some heath balds (Nos. 4, 8, 9). At one extreme the slopes are nearly vertical; in certain heath balds (Nos. 2, 3) the production of the second most productive vascular plant species is lower by several orders of magnitude, and there is no third species in the samples. In contrast to these communities, certain communities of intermediate species-diversity [Nos. 10 (illustrated) and 28] have moderate slopes approximating geometric series. The majority of the curves are of the sigmoid form illustrated for a spruce heath (No. 17) and pine heath (No. 12) and appearing in forests of low (Nos. 17, 29–31), intermediate (Nos. 11–13, 20–22, 24), and high (Nos. 15, 18, 23, 27) species-diversity, as well as in some heath balds (Nos. 6, 7) and grassy balds (Nos. 34–36). In a number of the curves [Nos. 6 (illustrated) and 19, 24, 31, 35, 49], the curve from the first to the second (or second and third) species is less steep than the apparently geometric slope

from these major species down to the less steep middle slope of the curve. A few curves (Nos. 5, 19, 25, 26, 30) have two separate middle portions of less steep slope. The floristically rich cove forests [Nos. 15, 18, 23 (all illustrated)] have sigmoid curves of moderate slope throughout. The rich oak forest (No. 27, illustrated) combines a steep initial slope, indicating strong dominance concentration, with a moderate middle slope expressing high herb-stratum diversity.

Several considerations bear on the confidence with which the curves can be interpreted.

1) Species are plotted by values for above-ground net production which are based on three different types of field measurements, and on conversion of these measurements to give above-ground net annual productions (17). Root production is omitted, but use of reasonable estimates for root production does not change the shape of the curves, though it changes the sequence of some species. The curves do not include all the vascular plant species in the communities. The species omitted (including the "additional herbs present" listed in Table 1) are of very low productivity and are believed to fit into the steep lower slopes of the curves, with production values scattered through orders of magnitude below 0.01 gram per square meter.

2) Curves have been plotted also by biomass and coverage. In forests the fraction of the community's biomass contributed by the dominant trees is even larger than the fraction of community production contributed by these trees. Use of biomass values steepens the initial slopes of the curves for the dominant trees but does not otherwise change their shapes. Coverage, being a lower power function than biomass and production, produces curves which are less steep throughout but which retain their essential geometric or sigmoid form. Coverage curves of similar forms have been obtained for a wide range of communities, from forest to desert, in the Santa Catalina Mountains (25).

3) In the sigmoid curves the initial slopes include mostly trees, but in some cases major shrub and herb species; the middle slopes include mainly herbs, but usually some minor tree and shrub species; and the final steep slopes are predominantly minor herbs. When the tree and shrub stratum and the herb stratum are plotted separately, geometric slopes in some cases result
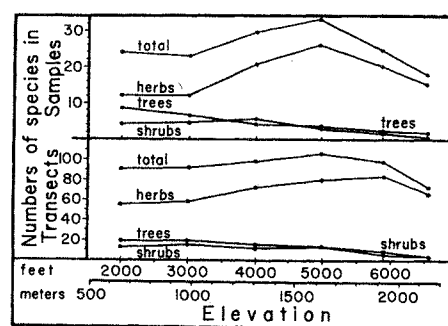

Fig. 2. Species diversities of vascular plants in relation to elevation in the Siskiyou Mountains, Oregon, based on data of Whittaker (18). (Top) Average numbers of tree and shrub species in 0.1-hectare quadrats and of herb species in 25 quadrats of 1 square meter each, and totals of these averages for all three strata. The averages are based on the 50 vegetation samples of a transect for each 300-meter elevation belt. (Bottom) Total numbers of herb, shrub, tree, and all vascular plant species occurring more than once in the 50 samples of a transect.

for one or both strata. In other cases curves for both strata have the sigmoid form, as do many of the curves for the single-stratum balds. The sigmoid curves are not simply products of different geometric slopes for canopy and undergrowth communities.

4) It is not possible to make statistical tests in most cases. Five replicate samples were taken, however, from a spruce-fir forest. The five gave somewhat different slopes and arrangements of species in the middle of the curves, but generally similar slopes and patterns for the curves as wholes. An indication of reliability results from superimposition of the curves for the three cove forest samples from different environments (Fig. 3, Nos. 15, 18, 23): curves representing different species sequences have remarkable identity of form. It is believed that, while individual points are affected by sampling error, the forms of the curves are reliable.

Models for Dominance-Diversity Curves

The geometric series was originally suggested as a fit for such curves by Motomura (1), but it fits only a minority of them. Both geometric and sigmoid curves may be generated, however, by quite modest models.

