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Source: *The American Naturalist*, Vol. 128, No. 6 (Dec., 1986), pp. 879-899

Published by: The University of Chicago Press for The American Society of Naturalists

Stable URL: <https://www.jstor.org/stable/2461769>

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THEORIES AND MODELS OF SPECIES ABUNDANCE

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Submitted March 8, 1985; Revised January 21, 1986; Accepted April 17, 1986

It is a common observation that in samples from animal and plant communities most of the individuals belong to a small number of abundant species, whereas most of the species are represented by a small number of individuals. The usual explanations for such patterns of species abundance are founded on one of two mathematical distributions, the log-series and the lognormal, which were initially used to *describe* species abundance in samples (see reviews in May 1975; Pielou 1975). These models may provide a quantitative description of the samples, which is assumed to reflect something of the abundance of the species in the community. However, recent criticisms of the use of these empirical models as descriptors of species abundance (Hughes 1984; Lambshead and Platt 1985) have also undermined their associated explanations, which have been separately criticized for their lack of ecological realism (Pielou 1975; Routledge 1980).

I recently suggested an alternative to these logarithmic models to explain the pattern of species abundance in samples from marine benthic communities (Hughes 1984). Recognized features of community dynamics were incorporated into an iterative model that consistently predicted species-abundance patterns similar to those in samples from natural communities. Although this dynamics model was based on features of the ecology of marine invertebrates, its predictions may be applicable to samples from other communities in which the abundance of species is influenced by recruitment, mortality, and competition.

The aims of this paper are to assess the ecological relevance of these different theories of explanation of species abundance, mainly by examining the accuracy of the three models in predicting the pattern of species abundance in a wide range of samples. In addition, the practice of using the log-series and lognormal models as models of community structure, as opposed to models of species abundance in samples, is examined. Other models, notably the gamma and negative binomial distributions, have been used to describe species-abundance patterns, but since they have not been used to provide explanations they contribute little to our ecological understanding and are not considered here.

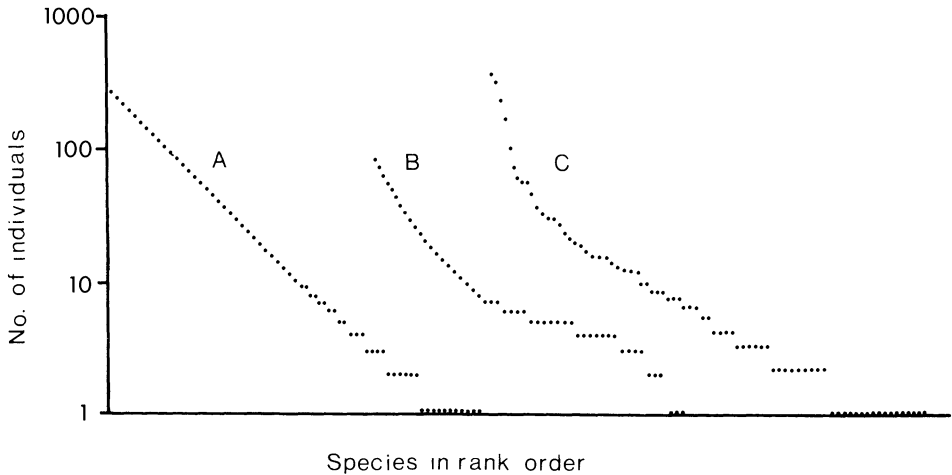


FIG. 1.—Dominance-diversity curves for A, a log-series distribution; B, a lognormal distribution truncated to the left of the mode; and C, a typical sample predicted by the dynamics model.

THE MODELS

The Log-Series Model

Fisher derived the log-series model to describe the species abundance of Malayan Lepidoptera in a collection made by Corbet (Fisher et al. 1943). In a log-series the expected number of species with n individuals is given by $\alpha x^n/n$, where x is a constant less than 1.0 dependent on sample size and α is a constant characteristic of the community, independent of sample size, and widely used as an index of diversity. When the abundance of each species is plotted on a logarithmic scale in rank order to produce a dominance-diversity curve, the log-series approximates a straight line (Taylor et al. 1976) with a slope of $-\alpha$ (fig. 1, curve A; May 1975). The line gradually expands as it approaches the horizontal axis because of a progressive increase in the number of rare species; more species are represented by one individual than by two, and progressively fewer by three, four, and so on. This feature of the log-series is often ignored by ecological texts. The log-series is usually thought to provide a particularly good description of samples from small, stressed, or pioneer communities (May 1975; Whittaker 1975). Caswell (1976), however, predicted the log-series distribution for “neutral” unstressed communities. In addition, the log-series has provided a statistically satisfactory description of samples from a wide range of communities (Williams 1964; Kempton and Taylor 1974; Gray 1978) with sufficient success for Taylor et al. (1976) to use it as their basic model of species abundance.

