The Statistics of Relative Abundance and Diversity

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Abstract.

When measurements of relative abundances or proportions are made on biological systems, regular patterns, related to the ordered broken-stick series, are sometimes observed. In this paper we show that these patterns arise predominantly because of the underlying mathematics of proportions. We also find that the detailed structure of the pattern may give information about the biology of the system being studied.

1 Introduction

In describing samples from natural populations, use is often made of the relative abundances p_i, where p_i is the proportion of a sample or population belonging to the ith species. Relative abundances are used to define more sophisticated quantities such as the diversity or the equitability. In this paper natural logarithms are used, so for a system of S species, the biological diversity D and the equitability E are defined by the equations,

$$D = -\sum_{i=1}^{S} p_i \log_e p_i, \tag{1.1}$$

$$E = D/\log_e S. \tag{1.2}$$

Diversity and equitability are used in comparing different biological systems and they may be relevant to the stability of such systems (Margalef, 1969; Deevey, 1969).

If relative abundances or related quantities are plotted in a suitable manner, regular patterns may be observed. Thus Preston (1948, 1962a,b) found that species abundance curves often follow a log-normal curve and MacArthur (1957), found that bird censuses from tropical forests and many temperate regions followed an ”ordered broken-stick series”[1]. Similarly Longuet-Higgins (1971) has shown that the diversity of Tramer’s (1969) breeding bird populations is similar to that calculated from the ordered broken-stick series.

In trying to understand the reason for these regularities, a number of models have been investigated. MacArthur (1957) showed that if the environment consisted of a set of non-overlapping niches, chosen in a particular way, then the ordered broken-stick series resulted. However Cohen (1968) showed that other models could give rise to the same series. Thus the relevance of the ordered broken-stick series remained unexplained. However it has been suggested that agreement with the ordered broken-stick distribution indicated ordering in the biological system (Deevey, 1969; King, 1964).

In this paper, we show that the similarity observed between some biological systems and the ordered broken-stick series arises essentially from the initial choice to work with proportions. This is because the mathematics of a broken-stick and the mathematics of proportions are just two ways of looking at what is mathematically the same thing.

We shall approach the subject from the point of view of proportionality space, that is the space of the p’s. Thus in sections 2 and 3 some of the basic properties of the space are discussed. In particular the mean values of quantities such as the diversity are calculated. The results obtained are very similar to those obtained directly from the ordered broken-stick series by Longuet-Higgins (1971). In section 4, the idea of taking averages over the space is developed, to investigate the distribution of both the diversity and the logarithmic standard deviation. It is found that these quantities are concentrated in a very narrow region around their mean values.

The process of taking averages can itself be looked on as a model in which we assume that the biological system is equally likely to be represented by any point in the space. Because of the context, we shall call this the ’proportionality space model’. It is equivalent to the ’broken-stick model’ used in statistics.

In section 5 the results of earlier sections are compared with measurements from a number of biological systems. One would expect to find most agreement with biological systems which similarly have an equal chance of being represented by a point anywhere in the space. Conversely one would expect to find disagreement if something in the biology constrains the system to a small region of the space.

In fact we find that the amount of agreement is surprisingly large. We also find that where there is significant disagreement, we are able to identify biological factors which constrain the system.

Finally the implications of these finding to the theoretical models of MacArthur and Cohen are

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[1] If a stick of unit length is broken randomly into n pieces then the expected length of the ith shortest piece $E<p_i>$ is,

$$E<p_i> = \frac{1}{n}\sum_{j=1}^{i}\frac{1}{n-j+1}.$$

The set of numbers $E<p_1>$, $E<p_2>$, ... , $E<p_n>$ is the ordered broken stick series.

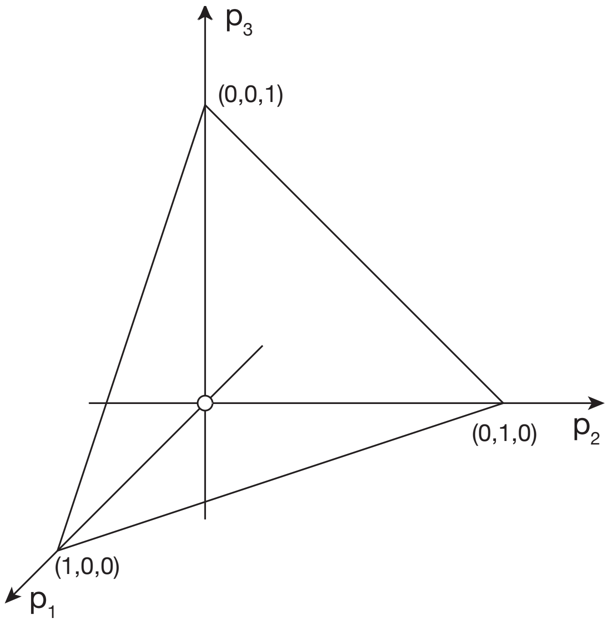

Fig. 1. Three dimensional proportionality space showing the biologically realistic region.

considered.

