Diversity as a Concept and its Measurement

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This paper puts forth the view that diversity is an average property of a community and identifies that property as species rarity. An intrinsic diversity ordering of communities is defined and is shown to be equivalent to stochastic ordering. Also, the sensitivity of an index to rare species is developed, culminating in a crossing-point theorem and a response theory to perturbations. Diversity decompositions, analogous to the analysis of variance, are discussed for two-way classifications and mixtures. The paper concludes with a brief survey of genetic diversity, linguistic diversity, industrial concentration, and income inequality.

KEY WORDS: Species rarity; Intrinsic diversity ordering; Sensitivity of diversity indices; Diversity decomposition; Lorenz curves.

1. INTRODUCTION

Diversity has been an important concept in ecological theory and application. Under various names, it appears in several biological, physical, social, and management sciences. See, for example, Atkinson (1970), Finkelstein and Friedberg (1967), Greenberg (1956), Hart (1971), Horowitz and Horowitz (1968), Lieberson (1969), Nei (1973), Pielou (1975), Sen (1974), and Theil (1972).

Despite extensive literature on diversity-related issues, a formal definition and logical development of diversity as a concept and of its measurement have been lacking. There are basic questions of importance: What is diversity? Can it be measured? If so, how and why?

The common theme is that of the apportionment of some quantity into a number of well-defined categories. The quantity may be in the form of resource, investment, time, energy, abundance, and so on. The important concern is about the nature and the degree of the apportionment being more diverse or less diverse expressed variously as diversification or concentration, spread or specialization, monopoly or lack of it, and so on. For example, suppose A devotes $\frac{6}{12}$ of his time to mathematics and the remaining $\frac{6}{12}$ to music, whereas B devotes $\frac{8}{12}$ of his time to mathematics, $\frac{3}{12}$ to music, and the remaining $\frac{1}{12}$ to literature. Then the questions to be answered are these: How much of a specialist is each one? Among the two, who is more of a specialist? This paper defines diversity and develops a related theory of diversity measurement and comparison in an ecological context. It concludes with a brief survey of genetic diversity, linguistic diversity, industrial concentration, and income inequality.

2. DIVERSITY AS AN AVERAGE PROPERTY OF A COMMUNITY

We view diversity as an average property of a community. But the average of what? To an outside observer, variety is a most striking feature of a diverse community. Alfred Russel Wallace's (1875, p. 65) description of a tropical forest is a vivid illustration:

> 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 colors 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.

In a *diverse* community, such as that described by Wallace, the typical species is relatively *rare*. Consequently, we propose that diversity be defined as the average rarity within a community.

Consider some quantity distributed among a countable set of categories, labeled $i = 1, 2, 3, \ldots$, with π_i as the proportionate share received by category i. This quantity may be continuous (income, biomass, etc.) or it may be discrete (word occurrences in a text, biological organisms, etc.). For concreteness, we will usually speak of biological organisms grouped into species and call $\boldsymbol{\pi} = (\pi_1, \pi_2, \pi_3, \ldots)$ the *species abundance vector*; arranging the components of $\boldsymbol{\pi}$ in descending order gives the ranked abundance vector, $\boldsymbol{\pi}^{\#} = (\pi_1^{\#}, \pi_2^{\#}, \pi_3^{\#}, \ldots)$ where $\pi_1^{\#} \geq \pi_2^{\#} \geq \pi_3^{\#} \geq \cdots$. For our purposes, a community may be identified with the pair $C = (s, \boldsymbol{\pi})$, where s is the number of nonzero components of $\boldsymbol{\pi}$, that is, the number of species that are physically present; s is assumed to be finite. A community is said to be *completely even* when $\pi_1^{\#} = \pi_2^{\#} = \cdots = \pi_s^{\#} = 1/s$.

Given the community, a numerical measure of rarity is to be associated with each species; denote the rarity of species i by $R(i; \boldsymbol{\pi})$.

The measures of rarity considered in this paper will be based on one of the following:

Dichotomy: The rarity of species i depends only on the numerical value of π_i. For notational simplicity, write

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$R(i; \pi)$ as $R(\pi_i)$. We use the term "dichotomy" because the rarity of species i would be unchanged if the other species were grouped into a single complementary category.

Ranking: The rarity of a species depends only on its (descending) rank and not explicitly on the numerical values of the components of π. Denoting the rarity of the ith ranked species by $R(i)$, the index takes the form $\Delta = \sum R(i)\pi_i^{\#}$. The ranks may be assigned arbitrarily within tied sets without affecting the value of Δ.

Now we are ready to propose our definition of the diversity of a community as follows.

Definition 2.1. The diversity measure of a community $C = (s, \pi)$ is its average rarity and is given by $\Delta(C) = \sum \pi_i R(i; \pi)$, where Δ is the *diversity index* associated with the measure of rarity R. Sometimes we write $\Delta(\pi)$ instead of $\Delta(C)$.

First, we note that in either of the two cases of dichotomy and ranking, the measure of rarity is uniquely determined by the diversity index. And then, in the sections to follow, we take up various diversity-related issues.

3. THE CONSTRUCTION AND INTERPRETATION OF DIVERSITY INDICES: EXAMPLES

Three widely used indices of ecological diversity are the Species Count, the Shannon index, and the Simpson index (Bhargava and Uppuluri 1975 attribute the Simpson index to C. Gini). These will be denoted as follows:

Species Count: $\Delta_{-1} = s - 1$.

Shannon index: $\Delta_0 = -\sum \pi_i \log(\pi_i)$.

Simpson index: $\Delta_1 = 1 - \sum \pi_i^2$.

All three assign diversity zero to a single-species community.

In Section 3.1 we show how these three indices can be interpreted in terms of the notion of interspecific encounters and in Section 3.2 we embed the three indices in a one-parameter family $\{\Delta_\beta : \beta \text{ real}\}$ of indices.

3.1 Interspecific Encounters

When rewritten in the form $\Delta_1 = \sum \pi_i(1 - \pi_i) = \sum \pi_i R(\pi_i)$, the Simpson index may also be interpreted as average community rarity, with the understanding that species rarity is measured by $R(\pi) = 1 - \pi$. Now contemplate Wallace's traveler who first comes upon a member of, say, the ith species. As his journey continues, the traveler encounters other organisms, sometimes of this species and sometimes not. The rarer the ith species, the more likely are the interspecific encounters. $R(\pi_i) = 1 - \pi_i$ is precisely the probability that a given encounter is interspecific. In what follows, this concept of interspecific versus intraspecific encounters is explored further. Three different schemes are considered.

Waiting time for an intraspecific encounter. Again consider the traveler in search of the ith species. With $Y + 1$ equal to the number of encounters up to and including the first intraspecific one, we have

$$E[Y \mid \pi_i] = (1 - \pi_i)/\pi_i, \quad E[Y + 1 \mid \pi_i] = 1/\pi_i,$$
$$E[1/(Y + 1) \mid \pi_i] = -\pi_i \log(\pi_i)/(1 - \pi_i),$$

when

$$P(Y = y \mid \pi_i) = \pi_i(1 - \pi_i)^y, \quad y = 0, 1, 2, \ldots.$$

Since large Y are associated with rare species, both Y and $Y/(Y + 1)$ are reasonable measures of rarity. But these are random variables and should be replaced by average quantities. There are several ways to interpret the "average" of a ratio; each gives rise to a different index.

1. Species Count:
$$R(\pi_i) = E[Y \mid \pi_i] = (1 - \pi_i)/\pi_i,$$
$$\sum \pi_i R(\pi_i) = s - 1.$$
2. Simpson index:
$$R(\pi_i) = E[Y \mid \pi_i]/E[Y + 1 \mid \pi_i] = 1 - \pi_i,$$
$$\sum \pi_i R(\pi_i) = \sum \pi_i(1 - \pi_i).$$
3. Shannon index:
$$R(\pi_i) = E[1/(Y + 1) \mid \pi_i] \cdot E[Y \mid \pi_i]$$
$$= -\log(\pi_i),$$
$$\sum \pi_i R(\pi_i) = -\sum \pi_i \log(\pi_i).$$
4. An unfamiliar index:
$$R(\pi_i) = E[Y/(Y + 1) \mid \pi_i]$$
$$= 1 + \pi_i \log(\pi_i)/(1 - \pi_i),$$
$$\sum \pi_i R(\pi_i) = 1 + \sum \pi_i^2 \log(\pi_i)/(1 - \pi_i).$$

Waiting time for an interspecific encounter. Here we suppose the traveler to be in search of a new species and put $Z + 1$ equal to the number of encounters up to and including the first interspecific one. We have,

$$E[Z \mid \pi_i] = \pi_i/(1 - \pi_i), \quad E[Z + 1 \mid \pi_i] = 1/(1 - \pi_i),$$
$$E[1/(Z + 1) \mid \pi_i] = -(1 - \pi_i)\log(1 - \pi_i)/\pi_i.$$

Small Z are associated with rare species and the variables of interest are $1/Z$ and $1/(Z + 1)$.

1. Species Count:
$$R(\pi_i) = 1/E[Z \mid \pi_i] = (1 - \pi_i)/\pi_i.$$
2. Simpson index:
$$R(\pi_i) = 1/E[Z + 1 \mid \pi_i] = 1 - \pi_i.$$
3. A second unfamiliar index:
$$R(\pi_i) = E[1/(Z + 1) \mid \pi_i] = -(1 - \pi_i)\log(1 - \pi_i)/\pi_i.$$

The index itself is $\sum \pi_i R(\pi_i) = -\sum (1 - \pi_i)\log(1 - \pi_i)$. Note that $E[1/Z \mid \pi_i] = \infty$ so that this third choice does not lead to a useful measure of rarity.

Fixed number of encounters. Here we let Y be the number of interspecific and Z the number of intraspecific encounters out of a fixed total of N encounters.

1. Species Count:

$$R(\pi_i) = E[Y \mid \pi_i]/E[Z \mid \pi_i] = (1 - \pi_i)/\pi_i.$$

2. Simpson index:

$$R(\pi_i) = E[Y \mid \pi_i]/E[Y + Z \mid \pi_i] = 1 - \pi_i.$$

Note that $E[Y/Z \mid \pi_i] = \infty$, while $E[Y/(Y + Z) \mid \pi_i] = 1 - \pi_i$.

Some biological motivations for considering interspecific encounters were discussed by Hurlbert (1971), who concluded that if an index is to be used, Simpson's is conceptually preferable to Shannon's. While it is curious that the Shannon index arises in only the first scheme, all the three indices popular in ecological literature can be given a common encounter-theoretic interpretation.

3.2 The Proportionality Equation

Consider a species with abundance π and a subspecies whose abundance is a fraction q of π $(0 < q \leq 1)$. We wish to compare the difference in rarity, $R(q\pi) - R(\pi)$, with the corresponding change in rarity that occurs in taking a fraction q of an entire community. For the Shannon index, the two changes are equal,

$$R(q \cdot \pi) - R(\pi) = R(q \cdot 1) - R(1),$$

while for the Species Count and the Simpson index we have, respectively,

$$R(q\pi) - R(\pi) = \pi^{-1}[R(q) - R(1)]$$

and

$$R(q\pi) - R(\pi) = \pi[R(q) - R(1)].$$

These suggest consideration of the functional equation

$$R(q\pi) - R(\pi) = W(\pi)[R(q) - R(1)]. \quad (3.1)$$

We call (3.1) the *proportionality equation* and $W(\pi)$ the *deflation factor*. Notice that (3.1) is invariant to affine transformations of R. A *degenerate solution* is given by $W(1) = 1$ and $W(\pi) = 0, 0 < \pi < 1$, and, up to an affine transformation, $R(\pi) = 1 - W(\pi)$. The next theorem gives essentially all other solutions.