The log-series may result from sampling or stochastic effects (Boswell and Patil 1971) and may simply describe small samples from a lognormal community (Preston 1948). Other authors believe that the log-series has greater ecological significance. The main ecological explanation for a log-series distribution of

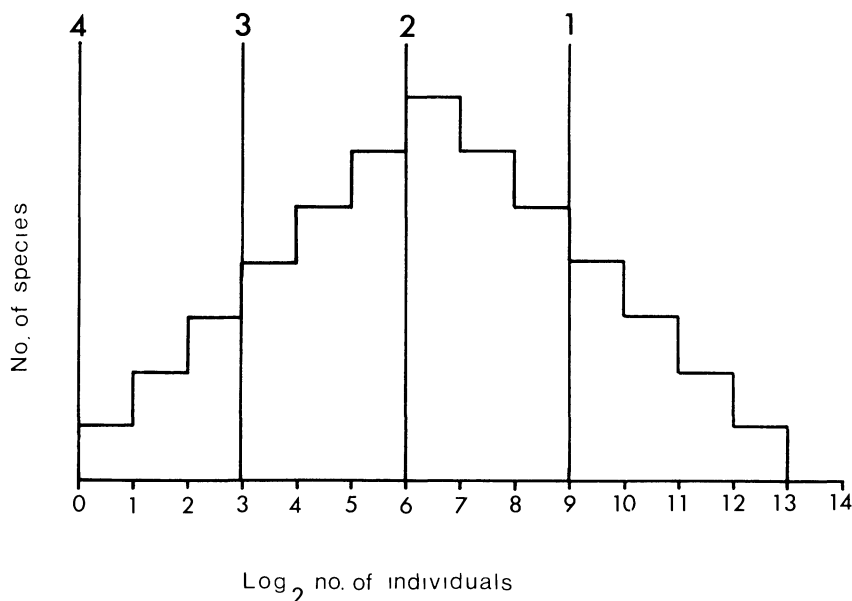


FIG. 2.—A lognormal distribution illustrating Preston's hypothesis of the moving veil line. Increasing sample size progressively reveals more of the underlying distribution by moving the veil line to the left (1–4).

species abundance was described by May (1975), who suggested that, as a statistically realistic variant of the geometric series, the log-series could be explained by a variation of the niche-preemption hypothesis associated with the geometric series. Briefly, May explained that a geometric series is expected if the species in a community are recruited at regular intervals, their abundance is governed by a major limiting resource, and the dominant species preempts a fraction of that resource and the next abundant the same fraction of the remainder, and so on. If these species are recruited randomly, rather than regularly, a log-series is the predicted distribution. The niche-preemption hypothesis has been criticized because it is not based on ecological criteria (Pielou 1975; Routledge 1980; Lamshead and Platt 1985) and, apart from the log-series distribution of species abundance, lacks supporting ecological evidence.

The Lognormal Model

Preston (1948) observed that in many samples the middle-ranking species were relatively numerous and there were fewer rare species than the log-series distribution predicted. Preston suggested that when plotted on a \log_2 scale, to give "octaves" of abundance, species abundance described a normal distribution (fig. 2). The log transformation was thought appropriate because populations tend to grow geometrically rather than arithmetically. Preston found that the distribution was always truncated, with a portion of the left-hand side missing. He attributed this to small samples that did not contain the rarer species, which were conse-

quently hidden behind a "veil line." Increasing the sample size would progressively collect the rarer species and move the veil line to the left, revealing more of the distribution (fig. 2). The lognormal distribution is characterized by three parameters, the number of species in the modal octave, the octave in which the mode occurs, and the standard deviation of the distribution around the mode. The dominance-diversity plot of a truncated lognormal, but one that shows a mode, is sigmoid, reflecting the preponderance of middle-order species and the relatively small number of rare species (fig. 1, curve *B*). A distribution that may be a lognormal truncated to the right of any mode is usually indistinguishable from a log-series.

Explanations for a lognormal distribution of species abundance are founded on the statistical properties of large numbers under the central-limit theorem (May 1975; Pielou 1975). If the abundance of each species in a large community is influenced differently by several variables and the species respond to these variables with different rates of geometric population growth, then a normal distribution on a logarithmic scale is expected. The direct application of the central-limit theorem in this context has been criticized because it does not include biological considerations, for example, the effects of extinction (Pielou 1975; Routledge 1980). The lognormal is considered almost ubiquitous as a descriptor of community structure, particularly for large communities that are stable and at equilibrium (May 1975; Whittaker 1975; Gray 1978; Preston 1980). However, Dennis and Patil (1979) and I (Hughes 1984, 1985) have argued the converse, that a truncated lognormal sample is most likely to describe samples from small or developing communities, where interspecific competition may be less important in restricting the abundance of the rarer species.

