COMPARATIVE EVALUATION OF FOUR SPECIES DIVERSITY INDICES RELATED TO TWO SPECIFIC ECOLOGICAL SITUATIONS

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ABSTRACT

Computer simulation was used to test the reliability of four diversity indices (Simpson, Shannon, Patil-Taillie, Margalef). The indices were calculated for two statistical universes (log-normal and gamma) representing pioneer and mature communities. Data were taken from four years of lepidoptera trapping published by Kempton and Taylor (1974).

The reliability of the indices was evaluated by calculating their bias and precision. The authors conclude that all the indices are independent of the type of community considered, while for both absolute and comparative estimates Simpson's is the most reliable.

INTRODUCTION

SPECIES diversity is a measurable characteristic of natural communities. The first index of diversity was that of Fisher-Williams (Fisher, Corbet and Williams, 1943) and it has been followed by many others. By far the most frequently used, both in theoretical and applied research, is the Shannon index (1949). Although many (perhaps too many!) indices have been proposed, little work has been done on the comparative evaluation of their statistical performance in specific ecological situations. Among the existing studies (Dickman, 1968; Bowman *et al.*, 1971; De Jong, 1975; Peet, 1974, 1975; Heltsche and Bitz, 1979; Cuba, 1981) there are no solid conclusions concerning the differential statistical behaviour of these indices in response to specific types of community or environment.

The relation between indices of diversity and species abundance distribution has been studied in detail by May (1973, 1975) and by Dennis and Patil (1979). These workers used various statistical distributions (log-normal, gamma, McArthur's broken-stick model, etc.) as models to describe the types of abundance distribution found for species of a natural community.

At the same time, they explicitly excluded from their discussion any comparison between the indices with respect to their sample behaviour within the given ecological/statistical model.

There is still considerable theoretical interest in species diversity and its relation to various aspects of the stability of a natural community (Margalef and Gutierrez, 1983; Connel and Sousa, 1983; King and Pimm, 1983), including the concepts of island bio-geography (Williamson, 1981). In applied work, on the other hand, indices of diversity are used more frequently as bioindicators in the quality control of aquatic (Mason, 1977; Rossi *et al.*, 1979; Dygert, 1981) and terrestrial (Menhimick, 1964; Solem, 1979) environments.

For the present computer simulation study, we considered two kinds of natural community, both described by well-known statistical distributions. The number of species is very different in the two communities and, from the general viewpoint of ecological succession, they might be classified as a pioneer community and a mature community.

Using computer-generated samples, they were compared with respect to two parameters that are important for species diversity estimates: bias and precision.

METHODS

The two statistical distributions employed, log-normal and gamma, were chosen for their importance as theoretical models in the study of the structure of natural communities. Both distributions have two parameters and are defined on the reals for $x = 0$ as follows:

$$\text{Log-normal } f(x) = \frac{1}{x\sigma\sqrt{2\pi}} \cdot e^{-1/2\sigma^2 \cdot (\log x - \mu)^2}$$

$\log(x)$ is distributed normally with mean $= \mu$ and variance $= \sigma^2$

x has mean $= e^{\mu + \sigma^2/2}$, variance $= e^{2\mu + \sigma^2} \cdot (e^{\sigma^2} - 1)$ and median $= e^\mu$

$$\text{Gamma } f(x) = \frac{k/m}{\Gamma(k)} \cdot \left(\frac{kx}{m}\right)^{k-1} \cdot e^{-kx/m}$$

with mean $= m$ and variance $= m^2/k$ (Kempton and Taylor, 1974).

The approximation resulting from the use of continuous distributions in real situations represented by frequencies is considered completely satisfactory when, as in our case, the range of the abundances of the individuals is very large and the probability that a species has the given abundance is, consequently, very low.

