Evolution and Measurement of Species Diversity
Author(s): R. H. Whittaker
Source: *Taxon*, Vol. 21, No. 2/3 (May, 1972), pp. 213-251
Published by: International Association for Plant Taxonomy (IAPT)
Stable URL: http://www.jstor.org/stable/1218190
Accessed: 03-11-2015 08:58 UTC

REFERENCES
Linked references are available on JSTOR for this article:
http://www.jstor.org/stable/1218190?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

EVOLUTION AND MEASUREMENT OF SPECIES DIVERSITY*

*R. H. Whittaker***

Summary

Given a resource gradient (e.g. light intensity, prey size) in a community, species evolve to use different parts of this gradient; competition between them is thereby reduced. Species relationships in the community may be conceived in terms of a multidimensional coordinate system, the axes of which are the various resource gradients (and other aspects of species relationships to space, time, and one another in the community). This coordinate system defines a hyperspace, and the range of the space that a given species occupies is its niche hypervolume, as an abstract characterization of its intra-community position, or niche. Species evolve toward difference in niche, and consequently toward difference in location of their hypervolumes in the niche hyperspace. Through evolutionary time additional species can fit into the community in niche hypervolumes different from those of other species, and the niche hyperspace can become increasingly complex. Its complexity relates to the community's richness in species, its alpha diversity.

Species differ in the proportions of the niche hyperspace they are able to occupy and the share of the community's resources they utilize. The share of resources utilized is expressed in species' productivities, and when species are ranked by relative productivity (or some other measurement) from most to least important, importance-value or dominance-diversity curves are formed. Three types of curves may represent manners in which resources are divided among species: (a) niche pre-emption with strong dominance, expressed in a geometric series, (b) random boundaries between niches, expressed in the MacArthur distribution, and (c) determination of relative importance by many factors, so that species form a frequency distribution on a logarithmic base of importance values, a lognormal distribution. The forms of importance-value curves do not permit strong inference about resource division, but are of interest for their expression of species relationships and bearing on measurement of diversity.

Two aspects of alpha diversity are to be measured. Diversity in the strict sense is richness in species, and is appropriately measured as the number of species in a sample of standard size. Slope measurements, in contrast, express the steepness of the importance-value sequence. Of the slope measurements the Simpson index expresses dominance or relative concentration of the importance values into the first or first few species, whereas the Shannon-Wiener index expresses the relative evenness or equitability of the importance values through the whole sequence. A new index, expressing equitability as number of species per logarithmic cycle of the importance-value sequence, is suggested.

Given a habitat gradient (e.g. elevation or soil moisture conditions) species evolve to occupy different positions along this gradient. The various habitat gradients of a landscape may also be conceived as a multidimensional hyperspace, and species evolve toward occupation of different positions in this hyperspace. Along a particular habitat gradient species populations have scattered centers and usually overlap broadly, forming a community continuum or coenocline. Through evolutionary time additional species can fit themselves in along the coenocline. As they do so the extent of change in community composition along

---

the gradient increases. The extent of differentiation of communities along habitat gradients is beta diversity. The total or gamma diversity of a landscape, or geographic area, is a product of the alpha diversity of its communities and the degree of beta differentiation among them. The species' position in a landscape of communities, as described in terms of both habitat and niche relationships, may be termed its ecotope.

Two approaches to measuring beta diversity have been most useful. For a transect along a given coenocline, the degree of species turnover or compositional change may be measured through sample similarities and expressed as half-changes. When a set of samples are taken to represent differences in communities of a landscape or range of habitat along more than one habitat axis, beta differentiation for these samples may be expressed by the ratio of the total number of species represented in the samples to the mean number per sample.

Diversity of communities seems a resultant of non-extreme conditions, stable conditions, evolutionary and successional time, and the kind of community developed in that time. It is difficult to separate the effects of chronic environmental rigor, amplitude of regular fluctuation, and irregularity or unpredictableness of fluctuation. Diversities are low in many unstable environments, but certain desert communities subject to wide and irregular variation in precipitation have evolved high diversities in relation to this variation. Evolutionary time is difficult to measure, but is important as the dimension through which increase in alpha and beta diversity occurs. Alpha diversities of birds, and gamma diverstities of islands, appear to reach saturation or steady-state levels. It is suggested, however, that for terrestrial plants and insects increase of species diversity, with elaboration of the niche hyperspace and division of the habitat hyperspace, is a self-augmenting evolutionary process without any evident limit.

INTRODUCTION

Ecologists and systematists alike are beneficiaries of the richness of the living world in forms and species. This richness appears on varied levels — in the many species accommodated to one another in a community studied by an ecologist, the relative numbers of species in areas with which the biogeographer is concerned, and the great wealth of species of the living world as a whole that the systematist tries to bring to understanding through evolution and classification. Different fields have thus common interests in the phenomenon, of richness in species, to which the term "diversity" applies. I shall discuss here some interpretations of diversity as a product of evolution and what these imply for measurement of diversity. We may note first the extraordinary development of the study of diversity during the last fifteen years. Articles by Hutchinson (1957) and MacArthur (1957) offered promise of a new area of a different kind of ecology, one of an orderly, formal system of mathematical relationships by which diversities and the importance-value relations of species should become predictable. An area of study with its own literature now exists, and it is of interest to see how its characteristics relate to the promise.

NICHES AND ALPHA DIVERSITY

Let us for this article accept without argument the formulations of Volterra (1931) and Lotka (1932), and the principle of Gause (1934) or of competitive exclusion: In general, in a stable community, two species will not persist as direct competitors for the same resources. We must qualify the statement: species in a stable community may be found to differ not in resources but in their limiting mechanisms (Levin 1970). In any case they differ in their positions in the community — in resource use, time of activity, vertical location, relation to horizontal pattern, manner of population interaction with other species, etc. Position within the community in
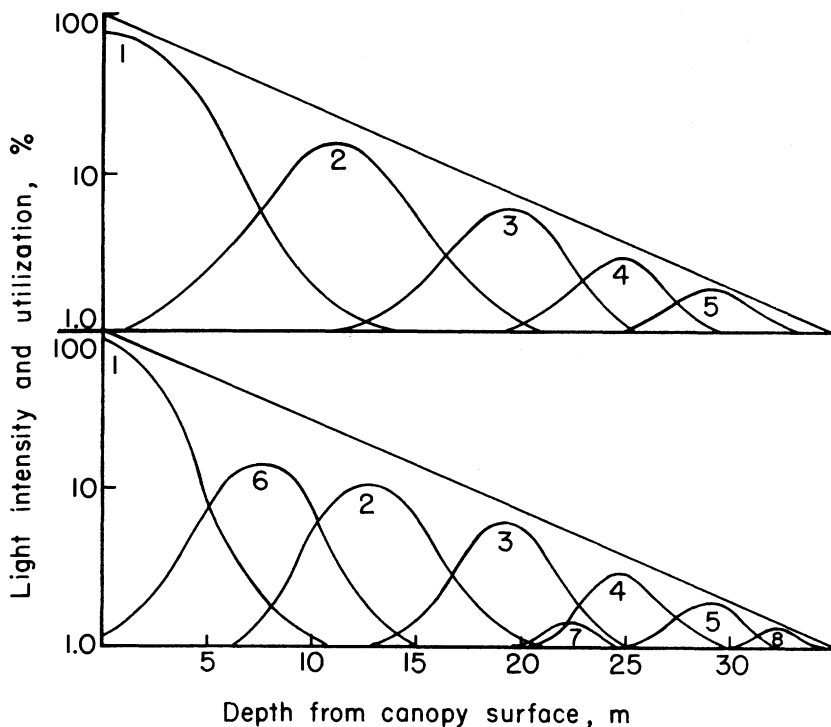
FIG. 1. Relations of species populations to a resource gradient (hypothetical). Light intensity as a resource is plotted on a logarithmic scale on the ordinate; available light decreases with increasing depth from the top of the forest canopy as indicated by the oblique lines. Species populations are adapted to different light intensities and have their centers scattered along the gradient. The bell-shaped curves represent relative utilization of light and relative population densities for the individual species. Five species occupy the gradient in the upper part of the figure; through evolutionary time three others enter and take positions along the gradient: Number 6, a strong competitor adapted to high light intensities fits in between 1 and 2, narrowing their distributions and increasing the "packing" of the resource gradient. Number 7, a weak competitor, while using a minor fraction of the resource, fits in with its adaptive center between 3 and 4. Number 8, a specialist adapted to very low light intensities, uses the low extreme of the gradient not effectively occupied before.

this sense is termed *niche*, a central concept of community theory derived from Elton (1927), Gause (1934), and earlier writings of Grinnell (1917). The community may be conceived as, in this respect, a system of variously interacting, niche-differentiated species populations.

We may consider a particular resource gradient, say, the gradient of light intensity from the top of the forest canopy downward. Along this gradient light is intercepted by foliage of plants for which it is a resource and suffers a logarithmic extinction (Fig. 1). Plant species must evolve to relate themselves to this gradient. If two species are competing in nearly the same positions along the resource gradient, their adaptations should tend, by the effects of selection, to diverge. From the divergence should ideally result, for a number of species, a staggering or spacing of their

populations along the gradient as indicated. There are some boreal forests in which the ideal structure is approached — five to seven major plant species that may include a canopy and a smaller tree species, a tall and a low shrub species, a tall and a low herb species, and a ground-level moss, with their foliages staged at heights that suggest a contracting geometric series from the canopy down. In most forests, however, a larger number of species occur with diverse adaptations to light and other factors, and with smaller differences in height between them. Given evolutionary time additional species can utilize a resource gradient; because of selective pressures their populations will in general fit in between the centers of the populations of other species (Fig. 1). As they do so their competition should reduce the breadths, or dispersions, along the gradient of species already present. The result of this process is the "packing" of an increasing number of species along the resource gradient (MacArthur 1970).

Evolution in response to light as a resource gradient produces a size-gradient of plants, and the plants are resources for herbivorous animals. The same principle of divergence applies to these animals; they will evolve to use different sizes and tissues of plants and in the process will evolve toward different sizes themselves. The herbivores will then form a third resource gradient, as prey of a range of sizes for predators. The predators in turn will form a size gradient, offering to secondary predators of different sizes different possibilities of harvest of primary predators, and of combinations of these with herbivores. Thus evolution of diversity on one level is transmitted upward, permitting evolution of further diversity in the trophic levels above it. Size is only one aspect of resource difference on a given level, and it is the full range of diversification on one level to which the level above may respond by diversification.

The last statement is improperly one-sided. Predators, by exerting different modes of control, make possible much of the diversity of their prey (Paine 1966, 1969). Grazing by herbivorous animals makes possible increased diversity of the plants they graze (Harper 1969). Effects of a given trophic level may thus enhance diversity of the level below it. For this effect we can offer at least two, overlapping interpretations: (a) The pressure of consumption from the upper level prevents over-dominance by any one species on the lower level. It thereby makes possible successful competition and survival of a larger number of lower-level species. (b) A number of upper-level species (and combinations among them) become, as different control mechanisms, a basis for increasing the number of niches on the lower level. Facilitation of increase in species number in interacting trophic levels is reciprocal. We should thus expect diversity to increase in parallel on any adjacent trophic levels and, in fact, throughout the various groups of interacting species that the community comprises.

For the community as a whole we can conceive an abstract niche "structure." Many of the attributes of niches can be treated as gradients — of organism size, vertical height, soil depth, diurnal time, seasonal time, proportions of different foods, intensities of different chemical defenses, etc. These gradients may be treated as axes defining a multidimensional, abstract "space", the niche hyperspace (Hutchinson 1957, Whittaker 1965, 1969, 1972). The niche hyperspace is a means of conceiving the way species relate to one another in the community as an interacting system. It is a conceptual construction about the evolution and organization of a community, and clearly should not be hypostatized or considered to have

existence except as an abstraction of some significant relationships in the community. As such it permits some interpretations of interest.

1. Each species evolves toward its own position in this space, different from that of any other species. Its position in and response to factors of the niche hyperspace defines its niche. If we think of the species as being limited to some range of each niche axis, then these limits outline for the species its niche hypervolume (Hutchinson 1957). To say that two species will not both survive if they have congruent hypervolumes, or if the hypervolume of the weaker competitor is wholly within that of the stronger, paraphrases the principle of Gause. It may be preferable, however, to think that each species occupies a vaguely outlined, cloud-like space that differs from, but may overlap broadly with, those of other species. Species evolve not so much toward mutually exclusive hyper-volumes as toward different locations of their centers in the hyperspace. If we knew enough about niche relationships it should be possible to "ordinate" species, arranging them by relative positions on niche axes in the niche hyperspace (Whittaker 1967, 1970a, Wuenscher 1969). Mac-Arthur et al. (1962) have, in fact, related the population clouds of bird species to one another in a hyperspace defined by foliage density axes; and structural dimensions of plant communities have been used as expressions for the dimensions of niche axes to predict species diversities of birds (MacArthur 1964, MacArthur & MacArthur 1961, Cody 1968) and desert lizards (Pianka 1967).

2. In evolutionary time the number of species in the community can grow — by fitting species in between other species along existing resource gradients, by the reciprocal facilitation of diversity growth by interacting groups, and by the extension of existing and addition of new niche axes. The possibilities for niche space division among species may increase exponentially with increase in number of niche axes — as shown by Mac-Arthur (1964) for the relation of bird species diversities to densities of different foliage layers as axes. There is no evident intrinsic limit on the increase in species number, with increased packing and elaboration of axes of the niche hyperspace. The addition of species to communities is a self-augmenting, self-facilitating evolutionary process (Hutchinson 1959, Whittaker 1969); the result of this process is community, within-habitat, or *alpha* diversity.

IMPORTANCE VALUES

There is a second consequence of this evolution of species in communities to be considered — the patterns of relative importances of species. Let us consider that the niche hyperspace, minus axes that are not interpretable as resources, is also a hyperspace of resource gradients. Species evolve characteristics that imply not only different positions in the hyperspace, but different sizes of the resource hypervolumes they occupy in different communities. In a given community species will differ in the ranges of resources they are able to command in competition with other species. The range of resources used is expressed in a species' productivity. We wish thus to ask how the resource hyperspace is divided among species, as this division is expressed in relative productivities of species. Productivities are not easily measured, and in many cases we must compare species by some other "importance value" — for animals population density or species
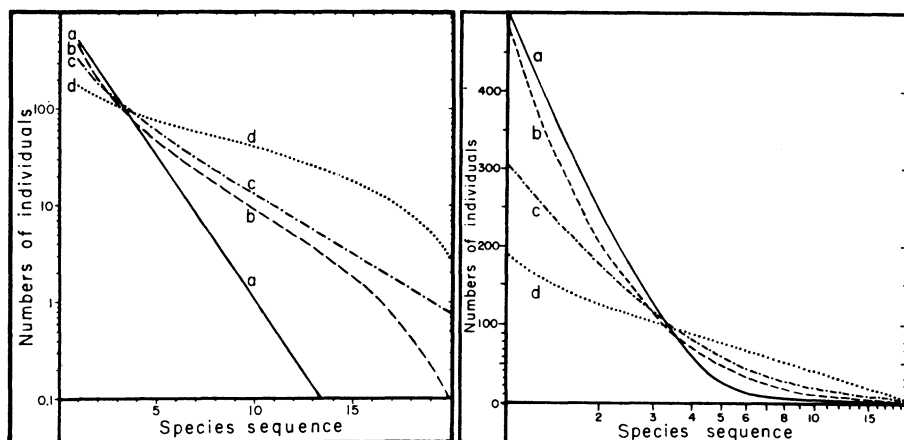
FIG. 2. Forms of dominance-diversity, or importance-value, curves for different treat-ments of the axes. Numbers of individuals, on the ordinate, are plotted against species number in the sequence from most to least abundant, on the abscissa. The four types of curves illustrated in both charts are: (a) geometric series, (b) lognormal distribution, (c) logarithmic series, and (d) MacArthur distribution. The curves are all computed for a hypothetical sample of 1000 individuals in 20 species; for curve a, $c = 0.5$, for curve b, $a = 0.2$ and $S_o = 2.26$, for curve c, $\alpha = 3.542$.