Theorem 3.1. Suppose R and W are defined on the interval $(0, 1]$ with R measurable and nonconstant. Then R and W satisfy the proportionality equation (3.1) if and only if either (a) R and W are the degenerate solution or (b) there is a real number β for which $W(\pi) = \pi^\beta$ and, up to an affine transformation,

$$R(\pi) = \begin{cases} (1 - \pi^\beta)/\beta & \text{if } \beta \neq 0 \\ -\log(\pi) & \text{if } \beta = 0. \end{cases}$$

Proof. Hardy, Littlewood, and Polya (1934, p. 69) give a proof under more stringent regularity assumptions; the present version requires only minor technical modifications in their argument.

For any real number β, we may now define the *diversity index of degree* β, denoted by Δ_β, as the dichotomous index whose rarity measure $R(\pi)$ is given by Theorem 3.1. Explicitly,

$$\Delta_\beta = (1 - \sum \pi_i^{\beta+1})/\beta,$$

where the usual limiting convention is understood when $\beta = 0$. It will be shown in Section 4 that a restriction $(\beta \geq -1)$ must be imposed if Δ_β is to have certain desirable properties.

3.3 The Numbers Equivalent

MacArthur (1965) has introduced a method for transforming diversity indices to a species richness scale. For a given community C and a given index Δ, he poses the question: how many species must a completely even community have in order that its diversity be $\Delta(C)$? This number is called the *equivalent number of species* and is denoted by $S_\Delta(C)$. The same transformation has appeared in the economics literature as the *numbers equivalent* (Adelman 1969). We will use the latter term.

The numbers equivalent remains invariant under one-one transformations of the index, that is, $S_{f(\Delta)} = S_\Delta$ whenever f is one-one. For a dichotomous index, $\Delta = \sum \pi_i R(\pi_i)$, the numbers equivalent is any solution of the equation $R(1/S_\Delta) = \Delta$; assuming that R is continuous and strictly monotonic, the solution is unique and may be written as

$$S_\Delta = 1/R^{-1}(\sum \pi_i R(\pi_i)). \quad (3.2)$$

The denominator of the right side of (3.2) has the form of a generalized average with R as the Kolmogorov-Nagumo function (cf. Rényi 1961). Specializing to the index Δ_β, the numbers equivalent,

$$S_\beta = 1/(1 - \beta\Delta_\beta)^{1/\beta} = 1/(\sum \pi_i \cdot \pi_i^\beta)^{1/\beta}, \quad (3.3)$$

is the reciprocal of the generalized mean of order β of $\pi_1, \pi_2, \pi_3, \ldots$ with weights $\pi_1, \pi_2, \pi_3, \ldots$. These indices have been proposed by Hill (1973), who gives several examples of their application ($S_\beta = N_{\beta+1}$ in Hill's notation).

The logarithmic numbers equivalent, $\log(S_\beta)$, is sometimes useful. For the index Δ_β,

$$\begin{aligned} \log(S_\beta) &= -\log(1 - \beta\Delta_\beta)/\beta \\ &= -\log(\sum \pi_i^{\beta+1})/\beta \end{aligned} \quad (3.4)$$

is Rényi's (1961) entropy of order $\beta + 1$, which might with equal justice be ascribed to Good (1954, 1956). Within the family of dichotomous indices, the Shannon index is characterized as being its own logarithmic numbers equivalent.

4. CRITERIA FOR DIVERSITY INDICES

Recalling the definition of dichotomous indices, $\Delta(C) = \sum \pi_i R(\pi_i)$, observe that $R(0)$ is inherently undefined, while the value $R(1)$ is germane only to a single-species community and, in fact, equals the diversity of such a community. $R(1) = 0$ is a natural normalizing requirement.

What else might be required of R? On intuitive grounds, $R(\pi)$ should be a decreasing function of π since rarer species correspond to smaller values of π.

Criterion C1. R is a decreasing function defined on the interval $(0, 1]$. If the normalizing condition $R(1) = 0$ is also imposed, R will, as a consequence, be nonnegative.

This monotonicity requirement, simple and intuitive though it is, has a striking implication. Consider two communities $C = (s, \boldsymbol{\pi})$ and $C' = (s', \boldsymbol{\pi}')$. We say that C leads to C' by *introducing a species* if $s' = s + 1$ and if there are two distinct positive integers, i and j, such that

$$\pi_k' = \begin{cases} \pi_k & \text{if } k \neq i, j \\ \pi_i - h & \text{if } k = i \\ h & \text{if } k = j \end{cases}$$

where $0 < h < \pi_i$. Note that $\pi_j = 0$. A possible biological interpretation is that species i shares its resources with a newly arrived, competing species.

Theorem 4.1. Assume $R(\pi)$ is decreasing in π. Then introducing a species increases the diversity measure of a community.

Proof. Straightforward.

Any community with finitely many species can be built up from a single-species community by successively introducing new species. Theorem 4.1 asserts that the diversity increases at each step. However, Criterion C1 does not ensure that diversity also increases with increasing evenness. For example, let $R(\pi) = 1/\pi^2 - 1$ and $\Delta = \sum_1^s (1/\pi_i^{\#}) - 1$. Criterion C1 is satisfied but, among communities with a fixed number of species, Δ is a minimum for the completely even community.

This defect can be remedied by imposing the additional requirement that diversity also increases when abundance is transferred from one species to another *strictly less abundant* species. The next definition formalizes this operation for many-species communities.

Definition 4.1. Let $C = (s, \boldsymbol{\pi})$ and $C' = (s', \boldsymbol{\pi}')$ be two communities. C leads to C' by a *transfer of abundance* if $s = s'$ and if there are positive integers, i and j, such that $\pi_i > \pi_j > 0$ and

$$\pi_k' = \begin{cases} \pi_k & \text{if } k \neq i, j \\ \pi_i - h & \text{if } k = i \\ \pi_j + h & \text{if } k = j \end{cases}$$

where $0 < h < \pi_i - \pi_j$.

For mathematical purposes, we may consider the operation of introducing a species as a special case of transferring abundance: in Definition 4.1, delete the requirement that $s = s'$ and permit π_j to be zero. The two operations are conceptually quite different, however; introducing a species increases the "species richness" while transferring abundance increases the "evenness."

Criterion C2. $\Delta(C) \le \Delta(C')$ whenever C leads to C' either by introducing a species or by transferring abundance.

Remark 4.1. The requirement that transferring abundance should increase the index is known in the economics literature as Dalton's (1920) "principle of transfers" and was originally proposed in connection with the measurement of income inequality. We discuss income inequality in Section 10.

To state conditions under which the two criteria will be satisfied, it is convenient to define an auxiliary function V by $V(0) = 0$ and $V(\pi) = \pi R(\pi)$ if $0 < \pi \le 1$. For the index $s - 1$, $V(\pi) = 1 - \pi$ for positive π, which shows that V may be discontinuous at the origin. We obtain the following theorems, which we state without proof:

Theorem 4.2. Criterion C2 is satisfied if and only if

$$V(\pi_j + h) - V(\pi_j) \ge V(\pi_i) - V(\pi_i - h) \quad (4.1)$$

whenever $\pi_i > \pi_i - h \ge \pi_j + h > \pi_j \ge 0$ and $\pi_i + \pi_j \le 1$. Assuming differentiability of V, (4.1) may be replaced by $V'(\pi_j) \le V'(\pi_i)$ whenever $\pi_i > \pi_j \ge 0$ and $\pi_i + \pi_j \le 1$.

Theorem 4.3. Criterion C1 and Criterion C2 are both satisfied if V is concave on the *closed* unit interval $[0, 1]$.

Remark 4.2. Because of the constraint $\pi_i + \pi_j \le 1$, the converse of Theorem 4.3 is not true. For example, let $R(\pi) = 1/\pi$ for $0 < \pi \le 1/2$ and $R(\pi) = 0$ for $1/2 < \pi \le 1$.

Corrollary 4.1. The index Δ_β satisfies Criterion C1 for all β. Criterion C2 is satisfied if and only if $\beta \ge -1$. In particular, the Species Count, the Shannon index, and the Simpson index satisfy both criteria.

5. DIVERSITY ORDERING

A *numerical*-valued diversity index imposes a linear ordering on the diversity of ecological communities. But, as emphasized by Hurlbert (1971), different indices may give inconsistent orderings. For example, the Species Count and the Simpson index order the two communities $C = (2, (.5, 0, .5))$ and $C' = (3, (.1, .8, .1))$ in the opposite sense:

$$\Delta_{-1}(C) = 1 < 2 = \Delta_{-1}(C'),$$

$$\Delta_1(C) = .5 > .34 = \Delta_1(C').$$

Inconsistent measures, such as these, are a familiar problem and should not be a cause for undue pessimism. The mean and the median are inconsistent measures of "central tendency"; the variance, the mean absolute deviation, and the range are inconsistent measures of "spread." However, in view of these inconsistencies, it becomes of interest to define an intrinsic diversity ordering without reference to indices. We propose the following:

Definition 5.1. Community C' is *intrinsically more diverse* than community C (written $C' \ge C$) provided C leads to C' by a finite sequence of the following operations:

1. Introducing a species;
2. Transferring abundance;
3. Relabeling species, i.e., permuting the components of the abundance vector.

This ordering is a *partial order* in the sense that (a) $C \ge C$; (b) $C' \ge C$ whenever $C'' \ge C'$ and $C' \ge C$; and (c) a given pair of communities need not be comparable. Solomon (1979) has also proposed a diversity ordering based on the notion of majorization. Fundamental theorems of Hardy, Littlewood, and Polya (1934) and Rado (1952) show that our definition is equivalent to Solomon's.

Theorem 5.1. Let $C = (s, \pi)$ and $C' = (s', \nu)$ be two communities. Then the following statements are equivalent.

(a) C' is intrinsically more diverse than C.

(b) ν is a convex linear combination of permutations of π.

(c) $\nu^{\#}$ is stochastically greater than $\pi^{\#}$, i.e.,

$$\sum_{i>k} \nu_i^{\#} \ge \sum_{i>k} \pi_i^{\#}, \quad k = 1, 2, 3, \ldots .$$

(d) $\pi^{\#}$ majorizes $\nu^{\#}$, that is,

$$\sum_{i\le k} \pi_i^{\#} \ge \sum_{i\le k} \nu_i^{\#}, \quad k = 1, 2, 3, \ldots .$$

Using statement (b) of the theorem, the intrinsic diversity ordering may be represented on the abundance simplex. Figure 1 shows a three-species community C together with the regions of the simplex that are intrinsically more or intrinsically less diverse than C. Also shown are the contours through C of the indices Δ_β. Any community whose abundance vector lies between two of these contours would be inconsistently ordered by the corresponding indices. As β decreases toward -1, the contours become increasingly elongated toward the vertices of the simplex and sweep out a region whose boundaries are labeled $\beta = \infty$ and $\beta = -1$. (The index Δ_{-1} does not have well-defined contours. The boundary labeled $\beta = -1$ has defining equation $\pi_1\pi_2\pi_3$ = constant while the boundary $\beta = \infty$ is defined by $\pi_1^{\#}$ = constant.) The contours do not sweep out the entire region of incomparability and there are communities that are consistently ordered by the entire family $\{\Delta_\beta : \beta \ge -1\}$ even though they are not intrinsically comparable. The communities labeled C and C' in Figure 1 are an example. A family of indices will be called *complete* if C is intrinsically more diverse than C'' when $\Delta(C) \ge \Delta(C'')$ for all indices Δ in the family. Thus $\{\Delta_\beta : \beta \ge -1\}$ is not complete.