The Community Concept and the Log Models

In the literature, communities are rarely defined outside of textbooks, which offer such examples as "an assemblage of populations of plants and animals that live in an environment and interact with one another" (Whittaker 1975, pp. 1–2). Such definitions are unsatisfactory largely because they cannot define the spatial (and temporal) limits of the environment and therefore say nothing of the size of communities. Nevertheless, it is clear that those that regard the lognormal and log-series models as descriptors of community structure hold different views about what constitutes a community. The prediction of a low number of rare species by the lognormal is considered intuitively reasonable because of the high risk of extinction associated with rarity (May 1975). Thus, under the lognormal model, communities are regarded as being mostly independent and large enough to survive with little immigration. Preston (1948) believed that such communities ("universes") would contain at least several hundred species. In contrast, the log-series model implies that communities are less independent, for there must be immigration to maintain the large number of rare species, and are therefore somewhat smaller than under the lognormal model. Indeed, Preston regarded the log-series as simply a small sample of a lognormal community. A further source of terminological confusion is that usually samples are from only some of the populations in a community (e.g., only the beetles, trees, or diatoms), when the terms

“assemblage” or “association” are preferentially applied, but the practice of referring to these as communities (e.g., the diatom community) remains widespread. The use of the term “community” in this paper follows the lognormal concept of a largely independent, self-sustaining assemblage of populations.

The Dynamics Model

The dynamics model was derived to explain (but not mathematically describe) the species abundance in samples from marine benthic communities, the dominance-diversity curves of which tend to be neither linear (log-series) nor sinusoidal (lognormal) but deeply concave, especially in the upper part, with a progressive increase in the number of rare species (fig. 1, curve C). The abundant species in these samples are more numerous than the log-series predicts and there are too many rare species for a mode to be revealed; consequently, it is uncertain whether the sample is part of a lognormal distribution or not. The dynamics model is an iterative model that simulates the development and progression of a theoretical community through time. The model constructs a three-dimensional matrix at each time interval with each element of the matrix representing the abundance of one species. The abundance (n) of the i th species at time $t + 1$ is calculated from the expression

$$n_{t+1}^i = S [n_t^i + R(1 + Zn_t^i)(K - N_t)/K] .$$

This is a simplified form of the model (given in full in Hughes 1984) to illustrate the main principles. The three axes of the matrix are factors affecting the abundance of each species, two for recruitment and one for mortality. The first axis is a survival parameter, S , set at different levels but including a predetermined level of catastrophe, C , which operates stochastically to periodically reduce the populations of each species. The second axis is a parameter for recruitment potential, R , representing the temporally variable quantity of potential recruits, either the number of dispersing immigrants (larvae) or the fecundity of established individuals that give birth to new recruits. The third axis is a “gregariousness” parameter, Z , which relates the number of recruits to the number of established conspecifics (n_t) and is important because it confers on each species the potential for geometric population growth. Thus, recruitment is the product of the two parameters R and Z but is limited by the total number of individuals, N_t , via the asymptotic expression, which introduces the element of competition (intraspecific and interspecific). Values for the parameters R , S , and Z cannot be estimated from natural communities and must be given arbitrary values. In the original model these values were 1–10, 0.1–0.9, and 0–0.5, respectively, producing a community with a maximum of 540 species. When the iterative model is run from $t = 0$ to, say, $t = 75$, it produces a community with a variable number of species (those with an abundance greater than 1.0) and individuals. Stability (where C is set at a relatively low level, or by chance temporarily does not reduce the community density) leads to an increase in community density, competition increases, and the number of species and the diversity of the community falls. Disturbance (the catastrophic mortality of one or more of the abundant species) reduces the community density, increasing recruitment which, in turn, causes an increase in

the number and diversity of species. These predictions of the model agree with the hypotheses of Connell (1978) and Huston (1979) that intermediate levels of disturbance maintain species diversity and with the hypothesis of Caswell (1976) that biological interactions reduce diversity.

