THE NONCONCEPT OF SPECIES DIVERSITY: A CRITIQUE AND ALTERNATIVE PARAMETERS[1]

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Abstract. The recent literature on species diversity contains many semantic, conceptual, and technical problems. It is suggested that, as a result of these problems, species diversity has become a meaningless concept, that the term be abandoned, and that ecologists take a more critical approach to species-number relations and rely less on information theoretic and other analogies. As multispecific collections of organisms possess numerous statistical properties which conform to the conventional criteria for diversity indices, such collections are not intrinsically arrangeable in linear order along some diversity scale. Several such properties or "species composition parameters" having straightforward biological interpretations are presented as alternatives to the diversity approach. The two most basic of these are simply:

$$\Delta_1 = \left[\frac{N}{N-1}\right]\left[1 - \sum_i \left(\frac{N_i}{N}\right)^2\right]$$

= the proportion of potential interindividual encounters which is interspecific (as opposed to intraspecific), assuming every individual in the collection can encounter all other individuals,

and

$$E(S_n) = \sum_i \left[1 - \frac{\left(\begin{array}{c} N-N_i \\ n \end{array}\right)}{\left(\begin{array}{c} N \\ n \end{array}\right)}\right]$$

= the expected number of species in a sample of n individuals selected at random from a collection containing N individuals, S species, and N_i individuals in the ith species.

Ever since Fisher, Corbet, and Williams (1943) proposed the diversity index α and, more recently, since MacArthur (1955) and Margalef (1958) proposed indices based on information theory, community ecologists have put much effort into the mathematical and statistical refinement of these indices, the devising of new indices, the calculation of diversity for various collections of organisms, and the correlation of diversity with other variables. These efforts have sometimes been at the expense of more substantive approaches to community ecology. The term "species diversity" has been defined in such various and disparate ways that it now conveys no information other than "something to do with community structure"; species diversity has become a nonconcept.

The present paper offers a critique of semantic, conceptual, and technical problems in the diversity literature and suggests that ecologists take more direct approaches to the study of species-numbers relations. It treats only empirical measures, i.e., those calculated directly from the observed relative abundances of the species in a collection. Theoretical indices, such as parameters of the log-series (Fisher, Corbet, and Williams 1943), log-normal (Preston 1948), or negative binomial distributions (Brian 1953) seem inadequate for critical comparisons. Since the fit of actual data to theoretical species-numbers distributions is always less than perfect, no clear interpretation can be attached either to numerical values yielded by theoretical indices or to differences between such values calculated for different collections. Attempts to discover mathematical regularity in species-numbers distributions are worthwhile but are to be distinguished from the empirical description of community structure.

SEMANTICS

Species diversity is a function of the number of species present (*species richness* or *species abundance*) and the evenness with which the individuals are distributed among these species (*species evenness* or *species equitability*) (Margalef 1958, Lloyd and Ghelardi 1964, Pielou 1966). If the term "species diversity" is to retain any usefulness (and this seems doubtful) its meaning probably should be restricted to at least this extent. Its use in other senses has been one cause of the term's present ambiguity. Some workers appear to synonymize species richness with

species diversity or at least consider species richness to be one of several possible measures of species diversity (e.g., MacArthur 1965, Whittaker 1965, Paine 1966, Pianka 1966, 1967, Hutchinson 1967: 372, Hessler and Sanders 1967, MacArthur and Wilson 1967, Odum 1967, McNaughton 1967, 1968, Johnson, Mason, and Raven 1968, Sanders 1968, Whittaker and Woodwell 1969). Margalef (1968:18) states that "an area with greater diversity of butterflies would yield more species, and . . . there would be a higher proportion of rare varieties." Although species diversity and species richness are often positively correlated, e.g., along latitudinal gradients, such positive correlation is neither a biological nor a mathematical necessity; gradients can exist along which *increases* in species diversity are accompanied by *decreases* in species richness.

Another problem concerns the distinction between abundance and importance and the occasional failure to recognize that diversity, as it is usually measured, is an aspect of community structure and that, structurally, rare species *are* minor components of their community. Complaints that an index such as Shannon's (Shannon and Weaver 1962)

$$H' = -\sum_i \frac{N_i}{N} \log \frac{N_i}{N} \qquad (1)$$

is inadequate because it is "insensitive to the rare species . . . [which may] play a substantial role in the ecosystem" (Sager and Hasler 1969) are as invalid as complaints that the weight of a tree is an inadequate measure because it is insensitive to the tree's functionally important leaves. Diversity indices do not assume "that the more abundant a particular species, the more important it is in the community" (Dickman 1968). A species' importance is not necessarily reflected by its relative contribution to the H' value for the community. Despite its past use in more static senses, the term "importance" connotes ecological function. Whittaker (1965) feels the "best single measure of a species' importance . . . is its productivity." This definition may suffice when one is dealing with a restricted group of organisms (e.g., green plants) among which competition is the major interaction (e.g., no predation, no parasitism); but otherwise it gives little weight to a species' actual impact on the rest of the community. For example, the fungus *Endothia parasitica* (Chinese chestnut blight) in the forests of the eastern United States and the cactus-eating moth *Cactoblastis cactorum* in Queensland, Australia, presently have very low productivities, yet we know that they exert major influences on the structure and function of their respective ecosystems. For similar reasons, MacFadyen (1936:236) has questioned the adequacy of populational metabolic rate as a measure of importance.