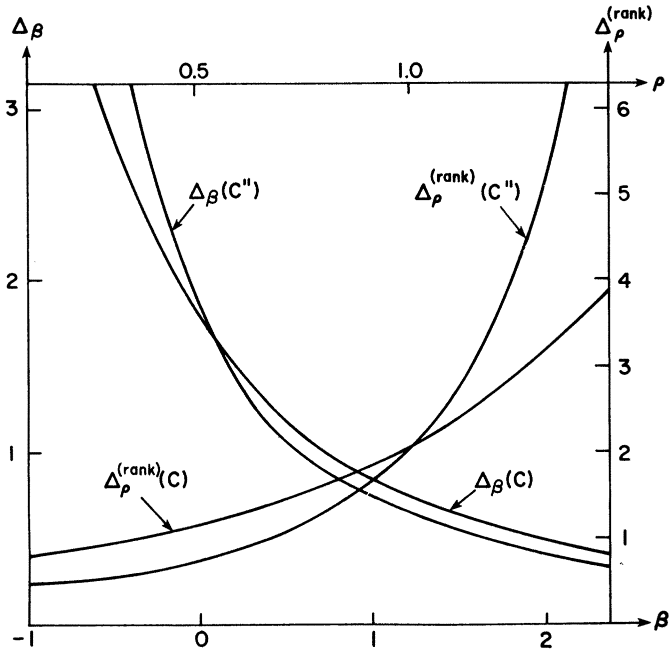

Figure 1. Geometric Representation of the Intrinsic Diversity Ordering: C = (3, (.49, .36, .15)), C'' = (3, (.62, .21, .17))

In view of Theorem 5.1(b), Criterion C2 may be restated as the requirement that $\Delta(\nu) \ge \Delta(\pi)$ whenever ν is a convex linear combination of permutations of π. Functions that satisfy this property are sometimes called *Schur concave* (see, for example, Marshall and Olkin 1974). Lewontin (1972) has suggested the following somewhat stronger requirement.

Criterion C3. $\Delta(\pi)$ is a concave function of π.

While we know of no intuitive motivation for this criterion, it will be essential to the mixture decomposition of Section 8.3. Criterion C3, unlike Criterion C2, is not preserved under increasing transformations of the index. For example, the numbers equivalent of the Simpson index, $1/\sum \pi_i^2$, satisfies Criterion C2 but not Criterion C3. We also note that the conclusion of Theorem 4.3 can be strengthened as follows.

Theorem 5.2. Criterion C3 is satisfied if the auxiliary function V is concave on the closed unit interval $[0, 1]$. In particular, Δ_β satisfies Criterion C3 if and only if $\beta \ge -1$.

6. INDICES BASED ON RANKING

The indices discussed in Section 3 and Section 4 were based on dichotomous measures of rarity. A measure of species rarity with a more detailed dependence upon community composition is the number of more abundant species. For the ith ranked species, this number is $i - 1$ and average community rarity becomes $\sum (i - 1)\pi_i^{\#} = \sum i\pi_i^{\#} - 1$ = Average Rank − 1. Solomon (1979), from quite another point of view, has introduced the Average Rank as a diversity index. (The -1 has the effect of assigning diversity zero to a single-species community and appears to be a generally useful convention.)

A related index is Fager's (1972) "Number of Moves," which is, in effect, the Average Rank rescaled to range between zero and one. However, Peet (1975) has given persuasive arguments against rescaling diversity indices. Fager's basic idea is attractive, though. As an alternative to Fager's number of moves needed to convert a sample to an even distribution, one may consider the "work (= mass × distance)" required to construct a given community from a single-species community. This "work" is seen to be Average Rank $-$ 1.

For the general measure of rarity based on ranks, the analog of Criterion C1 is the requirement that $R(i)$ be an increasing function of i. In contrast with the case of dichotomous indices, this monotonicity is sufficient for Criterion C2. In fact, we have the following theorem, whose proof is available from the authors upon request.

Theorem 6.1. For the rank-type index of the form $\Delta(\boldsymbol{\pi}) = \sum R(i)\pi_i^{\#}$, the following are equivalent.

(a) $R(i)$ is an increasing function of i.
(b) Δ satisfies Criterion C2 (Shur concavity).
(c) Δ satisfies Criterion C3 (concavity).

Lemma 6.1. Let $\mathbf{a}, \mathbf{b} \in R^n$ and assume that $a_1 \le a_2 \le \cdots \le a_n$. Then $f(\sigma) = \sum a_i b_{\sigma i}$ is maximized when the permutation σ arranges $\mathbf{b}$ in ascending order and is minimized when σ arranges $\mathbf{b}$ in descending order.

The proportionality equation (3.1) has the analog

$$R(k+i) - R(i) = W(i)[R(k+1) - R(1)], \qquad i, k = 1, 2, 3, \ldots,$$

whose solution is $W(i) = \rho^{i-1}$ and, up to an affine transformation,

$$R(i) = \begin{cases} (1-\rho^{i-1})/(1-\rho) & \text{if } \rho \neq 1 \\ i-1 & \text{if } \rho = 1 \end{cases} \tag{6.4}$$

where ρ is a constant. A necessary and sufficient condition for $R(i)$ to be increasing is that $\rho \ge 0$. The index based on (6.4) will be denoted by $\Delta_\rho^{(\text{rank})}$, $\rho \ge 0$. Average Rank $-$ 1 is included as the special case $\rho = 1$ and is the analog of the Shannon index in the sense that the deflation factor W is identically one for both indices. In Section 10 we need the numbers equivalent of Average Rank $-$ 1, which may be shown to be $2(\sum i\pi_i) - 1$. In general, however, it is not possible to obtain a closed form expression for the numbers equivalent of $\Delta_\rho^{(\text{rank})}$.

With the aid of the partial summation formula, $\Delta_\rho^{(\text{rank})}$ may be expressed as a right-tail probability-generating function,

$$\Delta_\rho^{(\text{rank})} = \sum_{i\ge 1} \Big(\sum_{j>i} \pi_j^{\#}\Big)\rho^{i-1}$$
$$= (1-\pi_1^{\#}) + (1-\pi_1^{\#}-\pi_2^{\#})\rho + \cdots. \tag{6.5}$$

Clearly, then, $\Delta_\rho^{(\text{rank})}(C)$ is an increasing function of ρ and is strictly increasing when $s > 2$.

Figure 1 shows some contours of $\Delta_\rho^{(\text{rank})}$ for three-species communities. As is true for all rank-type indices, the contours are piecewise linear. As ρ increases, the contours become increasingly elongated toward the vertices and, unlike those of Δ_β, sweep out the entire region of incomparability. Thus $\{\Delta_\rho^{(\text{rank})} : \rho \ge 0\}$ is complete for three-species communities (this fails for more than three species, however).

7. INDEX RESPONSE

The choice of an index implicitly involves a decision regarding the diversity-ordering of communities that are not intrinsically comparable. Peet (1975) discusses the need for a theory of index response to assist in this choice. For example, one may wish the index to be sensitive to the composition of the rare species but relatively indifferent to that of the abundant species. In Section 7.1, we give a definition of the sensitivity of an index and relate it to the question of index inconsistency. The term "sensitive to rare species" occurs frequently in the diversity literature, but to our knowledge no precise definition has previously appeared.

Peet (1974, p. 296) suggests that index response be determined by examining the change in index value that results from a given change in the abundance of two equally common species. Expanding upon this idea in Section 7.2, we define the deflation factor of an arbitrary index and characterize Δ_β and $\Delta_\rho^{(\text{rank})}$ by the form of their deflation factors.

7.1 Sensitivity to Rare Species

In this section we consider communities C, C', C'' with ranked abundance vectors $\boldsymbol{\pi}^{\#}$, $\boldsymbol{\pi}'^{\#}$, $\boldsymbol{\pi}''^{\#}$. Recall that C'' is intrinsically more diverse than C if all the tail-sum differences,

$$T_k = T_k(C'', C) = \sum_{i \ge k} (\pi_i''^{\#} - \pi_i^{\#}), \quad k = 1, 2, 3, \ldots,$$

are nonnegative. The next most complicated relation occurs when this sequence of differences has exactly one sign change. Taking the sign change to be from negative to positive, we say that C'' is *more diverse in the tail* than C if there is a positive integer m for which $T_1, T_2, \ldots, T_m$ are less than or equal to zero but not all zero while $T_{m+1}, T_{m+2}, \ldots$ are greater than or equal to zero but not all zero.

Definition 7.1. A vector $\mathbf{f} = (f_1, f_2, \ldots)$ is a *transfer vector* if all its tail sums are nonnegative and $f_1 + f_2 + \cdots = 0$. A pair $(\mathbf{b}, \mathbf{f})$ on nonzero transfer vectors is *separated at m* ($m = 2, 3, \ldots$) if $b_i = 0$ for $m < i$ and $f_i = 0$ for $i < m$. We call $\mathbf{b}$ the *backward* and $\mathbf{f}$ the *forward* component.

If C'' is intrinsically more diverse than C, the difference $\mathbf{f} = \boldsymbol{\pi}''^{\#} - \boldsymbol{\pi}^{\#}$ is a transfer vector that codes the information needed to obtain C'' from C by transfers to less abundant species (forward transfers). When C'' is more diverse in the tail than C, there is a pair $(\mathbf{b}, \mathbf{f})$ of nonzero transfer vectors separated at m for which $\boldsymbol{\pi}''^{\#} = \boldsymbol{\pi}^{\#} + \mathbf{f} - \mathbf{b}$. In this case, C'' may be obtained from C by a two-step operation: $\boldsymbol{\pi}^{\#} \to \boldsymbol{\pi}^{\#} + \mathbf{f} \to \boldsymbol{\pi}^{\#} + \mathbf{f} - \mathbf{b}$. The first step increases the diversity in the intrinsic sense and does so by forward transfers among the species ranked $m, m + 1, m + 2, \ldots$. The second step decreases the diversity by backward transfers among the species ranked $1, 2, 3, \ldots, m$.

Example 7.1. We illustrate the preceding with a numerical example similar to one given by Hurlbert (1971). Take

$$\boldsymbol{\pi}^{\#} = (.18, .18, .16, .16, .16, .16)$$

and

$$\boldsymbol{\pi}''^{\#} = (.50, .05, .05, .05, .05, .05, .05, .05, .05, .05, .05).$$

The sequence of tail sum differences T_k is

$$0, -.32, -.19, -.08, .03, .14, .25, .20, .15, .10, .05.$$

Since there is only one sign change, C'' is more diverse in the tail than C. Putting

$$\mathbf{b} = (-.32, .13, .11, .08, 0, 0, 0, 0, 0, 0, 0),$$

$$\mathbf{f} = (0, 0, 0, -.03, -.11, -.11, .05, .05, .05, .05, .05),$$

the pair $(\mathbf{b}, \mathbf{f})$ is separated at $m = 4$ and $\boldsymbol{\pi}''^{\#} = \boldsymbol{\pi}^{\#} + \mathbf{b} - \mathbf{f}$. Since the two communities C'' and C are not intrinsically comparable, they may be inconsistently ordered by a given pair of indices. But C'' is more diverse in the tail, so that we might anticipate the order $\Delta(C'') \geq \Delta(C)$ when Δ is "sensitive to rare species" and the opposite ordering when Δ is "insensitive." Figure 2 illustrates this behavior for the indices Δ_β. The figure includes plots of $\Delta_\beta(C)$ and of $\Delta_\beta(C'')$ versus β. Notice that both curves are decreasing and have exactly one crossing point. The analogous plots of $\Delta_\rho^{(\mathrm{rank})}(C)$ and $\Delta_\rho^{(\mathrm{rank})}(C'')$ are increasing in ρ but again have a unique crossing point.