The model, with various combinations of different (reasonable) parameter values, consistently produces communities with dominance-diversity curves similar to those of natural communities. This pattern of species abundance is explained by the interplay between the recruitment potential of each species, and mortality and exclusion by competitors. These factors combine to allow only a few species to approach their potential for rapid geometric population growth, and then for only a short period, before the increasing populations reduce further the recruitment of all species. The progressive decline in the importance of geometric growth through the species spectrum produces a concave dominance-diversity curve with a progressive increase in the number of rare species. The abundance of most species is, therefore, not the product of geometric population growth, because competition and mortality reduce the populations of established species and limit the recruitment of any new species to a small number of individuals. This is particularly true under stable conditions, which allow a few species to become dominant, and which through interspecific competition cause a large proportion of the remaining species to become rare (Hughes 1985). Geometric growth of populations may be more significant where interspecific competition is less important, because the number of species is temporarily or permanently low. This may occur naturally in pioneer communities, communities recovering from a disturbance, isolated communities with limited immigration, and communities in extreme or fluctuating environments (e.g., estuaries or deserts), where a relatively small number of species can tolerate the harsh conditions. Samples of marine invertebrates from such communities support this prediction of the model, for they usually have a relatively low proportion of rare species and often a mode in the species-abundance distribution (Hughes 1985). This prediction and these findings are opposite to the prevailing view that the lognormal is more applicable to large, stable, equilibrium communities. The dynamics model also indicates that communities exposed to more-severe or continual stress may more closely resemble a log-series distribution (Hughes 1985), in which no species is able to dominate to the extent seen in most samples. Many species are rare in these samples because their population growth is limited by the environment, rather than by competition. The dynamics model makes no prediction of the structure of the whole community but only of small segments (e.g., that taken in a sample) where immigration is a significant source of recruitment.

FITTING THE MODELS TO DATA

The literature was searched for data on species abundance in samples from a wide range of animal and plant communities. The data used were the number of individuals belonging to each species, because the dynamics model uses individuals as the units of recruitment and mortality. Where abundance was expressed in other ways (e.g., artificial abundance scales, biomass, productivity, or percentage

cover), the data could not be used. Samples with a small number of species (arbitrarily fewer than 30) or individuals (fewer than 1000) were not used. Some judgment had to be made to avoid duplication, which could influence any trends observed. If an author had taken many samples from a community, separated spatially or temporally, I used those samples that were judged not similar in species composition to those already selected. Janzen (1973) presented data from a large number of different tropical insect communities and Pearson (1975) sampled the same sea-loch sites over many years; to prevent bias in the accumulated data from these numerous samples, I used only three randomly selected samples from Janzen's study and the 1963 data from Pearson's.

For a given number of species and individuals there is only one predicted log-series, but often a large number of lognormals. The predicted log-series is easily calculated from these two figures (Williams 1964), but the lognormal that gives the best fit to the data is found by relatively complex iterative maximum-likelihood techniques (e.g., Bulmer 1974; Gauch and Chase 1974; Kempton and Taylor 1974). The fit of sample data to the prediction of the log models is usually assessed by goodness-of-fit tests (especially χ^2), which are of notoriously low discriminating power (Engen 1979; Routledge 1980). This is especially true in this context, where the data are reduced to a small number of points by being grouped into octaves and groups of octaves (even, inexplicably, when the test is for a log-series). The truncated lognormal and log-series distributions are similar over much of their range; the only differences may be a few points representing the predicted abundance of the most abundant and the rarest species. Consequently, the goodness-of-fit tests usually reject neither model as a description of the data (Gray 1978; Lambshead and Platt 1985). In the case of the lognormal this is not surprising because the comparison is between data and a prediction that is a best fit to that data. The question of which model is the most relevant is therefore unresolved. These statistical techniques are not used here to differentiate among the three models because (1) the failings outlined above preclude their use; (2) the predicted lognormal may not be accurate (see below); and (3) the dynamics model does not give a precise mathematical prediction that can be used in statistical tests.

Here a sample may be described by a truncated lognormal only if there is some evidence of a mode in the species-abundance distribution (usually because the octave with the most species is the second or third). This criterion is less stringent than that of Lambshead and Platt (1985), who required a more definite mode as evidence of a lognormal. Many authors have calculated a lognormal from a sample without a mode on the presumption that the data represent a portion of the right-hand side of a community lognormal distribution. This practice is untenable because none of the three parameters of the lognormal can be estimated without a mode (Taylor 1978, and see below). The dynamics model also predicts that samples from some communities may have relatively few rare species and may, therefore, be described by a truncated lognormal. Table 1 shows that these samples are from communities described as pioneer (P), isolated (I), disturbed (including polluted) (D), and environmentally stressed (H). The log-series model and, for most samples (other than those listed above), the dynamics model predict

a progressive increase in the number of species as abundance declines. The main difference between them is that for most samples the dynamics model predicts a dominance-diversity curve that is deeply concave in the upper part, whereas the log-series model predicts that this part of the plot is approximately linear (fig. 1). This feature was used to decide which of the two models best predicted species abundance. In most cases the difference was obvious, but in a small number of samples neither model better described the data. Some of the samples with a relatively low number of singleton species could be described by a lognormal as well as a log-series distribution. This is not surprising, since even a perfect log-series may have a mode in the species-abundance distribution (Lambshead and Platt 1985).