2 Proportionality Space

2.1 Three Species Populations

In considering a biological sample or population containing three species, it is convenient to introduce p_1, p_2 and p_3 where p_i is the proportion of the sample or population belonging to the ith species. A three-dimensional proportionality space can be introduced, whose basis axes correspond to each of the p_i's (Fig. 1). Any particular sample or population can be described by the sample vector $(p_1{,}p_2{,}p_3)$.

To be realistic the p's must satisfy the conditions,

$$\begin{gathered} p_1 + p_2 + p_3 = 1, \\ 0 \leq p_1 \leq 1, \quad 0 \leq p_2 \leq 1, \quad 0 \leq p_3 \leq 1. \end{gathered} \tag{2.1}$$

This biologically realistic region is a triangle with vertices at $(1{,}0{,}0)$, $(0{,}1{,}0)$ and $(0{,}0{,}1)$, This is shown in Fig. 2, which also shows the contours of biological diversity.

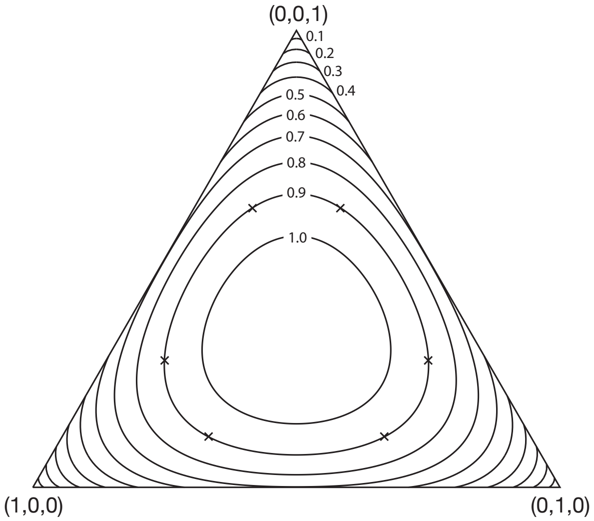

Fig. 2. The biologically realistic space for three species, showing contours of the diversity. Points marked with a cross correspond to the ordered broken-stick series (MacArthur, 1957) for three species.

2.2 Many Species Populations

For a larger number of species, say S species, one can again introduce the S-dimensional space of the p's. The biologically realistic portion of this space is defined by,

$$0 \leq p_i \leq 1, \quad \text{for} \quad i = 1, 2, \ldots, S.$$
$$\sum_{i=1}^{S} p_i = 1. \tag{2.2}$$

If a stick of unit length is broken into S pieces then the lengths of the pieces satisfy the same set of conditions. In fact one can show that the probability of breaking a stick randomly into S pieces is equivalent to the problem of choosing a point at random in the biologically realistic portion of S-dimensional proportionality space.

For the three-dimensional case, a result equivalent to this was obtained by Whitworth (1897). He showed that the problem of breaking a stick up randomly into three pieces was equivalent to choosing a point at random within an equilateral triangle. To do this he first assumed that the stick could be broken only at one of a large, but finite, number of equally spaced points. One can then show that the different ways in which the stick may be broken into three piece correspond to uniformly spaced points in the triangle. The limit as the number of points at which the stick can be broken tends to infinity corresponds to the broken stick problem. Then because of the uniform correspondence of the two approaches, expectations calculated with the broken-stick model will corresponds to integrals over the triangle.

It is straightforward to extend Whitworth's argument to the four dimensional space (a tetrahedron) and to higher dimensional spaces[2].

3 Mean properties of the Space

To calculate the mean properties of the biologically realistic space in S-dimensions, it is useful to introduce the weighting function W_S. This is useful because it is non-zero only in the biologically realistic part of the space. It gives equal weight to each point in the space and is normalised to give unity when integrated over the space (see Appendix 1).

$$W_S(p_1,...,p_S) = (S-1)!\,\delta\Big(1-\sum_{i=1}^{S} p_i\Big)\prod_{i=1}^{S}\theta(p_i), \tag{3.1}$$

where,

$$\begin{aligned}\theta(x) &= 1, \text{ if } x \geq 0\\ &= 0, \text{ if } x < 0,\end{aligned}$$

and $\delta(x)$ is the Dirac delta function (Dirac, 1930). This is defined so that,

$$\int_{-\infty}^{\infty} f(x)\delta(x)dx = f(0). \tag{3.2}$$

This can now be used to obtain some useful results.

