On richness and evenness within and between communities

Martin A. Buzas and Lee-Ann C. Hayek

Abstract.—Although there is extraordinary interest in the quantitative measurement of species diversity, published statements on the behavior of the components of species diversity are contradictory and lead to opposite conclusions. In this paper, we demonstrate that the confusion is due to two key oversights: (1) whether or not biological sampling is carried out within or between communities; and (2) determination of the statistical distribution underlying a biological community, which is crucial for the evaluation of all of the components of diversity measurement.

The problem of sampling "within" a population or community is basically distinct from the equivalent integration of structure and diversity measurement "between" differing multispecies populations. "Within-community sampling" is defined as a set of biological samples from a statistical population that has a particular statistical distribution or a constant value for the associated parameter(s). As the number of individuals increases along with the number of species, for a log series distribution, the diversity measures of Shannon's H, log series or Fisher's α, and Simpson's Index $1/\lambda$ remain constant while the evenness measures of Buzas-Gibson's E and Pielou's J decrease. For a log-normal distribution, J will remain constant while E decreases and α, $1/\lambda$, and H increase. No single measure of evenness remains constant over all statistical distributions, so if constancy as a type of independence is required, the appropriate distribution must first be determined. Each species ensemble is mathematically fixed by the applicable statistical distribution.

In contrast, "between-community sampling" is defined as a set of biological samples from different statistical distributions and/or the same distribution with differing parametric values. If sampling is between communities and S increases while the number of individuals remains constant, then all the other measures considered here increase. The exception is the broken stick, for which E remains constant while H, J, α, and $1/\lambda$ increase.

Herein we propose and justify the use of the log-series distribution (with regression on the information decomposition equation) as a null model for determination of community structure and demonstrate that the community structure of a Miocene bed at Calvert Cliffs, Maryland, is a log series by use of this new unified methodology.

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Introduction

In a biological multispecies community of $S = (s_1, s_2, \ldots, s_k)$ species with total size of N individuals, the focus of both ecological and paleoecological research is often on the proportions called relative abundances of each species. The relative abundances of species are denoted by $p_i = n_i/N$, each being the number of individuals within species divided by the total number of individuals in the community. It is most usual in diversity studies to rank these relative abundances from most to least abundant and list or table these data into a row or column to form a vector **p**. The rank of **p** is S, the species richness, or when N is obtained within a fixed area or volume, S is the species density (Simpson 1964; Magurran 1988). Before statistical methods were available to ecologists, S was plotted against N (or area or effort). Most often for current exposition and estimation purposes, N is not used directly with S but the focus is instead upon the species abundance and the set composed of the number of species represented by r individuals $\{n_r\}$ in the sample (Willis 1922; Fisher et al. 1943; Anscombe 1950; Engen 1974; Taylor et al. 1976). However, in this formulation it remains clear that the total number of species obtained, S, must be a function of the number of individuals sampled, N. Although other variations such as order statistics have been used (MacArthur 1957), the distribution of the number of species with r individuals depends strongly upon the originally obtained abundances (May 1975) and it is this "frequency of frequencies" distribution that

has been fit with a variety of statistical distributions for ecological purposes (e.g., Fisher et al. 1943; Preston 1948; Brian 1953; May 1975).

Clearly, the relative abundances form more than merely a list of values. As components of the vector **p** the $\{p_i\}$ can be described by or can be said to have some statistical distribution. Because this is true, every measure or index of both diversity and evenness, whose formula uses the quantities p_i, will have its values and range affected by this underlying distribution. That is, the functional relationship with both N and S of diversity as well as evenness measures will depend upon the pertinent statistical distribution for the vector **p**. Thus, any particular such measure may have its range restricted or expanded, or exhibit drastic changes, or indeed remain constant, depending upon the distribution underlying **p**. This fact appears to be recognized for diversity measurement (May 1975; Ulrich 2001) but not so clearly for the consideration of evenness (e.g., Tokeshi 1993; Bulla 1994; Camargo 1995; Bastow et al. 1999). In this paper we focus on the measurement of evenness and delineate specific distribution-dependent interrelationships with relative abundances and evenness.

Conceptual agreement exists on the maximum and minimum possible evenness for a multispecies community whereas measures to consider the interval between these extremes using deviations from uniformity have been the source of confusion. Although dependency upon distribution is a given for all of the most common such measures, empirical investigations still persist and authors of many empirical studies continue to exhibit surprise at their own, presumably confounded, results based upon both devised and actual data sets with unknown distributional properties (see, e.g., Smith and Wilson 1996; Stirling and Wilsey 2001; Weiher and Keddy 1999). Furthermore, values of measures and indices can vary across communities while adhering to the same distributional family, yet exhibiting differing parameter values such that some authors believe that most or all indices are sample-size dependent (e.g., Hill 1973; Gray 2000) while others advocate a form of independence (Smith and Wilson 1996). Indeed, it is a mathematical fact that no measure of evenness can

have all of these proposed properties (e.g., sample size independence, rare species adjustments, among others) as Routledge (1983) proved. Herein we shall elucidate the circumstances under which each of these measures has identifiable and well-defined but distinct properties for sampling either within or between communities.

As discussed above, establishing a relationship between the richness S and total community or sample, or number of individuals N, while gratifying, is only an initial part of the diversity problem. Because all species in a community do not equally utilize the niche hyperspace, some measure of the importance of each species is desirable. Further, because measurement of productivity and biomass is often difficult or impossible, the relative abundance of species is most often used as a measure of species importance. The relative abundances, or p_i's, are of course the components of the vector **p**. To discern whether or not the **p** vectors for the individual taxa and/or environments display recognizable patterns is a fundamental goal of diversity studies. The distribution of the number of individuals in each species over the community of S species has been a focal point for biodiversity study. We shall review the three most commonly fit distributions and present, with illustration, the definitive properties of the diversity and evenness measures identifiable for each distributional situation.

Popular Diversity Measures

In 1943 Fisher et al. derived the single-parameter log-series distribution. This distribution has proved to be one of the, if not the, most popular and widely applicable for explanation of species relationships (e.g., Williams 1953; Brian 1953; Buzas et al. 1977; Kempton 1979; Hughes 1986; Izsak and Hunter 1992; Buzas and Culver 1999). If the log series can be shown to fit the individual within-species data, then with only the observed values of N and S from the field data, the single parameter of this distribution, α, can be calculated or read from a table (Hayek and Buzas 1997).

Unlike species richness, which increases as we observe more individuals, for any particular log series or selected value of its param-
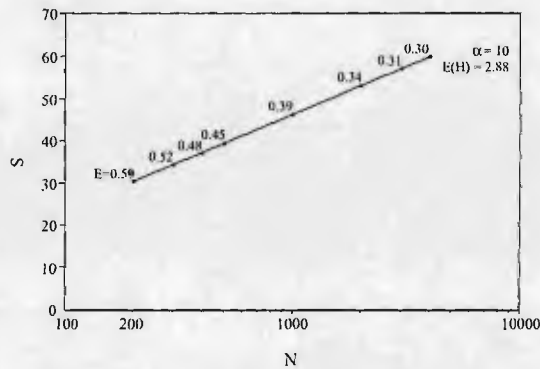
FIGURE 1. A semilog plot of S and N for a log series with an $\alpha = 10$ and expected value of the information function, $E(H) = 2.88$. Values of $E = e^{H}/S$ are shown at eight values of N and S.

eter, the parameter α remains constant regardless of the number of individuals (Fig. 1). Therefore, in this sense one can say that because α remains constant the parameter of the log series is "independent" of N. As Fisher suggested, α has become a reasonable measure of diversity because of this property. When used as a diversity measure this parameter has been advocated for data with an underlying log-series relationship (Fisher et al. 1943; Taylor et al. 1976). However, because ecological data do not conform consistently to a single distribution (Gray 1987; Peters and Bork 1999), α has also been used as a diversity index when the distribution is either unknown or known not to be log-series distributed (e.g., see Wiens et al. 1996).

The information function (Shannon 1948) $H = -\Sigma\, p_i \ln(p_i)$ came into common use because of the multiplicity of distributions that are possible for describing p. Because H incorporates both the p_i values and S, the value of H may vary greatly for multiple samples with equivalent numbers of species but different species proportions. It is this variability we address below relative to each distribution.

Alternative measures of evenness have been proposed (e.g., Pielou 1966; Buzas and Gibson 1969; Engen 1974; Smith and Wilson 1996; Ulrich 2001), each relying upon the most or least even case, yet a clear definition of unevenness remains elusive. Here we consider evenness as correlate or measure of the dispersion of the distribution of $\{n_i\}$: the less even, the more rare species—so that, in essence, evenness is a

transformation of distributional deviation. Below we shall outline methodology for fitting reference distributions to p. We shall present properties of the most common measures for biodiversity study as each is limited or defined for the three most widely used of the fitted distributions. In turn, we elucidate differences in application when sampling or observation is within or between communities, and finally we use results on our exemplar data sets to examine distribution, evenness, and community structure.

Fitting Distributions to Diversity Data

The distribution of the relative abundances $\{p_i\}$ must be known in order to know the properties of measures for diversity (Ulrich 2001) and evenness. If data from a natural population conformed exactly to some statistical distribution, or even multiple such distributions, we would be well served with theoretical description. However, each data set provides an error-prone picture of the multispecies community because a sample is never a perfect reflection. Thus, it is popular to perform goodness-of-fit tests with conventional statistical tools. Such tests each have their disadvantages (Engen 1974) and no one method nor possibly any such method will provide a definitive answer for a researcher. We outline below the usual as well as an alternative approach to identifying the distribution that can best describe p.