Dennis and Patil (1979), following previous results due to Capocelli and Ricciardi (1974), suggested that the abundances of $S^\star$ species forming a natural community at the pioneer stage of succession tend to follow the log-normal distribution. This same distribution was proposed by May (1975) as a description of ecological situations in which the distribution of the abundances is due to the multiplicative effect of infinite environmental factors. The fitting of the log-normal model to field data has been very successful for many taxa: for plants see Whittaker (1965, 1972), for several other species or genera of birds see Preston (1962, 1980). The abundances of $S^\star$ species in a community at the equilibrium, or climax, stage of succession might be characterised by the gamma distribution (Dennis and Patil, 1979). Kempton and Taylor (1974), analysing data from four years of lepidoptera trapping, showed that the log-normal distribution is better adapted to communities in unstable environments, while the gamma distribution characterises those in more stable environments. The latter communities tend to be more mature. Although the gamma distribution has been little used by ecologists studying the structure of natural communities, it is, in fact, a family of distributions from which one can derive, as limit forms, other well-known and frequently used distributions: the negative binomial, the logarithmic series, the beta distribution and so on. (For the connections between these distributions, see Ord, Patil and Taillie, 1979; or Douglas, 1980).

For our study we constructed two statistical universes corresponding to the two distributions. The essential characteristics are given in Table 1. They derive from experimental data published by Kempton and Taylor (1974). Using their data, we calculated the expected values (species frequencies) for the two distributions, rounded to the nearest integer.

The input data for the simulation was thus derived from two real situations studied during experimental research. The only manipulation of the data (required for the

Table 1. *Species frequency distributions of moth catches from Fort Augustus (log-normal universe) and from Geescroft Wilderness (gamma universe). By Kempton and Taylor (1974)*

	Log Normal Universe					Gamma Universe		
Number of individuals: 4543						Number of individuals: 52761		
Number of species: 165						Number of species: 296		
$\chi_5^2 = 7.1; P > 0.2$						$\chi_{10}^2 = 9; P > 0.5$		

	Individuals per species	Observed	Expected (rounded)			Individuals per species	Observed	Expected (rounded)
1	1	24	19		1	1	43	42
2	2+	22	26		2	2+	33	35
3	4+	30	31		3	4+	44	32
4	8+	22	29		4	8+	29	30
5	16+	30	24		5	16+	33	29
6	32+	21	16		6	32+	25	28
7	64+	9	10		7	64+	20	27
8	128+	7	9		8	128+	22	25
					9	256+	25	21
					10	512+	12	15
					11	1024+	8	8
					12	2048+	3	2

calculation of all the indices) involved the distribution of the total number of individuals among the species forming the two communities considered. All the species within a given abundance class are constituted by an equal number of individuals, in fact, by the central number of the reference interval (see Table 1).

The computer simulation used the following indices of species diversity:

(a) Simpson index (1949)

$$d_1 = 1 - \sum_{i=1}^{S} \frac{n_i(n_i - 1)}{N(N-1)}$$

(b) Shannon index (1949)

$$d_2 = -\sum_{i=1}^{S} \frac{n_i}{N} \log_{10} \frac{n_i}{N}$$

(c) Patil-Taillie index (1976)

$$d_3 = 1 + \sum_{i=1}^{S} \left(\frac{n_i}{N}\right)^2 \cdot \log_{10} \frac{n_i}{N} \Big/ \left(1 - \frac{n_i}{N}\right)$$

(d) Margalef index (1976)

$$d_4 = \frac{1 - \sum_{i=1}^{S} \frac{n_i (n_i - 1)}{N (N-1)}}{\sum_{i=1}^{S} \frac{n_i (n_i - 1)}{N (N-1)}}$$

These indices, especially the first two, are currently used by field ecologists and also by those (regional planning researchers, conservationists, etc.) who attempt to evaluate the impact of regional economic development plans promoted by public or private authorities on the natural environment (Nijkamp, 1979).

The last two (c–d) were considered because their relatively recent introduction could lead one to suppose that they have new and interesting characteristics. Margalef's index directly derives from that of Simpson and is conceptually interesting since it can be

interpreted as the ratio between the maximum number of interspecific interactions and the maximum number of intra-specific interactions.

As can be seen, we have excluded the well-known Fisher-Williams α index. It was not considered because the sample on which it is calculated derives from a statistical universe described by a logarithmic series.