Left, with number of individuals logarithmic and species sequence linear, the geometric series becomes a straight line and the lognormal and MacArthur distributions sigmoid curves of different slopes.

Right, with number of individuals linear and species sequence logarithmic, the MacArthur distribution approaches a straight line, but all other forms become ("Type IV") J-curves.

biomass, for plants coverage, biomass, frequency, basal area, or density. Such measurements are usually applied to "taxocenes," or taxonomically defined fractions of communities. When the species are thus measured and then arranged in sequence from most to least important, they may be plotted in semilog graphs to form importance-value or dominance-diversity curves. The most generally appropriate chart uses importance values on a logarithmic ordinate and species sequence on a linear abscissa; such charts distinguish the distributions characterized below as the linear geometric, sigmoid lognormal, and flat-sigmoid MacArthur distributions (Whittaker 1965, 1970a). For a taxocene that may approach a MacArthur distribution a chart with importance values linear and species sequence logarithmic is preferable (MacArthur 1960), for on this plot the MacArthur distribution is quasilinear, whereas the geometric and lognormal distributions become hollow J-curves (Fig. 2). Observations of importance-value curves have led to these interpretations:

1. The geometric series and niche pre-emption hypothesis (Motomura 1932, Whittaker 1965, 1969): If one assumes that a first species in the sequence, the dominant, occupies a fraction k of the resource hyperspace, the second a fraction approximating k of that not occupied by the first, and so on, the species importances will form a geometric series, $p_i = p_1 c^{i-1}$. In this p_i is the relative importance of a given species (i.e. as the decimal fraction of the sum of corresponding importance values for all species sampled), p_1 is the relative importance of the first species, i is the position of a species in the sequence from most to least important, and c is the

218   TAXON VOLUME 21
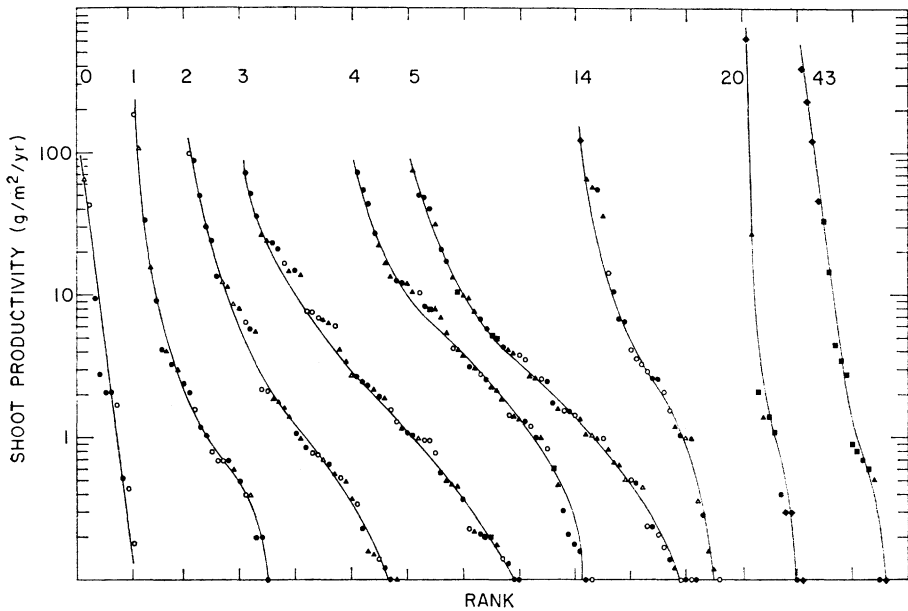
Fig. 3. Importance-value curves for an old field succession to oak-pine forest at Brookhaven National Laboratory, New York. The curve of the initial old field community (o) is roughly geometric (many such distributions lack the central cluster that appears in this case). With plant succession species are added until a later herbaceous stage (5) approaches a lognormal distribution. Similar relationships are shown by the old field data of Odum (1960) and Golley (1965). As woody plants enter the community (14), these establish strong dominance (20) with consequent steepening of the importance-value distribution and reduction of diversity. Sample (43) shows the beginning of a secondary increase in species diversity in the communities dominated by woody plants. Succession thus implies change both in species diversity and in slope of importance-value distributions. One measure of slope discussed below, E_c (measuring equitability, or the inverse of steepness, as mean number of species per log cycle of the sampled importance-value sequence), increased from 4.3 (sample o) to 17.1 (sample 5), then decreased to 2.7 (sample 20). (From unpublished data, courtesy of Buford Holt and G. M. Woodwell, Brookhaven National Laboratory.)

geometric series ratio and equals $1 - k$. There is no assumption that the first species was first in time, only that the species have struck competitive balances in which they take roughly equivalent fractions of resources not claimed by more effective competitors. The fractions, and the ratio c for their complements, may be expected to show random fluctuation from one species-pair to another in the sequence. (Alternatively the distribution itself can be interpreted as lograndom.) The occurrence of strong dominance in plant communities (and the relation to height and light shown in Fig. 1) suggest that the geometric form should often be observed in terrestrial plant communities (Fig. 3). Such is the case for the vascular plants of many communities of low species diversity, and for fractions or synusiae (such as each stratum or life-form taken by itself) of many communities of higher diversity (Whittaker 1965, 1969, Whittaker & Woodwell 1969, McNaughton 1968, Reiners et al. 1970). In some cases the strata as wholes are geometrically related (Whittaker 1969).

2. The MacArthur series and random niche boundary hypothesis: If one assumes that the boundaries between species hypervolumes in resource space are set at random, a very different distribution of importance values is predicted. MacArthur (1957, 1960, Vandermeer & MacArthur 1966) considered alternative modes of use of environment by species; the most interesting of these, in which species are limited by competition at randomly located boundaries, is fitted by the series (Whitworth 1897: 235, Barton & David 1956),

$$p_r = \frac{N}{S} \sum_{i=1}^{r} \frac{1}{S-i+1}.$$

S is the number of species in N individuals of the sample, i the sequence of species from least to most important, and r the position of a species with relative importance of p_r in the sequence. The series has come to be called the broken-stick or MacArthur distribution (probably against that author's wishes). By this hypothesis division of a given resource gradient is random on a linear scale; and the distribution of importance values implied is much "flatter" — of lower slope or less contrast between one species and the next in the sequence. Such importance value curves are approached by some samples of appropriate sizes for singing birds and some other animals (MacArthur 1960, King 1964, Hairston 1964). They are approached also, for what may be different reasons, by microcrustaceans deposited in sediments representing whole lake ecosystems (Goulden 1969, Deevey 1969). It is possible to interpret the geometric series as one limiting case approached by taxocenes or synusiae subject to scramble competition and the establishment of strong dominance, the MacArthur distribution as an opposite limiting case approached by other groups with contest competition and territorial relations stabilizing populations without development of dominance (Whittaker 1965, 1969).

3. The lognormal distribution: Both the niche pre-emption and random niche boundary interpretations are applicable to particular taxocenes of limited numbers of species in competitive contact with one another (contiguous niche hypervolumes). They should not be expected to apply to larger numbers of species most of which are not closely related in resource use (Whittaker & Woodwell 1969). As the number of species increases, the number of factors governing their relative importance increases. If relative importances are governed by many factors acting in partial independence, we should expect the importance values to form a frequency distribution, presumably a normal curve. If species importances are appropriately compared on a logarithmic, rather than a linear scale, as seems to be the case, then this frequency distribution becomes lognormal (Preston 1948, 1962). When species are classed by octaves or doubling units, a modal octave will contain the largest number of species, with intermediate importance values, and numbers of species per octave will decrease upward to a small number of dominants and downward to a small number of rarities, some of them beyond the reach of our sample from the community. The distribution of species in octaves may be expressed by,

$$S_r = S_o e^{-(aR)^2} , S_t = \sum S_r = S_o \sqrt{\pi/a},$$

in which S_r is the number of species in an octave R octaves distant from a modal octave containing S_o species, and a is a constant. Lognormal distributions are observed for a wide range of different kinds of samples (Preston 1948, 1962, Patrick et al. 1954, Williams 1953, 1964, Whittaker 1965, Batzli 1969); the samples must, however, be large if one is to observe the downslope of species numbers into octaves of increasing rarity. When a large sample is taken containing a good number of species, a lognormal distribution is usually observed, whether the sample represents a single community or more than one, whether distributions of the community fractions being combined are of geometric, lognormal, or MacArthur form. The constant a is usually around 0.2, but it is possible to make the lognormal curve reasonably fit most importance-value distributions from the near-geometric to the MacArthur form by varying the values of a and S_o.

4. The logarithmic series: A fourth treatment of importance value curves should be mentioned, the logarithmic series of Fisher et al. (1943, see also Williams 1953, 1964, Pielou 1969),

$$S = S_1 (1 + \frac{x}{2} + \frac{x^2}{3} + \ldots) = \alpha \log_e (1 + \frac{N}{\alpha})$$

In this S_1 is the number of species represented by single specimens, $S_1 x/2$ the number represented by two specimens . . .; x is a constant less than unity but approaching that value for large samples, and α is a constant and a slope-related diversity measurement. No theoretical justification is assumed for this series, which fits the ascending slope (of high importance values) of lognormal distributions.

Study of these curves leads not to a single characterization of the importance-value structure of communities, but to recognition of a range of intergrading forms of curves (Whittaker 1965, 1969). For interpretation of community process underlying these forms the curves are, unfortunately, a tactic of weak inference: a number of alternative hypotheses can be adduced to interpret a given form (Cohen 1968, Whittaker 1969). Study of the curves has given less insight into community organization than had been hoped, but has not been without value. There is, first, undoubted significance in contrast of pattern as marked as that between the geometric and the MacArthur distributions of a plant and a bird community, even if we are less than certain of the meaning of the difference. Second, the forms of these curves are important to problems of measuring diversity.

MEASUREMENT OF ALPHA DIVERSITY

Alpha diversity measurements are those applied to samples from particular communities. In principle it should be possible to characterize alpha samples by parameters of the lognormal distribution, S_t or S_o and a or σ, ($a = \sqrt{0.5}/\sigma$), but in practice it is often impossible to compute these. Two properties of samples — species numbers and relative importances — imply the need for measurements of two kinds: (a) diversity proper, or richness of the community in numbers of species, and (b) the character of the importance-value relations which, if we seek a single number, is a slope for the importance-value sequence. This slope relates to relative concentration of dominance, or to the inverse of this, relative flatness of the importance-value curves or evenness of the importance values. Diversity

and evenness are correlated; but the correlation is partial, and it is often desirable to measure species-richness and slope separately. The two aspects of slope — concentration of dominance in the first or first few species, and evenness for the whole sequence of species — bear a partial inverse correlation; and different measurements are appropriate for them. We thus desire more than one measurement and should like each to have such properties as: (a) relative independence of sample size, (b) low dispersion or vulnerableness to sample error, (c) conceptual appropriateness to the subject of measurement, and (d) dimensional correspondence with that subject and lucidity of expression of changes in it. The study of diversity is primarily about richness in species and we should prefer, though not necessarily require, diversity measurements to be interpretable in terms of numbers of species.

The most generally appropriate measure of diversity is simply S, the number of species per unit area as represented in some kind of standard sample. The sample is most often a quadrat of consistent (if arbitrarily chosen) area, in some cases a water volume. The virtues of standard samples by criteria (c) and (d) are balanced against weakness with regard to (a). Standard samples of different sizes are not simply comparable, though the approximately logarithmic relation of species number to sample area makes some comparisons possible. Species per quadrat measurements are also subject to rather large dispersions (b) because of irregularities of species distribution and different success in finding and determining rare species. Thus the measurement that is most appropriate, S, is by no means ideal.

Some limitations of species/quadrat as a measurement can be reduced by the relation of species number to the logarithm of sample size. The measurement is thus transformed from numbers of species per sample to a rate, d, at which species are added with expansion of the sample. A number of measurements of this type have been proposed: $d = S/\log A$ (Gleason 1922), $d = (S - 1)/\log N$ (Margalef 1958, 1967), or $d = S/\log N$ (Odum et al. 1960, Golley et al. 1965), $d = (S_m - \bar{S})/\log M$ (Dahl 1957, 1960), $d = S/\sqrt{N}$ (Menhinick 1964, 1967), $S = kA^d$ (Kilburn 1963, 1966), and the Fisher et al. (1943) relation given above (see also Auclair & Goff 1971). (A is sample area, M the number of sample quadrats with mean number of species $\bar{S}$ and a number of species S_m when combined.) Apart from the Fisher *alpha* they have not been much used or well evaluated for the study of community diversities. Several of them take the form, $S = a + d \log Q$, in which Q is sample size (usually N, number of individuals, M, number of samples, or A, area in m²). The constant a is in some cases set to zero, or for animal samples to 1. For areal samples from plant communities a is the y intercept of the line fitted to the quasilinear portion of the curve of S (as y) on $\log A$ (as x) and in some cases can be interpreted as a threshold diversity for a unit sample. Some non-areal diversity expressions, such as species per 1000 individuals or the number of species with relative importance values above a given percentage, describe points of the curve of S in relation to the log (or other function) of N. They thus do not measure areal diversity as such but (like H', to be discussed) infer relative diversity from slope. To the extent that the equation given (imperfectly) fits relations of species numbers to both areas and numbers of individuals (Hopkins 1955, Preston 1962, Greig-Smith 1964), a threshold area, A_o (for a diversity of $S = 1.0$) is suggested, $A_o = A/N$

$= \exp [(1-a)/d]$. A_0 appears to express the scale of the community as a mean area per individual for all species and, if known, should in principle permit conversion of a non-areal into an areal diversity measurement.

Measures of slope itself are more varied. One of the simplest is the index of Simpson (1949, Eberhardt 1969).

$$C = \sum_{i=1}^{S} p_i^2, \text{ or } = \sum_{i=1}^{S} \frac{n_i (n_i - 1)}{N (N - 1)}.$$

In the second expression n_i is an importance value, not relativized, for species i and N is the total of such importance values for all species. These expressions give the probability that two individuals drawn at random from the sample will be of the same species if the first individual drawn has been (first form) or has not been (second form) returned to the sample when the second individual is drawn. The second form can also be in-terpreted as a frequency of encounters between individuals of the same species, its complement $D_c = 1 - C$ as a frequency of encounters between individuals of different species. Such an assessment of encounters from importance values may have very limited meaning, however; for many of the species sampled may have no significant interactions, and many of the significant interactions may not be expressed in similarity of importance values in a community sample. The Simpson index does express degree of "dominance" and for this expression the first form given (which is also the limit of the second for a very large sample) seems more directly ap-propriate, is more easily computed as the sum of the squares of relative importance values, and escapes the problem of importance values less than 1.0 from which 1.0 is subtracted in the second form.