Goodness-of-Fit with Frequency versus Distribution Function.—Deviation from the hypothesized frequency or density distribution is what most envision when discussing goodness-of-fit. The frequency function or frequency distribution is a specification of the pattern of frequencies and how they are distributed according to the values of the variable of interest. For observed diversity data this specification may be a table, histogram, or list with categories/groupings/bins. Following this summary, a conceptual distribution is fit by some statistical method and test for fit is performed. Goodness-of-fit usually is measured by a criterion that depends upon the squares of the differences between observed and theoretical values. When a criterion attains a minimal value the fit is said to be "best." There is

a variety of such tests (e.g., chi-square, Kolmogoroff-Smirnoff, Anderson-Darling) but each criterion is devised under differing constraints so that the test results over criteria may be neither consistent nor comparable. Especially when more than one theoretical curve is to be tested, say log series versus log normal, there is no absolute choice of method by which to make the ultimate decision.

Uniquely related to each statistical density or frequency function is its distribution function. This function or curve is the graph of the cumulated frequency as the ordinate against the variate value as the abscissa. For diversity purposes, this distribution is the total frequency of species with number of individuals as the variate with values less than or equal to some numerical x-value. When standardized to unit area, the distribution describes the proportion of species with values of observed individuals less than or equal to some number, x.

For field data there are two choices. On the one hand, samples may be analyzed singly (e.g., Gray 2000) and we can calculate a diversity index with or without an evenness measure. Alternatively, data can be added together sample by sample; that is, data may be accumulated over time or space (e.g., Murray 2002; Osterman et al. 2002). In this latter case, we can calculate diversity and evenness measures at each step in the accumulation. This latter method yields an ordered list of increasing or decreasing index values such that a limiting value for these indices will be approached; the more numerous the sample values, the more closely the limit is approximated. This distribution function approach (Hayek and Buzas 1997), combined with theorems from information theory, is used for fitting distributions to diversity data.

Observed Information versus Expected Value.— Although Shannon's H is widely used in diversity study as an index, its grounding in physics and information theory has not been fully utilized by ecologists and paleoecologists. Indeed, the terms entropy, uncertainty, and information are subject to vast misunderstanding. Shannon first gave the basics of information theory a probabilistic basis. He succeeded in developing a usable measure of the

information we get from the occurrence of an event, having probability p. For our present work, given our discrete distribution $\mathbf{p} = \{p_i\}$ in which each probability or proportion is positive with sum of 1, we can define the entropy of a distribution to be the expected value of (Boltzmann-Gibbs-Shannon) information H. It is important to recognize that our definitions of information H and entropy as expected value of information $E(H)$ are uniquely related to the distribution of $\mathbf{p}$. Thus, the increase, decrease or change of any of these inter-related measures can only become understandable when the distribution $\mathbf{p}$ is specified.

The formulas for the entropy of the three most commonly applied distributions are known (Bulmer 1974; May 1975), and the Hayek and Buzas (1997) methodology based upon distribution functions uses this entropy as a limiting form. However, although this distributional entropy is unique, its use as a limit would not identify the best distribution to fit without some added facts. As the data are accumulated over space or time the pattern of the distribution function or the community structure is shown to emerge and each such pattern can also be determined uniquely.

It is hardly surprising that many of the conceptual and methodological problems of physics, the oldest of the quantitative sciences, have become important in more recently developed fields. The distinction between information and entropy is one such problem, which even Shannon admitted. In our ecological formulation, information is not entropy, nor is it uncertainty (Schneider 2003). Information as calculated on the observed N and S data is a measure of the decrease in uncertainty at the community or population level from that of the sample level. That is, decrease in uncertainty is gain in information. Entropy as expected value of information, $E(H)$, is a measure related to the randomness within the community. Whereas in communication theory we could evaluate information H both before and after signal reception, or H from the source and H from its receiver, in ecology, because of Shannon's probabilistic derivations we can evaluate the expectation, $E(H)$, or the H for a theoretical distribution and an observed H as it approaches its limit based upon

the sampled population. Thus, we examine the pattern of this decrease in uncertainty (as changes in the values of observed H) as we accumulate samples successively. Each such pattern is associated uniquely with some statistical distribution whose entropy is known and detectable as a limiting value from the accumulation table.

Using conditional probabilities and statistical marginal-distributional theory for the discrete entropy case, Buzas and Hayek (1996) provided the general solution that decomposed H into its maximum and an additive residual related to the distribution's dispersion. That is, residual $E = H_{max} - H_{observed}$. This residual is a measure of evenness as defined above. Shannon understood this distinction and called the subtracted quantity "equivocation." For our present application, the residual defined as distributional evenness allows for a loss of information from $E(H)$, the entropy as defined for a particular distribution p, to the maximum evenness for the sample from that distribution, or $\ln(S)$, the natural log ($\log_e[S]$) of S. Clearly then, the allocation of individuals within species, its evenness or spread, is the commonality across multispecies communities that keeps such a community from attaining its maximum, $E(H)$.

The decomposition equation can be rewritten to decompose any H from an observed data set into its separate components for richness and evenness as follows: $H = \ln S + \ln E$. Thus, it is possible to compute this separation of the index H into its maximum for a given data set ($\ln[S]$) and a residual ($\ln[E]$) that can be evaluated without regard to a particular conceptual distribution. Indeed, the index H has been applied to data sets representative of multiple or mixed communities, a fact that has introduced erroneous conclusions and interpretative error. However, when a particular distribution is relevant and known to be descriptive of p, the degree of ecological clarification is raised and its conceptual properties most clearly understood. For diversity study the need is to define quantities germane for the particular community under study, not merely to calculate isolated indices without regard to inter- or intracommunity characteristics. Thus, this information-based methodology can provide a total community synthesis and explanation.

An important aspect of this information theory-based approach is that when independent systems or separate communities are combined into larger groupings of taxa, the entropy of the combined system is the sum of the entropies of its component parts. Thus, after specifying properties of each diversity and evenness measure for each of the three distributions, we shall center our discussion and examples upon the dangers of confusing sampling that occurs within and sampling that occurs between communities. We shall examine the measures under each sampling condition as well.

The Log-Series Distribution and Properties of Diversity Components

Bulmer (1974) showed that for the log-series distribution unique statistical entropy is given by $E(H) = \ln(\alpha) + 0.58$, where 0.58 is Euler's constant. When sampling from within a single community for which p is log series distributed (that is, there is a single value for parameter α), it should be clear from that equation that this value of H must be a numerical constant. Notice also that for any data set fit by a log series the value of α and the value of H differ only by a transformation. Thus, if we know we have log series distributed data, then both diversity measures, α and H, will be constant, and certainly the selection of one over the other is irrelevant.

Hill (1973) showed that $\ln(1/\lambda) = H + $ constant, where λ is Simpson's (1949) well-known index Σp_i^2. Because H is constant for a log series, Hill's equation clearly reduces to the fact that $\ln(1/\lambda)$ and, in turn, Simpson's λ itself must also be a constant. May (1975) stated that $H = \ln(1/\lambda) + 0.58$, and a comparison of this with Hill's formulation tells us that $1/\lambda$ equates with the log-series parameter α.

Note here that the use of the information function H has been criticized (e.g., Magurran 1988; Gray 2000) for holding constant and thus allegedly not providing knowledge of diversity. In fact this constancy provides great insight; it can identify the distribution describing the community structure (Hayek and Buzas 1998) within a community or popula-

tion. Surprisingly, this same criticism appears not to have been made against λ or α, yet they, too, are constant for this distribution, and use of any one of these three measures provides an equivalent evaluation of diversity for log-series-distributed data.

Not only is it true that entropy decreases in a closed system, but because $E(H)$ and α are both constant for log-series-distributed data, any increase in species S that is experienced over sampling time or space must be accompanied by an exactly equivalent amount of decrease in the residual or evenness. This latter fact is evident from the decomposition equation.

Fisher et al. (1943) showed that another advantage of the log-series distribution is that any sample is also distributed as a log series with the same parameter value. As Figure 1 shows, for log-series-distributed data with $\alpha = 10$, $E(H)$ is always 2.88 regardless of which values of N and S we observe or select. Also from Figure 1 we can see that when $N = 200$, $S = 30$, evenness $E = 0.59$, but by the time we have reached a sample size of $N = 4000$, S has doubled and E has been halved. This illustrates that for log-series-distributed data, accompanying any unit increase in ln S will be a unit decrease in ln E. The Buzas-Gibson E is the measure of evenness we use to illustrate the concept with the log series. However, as we consider other distributions we shall show intrinsic relationships between our residual value $(H_{max} - H_{observed})$ and the formulas for other common evenness measures. Clearly, within a log series with a particular value of α, E is an exact (one-to-one) inverse measure of richness.