It may be assumed that productivity and species composition of the plant community are determined by environmental factors such as light, moisture, temperature, and nutrients. Intensities
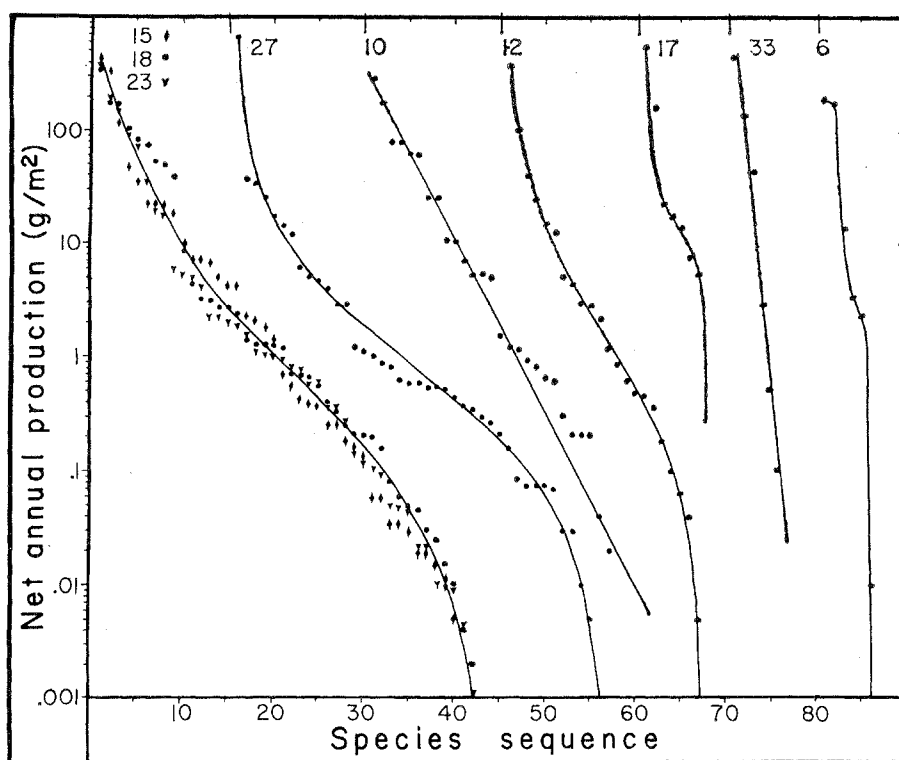
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Fig. 3. Dominance-diversity curves for vascular plant communities in the Great Smoky Mountains. Points represent species, plotted by net annual above-ground production (on the ordinate) against the species' number in the sequence of species from most to least productive (on the abscissa). In each curve the highest point represents the most productive species (species number 1 in the sequence) and the lowest point the least productive species. For the sake of graphic clarity, however, the curves have been arbitrarily spaced out, their origins being separated by 10 or 15 units along the abscissa. Positions of their origins on the abscissa are indicated by the vertical ticks along the top border of the figure.

of these factors in the soil and microclimate within the community are strongly affected by the character of the community, and most of the factors vary horizontally in a small-scale pattern or mosaic determined by microrelief and by root, shade, and leaf-fall effects of the plants themselves. Different species are differently adapted to various intensities of these factors, to different levels of above-ground vertical space and below-ground root space, and to different seasonal times of foliage production, flowering, and fruiting. A species' specialization in the community—its particular way of relating to other species and to intracommunity conditions of environment, space, and time (diurnal and seasonal)—is termed its "niche." Ranges of environmental factors, of space, and of time to which different species within a community are adapted represent axes of a "niche space," or hypervolume, in the sense in which the term is used by Hutchinson (26). The niche space is an arena in which the species populations compete and evolve in competition with each other. The word *competition* here

denotes the situation in which (i) environmental resources are limited in amount, (ii) each species population increases to a maximum determined by the resources available to it, (iii) amounts available to a given species are affected or determined by the use of these resources by other species of the community, and (iv) species populations are consequently limited by the presence of other species, a limitation which is often mutual. Each species occupies the part of niche space to which it is best adapted—the part in which it has competitive advantage over other species—and each species occupies as large an area, and occupies it as densely, as competition and other limitations permit.

The multidimensional niche space is represented in the model by a two-dimensional square in which species occupy rectangular niches (Fig. 4a). The size of a species' rectangle represents the fraction of the community's niche space which that species occupies. It is assumed that the fraction of environmental resources utilized and the fraction of total community production

realized by the species will be closely related to (though not identical with) the fraction of niche space occupied. If the community has a total green plant production N and the most successful species is able to appropriate a fraction k of the niche space and environmental resources with a production kN, if the second most successful species utilizes the same fraction of the remainder, and if each succeeding species utilizes the same fraction of the space not appropriated by more successful species, then,

$$y = N(1 - k)^{x-1}k = Ac^{x-1}, k = 1 - c,$$

—the familiar geometric series. With random variation in k, series closely resembling the data for some communities result. Although the model greatly simplifies relations in the community, as a model must, it may be a plausible representation of competitive relations, and their expression in production, in some communities with few species.