Perhaps the importance of a species is best defined as the sum, over all species,[3] of the changes (sign ignored) in productivity which would occur on removal of the particular species from the community.

In symbolic notation,

$$\text{Importance of } j\text{th species} = \sum_{i=1}^{S} \left| P_{i,t=1} - P_{i,t=0} \right|$$

where P_i is the productivity of the ith species before ($t = 0$) and after ($t = 1$) removal of the particular (jth) species being evaluated. This definition incorporates all aspects, quantitative and qualitative, of a species which might determine its influence in a community. Since the total productivity of green plants in a community is usually much greater than the total productivity of all other organisms (as a result of respiration losses), the most important species, by our definition, will include the commoner green plants and any organisms which, directly or indirectly, markedly influence their relative abundances.

DUBIOUS INDICES

The most widely used diversity indices, namely, H' [equation (1)] and

$$H = \frac{1}{N} \log \frac{N!}{\Pi N_i!} \qquad (2)$$

have been adopted from information theory and justified by cursory reference to "uncertainty of encounter" or by a dubious analogy between letters on a printed page and individuals in a community. Although these information theoretic indices have been examined and applied to ecological problems by many ecologists, no one has yet specified exactly what significance the "number of bits per individual" has to the individuals and populations in a community. It has not been shown that information theoretic indices have any greater biological relevance than do the infinite number of other potential indices which have a minimum value when $S = 1$ and a maximum value when $S = N$. MacArthur (1955) originally selected H' as a measure of stability (when calculated from data on energy flow) for the admittedly arbitrary reason that, in terms of Pielou (1967), hierarchical diversities are then additive. Information theory may have heuristic value for ecology, but at least for the present its " 'hard' usefulness in a practical sense seems doubtful" (Patten 1968). Similar criticisms apply to other diversity indices, such as those based on geometric analogies (McIntosh 1967).

The striking nonconcordance possible among various diversity indices has been ignored. Table 1 illustrates how two such indices can give different rank-

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[3] Including the species that was removed and also those species that may not have been present before its removal but invaded subsequently.

TABLE 1. The comparison of two species diversity indices calculated for two hypothetical communities, each containing 100,000 individuals. Both indices have a maximum value when $S = N$ and a minimum value when $S = 1$. Δ_3 is an index mentioned by MacArthur and Wilson (1967)

Com-munity	Abundances		Diversity, as measured by	
	S	N_i	$H^1 = \Sigma \pi_i \log \pi_i$	$\Delta_3 = 1/\Sigma \pi_i{}^2$
A	6	$N_i = 18{,}000$ $i = 1,2$ $N_i = 16{,}000$ $i = 3,4,5,6$	0.78	5.98
B	91	$N_i = 40{,}000$ $i = 1$ $N_i = 667$ $i = 2, \ldots, 91$	2.70	5.00

ings for a set of communities. Which is more diverse, A or B? The example shows the looseness of the question.

Several factors have motivated the creation of diversity indices, including (i) the observation that two collections could contain the same number of species and the same number of individuals but still have very different structures, and (ii) the intuitive feeling that the number of species and their relative abundances somehow could be combined into an index that would show a closer relation to other properties of the community and environment than would number of species alone. A central though unarticulated problem has been to determine the appropriate relative weights to be given to species richness and species evenness in the construction of such an index. And since diversity (everyone agrees on the word!) has never had a single, unequivocal definition, there has been no objective way to assign these relative weights; nor is one ever likely to be found. We therefore can muddle along with a plethora of indices, each supported by at least one person's intuition and a few recommended by fashion, or we can sharpen our thoughts and rephrase our questions in terms of biologically meaningful properties which, when calculable on a list of species and their abundances, we might collectively refer to as species composition parameters. The second alternative is recommended, and the remainder of this paper discusses a few such parameters.

PROBABILITY OF INTERSPECIFIC ENCOUNTER

Much of the interest in diversity has stemmed from its proposed relationship to community stability. Since stability is related to the number of links in a food web (MacArthur 1955, Leigh 1965) and since links imply interspecific encounters (e.g., fox eating woodchuck), the probability of interspecific encounters is a variable of interest. Potentially, each indi-

vidual in a community can encounter or interact with every other individual in the community. Of the $(N)(N-1)/2$ potential encounters in a community of N individuals, $\sum_i (N_i)(N-N_i)/2$ encounters involve individuals belonging to different species. Thus,

$$\Delta_1 = \sum_{i=1}^{S} \left(\frac{N_i}{N} \right) \left(\frac{N - N_i}{N - 1} \right)$$
$$= \left(\frac{N}{N-1} \right) \left(1 - \sum_{i=1}^{S} \pi_i{}^2 \right) \quad (3)$$

is the probability of interspecific encounter (PIE) or the proportion of potential encounters that is interspecific, where

N_i = number of individuals of the ith species in the community (or collection),

N = $\sum_i N_i$ = total number of individuals in the community,

π_i = N_i/N, and

S = number of species in the community.