During routine use, the values of $d_1 - d_4$ are considered sample estimates of the corresponding values $D_1 - D_4$ of the universe; the universe is considered as a compound of $N^\star$ individuals (N is the estimate of $N^\star$) divided into $S^\star$ species (S is the estimate of $S^\star$), $n_i^\star$ (n_i is the estimate of $n_i^\star$) being the true abundance of the ith species.

In the simulated sampling, each individual, independently of the species it belongs to, has the same probability of being included in the sample from which the four indices are calculated. This sampling scheme is approximate as regards the spatial cluster distribution of certain vegetable communities. It is, however, usable for many communities of organisms which exist as discrete individuals rather than as patches (forest trees, insects, etc.).

A C.D.C. Cyber 730 computer with the system random function RANF was used. The formulae given above were applied to the data relative to the two statistical universes under the following conditions:

—sample size n for both universes: 30, 50, 100, 400 and 800 individuals;

—200 replications with reintroduction for each sample size so as to calculate the following statistical parameters for each index: mean $\bar{d}$, standard deviation s, skewness g_1, kurtosis g_2, coefficient of variation $s/\bar{d}$, Student's "t" test for an estimate of the intensity of possible bias. The skewness and kurtosis of the distribution are defined as follows (Snedecor and Cochran, 1969):

skewness
$$g_1 = \frac{\Sigma(d-\bar{d})^3/n}{(\Sigma(d-\bar{d})^2/n)^{3/2}}$$

kurtosis
$$g_2 = \frac{\Sigma(d-\bar{d})^4/n}{(\Sigma(d-\bar{d})^2/n)^2} - 3$$

The statistical significance of g_1 and g_2 was evaluated using the tables published by Snedecor and Cochran (1969, page 532).

The bias or systematic error of an estimator is defined as the difference between the average value of the estimates obtained in many replications and the true value of what is being estimated.

The precision of an estimator is usually measured by the variance of the estimator or by its standard deviation. To compare the precision of the four indices considered, we used the coefficient of percentage variation:

$$\text{C.V.}\% = 100 \, s/\bar{d}$$

The larger the C.V., the larger the imprecision of the estimator. The intensity of the bias was measured as (see Fig. 1):

$$|\bar{d} - D|$$

Under column t, Table 2 shows the distance $|\bar{d} - D|$ in the standardised form $t = (\bar{d}/D)/(s/\sqrt{n})$ for each of the two universes, in order to take into account the variation of n and to also enable a comparison among the indices.
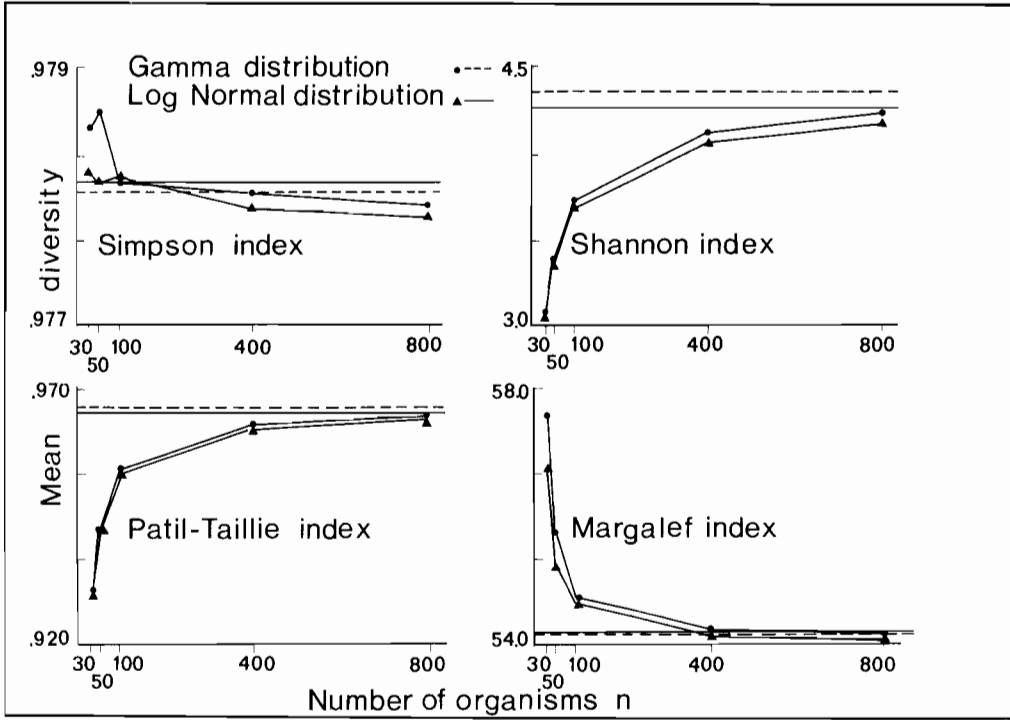
FIG. 1.