In many communities evolution has produced a larger number of competing species, among which no one has so great a competitive advantage over all the others. If the first species occupies a smaller, "central" area of the niche space, there may be several "peripheral" niches to be occupied, each representing a different pattern of adaptive specialization—adaptation to low intensities of light and other environmental factors; timing different from that of the dominants, as in the case of spring and late-summer herbs; and so on. For the model it has been assumed that each species will occupy a rectangle of somewhat flexible shape (the ratio of the sides being between 1.5 and 2.0) and will occupy, within the limits set by these ratios and by prior occupation of niche space by other species, the largest niche space available to it. There results the sigmoid curve of Fig. 4b, with three slopes: (i) an upper slope, representing a few dominant species, each appropriating a substantial fraction of niche space, with numerical relations between them approaching a geometric series; (ii) a middle, less steep slope representing a larger number of subordinate species, each adapted to some special portion of niche space, less widely separated from one another in productivity than the dominants; (iii) a terminal slope representing a few rare species occupying the remnants of space; since their number is small and the range of their production values is

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wide, the terminal portion of the curve slopes steeply to the last, rarest, species.

There is one further consideration relative to the forms of some of the curves. In many communities two species share dominance. The subarctic-subalpine forests (or taiga) which occur around the Northern Hemisphere in cool climates, below the tundra, and extend southward in mountain chains are such communities. In many areas, including the Great Smoky Mountains, the pair of dominants includes a spruce (*Picea* sp.) and a fir (*Abies* sp.). The two dominants have different optimum environments, where their populations reach maximum densities. Generally the fir population is centered in the higher, cooler, and moister part of the spruce-fir forest, the spruce population in the lower, warmer, and drier part. Along environmental gradients between the environments where spruce is most strongly dominant and those where fir is most strongly dominant, the population balance between the two shifts gradually and continuously. In some environments the two dominants are of equal importance; in many environments they are too nearly alike in importance to fit a geometric series. It is assumed that, because of differentiation between the environmental requirements of these species, they share the central niche space in the model. If the first species occupies a niche area to one side of the center and the rest of the niche space is assigned to the second and the remaining species in accordance with the rules discussed for Fig. 4*b*, there results a sigmoid curve with a flattened uppermost slope (Fig. 4*c*), resembling the curves for several of the field samples (for example, sample 6 in Fig. 3).

Types of Dominance-Diversity Curves

Dominance-diversity curves are thus not of a single form but represent a range of intergrading types. The variations observed in data for the Great Smoky Mountains and the curves produced by the models permit us to interpret the various mathematical relationships proposed to fit these curves (Fig. 1).

1) Curves approximating geometric series (*1, 2*) are of fairly wide occurrence. They appear for some communities which have rigorous environments and only a few species, widely scattered along the logarithmic scale of relative importance. Less steep geo-

metric slopes appear also for some communities with less severe environments and moderate species-diversity. Small samples from communities for which the curves are sigmoid (for example, samples limited to the first few species of sample Nos. 12, and 15, 18, and 23 of Fig. 3) will often have curves approaching geometric form (*27*).

2) Most communities, including many of those in relatively rigorous environments, have a small group of dominants, a larger middle class of moderately important species, and a smaller number of rare species, many of them ecological specialists. The curves are sigmoid on the semilogarithmic plot of Figs. 1 and 3, but various departures from simple sigmoid form result from the competitive relations among species in particular communities. Although competition is assumed to have a major role in deter-
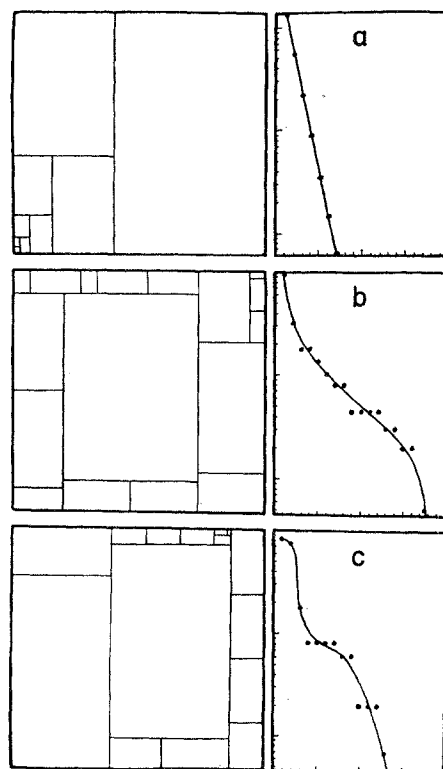

Fig. 4. Models for species and niche relations which may underlie dominance-diversity curves. The squares in each case represent a niche space which is divided among the species of the community, represented by rectangles. Sizes of the rectangles for species represent their share of niche space and environmental resources, as expressed in their population density, productivity, or other "importance" measurement. In the curves to the right of each model, species are plotted (on the ordinate) on a logarithmic scale by areas of their rectangles against species number in the sequence of species from most to least important (on the abscissa).

mining species abundance of vascular plants, at least two other factors should be allowed for. (i) The importance of some species may be controlled in part by animal consumption. Control of populations of plant species by different consumer species may represent a further aspect of niche differentiation, increasing the number of species which can occupy the niche space of the community beyond the number made possible by their niche differentiation in relation to factors of environment other than animal consumption. This and other forms of niche differentiation involving relations between species populations may affect the slope of the intermediate and lower portions of the curves and the species-diversity of the community. (ii) Because of the internal pattern of the community, which is affected by microrelief and other factors, only in scattered places in the community may niche requirements of some species be met. The importance of these species, and the number of species successfully occupying such niches, may be determined in part by balances of seed dispersal into, and mortality in, these scattered niche locations, analogous to the balances of immigration and extinction that affect island floras (*28*). The importance of rarer species, especially, and the slopes of the lower parts of curves, may be affected by this balance, for seed dispersal in some species may be inadequate to fill more than a fraction of the suitable niche locations in the community.