For the log series, the relationship between N and S is semilogarithmic. In the exact log series shown in Figure 1. A linear regression of ln S against ln E yields ln $S = 2.85 - 1.02$ ln E, $R^2 = 1.00$. This is an example to show that for a log series we can write a predictive equation: ln $S = \hat{H} + (-1)$ln E. That is, the constant (intercept) is always an estimate, $\hat{H}$, of the index H, and the slope is approximately equal to 1.00. The slope of the line is another indicator of the exact reciprocal relationship of richness and evenness for log series. When the distribution is log series we predict a unit de-
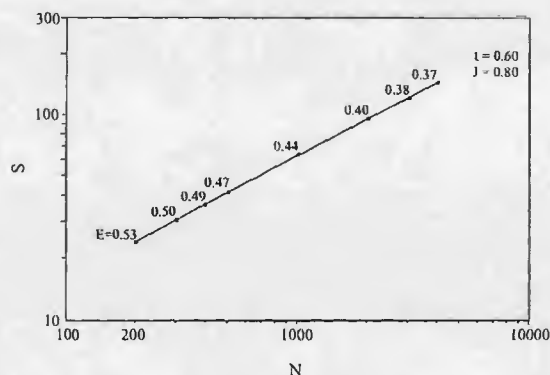

FIGURE 2. A log-log plot of S and N for a log-normal with $\iota = $ ln $S/$ln $N = 0.60$ and $J = H/$ln $S = 0.80$. Values of $E = e^H/S$ are shown at eight values of N and S. At each of the eight points $H = 0.80$ ln S.

crease in ln E for any unit increase in ln S. Thus, when sampling from a single biological community distributed according to a log series, for any observed N and S values and for any sample size, we can easily write an exact equation to predict the indices H and E and the richness S.

Two final observations for the log series are pertinent. First, if we regress S against ln N, a semilog plot, the slope of the regression line is an estimate of the parameter α. Second, if we express Pielou's index J in relation to H, we obtain $H = J$ ln S. Because this is true, as we observe an increase in richness S, then J will decrease for any log series.

The Log-Normal Distribution and Properties of Diversity Components

N and S have a perfect log-log relationship when the distribution is exactly log normal. In Figure 2 we plot ln S against ln N and define the relationship to have a constant ratio. We illustrate this both to select just one such distribution from the log-normal family and to indicate perfect fit in a quantitative way. The ratio was called iota by Hayek and Buzas (1997) and here $\iota = 0.6$, which produces results in the same sample space as those in Figure 1 for our log series. The regression pictured in Figure 2 is ln $S = 0.60$ ln N, with an $R^2 = 1.00$. Unlike the log series, this figure illustrates that the indices α and H both increase with increasing values of N and S for a log normal. Although May's (1975) equation

related H and Simpson's index for the log normal, the constant depends upon both ln S and the parameter of the log normal as well as other quantities.

For the log-normal distribution with parameter $\gamma < 1$, May (1975) gave the entropy as $E(H) = (1 - \gamma^2)$ ln S. From the formula, therefore, the entropy $E(H)$ must increase as ln S increases. As above, when the formula for index J (Pielou 1966) is rewritten as $H = J$ ln S by comparison Pielou's $J = (1 - \gamma^2)$. Furthermore, Hayek and Buzas (1997) derived the more usable formula: $J = 1 + \ln E/\ln S$. These authors also noted that because the parameter γ is constant, both J and ln $E/\ln S$ must also be constant for the log normal. In turn, for a log normal, to maintain a constant ratio of ln $E/\ln S$, evenness, E, will always decrease but the decrease will be less than the equivalent decrease for a log series' evenness. Thus for any log normal, the residual or evenness must decrease linearly with increasing richness but the rate of increase will be less than that for a log series. In addition, J will be constant for a log normal and α will increase with increase in richness.

For the log normal we do not have the same simple relationships we do with the log series. However, when we fit either a log series or a log normal to data, as we increase sampling effort or find more individuals (N increases), then richness increases and, consequently, evenness decreases. When N is accumulated from samples taken over space or time, a log-log plot of ln S or ln E against ln N is always linear for large or representative values of N. The slope of ln S versus ln N will be positive and the slope of ln S against ln E will be negative. For within-population determination of community structure or identification of an underlying statistical distribution from the data, the most important characteristic is this log-linear relationship of N, richness and evenness. When this relationship is recognized, we can use information-based methodology to evaluate the structure of the observations.

The Broken Stick Distribution and Properties of Diversity Components

Although this distribution is not often encountered in nature, it is well known and pro-

vides us with a third member of the negative binomial family (Brian 1953; Hayek and Buzas 1997). The relationship between N and S is strictly arithmetic for a broken stick distribution. For the broken stick distribution, ln E will remain constant and will not decrease with increasing ln N or ln S. May (1975) gave the formula for the entropy of the broken stick as $E(H) = \ln S - 0.42$. For $S < 100$, Buzas and Hayek (1996) determined that a constant of 0.40 gave a better estimate. Comparison of this entropy formula to the decomposition equation shows that for the broken stick ln E is the constant -0.40. In turn this relationship provides us with a constant value for this distribution's evenness of $E = 0.67$. Thus, as S increases, the value of H will increase, while evenness will remain constant. Using May's (1975) formula relating H and λ, we obtain $H = \ln(1/\lambda) + 0.27$. Our simulations show that 0.25 is more suitable for most sampling. However, if we then compare this with the decomposition equation we see that as $1/\lambda$ increases and accordingly Simpson's λ decreases, then calculated α will increase for a broken stick distribution on p.

In addition, because we have $J = (1 + \ln E/\ln S)$, if ln E remains constant while ln S increases, J also will increase, but only slightly. A comparison of the log series and the broken stick can be made via consideration of the most abundant species, which has in itself been suggested as a diversity measure (Berger and Parker 1970). For the log series the largest relative abundance, p_1 is estimated by ln α/α. However, for the broken stick $p_1 \approx \ln S/S$. Thus, the reason for the mythical evenness of the broken stick becomes more evident. As sample size increases, and richness increases, peak abundance decreases for the broken stick but not for a log series, in which abundance remains constant. So, as Table 1 clearly shows, because properties of the indices are functionally related to the distributional properties of p, no single measure can be all things or satisfy all concerns for all researchers.

Choice of a Base or "Null" Model for Evaluating Community Structure

We have now considered three relationships between N and S: log-log, semilog, and arith-

TABLE 1. Population evaluation with increasing or cumulative ln N and ln S.

Distribution	Entropy	Observed H	Fisher's α	Simpson's λ	ln E	J	Relation of N and S	β_i	Null model comparison ln $S = \beta_0 + \beta_i$ ln
Log series	ln α + 0.58	Constant	Constant	Constant	Large decrease	Small decrease	Semilog	ln α/α	$\beta_i = -1$
Log normal	J ln S or 1 + ln E/ ln S	Small increase	Increase	Decrease	Small decrease	Constant	Logarithm		$\beta_0 = H$ $\beta_i < -1$
Broken stick	ln S − 0.42 For $S < 100$, ln S − 0.40	Large increase	Increase	Decrease $2/S + 1$	Constant −0.40 $F = 0.67$	Small increase	Arithmetic	ln S/S	Not significant

metic. For each we have been able to determine (1) the most appropriate distribution for describing the vector **p**, and (2) deterministic properties of and interrelationships among the commonly used diversity and evenness measures. We have illustrated that these measures are intrinsically related within each distributional setting and that selection of any one particular measure to evaluate diversity or evenness does not necessarily provide the unequivocal information the researcher expects (e.g., H, α, and $1/\lambda$ provide equivalent information for any log-series-distributed data). Using these determinations we propose a null model scenario to be used as a basis for comparison with regression models for the data (Table 1).

For any single biological population or community we have shown some of the basic properties that are determinable once it is clear that **p** has a particular distribution. Using regression with data from Figures 1 and 2, it should be clear for ln E and ln N that both regressions are strictly linear. For the log-series data set ln $E = 0.60 - 0.22$ ln N, whereas for the log-normal ln $E = 0.01 - 0.12$ ln N. The R^2 for each rounds to 1.00. This illustrates that, in general, when predicting ln E with ln N when the distribution is log-normal, the slope will always be less than the comparable slope for log-series data.

In addition, for both log-series and log-normal distributions, regression of ln S and ln E will always be strictly linear. Indeed, as species richness increases with increasing or accumulating sample size N, then ln E will decrease linearly. However, we have shown above that for a regression of ln S and ln E on log-series data the slope is −1 and the intercept is the estimate $\hat{H}$ so that the elegant relationship of ln $S = \hat{H} + (-1)$ln E (equivalently ln $S = \hat{H} - 1($ln $E)$) always holds. The simplicity of this predictive relationship with constant values for H, α, and λ provides a convenient base or null model with which to compare ecological or paleoecological observations.

Many other authors have proposed the use of a base or null model (e.g., Lloyd and Ghelardi 1964; Caswell 1976; Ulrich 2001; Hubbell 2001). Herein we propose the use of the log se-

ries as a base model for multiple reasons as discussed above, in effect (1) simplicity of the distribution, and (2) the constancy of the related indices, as well as (3) the regression formulation that equates to the additive decomposition equation for the diversity components with slope $= -1$ and intercept $= \hat{H}$ (Table 1). Furthermore, many of the models previously suggested for use as a null in actuality are either subsumed by or approach the log series in the limit. For example, Hubbell (2001) states that α is an asymptote for his model parameter, and the neutral model of Caswell has been shown to be closely approximated by the log series as well (Hayek and Buzas 1997).

We continue by examining the repercussions of using these results, first for a single multispecies community evaluation and then across communities.

Within and between Multispecies Communities

Use and interpretation of diversity and evenness measures as indicative of community structure is appropriate under two conditions: (1) the relevant distribution of p is considered, and (2) sampling is clearly defined to be either within or between communities.

Within-community (or within-population) sampling is defined as the collection of a set of biological samples from a single statistical population, or the biological community, that adheres to a particular statistical distribution. When this obtains, use of the observed N, S and p provides the necessary elements for a complete evaluation of community structure in which each measure of diversity and of evenness has deterministic behavior within a mathematically fixed system. In any such closed system the degree of randomness or evenness will decrease as more individuals are collected and consequently more S are added.