Diversity indices mean values as a function of: (a) number of organisms for which the indices are computed; (b) type of universe (log-normal or gamma) from which each sample is obtained. Two hundred replications were performed for every n.

Table 2. *Skewness, kurtosis and bias for the four diversity indices with reference to the number of organisms for which each index is computed. The replication number is 200; g_1 and g_2 are, respectively, the skewness and the kurtosis coefficient. Student's t value measures the bias intensity: the symbol ★ represents a 5% statistical significance; the symbols + and −near the t values denote, respectively, over- and under-estimate when t is significant*

n	Log-normal universe				Gamma universe		
	g_1	g_2	t		g_1	g_2	t
30	− 0.32★	− 0.45	0.12		− 1.03★	1.94	0.71
50	− 0.68★	0.43	− 0.03		− 0.81★	0.72	1.30
100	− 0.39★	− 0.18	0.10	Simpson	− 0.73★	0.48	0.28
400	− 0.41★	0.39	− 1.80		0.44★	0.27	− 0.17
800	− 0.16	0.20	− 3.56★		− 0.05	0.35	− 1.11★
30	− 0.27	− 0.26	− 142.34★		− 0.26	− 0.32	− 147.36★
50	− 0.06	0.00	− 113.39★		− 0.08	0.35	− 112.26★
100	− 0.15	0.18	− 91.38★	Shannon	0.00	− 0.33	− 94.81★
400	− 0.29★	0.31	− 52.16★		− 0.09	− 0.34	− 58.87★
800	0.06	0.42	− 36.04★		0.11	0.39	− 45.16★
30	− 0.58★	− 0.07	− 67.86★		− 1.01★	1.66	− 67.25★
50	− 0.58★	0.49	− 57.92★		− 0.73★	0.76	− 48.51★
100	− 0.34★	− 0.37	− 48.31★	Patil-Taillie	− 0.27	− 0.51	− 44.64★
400	− 0.35★	− 0.01	− 22.71★		− 0.31★	− 0.23	− 20.75★
800	− 0.09	0.40	− 17.48★		− 0.28	− 0.00	− 16.78★
30	+ 2.60★	+ 10.70★	+ 4.49★		+ 2.39★	+ 8.41★	+ 5.32★
50	+ 0.68★	0.21	+ 3.61★		+ 0.75★	0.38	+ 5.11★
100	+ 0.69★	1.27	+ 2.55★	Margalef	+ 0.51★	0.94	+ 3.02★
400	0.04	− 0.08	− 0.79★		0.08	− 0.09	+ 1.09★
800	0.17	0.46	− 2.90★		+ 0.39★	0.95	− 0.28

RESULTS

The results are shown in Fig. 1, Fig. 2 and in Table 2. With regard to imprecision we can make the following observations (Fig. 1):

—The imprecision obviously decreases with an increase in the abundance of the individuals in the sample of organisms. One can see that the behaviour of the four indices is largely the same for the two types of statistical universes.

—Assuming an imprecision of 1% as a conventional discriminating value, valid for the purpose of the present study, one can see that the Simpson and Patil-Taillie indices are always much more precise than those of Shannon and Margalef.