Consider an S species system, whose probability distribution is uniform throughout the space. Then if $F_S(p)dp$ is the probability that the relative abundance of a particular species has a value between p and $p+dp$, then,

$$F_S(p) = F_S(p_S) = \int dp_{S-1}...\int dp_1 W_S(p_1,...,p_S). \tag{3.3}$$

This integral is considered in Appendix 1. One find that,

$$F_S(p) = (S-1)(1-p)^{S-2}. \tag{3.4}$$

If the number of species is large, then,

$$F_S(p) \sim S\,e^{-Sp}. \tag{3.5}$$

This is the same result as found by Longuet-Higgins (1971) for the ordered broken-stick series.

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[2] The equivalence between the two approaches can readily be checked by calculating the mean length of the shortest stick or the smallest relative abundance. The solution obtained by integrating over the biologically realistic S-dimensional space (see Appendix II) is the same as that obtained by the more classical methods of treating the broken-stick problem.

The mean diversity of the space D_S, is given by,

$$D_S = -\int dp_S ... \int dp_1 \, W_S(p_1,...,p_S) \sum_{i=1}^{S} p_i \log_e p_i, \tag{3.6}$$

$$= -S \int dp_S \; p_S \; \log_e p_S \int dp_{S-1} ... \int dp_1 \, W_S(p_1,...,p_S),$$

$$= -S(S-1) \int_0^1 dp_S \, p_S \; \log_e \; p_S \; (1-p_S)^{S-2}. \tag{3.7}$$

Using the relation,

$$\int_0^1 dx \, x^S \log_e(1-x) = -\frac{1}{S+1} \sum_{i=1}^{S+1} \frac{1}{i}, \tag{3.8}$$

one can show that[3],

$$D_S = \sum_{i=1}^{S} \frac{1}{i} - 1. \tag{3.9}$$

If the number of species is large,

$$D_S \sim \log_e \; S - (1-\gamma). \tag{3.10}$$

where $\gamma = 0.57721 \; 56649...$ (Euler's constant). Again this is the same asymptotic form as Longuet-Higgins (1971) obtained for the ordered broken-stick series.

To illustrate the geometric properties of the space it is useful to calculate the mean value of r^2, where r is the distance from the centre of the space,

$$< r^2 > = \int dp_s \; ... \int dp_1 \sum_{i=1}^{S} \left(p_i - 1/S\right)^2 W_s(p_1,...,p_S). \tag{3.11}$$

This simplifies to,

$$< r^2 > = \frac{1}{S} \frac{S-1}{S+1}. \tag{3.12}$$

Comparing this with the maximum value that r^2 can have, which is,

$$(r^2)_{max} = 1 - \frac{1}{S}, \tag{3.13}$$

one sees that when S is large, most of the volume must lie very near the centre of the space.

A direct comparison between proportionality space and Preston's (1948) log-normal curves is rather involved. However, it is straightforward to calculate the square of the logarithmic standard

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[3] This result was originally obtained by H. Irrgang (personal communication).

deviation σ, for,

$$\sigma^2 = \frac{1}{S}\sum_{i=1}^{S}\bigl(\log_e p_i - \frac{1}{S}\sum_{j=1}^{S}\log_e\ p_j\bigr)^2. \tag{3.14}$$

If the log-normal hypothesis is correct, then this is an estimate of the variance of the log-normal distribution from which the sample was taken. The mean value of σ^2 over the biologically realistic space is given by,

$$<\sigma^2> = \int dp_s\ ...\int dp_1\, W_S(p_1,...,p_S)\left[\frac{1}{S}\sum_{i=1}^{S}\bigl(\log_e p_i - \frac{1}{S}\sum_{j=1}^{S}\log_e\ p_j\bigr)^2\right]. \tag{3.15}$$

This simplifies to,

$$<\sigma^2> = \frac{S-1}{S}\times\frac{\pi^2}{6}. \tag{3.16}$$

4 The Distribution of Diversity and Log-normal Variance

Equations (3.9) and (3.10) show that the mean value of the diversity lies very near to its maximum possible value, which is $\log_e S$. To learn more about the distribution of diversity, it was calculated using a Monte-Carlo technique.