The Simpson index is strongly affected by the importances of the first one, two, or three species; it is primarily a measure of dominance as degree of concentration of importance values in one or a few species. As such it is most appropriate to kinds of samples for which degree of dominance is of concern, as with samples from land plant communities. For these the Simpson index is suitable as judged by criteria (a) and (c) and, assuming the samples are large enough to represent effectively the proportions of the major species, criterion (b). As regards criterion (d), the Simpson index is not dimensionally related to species number or species importance values; but the square root of the Simpson index is strongly related to (but larger than) the importance of the first species, or a weighted estimate of the first species' importance from those of the first few species. A number of other variants on the Simpson index and related indices have been proposed (McIntosh 1967, Pielou 1969, Hurlbert 1971, Hendrickson & Ehrlich 1971), but I do not see sufficient reason to prefer any of these to the Simpson index itself. For sequences of geometric form the ratio c from a least squares fit is a slope measure (Whittaker 1961a), and its complement k is then also a weighted estimate of first-species dominance. McNaughton (1967, 1968, McNaughton & Wolf 1970) used as a dominance index $DI = p_1 + p_2$, the sum of the two highest relative importance values in a sample, and showed inverse correlation of this expression with diversity; Berger & Parker (1970) used for dominance $Dd = p_1$ and showed correlation with the Simpson Index. The Simpson C and these other expressions are

less appropriate when concern is not dominance of the first species but slope of importance-values through all the sampled species.

This over-all slope, approached as relative evenness of importance values from one species to the next throughout the sequence, is "equitability" (Lloyd & Ghelardi 1964). The most widely used equitability measure is the Shannon-Wiener information index, $H' = - \sum_{i=1}^{S} p_i \log p_i$.

There is no particular reason to interpret diversity or equitability as information or uncertainty, but the index has distinctive and appropriate qualities. It is most strongly affected by importances of species in the middle of the sequence. For large samples the index is consequently somewhat damped against effects of differences in quantitative proportions of the first few species. Effects of the rarer species are also damped, rendering the index, like C, relatively independent of sample size, criterion (a), for samples that are not too small. Low dispersions (b) for H' compared with S result, but the low dispersions are in part deceptive because H' is logarithmically related to species number. For samples with few species H' is neither of low dispersion nor stable against effects of quantitative relations among dominant species. For a given sample H' will, like other slope measures, change with change in the kind of importance value (density, coverage, productivity, biomass, etc.) to which it is applied (Dickman 1968, Wihlm 1968).

In application to some communities H' can give misleading results. Along an elevation gradient from 1720 to 1800 and 1920 m in subalpine forests of the Great Smoky Mountains, vascular plant species diversity declines in a trend as expressed in 21, 19, and 16 species per 0.1 ha, whereas H' increases from 1.22 to 1.46 and then decreases to 1.12 ($\log_2$) in response to change in dominance proportions between *Picea rubens* and *Abies fraseri* (data of Whittaker 1965). For bird communities with generally consistant importance-value curves H' is a strong correlate of S and a reliable index of species diversity (Tramer 1969). Even for birds, however, H' may fail to express significant differences in numbers of rare species (Karr 1971). For lake phytoplankton H' is strongly affected by importance values of the first 10-15 species and little affected by additional species (Sager & Hasler 1969); for these samples it is a weak correlate and poor expression of diversity. Further limitations of H' involve its curvilinear relation to diversity. Addition of 10 species to a MacArthur distribution of 10 species increases H' from 2.84 to 3.78; addition of 10 species to a distribution of 50 species increases H' from 5.07 to 5.32. In rich tropical communities the expression of diversity increase in H' is damped. The richer the community the less expressive the measurement, for H' asymptotically approaches a maximum that for many kinds of samples is around 5 (Margalef 1969). If, for example, the rate of diversity change along an elevational or latitudinal gradient is in question, diversity increase as expressed in S or α may accelerate into the low-elevation or tropical communities (Yoda 1967), whereas H' suggests a decreasing rate of increase. H' does not merit the unquestioning trust as an expression of diversity it has sometimes been granted. Pielou (1966b, 1967, 1969) has advocated the use in some circumstances of the Brillouin information index (Lloyd et al. 1968). I will differ, not with the mathematical quality of Pielou's treatment, but with suggested applications to community data. I doubt that for ecological

data the Brillouin index, which is more difficult to compute, more obscure in relation to importance-value slope, more sample-size dependent, and more questionable on theoretic grounds for samples that are never complete than the Shannon-Wiener index, is ever to be preferred to the latter.

As a more directly interpretable alternative to H' for non-areal samples, numbers of species in some such standard sample as 1000 individuals (Sanders 1968) can be used. The function of H' itself for ecological material may be clarified by observation of its antilogarithm. The expH' bears a strong and quasilinear relation to number of species per decimal cycle of geometric distributions, species number in the modal octave or cycle of lognormal distributions, and species per cycle or total species number for MacArthur distributions. H' thus expresses equitability of an importance-value distribution as a function related to the logarithm of the number of species per cycle. The manner in which H' gives an integrated expression of equitability from importance values through the full ranges of different types of distributions is convenient. H' seems the best all-purpose expression of equitability now in use. There are, furthermore, studies in which diversity cannot be directly measured but must be inferred from equitability of non-areal samples; H' (or exp H') is a useful measurement for this purpose. The Simpson index in the forms 1—C (Pielou 1969) and 1/C (Williams 1964), because of the strong influence on it of the importance values of the first or first few species, is a less effective index for inferring diversity than H'.

The relation of expH' to species per cycle suggests, however, the possibility of a more directly appropriate measure. Equitability may be conceived as a function of the variance of species importance values: the wider the dispersion of the importance values, the lower the equitability (Peet 1971). The variance is most simply stated, for relative importance values, as $V_e = \Sigma \, (p_i - \bar{p})^2$; V_e is related to the Simpson index, $V_e = C - 1/S$. For unrelativized importance values Peet (1971) develops the form,

$$V'_e = \frac{\Sigma \, n_i{}^2 - (N^2/S)}{(1 - 1/S) \, (N - S)^2}$$

The measure is relatively stable for sample size (for samples that are not too small) and is standardized to give values from zero, if all species are represented by equal numbers of individuals, to 1.0 for maximum concentration of individuals into the dominant species (with one individual each for the remaining species). Equitability is thus expressed by $1 - V'_e$.

From V_e an equitability expression in species per cycle may be developed. (i) The dispersion dimensionally most appropriate to importance values uses the logarithms of these to compute a standard deviation or hence, mean deviation, hence,

$$\sigma_e = \sqrt{\Sigma \, (\log n_i - \log \bar{n})^2/S}, \qquad MD_e = \Sigma |\log n_i - \log \bar{n}|/S,$$

in which $\bar{n}$ is the geometric mean. (ii) When computed from logarithms of importance values, the standard deviation (σ_e) and mean deviation (MD_e) express dispersions directly in cycles (those of the base of the logarithms) as units. Four times either σ_e or MD_e (including, for a lognormal distribution, about 95% of the importance-value sequence) is an expression of the range of the importance values in logarithmic cycles, and should be closely related to the distance in logarithmic cycles between the most and least important species in the sample, $D_e = \log n_1 - \log n_s$. (iii) The number of

species, S, divided by $4\sigma_e$, $4MD_e$, or D_e then expresses equitability as an average density or "packing" of species per cycle of the importance-value distribution (Fig. 3). The three expressions of range of importance values, and different logarithmic bases, provide a number of ways of computing equitability measures by this concept. The simplest measurement is $E_c = S/D_e$ using logarithms to the base 10. Mathematically the most interesting form may be $E'_c = S/4\sigma_e$ (using $\log_2$). When computed for a lognormal distribution (the sample for which is complete), E'_c bears a strict relation to the lognormal parameters, $E'_c = 0.354Sa = 0.628S_0$. E_c and E'_c are relatively, though not fully, independent of sample size and appear to have the advantage over H' by the other criteria given. Peet's (1971) and these equitability measures have not yet been adequately evaluated in practice, but they suggest that a better measure of equitability and means of inferring diversity than H' can be found.

Some other equitability expressions should be mentioned. Lloyd & Ghelardi (1964), observing the distinction of diversity and equitability, sought expression of the latter by the ratio of H' of a sample to that of a MacArthur distribution for the same number of species, H_m. The Mac-Arthur distribution was considered to represent maximum feasible equitability, in communities. Direct comparison of Shannon-Wiener indices $E = H'/H_m$, was rejected because of the logarithmic scale of H'. The ratio, $\varepsilon = S'/S$, was suggested instead, comparing actual number of species in a sample (S) with the number that would occur (S') in a sample with a MacArthur distribution and the same H'. Pielou (1966b, 1969) suggested $J = H'/\log S$, in which $\log S$ is equal to H' for S species given perfect equitability — identical importance values for all. Pielou did not refer to Lloyd & Ghelardi's rejection of the logarithmic ratio, but Buzas & Gibson (1969) have used an antilog equivalent, $\exp H'/S$. The index ε would in principle have the advantage because it is interpretable in terms of both species as units and a biologically realistic maximum equitability. However, all these indices suffer from the fact that they compare a stable with an unstable value (cf. Sheldon 1969, Hurlbert 1971). H' is relatively independent of sample size, but S, and hence $\log S$ and H_m are strongly influenced by sample size. There is no area-independent number of species in a community that may be used as a comparison. S, $\log S$, and H_m will change both more rapidly than H' with change in sample size, and more slowly than H' but in parallel with H' as equitability increases for samples of constant size. For standard samples of geometric or lognormal form E, ε, and J are functions of H'; they increase with increasing equitability but may offer no information on equitability beyond that expressed in H'. As sample size for the same importance distribution is varied, E, ε and J will vary, but interpretation of the variation as change in equitability will be in error. J, which has no biological standard of comparison, seems a rather unrevealing number. For samples that should be compared with the MacArthur distribution ε is still useful (Goulden 1966, 1969, Deevey 1969). In this use ε expresses not over-all evenness of importance values through the whole sequence (as H' does), but degree of departure of that sequence from the MacArthur form, departure usually in the direction of stronger dominance and geometric or lognormal form. The greater the departure the more the value of ε will be influenced by sample size as well as that departure. Other tests of goodness of fit to the MacArthur distribution are used by Hairston (1959), King (1964), and Kohn (1968).

One regrets the limitations of these ingenious efforts to obtain a second slope measure from H'. The reason for the effort may lie in the popularity of H' as a measurement for the inference of diversity; it has not been sufficiently emphasized that H' is itself an equitability measure. Some authors have gone beyond use of H' as the best equitability measure for inferring relative diversity, to try to solve the problem of biological interpretation of diversity by the simple postulation that H' *is* diversity. From this identification of diversity with a particular index of mixed meaning an unforeseen line leads to Hurlbert's (1971) conclusion that, since diversity can be identified with any of a number of indices, diversity per se does not exist.

For the measurement of alpha diversity relations I suggest, first, use of a direct diversity expression, S, as a basic measurement whenever possible, second, accompaniment of this by a suitable slope expression when the data permit. For vascular plants and other samples involving strong dominance S and C or $\sqrt{C}$ may be the most effective combination, for many kinds of samples S and H' or E_c may be desired, and when the MacArthur form is in question ε or one of the other tests of fit is of interest in combination with S, H', or E_c.

HABITATS AND BETA DIVERSITY

The environment of a species, as characterized primarily by physical and chemical qualities rather than position within a community, is the species' *habitat*. The habitats occupied by species in a given landscape intergrade along environmental gradients, and we can use these gradients as axes of a quite different kind of abstract space, a habitat hyperspace (Goodall 1963, Whittaker 1967, 1969, Whittaker & Levin 1972). The qualities of environments in a landscape are many. It simplifies treatment to abstract from the many factor-gradients a few major directions of environmental variation, complex-gradients along which many particular factors vary together. The habitat hyperspace for a landscape may thus be reduced to a manageable two to four or five axes, which may include such variables as elevation, moisture conditions as influenced by topographic position, soil fertility, and severity of disturbance. For each of these axes a species has a range of tolerance, a span of environmental conditions over which it is able to maintain a population in interaction with other species. The limits of these ranges outline in the hyperspace a hypervolume, as an abstract formulation of the species' habitat (Whittaker & Levin 1972, cf. Hutchinson 1957).

Extensive work in gradient analysis has dealt with the manner in which species populations relate to environmental complex-gradients (Whittaker 1956, 1967, 1970c). In general (a) each species has a bell-shaped distribution of binomial or Gaussian form, and (b) the modes or centers of these distributions are scattered along the gradient, while (c) in most cases the curves overlap broadly with one another, so that (d) the many species together form a population continuum, a community-gradient or coenocline (Fig. 4). The scattering of species centers along the gradient is of particular interest for it suggests that, even as species evolve toward difference of niche in a community as implied by the principle of Gause, they evolve also toward difference of habitat by which competition between them in their distributional centers is reduced. One expression of the result
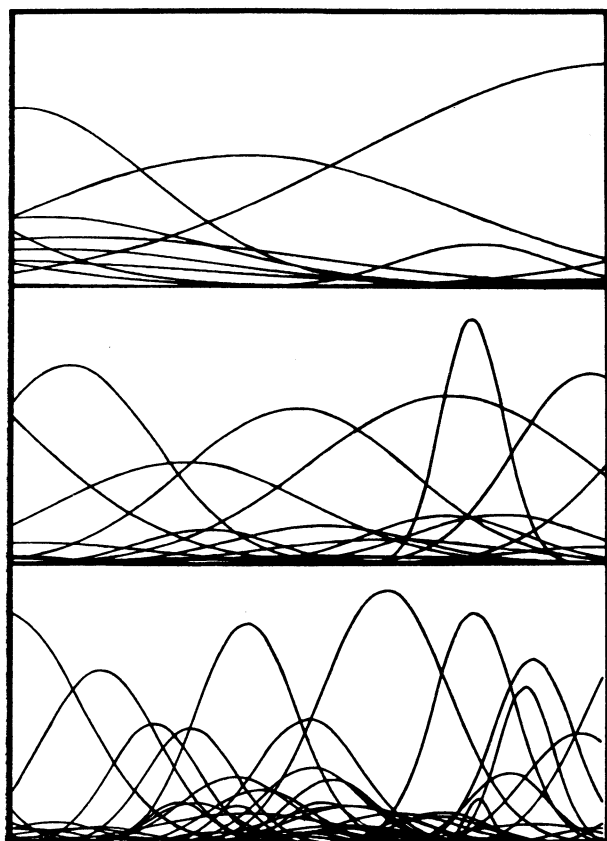
FIG. 4. Species distributions and community continuity along environmental gradients. Densities (or other importance values) of species form overlapping bell-shaped curves; the centers or modes of these curves are scattered rather than clustered along the gradient. Communities intergrade continuously along the gradient to form a "coenocline." The three coenoclines illustrated are from simulated data (Gauch & Whittaker 1971); with alpha and beta diversity doubling from the top to the middle and from the middle to the bottom coenoclines. The patterns of species distributions in these simulated coenoclines fit those of actual data as given by Whittaker (1956, 1960, Whittaker & Niering 1964, 1968).

is the principle of species individuality (Ramensky 1924, Gleason 1926): Each species is distributed according to its own physiological and life-cycle characteristics and ways of relating to environment (including other species); in general no two species have the same distribution. The fact species distributions much more commonly overlap broadly than exclude one another (Whittaker 1956, 1962, Terborgh 1971) implies that where these overlapping species meet they occupy niches at least partly different. The coenocline as a continuum of populations with scattered centers is a consequence of evolution of both niche and habitat difference among the species of a landscape (Whittaker 1965, 1969, 1970c). As additional species enter a landscape, they may fit into positions along particular coenoclines by location of their centers between those of species already present (Whittaker 1969, 1970a).