RESULTS AND DISCUSSION

Data for 222 samples from a wide range of communities were examined. These are listed in table 1, with a brief label for identification, together with the model or models that most accurately predicted the pattern of species abundance.

The Occurrence and Use of the Lognormal Distribution

Only 65 samples could be described by a truncated lognormal because most of the samples (71%) do not have a mode in the species-abundance distribution. Preston (1948) and subsequent authors following his example have fitted lognormals to such data and, using the derived lognormal parameters, have predicted the structure of the whole community by estimating the number and abundance of the species not collected. The usefulness of the lognormal in describing, and hence explaining, species abundance rests upon the validity of this practice.

Samples without a mode.—Preston (1948) postulated that the graph of the abundance of the species in a sample plotted in octaves was identical in shape to the graph of the whole community except that a variable portion of the left-hand side was uncollected and therefore missing behind a “veil line.” Preston investigated the validity of this postulate and showed that if the first octave of the sample was to the left of, or close to, the mode of an underlying distribution, the graph of the sample was indeed similar in shape to the right-hand side of the community graph. However, he also demonstrated that if the veil line was significantly to the right of the community mode, the graphs were dissimilar with more species in the lowest octaves of small samples than in the modal octave of the community. Having identified this sampling effect, Preston considered it insignificant, claiming that most samples collect close enough to the community mode that the difference between the two graphs was negligible. However, if a sample contains a small proportion of the individuals in a community, even if it contains most of the species, the graph of the species abundance will differ significantly from that of the right-hand side of the assumed underlying distribution. This is demonstrated by figure 3, which shows the effect of increasing the size of samples taken randomly from a small contrived lognormal community. For example, when the sample contains 1% of the individuals, the mode contains 22 species, 9 more than the community mode. Moreover, since the sample has no

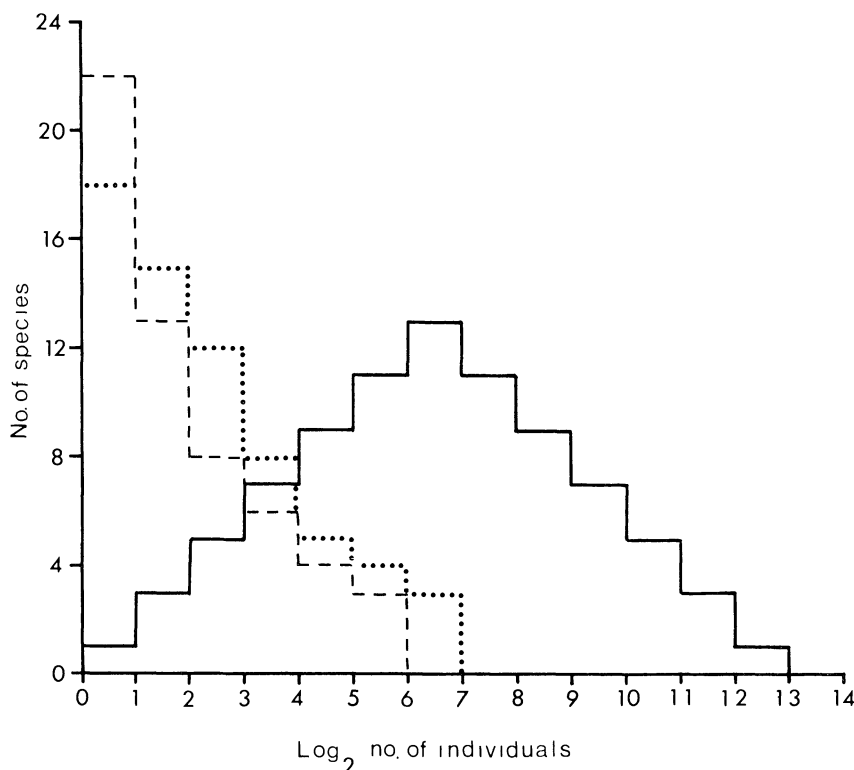


FIG. 3.—The species-abundance distribution of a small, contrived lognormal community (solid line) and of random samples from this community containing 1% (dashed line) and 2% (dotted line) of the individuals.

mode, this would, according to Preston, mean that the veil is to the right of the community mode, indicating that less than half of the species have been caught. However, 66% of the species are in the sample. This sampling effect reflects the small probability of catching individuals of each of the rarer species. Because these species are numerous, some will be caught by chance and, as rarities, be added to the lowest octaves, which may then contain more species than the community mode. In nature this sampling effect is further complicated by the patchy distribution of most species, which means that truly random samples are probably never taken; some species are overcollected while others are undercollected. A sample from a community of aggregated species will contain fewer species than a sample from a community of species more randomly dispersed.