Points were chosen at random in the biologically realistic portion of the S-dimensional space. This was done by using the analogy with the broken-stick problem. Thus for 16 species, 15 random numbers[4] between 0 and 1 were obtained and, together with 0 and 1 ranked in order of their magnitude. The differences between adjacent values gave the 16 co-ordinates required.

The diversity of each point was calculated and the results used to create a histogram. This was done for different numbers of species and the results are given in Fig. 3. For a given number of species 99% (1%) of points had a diversity greater than that given by the curve marked 99% (1%). The mean value obtained from Eqn. (3.9) is also shown.

The results indicate that the distribution of diversity is strongly peaked about its mean value. The peak becomes narrower as the number of species increases.

A similar procedure was carried out to estimate the distribution of the logarithmic standard deviation [5]. The results are shown in Fig. 4. Again the distribution is peaked about its mean value and the peak becomes narrower as the number of species is increased. We thus conclude that over most of the space both the diversity and the logarithmic standard deviation lie within very narrow limits.

This means that if the random elements acting on a biological system are important enough so that the system has a reasonable chance of being found in more than, say 5%, of the total volume of

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[4] The method used here for Figs 3 and 4 differs from earlier versions in that more samples are generated so smoothing is not needed. Also the random number generator 'ran2' of Press et al. (2001) was used instead of the Knuth (1969) generator.

[5] Defined in Eqn. (3.14).

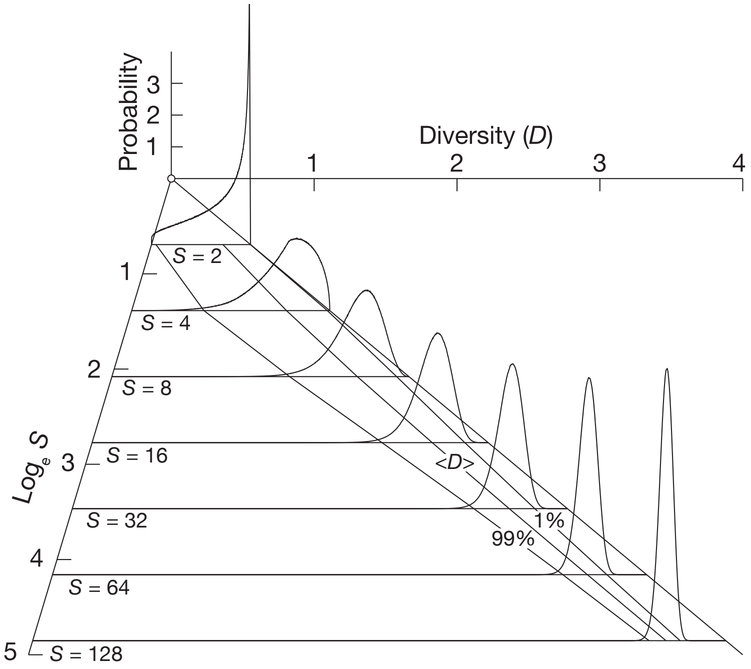

Fig. 3. The probability distribution of diversity for different numbers of species S. $< D >$ is the mean value calculated from Eqn. 3.9. Each of the distributions was calculated using a Monte-Carlo technique with 2^{24} samples, sorted into 1024 bins and plotted without smoothing. 99% (1%) of the samples had a diversity greater than that given by the curve marked 99% (1%).

proportionality space, then many of the measurements made on the system will give results which are near to the mean value of the space.

In the case of the diversity, one can see from Fig. 2 that part of the reason for this behaviour is that low diversities are found only at the very edge of the space. There is however a more fundamental reason for the behaviour which holds for any function that can be expanded in the form,

$$F = \sum_{i=1}^{S} f(p_i). \tag{4.1}$$

Let $< F >$ be the mean value of the quantity. The variance about this mean value is,