As an equivalent interpretation, note that if an individual (a biologist or any other organism) enters a community and encounters two individuals at random, Δ_1 is the probability that they belong to different species. When the first individual encountered risks being the subject of the second encounter also, as in nonlethal encounters, this probability is simply

$$\Delta_2 = 1 - \sum_{i=1}^{S} \pi_i{}^2 \ , \quad (4)$$

the complement of Simpson's (1949) "measure of concentration."

The concept of PIE finds perhaps its first expression in one of Alfred Russell Wallace's (1876:65) observations on the structure of Amazonian forests: "If the traveller notices a particular species and wishes to find more like it, he may turn his eyes in vain in any direction. Trees of varied forms, dimensions and colours are around him, but he rarely sees any one of them repeated. Time after time he goes towards a tree which looks like the one he seeks, but a closer examination proves it to be distinct. He may at length, perhaps, meet with a second specimen half a mile off, or may fail altogether, till on another occasion he stumbles on one by accident."

If we think of the "traveller" as a phytophagous insect seeking its host plant, the biological significance of PIE is apparent. In communities with high PIE we can expect that the sensory abilities of animals, especially host-specific ones, will be more highly developed, on average, than would those of animals living in communities with low PIE. Or perhaps we should simply say that in communities characterized by high PIE, fewer random components can be tolerated in searching (for mates, hosts, or prey) be-

havior of animals. In flowering plants the most random method of mate-seeking is wind dispersal of pollen, a method notably absent in high PIE communities such as tropical rainforests (the year-round presence of wind-obstructing foliage in such communities may also be a factor) (Corner 1964:199).

Since Δ_1 (and Δ_2) ranges only from 0 to 1, three communities consisting, respectively, of 2, 10, and 100 equally abundant species yield Δ_1 (or Δ_2) values of .50, .90, and .99. These suggest that from the viewpoint of an individual functioning in the community, even large increases in species richness may add little to community complexity after a moderate degree of species richness has been attained.

STATISTICS OF PIE

For those rare occasions when it is possible to take a truly random sample of individuals from a community or other collection, the sample estimators of Δ_2 and Δ_1 are provided by Simpson (1949):

$$D_2 = \sum_{j=1}^{S_n} \left(\frac{n_j}{n}\right)\left(\frac{n - n_j}{n - 1}\right) \qquad (5)$$

$$D_1 = \frac{N}{N-1} D_2 \qquad (6)$$

where n_j = number of individuals of the jth species in the sample,

$n = \sum\limits_{j} n_j$ = total number of individuals in the sample, and

S_n = number of species in the sample, $S_n \leqq$ S (Simpson 1949).

D_1 and D_2 are consistent, unbiased estimators so long as $n \geqq 2$ and do not require knowledge of the number of species in the community. As n increases, the distributions of D_1 and D_2 tend to normality (except when $S = N$). The variance of D_2 is given by Simpson (1949; he gives the variance of $1 - D_2$, which is identical to that of D_2) and the variance of D_1 is simply

$$\text{Var}(D_1) = \left(\frac{N}{N-1}\right)^2 \text{Var}(D_2). \qquad (7)$$

A TRANSFORMATION OF PIE

Adopting a transformation applied by MacArthur (1965) to H', we can obtain an alternative way of expressing PIE by asking, "If species are equally abundant, how many would a hypothetical collection have to have in order to yield a PIE value equal to the PIE value of some real collection containing S unequally abundant species?" If S_h is the number of species in the hypothetical collection and if π_i is the relative abundance of the ith species in the real collection, then we set

$$\Delta_2 = 1 - \sum_{i=1}^{S} \pi_i^2 = 1 - S_h\left(\frac{1}{S_h}\right)^2 \qquad (8)$$

and obtain

$$S_h = 1/(1 - \Delta_2) = 1/\Sigma \, \pi_i^2 = \Delta_3. \qquad (9)$$

The same result is obtained if we use Δ_1 as our measure of PIE.

Δ_3 is a useful transformation for dealing with collections having high PIE's distributed over a narrow range (for instance, Δ_2 values of .95 and .99 yield Δ_3 values of 20 and 100) or if we simply wish to express results in familiar units, i.e., number of species.

RELATIVE IMPORTANCE OF INTERSPECIFIC COMPETITION

When calculated on a collection of closely related species on the same trophic level, Δ_1 measures the importance of interspecific competition relative to total competition, assuming that encounters occur at random and that each encounter represents a unit of competition. The remainder, $1 - \Delta_1$, is the proportion of total competition which is intraspecific. Alternatively, we can calculate the ratio of interspecific to intraspecific competition (= encounters), i.e.,

$$\Delta_4 = \frac{\Delta_1}{1 - \Delta_1} = \frac{1 - \Sigma\pi_i^2}{(\Sigma\pi_i^2) - 1/N}. \qquad (10)$$

If N is large and PIE is low (i.e., $\Sigma\pi_i^2$ is high), we have the approximation,

$$\Delta_4 \cong \frac{1 - \Sigma\pi_i^2}{\Sigma\pi_i^2} = \Delta_3 - 1 = \Delta_5. \qquad (11)$$

The percentage error arising from use of Δ_5 as an approximation of Δ_4 is

$$\frac{\Delta_4 - \Delta_5}{\Delta_4} = \frac{1}{N\Sigma\pi_i^2}. \qquad (12)$$

If we assume that, in some sense, an individual can compete with himself, then the ratio of interspecific intraspecific competition is given exactly by Δ_5.