Species distributional relations to one another in the landscape can be represented by species ordination in relation to the habitat hyperspace (Whittaker 1967). Fig. 5 represents the population centers and distributions of seven major tree species in relation to the range of habitats in the Great Smoky Mountains (Whittaker 1956); a number of other techniques of species ordination have been described (Bray & Curtis 1957, Dagnelie 1960, Loucks 1962, Whittaker 1967, Green 1971, James 1971). For the distributional relations of species in habitat space two measures are of interest, to express
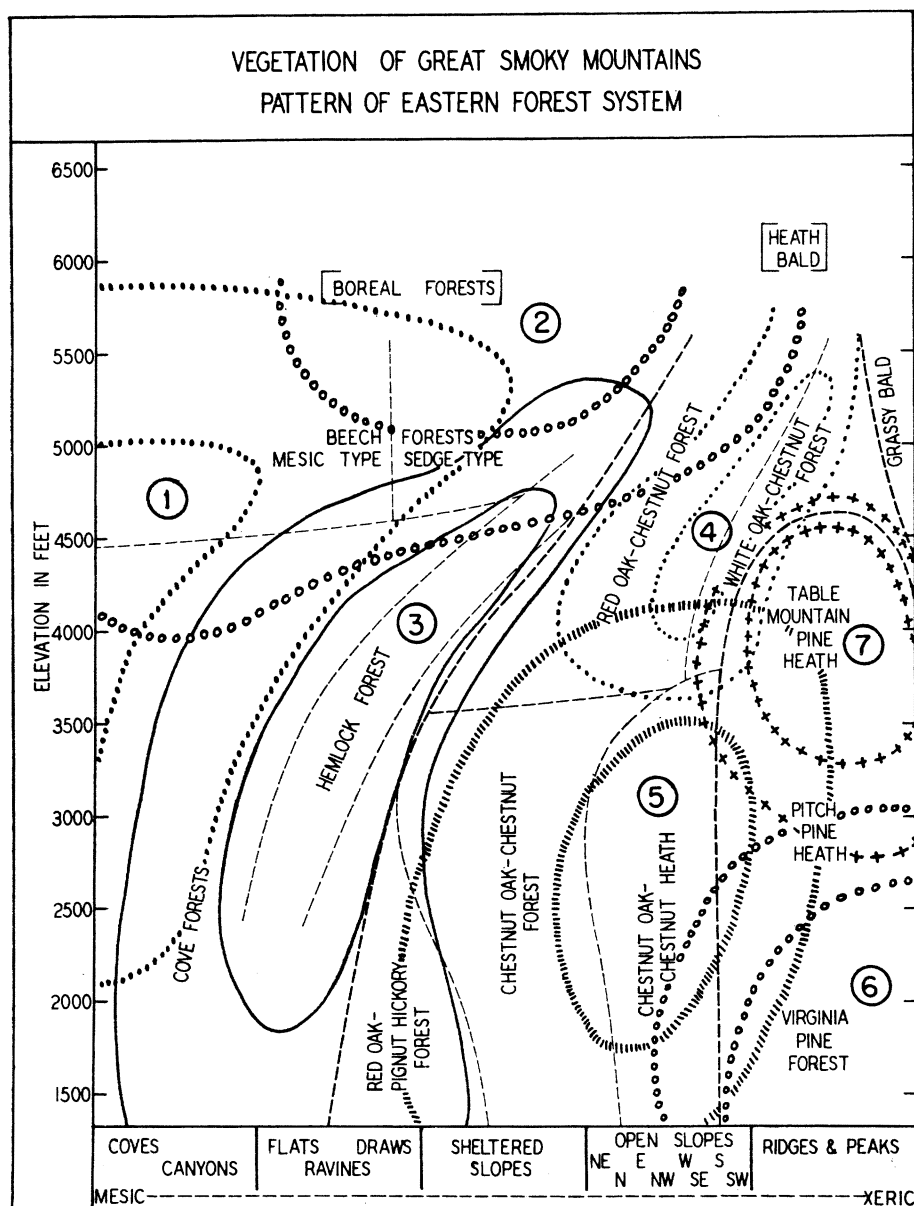
FIG. 5. A community pattern, with distributions of major tree species superimposed. Vegetation samples from the Great Smoky Mountains were plotted on the chart in relation to elevation and topographic position, and the boundaries of major types of communities were outlined (Whittaker 1956). Locations of the boundaries of these types are largely arbitrary, for the whole pattern forms a continuum of intergrading communities. Populations of seven major tree species are outlined: 1 *Aesculus octandra*, 2 *Fagus grandifolia*, 3 *Tsuga canadensis*, 4 *Quercus alba*, 5 *Quercus prinus*, 6 *Pinus virginiana*, and 7 *Pinus pungens*. Each population forms a binomial solid or "hill", with a center of maximum density at the circled number and lower densities (15% and 5% of stems in forest stands) outlined by the two contour lines. A transect, measuring species populations along an environmental gradient either vertically or horizontally across the pattern, gives a coenocline of apparently Gaussian species distributions like those of Fig. 4 (Whittaker 1956).

widths or amplitudes and degrees of overlap. Habitat width can be measured as a dispersion when data are adequate for species distributed along a particular gradient (McNaughton & Wolf 1970); but habitat breadth is often more easily measured by analogs of the Shannon-Wiener equitability index,

$$B' = -\sum_{j=1}^{M} p_j \log p_j, \text{ and of the reciprocal of the Simpson index, } B = 1 \bigg/ \sum_{j=1}^{M} p_j^2,$$

in which p_j is now the relative importance of a species in a given sample j as a decimal fraction of its total importance values in M samples, $\Sigma\, p_j = 1.0$ (Levins 1968, Price 1971, Colwell & Futuyma 1971). The simplest overlap measures are species association (considering presence and absence in samples only) as an analog of the Jaccard or Sørensen index indices given below, "percentage co-occurrence," $SA = 2M_c/(M_h + M_i)$ (Agrell 1945, Iversen 1954, Whittaker & Fairbanks 1958), and species correlation (comparing species importance values in samples) as an analog of percentage similarity,

$$SC = \sum_{j=1}^{M} \min\,(p_{hj}, p_{ij}) = 1 - 0.5 \sum_{j=1}^{M} \left| p_{hj} - p_{ij} \right|$$

(Whittaker & Fairbanks 1958, Schoener 1970, Price 1971, Colwell & Futuyma 1971). (M_h and M_i are the numbers of samples in which species h and i, respectively, occur and M_c the number in which both occur; p_{hj} and p_{ij} are importance values for species h and i in sample j when relativized as for the measures B and B'.) Point and rank correlation coefficients and a number of other measures can also be used (Goodall 1972, see also Levins 1968, Fienberg 1970, Colwell & Futuyma 1971), but some of these are more complex than the quality of community data is likely to justify. These measures when applied to habitat width and overlap, though they are sometimes termed "niche" measurements, should be clearly distinguished from niche measurements that express intracommunity relationships. Schoener (1970) and Price (1971) have applied measurements of the forms given to combinations of niche and habitat factors, thereby using them to express "ecotope" relations as these are considered below.

As additional species are packed into a coenocline, competition among species tends to narrow their distributions along the gradient. As species distributions become narrower, the extent of change in species composition of communities along the coenocline increases (Fig. 4). This extent of species replacement or biotic change along environmental gradients is *beta* or between-habitat diversity. To the habitat hyperspace there corresponds a community pattern or hyperspace, the axes of which are gradients of community composition or coenoclines (Whittakker 1956, 1967). One of the products of an indirect ordination of community samples should be a representation of such a compositional or community hyperspace. An ordination of species, rather than samples, generally reveals the scattering of their positions in habitat or community hyperspace (Whittaker 1967). Species, through evolutionary time, are added to the biota of the landscape, and each species fits itself into a habitat — and a corresponding hypervolume in the habitat hyperspace and central position in the community hyperspace — different from those of other species. Thus beta diversity may increase with time along each of the major axes of the community hyperspace. The com-

munity hyperspace may be conceived to "grow" by the addition of species and extension of the compositional lengths of its axes. Like alpha diversity, the community pattern of a landscape is an evolutionary product that tends by addition of species further to complicate itself in evolutionary time.

Richness in species of a range of habitats (a landscape, a geographic area, an island) is a *gamma* diversity and is consequent on the alpha diversity of the individual communities and the range of differentiation or beta diversity among them. We may, once more, employ the hyperspace formulation. If we combine the set of axes of the niche hyperspace with the set of axes for the habitat hyperspace (and axes for succession and disturbance that we may or may not wish to include among the latter), we derive a compound hyperspace (Whittaker 1969). The axes of this (niche + habitat + succession) hyperspace are now assumed to include all the ecological variables to which species in the landscape respond in their evolution. There is no established name for this compound hyperspace; we may refer to it here as the "ecotope hyperspace." A given species has its place in this hyperspace, set by the limits of its population tolerances in the face of interaction with other species, along those axes that affect its population. This place is its ecotope hypervolume as an abstract formulation of its place in a landscape of communities and species, its relation to the full range of habitat and niche factors affecting it (Whittaker & Levin 1972). The habitat + niche, as the species' position in (and response to) the landscape and its community, we may call "ecotope." The abstract ecotope hypervolume largely corresponds to the "fundamental niche" of Hutchinson (1957, 1965, Whittaker & Levin 1972).

The concept of "niche" should be kept in clear distinction from "fundamental niche" and "ecotope hypervolume." "Niche" and "habitat" are, like "diversity" and "equitability," a complementary pair of terms representing complementary concepts. In both cases confusion has resulted from appropriation of one of the terms to denote the combination of the two concepts. The concept of "niche" has its functional "place" in community theory, its "role" in interpretation of species evolution in communities. Confusion results from a sequence of changes in usage in which, first, the term "fundamental niche" for Hutchinson's abstract formulation is applied to the actual ecotopes of species, second the qualification "fundamental" is dropped so that niche + habitat is now termed "niche," and third intracommunity factors are left out of active consideration, so that in some cases "niche" is used as a term for habitat and "niche breadth" for habitat width. I intend no detraction from the incisiveness of Hutchinson's concept that is, along with work in gradient analysis, a source of the formulation offered here. As observed by Clarke (1954) separate terms are needed for the functional niche of Elton (1927) and Gause (1934) and the place niche or habitat-niche of later writings of Grinnell (1928) and as formulated by Hutchinson. For clarity "niche" should apply to a species' position in the community. The species' habitat + niche may be given abstract formulation as its "ecotope hypervolume"; and habitat + niche may be termed "ecotope" in application to actual relations of a species population to both environmental gradients and other species in communities in the field (Whittaker & Levin 1972).

The present formulation can be completed in terms of the ecotope hyperspace. The hyperspace may be conceived as an arena in which the species of a geographic area evolve in relation to one another. Under the influence of selection species move in the hyperspace; their movements are maneuvers

toward positions in the hyperspace that differ from those of other species in both niche and habitat factors (Whittaker 1969). If we might, in our view of the hyperspace, hold constant the niche axes and observe the relations of species and communities to habitat axes, we would observe the individualistic scattering of species in relation to habitats, their varied habitat widths and degrees of overlap, the community continua formed, the degrees of beta differentiation along these, and the the pattern of communities in relation to environmental gradients. If we held constant the habitat axes we would observe niche differentiation and importance-value relations, alpha diversity and equitability, and the community as a system of interacting species. I hope thus to justify the abstract course of this article through more than one hyperspace. The conception links together, as connected by common evolutionary roots in selection toward divergent uses of resources and reduction of competition, various properties of species and communities, research results from diversity studies and gradient analysis (Whittaker 1967, 1969, 1970c).

MEASUREMENT OF BETA AND GAMMA DIVERSITY

Gamma samples are usually alpha samples combined from several communities, or lists of species for geographic units, or non-areal samples (such as those of light traps) drawing species from a number of communities. Since gamma samples have the same dimensional characteristics (numbers of species, relative importance values) as alpha samples, the same measurements of diversity and slope are appropriate. The most extensive current research on gamma relationships uses numbers of species in areas (e.g. islands) as a diversity measure; for the non-areal samples a slope measure such as H' or E_c is appropriate.

Beta diversities, in contrast, are of different dimensional character; they are based on ratios or differences. For different research purposes such ratios or differences are to be measured either along particular coenoclines, or for sets of samples differing from one another along several axes of habitat or community hyperspace. A number of approaches are, however, possible (Whittaker 1960).

The essential relationship is most simple $\beta = \gamma/\alpha$. A generally appropriate measure is consequently, $BD = S_c/\bar{S}$, in which S_c is the number of species in a composite sample (combining a number of alpha samples), and $\bar{S}$ the mean number of species in the alpha samples. An analogous measure based on H' and comparing H_c' for a composite sample with the mean $\bar{H}'$ for alpha samples, $H'_c/\bar{H}'$, is subject to the damping effect of a ratio of logarithms. For non-areal samples a ratio of equitabilities as antilogs,

$$BD' = \exp H'_c/\exp H', \text{ or } BD_e = E_{cc}/E_c,$$

in which E_{cc} is calculated for the composite sample, is suggested. It is possible also to approach the measure as the ratio of the habitat range of the set of samples to the average habitat amplitudes of species in samples of the set, $BD = M_n/\bar{M}_s$, in which M_n is the number of samples in the set, and $\bar{M}_s$ is the number of these samples in which particular species occur, averaged for all species. The calculation is converse to that of $BD = S_c/\bar{S}$ and will give the same result. These measures are somewhat affected by sample size, but seem otherwise suitable in relation to the criteria given above. The units in which they express beta differentiation are full changes

in, or turnovers of, species composition. Identical samples (if such existed) would give $BD = 1$, two samples completely different in species composition a value of 2.0, etc. Since a single sample may be considered to have zero beta differentiation, it is appropriate to modify BD, BD' and BD_c as the ratios given minus 1.0.