Between-community (or between-population) sampling is defined as the collection of a set of biological samples from different communities/distributions or equivalent distributions (from the same parametric family) that have different parametric values. Often
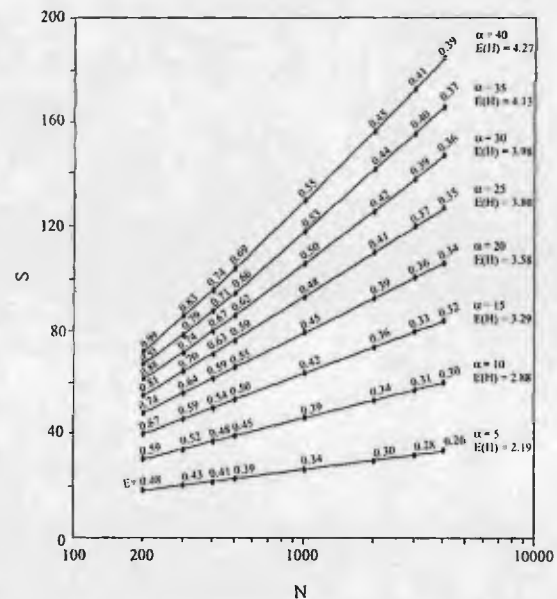

FIGURE 3. A semilog plot of S and N for log-series populations with eight values of α and their respective $E(H)$'s. Values of $E = e^{H}/S$ are shown for 64 values of N and S. Each line depicts a log series population with a particular α and shows an increase in S with increasing N. Within-population sampling follows the path along the particular line for the α value. For sampling between populations, lines can occur either vertically at any value of N or diagonally across the lines with increasing values of N.

fieldwork is undertaken to discover patterns or changes in diversity between populations. The researcher expects to describe or recognize distinct biological populations when sampling is over distinct environments, habitats, biomes, or faunal assemblages. Because of the additive property of information, data can be collected across community or population boundaries, but the entropy of the total system will not always decrease. Despite this, we show that properties of diversity and evenness measures can be determined for this intracommunity situation.

Multiple Log-Series Communities or Populations.—Let us first assume we have two log-series-distributed data sets and illustrate this sampling. Figure 3 shows an expanded Figure 1 that includes multiple log-series-distributed data sets in the same sample space. Because each line depicts a log-series sampling, each has constant $E(H)$ and α. To envision sampling between these populations, which implies increasing values of N and S, we go up diago-

nally across the lines. For example, if we first select a sample of size $N = 300$ from the population with $\alpha = 10$ and the second sample is of size $N = 500$ from the population with $\alpha = 15$, we must read diagonally up to the right. As a shorthand we shall call this "sampling diagonally." Examining species richness between or across populations with equal-sized samples will be termed "sampling vertically."

Equal-sized samples are obtained by setting limits before field observation, observing or collecting under a stop rule, making an a posteriori decision, biological sample partitioning, or just luck. Regardless of the method, if one samples with constant sample size across log-series populations then as S increases (non-monotonic increase) both H and α will also increase. Importantly, ln E becomes less negative, so evenness is increasing as well. Consequently, unlike when sampling within a single biological community, when we perform intracommunity (intrapopulation) sampling, with attendant increasing species richness S, there must be an accompanying increase in evenness. That is, from an information perspective, the randomness is increased over that of a closed system.

Notice that the lines in Figure 3 radiate out from the origin. This illustrates that at small sizes the observed richnesses in differing log-series distributions (with unequal parametric values) will be relatively indistinguishable. However, as sample size becomes larger, differences between observed richness, or S values, from these populations will become more pronounced.

The opposite is true for evenness. For example, at size $N = 200$ the two populations with $\alpha = 20$ and $\alpha = 10$ show that evenness has decreased from 0.74 to 0.59, a difference of 0.15. When sample size is $N = 2000$ for these populations this difference is only 0.05. An alternative view is that the larger the sample size the larger the regression coefficient or slope of the line.

Multiple Log-Normal Populations.—Figure 4 presents S and N on a log-log scale with lines showing the accompanying constant J for distinguishable log-normals. Surprisingly, sampling (vertically) at constant sample size $N = 300$, as above, shows that results for log nor-
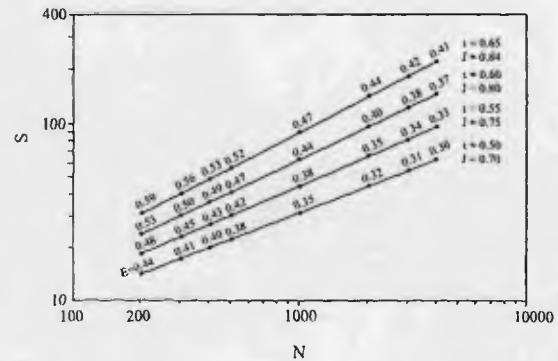

FIGURE 4.   A log-log plot of S and N for log-normal populations with four values of J. Values of $E = e^H/S$ are shown for 32 values of N and S. Sampling pathways for within and between populations are the same as in Figure 3.

mals are similar to those for log series. Evenness increases as we sample between differing populations. In summary, for equal-sized samples from within a single biological population, evenness will always decrease. Alternatively, when sampling crosses over distinct populations (e.g., either log series or log normal), evenness can increase when richness increases.

However, when samples are not of equal size, as we observe more species, i.e., as S increases when sampling crosses populations, then evenness can be observed to increase, decrease, or even remain constant. This variability does not indicate that there is some inherent logical or conceptual failure in the measures for evenness; an evenness measure is indicative of a unified biological community's structure. The existence of change is a deterministic indicator that we are no longer sampling within a single community but have crossed a population boundary. Clearly, this is an instance in which a lack of understanding of the components of diversity and their relationship to the distribution of p has led many authors unjustly to fault diversity studies and the measurement of evenness in particular (e.g., Hurlbert 1971).

Any biological community, population, biome, or biofacies can be identified a priori by experience, analytically by SHEBI, clustering with probabilistic assessment, or possibly other methods. Regardless of the method selected for biological population identification, an

evaluation of community structure is ensured, with all the attendant and interrelated measures for diversity and evenness, if we have correctly identified and considered the distribution of p. However, because of convergence of the values of these distributions, no single sample can assess the distribution accurately enough for biodiversity purposes; the information in the serial accumulation of all the samples, that is, of the total field experience, must all be considered.

Between-Population Comparisons

Because richness and evenness change with increased sampling (except for the broken stick), a comparison of these quantities between populations must be made at a constant total N (Hurlbert 1971; Gray 2000). This can be accomplished in two ways: (1) keep N constant when sampling or collecting, in which case mean values of S and evenness are appropriate statistics, and (2) rarefy to some common value of N within each of the populations being compared (Gotelli and Colwell 2001). There are several ways to accomplish rarefaction (for a discussion, see Hayek and Buzas 1997) depending on the statistical distribution of p and the degree of spatial aggregation (Fager 1972). If values of N are similar between populations, regressions of ln S with ln N and ln E with ln N within each of the populations to be compared are probably the best way to obtain a common N and thereby richness and evenness estimates for between population comparisons.

Unequal Sample Sizes.—If the biological samples are of unequal sizes, then the statistical relationship between ln S and ln E may be positive or negative depending on the degree of variability in the sample sizes; if the difference is small the relationship is positive; if large, negative. The former case is similar to the situation in which N is constant and the latter is similar to that of an accumulated N within-population analysis. Regression on individual observations or samples with unequal values of N is a risky business. Figure 4 depicts a virtual minefield for the wanderer.

Equal Sample Sizes.—When comparing equal-sized samples between populations (N is kept constant) and considering separate samples (sampling vertically on Fig. 4), then for a known statistical distribution the relationship between richness and evenness is always positive (DeBenedictis 1973). When differences between sample sizes are relatively minor, this relationship will still be positive. Depending on the statistical distribution of p, as well as on the value of the distribution's parameters, regressions of ln S versus with ln E on individual, unaccumulated biological samples will have positive but highly variable slopes.

Accumulated Samples.—If observations are accumulated over biological samples obtained from multiple populations, the statistical relationship between ln S and ln E will be negative just as it was when sampling within populations. Although a regression of ln S against ln E may be negative and significant, a plot of ln S against ln E will not show a consistent linear trend and will have a smaller value for R^2 than when examining within-population observations.

In the following sections we shall present two examples of real data sets and assess structure and diversity both within and between the communities.

A Within-Community Example

For a spatial distribution study of Miocene Foraminifera at Calvert Cliffs, Maryland, Buzas and Gibson (1990) extensively sampled bed 18 of the Choptank Formation. Using a plane table and alidade to ensure a horizontal surface, they established nine stations, each 3.56 m apart, in a 3 × 3 grid. A template with a square grid of 100 cells was centered at each station and five sediment samples, each 3.5 cm in diameter and 1 cm in thickness, were taken by using a table of random numbers. The number of individuals and species were enumerated in each of the 45 samples. The grand total for individuals in this single population is N = 34,454 and S = 45 species.