3) Some samples from communities of high species-diversity, among them the cove forests, have sigmoid distributions of moderate slope throughout. These same communities have "lognormal" distributions when plotted by Preston's method (*6, 7, 29*) (Fig. 5). The numbers of species in octaves of importance measurements (production of 1-2, 2-4, 4-8 . . . g/m², and so on) are determined, and these numbers of species, on the ordinate, are plotted against the octaves (hence, according to a logarithmic scale of importance values) on the abscissa. Species numbers then form a binomial curve on a logarithmic base, a lognormal distribution fitted by the relation

$$n = n_o e^{-(aR)^2}, \quad \Sigma n = S = n_o(\pi)^{1/2}/a,$$

in which n is the number of species in an octave R octaves distant from the modal octave containing n_o species, and a is a constant which often approximates 0.2. Here, as in the treatment
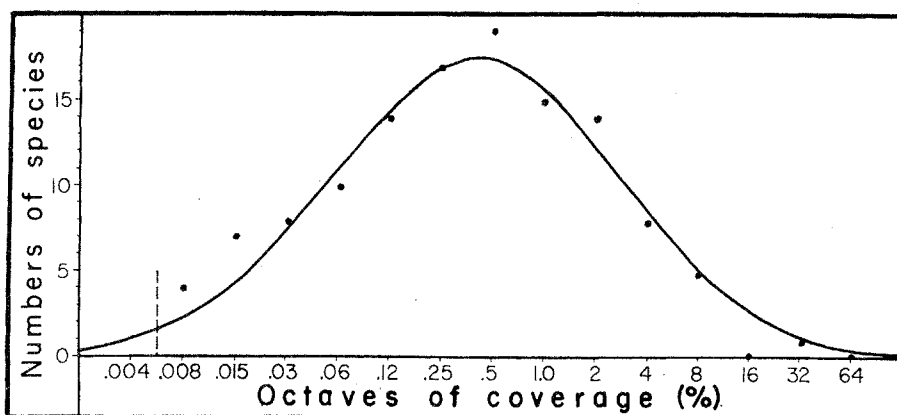
Fig. 5. The lognormal distribution of Preston (6), applied to rich north-slope, shrub-phase Sonoran desert communities on lower mountain slopes of the Santa Catalina Mountains, Arizona (19). Points are numbers of species (on the ordinate) plotted against their coverage values within the octaves of coverage (on the abscissa). The coverage values indicated on the abscissa are upper limits of octaves. Coverage values (for 122 species) are averages of measurements for ten similar stands (19). The fitted curve is described by $y = 17.5e^{-(0.215R)^2}$, where y is the number of species in an octave R octaves distant from the modal octave (which contains $n_o = 17.5$ species). The dashed vertical line is the "veil line," to the left of which no data on species numbers and importances are available. (Field methods did not measure coverages below 0.004 to 0.008 percent.) The data form a sigmoid curve of gentle slope in a plot of the type of Figs. 1 and 3.

in terms of geometric series, it is assumed that importance values of species are best compared on a logarithmic scale, and the results indicate that this is the case. The lognormal distribution implies that there are many species of intermediate importance, and that numbers of species decrease according to a probability curve with increasing departure from the modal importance value. Incomplete data for tropical forests (30) suggest that for these, as for the cove forests, geometric and logarithmic plots give sigmoid and lognormal curves, respectively, but the curves represent many more species than the curves for the cove forests do. It is possible to interpret the curves of Fig. 3 as small-sample departures from the lognormal distribution. It may be preferable to consider that the varied forms of the curves express the particular competitive (and other) relationships of species populations in communities. When the number of species is large and the factors determining their relative importance are complex and multiplicative in effect (31), the distribution of species by relative importance approaches the lognormal.

4) None of the vascular plant communities studied fits the MacArthur (10) curve a (random division of constant total niche space, niches nonoverlapping, see Fig. 1) or curve b (random division of niche space without reciprocal competitive limitation, niches overlapping). Data for animal communities also generally fail to fit these

curves (32, 33); curve a is fitted by some small samples of bird (10) and snail (34) populations. The bird samples compiled by Udvardy (35) show, on the semilogarithmic plot of Figs. 1 and 3, a range of forms from geometric slopes to sigmoid curves approximating the MacArthur curve a. MacArthur's studies (14, 36) of niche relationships in birds are among the most significant contributions to the species-diversity problem. It is probably not the case, however, that division of niche space is in general random in the sense assumed in MacArthur's models (see 29, 32). Species of singing birds combine self-limitation of population density (by territoriality) with self-limitation of niche space, each species having behavior which limits the fraction of community space in which it nests and takes food: they "cartelize" niche space. Consequently, no species reaches the degree of dominance which might be possible with unrestricted competition, and the relative importances of species are much less widely divergent than is the case with vascular plants and may fit the MacArthur curve a. The steep geometric series and the MacArthur curve may thus represent different limiting cases in organisms with widely different kinds of interaction and modes of population limitation.