Having both species richness and species evenness components, Δ_1, Δ_2, Δ_3, Δ_4, and Δ_5 conform to the conventional criteria for diversity indices. Hopefully, they can be spared that unhelpful label, however.

McIntosh (1967) has referred to Δ_2 as "directly related to diversity" after implying a few pages earlier that it is a measure of equitability. Yule (1944) employed the index $K = (1 - \Delta_1) \left(\frac{N-1}{N}\right)$ in his statistical studies of literature. Williams (1964:148) suggested $1/(1 - \Delta_1)$ as a diversity index; it approximates Δ_3 if N is large. MacArthur and Wilson (1967:187) listed Δ_3 as a possible measure of diversity, and Levins (1968:43) has used it to measure "niche breadth."

SPECIES RICHNESS

Species richness can refer to the number of species present, without any particular regard for the

exact area or number of individuals examined. However, it is useful to distinguish between *numerical species richness* (hereinafter referred to simply as species richness), the number of species present in a collection containing a specified number of individuals, or, possibly, amount of biomass; and *areal* species richness or species density (Simpson 1964), the number of species present in a given area or volume of the environment (e.g., square kilometer of grassland, a liter of lake water). Species density is another parameter to which the term "species diversity" has been applied (e.g., Woodwell 1967, Whittaker and Woodwell 1969). By varying area or number of individuals, we can generate species density (= species-area) or species richness curves. Species density is of considerable interest but falls outside the scope of the present discussion.

Since the species richness of a collection generally increases with N, comparison of species richnesses of different collections requires that collections be reduced to a common size (n). This can be effected with the equation

$$\mathrm{E}(S_n) = \sum_{i=1}^{S} \left[1 - \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right] \qquad (13)$$

= the expected number of species in a sample of n individuals selected at random (without replacement) from a collection containing N individuals and S species.

For example, if we have two collections, A ($N_A = 1013$, $S_A = 70$) and B ($N_B = 780$, $S_B = 65$), we can calculate

$$\mathrm{E}(S_{A, n=780}) = \sum_{i=1}^{70} \left[1 - \frac{\binom{1013 - N_{Ai}}{780}}{\binom{1013}{780}} \right]$$

and compare $\mathrm{E}(S_{A, n})$ directly with S_B. Such comparisons will have greatest validity when each collection is comprised either of all individuals in a given area, size of area being the same for each collection, or of a truly random sample of these individuals. If this method is applied to other types of collections, interpretation of results will be less conclusive.

Species richness comparisons made at a single sample size (n) permit only limited conclusions. Since the manner in which sample species richness increases with sample size varies according to the number of species and their relative abundances in the collection, it is possible that at one sample size, collection A will have a greater sample species richness than collection B, while at a larger sample size, collection B will have the greater sample species rich-

ness. This same relativity plagued Yule (1944:83) in his attempts to compare different authors with respect to vocabulary richness. He concluded, "To transform the correct statement 'in a sample of n occurrences the vocabulary of author A is twice as great as that of author B' into the general statement 'the vocabulary of author A is twice as great as that of author B' may be an entirely fallacious proceeding."

Probably the most instructive approach is to calculate, plot, and compare the species richness curves [n vs. $\mathrm{E}(S_n)$] of the different collections, as suggested by Sanders (1968). Although Sanders refers to these as "species diversity curves," two collections can have identical diversities, as measured by one of the conventional indices, and yield radically different species richness curves, as they are termed here. It may also be noted that Sanders' "rarefaction methodology" generally overestimates the "expected number of species present in populations [= samples] of different sizes." In Table 2 expected sample species richness (for $n = 100$) has been determined both by $\mathrm{E}(S_n)$ and by the "rarefaction methodology" for five hypothetical collections of varying species evenness: in the first four collections, the error ranges from 12% to 53%.

Despite its dependence on sample size, sample species richness is not without biological significance. Consider an individual which enters a community and in a certain period of time encounters n individuals at random, the exact number being determined by his mobility or sedentariness. If the intruder eats or destroys each individual encountered, then he can expect to encounter $\mathrm{E}(S_n)$ species. If the intruder eats none of the individuals encountered, the number of species he will meet with is, on average,

$$\mathrm{E}(S'_n) = \sum_{i=1}^{S} \left[1 - (1 - \pi_i)^n \right] \qquad (14)$$

the "with replacement" equivalent of $\mathrm{E}(S_n)$. For a member of the community, rather than an intruder into it, the number of species encountered would be, on average,

$$\mathrm{E}(S''_n) = \sum_{j=1}^{S} \left[\frac{N_j}{N} \right] \left[E_j (S_n) \right] \qquad (15)$$

if each individual encountered is eaten, or

$$\mathrm{E}(S'''_n) = \sum_{j=1}^{S} \left[\frac{N_j}{N} \right] \left[\mathrm{E}'_j (S_n) \right] \qquad (16)$$

if no individuals are eaten. $E_j(S_n)$ and $\mathrm{E}'_j(S_n)$ are the number of species an individual of the jth species could be expected to encounter; they are defined exactly in equations (28) and (29). These four measures of species richness [equations (13–16)] yield similar values when N is large relative to n and S.