Although the original study analyzed the data for spatial variation only (a remarkable degree of spatial homogeneity was observed), the data are also ideally suited for an analysis of community structure. To accomplish this we used both methods of determining fit to select the most representative model. First, we
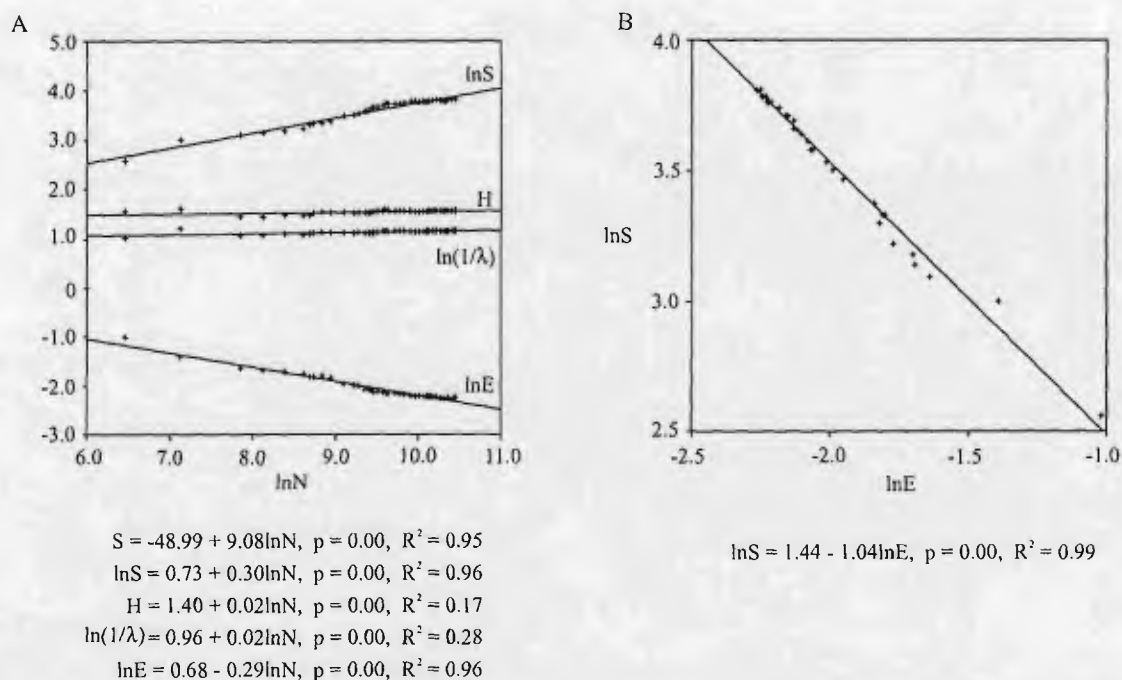
$$S = -48.99 + 9.08\ln N, \quad p = 0.00, \quad R^2 = 0.95$$
$$\ln S = 0.73 + 0.30\ln N, \quad p = 0.00, \quad R^2 = 0.96$$
$$H = 1.40 + 0.02\ln N, \quad p = 0.00, \quad R^2 = 0.17$$
$$\ln(1/\lambda) = 0.96 + 0.02\ln N, \quad p = 0.00, \quad R^2 = 0.28$$
$$\ln E = 0.68 - 0.29\ln N, \quad p = 0.00, \quad R^2 = 0.96$$

$$\ln S = 1.44 - 1.04\ln E, \quad p = 0.00, \quad R^2 = 0.99$$

FIGURE 5. SHECSI analysis of Miocene bed 18 at Calvert Cliffs, Maryland. A, Plot of ln S, H, $\ln(1/\lambda)$ and ln E vs. ln N for accumulated 45 samples. B, Plot of ln S vs. ln E for 45 sample accumulation. For a perfect log series value of coefficient is -1.00.

used N, S, and the frequency distribution of p in histogram form to attempt to fit a statistical distribution to the single sample. We tried both log-normal and log-series fits.

Following both the procedures of Preston (1948) and of Pielou (1975) we wrote a Mathcad routine to fit a truncated log normal to our relative species abundances. Results of these two computational procedures were disparate. However, in each case, when assessed by chi-square and Darling-Anderson goodness-of-fit tests, a log normal was not significantly different from the observed data distribution. In addition, we used the program Species Diversity and Richness III (Pisces Conservation 2002) to fit a truncated log normal and to calculate chi-square goodness-of-fit. These results likewise could not reject that the data could be fit by a truncated log-normal model.

We then programmed Mathcad to fit a log series directly. According to each goodness-of-fit test result there was no reason to reject an underlying log-series distribution. Finally, the program Species Diversity and Richness III was used to fit an equivalent log series with α approximately equal to 5 and $x = 0.9999$.

Again, each goodness-of-fit result provided no reason to reject the log series as a reasonable fit to the data distribution.

Secondly, the data set was accumulated over individual samples and evaluated sample by sample successively to determine the most appropriate model for the data using the Hayek-Buzas methodology. At each step we computed the most familiar measures for diversity and evenness: H, J, λ, α, S, E. We applied the decomposition equation and calculated its components at each step.

In Figure 5 we show the analysis as successive values of the indices along with linear regressions of the components. In addition to the components of the decomposition equation, the regression equations (Fig. 5A) show that both S versus ln N (semilog) or ln S versus ln N (log-log) could well-describe the relationship between the cumulative number of species and the cumulative number of individuals. This result is in keeping with the frequency fit and goodness-of-fit test results. We continue by examining additional relationships for the accumulation distribution, which can
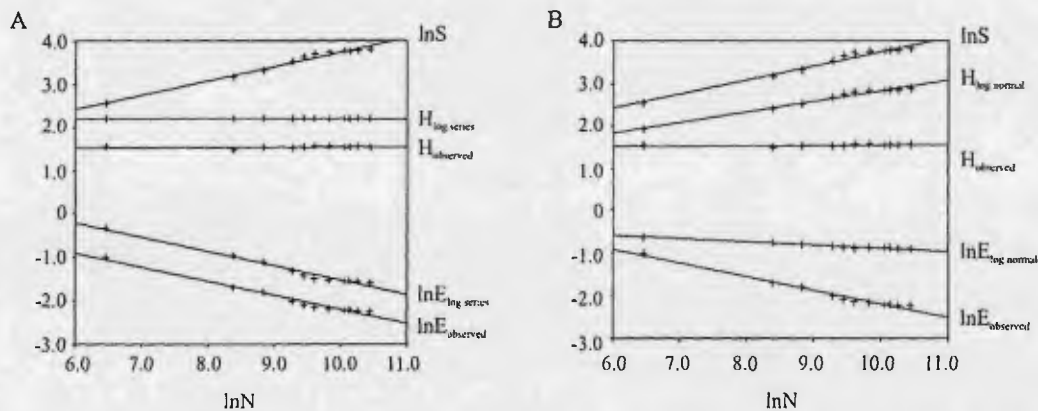
FIGURE 6. Plots of ln S, H, and ln E vs. ln N for accumulated 45 samples of bed 18 at Calvert Cliffs, Maryland. A, Plots of observed vs. log series constructed using mean value of H as constant. B, Plots of observed vs. log normal constructed using mean value of J as a constant.

shed further light on the selection of a model for p.

For both H and $\ln(1/\lambda)$ the regression slopes are equivalent (0.02), and are almost zero. The regression slope for ln E versus ln N is approximately equivalent to, but opposite in sign (that is, multiplied by -1) from, that for the regression for ln S versus ln N (-0.29 versus $+0.30$). Because H is observed as almost horizontal (constant) with ln N, we know from the decomposition equation that under this condition within a population, as S increases, E must decrease by exactly the same amount.

Finally, using the log series as our yardstick or null model we note that when we write $\ln S = \hat{H} - \ln E$, then, when H is constant, regression of ln S versus ln E will yield ln $S = \hat{H} - 1.00(\ln E)$. We compare our Miocene foram results shown in Figure 5B with this equation to see that the fitted slope of -1.04 closely approximates that of the log series. The intercept constant, which is our estimate $\hat{H}$, is convincingly near the mean value of the observed cumulative H. Although both log series and log normal can be said to "fit" within the stated statistical conditions, this methodology shows that the form and pattern of the data are closest to log series.

Continuing with the analysis of these data, consider that for $N = 34,454$ and $S = 45$, we calculate an $\alpha = 5.10$ so that, in turn, $E(H) = \ln \alpha + 0.58 = 2.21$. The observed mean is $H = 1.54$ and the last observed cumulative $H =$

1.55. The terminal accumulation value of ln $E = -2.25$ giving an $E = 0.10$, while at the point at which $E(H) = 2.21$ and $S = 45$, then $E = 0.20$. Thus, although we affirm that the data adhere to a log-series pattern, the observed values show dominance that is excessive for this log-series formulation. This two-part procedure is called SHE analysis for community structure identification, SHECSI (Buzas and Hayek 1998).

Although the structure of p from Calvert Cliffs has been identified as that of a log series, for comparison purposes, we also calculated the expected value or entropy of a log normal. The expected value for an applicable log normal is $E(H) = (1 - \gamma^2)\ln S$. Using the method given by Magurran (1988; after Pielou's method [1975]) we calculated that $\gamma = 0.49$ so that $(1 - \gamma^2) = 0.76$. Note, this is also the expected value of Pielou's (1966) measure of evenness, $J = H/\ln S$, which equals $1 + \ln E/\ln S$ (Hayek and Buzas 1997). For a log normal, we know that all of the indices γ, J, and ln $E/\ln S$ must be constant. Thus, for observed values of S from bed 18, we calculated $H = 0.76 \ln S$. These results, along with the log series' expected values for $\alpha = 5.10$, are shown in Figure 6. Neither the accumulation pattern nor the expected values of the log normal are in agreement with the observations. We again conclude that the community structural pattern for bed 18 is not a log normal but a log series. However, we have also found that the

values of H and evenness are less than expected, with higher than expected dominance.