A second set of possible expressions are based on measurement of relative similarity of samples. Three principal indexes of sample similarity are in use: (a) Coefficient of community,

$$CC = S_s/(S_j + S_k - S_s) \text{ (Jaccard 1902), or } CC = 2S_s/(S_j + S_k) \text{ (Sørensen 1948),}$$

in which S_s is the number of species shared by two samples, S_j is the number in the first and S_k the number in the second sample. (b) Percentage similarity,

$$PS = \sum_{i=1}^{s} \min(p_{ij}, p_{ik}) = 1 - 0.5 \sum_{i=1}^{s} |p_{ij} - p_{ik}| \text{ (Renkonen 1938, Whittaker 1952),}$$

$$\text{or } PS = 2 \sum_{i=1}^{s} \min(n_{ij}, n_{ik}) / (N_j + N_k) \text{ (Bray \& Curtis 1957),}$$

in which p_{ij} and p_{ik} are relative and n_{ij} and n_{ik} unrelativized importance values, for a given species in samples j and k with total unrelativized importance values of N_j and N_k. (c) Euclidean distance,

$$ED = \sqrt{\Sigma(n_{ij} - n_{ik})^2}, \text{ (Orloci 1966).}$$

Euclidean distance, though it is part of some current ordination techniques, has properties that do not recommend it for diversity studies (Gauch & Whittaker 1972). A number of more complex measures have been proposed (Dagnelie 1960, Whittaker 1967, Goodall 1972). MacArthur (1965, MacArthur et al. 1966, MacArthur & Wilson 1967) has used a measure of bird species difference based on H', $BSD = H'_c - (\bar{H}_j' + H_k')/2$, in which H_c' is computed for the two samples combined, $\bar{H}_j'$ and H_k' for the samples separately. BSD has served well as one of several measurements based on H' applied to bird communities, but is much more difficult to compute than CC and PS and is affected by its logarithmic scale. CC expresses the degree to which two samples are alike in species present, PS the degree to which they are alike in the quantitative proportions of their species. CC (Sørensen form) may be the more appropriate for diversity measurement, and the mean CC for samples of a set compared with one another in all possible directions is one expression their relative dissimilarity, or beta differentiation (cf. Koch 1957).

There are difficulties with such measurement. It is not the mean CC but its one complement that expresses relative dissimilarity. CC should not, however, be subtracted from 1.0 but from the smaller fraction that represents CC for comparison of replicate samples from the same community. This "internal association" or threshold dissimilarity, CC_o, ranges often between 70 and 90 per cent, and is not known for a given kind of sample until measured. It decreases with increasing alpha diversity and decreasing sam-

ple size (Whittaker 1952). The difference, $CC_0 - CC$, bears a curvilinear re-
lation to distance along a complex-gradient or coenocline (Gauch 1972).
Furthermore, the mean CC will be affected by sample density in the com-
munity pattern — the number of samples taken from a given range of com-
munity variation with environment.

   These points make difficult use of sample similarities for expression of beta
diversity in sets of samples having multidirectional relationships to one
another. Sample similarities can, however, be used to measure beta diversity
as degree of change in species composition along a particular coenocline (Fig.
6). Mean sample similarities are computed for different unit distances along
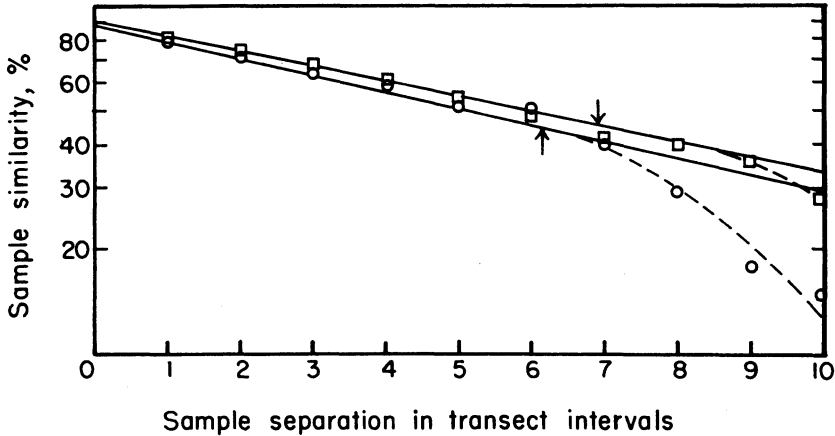

Sample separation in transect intervals

FIG. 6. Measurement in half-changes of the beta diversity of a coenocline. Mean similarities
of community samples decrease with increasing separation along a topographic moisture
gradient. The upper curve (squares) is for coefficients of community, the lower (circles) for
percentage similarities, for a transect of the topographic moisture gradient, 600-900 m
elevation belt, Siskiyou Mountains, Oregon (Whittaker 1960). The fitted lines permit
calculation of degree of turnover of species populations along the gradient in half-change
units; the arrows indicate points at which sample similarity is reduced to 50% of control
(for comparison of replicate samples). Half-change values for the coenocline are 1.59
using percentage similarity, 1.47 using coefficient of community.

the complex-gradient (for example, different numbers of 100 m elevation
intervals apart). A semilog plot of these sample similarities against distance
along the gradient permits extrapolation of the first part of the resulting
curve to zero distance, to estimate CC_0, and to the full length of the gradient
studied, to give an estimate of CC_n. (Because of the curvilinear relation of
CC to sample separation and the limited significance of very low values
(Gauch 1972), this estimate is preferred to the actual value for the ex-
treme samples.) A beta diversity expression is then, in "half-changes" $\beta = (\log CC_0 - \log CC_n)/\log 2$, $CC_n = CC_0 (0.5)^{\beta}$. The technique has been applied,
using PS, by Whittaker (1960) and Whittaker & Niering (1965, 1968); when
the Sørensen CC is used the result expresses beta diversity along an environ-
mental gradient in terms of half-units of species turnover. The measure seems
appropriate by the criteria given; in use with vegetation transects it is
reasonably, though not wholly, independent of sample size, and dispersions
of repeated measurements are not large if sufficient numbers of samples
are used and similarity measurements averaged. Different half-change values

are obtained for the different strata of the same communities; this fact reflects the relative independence of diversity relations of different strata and taxocenes (Fig. 7), rather than limitations of the technique.

Measures of the same form as those given for beta diversity are appropriate on other levels of community differentiation than that in relation to topography, elevation, and soils of a given landscape or limited geographic area. MacArthur (1969) shows that the ratios of species numbers for tropical and temperate faunas from corresponding areas increase as the areas are expanded, implying greater geographic, as distinguished from topographic, differentiation of tropical communities. Cody (1970) used BSD to compare Chilean bird samples and found that topographic beta diversity is lower than in the United States, but that geographic differentiation is about the same. Measurement of differentiation may also be extended downward to intracommunity pattern. Pielou (1966a) suggests as a measure of pattern diversity, $D = \bar{H}(n)/E[H(n)]$, in which $\bar{H}(n)$ is the mean Brillouin measure for a set of local subsamples and $E[H(n)]$ is the expected measure for the community as a whole. Pielou defines as low pattern diversity marked segregation of species and differentiation of subsamples, the reverse of the definition that seems appropriate for intracommunity patterning as an aspect of niche differentiation among species. As appropriate measures of pattern diversity,

$$DP = (S_c/S) - 1, DP' = (\exp H'_c/\exp H') - 1, \text{ and } DP_c = (E_{cc}/E_c) - 1,$$

are suggested, applied to small quadrats or subsamples within the community. These indices (like other measures of intracommunity pattern) are strongly affected by the size of the subsamples.

DIVERSITY AND ENVIRONMENT

As a final question, to what knowledge have diversity measurements led? I shall limit myself to terrestrial plant communities and certain comparisons because of the extent of the literature and discussions by other participants in the symposium. As a general statement: Alpha diversity of terrestrial plant communities seems a resultant of the combined influences of: — non-extreme conditions, stable conditions, evolutionary and successional time, and the kind of community developed in that time.

Environmental Favorableness

It is a natural first guess that alpha diversity and primary productivity should vary in parallel as community expressions of environmental "favorableness." However, different observers have suggested both direct (Connell & Orias 1964, MacArthur 1969) and inverse (Grice & Hart 1962, Margalef 1969, Whiteside 1970) correlations of diversity and productivity. It is likely that for land plant communities in general, over a broad range of environments, these two dimensions are non-correlated (Whittaker 1965, 1969).

Considered apart from productivity, diversities bear no simple relation to what we might regard as environmental "favorableness." In some areas maximum diversities are in most mesophytic communities (Ilvessalo 1922, Ogawa et al. 1961, 1965, Daubenmire & Daubenmire 1968, Carbiener 1970). In the Great Smoky Mountains maximum vascular plant diversity (and foliage insect diversity) is in the intermediate ranges of topographic moisture

FIG. 7. Species diversity of four taxocenes in the Great Smoky Mountains (data of Whittaker 1952, 1965). Contours outline numbers of tree, shrub and summer herb species in 0.1 ha quadrats, and alpha indexes for sweep samples of summer foliage insects.

gradients (Fig. 7, Whittaker 1956, 1952, cf. Curtis 1959, Monk 1965, 1967, Auclair & Goff 1971). In Washington diversities increase with increasing elevation and moisture from grasslands into the lower forests (Daubenmire 1970), whereas in the Santa Catalina Mountains, Arizona, plant diversities increase with decreasing elevation and increasing drought, from forest through woodland and grassland to the less extreme deserts (Whittaker &

Niering 1965). In many cases diversities increase with increasing soil fertility and (apart from saline soils) pH (Dahl 1957, Loucks 1962, Monk 1965, 1967, Frydman & Whittaker 1968, Prusinkiewicz 1970). Maarel & Leertouwer (1967), however, observed maximum diversity of dune vegetation at intermediate pH values (see also Thalen 1971). Diversity is in some cases higher on serpentine soils with their peculiar chemical characteristics, than on nearby non-serpentine soils (Whittaker 1954, 1960, McNaughton 1968). Diversity is generally reduced by chronic environmental stress on the community — overgrazing (Itow 1963), air pollution (Gordon & Gorham 1963, Skye 1968, Gilbert 1968, Hadjúk 1970), and gamma irradiation (Woodwell 1967, 1970, Woodwell & Whittaker 1968) —, but, as observed above, light or moderate grazing may increase diversity (Harper 1969).

Extreme conditions, however, act as a filter, demanding adaptations for which not all genetic lines have the potentiality, limiting the number of species that are able to cope with a harsh environment and survive there. As we should expect, diversities of vascular plants are low in extreme deserts, the high Arctic and Alpine, and on the salt soils of playas, salt-marshes, and mangrove swamps. Apart from extreme desert, the effect of drought on diversity is less marked than that of cold. Some warm and dry environments are rich in species; and it seems likely that cold, through physiological stress that must be complex but should include tissue freezing and more profound alterations of enzymatic and other function than those required for a warm dry season, exerts a major filtering effect on vascular plant diversity. The nature of the cold period differs between the seasonal cold of the Arctic and temperate Alpine and the nocturnal cold of the tropical Alpine, but the correlation of diversity with temperature is strong. In relation to temperature and other factors, however, it is difficult to distinguish the effects on diversity of three aspects of environmental rigor: (a) average conditions and chronic environmental hardship or rigor or shortage, (b) the relative amplitudes of regular environmental fluctuation, and (c) irregularity of fluctuation, environmental unpredictableness.

Instability

A number of observations suggest the strong effects of environmental instability, grouping together in this (b) and (c). The master gradient of diversity from the lowland Tropics to high latitudes and altitudes on land may be more a matter of extreme temperatures and their duration than of mean temperatures. The response of diversity to stability seems clearer in the increase in benthic diversity with increasing depth in the oceans (Sanders 1968, 1969, Hessler & Sanders 1967, Slobodkin & Sanders 1969).

Stability may act in large part through its effect on dependableness of resources. If fluctuation in resource levels is imposed on a resource gradient such as illustrated in Fig. 1, two effects will be expected. First, species occupying extremes of resource gradients, corners of the niche hyperspace, can no longer survive. Fluctuation has thus the effect of reducing the "size" of the niche hyperspace (Fig. 8). Second, species that have found positions along a resource gradient between other species may be subject to a periodically intensified competitive squeeze, against which the more vulnerable are not able to maintain their populations. Fluctuation thus limits the species packing, the number of species able to differentiate themselves in use of the gradient; the relation is given more formal discussion by MacArthur (1970,

MacArthur & Levins 1967). Fluctuation reduces both the lengths of niche axes that may be feasibly occupied, and the feasible extent of division of these axes among species.

Periodic resource shortage has further effects involving relations between trophic levels. Reliability throughout the year of prey species as resources permits increased survival and differentiation of predator species; and, as indicated above, the increased intensity and variety of control effects ex-
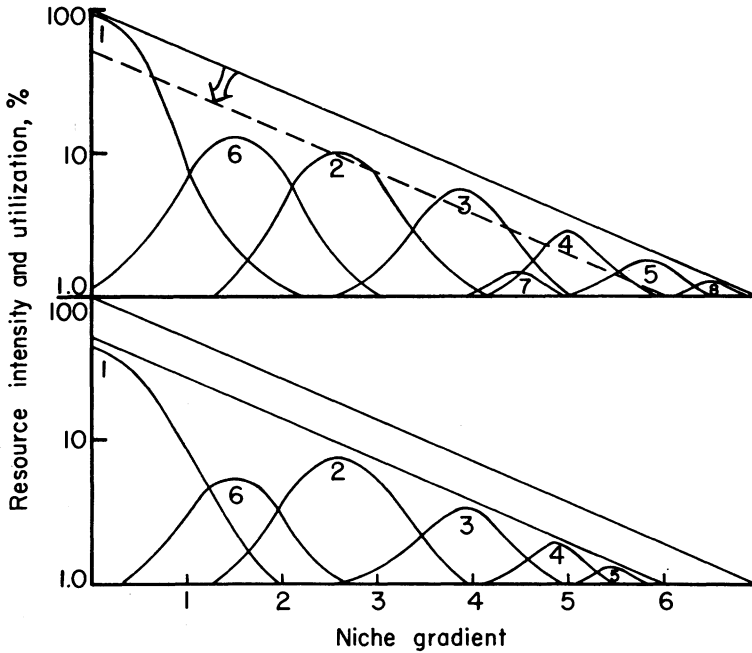

FIG. 8. Effect of environmental instability on the populations of species along a resource gradient. Contraction of resource availability by environmental fluctuation is indicated by the arrow and dashed line of the upper part of the figure. In the unstable environment species 7 and 8 are unable to maintain themselves, the latter because of resource failure and the former because of intensified competition with species 3 and 4 during the adverse period.

erted by the predators permits increased diversification of prey species. The more fluctuant the environment, the more this positive feed-back in diversity evolution between trophic levels may be limited by periodic failure of prey resources for the predators. The formulation should apply to other interacting groups: to plants and their consumers, to both plants and animals in relation to parasites and pathogens, and to plants in relation to pollinators and fungal symbionts. If, for example, the equable conditions of a tropical rainforest make possible survival of a larger number of species of mycorrhizal fungi, then these offer an increasing range of collaborative possibilities to vascular plants and their seedlings and an increasing differentiation of the forest-floor pattern in terms of fungal species present, while increasing diversity of vascular plant species and chemistry of their roots and decaying foliage offers an increasing range of possibilities to the fungal species. It thus appears that environmental instability, as it acts upon the feasibility of

marginal niches, competitive effects on niche packing, and implications of interactions for niche differentiation, is a major factor limiting species diversity. Instability acts to limit what is, by the formulation of this paper, the essential mode of evolutionary increase in alpha diversity — reciprocally influenced, self-augmenting increase in the range, complexity, and density of occupation by species of the niche hyperspace.