TABLE 2. A comparison of expected sample species richness as determined by $E(S_n)$ and by Sanders' (1968) "rarefaction methodology." Collections 1, 2, 4, and 5 each contain 1,000 individuals and 100 species; collection 3 contains 1,002 individuals and 40 species. Sample species richness is calculated for a sample size of 100 individuals

Collection type	Sample species richness ($n = 100$)	
	$E(S_n)$	Sanders' method
1. Maximum evenness..	65.3	100.0
($N_i = 10$, for all i)		
2. High evenness...	46.5	53.4
($N_1 = 76, N_2 = \ldots = N_6 = 50, N_7 = \ldots = N_{26} = 20,$		
$N_{27} = \ldots = N_{76} = 5, N_{77} = \ldots = N_{100} = 1$)		
3. Moderate evenness...	20.4	22.9
(Collection in Table 1, Sanders 1968)		
4. Low evenness..	41.6	51.0
($N_1 = 505, N_i = 5$, for $i = 2, 3, \ldots 100$)		
5. Minimum evenness...	10.9	10.9
($N_1 = 901, N_i = 1$, for $i = 2, 3, \ldots, 100$)		

Of course, if an individual is considered to examine a given area, rather than encounter a given number of individuals, then species density becomes the variable of prime interest.

The occasional intersection of species richness curves calls attention to the mobility of the individual as a factor determining effective species richness. If community A and community B have intersecting species richness curves, one might conclude that community A has greater richness for an individual (or species) of low mobility, but that community B has greater richness for an individual of high mobility.

Species richness curves rise rapidly at first and then flatten out, so at sufficiently large sample sizes, the results of species richness comparisons tend to stabilize. Therefore, if a single measure of richness is desired, as when richness is being examined for correlation with other factors, one might compare $E(S_n)$ values calculated for some high, standardized value of n. Odum (1967), for example, found a relationship between sample species richness (for $n = 1000$) and organic matter in marine systems, although he did not specify how his species richness values were calculated.

SPECIES EVENNESS

Species evenness usually has been defined as the ratio of observed diversity to maximum diversity, the latter being said to occur when the species in a collection are equally abundant (Margalef 1958, Patten 1962, Pielou 1966). Reasoning that "numerical equality among the species is too much to expect," Lloyd and Ghelardi (1964) defined maximum diversity to exist when the species' abundances were as predicted by one of MacArthur's (1957) broken stick models. However, this causes their species equitability measure to be expressed in somewhat arbitrary units, especially considering MacArthur's (1966) own comments on the model. The clearest

approach seems to lie in taking complete numerical equality as the standard of comparison.

Historically, two types of evenness measures have been defined, viz.

$$V' = \frac{\Delta}{\Delta_{max}} \qquad (17)$$

and

$$V = \frac{\Delta - \Delta_{min}}{\Delta_{max} - \Delta_{min}} \qquad (18)$$

where Δ = observed value of parameter

Δ_{max} = value parameter would assume if all S species were equally abundant

Δ_{min} = value parameter would assume if one species was represented by $N - (S + 1)$ individuals and the other species by one individual each.

V' indices have been defined for H and H' (Pielou 1966), and Patten (1962) defined for H an index of the form $R = 1 - V$, terming it "redundancy"; it can also be thought of as a measure of relative species unevenness. Kohn (1968) defined for H' an index of the form $R = 1 - V'$ and used it to measure degree of food specialization.

Below, Δ_{max} and Δ_{min} are given for Δ_1, Δ_3, and Δ_4; one can utilize the relationships $\Delta_2 = \left(\dfrac{N-1}{N}\right)(\Delta_1)$ and $\Delta_5 = \Delta_3 - 1$ to obtain Δ_{max} and Δ_{min} for Δ_2 and Δ_5. By substitution into equations (17) and (18), V' and V indices can be fashioned as needed.

$$\Delta_{1, max} = \left(\frac{N}{N-1}\right)\left(\frac{S-1}{S}\right) \qquad (19)$$

$$\Delta_{1, min} = \left(\frac{N}{N-1}\right)\left(\frac{(2N-S)(S-1)}{N^2}\right) \qquad (20)$$