A Between-Multispecies-Communities Example

Communities or habitats are often not as extensively sampled as was Calvert Cliffs. It is more usual that a set of samples or observations may be distributed, or quadrats may be placed along a traverse encompassing several habitats. As an example, we consider benthic foraminifera from a traverse (no. 6) in the Northeastern Gulf of Mexico (Parker 1954). In all, Parker recorded 201 taxa from 35 stations ranging in depth from 20 m to 2697 m. The data consist of the numbers of individuals of each taxon at each station. A universal characteristic of benthic foraminifera is that they exhibit depth zones or biofacies. Considering the depth range covered by traverse 6, several depth zones or biofacies could be expected.

In 1998, using SHE for biofacies identification (SHEBI) with traverse data, Buzas and Hayek identified seven depth zones over the entire range. This depth pattern was corroborated by using canonical variate (multigroup discriminant) analysis. Before breaking up the traverse into biofacies, regression models were developed using the entire traverse as a single unit, accumulating N and S from the shallowest station (20 m) to the deepest (2697 m) because a useful feature of SHE analysis is that if the observed samples are from a single statistical population, a plot of ln E versus ln N will be linear. Any deviation from a linear trend indicates a change in the parameter of the applicable statistical distribution or a new distribution. Consequently, when viewing a plot of ln E versus ln N in which there is a break in a linear sequence, the samples preceding the break are designated as distinct biofacies (Osterman et al. 2002) and the remaining samples reexamined. After this identification process and for our present purposes, because we wish to examine within-population community structure, we selected the largest of the biofacies, numbers 2 and 4, which each have seven stations, and biofacies 6, with ten stations. Using these data we examine the similarities and differences among the indices and structure for each biofacies

and continue by identifying the characteristics and changes that occur in indices when we consider a between-biofacies analysis of this sampled data.

Assessment within Each Biofacies.—Given nature's variability as well as the close statistical relationship between the two alternatives of log-log versus semilog over the range of observations we cannot expect the variables S and N alone to discriminate the most applicable formulation in every case. However, regression equations can provide key discriminatory evidence when considered against a base model. For example, if we consider biofacies 2 from the Parker (1954) data, the regression equation for the plot of ln E in Figure 7A is shown with a slope of -0.24. This quantity is of equivalent magnitude in absolute value and nearly the opposite of the regression slope of ln S, which is $+0.30$. An exact inverse relationship is representative of a log-series specification. Also, the biofacies 2 regression equation shown in Figure 7B has a slope (-1.05) whose value of approximately minus one is what we would expect for a log series distribution. Recall here that the regression equation ln $S = 3.04 - 1.05$ ln E indicates the constant value of 3.04 is the estimate $\hat{H}$. The mean H for the observations of the SHE analysis of biofacies 2 is 3.09. Thus, both the regressions and the estimated value of H from the data of biofacies 2 are indicative of a log-series distribution.

Results of regressions on biofacies 4 indicate that the relationship between N and S could be modeled as either semilog or log-log (Fig. 9A,B). Recall that in biofacies 2 the regression coefficients for ln S versus ln N and ln E versus ln N were nearly equal but with opposite sign. When considering the data results of biofacies 4 against the base log-series model, the coefficients are opposite in sign but not of equivalent magnitude. In addition, the regression coefficient for ln S versus ln E is larger than one (-1.72) and the constant (3.02) is less than the mean value of the observed H, which is 3.68. In addition, evenness as measured by E decreases from 0.46 to 0.38, J goes from 0.82 to 0.80, while Simpson's lambda changes over the accumulated samples from 0.0489 to 0.0414. All the measures therefore have a de-
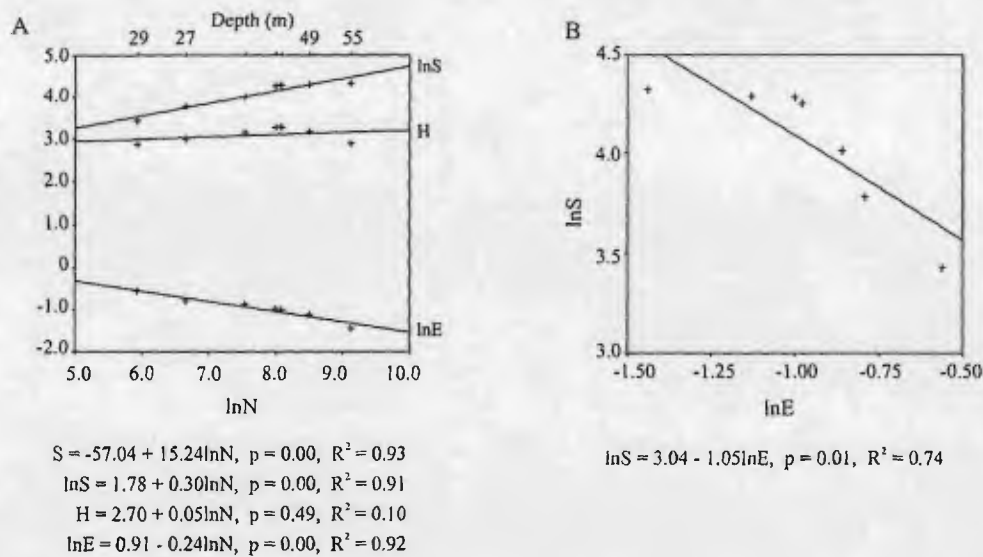
FIGURE 7. SHECSI analysis of Parker (1954) traverse 6 biofacies 2 (Buzas and Hayek 1998) data from the Gulf of Mexico. A, Plot of ln S, H, and ln E against ln N. B, Plot of richness (ln N) and evenness (ln E).

creasing pattern, with the largest decrease seen over the values for E. Thus, we conclude that biofacies 4 is not a log normal yet not a perfect log series, or that the results are between a log series and a log normal.

As a third and final within-population example before we examine the entire transect across the three depth-delineated populations, results of regressions on biofacies 6 are presented in Figure 8 and show that the co-

efficient of determination (the square of the correlation coefficient) R^2 for ln S versus ln N is slightly but not significantly higher than the R^2 for the semilog relationship. The difference between the two fits as expressed by the R^2 values is not sufficient to allow us to choose one relationship over the other. As we accumulate over increasing depth the common measures of evenness decrease: the value of E decreases from 0.47 to 0.32, J goes from 0.81
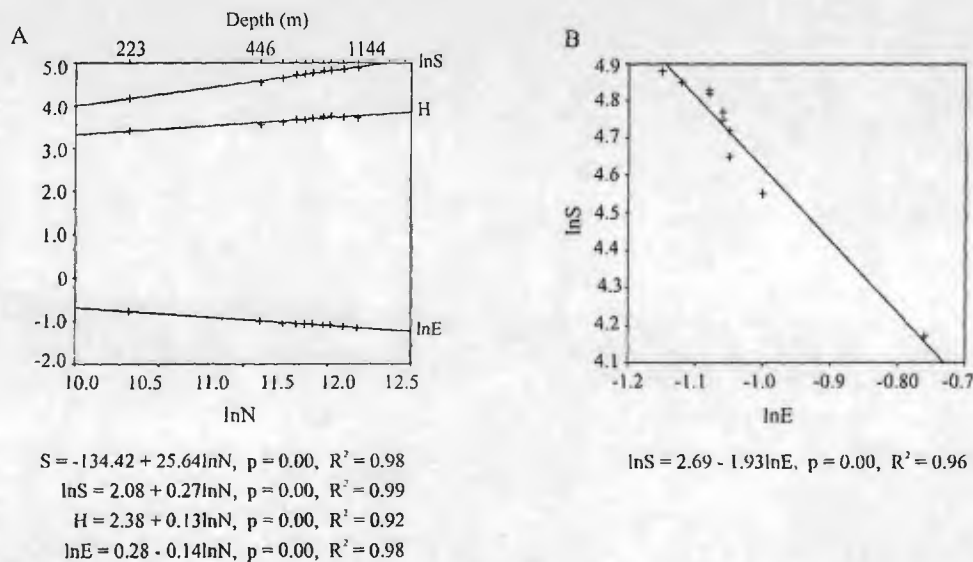

FIGURE 8. SHECSI analysis of Parker (1954) traverse 6 biofacies 6 (Buzas and Hayek 1998) data from the Gulf of Mexico. A, Plot of ln S, H, and ln E against ln N. B, Plot of richness and evenness on log scale.
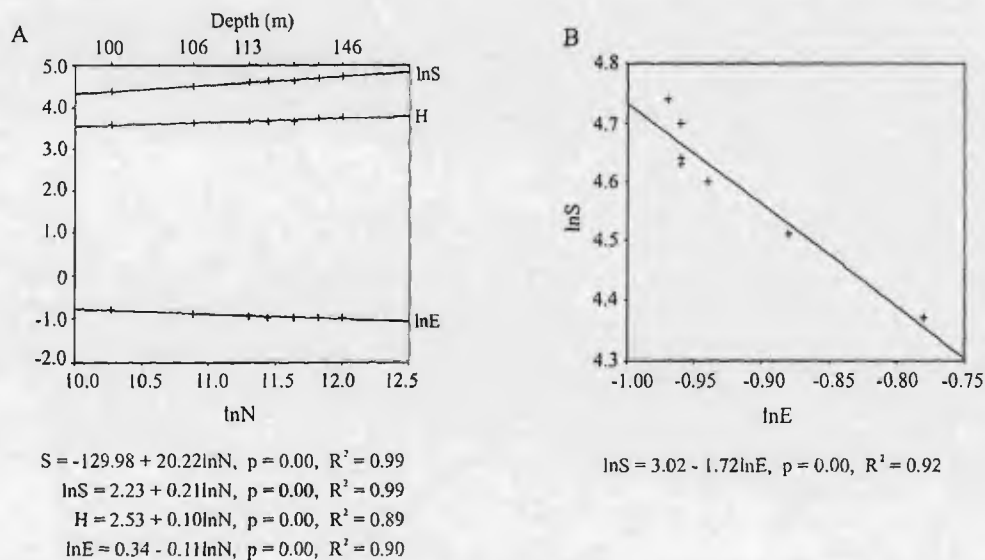
FIGURE 9. SHECSI analysis of Parker (1954) traverse 6 biofacies 4 (Buzas and Hayek 1998) data from the Gulf of Mexico. A, Plot of ln S, H, and ln E against ln N. B, Plot of richness and evenness on log scale.

down to 0.76, while Simpson's index decreases from 0.0562 to 0.0419. However, as in biofacies 4 (Fig. 9) the regression coefficients for ln S versus ln N and ln E versus ln N are opposite in sign though not equally opposed. The regression coefficient for ln S versus ln E (−1.93) is slightly larger than for biofacies 4 and the constant of 2.68 is farther from the mean of H, which is 3.66. Again, results indicate an imperfect log series or a distribution in between that of a log series and a log normal.