We may pursue the relation further in relation to two rich communities, the tropical rainforest and the Sonoran desert. It is in the tropical rainforest in its warm, humid, and equable climate that we find diversity to be highest on land (Dobzhansky 1950, Cain & Castro 1959, Richards 1952, Fischer 1960, Pianka 1966, Ashton 1969, Baker 1970). Among plants the diversity appears not only in the wealth of tree species, but in the occupation of special niches (such as those of the many vascular epiphytes and micro-epiphytes of leaves), representation of groups largely intolerant of more rigorous environments (rosette trees, lianas, and the vascular epiphytes), difference in mode of flowering and fruiting between the seasonal pulse of major species and more continuous staggering through the year of others (Janzen 1967b, Smythe 1970), and narrow specificities of biotic relations. Appropriateness of the niche concept for tropical rainforest trees has been doubted (Poore 1964, Fedorov 1966, Richards 1969), for it is difficult to conceive of differentiation in primarily non-biotic niche dimensions, such as vertical height, seasonal time, and soil depth and nutrient selection, that could account for the extent to which numbers of species in tropical forests exceed those in temperate forests. The dimensions of niche differentiation responsible for the contrast must be biotic, involving the relations of plants to other organisms (Ashton 1969). The species are of narrow morphological variability (Ashton 1969) and environmental tolerance (Janzen 1967a, Ashton 1969) including, probably, sensitivity to the complex internal pattern of niche loci available for plant seedlings (Whittaker 1969). Janzen (1970) has stressed as an aspect of this patterning the effect of the consumer species of a given tree species in preventing seedling growth beneath trees of that species. The effect may well be important in its context among the full range of interactions of the trees with other species, including effects through litter, soil chemistry, and mycorrhizal species on the environments of one anothers' seedlings. The enigma of the diversity of the tropical rainforest should be expected to open itself to no single key, and may be enigmatic to the extent we have yet to comprehend the full implications of biotic differentiation and interaction, the complexity of niche hyperspace that is feasible and has evolved in these forests.

In relation to this, the Sonoran desert is a paradox, as much so as the plankton (Hutchinson 1961). The environment is (a) chronically arid or semiarid, as expressed in its low mean annual precipitation, (b) widely fluctuant, with winter and summer rainy seasons and intervening periods of 2-4 months with little or no rain, and (c), unstable, with the precipitation during the rainy seasons varying widely from year to year, as expressed in a much higher coefficient of variation of annual precipitation than in the eastern forests (McDonald 1956, Whittaker & Niering 1965). Yet the perennial vascular plant diversity of the Sonoran desert of mountain slopes is higher than that of all but a few of the eastern forests, and on this diversity of perennials is superimposed a number of annual species several times larger in a given sample than in the eastern forests (Whittaker 1965, Whittaker & Niering 1965). One notes two kinds of adaptive calculus in relation to the

unstable climate. The perennials include a wide range of different growth-forms adapted to different timings and degrees of leaf persistence, supplementation or replacement of leaf by stem photosynthesis, means of water storage and reduction of aboveground surface — a diversity of ways of integrating year-around the unreliable precipitation resources. The annuals, in contrast, appear irregularly; a given 0.1 ha quadrat may include 30-40 species one spring, and 20-30 species, some of them uncollected the previous year, the following spring. Germination responses of desert annual species are acutely programmed to different environmental cues (Went 1949, Juhren et al. 1956, Cohen 1966, 1967). By specificity of germination behavior probability of survival is enhanced, but the species' appearance becomes irregular in response to year-to-year and place-to-place differences in environmental cues offered. The Sonoran desert includes some hundreds of annual plant species with differential responses to either the winter or the summer rainy season (Shreve 1964).

One must thus compromise the generalization that environmental instability inhibits the evolution of diversity. Given warm temperatures, a climate that is arid but not excessively arid, and time, evolution of many species with different responses to climatic fluctuation is possible. In a climate that is chronically variable from year to year, predictably unpredictable, specialization in response to that irregularity becomes a major means of niche differentiation. The Sonoran desert is rich on the basis of a niche hyperspace that differs from that of a rich forest in design, in the kinds and relative lengths of niche axes most significant in the evolution of species differentiation in the community.

Time

Diversity increases during many successions (Odum 1960, 1969, Richards 1952, Tagawa 1964, Margalef 1963, Monk 1967, Reiners et al. 1970). In some successions, however, diversity decreases from a late successional stage to the climax (Cajander 1925, Margalef 1969, Loucks 1970, Auclair & Goff 1971); such decrease may be characteristic of temperate forests of favorable environments, in which canopy closure and strong dominance in the climax suppress subordinate species that had occurred during succession. Reiners et al. (1970) followed changes in diversity and importance-value slope in far-northern forests in Alaska on glacial moraines of known age. Diversity increased rapidly during the first century and then more slowly, to an apparently stable maximum in a final muskeg stage. Diversity increased by a wave-like sequence of invasions by plants of the different strata, largely in order of increasing height. Diversity generally declined and dominance concentration increased in a particular stratum after the early period of its wave, while the stratum dominated the community. Diversity increases and decreases in different ways in different successions, and the decrease from subclimax to climax in some forests with closed canopies may contrast with continued increase into the climax in more open communities of incomplete coverage in less favorable environments (Auclair & Goff 1971). Auclair & Goff (1971) suggest a model describing diversity relations of terrestrial plant communities by such difference in successional change in diversity combined with relations of diversity to environmental gradients.

It is difficult, since communities include species with long histories in other communities, to treat evolutionary time as a variable to which diver-

sity can be related. Even the land exposed by retreat of continental glaciers recently (some thousands of years ago) is occupied by communities whose species migrated in from other areas, in which those species had evolved niche differentiations that made possible the diversity of the new communities. Some communities north of the limits of continental glaciation are poorer in species than comparable communities south of the glacial border, but the relation is not consistent. The effect of time seems clearest where communities of very distinctive soils, notably serpentines, may be compared in glaciated and unglaciated areas. The serpentine outcrops are for many plants islands; for species narrowly confined to serpentine cannot easily cross a considerable distance of normal soils between outcrops, and species not adapted to serpentine may be able to colonize an outcrop only in time, with evolution of serpentine ecotypes, if at all. Unglaciated serpentine mountains in the Klamath Region of northern California and southern Oregon support distinctive plant communities of high species diversity and very large numbers of narrowly endemic species that have accumulated on these land surfaces through millions of years (Whittaker 1954, 1960, 1961b). Glaciated serpentine mountains north from the Klamath Region in Washington, in contrast, bear vegetation of much less floristic distinction from surrounding communities, largely lacking in narrowly endemic species, and of low species diversity (Kruckeberg 1969a, 1969b). The floras of both serpentine areas may be in equilibrium with the surrounding floras (as regards short-term plant invasion and succession), but time has permitted evolution of a far richer equilibrium in the unglaciated mountains.

Diversity expresses both time and effects of environmental rigor and instability on the rates at which species are added to communities. As new species enter and find their niches in communities, some species already in these will become extinct. It is the accumulated difference in the rates of species addition and extinction, as both are affected by environmental severity, that should be expressed in difference of diversity observed in the present. If, however, the rate of species extinction increases as diversity increases, while the rate of species addition does not increase or increases more slowly, then extinction and addition may come eventually into balance and diversity into a steady state. The effect has been shown for island biotas (MacArthur & Wilson 1963, 1967, Simberloff & Wilson 1970, Diamond 1969), and alpha diversities of bird communities on continents appear to approach a saturation level or maximum correlated with stratal structure (MacArthur 1965, Cody 1966, 1968, Recher 1969). The saturation appears to be relative, for alpha diversities of bird communities are somewhat higher in tropical than in temperate forests because the tropical forests include larger numbers of rare species and food habits unrepresented in temperate forests (Orians 1969, Karr 1971). The observation suggests, however, the question: Does the saturation concept apply to land communities in general, or is their species diversity subject to indeterminate increase?

The time scale for this question is different from that of the steady states studied for island faunas (MacArthur & Wilson 1967, Wilson 1969), for those steady states relate to a continental source of species that is normally treated as constant. In the occurrence of saturation, as in their importance-value relations, birds may be a rather special case. There are limits to the extent to which passerene birds can divide their niche hyperspace, major axes of which are vertical position and food kind and size, while still obtaining resources sufficient for survival. No such limitation is apparent for

vascular plants, evolution of which has featured chemical coadaptation (Ehrlich & Raven 1965, Janzen 1968, Whittaker 1969, Whittaker & Feeny 1971) and elaboration of niche difference through more narrowly specific relationships with consumers, symbionts, and pollinators. The wide contrasts in diversities of plant communities in similar environments on the same and different continents suggests that these communities are not saturated. It is likely that evolutionary increase in diversity is, for the vascular plants and the animals and fungi with which they interact, indeterminate, or subject at least to no saturation limit that can be recognized in present communities (Whittaker 1969, cf. Simpson 1969, Stehli et al. 1969).

Dominance Structure

Contrasts among present communities reflect in part effects of dominance structure on diversity. The diversities of the different strata of plant communities are partially independent of one another (Fig. 7, Whittaker 1956, 1969, Daubenmire & Daubenmire 1968, Auclair & Goff 1971); they show in some cases inverse correlations. The effect of stratal relationships is marked in the diversity contrast of closed forests and open woodlands of drier environments or special soils in the same areas (Whittaker 1960, Whittaker & Niering 1965). The woodlands may offer more varied ground-level mosaics of shade and sun and soil characteristics than forests, in which light and soil conditions are strongly dominated by the trees. The range of undergrowth niches and number of undergrowth species is generally greater in a woodland, though the number of tree species may be higher in a forest. In temperate climates undergrowth species numbers generally exceed tree species numbers, and the woodlands are consequently in most cases richer in total vascular plant species.

Implications of dominance for diversity go beyond such relationships involving stratal coverage, to effects of particular dominant species. Forests dominated by evergreen tree species average lower in species diversity than deciduous forests of the same canopy coverage in summer. Mean numbers of vascular plant species in sets of 5 samples of o.1 ha each were 15 in evergreen vs. 41 in deciduous forests in the Great Smoky Mountains (Whittaker 1969). In some communities strongly dominated by a given species, allelopathic effects strongly limit the diversity of the undergrowth and thereby of the community as a whole (Muller 1966, Whittaker 1970b). It would be gratifying if the diversities of plant communities could be well predicted from correlations with time and the three aspects of environmental rigor. The correlations may be of interest but poorly predictive, for diversity is much affected by characteristics, especially dominance structure, of the particular communities that have evolved through the time available in the environments in question (Whittaker 1965, 1969).

Beta Diversity

Measurements are too few for extended comment on beta diversity relationships. In temperate-zone observations both alpha and beta diversities increase from maritime into continental climates (Whittaker 1960, Whittaker & Niering 1965, see also the boreal forest data of Kujala 1945 and LeRoi 1967). The continental climate has the wider annual fluctuation of temperature, but the maritime precipitation is at its minimum during the growing

season. Summer drought may be the stress responsible for lower diversity in the temperate maritime climate. There is contrast in this respect between the two great centers of forest diversity for the United States — the Southern Appalachians and the Klamath Region (Whittaker 1956, 1960, 1961b). The Southern Appalachians, in a more continental climate, have forests rich in alpha and topographic beta diversity; and the high gamma diversity for the area reflects primarily these aspects of diversity. The Klamath Region, in a maritime climate, has forests which from the *Sequoia* belt inland are low to intermediate in alpha and topographic beta diversity. The richness of the area flora results not so much from richness of individual communities and local topographic patterns, as from differentiation of communities in relation to steep climatic gradients and the remarkable mosaic of different parent materials (Whittaker 1960).

Beta diversities, like alpha diversities, in some cases show relatively independent variation in different strata of plant communities (Whittaker 1956, 1960). Low-elevation forests of the Great Smoky Mountains have comparably high beta diversities of the tree and herb stata; but at high elevations the low beta diversity of the tree stratum (strongly dominated by two species along the whole of the topographic moisture gradient) contrasts with the higher beta diversity of the undergrowth along the same gradient. The greater differentiation of the undergrowth than of the tree stratum in boreal forests is part of the basis of the Finnish approach to forest classification based on site-types distinguished primarily by undergrowth (Cajander 1949, Ilvessalo 1922, Kujala 1945). It is likely that forests show a broad trend of diversity relations (though complicated by other factors) from boreal forests with very low alpha and beta diversity of the tree stratum combined with somewhat higher alpha and beta diversity of the undergrowth, to warm temperate forests with intermediate or moderately high alpha and beta diversities of both tree stratum and undergrowth. It seems likely that the trend, extrapolated from the latter, implies tropical forests with very high alpha and beta diversity of the tree stratum but lower alpha and beta diversity in the undergrowth — the reverse relation to that in boreal forests.

The reasoning on evolution of diversity suggests that beta diversity for many groups should be higher in the lowland Tropics than in the Temperate Zone. There are suggestions that such is the case. MacArthur (1965, 1969) found local beta diversity and geographic differentiation were higher in tropical than in temperate bird communities. Work of Janzen & Schoener (1968) suggests high beta diversity in tropical insects, to which should correspond high beta diversity in the plants on which they feed. Janzen (1967) observes that species evolved in stable tropical climates may be narrow in habitat tolerances and consequently sensitive to geographic barriers that temperate species could more easily cross. A striking illustration of the principle appears in the limitations of many lowland tree species in Borneo by river systems (Ashton 1969). In birds, because of the occurrence of relative saturation of alpha diversity, alpha and beta diversity may show different geographic relationships (MacArthur 1965, 1969, Cody 1970). The observations available do not conflict with the expectation that in other groups alpha diversity, topographic beta diversity, and geographic differentiation of biotas should, as related evolutionary products, show largely parallel variation in relation to differences in climate and history.

CONCLUSION

The development of diversity theory in the past 15 years may have disappointed those who expected the construction in ecology of an area of neat, tight, rigorously formulated relationships as bases of prediction. To this statement the study of island biogeography (MacArthur & Wilson 1963, 1967) is a partial exception. Dealing with problems made more manageable by treatment of islands as bounded units whose biotas relate to a constant source, MacArthur & Wilson (1967) create an impressive mathematical analysis the complexity of which is their effort to do justice to this somewhat simplified case. Some biotas on continents, such as those of water bodies (Cairns et al. 1969), special parent-material outcrops (Whittaker 1960), caves (Culver 1970), and mountain summits (Vuilleumier 1970, Brown 1971) are partly island-like. For these as for true islands (Hamilton et al. 1963, Johnson et al. 1968) the study of diversity through correlations may be rewarding. More generally for continental biotas, however, the complex effects of time, aspects of environmental rigor, historic differences in availability of species from adjacent areas, and effects of community structure on diversity may be only partly disentangled by correlations. Correlation analysis serves as an aid to conceptual interpretation, but not as a basis of formal statement and deductive prediction.

This is to emphasize the importance of the biological and evolutionary, as well as of the formal and mathematical, perspective in the interpretation of diversity. Formal treatment has contributed much to the field, and the concepts of Hutchinson and MacArthur in particular have been the basis on which many biological and evolutionary questions were effectively asked. Yet there remains much of interest in this, as in other areas of biology, that will resist formal treatment. The biological perspective applies especially to problems of measurement. There is some hazard, in applying complex measurements and mathematical treatments to community data, of obscuring rather than clarifying relationships. Simple and more direct measurements are in general to be preferred; biological clarity should be valued above mathematical elegance when these do not coincide. If diversity is recognized as an evolutionary product, it may cause no surprise that no single measurement serves all purposes. The problems of measurement of such other products of evolution as intelligence, organic complexity, phylogenetic relationship, and organization may be noted.

Understanding of diversity has advanced by a tripartite exchange among field research, biological interpretation, and formal statement, with concepts and measurements the means of exchange among the three. More than any other author Robert MacArthur has maintained a range of interest and inquiry through the three areas, in a balance that supported his singularly effective development of theory. I should like in consequence to end with a reference of respect beyond the usual ways of citation, to one who has made the study of diversity so much his own and contributed so much.