5) Samples which are not taken from a single community of interacting species (for example, collections of insects caught in light-traps) will often approximate a geometric series because

(i) a small number of species, not competitively related, will tend to have their relative abundances widely scattered along the logarithmic scale; (ii) such samples may include mainly major species, among which geometric relations are frequent; and (iii) hierarchial relations (in which one secondary predator feeds on n_1 individuals of a primary predator species and each of these feeds on n_2 individuals of a herbivorous species) may be involved when more than one trophic level is represented (37).

6) Larger samples which are not from a given, integrated community will often approximate lognormal distributions (6, 7, 38, 39); these distributions imply that there are many species of intermediate abundance and fewer rare and common species. The logarithmic series (4, 38, 40) often fits the steep upper and flatter middle parts of such curves but predicts an excessive number of rare species. The lognormal distribution seems to be the most satisfactory interpretation of the relative abundances of species in nature in general, as distinguished from sets of interacting species in particular communities.

Diversity in Relation to Environment

These observations may also place in perspective the results on species-diversity and concentration of dominance. The inverse relation of these is weak. In temperate-zone communities, at least, no strong and consistent relationship should be expected between the steep initial slopes of curves, which relate the dominant species, and the middle slopes, which primarily affect species-diversity. There is no reason why species-diversity relations for different strata or fractions of the community, subject to different environmental factors and modes of population limitation, should parallel one another; and they often do not (18, 22, 24). Species-diversities of vascular plant communities are affected most strongly by richness in subordinate species; in temperate-zone forests these subordinate species are mainly the herbs. High species-diversities consequently occur under such divergent conditions (all favoring the growth of subordinate species) as those of the southern Appalachian cove forests, open woodlands of drier environments and woodlands on serpentine soils in the Siskiyou Mountains (18), and certain deserts of

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less severely arid environments (*19*). In contrast to these, eastern hemlock (*Tsuga canadensis*) forests, in favorable moist sites intermediate to the rich upper cove forests and the red oak (*Quercus borealis*) forests (samples No. 16, 23, 27), are of very low species-diversity—as low as the diversities of some communities of highest elevations.

Although the external, topographic environment of the hemlock forest is as favorable as that of the cove and red oak forests, the needle-litter and root relations of the dominant hemlocks render the environment *within* the community, affecting subordinate species, unfavorable (*24, 41*). The deciduous cove forest and serpentine woodland offer, for very different reasons, more favorable conditions for undergrowth plants. In the deciduous cove forest, although the intensity of the light reaching the herb stratum in the summer is low, soil nutrients and moisture conditions are favorable. The serpentine woodland is believed to offer undergrowth plants relatively favorable conditions of light, soil moisture, and some nutrients, because the special nutrient conditions of serpentine soil permit the development of only an open tree stratum (*18, 42*). An intensity of one of these environmental factors that is more favorable for the community as a whole may imply a wider range of tolerable variations in that factor, from place to place within the community, to which different species are adapted. The serpentine woodland, for example, offers herb species a wide range of light intensities, from sunlight to shade, beneath its open tree and shrub strata, in contrast to the more uniform shade beneath canopies of evergreen forests of lower species-diversities on other soils nearby. The factors are also variously interrelated in their effects on plants. The favorable moisture conditions of the cove forest permit spring herbs to grow and fruit rapidly before trees are in leaf; these spring herbs are largely absent from the drier forests of the area. The greater soil moisture of the cove forest makes possible wider niche differentiation in relation to season than that which occurs among herbs in drier forests. It is suggested that the effect of environmental "favorableness" on undergrowth diversity results from the fact that favorable conditions for a given environmental factor permit a wider range of adaptations, by different species, to different intensities of that and

other environmental factors within the community.

Two broad geographic trends in species-diversity have been observed.

1) One of the major generalizations of biogeography is the increase in numbers of species in many plant and animal groups from high latitudes into the tropics. Numbers of tree species in forests, for example, increase from high elevations downward and from high latitudes equatorward—from one to three species in many subarctic-subalpine forests to more than 100 species in some tropical forests (*30, 43*). The effects of glaciation in northern latitudes are one source of contrast, as illustrated in the low diversity and distinctiveness of serpentine-soil floras of glaciated areas compared with serpentine floras of nonglaciated areas (*42*). There has been less time, in the younger communities which have developed on surfaces exposed by the retreat of glaciers, for numerous species to evolve while interacting with one another in these communities and to evolve niche differentiation. To state this more generally, tropical environments have changed less
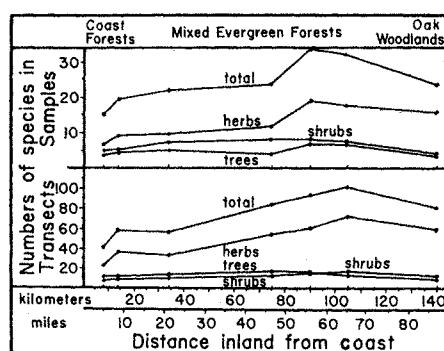