Assessment of Distribution of p.—To more fully comprehend and compare the analyses performed in the examination of community structure within each of the three biofacies, we constructed distributions with constant values of H and J for comparison. The constants used were the mean values for H and J calculated from each set of field observations. Recall that when we find a constant H, the slope for the regression ln S versus ln E must be −1. For a constant J, the slope will be about −4 to −5. In Figure 10 the regressions for ln S versus ln E from the three biofacies are plotted alongside values for constant H and J. For biofacies 2, the regression equation for the observations and the line for a constant H are approximately collinear in the range of observations. The regressed observations lie closer to the line for constant H than to the line for constant

J (Fig. 10A), but this is not the case for biofacies 4 and 6, whose observed slopes are −1.72 and −1.93, respectively. Note also that the ranges of observed values are smaller than for biofacies 2.

As Figure 10 illustrates, the slopes of ln S versus ln E for each of the three biofacies become increasingly negative with depth of water. The regression equation for biofacies 2 is very similar to that of a predicted log series (Fig. 10). Although the regression equations for biofacies 4 and 6 are not as similar, they are still closer to log series than to log normal. Because we are making comparisons to separate choices of model only, the best we can say is that we have imperfect log series or that distributions are in between log series and log normal. Forcing a discrete structural classification on the observations does an injustice to the subtlety of the change in slope with increasing water depth.

Assessment of Diversity, Richness, and Evenness of Foraminifera between Biofacies in the Gulf of Mexico.—The next step in the process is to examine the species richness and evenness across biofacies. At the end of the accumulation steps, we observed 75 species in biofacies 2, 115 species in biofacies 4, and 131 species in biofacies 6, and this appears to show increasing richness with depth.
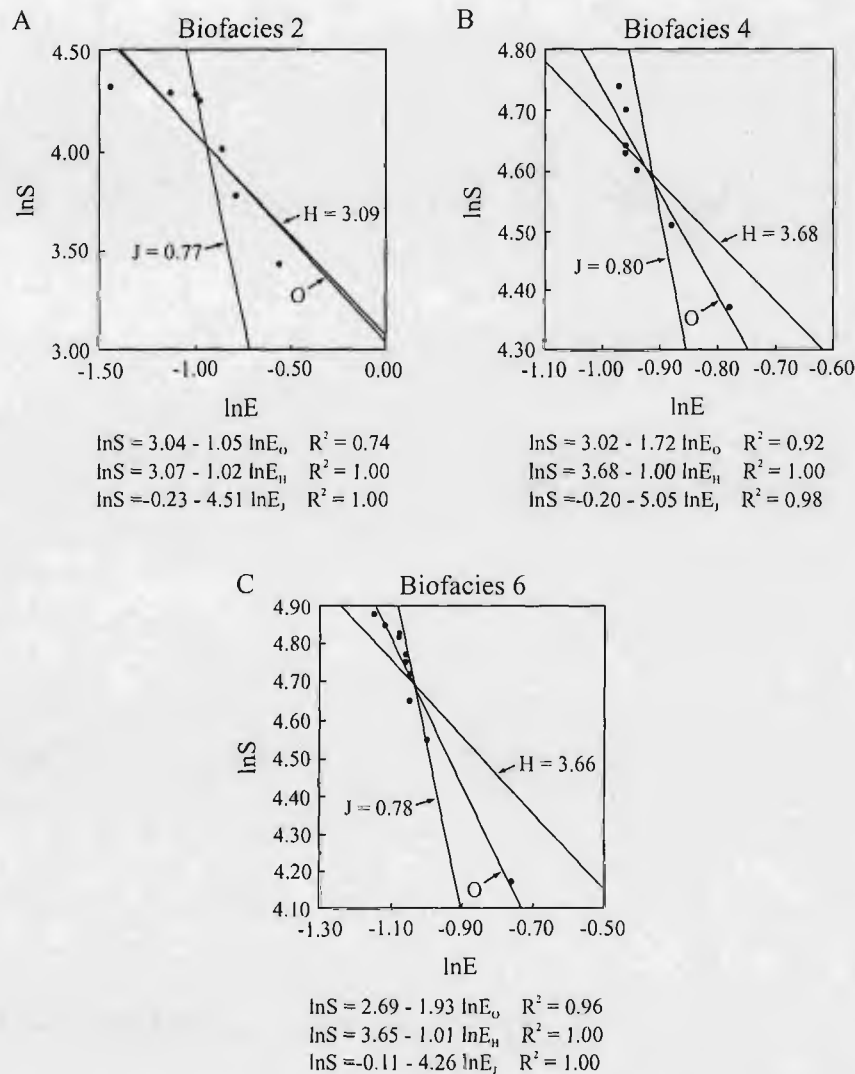
FIGURE 10.   Comparison of plots of ln S versus ln E for observed (O), log-series (H), and log-normal (J) populations for biofacies 2 (A), biofacies 4 (B), and biofacies 6 (C), Gulf of Mexico.

However, any examination of richness or evenness must incorporate the fact that indices that measure these facets are functions of sample size as well as distribution. In our three biofacies the sample sizes are quite disparate. In biofacies 2 the accumulated ln N ranges from 5.93 to 9.12, in biofacies 4, from 10.27 to 12.00, and in biofacies 6, from 7.64 to 10.36. Using the regressions for ln S versus ln N given in Figures 8, 9, and 10, we rarified (the common N is the minimum) and abundified (the common N is the maximum) to obtain predicted values of S for representative values of ln 9, ln 10, and ln 12. Regardless of the size

of samples we use for comparison, predicted richness values demonstrate the same pattern, namely, that biofacies 2 and 6 are similar in terms of species richness and biofacies 4 has fewer species at any given N. For example, at sample size ln 10 the predicted values of S are as follows: for biofacies 2, $S = 114$; for biofacies 4, $S = 75$; and for biofacies 6, $S = 123$. Had we not incorporated a constant sample size N and instead used for comparison the average values of S obtained from the samples in each biofacies, or the total number of species observed in each biofacies, the results would have been quite different, and most probably

incorrect. Thus, the raw data alone indicate that the trend of increasing mean and total species richness from biofacies 2 to 4, without concern for the unequal sample sizes, occurs because biofacies 4 has a larger sample size than the others. It should be obvious that any question concerning species richness within or between the biofacies must have a value of N attached for presentational clarity.

Each of the observed evenness values as well as values estimated for sizes of ln 9, ln 10, and ln 12 exhibit the same pattern, namely, that biofacies 4 has higher values of evenness than the other two.

Putting all this together, there is a distinct decrease in richness and an increase in evenness at biofacies 4, these factors offsetting one another and resulting in an increase in proportional diversity from biofacies 2 to 6. As an example, using regression to estimate values of ln S and ln E at a constant sample size of ln $N = 9$ makes it clear that both evenness and richness affect diversity. We have the following results: for biofacies 2, $H = 4.44 + (-1.27) = 3.17$; for biofacies 4, $H = 4.11 + (-0.65) = 3.46$; for biofacies 6, $H = 4.54 + (-0.96) = 3.58$. In this decomposition we see precisely how the high value of evenness in biofacies 4 results in increasing values of H across the set of three biofacies. Therefore, at a constant sample size, we observe an increase in the value of H, but not richness or evenness, from biofacies 2 to 6, showing that diversity is actually increasing with depth.

Discussion

With usage, various indices have become typified as measuring either richness or evenness (for summary, see Tokeshi 1993). But we have shown here that, depending on circumstances, the same index may measure different properties.

The mathematical relationships of statistical distributions to an information/entropy system (May 1975) along with their application in ecology, incorporating decomposition of richness and evenness and other common measures within that system (Buzas and Hayek 1996; Hayek and Buzas 1997), are now well established. Consequently, for the first time we can examine the behavior of indices for the

commonly encountered distributions governing the species abundance vector $\mathbf{p}$. With this approach, measurement and field observations can be reconciled. In past works on this subject, most studies of behavior of indices relied upon only observed or simulated data without assessment of or reference to the statistical distribution of $\mathbf{p}$ (Stirling and Wilsey 2001). Of additional concern are the studies that fail to clarify or determine when sampling has transcended community boundaries. Our results from diversity, richness, and especially evenness measurement showed that disparate yet deterministic patterns will obtain (1) when application is within as opposed to between communities, and (2) for different distributions descriptive of the relative abundances or from the same distribution with different values of the parameters.