To give a precise definition of the sensitivity of an index to rare species, start with an s-species community $C = (s, \boldsymbol{\pi}^{\#})$ and let $(\mathbf{b}, \mathbf{f})$ be a pair of nonzero transfer vectors that are separated at m $(1 < m \leq s)$. With h and k two small positive numbers, use $\mathbf{b}$ and $\mathbf{f}$ as direction vectors to construct the two communities,

$$C' : \boldsymbol{\pi}'^{\#} = \boldsymbol{\pi}^{\#} + h\mathbf{f}$$

$$C'' : \boldsymbol{\pi}''^{\#} = \boldsymbol{\pi}^{\#} + h\mathbf{f} - k\mathbf{b}.$$

To ensure that $\boldsymbol{\pi}'^{\#}$ and $\boldsymbol{\pi}''^{\#}$ are ranked, we assume that $f_i \geq f_{i+1}$ and $b_i \leq b_{i+1}$ whenever $\pi_i^{\#} = \pi_{i+1}^{\#}$. Now C' is intrinsically more diverse than C and $\Delta(C') \geq \Delta(C)$ for any index Δ that satisfies Criterion C2. On the other hand, $\Delta(C'')$ is a decreasing function of k and, for sufficiently small h, there is a $k = k(h)$ for which $\Delta(C'') = \Delta(C)$. We define the *sensitivity* of the index Δ to be $dk/dh\,|_{h=0}$ and denote it by $\sigma(\Delta; C; \mathbf{b}, \mathbf{f})$. Figure 3 shows the communities C, C', C'' along with the contour of Δ that passes through C. The sensitivity is the slope of this contour at $h = 0$. Comparison of Figure 3 with Figure 1 reveals that a sensitive index has contours that are elongated toward the vertices of the abundance simplex. Since contours are unaffected by strictly monotonic transformations, the sensitivity of an index is invariant to such transforma-

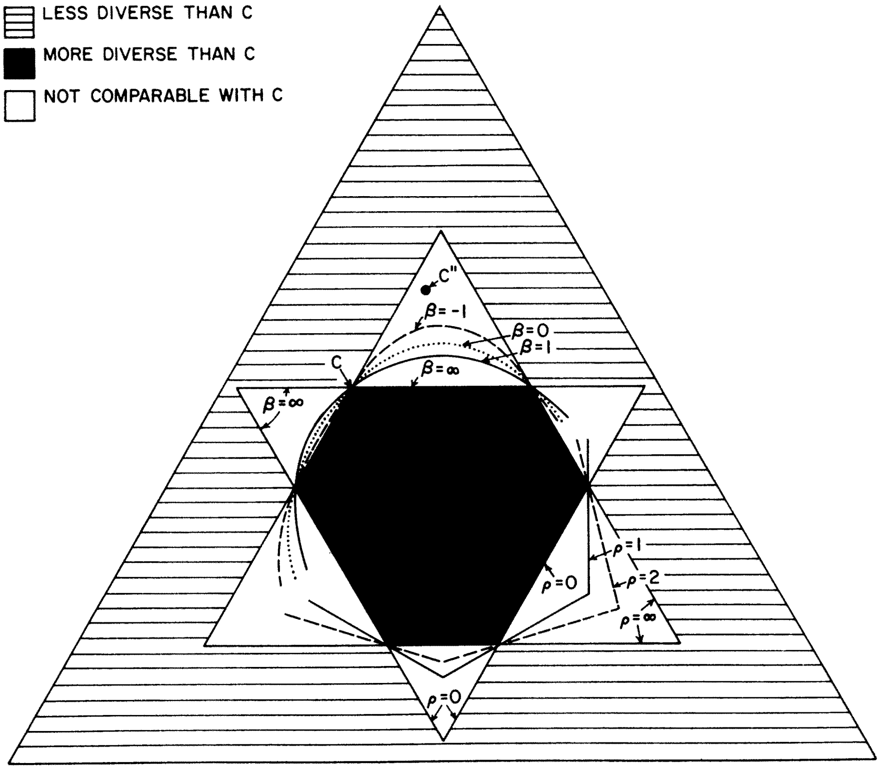

Figure 2. Illustration of the Crossing Point Theorem

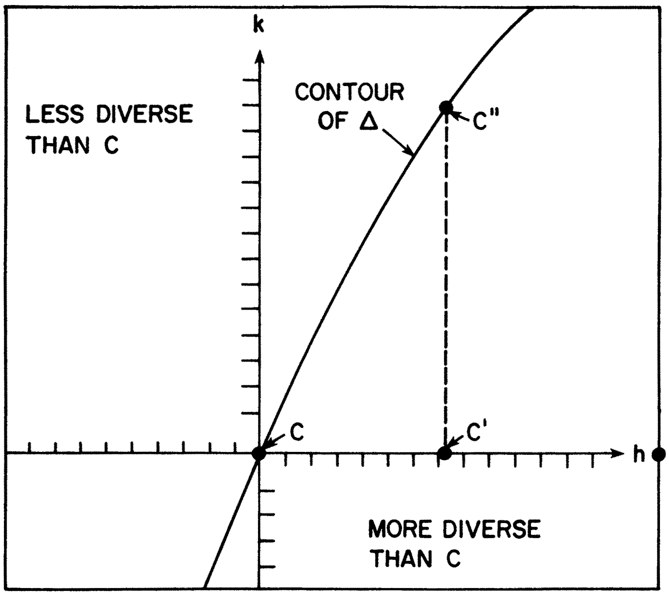

Figure 3. Defining the Sensitivity of Δ

tions. In particular both Δ and its numbers equivalent have the same sensitivity.

It can be shown that the sensitivity of Δ_β is a strictly decreasing function of β, while the sensitivity of $\Delta_\rho^{(\text{rank})}$ is a strictly increasing function of ρ. Also, the existence and uniqueness of the crossing points described in Example 7.1 can be proved.

7.2 Response to Perturbations

We consider a community C and a subcollection of species from this community. Label the members of the subcollection as $i = 1, 2, \ldots, n$, denote their abundances by $\pi_1, \pi_2, \ldots, \pi_n$ and let $\pi = \pi_1 + \pi_2 + \cdots + \pi_n$ be their combined abundance. The subcollection forms a community C' with abundance vector $(\pi_1/\pi, \pi_2/\pi, \ldots, \pi_n/\pi)$. Keeping π fixed, we subject the subcollection to an infinitesimal perturbation of form

$$\tilde{\pi}_i = \pi_i + hb_i, \quad i = 1, \ldots, n, \quad h > 0,$$

$$\sum b_i = 0.$$

The perturbation induces a change $\delta\Delta(C)$ in the diversity index of C and also a change $\delta\Delta(C')$ in that of C'. We wish to compare the magnitudes of these two changes and we define the *response function* of Δ to be the ratio $\delta\Delta(C)/\delta\Delta(C')$. The dependence of the response function on the combined abundance π will be of particular interest. The most natural dependence occurs when the response function equals π (i.e., $\delta\Delta(C) = \pi\cdot\delta\Delta(C')$). More generally we write the response function as $\pi \cdot W$ and call W the *deflation factor*. (Values of W greater than 1 act as an inflation factor.) In general, W depends on the direction vector **b** as well as on the parameters of C and of C'. We also remark that W is invariant to affine transformations of the index but not to monotone transformations in general.

An easy calculation shows that the dichotomous index with auxiliary function V has deflation factor $W = \sum b_i V'(\pi_i)/\sum b_i V'(\pi_i/\pi)$. For the index Δ_β, this expression reduces to $W = \pi^\beta$ which depends only on π. The deflation factor of the rank-type index is bound to be $W = \sum b_j R(i_j)/\sum b_j R(j)$, where $i_1 < i_2 < \cdots < i_n$ are the ranks (within C) of the various species in the subcollection. In particular, $\Delta_\rho^{(\text{rank})}$ has deflation factor $W = \sum b_j \rho^{(i_j - 1)}/\sum b_j \rho^{i-1}$; in general, this expression depends on **b**, but when the species are consecutively ranked ($i_1 = i, i_2 = i + 1, \ldots, i_n = i + n - 1$) it reduces to ρ^{i-1}, which depends only on the rank of the most abundant species. In fact, the indices $\Delta_\rho^{(\text{rank})}$ are characterized by this last property.

Theorem 7.1. Let Δ be a rank-type index whose deflation factor depends only on the rank of the most abundant species when the species are consecutively ranked. Then there is a real number ρ such that Δ is an affine transformation of $\Delta_\rho^{(\text{rank})}$.

Proof. Let i be the rank of the most abundant species and let k be a positive integer. Taking $b_1 = -1$, $b_2 = b_3 = \cdots = b_k = 0$, $b_{k+1} = 1$, we find that

$$W = W(i) = (R(i + k) - R(i))/(R(k + 1) - R(1)).$$

Thus R satisfies the proportionality equation of Section 6 and the theorem follows from (6.4).

8. DIVERSITY DECOMPOSITION

The calculated value of a diversity index provides only limited information concerning the overall structure of a community. Often it is possible to decompose the community in some natural way and, as in the analysis of variance, apportion the total diversity among and between the various components. We consider two types of decompositions: two-way classifications and mixtures. Allan (1975) has discussed both types for the Shannon index. Multiplicative decompositions sometimes appear in the literature, but we restrict ourselves to additive decompositions.

As measured by the Shannon index, the total diversity of a two-way classification decomposes into the sum of two terms: the diversity of the row marginals and the average diversity of the normalized rows. In Section 8.2 we replace this last average by a "deflated" average and extend the decomposition to a wider class of indices. In the important special case of a hierarchial classification, the total diversity equals the diversity of the column marginals and the decomposition becomes a decomposition of marginal diversity. Pielou (1967), Lloyd, Juger, and King (1968), and Wilson (1974) have used this hierarchial decomposition to apportion taxonomic diversity. Theil (1967, 1972) has discussed numerous applications in the social and administrative sciences.

Lewontin (1972) has pointed out a general method of decomposing marginal diversity even for nonhierarchial classifications. In a two-way classification, the vector of column marginals is a mixture of the normalized rows and, when the index is concave, the diversity T of the column marginals is greater than or equal to the average diversity W of the normalized rows. Lewontin proposes that the "within" and the "between" components of diversity be defined as W and $T - W$, respectively. Lewontin explicitly gives the decomposition only for the Shannon index, but Nei (1973) has given it for the Simpson index. In Section 8.3 we discuss this mixture decomposition for the general dichotomous index. However, in the case of a hierarchial classification, the mixture decomposition coincides with the hierarchial decomposition only for the Shannon index. At present, we are aware of no reason for preferring one decomposition over the other.

We begin by making an analogy between diversity and variance; the analogy is strengthened in Section 10.4.

8.1 Diversity and Variance

Let X_1 and X_2 be independent realizations of a random variable X. The variance of X is given by $\sigma^2 = (1/2)E[(X_1 - X_2)^2]$ and may be interpreted as the average difference (or differentness) between the two independent observations. By analogy, define the differentness between species i and species j to be $1 - \delta_{ij}$, where (δ_{ij}) is the identity matrix. Simpson's index can be written as $\Delta_1 = \sum \pi_i(1 - \delta_{ij})\pi_j$ so that diversity (at least as measured by Simpson's index) is the average differentness between two randomly selected members of the community.

Now Δ_1 is a measure of diversity while σ^2 is a measure of spread. The analogy may be extended to one between diversity and spread in general. Given a ranked abundance vector $\boldsymbol{\pi}^{\#}$, define a symmetric, unimodal probability distribution on the integers by $P(0) = \pi_1^{\#}$ and $P(i) = P(-i) = \pi_{i+1}^{\#}/2$ for $i = 1, 2, 3, \ldots$. It is intuitively clear that introducing a species or transferring abundance will increase the spread of this distribution with any reasonable interpretation of spread. In fact, some of the standard measures of spread, when applied to this distribution, become identified with previously considered diversity indices. The half-range, for example, is the Species Count while the mean absolute deviation is the reduced Average Rank.

8.2 Diversity of a Two-Way Classification

Pielou (1975, p. 7) listed three desirable properties of a diversity index:

P1. For a given number of species, the index should assign maximum diversity to the completely even community.