$$\Delta_{3, max} = S \qquad (21)$$

$$\Delta_{3, min} = \frac{N^2}{N^2 + (S - 2N)(S - 1)} \qquad (22)$$

$$\Delta_{4,\max} = \frac{S-1}{1 - \dfrac{S}{N}} \qquad (23)$$

$$\Delta_{4,\min} = \frac{(2N-S)(S-1)}{N(N-1)+(S-2N)(S-1)} \qquad (24)$$

As V' indices are dependent on species richness (Sheldon 1969), their principal value is as good approximations, under some circumstances, of the corresponding V indices, which are independent of S. (The difference between V and V' values will be negligible except when Δ is low or when $\Delta_{\min}$ is high—e.g., as it would be if the ratio S/N approaches unity.) This conclusion derives from the premise that all collections (of the same size) having every species but one represented by a single individual are equally "uneven."[4] Thus these two collections—(17, 1, 1, 1) and (15, 1, 1, 1, 1, 1)—are regarded as differing in species richness but not in species evenness (V). These collections would not yield the same V' values because V' indices use S, the observed number of species, to determine $\Delta_{\max}$ but, implicitly, let S go to unity to determine $\Delta_{\min}$—as result of which $\Delta_{\min}$ always equals zero, and so does not appear in the general expression [equation (17)]. This procedure seems inconsistent; it is more logical to use observed S to determine both $\Delta_{\min}$ and $\Delta_{\max}$. Differences in species richness pose no problem to statistical comparisons of species evenness so long as V indices are used.

The same cannot be said of sample or collection size. As species richness tends to increase with sample size, so species evenness tends to decrease with sample size. Thus, the species evenness of a community cannot be estimated by sampling except to the extent that an indefinitely large sample will provide an estimate containing an indefinitely small amount of bias (Lloyd and Ghelardi 1965, Pielou 1967). As with species richness, comparisons of species evenness are meaningful only when all collections are adjusted to a common size. Other things being equal, larger collections have more rare species, and these always lower the value of V or V'. This fact usually has been ignored (e.g., Patten 1962, Goulden 1966, Monk 1967, Barrett 1968, Pulliam, Odum, and Barrett 1968, Buzas and Gibson 1969, Sager and Hasler 1969), and it is probable that some of the variation in species evenness (or equitability) dis-

[4] Sheldon's (1969) premise that all collections where the abundances of species conform to MacArthur's (1957) broken stick model should possess the same degree of evenness seems less valid. There are many possible models for predicting the relative abundances of species, but probably no one of them bears any constant relationship to species evenness unless species evenness is defined specifically in terms of the model, e.g., Lloyd and Ghelardi's (1964) "equitability."

covered by these workers resulted entirely from variations in collection size (N). Even when one's collections consist of all organisms found in areas of equal size, species evenness should be adjusted for collection size differences before comparisons are made; whether two areas differ in species evenness and whether they differ in density (= total no. individuals/unit area) are best treated as independent questions.

To effect comparisons, we require the ability to predict the expected species evenness, $E(V_n)$, of a sample of n individuals selected at random (without replacement) from a larger collection. An exact estimator is beyond the abilities of the writer; for the present, valid comparisons of species evenness are possible only (i) for collections of equal size, or (ii) if a computer is used to draw and replace successive random samples, calculating V_n for each until the mean value of V_n reaches a specified and satisfactory degree of constancy. (V_n can be calculated with the formula for V.)

Unlike species richness, species evenness has been defined only in terms of PIE or other parameters and not as an independent entity. Species evenness therefore has significance only to the extent that the parameter on which it is defined is significant. Interpretation of species evenness values also must consider that even for closely related parameters, such as Δ_2 and Δ_3, differing species evenness values result from the same set of data; if $N = 1000$, $\pi_1 = .70$, $\pi_2 = .20$, and $\pi_3 = .10$, then $V = .85$ (for Δ_2), while $V = .76$ (for Δ_3).

PARAMETERS FOR INDIVIDUAL SPECIES

So far I have presented parameters useful for comparing different communities. Most of them actually are average values of parameters defined on individuals. For example, Δ_1 is the probability of interspecific encounter averaged over all individuals in all species. One may define similar parameters which describe the community from the viewpoint of (the individuals in) a particular species. Such parameters can be used for comparing the biotic environments of different species in the same community and of the same species in different communities.

Simplest of all is π_j, relative abundance. Closely related are

$$1 - \Delta_{1j} = \frac{N_j - 1}{N - 1} = \left(\pi_j - \frac{1}{N}\right) \bigg/ \left(1 - \frac{1}{N}\right) \qquad (25)$$

which is the proportion of potential encounters that is intraspecific for an individual of the jth species, and

$$\Delta_{1j} = (1 - \pi_j)\left(\frac{N-1}{N}\right) \qquad (26)$$

which is the proportion that is interspecific. The ratio of potential inter- to intraspecific encounter is then, for the jth species,

$$\Delta_{4j} = \frac{N - N_j}{N_j - 1}. \tag{27}$$

Δ_4 equals infinity when every species is represented by a single individual, and, similarly, Δ_{4j} equals infinity when the jth species is represented by a single individual. Δ_1 and Δ_{1j} are clearly more amenable to statistical treatment than are Δ_4 and Δ_{4j}. One can define similar parameters on Δ_2, Δ_3, and Δ_5.

Species richness also can be defined from the viewpoint of particular species. If an individual of the jth species encounters other individuals at random, then the number of species it will encounter is, on average,

$$E_j(S_n) = \left[1 - \frac{\binom{N - N_j}{n}}{\binom{N - 1}{n}} \right] +$$

$$\sum_{i \neq j} \left[1 - \frac{\binom{N - N_i - 1}{n}}{\binom{N - 1}{n}} \right] \tag{28}$$

if an individual cannot be encountered more than once, or

$$E'_j(S_n) = \left[1 - \left(\frac{N - N_j}{N - 1} \right)^n \right] +$$

$$\sum_{i \neq j} \left[1 - \left(\frac{N - N_i - 1}{N - 1} \right)^n \right] \tag{29}$$

if an individual can be encountered more than once. To obtain the expected number of *other* species encountered, simply omit the term in the first set of brackets.