Fig. 6. Species-diversities of vascular plants in relation to the climatic gradient from maritime climates inland to continental climates at low elevations in the Siskiyou Mountains, Oregon and California, based on data of Whittaker (*18*). (Top) Average numbers of tree and shrub species in 0.1-hectare quadrats and of herb species in 25 quadrats of 1 square meter each, and totals of these averages for all three strata. The averages are based on six samples representing the topographic moisture gradient in each study area (ravine, lower north-facing slope and open north-, east-, southeast-, and southwest-facing slopes). (Bottom) Total numbers of herbs, of shrubs, of trees, and of all vascular plant species occurring in the six samples of a study area. The diversities in the plot at top are alpha diversities of individual plant communities; those in the plot at bottom are gamma diversities of vegetation patterns in relation to topography. The points at far left are for the coastal redwood forests. The lower diversities of the points at far right may result from grazing disturbance.

during evolutionary time than temperate and arctic ones, and have been freer from severe environmental conditions of catastrophic consequence to natural populations. Evolution under tropical conditions may consequently be more strongly influenced by selection for survival relative to other organisms than by selection for survival in a severe environment. Over longer periods of evolutionary time larger numbers of species evolve in accommodation to each other in the tropics, and they evolve with smaller differences in niche requirements; because of this they are able to exist together in communities of high species-diversity (*44*).

2) Paradoxically, species-diversities have been found to increase from maritime climates inland to continental climates which have apparently less favorable, more widely fluctuating present climates, which one would expect to be less favorable to species-diversity (Fig. 6) (*18, 19*). The increase occurs on three levels, distinguished as "alpha" diversities (diversities within individual communities), "beta" diversities (or relative extents of differentiation of communities along topographic gradients), and "gamma" diversities (diversities of vegetation patterns, resulting from both alpha and beta diversities). It is not known whether these trends are worldwide. Possible bases for them have been discussed (*18, 19*); it is likely that during the dry summers of temperate maritime climates most of the limited available soil moisture is used by dominant plants and soil drought limits the growth and diversification of subordinate plants.

Various interpretations of these trends may be suggested. (i) Severe, unstable, and recent environments limit the numbers of species which have evolved to maintain themselves in those environments. In older and less severe environments larger numbers of species tolerate environmental conditions and maintain themselves with finer differentiation of their environmental requirements. (ii) In both severe and favorable environments species-diversity results mainly from utilization by subordinate species of environmental resources "left over" beyond the resources requisitioned by the dominant species and from niche differentiation among these subordinate species. (iii) Species-diversity of a community is a resultant of at least three interrelated determinants—characteristics of environment, time during which species have evolved niche differentiation in

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relation to one another, and characteristics of the particular species which have evolved to form communities in that environment, especially characteristics of the dominants which affect environmental conditions for subordinate species. (iv) Certain broad trends in relation to climate exist. Apart from these, species diversity can be interpreted, but is not simply predictable, from characteristics of the environment or from such community characteristics as dominance, productivity, maturity, and structure or physiognomy.
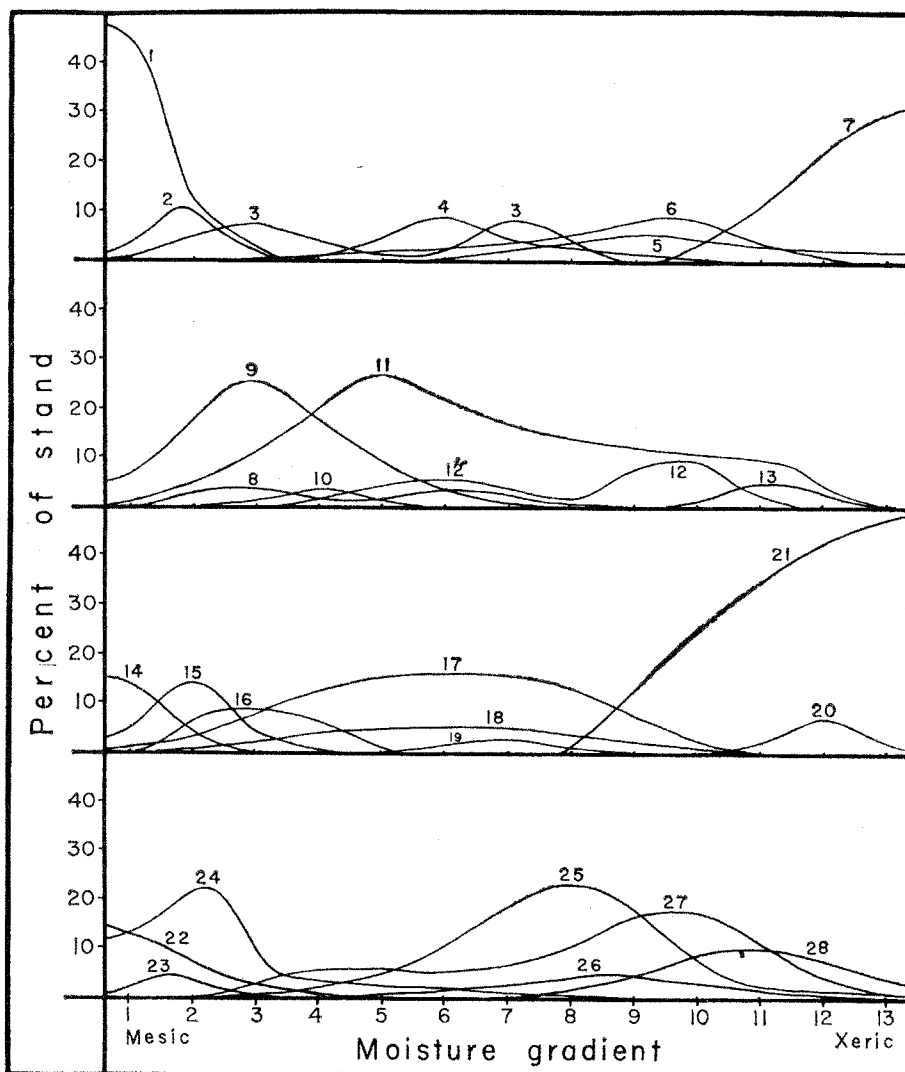