It must be concluded that the shape of any underlying lognormal cannot be reasonably predicted from a small sample. The validity of fitting a lognormal to a sample without a mode therefore depends on the implicit assumption that the first octave of a sample is close to the community mode. In individual cases this assumption is not testable; that the calculated community mode is invariably in the first octave of the sample (e.g., Gray 1978) is a product of the assumption, and

TABLE 1

SAMPLES USED IN THIS STUDY AND THE MODEL OR MODELS THAT GAVE THE BEST PREDICTION OF THEIR SPECIES-ABUNDANCE PATTERN

REFERENCE	MODEL			REFERENCE	MODEL		
	Log-normal	Log-Series	Dynamics*		Log-normal	Log-Series	Dynamics*
ALGAE				FISH			
McClatchie et al. 1982	×		×	Brock et al. 1979			
Patrick 1971				1966	×		×
Jan			×	1967	×		×
Mar			×	Iglesias 1981			
Apr			×	JB	×		×
Oct			×	JM			×
				JR	×		×
HIGHER PLANTS				Loeb 1979			
Williams 1964				IKPT			×
T38 WF			×	BONGO			×
WU			×	Molles 1978			
SF			×	Jan	×		×
SU	×		×	June	×		×
ARTHROPODS				REPTILES			
Ashmole et al. 1983 1-7			×	Dunn (1949)			
Bailey et al. 1978			×	CO		×	
Bultman & Uetz 1982				SA			×
AF	×		×	CH	×	×	×
AN	×		×	DA			×
NF			×	Heyer & Bevren 1973			
NN	×		×				
AC	×		×	BIRDS			
NC			×	Halla 1983			
Crighton & Fisher 1982				3 1980	×		×
RYC 1966			×	5 1980	×		×
RYC 1967			×	6 1980	×		×
RYC 1969			×	7 1980	×	×	×
PM 1967			×	Williams 1964			
PM 1969			×	App. C			×

TABLE 1 (Continued)

REFERENCE	MODEL			REFERENCE	MODEL		
	Log-normal	Log-Series	Dynamics*		Log-normal	Log-Series	Dynamics*
Buchanan & Warwick 1975			×	Pearson (continued)			
Chamberlain 1973	×		×	24			×
Heck 1976			×	1			×
Eco			×	27			×
Fen	×		×	8			×
Heck 1977	×		×	28			×
1			×	9			×
2			×	34			×
3			×	33			×
4			×	10			×
Hicks 1980			×	36			×
SA			×	37	×		×
RHB			×	39	×		×
Hughes 1984			×	42			×
LAM			×	53			×
UG			×	Pearson 1975			×
NEM			×	1963 2	×		×
Gage 1972			×	34	×		×
FL1			×	1	×		×
C5			×	53	×		×
C12			×	24	×		×
E2			×	Poiner & Kennedy 1984			×
E6			×	Probert 1981			×
E11			×	A70			×
E24	×		×	O70			×
TOT			×	JU72			×
Josefson 1981			×	Rosenberg 1975			×
100 m			×	Rosenberg 1974			×
300 m			×	0-5 m			×
Lewis 1984			×	5-10 m			×
AM			×	Total (0-10 m)			×
HA			×	Rosenberg 1977			×
TH	×	×	×	BY			×

not a test of it. If this assumption is correct, the largest communities so far sampled will cover about 20 octaves, with the population of the most abundant species between 1.05 and 2.1 million. This is clearly an underestimate. In benthic marine communities familiar to the author, species of barnacles, nematodes, copepods, mud snails, and amphipods may occur in such numbers in only 1–2 m² of substrate. The assumption that a sample without a mode represents most of the right-hand side of an underlying lognormal distribution is, in most (possibly all) cases, almost certainly erroneous. Communities are implicitly defined by the lognormal as being large, and it is therefore likely that samples will contain only a small proportion of the individuals and that the first octave of a sample is probably not close to any community mode. Therefore, predicting the structure of a community from lognormal parameters calculated for a sample without a mode is unreasonable, even allowing for the assumption that the community conforms to a lognormal, which may or may not be correct.

Samples with a mode.—The presence of a mode in a sample may be a reflection of the community species-abundance distribution or it may have little ecological significance. For a truncated lognormal sample to accurately reflect part of an underlying distribution, it must contain many more than half of the species and, evidently, an unusually large proportion of the individuals. Preston (1962) estimated 70%–80% of the species should be sampled, but this may be an underestimate because random samples from the contrived community (referred to above) need to contain about 85% of the species before a mode is revealed. It is therefore logical, simply on arithmetical grounds, to expect a lognormal community to be confirmed only by samples from very small communities.