$$< (F - < F >)^2 > = < F^2 > - < F >^2 . \tag{4.2}$$

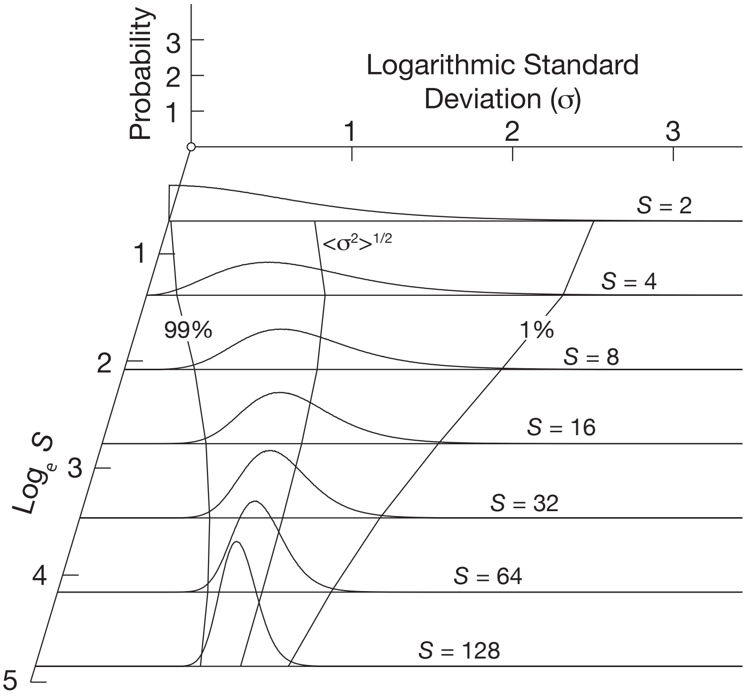

Fig. 4. The probability distribution of logarithmetic standard deviation for different number of species S using the same method as for Fig. 3. $<\sigma^2>^{1/2}$ is the mean value calculated from Eqn. 3.16. 99% (1%) of the samples had a diversity greater than that given by the curve marked 99% (1%).

Now,

$$
\begin{aligned}
<F> &= \int dp_1 ... \int dp_S \Big[\sum_{i=1}^{S} f(p_i)\Big] \; W(p_1,...,p_S), \\
&= S \int dp \; f(p)(S-1)(1-p)^{S-2}. \qquad (4.3) \\
<F^2> &= \int dp_1 ... \int dp_S \Big[\sum_{i=1}^{S} f(p_i)\Big]^2 \; W(p_1,...,p_S), \\
&= S \int \; dp \, f(p)^2 (S-1)(1-p)^{S-2} \\
&\quad + S(S-1) \int dp \int dq \, f(p) f(q)(S-1)(S-2)(1-p-q)^{S-3}. \qquad (4.4)
\end{aligned}
$$

If the function f is reasonably well behaved then the second term in this expression is S times larger than the first. Also the main contribution to the integral will come from the region where p or q have the same order of magnitude as $1/S$.

In this region,

$$(1-p-q)^{S-3} = (1-p)^{S-2}(1-q)^{S-2}(1+O(\frac{1}{S}).$$

$O(1/S)$ indicates that the correction terms will be in the form of a constant decided by S. Using these properties,

$$
\begin{aligned}
<F^2> &= S^2 \Big[\int dp\, f(p)(S-1)(1-p)^{S-2} \Big]^2 \big(1+0(\frac{1}{S})\big) \\
&= <F>^2 \big(1+O(\frac{1}{S})\big).
\end{aligned} \tag{4.5}
$$

Thus we obtain the result,

$$
<(F-<F>^2> = <F>^2\, O(\frac{1}{S}). \tag{4.6}
$$

Thus because of their mathematical properties, the functions which can be expanded in the form of Eqn. (4.4) have a variance which decreases relative to $<F>^2$ as the number of dimensions (or species) increases. If the mean value, $<F>$, increases more slowly than $S^{1/2}$, then the variance will decrease. This is true for the diversity and for the logarithmic standard deviation.

This result implies that the functions have a limited range of values over most of proportionality space. In the case of the diversity, low diversities are only found in the remote outer regions of the biological space. Large values of the logarithmic standard deviation are also only found at the outer surface of the space.

5 Comparison with Natural Systems

The importance of the mathematics discussed so far arises from the way it helps our understanding of the patterns that arise in biological data. Figure 5 compares the 1 and 99% curves from Fig. 3, with the diversity of the bird populations studied by Tramer (1969). Longuet-Higgins (1971) has noted previously how the mean value of the diversity, for a given number of species, agrees with the broken-stick distribution.

We now see that most of the points lie between the 1 and 99% lines. They are spread out over the region and have a slight tendency to lie above the mean value. In terms of proportionality space, these observations indicate that Tramer's breeding bird populations are fairly uniformly distributed over the space, with a slightly higher probability of lying near the centre of the space.