We could also assume that all n encounters are with other species (or simply that intraspecific encounters are of no import), in which case the average number of species encountered per n interspecific encounters is

$$E'_j(S_{n, \neq j}) = \sum_{i \neq j} \left[1 - \left(\frac{N - N_j - N_i}{N - N_j} \right)^n \right] \tag{30}$$

assuming the possibility of repeat encounters, or

$$E_j(S_{n, \neq j}) = \sum_{i \neq j} \left[1 - \frac{\binom{N - N_j - N_i}{n}}{\binom{N - N_j}{n}} \right] \tag{31}$$

assuming the impossibility of repeat encounters.

All these parameters possess only abstract signif-

icance, as in nature both spatial distributions and interindividual encounters are generally nonrandom in the extreme. However, they do have the benefit of measuring, within the limits of the assumptions, concrete and biologically significant properties. Moreover, these parameters are all amenable to modification when data on the distributions of encounters and populations are available. A first step toward refinement might be to determine, still assuming random movement of individuals (in space), the extent to which patchiness of spatial distributions decreases PIE and species richness for species of differing mobilities and spatial distributions.

COLLECTION DELIMITATION

For what types of collections is it appropriate or at least permissible to apply the holistic mathematical approach implicit in such parameters as Δ_1, Δ_2, $E(S_n)$, etc.? In preceding sections I have sometimes used the term "community" in lieu of "collection" to make discussion a bit less abstract. Actually, I cannot imagine that there would ever be value in calculating a species composition parameter on an entire community, i.e., on all producers, herbivores, carnivores, and decomposers present, and must disagree with Dickman's (1968) suggestion that "an index of community diversity [or species composition parameter] sensitive to changes in relative abundance of all trophic levels . . . appears to be a necessary prerequisite to comparative studies." Two factors in particular argue against that approach. First, the value of any given species composition parameter would be determined almost entirely by relative abundances within one group of organisms (e.g., bacteria, phytoplankton, trees), depending on our units of representation (numbers, biomass, productivity, etc.) and the type of community being studied. Secondly, real and interesting differences between different trophic or taxonomic groups could cancel each other out and thus yield parameter values of little interest. A mathematical approach does not oblige a biologist to be modest about his ability to make biological distinctions.

A *taxocene* is a taxonomic segment of a community or association (Chodorowski 1959, Hutchinson 1967), and since "members of a taxocene are likely to be of about the same size, to have similar life histories, and compete over both evolutionary and ecological time" (Deevey 1969), species composition parameters probably will have clearest significance when calculated on a taxocene. If a taxocene spans more than a single trophic level, whether or not we calculate parameters for each trophic level separately may depend on the extent to which our questions relate to contemporary (ecological) versus historical (evolutionary) phenomena.

Taxocenes can be defined at various taxonomic

levels. The chydorids of a pond constitute a taxocene, as Deevey (1969) notes, but so do the cladocerans, the crustaceans, or even the arthropods. If a taxocene is defined so exclusively as to contain only one or a few species, then obviously calculation of species composition parameters offers little advantage over simple verbal analysis of the situation. If the taxocene is too inclusive, then interpretation of calculated parameters becomes weak because individuals belonging to different species will be highly nonequivalent (e.g., in size, life history, etc.) and because no or even negative correlation may exist between parameters for different subgroups in the taxocene. Finding the middle ground may be simple enough in any given problem, but specific guidelines are not available.

A taxocene also has a restricted spatial or environmental dimension; Chodorowski (1959) distinguished in a single lake nine different taxocenes each spanning the order Turbellaria and distinguished by differences in microhabitat. Since individuals sharing the same habitat or microhabitat are much more likely to encounter each other than are individuals in different habitats, interpretation of species composition parameters in terms of "encounters" will be most valid when our collection or sample has been taken from a restricted environment. The appropriate size and uniformity of this piece of environment will be determined by the organisms' size, mobility, and fidelity to particular microhabitats. Thus in a particular pond we might distinguish a single fish taxocene, two to five chironomid taxocenes, and 10 to 50 protozoan taxocenes.

CONCLUSIONS

Communities having different species compositions are not intrinsically arrangeable in linear order on a diversity scale. Diversity per se does not exist. There are many statistical properties relating to species composition and species-numbers relations and each one may give a different ordering of the communities. Although I have defined a few parameters with simpler and more direct biological interpretations than possessed by some commonly used diversity indices, it is not intended that these parameters be adopted simply as a new set of such indices. In fact, it is hoped that these parameters will be used much less than have diversity indices in the past, for problems that can be fruitfully investigated by this general approach are fewer than the volume of the diversity literature might seem to suggest. Just as there is no value in calculating H or H' unless one is specifically interested in the number of bits per individual, so there will be no value in calculating Δ, unless one is specifically interested in the probability of interspecific encounter. The fact that a particular index shows a correlation with other proper-

ties of the community or environment is not evidence that the index is either appropriate or useful.