For illustration, the log-series and the broken stick distributions can serve as ends of a spectrum of possibilities encountered in nature. We first examine results for these two in detail and then compare the log normal.

In Table 2, we illustrate the general case of richness increase by documenting changes in the common indices for these two distributions as the species richness is increased from 25 to 50. Recall that when sampling within a particular log series the parameter α of the log series is constant. Interestingly, because the parameter for the broken stick is S, the categories of within and between populations are no longer germane. Therefore, any change in richness can be thought of as between-population for a broken stick distribution. When sampling within a log series population, the number of individuals observed must, of course, increase (Fig. 4). For the broken stick distribution, as long as N is large enough to ensure a reasonably accurate and representative vector $\mathbf{p}$, this increase in N is irrelevant.

The Log-Series Distribution.—We arbitrarily chose a log-series α value of 10. We then showed that within communities, for a log series α is the slope of the line for a semilog plot of S versus ln N (Fig. 3). As an example, for $\alpha = 10$ and $S = 25$, then $N = 112$, whereas for $\alpha = 10$ and $S = 50$, $N = 1475$ and the expected proportion of the most dominant species is ln (α/α) or 0.23. For a log-series-distributed

TABLE 2. Values for biodiversity measures for within a log series distribution and between broken stick distributions for an increase in species richness from $S = 25$ to $S = 50$.

Distribution	S	ln S	H	ln E	E	α	λ	$1/\lambda$	$1/\lambda/S$	J	ln α/α or ln S/S
Within log series	25	3.22	2.88	−0.34	0.71	10.00	0.10	10.00	0.40	0.89	0.23
	50	3.91	2.88	−1.03	0.36	10.00	0.10	10.00	0.20	0.74	0.23
Δ		0.69	0	−0.69	−0.35	0	0	0	−0.20	−0.15	0
Change		+	0	—	—	0	0	0	—	—	0
Between broken stick	25	3.22	2.82	−0.40	0.67	4.66	0.08	13.00	0.52	0.88	0.13
	50	3.91	3.51	−0.40	0.67	11.08	0.04	25.50	0.51	0.90	0.08
Δ		0.69	0.69	0	0	6.42	−0.04	12.50	−0.01	0.02	−0.05
Change		+	+	0	0	+	—	+	0	+	—

community, then, regardless of the increase in richness, H, λ, α, and $p_1 = \ln \alpha/\alpha$ are all constants. Table 2 also shows the actual values at $S = 25$ (ln $S = 3.22$) and $S = 50$ (ln $S = 3.91$). The row labeled Δ for difference indicates the change, positive or negative with increasing richness for our example of $S = 25$ to $S = 50$. The change in ln S is $+0.69$, and in ln E it is -0.69, while for the constants, of course, it is 0. From our earlier examination of the log series it is clear that for any given or observed N and S there is a value of α that remains constant as sampling increases on a semilog plot. Therefore, although the actual value of α is a measure of species richness, the fact that it is the slope of the line of the semilog plot shows that for a log series population it is also a measure of evenness. In addition, H and λ for a within-community log series behave in exactly the same way, namely, they are constant. Just as H and λ are easily seen as measures of evenness when S is constant, so they can also be thought of as measures of evenness within a log series, because the only way in which their values can change is if evenness changes. In a sense, then, if the measure is constant with changing S many investigators call this independence. Consequently ratios with S in the denominator are popular measures despite both warnings (e.g., Peet 1975) and the existence of mathematical consequences such as discontinuities when used with large numbers of rare species or even minor polymorphisms. This constancy can be obtained with H, α, or λ for a log series distribution but not with any single measure for all distributions of p.

Table 2 also shows that what we do not have as constants are some of the traditional measures of evenness, namely, E, J, $(1/\lambda)/S$, even though the latter has S as divisor. As the difference (Δ) row shows, the logarithmic difference is an increase of 0.69 between the increasing richness values S of 25 to 50. From the decomposition equation, $H = \ln S + \ln E$, there must be an equivalent decrease in ln E because H is constant. Table 2 shows this is exactly the case, so that ln E is measuring a (negative or residual) value compensating for the equivalent increase in species richness. If we were to transform the values of $(1/\lambda)/S$ to logs, the

TABLE 3. Changes in biodiversity measures for four different situations as species richness increases from $S = 25$ to $S = 50$. + indicates an increase, − a decrease, 0 no change or constant.

Distribution	ln S	H	ln E	E	α	λ	$1/\lambda$	$1/\lambda/S$	J
Within log series	+	0	−	−	0	0	0	−	−
Within log normal	+	+	−	−	+	−	+	−	0
Between combinations of log series and log normals	+	++	+	+	+	−	+	+	+
Between broken stick	+	+	0	0	+	−	+	0	+

difference would also be −0.69. Within a log series distribution, then, as richness increases the value of E or ln E is measuring the change in species richness. In addition, for a log series, E is a measure of evenness only between distributions. The evenness of the distribution is actually being measured by α, λ, and H, and not by the traditional evenness measures that are responding negatively to a positive change in S. Clearly, the measures α, λ, and H do not conform to the "repeat" criterion of Smith and Wilson (1996). However, if sample sizes are equal, that is, if N is kept constant when comparing biodiversity between populations, then both E and $1/\lambda/S$ will have constant value for any particular log series and they do satisfy this repeat criterion.

The Broken Stick Distribution.—For the broken stick distribution, the situation is quite disparate and consequently the behavior and interpretation of the indices is likewise different. Once again the change in the number of species is 25 (50 − 25) so that the difference (Δ) for ln S is +0.69. For the broken stick, $E(H) = $ ln $S - 0.40$, which is not constant but increases with richness. Table 2 shows the increase in observed H also is exactly +0.69. H, then, behaves like ln E for the log series, namely, it parallels exactly ln S. Consequently, H for the broken stick actually is measuring species richness. The constant 0.40 is equivalently the value of ln E so that this measure of evenness will be constant regardless of the value of S. The behavior of λ, on the other hand, no longer has the desirable property of independence from S and, instead, decreases as S increases because $\lambda = 2/(S + 1)$ (May 1975). The evenness measure $(1/\lambda)/S$ behaves like E. The expected proportion for the most abundant species in a broken stick is (ln $S)/S$, and unlike the log series, as richness increases the proportion of the most abundant species therefore must decrease.

To simplify the pattern of changes in the measures we placed a "+" under the measure if it increased, "−" if it decreased, and 0 if it remained constant with richness increase. Thus, at a glance, the two distributions shown in Table 2 are easily distinguished.

The Log-Normal Distribution.—Table 3 illustrates the visual +, −, 0 scheme for the other possibilities we might encounter with field data. Both log series and broken stick are included for comparison with the two new entries. For the log-normal distribution, the only measure whose behavior is constant with richness increase is J; H and ln E for the log normal do not measure changes merely in the single aspect of either richness or evenness. When comparing changes in measures within a single log-normal community, the change or difference (Δ) will be smaller than the corresponding change in S. However, when comparing between log normals with different parameters, or between distributions, then none of these measures remain constant. Furthermore as S increases each of the measures of evenness increases as we go between distributions. The value of H will increase more, or Δ will be larger for H than for S. We have placed a "++" on H when considered between distributions to indicate the relative size of increase in H with that in richness.

The exercises we have just examined illustrate how sensitive are the standard measures we use for biodiversity analysis to the underlying statistical distribution of **p**. It is clear that what and how they measure changes precisely with the distribution.

Although we have shown that the distribution of **p** is crucial for understanding evenness measures, it has never been mentioned when

drawing up a list of desirable criteria (Routledge 1983; Smith and Wilson 1996). Authors seeking to develop measures of evenness that are independent of species richness continue to devise allegedly new evenness measures without considering the mathematical consequences of distribution or algebraic equivalents (e.g., Peters 2004).

Summary.—Consideration of the entropy-based methodology indicates that there exists a constant measure for each of the three distributions discussed herein, but that no one measure is constant for all distributions. In order to realize an ecological reward for use of an evenness or diversity measure in a study, one must identify and appraise (1) the appropriate distribution of p; (2) the deterministic behavior of diversity, richness, and evenness measures for each distribution; (3) the role of unequal, equal-sized, or accumulated samples; and (4) whether the evaluation is within or between communities or populations. Interpretation must then proceed accordingly.

Our recommendation to use the log series as a null model is enhanced by the unified theory of biogeography of Hubbell (1997, 2001). The fundamental biodiversity number, θ, is asymptotically identical to Fisher's α, and the log series is the expected distribution for metacommunities. In accordance with the unified theory, for both molluscs and foraminifera Buzas et al. (1982) and Buzas and Culver (1999) have found that the regional distribution of species occurrences is a log series. When immigration or dispersal rates are high, as they are with many marine organisms, the unified theory also predicts the log series distribution for local communities. For local foraminiferal communities, the log series distribution of individuals has been established and identified by Buzas et al. (1977) and Murray (2002). The simplicity and elegance of Fisher's and Hubbell's models make the log series the ideal yardstick by which to compare observations in the field. The use of the entropy-based approach with the decomposition equation allows not only for the evaluation of biological populations' adherence to specific statistical distributions, but also for an objective assessment of the observations regardless of known statistical distributions.

Past work has established that the distribution of a community is of importance. The present work quantifies this importance, emphasizes the commutations when sampling between communities versus sampling within a community, and shows that without knowledge of the statistical distribution of p, the relative abundances from a community, the usual indices for diversity and evenness are not interpretable in the expected ways. We suggest that this work has illustrated that the entire concept of what constitutes evenness and its measurement must be reconsidered in any ecological application.

Acknowledgments

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