Considering now the bias (Fig. 2 and Table 2), it can be seen that:

—With the exception of the Simpson index, all the other indices nearly always give either an underestimation (Shannon, Patil-Taillie) or an overestimation (Margalef).

—The bias is independent of the type of ecological/statistical universe.

The skewness test suggests that there is a tendency for most of the indices (except Shannon) to deviate significantly: the values tend to be more numerous to the right of the corresponding sample mean. This behaviour may be independent of the fact that an index gives an underestimate: in fact, a non-asymmetrical distribution (see the Shannon index) may be accompanied by a marked systematic underestimate (Fig. 3). In the same figure, we give histograms for the remaining indices. The sample size for all of them is 100. The kurtosis test shows (with the exception of Margalef's index for small n) that none of the
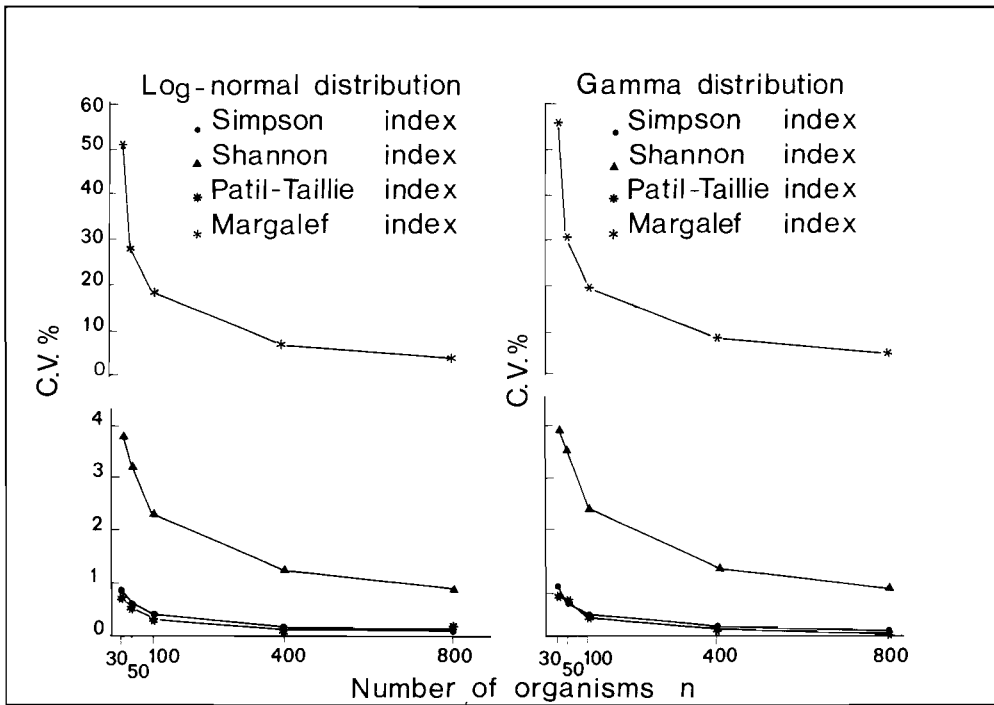