Figure 6 is made up of data from a number of other sources. Systems such as Red Sea corals and the benthos of Kingston Harbour appear to be spread out over proportionality space. The same is true of most of the copepod and other plankton samples from the Antarctic and Indian Oceans. The exceptional samples, with low equitability, correspond to systems in the extreme outer regions of the space. On inspection these samples were found to correspond to plankton blooms, dominated by a few species.

Gueredrat (1971), studying copepods in the Equatorial Pacific observed a similar pattern. His samples showed that the lowest diversity occurred in regions where the water was high in nutrients

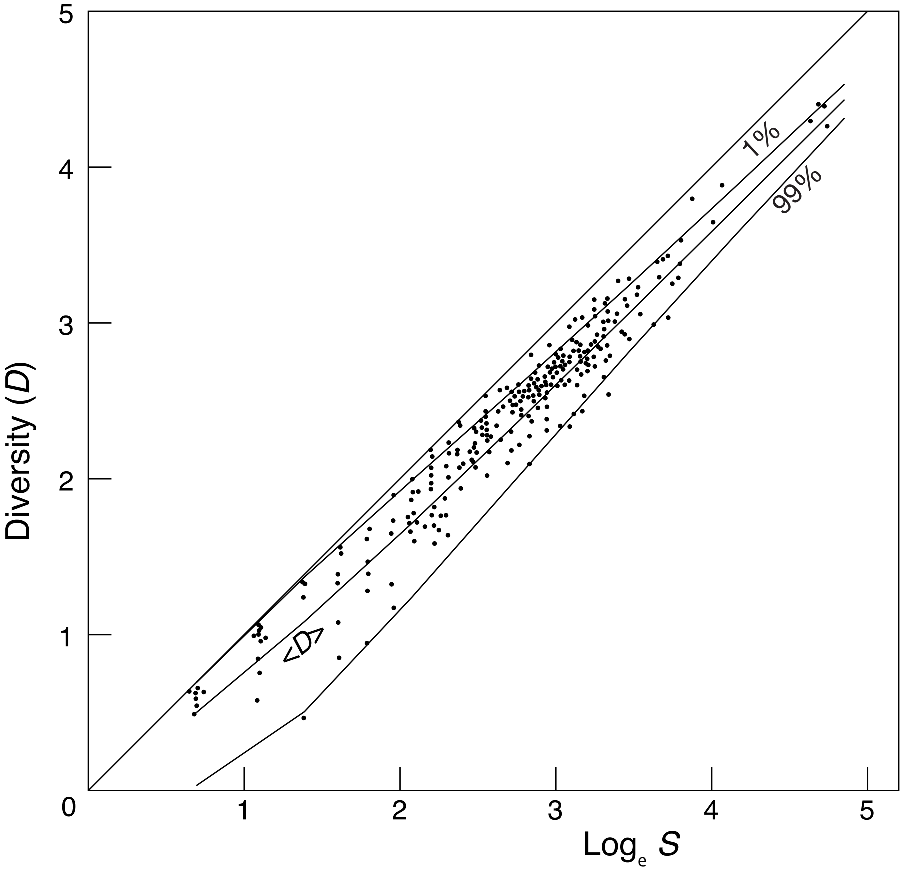

Fig. 5. A comparison of Tramer's (1969) bird species diversity with the proportionality space distribution of diversity.

and the primary productivity was large. As the systems became more mature the diversity was found to increase.

The trees studied by Whittaker (1956), consistently have a low equitability. This is probably related to the tendency of these trees to form stands of the same species, similar to, but not as extreme as the plankton blooms.

It should be borne in mind that the results may be affected by the method of sampling. An example shown here is Karr's (1971) bird samples. These were each taken over the course of a whole year. This procedure weights the samples in favour of resident species as compared with seasonal visitors and thus tends to lower the equitability. At any one period during the year, the equitability within each region would usually have been much higher.

Figure 7 compares the 1 and 99% curves from Fig. 4, with Preston's plot of logarathmic standard deviation σ (Preston, 1962a, Fig. 17). The samples studied by Preston were taken mainly from bird populations. They fall into two groups. The group with large values of σ are concentrated in the