P2. Given two completely even communities, the one with more species should be assigned the greater diversity.

P3. An ANOVA formula (equation 8.2, with $W(\pi) = 1$) should hold for two-way classifications.

Theorem 8.1. Any diversity index $\Delta(C)$ that satisfies Criterion C2 also satisfies properties P1 and P2.

Proof. Let $C' = (s', \boldsymbol{\nu})$ and $C = (s, \boldsymbol{\pi})$ be two communities with C' completely even. Clearly $\boldsymbol{\nu}$ is a convex linear combination of permutations of $\boldsymbol{\pi}$ when $s \le s'$. Applying Theorem 5.1, it follows that $\Delta(C') \ge \Delta(C)$.

As has been shown by Khinchin (See Aczél and Daroczy 1975, p. 67), the three properties P1, P2, and P3 together with some regularity assumptions characterize the Shannon index up to a constant multiple. However, deflated ANOVA formulas can be associated with certain other indices. Consider a two-way classification, $A \times B$, with cell proportions π_{ij}, $i = 1, 2, \ldots, a$, $j = 1, 2, \ldots, a$, and $\pi_{\cdot j}$, $j = 1, 2, \ldots, b$, are all nonzero. We restrict attention to dichotomous indices with rarity measure R. Putting

$$\Delta(A) = \sum_{i=1}^{a} \pi_{i\cdot} R(\pi_{i\cdot}),$$

$$\Delta(B \mid A_i) = \sum_{j=1}^{b} (\pi_{ij}/\pi_{i\cdot}) R(\pi_{ij}/\pi_{i\cdot}),$$

and

$$\Delta(A \times B) = \sum_{i=1}^{a} \sum_{j=1}^{b} \pi_{ij} R(\pi_{ij}),$$

the total diversity may be written as

$$\Delta(A \times B) = \Delta(A) + \sum_{i=1}^{a} \pi_{i\cdot} \sum_{j=1}^{b} (\pi_{ij}/\pi_{i\cdot})[R(\pi_{ij}) - R(\pi_{i\cdot})]. \quad (8.1)$$

For the index Δ_β with rarity measure $R(\pi) = (1 - \pi^\beta)/\beta$ and with deflation factor $W(\pi) = \pi^\beta$, (8.1) reduces to the *deflated ANOVA formula*

$$\Delta(A \times B) = \Delta(A) + \sum_{i=1}^{a} \pi_{i\cdot} W(\pi_{i\cdot}) \Delta(B \mid A_i), \quad (8.2)$$

or, more schematically,

$$\Delta(A \times B) = \Delta(A) + E_A[W(\pi_{i\cdot})\Delta(B \mid A_i)]. \quad (8.3)$$

Interchanging A and B in (8.3) leads to the equation

$$\Delta(B) = \Delta(A) + E_A[W(\pi_{i\cdot})\Delta(B \mid A_i)] - E_B[W(\pi_{\cdot j})\Delta(A \mid B_j)]. \quad (8.4)$$

With $A \times B$ classification as habitat × species, various ecologists, using the Shannon (or the Brillouin) index, have attempted to interpret the last two terms of (8.4) as measures of "niche overlap" and "niche width," respectively (see Allan 1975; Colwell and Futuyma 1971; Horn 1966; Pielou 1972). These interpretations are also reasonable for the Species Count and for the Simpson index; for example, with the Simpson index, $E_A[W(\pi_{i\cdot})\Delta(B \mid A_i)]$ is the probability that two randomly selected organisms belong to the same habitat but different species. Accepting these interpretations, (8.4) states that

$$\text{species diversity} = \text{habitat diversity} + \text{niche overlap} - \text{niche width}. \quad (8.5)$$

Arguing from the Lotka-Volterra competition equations, MacArthur (1972, p. 195) has obtained a multiplicative version of (8.5).

A two-way classification is hierarchial if the rows are mutually orthogonal or, more specifically, if, for each j, all but one of the proportions π_{ij}, $i = 1, 2, \ldots, a$, are zero. In this case $\Delta(A \times B) = \Delta(B)$ and (8.3) becomes a decomposition of marginal diversity,

$$\Delta(B) = \Delta(A) + E_A[W(\pi_{i\cdot})\Delta(B \mid A_i)]. \qquad (8.6)$$

For example, taking the $A \times B$ classification as genus × species, (8.6) expresses the overall species diversity as the sum of the genus diversity and a deflated within-genus species diversity.

The indices Δ_β are essentially the only indices satisfying the deflated ANOVA formula (8.3). This can be proved under a variety of regularity assumptions.

8.3 Diversity of a Mixture

For random variables, the variance of a mixture is greater than or equal to the average variance of the components; the difference is the between-component variance and is nonnegative. Here, we exploit the analogy between diversity and variance to effect an ANOVA-like decomposition for the diversity of a community $\bar{C} = (\bar{s}, \bar{\boldsymbol{\pi}})$ that is a mixture of subcommunities $C_1 = (s_1, \boldsymbol{\pi}^{(1)})$, $C_2 = (s_2, \boldsymbol{\pi}^{(2)}), \ldots, C_n = (s_n, \boldsymbol{\pi}^{(n)})$ with $w_1, w_2, \ldots, w_n$ as the mixing proportions. Then $\bar{\boldsymbol{\pi}} = \sum w_k \boldsymbol{\pi}^{(k)}$.

Throughout this subsection the diversity index is assumed to satisfy Criterion C3 so that $\Delta(\bar{C}) \geq \sum w_k \Delta(C_k)$. The within-community diversity may then be defined as the average $\sum w_k \Delta(C_k)$ and the between-community diversity as the difference $\Delta(\bar{C}) - \sum w_k \Delta(C_k)$. The structure of the between-community component of diversity will be discussed only for the dichotomous type of index $\Delta = \sum \pi_i R(\pi_i)$. Randomly select an individual from the subcommunity C_k. This individual may be regarded as a member of either C_k or $\bar{C}$. Comparing these two viewpoints, the difference in average rarity is

$$\Gamma(C_k; \bar{C}) = \sum_i \pi_i^{(k)}[R(\bar{\pi}_i) - R(\pi_i^{(k)})],$$

which we call the *rarity gain*. With Δ as the Shannon index, $\Gamma(C_k; \bar{C})$ is known as the "information gain (of order 1)" and measures the increase in information attributable to the knowledge that the individual is a member of the particular subcommunity C_k. While the information gain is known to be nonnegative, the rarity gain may be negative for indices other than the Shannon index (see Aczél and Daroczy 1975). However, as is stated by the next theorem, the between-community diversity is the rarity gain averaged over all the subcommunities so that this average is nonnegative.

Theorem 8.4. Assume that the index $\Delta = \sum \pi_i R(\pi_i)$ satisfies Criterion C3. Then

$$\Delta(\bar{C}) = \sum w_k \Delta(C_k) + \sum w_k \Gamma(C_k; \bar{C}).$$

Proof. Straightforward.

Nei (1973) studied the decomposition of Theorem 8.4 in the case of the Simpson index and showed that the between-community diversity may be written as

$$\sum w_k \Gamma(C_k; \bar{C}) = (1/2) \sum w_i w_j \mid \boldsymbol{\pi}^{(i)} - \boldsymbol{\pi}^{(j)} \mid^2, \qquad (8.7)$$

where $| \cdot |$ is the ordinary Euclidian distance. It is clear from (8.7) that (for the Simpson index) the between-community diversity is zero if and only if all the subcommunities with nonzero mixing proportions have identical abundance vectors. In fact this will be true for any index whose auxiliary function $V(\pi) = \pi R(\pi)$ is strictly concave. In particular, it is true for the index Δ_β when $\beta > -1$.

The decomposition of Theorem 8.4 is easily extended to higher-order mixtures. For example, with a doubly indexed family of subcommunities C_{ij} and with mixing proportions w_{ij}, one obtains, with the obvious notation,

$$\Delta(\bar{C}_{\cdot\cdot}) = \sum w_{ij} \Delta(C_{ij}) + \sum w_{ij} \Gamma(C_{ij}; \bar{C}_{i\cdot}) + \sum w_{i\cdot} \Gamma(\bar{C}_{i\cdot}; \bar{C}_{\cdot\cdot}). \qquad (8.8)$$

9. THE DIVERSITY CONCEPT IN OTHER FIELDS

The previous sections have emphasized ecological diversity. Here we survey several additional areas in which the diversity concept has been found to be of some value.

9.1 Genetic Diversity

What proportion of human genetical variation is accounted for by a system of racial classification that is largely based on morphological characteristics? The question has generated a good deal of controversy. To obtain some quantitative answers, Lewontin (1972), subdividing the human species into races and the races into populations, develops the mixture decomposition (8.8) for the Shannon index. Examining the gene frequencies at 17 loci, he finds that, on the average, 6.3 percent of the genetic diversity is accounted for by racial classification, 8.3 percent by population differences within a race, and 85.4 percent by variation among individuals.

9.2 Linguistic Diversity

In a quite interesting paper, Greenberg (1956) describes eight diversity indices that might be applied to the measurement of the potential for communication among the inhabitants of a geographical region. The languages spoken within the region correspond to the species; π_i is the proportion of inhabitants who speak language i.

Observing that a geographical region may be an aggregate of several subregions, Greenberg also raises the question, as in the mixture decomposition of Section 8.3, of how the diversity of the whole can be computed from knowledge of the parts. He cites the example of Mexico and its 32 provinces and points out that the diversity of the whole may exceed the diversity of any or of all of its parts, but he carries the analysis no further. Lieberson (1964,1969) has extended Greenberg's indices to a measure of the "diversity between two subpopulations."

Diversity also occurs in studies of word frequency as an index of literary style (cf. Guiraud 1959; Herdan 1964,1966; Yule 1944). The word-types in an author's lexicon correspond to the species and the relative frequency of occurrence of these word-types to the species proportions.

9.3 Industrial Concentration

Consider s business firms whose proportionate shares of the market are $\pi_1, \pi_2, \ldots, \pi_s$. According to Horowitz (1970), the diversity of the market shares will serve as a meaningful index of industrial competition. Usually economists prefer the dual notion of concentration, but to avoid confusion we will stick to diversity. Both the Shannon index and the Simpson index are widely used (Finkelstein and Friedberg 1967; Hexter and Snow 1970; Horowitz and Horowitz 1968), the latter under the name of Herfindahl index. Theil (1972) advocates the Shannon index because of its ANOVA decomposition. Hall and Tideman (1967) have suggested a variant of the average rank; they also advocate the "principle of transfers."

Arguing that the competitive patterns within an industry are largely determined by the dominant firms, Hart (1971,1975) claims that the Simpson index is sometimes overly sensitive to the entry of a few small firms. (As discussed in Section 7, the Shannon measure is even more sensitive.) This is interesting since the highly sensitive index, $s - 1$, is fashionable among ecologists.

10. INCOME INEQUALITY

10.1 Inequality as Relative Unevenness

Suppose there are s individuals in a population and that the ith individual receives a fraction π_i of the total income. At first glance it might seem that the diversity of $\boldsymbol{\pi} = (\pi_1, \pi_2, \ldots, \pi_s)$ would serve as an inverse measure of income inequality. Indeed, Theil (1967, p. 128) asserts that "concentration and inequality are essentially the same concepts" and that $\sum \pi_i^2$ (which is a decreasing transformation of the Simpson index) can be used as a measure of inequality. This is not the case, however. Perfect equality occurs when the income shares π_i are all the same; in these circumstances, a measure of inequality should take on the same value irrespective of the number of recipients. On the other hand, industrial concentration decreases with an increase in the number of firms in an equally distributed market. Thus $\sum \pi_i^2$ is a suitable measure of concentration but not of inequality.