FIG. 2.
Relation between the C.V.% values related to the four diversity indices and the number of organisms utilised in computing the indices. Log-normal universe and gamma universe are presented separately.
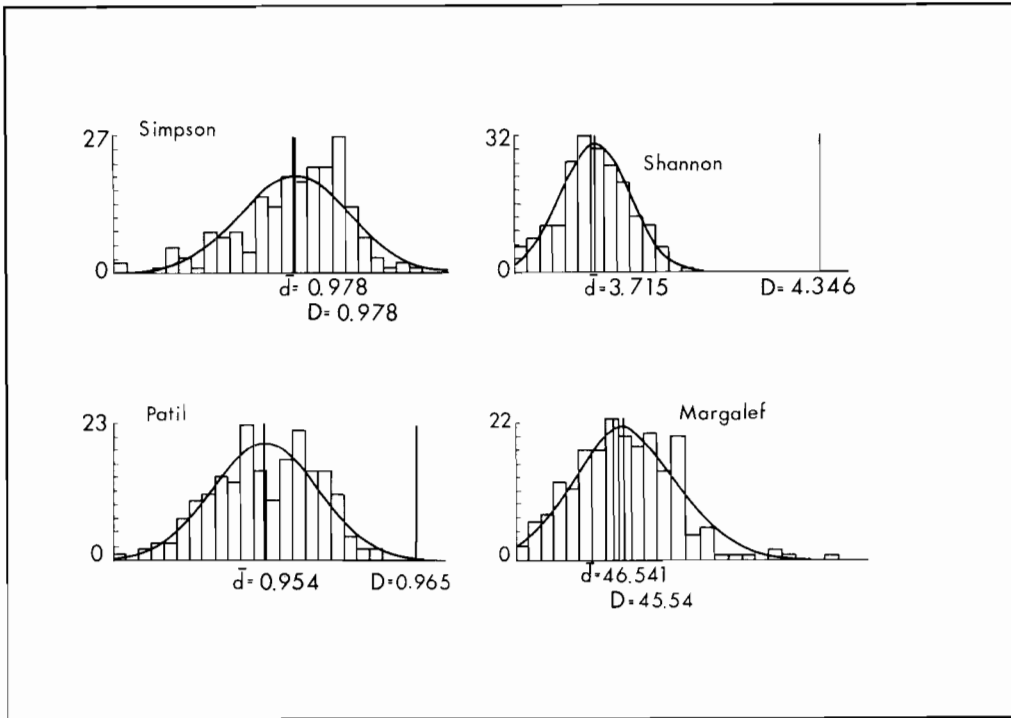
Fig. 3.

Histograms representing the frequency distribution for the four species diversity indices. On abscissa the sample d for 200 replications and the "true" D value when the index is referring to the statistical gamma universe. Each value for each index is computed on a 100 organisms sample.

other indices is significantly off a normal distribution for the two universes considered (Table 2).

DISCUSSION

It is clear that the characteristics of the indices hardly ever depend on the type of distribution of individuals within the species forming the community, nor on the number of species present: in other words, the type of universe, or perhaps the stage of succession, probably does not need to be taken into consideration when choosing an index of species diversity for a natural community. Figure 4 shows an arrangement of the four indices according to reliability as it is reflected in the bias and the precision. The arrangement given suggests that the Simpson index is the most precise of the four and, in addition, the precision is accompanied by a substantial lack of bias. The Patil-Taillie index is as precise as Simpson's but presents a systematic underestimate.