However, a mode can be present simply through chance or sampling effects. In most samples the first octave usually has more species than the second, the second more than the third, and so on, but the difference between these adjacent octaves is often small and the chance absence or misidentification of a few individuals of rare species may make the difference between the presence or absence of a mode (Lambshead and Platt 1985). Moreover, many of the data listed in table 1 represent repeated samples grouped together. The practice of adding together non-replicate data may, for statistical reasons, produce a truncated normal distribution (Routledge 1980; Shaw et al. 1983). It is perhaps significant that much of the data used by Preston are from compiled samples; he noted that the average of many years of data usually fit a lognormal distribution better than one sample (Preston 1980). Lambshead and Platt (1985) concluded that a lognormal has yet to be demonstrated in genuine ecological samples. Even if a genuine mode could be identified, it would reflect only the relative abundance of species in the small area sampled and not the whole community. This may be particularly significant in samples of gregarious species (e.g., fish or birds) that have a tendency to form social groups (shoals, flocks, etc.). In sampling from aggregations, the capture of one individual of a species positively enhances the likelihood of catching another (and reduces the probability of catching other species). Consequently, the number of species with a small number of individuals may be relatively low. This may partly explain why 16 of the 31 samples from vertebrate communities have a mode, whereas only 24% of the 182 invertebrate samples have one.

A mode may also be an artifact of the methods used to plot the data. Williams (1964) argued against the use of \log_2 because the boundaries between adjacent octaves are integer values. He preferred the use of \log_3 because the integer values for abundance were within groups rather than on the boundary. (Despite the logic of Williams' argument, most authors have followed Preston and used \log_2 , presumably because this gives more abundance groups.) Williams used \log_3 throughout his book, and these species-abundance distributions often showed a mode when one would not be present if \log_2 were used, because the middle and higher-order groups cover larger abundance ranges. (Almost any large data set may be described by a truncated lognormal if the logarithmic base is sufficiently large.) This raises the question of which logarithmic scale is more appropriate for the presentation of species-abundance data, since the presence of a mode may owe more to the logarithmic transformation, which normalizes data, than to the ecology of the community. The dynamics model indicates that species rarely show geometric population growth and that there is, therefore, no justification for using any logarithmic scale. This finding concurs with those of population ecologists who, since Malthus, have investigated the mechanisms that tend to regulate natural populations by preventing continued geometric population growth.

One must conclude that the crucial assumptions underlying the relevance of the lognormal in community ecology are untenable. The model does not provide a satisfactory description of most samples; where data can be described by a truncated lognormal, the distribution probably does not reflect the relative abundance of the sampled species in the community and cannot reasonably be used to estimate the absolute abundance of the collected and uncollected species. There is, therefore, no convincing evidence that the numbers of individuals belonging to each species in a community are lognormally distributed. This conclusion concurs with the views of Lambshead and Platt (1985), who pointed out that a lognormal distribution has not been demonstrated by increasing the sample size to progressively unveil a mode. However, it seems reasonable to suppose that there will be few species close to (local) extinction and a small number of very abundant species. Therefore, the species-abundance distribution may conform to a normal distribution but on an unknown appropriate scale.

The Occurrence and Use of the Log-Series Distribution

The log-series distribution provides a better prediction than the dynamics model of the structure of only eight (4%) of the samples, because in most samples the abundant species have much larger numbers than the log-series predicts. The abundance patterns of the rarer species usually fit the log-series reasonably well. The log-series was conceived to describe the species abundance in data from Corbet's collection of Lepidoptera. Fisher used only the data for the species with less than 25 individuals because individuals of the most-abundant species were ignored after a certain number had been collected (Fisher et al. 1943). The most-abundant species in these truncated data had only 24 individuals and therefore would not show the high degree of dominance seen in most complete samples. Once the log-series was available as a description of data, it was accepted, despite the apparent consistent difference between the sample data and the prediction, because the data could be easily fitted by the use of indiscriminating techniques

emphasizing the rarer species that more closely fit the model. Fisher also thought that a log-series described Williams' sample of English Lepidoptera, but the dominance-diversity curve of these data show the typical form with a deeply concave upper curve rather than the linear curve produced by the log-series model. These data and 94% of the others examined here better approximate a straight line when log-transformed data are plotted on the log scale of a dominance-diversity graph. The log-series parameter α , which may also be derived from the lognormal (Kempton and Taylor 1976), does not therefore provide a good description of most data sets, and this must cast considerable doubt on its usefulness as an index of diversity.