We have pointed out that diversity is influenced by two factors: evenness and richness. In the light of the preceding paragraph, it appears that a measure of inequality should account for only the uneveness of the income distribution. In fact, it is desirable to qualify this last statement. If the population is partitioned into subpopulations, we identify income inequality with the unevenness of the income shares of the subpopulations relative to their population shares. In general, we suppose that there are s subpopulations and let π_i be the fraction of total income and ν_i the proportion of individuals in the ith subpopulation. Some of the π_i may be zero but, in any case, $\boldsymbol{\pi}$ is absolutely continuous with respect to $\boldsymbol{\nu}$. As Theil (1967, p. 102) points out, per capita income in the ith subpopulation is proportional to the ratio π_i/ν_i; the constant of proportionality is the per capita income in the overall population. We refer to π_i/ν_i as the *standardized per capita income.*

10.2 The Lorenz Ordering

An intrinsic inequality ordering, similar to the diversity ordering of Section 5, may be defined on the set of pairs $(\boldsymbol{\pi}, \boldsymbol{\nu})$ by considering finite sequences of the following operations.

I1. Simultaneously permuting the components of $\boldsymbol{\pi}$ and $\boldsymbol{\nu}$ does not change the inequality of $\boldsymbol{\pi}$ relative to $\boldsymbol{\nu}$.

I2. Combining two subpopulations that have the same per capita income does not change inequality. Specifically, if $\pi_i/\nu_i = \pi_j/\nu_j$, this operation replaces the two components π_i and π_j by the single component $\pi_i + \pi_j$ and also replaces ν_i and ν_j by $\nu_i + \nu_j$. Conversely, splitting a subpopulation into two subpopulations with the same per capita income does not change inequality.

I3. (Principle of transfers). Inequality is increased by a transfer of income from one subpopulation to another provided the second has a larger per capita income. This operation changes $\boldsymbol{\pi}$ but not $\boldsymbol{\nu}$.

Operations I1 and I2 are symmetrical in $\boldsymbol{\pi}$ and $\boldsymbol{\nu}$ but I3 is not; consequently measures of inequality need not be symmetrical in $\boldsymbol{\pi}$ and $\boldsymbol{\nu}$. Operation I2 permits the comparison of populations with different numbers of individuals and was suggested to us by axiom A5 of Dasgupta, Sen, and Starrett (1973).

The intrinsic diversity ordering admitted a simple geometric representation on a simplex. The inequality ordering can also be represented on the cartesian product of two simplices but this requires too many dimensions to be useful. Easier to visualize is the Lorenz curve, which is discussed by Theil (1967, p. 121) for discrete distributions, by Kendall and Stuart (1958, p. 48) for continuous distributions, and by Gastwirth (1971) and Thompson (1976) in general. Thompson also suggests some interesting biological applications. If the subpopulations are arranged in order of decreasing per capita income

$$\pi_1/\nu_1 \geq \pi_2/\nu_2 \geq \cdots \geq \pi_s/\nu_s,$$

the Lorenz curve is the polygonal path joining the successive points $P_1, P_2, \ldots, P_{s+1}$, where $P_{s+1} = (0, 0)$ and

$$P_k = \Big(\sum_{i \geq k} \nu_i, \sum_{i \geq k} \pi_i\Big), \quad k = 1, 2, \ldots, s.$$

The slope of the segment $P_k P_{k+1}$ is the standardized per capita income π_k/ν_k of the kth subpopulation. Operation I2 has the effect of inserting or removing "extra" vertices on any straight line segment. Transferring income lowers the Lorenz curve. A simple inductive argument shows that $(\boldsymbol{\pi}', \boldsymbol{\nu}')$ is intrinsically more unequal than $(\boldsymbol{\pi}, \boldsymbol{\nu})$ if and only if the Lorenz curve of $(\boldsymbol{\pi}', \boldsymbol{\nu}')$ is uniformly below that of $(\boldsymbol{\pi}, \boldsymbol{\nu})$. This generalizes a previous result of Kolm (1969).

10.3 Measures of Inequality

An obvious measure of income inequality, the Gini coefficient, $G(\boldsymbol{\pi}; \boldsymbol{\nu})$, is twice the area between the Lorenz curve and the 45° line. Still supposing that the subpopulations are arranged in order of decreasing per capita income, Theil (1967, p. 121) and others have shown that $G(\boldsymbol{\pi}; \boldsymbol{\nu})$ is symmetrical in $\boldsymbol{\pi}$ and $\boldsymbol{\nu}$ and that

$$G(\boldsymbol{\pi}; \boldsymbol{\nu}) = (1/2) \sum \nu_i \nu_j \mid \pi_i/\nu_i - \pi_j/\nu_j \mid \qquad (10.1)$$

and

$$G(\boldsymbol{\pi}; \boldsymbol{\nu}) = 1 - 2 \sum_i \pi_i \Big(\sum_{j \le i} \nu_j\Big) + \sum_i \pi_i \nu_i. \qquad (10.2)$$

From (10.1) the Gini coefficient is one-half the mean absolute difference between the standardized per capita incomes of two randomly selected subpopulations. When $\boldsymbol{\nu}$ is completely even (i.e., when each $\nu_i = 1/s$), (10.2) simplifies to

$$G(\boldsymbol{\pi}; \boldsymbol{\nu}) = 1 - [2 \sum (i\pi_i) - 1]/s, \qquad (10.3)$$

where $\pi_1 \ge \pi_2 \ge \cdots \ge \pi_s$. Sen (1974) gives an axiomatic characterization of $G(\boldsymbol{\pi}; \boldsymbol{\nu})$ when $\boldsymbol{\nu}$ is completely even.

The Gini coefficient and several other standard measures of inequality can be constructed by adapting a method that has been employed by ecologists to measure the evenness of a distribution. They use the ratio of the actual value of a diversity index to the maximum value that the index could assume in a community with the same number of species (Pielou 1975, p. 15). This ratio, however, is not invariant to monotone transformations of the index and it is preferable to replace the index by its numbers equivalent and use the ratio S_Δ/s as a measure of (absolute) evenness. To convert this ratio to a measure of inequality several decreasing transformations are possible: $1 - (S_\Delta/s)$, $\log(s/S_\Delta)$, or $(s/S_\Delta) - 1$. All three are instances of the transformation

$$S_\Delta/s \rightarrow [(s/S_\Delta)^\alpha - 1]/\alpha, \ \alpha \text{ real}. \qquad (10.4)$$

Applying (10.4) with $\alpha = -1$ to the Average Rank index gives Gini's coefficient in the form (10.3). Applying (10.4) with $\alpha = \beta$ to the index Δ_β gives

$$[\sum \pi_i(\pi_i/s^{-1})^\beta - 1]/\beta \qquad (10.5)$$

as a measure of absolute inequality. To obtain a measure of relative inequality, we replace s^{-1} by ν_i in (10.5), which yields

$$\delta_\beta(\boldsymbol{\pi}; \boldsymbol{\nu}) = [\sum \pi_i(\pi_i/\nu_i)^\beta - 1]/\beta. \qquad (10.6)$$

The measure δ_β is proportional to the directed divergence of type $\beta + 1$ (Rathie and Kannappan 1972) and $\log(1 + \beta\delta_\beta)/\beta$ is the information gain of order $\beta + 1$ (Renyi 1961).

Remark 10.1. Hill (1973) has proposed the ratio S_β/S_α, $\alpha, \beta \ge -1$, as a measure of evenness (S_β is the numbers equivalent of Δ_β). Peet (1975, p. 301) remarks that "These ratios do not measure equitability (evenness) as it is normally defined . . . ." While it is unclear what Peet means by this statement, it can be verified that Hill's ratios violate the principle of transfers unless $\alpha = -1$ or, trivially, unless $\alpha = \beta$. Thus only the ratio S_β/s is a suitable measure of evenness.

When $\beta = -1$, $\delta_\beta(\boldsymbol{\pi}; \boldsymbol{\nu})$ reduces to the proportion of the population that has no income. Here we have used the convention that $0 \cdot \infty = 0$. Some other special cases should be mentioned:

Pearson's X^2: Putting $\beta = 1$ in (10.6) gives

$$\delta_1(\boldsymbol{\pi}; \boldsymbol{\nu}) = \sum (\pi_i - \nu_i)^2/\nu_i = \sum \nu_i(\pi_i/\nu_i - 1)^2,$$

which is the variance of the standardized per capita incomes or, equivalently, the squared coefficient of variation of the unstandardized per capita incomes.

Theil index: With $\beta = 0$, (10.6) becomes

$$\delta_0(\boldsymbol{\pi}; \boldsymbol{\nu}) = \sum \pi_i \log(\pi_i/\nu_i),$$

which has been used by Theil as a measure of income inequality.

Bhattacharyya's divergence: Putting $\beta = -.5$ in (10.6) gives

$$\delta_{-.5}(\boldsymbol{\pi}; \boldsymbol{\nu}) = 2[1 - \sum (\pi_i \nu_i)^{1/2}] = 4 \sin^2(\theta/2) \approx \theta^2,$$

where θ is the angle between the two unit vectors $(\sqrt{\pi_1}, \sqrt{\pi_2}, \ldots, \sqrt{\pi_s})$ and $(\sqrt{\nu_1}, \sqrt{\nu_2}, \ldots, \sqrt{\nu_s})$. Bhattacharyya (1946) uses θ^2 as a measure of the distance between two multinomial populations. Note that $\beta = -.5$ is the only instance in which $\delta_\beta(\boldsymbol{\pi}; \boldsymbol{\nu})$ is symmetrical in $\boldsymbol{\pi}$ and $\boldsymbol{\nu}$.

Assuming that $\beta \ge -1$, we have the following properties: (a) $\delta_\beta(\boldsymbol{\pi}; \boldsymbol{\nu}) \ge 0$; (b) $\delta_\beta(\boldsymbol{\pi}; \boldsymbol{\nu}) = 0$ if and only if $\boldsymbol{\pi} = \boldsymbol{\nu}$, provided $\beta \ne -1$; (c) $\delta_\beta(\pi'; \nu') \ge \delta_\beta(\pi; \nu)$ whenever $(\boldsymbol{\pi}', \boldsymbol{\nu}')$ is intrinsically more unequal than $(\boldsymbol{\pi}, \boldsymbol{\nu})$. There is also a decomposition for two-way classifications $A \times B$ (occupation × age-group, for instance); it takes the form

$$\delta_\beta(\boldsymbol{\pi}; \boldsymbol{\nu}) = \delta_\beta(\boldsymbol{\pi}(A); \boldsymbol{\nu}(A)) + \sum \pi_i(A)[\pi_i(A)/\nu_i(A)]^\beta \, \delta_\beta(\boldsymbol{\pi} \mid A_i; \boldsymbol{\nu} \mid A_i), \qquad (10.7)$$

where: $\boldsymbol{\pi}$ and $\boldsymbol{\nu}$ are the arrays of income shares and population shares, respectively; $\boldsymbol{\pi}(A)$ and $\boldsymbol{\nu}(A)$ are the vectors of row marginals; and $\boldsymbol{\pi} \mid A_i$ and $\boldsymbol{\nu} \mid A_i$ are the normalized ith row vectors. The last term of (10.7) is an average with respect to the income shares but, when β is *strictly* greater than -1, it may be written more naturally as an average with respect to the population shares:

$$\sum \nu_i(A)[\pi_i(A)/\nu_i(A)]^{\beta+1} \, \delta_\beta(\boldsymbol{\pi} \mid A_i; \boldsymbol{\nu} \mid A_i)$$

The factor $[\pi_i(A)/\nu_i(A)]^{\beta+1}$ inflates the contribution of inequality within high per capita income groups while deflating that of low income groups. Such an effect is desirable in a measure of industrial concentration (Sec. 9.3) but may be undesirable in a measure of income inequality (Chiswick 1976). If desired, the contribution of low per capita income groups can be inflated by interchanging $\boldsymbol{\pi}$ and $\boldsymbol{\nu}$ and adopting $\delta_\beta(\boldsymbol{\pi}; \boldsymbol{\nu}) = \delta_\beta(\boldsymbol{\nu}; \boldsymbol{\pi})$, $\beta \geq -1$ as the inequality measure. This measure preserves the Lorenz ordering on the pairs $(\boldsymbol{\pi}; \boldsymbol{\nu})$ but becomes infinite when any of the subpopulations have zero income.