The frequently used Shannon index is known for being almost insensitive to rare species (Sager and Hasler, 1969), but it is also characterised by an imprecision almost four times larger than that of the Simpson and Patil-Taillie indices for all sample sizes considered here. The underestimate of this index is always large, for whatever sample size and whatever successional stage of the natural community. Zahl (1977) and Adams and McCune (1979) proposed some Jack-knife statistical techniques to reduce it.
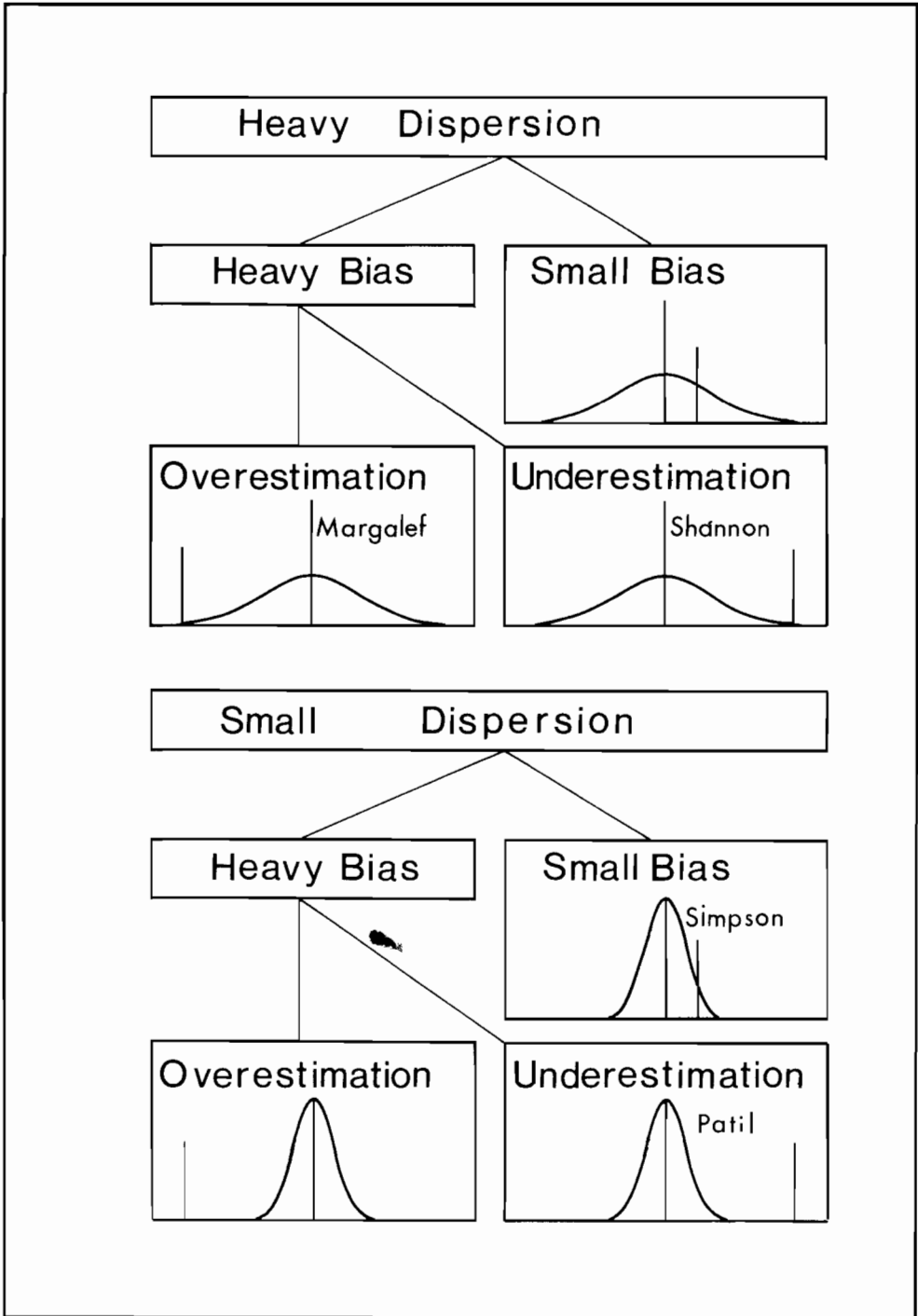
FIG. 4.
Indices classification with reference to bias and precision intensity.

These statistical techniques do not, however, appear to be normally used by scientists using the Shannon index. So for an absolute estimate of the species diversity in a given community, the Simpson index seems to be the most reliable. This conclusion is in agreement with the results of Yapp (1979) and Usher (1983).

In environmental quality control based on a threshold value established on the basis of species diversity, the indices (with the exception of Margalef index) would give a much larger than necessary number of environmental alarms. This could be useful for pollution containment but in the long term could become expensive. To compare the species diversity of more than one ecological situation, one needs an index with the following properties:

(a') A precision that is almost independent of possible differences in sample size for the ecological situation to be compared.

(b') If a bias exists, it should be as far as possible independent of a sample size and in the same direction for the situations compared.

Of the two older diversity indices (Simpson and Shannon), Simpson's is certainly the best from this point of view, whichever the ecological/statistical universe considered; it does in fact (see Figures 1 and 2) satisfy the (a') and (b') conditions.

Of the most recent indices (Patil-Taillie and Margalef), Patil-Taillie's is very precise (condition a') but can only satisfy condition b' if the dimensions of the samples relative to two or more ecological situations are very similar to each other.

The recent index of Margalef and the old one of Shannon appear less suitable for comparisons as, even if the samples have very similar dimensions, they are characterised by a notable imprecision.

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