Fig. 7. Plant populations along an environmental gradient. The gradient is the topographic moisture gradient from mesic (moist) ravines (at left) to xeric (dry) southwest-facing slopes (at right), between elevations of 460 and 760 meters in the Great Smoky Mountains. Populations of major tree species are plotted by percentages of the total numbers of tree stems over 1 centimeter in diameter 1.4 meters above the ground; the curves are smoothed from data summarized in Table 1 of Whittaker (54). All the species illustrated are part of the same vegetation gradient, but they are separated into four panels for the sake of clarity. Although, with 28 species and 13 steps of the gradient, some species must have their modes in the same step, the modes of species populations appear to be scattered along the gradient. Pairs of species having their modes in the same step of the moisture gradient may be shown to be differently distributed in relation to the elevation gradient (24). Some species are bimodal, with two ecotypes having different population centers (24). Plant communities intergrade continuously from cove forests (transect steps 1–4), through oak forests (steps 6–8), to pine forests (steps 10–13). The species are as follows: 1, *Halesia monticola*; 2, *Acer saccharum*; 3, *Hamamelis virginiana*; 4, *Carya tomentosa*; 5, *Nyssa sylvatica*; 6, *Pinus strobus*; 7, *P. rigida*; 8, *Quercus borealis*; 9, *Tsuga canadensis*; 10, *Fagus grandifolia*; 11, *Acer rubrum*; 12, *Qu. alba*; 13, *P. echinata*; 14, *Aesculus octandra*; 15, *Betula alleghaniensis*; 16, *B. lenta*; 17, *Cornus florida*; 18, *Carya glabra*; 19, *C. ovalis*; 20, *Qu. marilandica*; 21, *P. virginiana*; 22, *Tilia heterophylla*; 23, *Cladrastis lutea*; 24, *Liriodendron tulipifera*; 25, *Qu. prinus*; 26, *Qu. velutina*; 27, *Oxydendrum arboreum*; 28, *Qu. coccinea.*

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Conclusion

Dominance and diversity form an area of complex and often obscure relationships, not subject to neat, unitary formulation. The preceding discussion may illustrate, in this area of ecological study, the "loosely ordered complexity" of natural communities (45), and the consequent need for sufficiently wide observations to allow one to judge which observations are of general and which are of exceptional phenomena. In this, as in other areas, the ecologist needs to seek a balanced perspective in which he neither loses sight of complexities in his fondness for theory, model, and generalization nor loses sight of significant general relationships in his fondness for the professional's knowledge of details, complexities, and exceptions. Recognition that dominance-diversity relations lack neatness is essential to a realistic understanding of these relations; this lack of neatness does not reduce their significance or the fascination of the suggestions about community organization which they offer.

The interpretations suggested follow Hutchinson (8, 26, 46) in applying the concepts of "niche" and "niche space" to diversity problems and assume that the principle of Gause applies to vascular plant species. According to the principle of Gause (and Volterra), or the principle of competitive exclusion (26, 47), no two species in a stable community occupy the same niche and compete for the same environmental requirements in the same part of intracommunity space at the same time. The idea may suggest another idea from across the sciences—the principle of Pauli, that no two electrons occupy the same atomic "niche." Theory of population dynamics, experiments with laboratory populations, and some observations of competitive relations of species in the field support the belief that if two species are in direct competition, one or the other must become extinct or one or both must so evolve that their requirements are no longer identical. Competition among vascular plants has been investigated (48), and aspects of niche differentiation in plant communities observed (49); but the application of the principle of Gause to vascular plants is often obscure. It must for the present be assumed that differences of degree in the requirements for different environmental resources exist among the vascular plant

species in a community. These differences of degree among plants would be analogous to the phenomenon of character displacement (46, 50) among animals—quantitative differences in dimensions (of the order of 1.2 to 1.0 or 1.3 to 1.0) between related species, differences which permit them to occur together in communities as partial competitors in those parts of their geographic areas in which both species occur. Some differences in environmental requirements of plant species are expressed in morphology, but others which result from physiological differences and are not expressed in morphology are likely to be unknown to us.