References

AGRELL, I. 1945 — An objective method for characterization of animal and plant communities. Förhandl. K. Fysiogr. Sällsk., Lund 15(9): 63-77.
ASHTON, P. S. 1969 — Speciation among tropical forest trees: some deductions in the light of recent evidence. Biol. J. Linn. Soc. London 1: 155-196.

AUCLAIR, A. N. & F. G. GOFF 1971 – Diversity relations of upland forests in the western Great Lakes area. Amer. Nat. 105: 499-528.

BAKER, H. G. 1970 – Evolution in the tropics. Biotropica 2: 101-111.

BARTON, D. E. & F. N. DAVID 1956 – Some notes on ordered random intervals. J. Roy Stat. Soc., B, 18: 79-94.

BATZLI, G. O. 1969 – Distribution of biomass in rocky intertidal communities on the Pacific Coast of the United States. J. Anim. Ecol. 38: 531-546.

BERGER, W. H. & F. L. PARKER 1970 – Diversity of planktonic Foraminifera in deep-sea sediments. Science 168: 1345-1347.

BRAY, J. R. & J. T. CURTIS 1957 – An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27: 325-349.

BROWN, J. H. 1971 – Mammals on mountaintops: nonequilibrium insular biogeography. Amer. Nat. 105: 467-478.

BUZAS, M. A. & T. G. GIBSON 1969 – Species diversity: benthonic Foraminifera in western North Atlantic. Science 163: 72-75.

CAIN, S. A. & G. M. de OLIVEIRA CASTRO 1959 – Manual of vegetation analysis. Harper, New York. 325 pp.

CAIRNS, J. Jr., M. L. DAHLBERG, K. L. DICKSON, N. SMITH, & W. T. WALLER 1969 – The relationship of fresh-water protozoan communities to the MacArthur-Wilson equilibrium model. Amer. Nat. 103: 439-454.

CAJANDER, A. K. 1925 – Der gegenseitige Kampf in der Pflanzenwelt. Veröff. Geobot. Inst. Rübel, Zürich 3: 665-684.

CAJANDER, A. K. 1949 – Forest types and their significance. Acta Forest. Fennica 56(4): 1-71.

CARBIENER, R. 1970 – Un exemple de type forestier exceptionnel pour l'Europe occidentale: la forêt du lit majeur du Rhin au niveau du fossé rhénan. (Engl. & Germ. summs.) Vegetatio 20: 97-148.

CODY, M. 1966 – The consistency of intra- and inter-continental grassland bird species counts. Amer. Nat. 100: 371-376.

CODY, M. L. 1968 – On the methods of resource division in grassland bird communities. Amer. Nat. 102: 107-147.

CODY, M. L. 1970 – Chilean bird distribution. Ecology 51: 455-464.

COHEN, D. 1966 – Optimizing reproduction in a randomly varying environment J. Theoret. Biol. 12: 119-129.

COHEN, D. 1967 – Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. J. Theoret. Biol. 16: 1-14.

COHEN, J. E. 1968 – Alternate derivations of a species-abundance relation. Amer. Nat. 102: 165-172.

COLWELL, R. K. & D. J. FUTUYMA 1971 – On the measurement of niche breadth and overlap. Ecology 52: 567-576.

CONNELL, J. H. & E. ORIAS 1964 – The ecological regulation of species diversity. Amer. Nat. 98: 399-414.

CULVER, D. C. 1970 – Analysis of simple cave communities. I. Caves as islands. Evolution 29: 463-474.

CURTIS, J. T. 1959 – The vegetation of Wisconsin: an ordination of plant communities. Univ. Wisconsin, Madison. 657 pp.

DAGNELIE, P. 1960 – Contribution à l'étude des communautés végétales par l'analyse factorielle. (Engl. summ.) Bull. Serv. Carte Phytogéogr., Paris, Sér. B, 5: 7-71, 93-195.

DAHL, E. 1957 – Rondane; mountain vegetation in South Norway and its relation to the environment. Skr. Norske Vidensk.-Akad. Oslo, I. Mat.-Naturv. Kl. 1956(3): 1-374.

DAHL, E. 1960 – Some measures of uniformity in vegetation analysis. Ecology 41: 805-808.

DAUBENMIRE, R. 1970 – Steppe vegetation of Washington. Washington Agr. Expt. Sta. Tech. Bull. 62: 1-131.

DAUBENMIRE, R. & J. B. DAUBENMIRE 1968 – Forest vegetation of eastern Washington and northern Idaho. Washington Agr. Expt. Sta. Tech. Bull. 60: 1-104.

DEEVEY, E. S., Jr. 1969 – Specific diversity in fossil assemblages. Brookhaven Symp. Biol. 22: 224-241.

DIAMOND, J. M. 1969 – Avifaunal equilibria and species turnover rates on the Channel Islands of California. Proc. Nat. Acad. Sci. Washington 64: 57-63.

DICKMAN, M. 1968 – Some indices of diversity. Ecology 49: 1191-1193.

DOBZHANSKY, T. 1950 – Evolution in the tropics. Amer. Scient. 38: 209-221.

EBERHARDT, L.L. 1969 – Some aspects of species diversity models. Ecology 50: 503-505.

EHRLICH, P. R. & P. H. RAVEN 1965 – Butterflies and plants: a study in coevolution. Evolution 18: 586-608.

ELTON, C. 1927 – Animal ecology. Sidgwick & Jackson, London. 209 pp.

FEDOROV, An. A. 1966 – The structure of the tropical rain forest and speciation in the humid tropics. J. Ecol. 54: 1-11.

FIENBERG, S. E. 1970 – The analysis of multidimensional contingency tables. Ecology 51: 419-433.

FISCHER, A. G. 1960 – Latitudinal variations in organic diversity. Evolution 14: 64-81.

FISHER, R. A., A. S. CORBET & C. B. WILLIAMS 1943 – The relation between the number of species and the number of individuals in a random sample of an animal population. J. Anim. Ecol. 12: 42-58.

FRYDMAN, I. & R. H. WHITTAKER 1968 – Forest associations of southeast Lublin Province, Poland. (Germ. summ.) Ecology 49: 896-908.

GAUCH, H. G., Jr. 1972 – Sample similarity and coenocline distance. Manuscript.

GAUCH, H. G., Jr. & R. H. WHITTAKER 1971 – Coenocline simulation. Ecology (in press).

GAUCH, H. G., Jr. & R. H. WHITTAKER 1972 – Comparison of ordination techniques. Ecology (in press).

GAUSE, G. F. 1934 – The struggle for existence. Reprint, Hafner, New York, 1964. 163 pp.

GILBERT, O. L. 1968 – Bryophytes as indicators of air pollution in the Tyne Valley. New Phytol. 67: 15-30.

GLEASON, H. A. 1922 – On the relation between species and area. Ecology 3: 158-162.

GLEASON, H. A. 1926 – The individualistic concept of the plant association. Bull. Torrey Bot. Club 53: 7-26.

GOLLEY, F. B. 1965 – Structure and function of an old-field broomsedge community. Ecol. Monogr. 35: 113-137.

GOLLEY, F. B., G. A. PETRIDES & J. F. McCORMICK 1965 – A survey of the vegetation of the Boiling Springs Natural Area, South Carolina. Bull. Torrey Bot. Club 92: 355-363.

GOODALL, D. W. 1963 – The continuum and the individualistic association. (French summ.) Vegetatio 11: 297-316.

GOODALL, D. W. 1972 – Sample correlation and species similarity. In: Handbook of Vegetation Science, ed. R. Tüxen, Part V: "Ordination and classification of communities," ed. R. H. Whittaker. Junk, The Hague. (In press).

GORDON, A. G. & E. GORHAM 1963 – Ecological aspects of air pollution from an ironsintering plant at Wawa, Ontario. Canad. J. Bot. 41: 1063-1078.

GOULDEN, C. E. 1966 – La Aguada de Santa Ana Vieja: an interpretive study of the cladoceran microfossils. (Germ. summ.) Arch. Hydrobiol. 62: 373-404.

GOULDEN, C. E. 1969 – Temporal changes in diversity. Brookhaven Symp. Biol. 22: 96-102.

GREEN, R. H. 1971 – A multivariate statistical approach to the Hutchinsonian niche: bivalve molluscs of central Canada. Ecology 52: 543-556.

GREIG-SMITH, 1964 – Quantitative plant ecology. 2nd ed. Butterworths, London. 256 pp.

GRICE, G. D. & A. D. HART 1962 – The abundance, seasonal occurrence and distribution of the epizooplankton between New York and Bermuda. Ecol. Monogr. 32: 287-309.

GRINNELL, J. 1917 – The niche-relationships of the California Thrasher. Auk 34: 427-433.

GRINNELL, J. 1928 – Presence and absence of animals. Univ. Calif. Chron. 30: 429-450.

HADJÚK, J. 1970 – Einwirkung von Industrie-Exhalationen auf die Struktur der Phytocoenosen. (Engl. summ.) In, "Gesellschaftsmorphologie (Strukturforschung)," ed. R. Tüxen. Ber. Symp. Int. Vereinig. Vegetationskunde, Rinteln 1966, 10: 340-349.

HAIRSTON, N. G. 1959 – Species abundance and community organization. Ecology 40: 404-416.

HAIRSTON, N. G. 1964 – Studies on the organization of animal communities. J. Ecol. 52 (Suppl): 227-239.

HAMILTON, T. H., I. RUBINOFF, R. H. BARTH, Jr. & G. L. BUSH 1963 – Species abundance: natural regulation of insular variation. Science 142: 1575-1577.

HARPER, J. L. 1969 – The role of predation in vegetational diversity. Brookhaven Symp. Biol. 22: 48-62.

HENDRICKSON, J. A., Jr. & P. R. EHRLICH 1971 – An expanded concept of "species diversity." Notulae Nat. (Acad. Nat. Sci. Philadelphia) 439: 1-6.

HESSLER, R. R. & H. L. SANDERS 1967 – Faunal diversity in the deep-sea. Deep-Sea Res. 14: 65-78.

HOPKINS, B. 1955 – The species-area relations of plant communities. J. Ecol. 43: 409-426.

HURLBERT, S. H. 1971 – The nonconcept of species diversity: a critique and alternative parameters. Ecology 52: 577-586.

HUTCHINSON, G. E. 1957 – Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22: 415-427.

HUTCHINSON, G. E. 1959 – Homage to Santa Rosalia, or why are there so many kinds of animals? Amer. Nat. 93: 145-159.

HUTCHINSON, G. E. 1961 – The paradox of the plankton. Amer. Nat. 95: 137-145.

HUTCHINSON, G. E. 1965 – The ecological theater and the evolutionary play. Yale Univ., New Haven. 139 pp.

HUTCHINSON, G. E. 1967 – A treatise on limnology. Vol. II. New York.

ILVESSALO, Y. 1922 – Vegetationsstatistische Untersuchungen über die Waldtypen. Acta Forest. Fennica 20(3): 1-73.

ITOW, S. 1963 – Grassland vegetation in uplands of western Honshu, Japan. II. Succession and grazing indicators. Japan. J. Bot. 18: 133-167.

IVERSEN, J. 1954 – Über die Korrelation zwischen den Pflanzenarten in einem grönländischen Talgebiet. Vegetatio 5-6: 238-246.

JACCARD, P. 1902 – Lois de distribution florale dans la zone alpine. Bull. Soc. Vaudoise Sci. Nat. 38: 69-130.

JAMES, F. C. 1971 – Ordinations of habitat relationships among breeding birds. Wilson Bull. 83: 215-236.

JANZEN, D. H. 1967a – Why mountain passes are higher in the tropics. Amer. Nat. 101: 233-249.

JANZEN, D. H. 1967b – Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution 21: 620-637.

JANZEN, D. H. 1968 – Host plants as islands in evolutionary and contemporary time. Amer. Nat. 102: 592-595.

JANZEN, D. H. 1970 – Herbivores and the number of tree species in tropical forests. Amer. Nat. 104: 501-528.

JANZEN, D. H. & T. W. SCHOENER 1968 – Difference in insect abundance and diversity between wetter and drier sites during a tropical dry season. Ecology 49: 96-110.

JOHNSON, M. P., L. G. MASON & P. H. RAVEN 1968 – Ecological parameters and plant species diversity. Amer. Nat. 102: 297-306.

JUHREN, M., F. W. WENT & E. PHILLIPS 1956 – Ecology of desert plants. IV. Combined field and laboratory work on germination of annuals in the Joshua Tree National Monument, California. Ecology 37: 318-330.

KARR, J. R. 1971 – Structure of avian communities in selected Panama and Illinois habitats. Ecol. Monogr. 41: 207-233.

KILBURN, P. 1963 – Exponential values for the species-area relation. Science 141: 1276.

KILBURN, P. D. 1966 – Analysis of the species-area relation. Ecology 47: 831-843.

KING, C. E. 1964 – Relative abundance of species and MacArthur's model. Ecology 45: 716-727.

KOCH, L. F. 1957 – Index of biotal dispersity. Ecology 38: 145-148.

KOHN, A. J. 1968 – Microhabitats, abundance and food of *Conus* on atoll reefs in the Maldive and Chagos Islands. Ecology 49: 1046-1062.

KRUCKEBERG, A. R. 1969a – Plant life on serpentinite and other ferromagnesian rocks in northwestern North America. Synthesis 2: 15-114.

KRUCKEBERG, A. R. 1969b – Soil diversity and the distribution of plants, with examples from western North America. Madroño 20: 129-154.

KUJALA, V. 1945 – Waldvegetationsuntersuchungen in Kanada mit besonderer Berücksichtigung der Anbaumöglichkeiten kanadischer Holzarten auf natürlichen Wald-

böden in Finnland. Ann. Acad. Sci. Fennicae, Ser. A, 4 Biol. 7: 1-434.

LeRoi, G. H. 1967 – Ecological studies in the boreal spruce-fir forests of the North American taiga. I. Analysis of the vascular flora. Ecol. Monogr. 37: 229-253.

Levin, S. A. 1970 – Community equilibria and stability, and an extension of the competitive exclusion principle. Amer. Nat. 104: 413-423.

Levins, R. 1968 – Evolution in changing environments. Princeton Univ. Press, Princeton, N. J. 120 pp.

Lloyd, M. & R. J. Ghelardi 1964 – A table for calculating the "equitability" component of species diversity. J. Anim. Ecol. 33: 217-225.

Lloyd, M., J. H. Zar & J. R. Karr 1968 – On the calculation of information-theoretical measures of diversity. Amer. Midland Nat. 79: 257-272.

Lotka, A. J. 1932 – The growth of mixed populations: two species competing for a common food supply. Jour. Washington Acad. Sci. 22: 461-469.

Loucks, O. L. 1962 – Ordinating forest communities by means of environmental scalars and phytosociological indices. Ecol. Monogr. 32: 137-166.

Loucks, O. L. 1970 – Evolution of diversity, efficiency, and community stability. Amer. Zool. 10: 17-25.

Maarel, E. van der & J. Leertouwer 1967 – Variation in vegetation and species diversity along a local environmental gradient. Acta Bot. Neerlandica 16: 211-221.

MacArthur, R. H. 1957 – On the relative abundance of bird species. Proc. Natl. Acad. Sci. Washington 43: 293-295.

MacArthur, R. 1960 – On the relative abundance of species. Amer. Nat. 94: 25-36.