We have motivated the inequality measure δ_β by transforming a numbers equivalent. Atkinson (1970) has given a similar justification for $\delta_\beta{}^*$ by transforming an income equivalent.

10.4 Completing the Circle

Our starting point for the inequality measure δ_β was the diversity index Δ_β. Conversely, Δ_β may be obtained from δ_β by regarding the latter as a measure of distance and by further exploiting the analogy between diversity and variance. Recall that the variance of a random variable X is the minimum value of the mean squared error $E[(X - a)^2]$ and that the minimum is achieved when $a = \mu = E[X]$. This is usually proved by noting the decomposition

$$E[(X - a)^2] = (\mu - a)^2 + \sigma_X{}^2.$$

Consider an abundance vector $\boldsymbol{\pi}$ and write it in the form $\boldsymbol{\pi} = \sum \pi_k \boldsymbol{\epsilon}^{(k)}$ where $\boldsymbol{\epsilon}^{(k)}$ is the kth coordinate vector. The mean deflated distance between an arbitrary abundance vector $\boldsymbol{\nu}$ and a random observation on $\boldsymbol{\pi}$ decomposes as

$$\sum \pi_k \cdot \pi_k{}^\beta \cdot \delta_\beta(\boldsymbol{\epsilon}^{(k)}; \boldsymbol{\nu}) = \delta_\beta(\boldsymbol{\pi}; \boldsymbol{\nu}) + \Delta_\beta(\boldsymbol{\pi})$$

and is minimized, with minimum value $\Delta_\beta(\boldsymbol{\pi})$, when $\boldsymbol{\nu} = \boldsymbol{\pi} = \sum \pi_k \boldsymbol{\epsilon}^{(k)}$.

Using the mixture notation of Section 8.3, one might similarly attempt to minimize, with respect to $\boldsymbol{\nu}$, the expression

$$\sum w_k \cdot w_k{}^\beta \cdot \delta_\beta(\boldsymbol{\pi}^{(k)}; \boldsymbol{\nu}). \qquad (10.8)$$

Here the situation becomes somewhat unpleasant; in particular, (10.8) is minimized by $\boldsymbol{\nu} = \boldsymbol{\pi} = \sum w_k \boldsymbol{\pi}^{(k)}$ in only two cases: (a) when $\beta = 0$ (the Shannon index) and (b) when the abundance vectors $\boldsymbol{\pi}^{(1)}, \boldsymbol{\pi}^{(2)}, \ldots, \boldsymbol{\pi}^{(n)}$ are mutually orthogonal. This anomaly appears to be related to the failure of the mixture decomposition (Theorem 8.4) to coincide with the hierarchial decomposition (8.6). Sibson (1969) or Jardine and Sibson (1971, Ch. 2) may be consulted for more details concerning the problem of minimizing (10.8).

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Comment

I.J. GOOD*

Even after so substantial a paper there is more that can be said about diversity, especially about its history and its applications, and matters of terminology. If $p_1, p_2, \ldots, p_t$ are the probabilities of t mutually exclusive and exhaustive events, any statistician of this century who wanted a measure of homogeneity would have taken about two seconds to suggest $\sum p_i^2$, which I shall call ρ. Both ρ and an unbiased estimate of it, $\hat{\rho} = \sum n_i(n_i - 1)/(N(N - 1))$ in a self-explanatory notation, are mentioned in books on cryptanalysis. See, for example, Saccho (1951, p. 185)—who cites Friedman (1922)—Sinkov (1968, p. 68), and Kullback (1976), which was written I think in the early 1940's, but classified at that time. Kullback, on page 152, derived the variance of $\sum n_i^2$, from which the variance of $\hat{\rho}$ can of course be at once derived. It can also be quickly inferred from the more general formula (Patnaik 1949) for the variance of $\sum [(n_i - Nq_i)^2/(Nq_i)]$ when the true probabilities are (p_i), after replacing each q_i by $1/t$. Patnaik used the methods exemplified by Haldane (1937). Patnaik's formula, rearranged in powers of N for convenience, is

$$\begin{aligned} &4N(\rho_{-2,3} - \rho_{-1,2}^2) + 2(5\rho_{-1,2}^2 - 2\rho_{-1,1}\rho_{-1,2} \\ &\qquad - 6\rho_{-2,3} + 3\rho_{-2,2}) \\ &+ N^{-1}(4\rho_{-1,1}\rho_{-1,2} - 6\rho_{-1,2}^2 + 8\rho_{-2,3} \\ &\qquad - \rho_{-1,1}^2 - 6\rho_{-2,2} + \rho_{-2,1}) \end{aligned}$$

where $\rho_{r,s} = \sum_i(q_i^r p_i^s)$. Note the neat checks that the coefficients of each power of N add up to zero and also that the variance vanishes when $N = 1$. The former of these checks is necessary because $\rho_{-r,r+1} = 1$ in the "equiprobable" case $q_i = p_i = 1/t$ for all i. The same checks would apply to any higher moments and should be held in mind by anyone energetic enough to derive these moments. On putting $q_i = 1/t$ and $\rho_{0,s} = \rho_s$, we obtain the variance of $\hat{\rho}$ in the convenient form

$$\begin{aligned} V(\hat{\rho}) = 2N^{-1}(N - 1)^{-2}[&2N^2(\rho_3 - \rho^2) \\ &+ N(5\rho^2 + \rho - 6\rho_3) + (4\rho_3 - \rho - 3\rho^2)]. \end{aligned}$$

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In 1941, A.M. Turing, probably unaware of previous uses, gave ρ its most natural name "the repeat rate," noticed its unbiased estimate, and made very important use of ρ in cryptanalysis. (The unbiased estimate of $\hat{\rho}$ is not necessarily as good as $\sum n_i^2/N^2$ in some applications.) Turing is best known for his work in the foundations of mathematics, which work involved the concept of what is now called the "Turing machine." He was for a time head of the section of the Government Code & Cypher School in Bletchley, Buckinghamshire, working on the cryptanalysis of the German naval use of the cryptographic machine called the Enigma. For a description of Turing's statistical contributions at that time see Good (1979). Many of us, working at Bletchley, obtained the idea of the repeat rate and of its unbiased estimate directly or indirectly from Turing. The repeat rate had previously been used by Polish cryptanalysts in work on the Enigma (Rejewski 1981). When E.H. Simpson, who also worked at Bletchley, later suggested the use of 1 minus the repeat rate as an index of diversity he did not acknowledge Turing, fearing that to acknowledge him would be regarded as a breach of security. Recently Bhargava and Uppuluri (1975) called $1 - \rho$ the Gini index and cited Gini (1912). It might also be reasonable to ascribe the repeat rate, or some simple function of it, to Lexis (1879), judging by Keynes (1921, pp. 398–399). Weaver (1948) used ρ/p_i as a "surprise index" (where i is the event that obtains) and he regarded ρ as the average value of the p's. Thus it is unjust to associate ρ with any one person. It would be better to use such names as "repeat rate" or "quadratic index of homogeneity" for ρ and perhaps "quadratic index of heterogeneity or diversity" for $1 - \rho$. This name could well be shortened to "the quadratic index" in appropriate contexts.

The repeat rate is of course the probability that two units or animals, selected at random, will belong to the same category or species. Similarly ρ_s is the corresponding probability when s units are selected, and its unbiased estimate is $\sum n_i^{(s)}/N^{(s)}$.

The most familiar alternative index of diversity is the "entropy" $-\sum p_i \log p_i$. It is reasonable to call it Shannon's index (as do Patil and Taillie) because Shannon's work on communication theory was a major contribution, but "Gibbs's index" would be equally reasonable. It is, however, closely related to the equally useful "expected weight of evidence" that predated it. A brief history of the concept of expected weight of evidence is given by Good (1980), but the description there of C.S. Peirce's use of "weight of evidence" is inaccurate and is corrected by Good (1981). Another possible name for the entropy would be the logarithmic index (of diversity). There is some truth in saying that both the quadratic and the logarithmic indexes have histories dating back a hundred years. One can simultaneously in effect generalize these indexes by $c_{m,n} = \sum p_i^m (-\log p_i)^n$ (Good 1953, p. 245; 1954; 1969). A better way of doing so was proposed by Good (1956, 1957), when generalizing Weaver's surprise index, and later by Rényi (1961). I expressed the generalized surprise index as the ratio to p_i of a generalized average of all the p's. This use of an average is analogous to the theme expressed in the first sentence of the abstract of the paper by Patil and Taillie. The analogy is to be expected because there is a strong relationship between surprise and diversity or heterogeneity. In fact, in a very heterogeneous population, it is less surprising to meet a unit that belongs to an unspecified rare category than it would be in a more homogeneous population. So, if p is the probability of the category just encountered, it is natural to divide p into a measure of homogeneity to obtain an index of surprise.

Weaver (1948) mentioned the difficulty of evaluating his surprise index for the Poisson and binomial distributions. For the former the answer can be obtained as a Bessel function and, for the latter, from the convenient identity (Good 1955)

$$\sum_{r=0}^{t} \left[\tbinom{t}{r} p^r (1-p)^{t-r}\right]^2 = \frac{1}{u} \sum_{r=0}^{u-1} \left[1 - 4p(1-p)\sin^2 \frac{\pi r}{u}\right]^t$$

whenever $u > t$, because nearly all the terms on the right are negligible. There is also an expression in terms of Legendre polynominals.

Just as an index of surprise depends on the categorization of the population so does an index of diversity. If we can't decide whether "chair" and "chairs" are the same word, then our index of diversity of English words is made ambiguous, even if the population can be held constant. One way to begin to get round this difficulty is to introduce a measure S of similarity between any pair of animals (or more general units). Then we could call $\rho^* = E(S)$ the *weighted* index of homogeneity or the *index of uniformity*. Of course $\rho^* = \rho$ if S can take only the values 0 and 1. Perhaps we should multiply S by the sum or product of the weights or diameters of the two animals. To use the product of the weights would roughly mean that we were producing an index of uniformity of all the cells in the entire population of animals!

One measure of similarity is by the proportional agreement of DNA strands (Johnson 1973), but it is time-consuming to obtain such a measure. Of course a DNA homology measure lies between 0 and 1 and takes the value 1 only for clones or identical twins. In principle this measure might resolve the difficult "species problem," and it avoids the Platonic all-or-none approach to the definition of species. Unlike one of the standard definitions of species, the proportional homology is applicable even to organisms that reproduce asexually.

A similar definition for an index of nonuniformity or weighted index of diversity is the expected discrepancy (where discrepancy might be defined as $1 - S$) between two randomly selected organisms or units, again possibly allowing for the sizes of the units. When *discrepancy* is interpreted as distance, this definition provides problems in geometrical probability; for example, presumably a disc is the region of given area of minimum mean distance between pairs of infinitesimal elements. In a biological context, instead of using the DNA homology method, or assuming with Plato that species are sharply defined in the mind of God, we can measure discrepancy between two organisms by $1 - \exp(-kx)$ where x is the length of the shortest path connecting them on a taxonomic tree and k is a positive constant. The quadratic index of diversity corresponds to $k = \infty$, but it ignores the fact that tigers and lizards are more dissimilar than tigers and lions. Also, if we don't allow for size, we might find that the index of diversity of animal life on earth is almost determined by the insects alone, or by even smaller organisms.