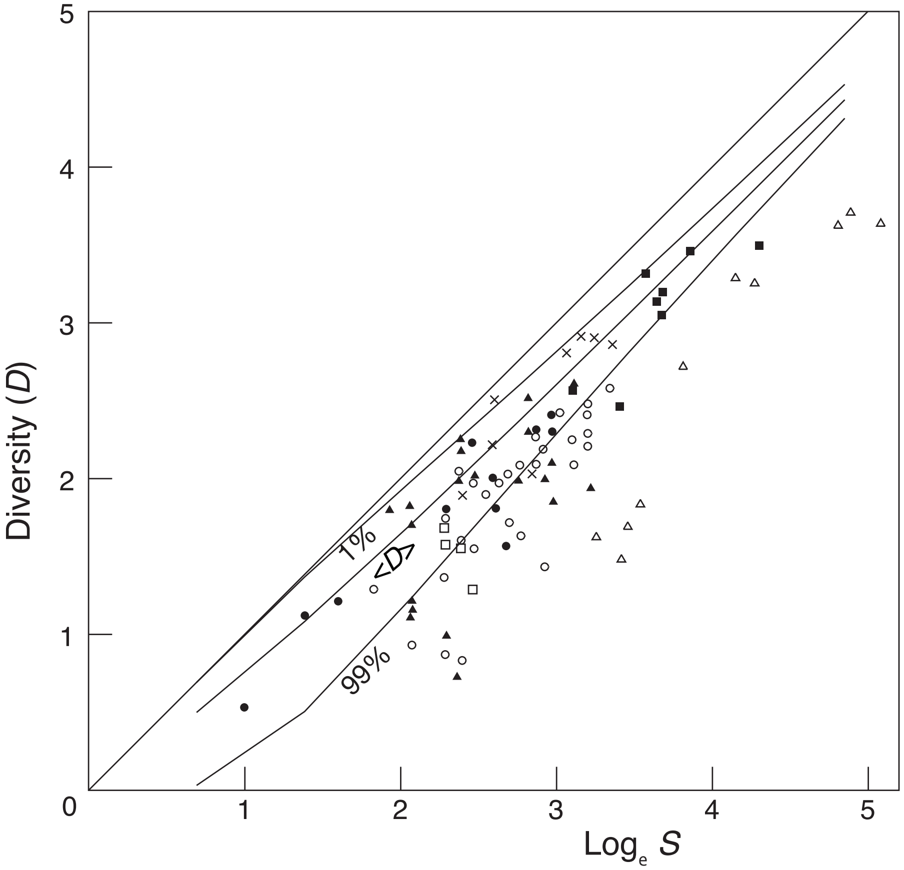

Fig. 6. A comparison of the proportionality space distribution of diversity with samples from a number of biological systems. ×, Red Sea corals (Loya, 1972); ■, Benthos communities, Jamaica (Wade, 1972); ●, Antarctic copepods (Vervoort, 1957); ▲, Indian Ocean plankton (Tranter, personal communication); □, equatorial copepods (Gueredrat, 1971); ○, Smokey mountain trees (Whittaker, 1956); △, birds in Illinois and Panama (Karr, 1971).

outer regions of proportionality space. The group with a small value of σ is not so concentrated, but the samples tend to lie near the centre of the space. Preston found that samples in the former group included birds that were gregarious, while the samples in the latter group contained birds which defended their territory.

We therefore conclude that a biological tendency for a species to be gregarious or form clumps, drives the system into the outer reaches of proportionality space. Similarly a tendency to defend territory or be infradispersed will act in the opposite direction. Plankton which except during blooms are not known to be particularly gregarious or territorially minded appear to be uniformly spread over the space. As Tramer's (1969) and Preston's (1962a) territory defending birds show only a slight concentration towards the centre of the space, it seems probable that their territorial behaviour does

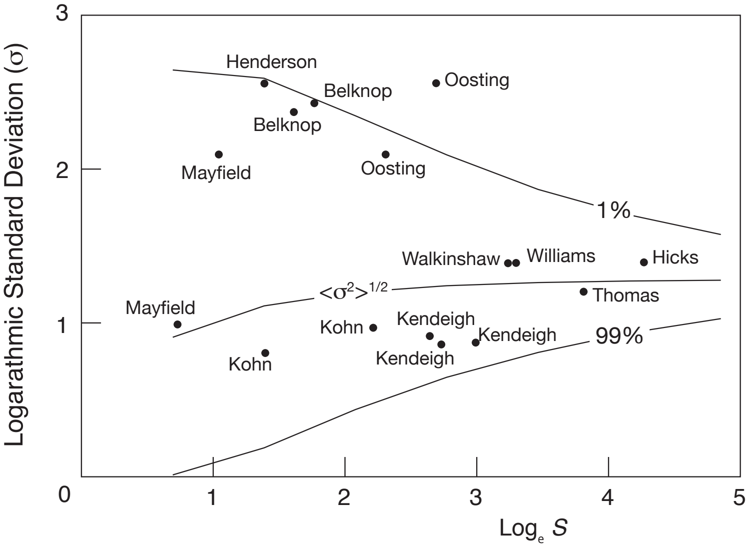

Fig. 7. A comparison of the proportionality space distribution of logarithmic standard deviation, with the samples considered by Preston (1962a, Fig. 17).

little more than neutralize their other biological tendency to form clumps, e.g. families of nestlings.