MacArthur, R. 1964 – Environmental factors affecting bird species diversity. Amer. Nat. 98: 387-397.

MacArthur, R. H. 1965 – Patterns of species diversity. Biol. Rev. 40: 510-533.

MacArthur, R. H. 1969 – Patterns of communities in the tropics. Biol. J. Linn. Soc. London 1: 19-30.

MacArthur, R. 1970 – Species packing and competitive equilibrium for many species. Theoret. Popul. Biol. 1: 1-11.

MacArthur, R. & R. Levins 1967 – The limiting similarity, convergence, and divergence of coexisting species. Amer. Nat. 101: 377-385.

MacArthur, R. H. & J. W. MacArthur 1961 – On bird species diversity. Ecology 42: 594-598.

MacArthur, R. H., J. W. MacArthur & J. Preer. 1962 – On bird species diversity. II. Prediction of bird census from habitat measurements. Amer. Nat. 96: 167-174.

MacArthur, R., H. Recher & M. Cody 1966 – On the relation between habitat selection and species diversity. Amer. Nat. 100: 319-332.

MacArthur, R. H. & E. O. Wilson 1963 – An equilibrium theory of insular zoogeography. Evolution 17: 373-387.

MacArthur, R. H., & E. O. Wilson 1967 – The theory of island biogeography. Princeton Univ. Press, Princeton. 203 pp.

Margalef, D. R. 1958 – Information theory in ecology. General Systems 3: 36-71. Transl. from Mem. R. Acad. Cienc. Arts, Barcelona 32: 373-449, 1957.

Margalef, R. 1963 – On certain unifying principles in ecology. Amer. Nat. 97: 357-374.

Margalef, R. 1967 – Some concepts relative to the organization of plankton. Oceanogr. Mar. Biol. Ann. Rev. 5: 257-289.

Margalef, R. 1969 – Diversity and stability: a practical proposal and a model of interdependence. Brookhaven Symp. Biol. 22: 25-37.

McDonald, J. E. 1956 – Variability of precipitation in an arid region: a survey of characteristics for Arizona. Univ. Ariz. Inst. Atmospheric Phys., Tech. Rept. 1: 1-88.

McIntosh, R. P. 1967 – An index of diversity and the relations of certain concepts to diversity. Ecology 48: 392-404.

McNaughton, S. J. 1967 – Relationships among functional properties of Californian grassland. Nature 216: 168-169.

McNaughton, S. J. 1968 – Structure and function in California grasslands. Ecology 49: 962-972.

McNaughton, S. J. & L. L. Wolf 1970 – Dominance and the niche in ecological systems. Science 167: 131-139.

MENHINICK, E. F. 1964 – A comparison of some species-individuals diversity indices applied to samples of field insects. Ecology 45: 859-861.

MENHINICK, E. F. 1967 – Structure, stability, and energy flow in plants and arthropods in a sericea lespedeza stand. Ecol. Monogr. 37: 255-272.

MONK, C. D. 1965 – Southern mixed hardwood forest of northcentral Florida. Ecol. Monogr. 35: 335-354.

MONK, C. D. 1967 – Tree species diversity in the eastern deciduous forest with particular reference to north central Florida. Amer. Nat. 101: 173-187.

MOTOMURA, I. 1932 – A statistical treatment of associations (In Japanese). Japan. J. Zool. 44: 379-383.

MULLER, C. H. 1966 – The role of chemical inhibition (allelopathy) in vegetational composition. Bull. Torrey Bot. Club 93: 332-351.

ODUM, E. P. 1960 – Organic production and turnover in old field succession. Ecology 41: 34-49.

ODUM, E. P. 1969 – The strategy of ecosystem development. Science 164: 262-270.

ODUM, H. T., J. E. CANTLON & L. S. KORNICKER 1960 – An organizational hierarchy postulate for the interpretation of species-individual distributions, species entropy, ecosystem evolution, and the meaning of a species-variety index. Ecology 41: 395-399.

OGAWA, H., K. YODA & T. KIRA 1961 – A preliminary survey on the vegetation of Thailand. Nat. Life SE Asia 1: 21-157.

OGAWA, H., K. YODA, T. KIRA, K. OGINO, T. SHIDEI, D. RATANAWONGSE & C. APASUTAYA 1965 – Comparative ecological study on three main types of forest vegetation in Thailand. I. Structure and floristic composition. Nat. Life. SE Asia 4: 13-48.

ORIANS, G. H. 1969 – The number of bird species in some tropical forests. Ecology 50: 783-801.

ORLOCI, L. 1966 – Geometric models in ecology. I. The theory and application of some ordination methods. J. Ecol. 54: 193-215.

PAINE, R. T. 1966 – Food web complexity and species diversity. Amer. Nat. 100: 65-76.

PAINE, R. T. 1969 – A note on trophic complexity and community stability. Amer. Nat. 103: 91-93.

PATRICK, RUTH, M. H. HOHN & J. H. WALLACE 1954 – A new method for determining the pattern of the diatom flora. Notulae Nat. (Acad. Nat. Sci. Philadelphia) 259: 1-12.

PEET, R. K. 1971 – Problems in the study of diversity in southern Wisconsin forests. M.S. thesis, Univ. Wisconsin, Madison. 174 pp.

PIANKA, E. R. 1966 – Latitudinal gradients in species diversity: a review of concepts. Amer. Nat. 100: 33-46.

PIANKA, E. R. 1967 – On lizard species diversity: North American flatland deserts. Ecology 48: 333-351.

PIELOU, E. C. 1966a – Species-diversity and pattern-diversity in the study of ecological succession. J. Theoret. Biol. 10: 370-383.

PIELOU, E. C. 1966b – The measurement of diversity in different types of biological collections. J. Theoret. Biol. 13: 131-144.

PIELOU, E. C. 1967 – The use of information theory in the study of the diversity of biological populations. Proc. 5th Berkeley Symp. Math. Stat. Prob., 1966, 4: 163-177.

PIELOU, E. C. 1969 – An introduction to mathematical ecology. Wiley-Interscience, New York. 286 pp.

POORE, M. E. D. 1964 – Integration in the plant community. J. Ecol. 52 (Suppl): 213-226.

PRESTON, F. W. 1948 – The commonness, and rarity, of species. Ecology 29: 254-283.

PRESTON, F. W. 1962 – The canonical distribution of commonness and rarity. Ecology 43: 185-215, 410-432.

PRICE, P. W. 1971 – Niche breadth and dominance of parasitic insects sharing the same host species. Ecology 52: 587-596.

PRUSINKIEWICZ, Z. 1970 – Die Zahl der auf dem Minimi-Areal vorkommenden Gefäss-pflanzenarten als Mass für die Fruchtbarkeit der Waldböden, (Engl. summ.) In, "Gesellschaftsmorphologie (Strukturforschung)," ed. R. Tüxen. Ber. Symp. Int. Vereinig. Vegetationskunde, Rinteln 1966, 10: 282-296.

RAMENSKY, L. G. 1924 – Die Grundgesetzmässigkeiten im Aufbau der Vegetationsdecke

(Russian). Vêstnik Opytn. dêla Sredne-Chernoz. Obl., Voronezh. (Bot. Centbl., N.F. 7: 453-455, 1926).

RECHER, H. F. 1969 – Bird species diversity and habitat diversity in Australia and North America. Amer. Nat. 103: 75-80.

REINERS, W. A., I. A. WORLEY & D. B. LAWRENCE 1970 – Plant diversity in a chronosequence at Glacier Bay, Alaska. Ecology 52: 55-69.

RENKONEN, O. 1938 – Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. (Finn. summ.) Ann. Zool., Soc. Zool.-Bot. Fennica Vanamo 6(1): 1-231.

RICHARDS, P. W. 1952 – The tropical rain forest: an ecological study. Cambridge Univ., Cambridge. 450 pp.

RICHARDS, P. W. 1969 – Speciation in the tropical rain forest and the concept of the niche. Biol. J. Linn. Soc. London 1: 149-153.

SAGER, P. E. & A. D. HASLER 1969 – Species diversity in lacustrine phytoplankton. I. The components of the index of diversity from Shannon's formula. Amer. Nat. 103: 51-59.

SANDERS, H. L. 1968 – Marine benthic diversity: a comparative study. Amer. Nat. 102: 243-282.

SANDERS, H. L. 1969 – Benthic marine diversity and the stability-time hypothesis. Brookhaven Symp. Biol. 22: 71-81.

SCHOENER, T. W. 1970 – Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51: 408-418.

SHELDON, A. L. 1969 – Equitability indices: dependence on the species count. Ecology 50: 466-467.

SHREVE, F. 1964 – Vegetation of the Sonoran Desert. In: "Vegetation and Flora of the Sonoran Desert," by F. Shreve & I. L. Wiggins, 1: 9-186. Stanford Univ., Stanford.

SIMBERLOFF, D. S. & E. O. WILSON 1970 – Experimental zoogeography of islands. A two-year record of colonization. Ecology 51: 934-937.

SIMPSON, E. H. 1949 – Measurement of diversity. Nature 163: 688.

SIMPSON, G. G. 1969 – The first three billion years of community evolution. Brookhaven Symp. Biol. 22: 162-177.

SKYE, E. 1968 – Lichens and air pollution: a study of cryptogamic epiphytes and environment in the Stockholm region. Acta Phytogeogr. Suecica 52: 1-123.

SLOBODKIN, L. B. & H. L. SANDERS 1969 – On the contribution of environmental predictability to species diversity. Brookhaven Symp. Biol. 22: 82-95.

SMYTHE, N. 1970 – Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. Amer. Nat. 104: 25-35.

SØRENSEN, T. A. 1948 – A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. Biol. Skr., K. Danske Vidensk. Selsk. 5(4): 1-34.

STEHLI, F. G., R. G. DOUGLAS & N. D. NEWELL 1969 – Generation and maintenance of gradients in taxonomic diversity. Science 164: 947-949.

TAGAWA, H. 1964 – A study of the volcanic vegetation in Sakurajima, south-west Japan. I. Dynamics of vegetation. Mem. Fac. Sci. Kyushu Univ., Ser. E (Biol.) 3: 165-228.

TERBORGH, J. 1971 – Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. Ecology 52: 22-40.

THALEN, D. C. P. 1971 – Variation in some saltmarsh and dune vegetations in the Netherlands with special reference to gradient situations. Acta Bot. Neerlandica 20: 327-342.

TRAMER, E. J. 1969 – Bird species diversity: components of Shannon's formula. Ecology 50: 927-929.

VANDERMEER, J. H. & R. H. McARTHUR 1966 – A reformulation of alternative (b) of the broken stick model of species abundance. Ecology 47: 139–140.

VOLTERRA, V. 1931 – Variations and fluctuations of the number of individuals in animal species living together. "Animal ecology with especial reference to insects," by R. N. Chapman, pp. 409-448. McGraw-Hill, New York.

VUILLEUMIER, F. 1970 – Insular biogeography in continental regions. I. The northern Andes of South America. Amer. Nat. 104: 373-388.

WENT, F. W. 1949 – Ecology of desert plants. II. The effect of rain and temperature on germination and growth. Ecology 30: 1-13.

WHITESIDE, M. C. 1970 – Danish chydorid Cladocera: modern ecology and core studies. Ecol. Monogr. 40: 79-118.

WHITTAKER, R. H. 1952 – A study of summer foliage insect communities in the Great Smoky Mountains. Ecol. Monogr. 22: 1-44.

WHITTAKER, R. H. 1954 – The ecology of serpentine soils. IV. The vegetational response to serpentine soils. Ecology 35: 275-288.

WHITTAKER, R. H. 1956 – Vegetation of the Great Smoky Mountains. Ecol. Monogr. 26: 1-80.

WHITTAKER, R. H. 1960 – Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30: 279-338.

WHITTAKER, R. H. 1961a – Estimation of net primary production of forest and shrub communities. Ecology 42: 177-180.

WHITTAKER, R. H. 1961b – Vegetation history of the Pacific Coast states and the "central" significance of the Klamath Region. Madroño 16: 5-23.

WHITTAKER, R. H. 1962 – Classification of natural communities. Bot. Rev. 28: 1-239.

WHITTAKER, R. H. 1965 – Dominance and diversity in land plant communities. Science 147: 250-260.

WHITTAKER, R. H. 1967 – Gradient analysis of vegetation. Biol. Rev. 42: 207-264.

WHITTAKER, R. H. 1969 – Evolution of diversity in plant communities. Brookhaven Symp. Biol. 22: 178-196.

WHITTAKER, R. H. 1970a – Communities and ecosystems. Macmillan, New York, 162 pp.

WHITTAKER, R. H. 1970b – Biochemical ecology of higher plants. In "Chemical ecology," ed. E. Sondheimer & J. B. Simeone, pp. 43-70. Academic Press, New York.

WHITTAKER, R. H. 1970c – The population structure of vegetation. (Germ. summ.) In "Gesellschaftsmorphologie (Strukturforschung)," ed. R. Tüxen. Ber. Symp. Int. Vereinig. Vegetskunde., Rinteln, 1966: 39-62.

WHITTAKER, R. H. & C. W. FAIRBANKS 1958 – A study of plankton copepod communities in the Columbia Basin, southeastern Washington. Ecology 39: 46-65.

WHITTAKER, R. H. & P. P. FEENY 1971 – Allelochemics: chemical interactions between species. Science 171: 757-770.

WHITTAKER, R. H. & S. A. LEVIN 1972 – Niche, habitat, and ecotope. Manuscript.

WHITTAKER, R. H. & W. A. NIERING 1965 – Vegetation of the Santa Catalina Mountains, Arizona. (II). A gradient analysis of the south slope. Ecology 46: 429-452.

WHITTAKER, R. H. & W. A. NIERING 1968 – Vegetation of the Santa Catalina Mountains, Arizona. IV. Limestone and acid soils. J. Ecol. 56: 523-544.

WHITTAKER, R. H. & G. M. WOODWELL 1969 – Structure, production and diversity of the oak-pine forest at Brookhaven, New York. J. Ecol. 57: 155-174.

WHITWORTH, W. A. 1897 – DCC exercises in choice and chance. (5th ed.) Reprint 1965 by Hafner, New York. 237 pp.

WIHLM, J. L. 1968 – Use of biomass units in Shannon's formula. Ecology 49: 153-156.

WILLIAMS, C. B. 1953 – The relative abundance of different species in a wild animal population. J. Anim. Ecol. 22: 14-31.

WILLIAMS, C. B. 1964 – Patterns in the balance of nature, and related problems of quantitative ecology. Academic Press, London & New York. 324 pp.

WILSON, E. O. 1969 – The species equilibrium. Brookhaven Symp. Biol. 22: 38-47.

WOODWELL, G. M. 1967 – Radiation and the patterns of nature. Science 156: 461-470.

WOODWELL, G. M. 1970 – Effects of pollution on the structure and physiology of ecosystems. Science 168: 429-433.

WOODWELL, G. M. & R. H. WHITTAKER 1968 – Effects of chronic gamma irradiation on plant communities. Quart. Rev. Biol. 43: 42-55.

WUENSCHER, J. E. 1969 – Niche specification and competition modeling. J. Theoret. Biol. 25: 436-443.

YODA, K. 1967 – A preliminary survey of the forest vegetation of eastern Nepal. II. General description, structure and floristic composition of the sample plots chosen from different vegetation zones. J. College Arts Sci., Chiba Univ., Nat. Sci. Ser. 5(1): 99-140.