The Dynamics Model

The dominance-diversity curves of 94% of the samples examined are similar in shape to figure 1, curve C, and thus accord with the predictions of the dynamics model. This does not imply that the parameters as specified and arranged in the original model are relevant to all these samples. The model was devised from criteria thought to be pertinent to marine fouling communities, where competition (for space) is important. However, subsequent tests with different parameter values that shift the emphasis from competitive interactions to mortality (via C or S) produce similar species-abundance patterns. (Further increases in the level of mortality produce species-abundance patterns that begin to resemble log-series distributions.) Thus, the model indicates that this pattern of species abundance is common because it is the almost inevitable result of many species having variable success in approaching their different potentials for geometric growth, irrespective of the precise mechanisms that restrict population growth. The prediction that the proportion of rare species may be smaller where population growth is less restricted by interspecific competition or mortality was supported by the data from various marine communities (listed in table 1) and is similarly supported by other data here. Of the 65 samples that have a mode in the species-abundance distribution, 39 may be expected to have a relatively low proportion of rare species from this prediction of the dynamics model, because 13 are from isolated communities, 10 from pioneer communities, 9 from disturbed or stressed communities, and 7 from communities in harsh conditions. Further support for this prediction may be found by more detailed examination of studies that are unusual in having several samples that may be truncated lognormals. Arntz and Rumohr (1982) examined the colonization of experimental containers by benthic invertebrates in the Baltic Sea. Of the 13 samples from these pioneer communities, 7 show a mode but only 1 of the 7 samples from the natural communities has one. Similarly, in Bultman and Uetz (1982) the three samples of immigrant forest spiders have modes, but the three samples from the established communities do not. After censusing the land birds that had recently colonized 44 islands off the coast of Finland, Haila (1983) found that, when the data were grouped into 7 island types, most of these showed a mode (only the 1980 data for 4 groups are used in this study). The insular nature of these communities, the social behavior of the birds, or the grouping of the data may all be partly responsible for this. Pearson (1975) gathered comprehensive data on the changes in the benthos of semi-

enclosed sea lochs associated with the discharge of pulp-mill effluent. Many of his samples may be described by a truncated lognormal, including those used here taken in 1963 before the discharge began. This is an unusual feature of marine samples and may reflect the degree of isolation of these communities in the lochs, where the levels of immigration may be reduced (Hughes 1984).

This prediction, and these findings, contradict the prevailing opinion that samples from large, stable communities at equilibrium are those most likely to be described by a truncated lognormal. The view that equilibrium communities belong to a lognormal distribution, while disturbed communities do not, is often supported by Patrick's (1963) observations of diatoms in polluted and unpolluted streams (Preston 1980) and by data on the development of pasture communities (May 1981). Patrick actually found that in natural soft-water rivers most species had relatively small populations, but under polluted conditions few species had relatively small populations. Patrick's most convincing truncated-lognormal sample (Back River) was from a community subject to organic pollution. Patrick (1967) later found that a number of samples of diatoms had modes in the species-abundance distribution, but these were pioneers from experiments designed to investigate the influence of immigration on species-abundance patterns. These observations by Patrick agree with this dynamics-model prediction. The data on abundance of plants in the pasture communities is expressed as "cover values" and are not strictly comparable to data expressed as numbers of individuals. The addition of the extra variable of size may be expected to increase the normality of the data.

The dynamics model also predicts that a distribution resembling a log-series may be found in samples from stressed or disturbed communities where mortality prevents the most-abundant species from achieving the high degree of dominance seen in most samples. There is, however, no evidence that any of the log-series samples identified in table 1 are from stressed communities, although it is interesting that six of these samples have a mode in the species-abundance distribution, a feature that the dynamics model indicates may be a feature of some samples from stressed communities.

SUMMARY

Three theories of explanation for the observed patterns of species abundance in samples from animal and plant communities are reviewed. These are the niche-preemption hypothesis associated with the log-series distribution, the theory based on the central-limit theorem to explain the truncated lognormal distribution, and the explanations associated with a recently published model of community dynamics. The relative performance of the log-series, lognormal, and dynamics models in predicting the species abundance in 222 samples from a wide range of communities is examined. The log-series provides the best prediction of only 4% of the samples, because there were either too few rare species or, more usually, the common species were too abundant. Only 28% of samples, those with a mode in the species-abundance distribution, may be described by a truncated lognormal, but even in these cases the lognormal parameters cannot reasonably be used

to predict the abundance of species in the whole community. The species abundance in 94% of the samples may be explained by one of the predictions of the dynamics model. For most samples, the model predicts a concave dominance-diversity curve with a large number of rare species, but indicates that there may be a smaller proportion of rare species in communities where population growth is less restricted by competition or mortality.

It is concluded that the theories associated with the log-series and lognormal models, which have been criticized previously for a lack of ecological realism, provide unsatisfactory explanations for species abundance because they are conceptually unsound and the models on which they are based rarely provide a satisfactory description of samples. This conclusion undermines the use of the diversity index α associated with these models. The dynamics model predicts the species-abundance pattern of most samples with greater accuracy and provides an explanation of species abundance based on recognized and testable ecological principles.

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