The behaviour of the plankton also imply that proportionality space may be biological neutral, in the sense that a biological system is equally likely to be represented by any point in the space, unless some biological process constrains the system.

6 The Theoretical Models

We have shown that as long as there is enough randomness in a biological system, one will obtain reasonable agreement with the results of the 'proportionality space or broken-stick model'. In a similar manner, the fact that the models of MacArthur and Cohen can also give the broken-stick series arises not because of the biological principals that they used, but because they included enough randomness.

The biological principals that they used, for example the concept of overlapping or non-overlapping niches, may or may not still be correct. To test those principals it will be necessary to study in detail those results, if any, predicted by the models which are not also predicted by the 'proportionality space model'.

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Appendix I

To check to normalization, we consider the integral,

$$
\begin{aligned}
I &= \int dp_S \int dp_{S-1} \dots \int dp_1 \, W_S(p_1, \dots, p_S), \qquad \text{(A1)}\\
&= \int_0^1 dp_S \int_0^1 dp_{S-1} \dots \int_0^1 dp_1 \, (S-1)! \; \delta\big(1-\sum_{i=1}^{S} p_i\big),\\
&= (S-1)! \int_0^1 dp_S \int_0^{a_{S-1}} dp_{S-1} \dots \int_0^{a_2} dp_2 \; C_2. \qquad \text{(A2)}
\end{aligned}
$$

Where,

$$a_j = 1 - \sum_{i=j+1}^{S} p_i,$$

and,

$$C_j = \frac{1}{(j-2)!}(a_j - p_j)^{j-2}. \qquad \text{(A3)}$$

One can show that,

$$\int_0^{a_j} dp_j \, C_j = C_{j+1}. \qquad \text{(A4)}$$

Thus,

$$
\begin{aligned}
I &= \int_0^1 dp_S \; C_S (S-1)!,\\
&= \int_0^1 dp_S \; (S-1)(1-p_S)^{S-2},\\
&= \big[-(1-p_S)^{S-1}\big]_0^1.
\end{aligned}
$$

$$\therefore I = 1. \qquad \text{(A5)}$$

Thus the weighting function is properly normalized.

To calculate the distribution function for one co-ordinate we consider the integral,

$$
\begin{aligned}
F_S(p_S) &= \int dp_{S-1} \dots \int dp_1 \, W_S(p_1, \dots, p_S),\\
&= (S-1)! \; C_S.
\end{aligned}
$$

$$\therefore F_S(p_S) = (S-1)(1-p_S)^{S-2}. \qquad \text{(A6)}$$

Similarly the joint distribution for two coordinates is,

$$
\begin{aligned}
F_S(p_S{,}p_{S-1}) &= \int dp_{S-2} \dots \int dp_1 \, W_S(p_1, \dots, p_S), \\
&= (S-1)! \; C_{S-1}. \\
\therefore F_S(p_S{,}p_{S-1}) &= (S-1)(S-2)(1-p_S-p_{S-1})^{S-3}. \qquad \text{(A7)}
\end{aligned}
$$

Appendix II

Let $s(p)$ be the probability distribution for the smallest stick. This will be S times the probability that the Sth stick is the smallest. Thus,

$$
\begin{aligned}
s(p) &= S \int_p^1 dp_{S-1} \dots \int_p^1 dp_1 \; W_S(p_1, \dots, p_S), \\
&= S(S-1)! \int_p^{b_{S-1}} dp_{S-1} \dots \int_p^2 dp_2 \; D_2, \qquad \text{(A8)}
\end{aligned}
$$

where,

$$b_j = a_j - (j-1)p,$$

and

$$D_j = \frac{1}{(j-2)!}(b_j - p_j)^{j-2}. \qquad \text{(A9)}$$

One can show that,

$$\int_p^{b_j} dp_j \, D_j = D_{j+1}. \qquad \text{(A10)}$$

Thus,

$$
\begin{aligned}
s(p) &= S(S-1)! \, D_S. \\
\therefore s(p) &= S(S-1)(1-Sp)^{S-2}. \qquad \text{(A11)}
\end{aligned}
$$

This is the result obtained by the more usual methods (Barton & David, 1956).

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