An advantage of the adjectives quadratic and logarithmic is that they can also be applied to the "proper" payoff rules that were independently suggested by Brier (1950) and by Good (1952), respectively. Thus we would have a unified terminology that would be less of a burden on the memories of those who come new to these topics and we would avoid the distortion of history that is so often caused by the naming of concepts by the names of people.

A potentially important application of measures of diversity is in the logic of medical or nonmedical diagnosis. If the probabilities of t diseases, at some stage of a medical diagnostic procedure, are $p_1, p_2, \ldots, p_t$, then the rougher or more heterogeneous the set of probabilities, the closer we are to a unique diagnosis. Several measures were suggested for this purpose, including the repeat rate and the negentropy, by Good (1968,1970) and by Good and Card (1971). There has not yet been enough experience with numerical medical diagnosis to decide which of the various measures of heterogeneity is the best for this purpose, but it might well turn out that many of them are about equally useful.

For some purposes the homogeneity or heterogeneity of a population may be better described by the parameters in a distribution such as the Pareto or Zipf distribution. A three-parameter distribution that is capable of simultaneously describing both common and rare species was called hypothesis H_4 by Good (1953, p. 249) and was developed in great detail by Sichel (1975).

It may sometimes be best to try to apprehend the statistical composition of a population by means of a density curve of the probabilities of the categories, without worrying about its analytical properties.

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Comment

GEORGE SUGIHARA*

Patil and Taillie have given us a lucid and well-defined analytic framework for studying the mathematical properties of diversity indices. By defining ecological diversity very sensibly as average species rarity and by establishing a set of general criteria for measures of diversity, they are able to bring rigor to issues such as the ambiguity of diversity orderings and the sensitivity of indices to rare species. A similar although less comprehensive attempt at a unifying notation has been made by Hill (1972), who insightfully derived the family Δ_α based on Renyi's entropy. Whereas Hill's essay was aimed at an ecological audience, Patil and Taillie's paper is clearly aimed to provide signpost entry into the subject for statisticians. For this reason I thought that it might be useful here to enumerate a few criticisms and philosophical nitpickings that many ecologists and even born-again mathematical ecologists have raised about the study of species diversity and especially the proliferation of diversity indices in the literature. These should be taken less as criticisms of this particular paper, than as counsel for statisticians who may be interested in contributing to the literature on species diversity.

WHY DIVERSITY?

There are two broad reasons why attention has been focused on characterizing the diversity of an ecological assemblage. These depend on whether one treats diversity as an abstract phenomenological property or a specific biological one. That is, whether one treats diversity in its general sense, as a property in itself, or as an indicator of the functioning and organization of communities. First, diversity per se, as a phenomenological property, contains intrinsic interest, and as a fundamental quality of perception seems to demand quantification. It is not surprising, therefore, that one finds diversity measures emerging in such varied disciplines as genetics, linguistics, and economics. The special significance of *species* diversity as a phenomenological property arises from its association, in a political context, with human values and environmental quality. Such species diversity indices have the practical importance of enabling one to speak precisely (albeit no less arbitrarily) about the qualitative effects of human disturbance on the environment. Here justification for a particular index rests more on philosophy than science, since the primary purpose of the index is to reflect a human value rather than to capture an important property of state in the functioning of communities. This does not detract from the significance of the problem, however, as underscored by the multitude of indices that have been proposed.

Apart from politics there are the more ontological concerns of diversity as a biological property. To the ecologist, diversity is interesting as a property of state in so far as it has the potential to reflect the nature of the underlying processes and organization that structure the community. Therefore, beyond arbitrary or weakly motivated definitions, the scientific interest in and importance of ecological diversity hinges directly on its possible connection with the functioning and organization of communities. The principal aim of such scientific study, therefore, is to find a characterization of species diversity that most clearly reveals this functional connection.

One can group approaches to this problem into three alternative strategies, depending on whether preliminary emphasis is given to the index, the model, or the data. Choosing initially to focus on the index necessarily invokes a phenomenological view of diversity. One does not know whether the index chosen is capturing interesting phenomena or is the best one for revealing the nature of the underlying community structure. To take this approach is in some sense putting the cart before the horse, since the analysis that follows can only have meaning after the index has been justified with a functional model and established with data. The problem of diversity ordering for example, as considered by Patil and Taillie, is really an epistemological one, and it is only when diversity is related to a functional model that the question of "what is more diverse" becomes more than sterile controversy.

In view of how little is known about the connection between diversity patterns and community processes, it seems premature at this early stage to restrict attention to indices and risk losing information by condensing the complete abundance vector into a single statistic. It would be more prudent in these initial stages to consider the complete abundance vector as represented by ranked abundance plots or species frequency distributions (see May 1975 or Pielou 1975). Regularities in these empirical distributions may then be found (Fisher et al. 1943; Preston 1948; May 1975; Kempton 1979) that could provide insight into the underlying processes that structure the community. Only after obtaining a verified model can one

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properly derive an appropriate diversity index that reveals the connection between process and pattern.

Fitting data to theoretical distributions has the added advantage of enabling one to make inferences about the community from incomplete samples. In this sense, the title of Patil and Taillie's essay is somewhat misleading, in that they do not address the crucial practical concerns of inferring community diversity measures from samples. All of the indices discussed are in general sample-size dependent. Questions of the philosophy of approach aside, historical inertia in the wide usage of indices suggests that this is a problem that in the future could benefit from the sort of systematic treatment given to the question of ordering. Simpson's index, for example, can be shown to be independent of sample size if the underlying pattern of abundances has a logseries distribution (May 1975).

Although Patil and Taillie have, for the most part, focused on diversity as a phenomenological property, it is notable that some attempt was made to motivate Simpson's index, species count, and the information-theoretic measure in terms of interspecific encounter probabilities, waiting times, and niche theory. None of these interpretations, however, has yet proved to be very fruitful, as they suffer from such real-world concerns as spatial patchiness and clumping in species distributions, differential mobility, and problems associated with interpreting niche overlap between species from their spatial covariance. Approaching the study of species diversity through a priori models is a valid enterprise, but requires a clear intuition of how communities operate, which thus far seems to be lacking.

In closing, I believe that Patil and Taillie's paper, although interesting and useful in its own right, will be regarded by ecologists not so much as a contribution to the theory of species diversity as a constructive and insightful essay in tidying up a messy literature on diversity indices. Truly ground-breaking contributions to the theory of species diversity are not likely to arise in vitro from a mathematical analysis of indices but will most probably depend on an interplay of analysis with real data.

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Rejoinder

G. P. PATIL AND C. TAILLIE*

1. INTRODUCTION

We greatly appreciate the comments by I. J. Good and George Sugihara. In this rejoinder, we simply review recent literature on diversity. In so doing, we hope to have touched base with some of the comments of Good and Sugihara.

2. DIVERSITY IN CONSERVATION AND MANAGEMENT

The National Forest Management Act of the United States (Federal Register 44(181), 219.13(6), 1979) requires that the management practices should maintain the diversity of the forest ecosystems. These regulations further require quantitative comparisons of the diversities of the natural and the managed forests.

The Committee to Review Methods for Ecotoxicology of the Environmental Sciences Board of the U.S. National Academy of Sciences (1981, John Cairns, Jr., Chairman) has concluded in their report on testing for effects of chemicals on ecosystems that "diversity is a system property that is likely to be a sensitive measure of ecosystem contamination." The Committee has further recommended that "methods should be developed

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for detecting change in such properties related to systems as diversity, productivity and biomass, connectivity, resistance and resilience, and genotypic or taxonomic variability."

The United States Strategy Conference on Biological Diversity was sponsored by the U.S. Department of State (1981). The principal objective of the conference was to consider steps the U.S. might pursue to maintain the earth's biological diversity in a manner that serves a range of economic, social, and ecological interests over the long term.

The Committee on Germplasm Resources of the Division of Biological Sciences of the U.S. National Academy of Sciences (1978) identified the diversity of germplasms as an essential natural resource. It found that the value of these resources is being rapidly eroded by a variety of encroachments, and recommended that action must be taken soon to protect and maintain the remaining genetic diversity.

The Royal Entomological Society sponsored a symposium and its publication on diversity of insect faunas. In his inaugural address, L. R. Taylor (1978) said ". . . diversity so pervades every aspect of biology that each author may safely interpret the word as he wishes. . . . We have three approaches to the study of diversity: mathematical, statistical, and biological, all of which are necessary. . . ."

The International Statistical Ecology Program sponsored a series of research workshops and a publication on diversity in theory and practice (Grassle et al. 1979) with a view to put together current state-of-the-art for use in the ongoing efforts of resource conservation and environmental protection.

3. DIVERSITY AS A MULTIDIMENSIONAL CONCEPT AND ITS QUANTITATIVE REPRESENTATION

Like most any other major concept, diversity is a multidimensional concept. With this in view, Patil and Taillie (1979a) introduce the concept of diversity profile and its representation through suitably chosen plots. One has then a pictorial representation of diversity comparisons of communities. Further, it turns out that isotonic diversity indices play the role of test statistics and that the multitude of indices then becomes an advantage because of their use in the development of appropriate tests powerful against possible changes in community structure. For further information, see Hill (1973), May (1975), Dennis and Rossi (1979), Kempton (1979), Kempton and Taylor (1979), Patil and Taillie (1977,1979b), Routledge (1979), and Tong (1982).

By tradition, diversity has been primarily viewed in ecology as a two-dimensional concept with components of richness and evenness. Based on his analysis of empirical data, Preston (1948,1962) stipulated a "canonical hypothesis," which, in certain situations, has an implication of a trade-off between richness and evenness, leading to a scalar concept of the composite diversity. For further discussion, see MacArthur and Wilson (1967), May (1975), and Patil and Taillie (1979c).

4. DIVERSITY AS AN OUTPUT AND INPUT PARAMETER

A scalar or nonscalar measurement of diversity may serve as an indicator or as a regulatory criterion, in which case it plays the role of an output parameter. In this role, it may be a process parameter, a phenomenological parameter, or both. Some of the relevant statistical and ecological references are: Cairns (1969), Cairns and Dickson (1971), May (1974,1975,1978), Pielou (1975), Dennis and Patil (1977), Engen (1978), Colwell (1979), Dennis, Patil, and Rossi (1979), and Cancela Da Fonseca (1980).

Research on diversity as an input parameter is relatively in its embryonic stage. A major question is, What of consequence, if any, does the diversity of a system help predict or determine? Some of the questions that have been pursued are, Does the diversity of a community help predict its stability? Does the biotic diversity of a habitat help predict its abiotic classification? Does the geological diversity of a region help predict its mineral diversity? The reader will find the following references of interest: Woodwell and Smith (1969), Goodman (1975), Cairns, Patil, and Waters (1979), Kempton and Taylor (1979), Rossi et al. (1979), Griffiths, Watson, and Menzie (1980), Abugov (1982), and Zaret (1982).

5. DATA ANALYSIS FOR DIVERSITY ESTIMATION AND COMPARISON

Meaningful diversity analysis and interpretation of data is a challenging task for both the scientist and the statistician. Several papers are now in print that discuss one aspect or the other. And there is abundant scope for further work. References to start off may include Simberloff (1972), May (1975), Pielou (1975), Smith and Grassle (1977), Engen (1978), Grassle et al. (1979), Patil and Taillie (1979a), Rao (1982a,b), and Siegel and German (1982).

6. BIBLIOGRAPHIC SOURCES ON DIVERSITY-RELATED LITERATURE

The following books should provide a good start. Gatlin (1972), Sen (1973), Pielou (1975), Engen (1978), Mound and Waloff (1978), Patil and Rosenzweig (1979), and Grassle et al. (1979). The last reference includes a comprehensive bibliography of literature on ecological diversity and related methodology consisting of 1,046 publications as of 1979. Most of the references cited in the rejoinder appear in the main paper or in this comprehensive bibliography. Additional references are given below.

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