LITERATURE CITED

Barrett, G. W. 1968. The effects of an acute insecticide stress on a semi-enclosed grassland ecosystem. Ecology **49**: 1019–1035.

Brian, M. V. 1953. Species frequencies in random samples from animal populations. J. Anim. Ecol. **22**: 57–64.

Buzas, M. A., and T. G. Gibson 1969. Species diversity: benthic foranimifera in western North Atlantic. Science **163**: 72–75.

Chodorowski, A. 1959. Ecological differentiation of turbellarians in Harsz-Lake. Polsk. Archwm. Hydrobiol. **6**: 33–73.

Corner, E. J. H. 1964. The life of plants. World Publishing Company, New York. 315 p.

Deevey, E. S. 1969. Coaxing history to conduct experiments. Bioscience **19**: 40–43.

Dickman, M. 1968. Some indices of diversity. Ecology **49**: 1191–1193.

Fisher, R. A., A. S. Corbet, and C. B. Williams. 1943. The relation between the number of individuals and the number of species in a random sample of an animal population. J. Anim. Ecol. **12**: 42–58.

Goulden, C. E. 1966. The history of Laguna de Petenxil: the animal microfossils. Mem. Conn. Acad. Arts Sci. **17**: 84–120.

Hessler, R. R., and H. L. Sanders. 1967. Faunal diversity in the deep sea. Deep-Sea Res. **14**: 65–78.

Hutchinson, E. H. 1967. A treatise on limnology. Vol. II. John Wiley & Sons, New York. 1115 p.

Johnson, M. P., L. G. Mason, and P. H. Raven. 1968. Ecological parameters and plant species diversity. Amer. Natur. **102**: 297–306.

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

Leigh, E. 1965. On a relation between the productivity, biomass, stability and diversity of a community. Proc. Nat. Acad. Sci. **53**: 777–783.

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

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

MacArthur, R. H. 1955. Fluctuations of animal populations, and a measure of community stability. Ecology **36**: 533–536.

———. 1957. On the relative abundance of bird species. Proc. Nat. Acad. Sci. **43**: 293–295.

———. 1965. Patterns of species diversity. Biol. Rev. **40**: 510–533.

———. 1966. Notes on Mrs. Pielou's comments. Ecology **47**: 1074.

MacArthur, R. H., and E. O. Wilson. 1967. The theory

of island biogeography. Princeton Univ. Press, Princeton, N. J. 203 p.

MacFadyen, A. 1963. Animal ecology. 2nd ed. Sir Isaac Pitman & Sons, London. 344 p.

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

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

————. 1968. Definition and quantitation in ecology. Nature **219**: 180–181.

Margalef, D. R. 1958. Information theory in ecology. Gen. Syst. **3**: 36–71.

————. 1968. Perspectives in ecological theory. Univ. Chicago Press, Chicago. 111 p.

Monk, C. D. 1967. Tree species diversity in the eastern deciduous forest with particular reference to North Central Florida. Amer. Natur. **101**: 173–187.

Odum, H. T. 1967. Biological circuits and the marine systems of Texas, p. 99–157. *In* T. A. Olson and F. J. Burgess [ed.] Pollution and marine biology.

Paine, R. T. 1966. Food web complexity and species diversity. Amer. Natur. **100**: 65–75.

Patten, B. C. 1962. Species diversity in net phytoplankton of Raritan Bay. J. Mar. Res. **20**: 57–75.

————. 1968. Mathematical models of plankton production. Internationale Review der Gesamten Hydrobiologie und Hydrographie **53**: 357–408.

Pianka, E. R. 1966. Latitudinal gradients in species diversity. Amer. Natur. **100**: 33–46.

————. 1967. On lizard species diversity: North American flatland deserts. Ecology **48**: 333–351.

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

————. 1967. The use of information theory in the study of the diversity of biological populations. Proc. Fifth Berkeley Symp. Math. Statist. Probab. **4**: 163–177.

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

Pulliam, H. R., E. P. Odum, and G.W. Barrett. 1968. Equitability and resource limitation. Ecology **49**: 772–774.

Sager, P. E., and A. D. Hasler. 1969. Species diversity in lacustrine phytoplankton. I. The components of the index of diversity from Shannon's formula. Amer. Natur. **103**: 51–59.

Sanders, H. L. 1968. Marine benthic diversity: a comparative study. Amer. Natur. **102**: 243–282.

Shannon, C. E., and W. Weaver. 1963. The mathematical theory of communication. Univ. Illinois Press, Urbana. 117 p.

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

Simpson, E. H. 1949. Measurement of diversity. Nature **163**: 688.

Simpson, G. G. 1964. Species density of North American recent mammals. Syst. Zool. **13**: 57–73.

Wallace, A. R. 1878. Tropical nature and other essays. MacMillan and Co., London. 356 p.

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

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

Williams, C. B. 1964. Patterns in the balance of nature. Academic Press, New York. 324 p.

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

Yule, G. U. 1944. The statistical study of literary vocabulary. Cambridge Univ. Press, London. 306 p.