Such marginal differentiation in environmental requirements may also permit competing plant species to have widely overlapping distributions. Cases are observed in which two animal species in direct competition replace one another abruptly along an environmental gradient (26, 51). The principle of Gause may imply, for these direct competitors, a sharp boundary of competitive exclusion at the point along a gradient where the competitive advantage shifts from one to the other. Such population discontinuities are, though of much theoretical significance, of rare occurrence in relation to the immense number of cases in which distributions of competing species overlap broadly (24, 52, 53). Because plant species populations in general overlap broadly along an environmental gradient and population densities of the species change gradually along the gradient, composition of the communities changes gradually and continuously along the gradient (Fig. 7) (18, 24, 54, 55). Some relatively steep transitions or "zonal" boundaries between communities occur, but these appear to be of exceptional rather than general significance and are apparently not based on competitive exclusion (24). Green plant species are undoubted competitors for light, water, and nutrients, but they must be partial competitors with small differences in requirements which make possible their occurrence together in communities, their broad distributional overlap, and the continuity along environmental gradients of the communities they form.

The environmental gradients of a landscape may be conceived as forming a multidimensional habitat-space, to which there corresponds a multidimensional pattern of populations and communities. In this pattern each spe-

cies has its own population center and distribution, differing from those of all other species according to the principle of species individuality (56). Along a given environmental gradient, and probably in habitat-space, the centers or modes of species populations are scattered, as if randomly located (Fig. 7) (24, 54). It has been thought that species evolution in communities might produce clusters of species with distributional centers close together in habitat-space and separated from the clusters of other species (18, 24, 52, 57). It is probable, however, that if such clusters exist they are exceptional (18, 24). It is suggested that, rather than evolving to form clusters of associates, green plant species predominantly evolve toward dissociation (in the sense of scattering of distributional centers in habitat-space and in geographic areas), by which means they escape direct competition within their population centers.

Niche differentiation and habitat differentiation may thus be very closely related aspects of the same tendency to evolve away from direct competition. Alpha diversities of communities and gamma diversities of landscapes are expressions on different levels of the same evolutionary processes. The evolution of differences in environmental requirements permits many species to exist together in the landscape, broadly and continuously overlapping in varied combinations to form the landscape's many, intergrading communities. A common principle of evolutionary diversification in environmental relations and interrelations of species, by which direct competition is avoided, may thus relate such varied ideas and observations as the principle of Gause and the phenomenon of character displacement, adaptive radiation and the richness in species of the living world, the rare occurrence of discontinuities of competitive exclusion and the more general broad overlap of partial competitors, the principle of species individuality, and the continuity of natural communities.

Summary

Most plant communities consist of several or many species which compete for light, water, and nutrients. Species in a given community may be ranked by their relative success in competition; productivity seems to be the best meas-

ure of their success or importance in the community. Curves of decreasing productivity connect the few most important species (the dominants) with a larger number of species of intermediate importance (whose number primarily determines the community's diversity or richness in species) and a smaller number of rare species. These curves are of varied forms and are believed to express different patterns of competition and niche differentiation in communities. It is probably true of plants, as of animals, that no two species in a stable community occupy the same niche. Evolution of niche differentiation makes possible the occurrence together of many plant species which are partial, rather than direct, competitors. Species tend to evolve also toward habitat differentiation, toward scattering of their centers of maximum population density in relation to environmental gradients, so that few species are competing with one another in their population centers. Evolution of both niche and habitat differentiation permits many species to exist together in communities as partial competitors, with distributions broadly and continuously overlapping, forming the landscape's many intergrading communities.

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17. Measurements used to compute Simpson indexes for the tree stratum are estimated volume increments (apparent volume growth of wood, computed from half the area of wood growth per year at 1.4 meters above the ground times tree height, summed for all individuals of the species of trees and arborescent shrubs in the 0.1-hectare quadrats). Simpson indexes for the shrub stratum are based on dry weights of current twigs with leaves, clipped in the 20 1-square-meter undergrowth quadrats; those for herbs are based on dry weights of clippings at ground level in the same quadrats. The curves of Fig. 3 are based on multiplication of the same field data by conversion factors to obtain estimated above-ground net annual production [R. H. Whittaker, *Ecology* **43**, 357 (1962); ———, N. Cohen, J. S. Olson, *ibid.* **44**, 806 (1963)]. Although conversion factors vary with plant species, plant size, and environment, the reader can obtain curves similar to those of Fig. 3 for the other published samples (*16*) by using average conversion factors for strata: above-ground net annual production of trees per unit of estimated volume increment $= 2.0$ g/cm³; above-ground net annual production of shrubs per weight of current-twig clipping $= 3.0$ g/g; above-ground net annual production of herbs per weight of clipping $= 1.0$ g/g.

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