DIVERSITY AND EVENNESS: A UNIFYING NOTATION AND ITS CONSEQUENCES[1]

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Abstract. Three commonly used measures of diversity, Simpson's index, Shannon's entropy, and the total number of species, are related to Rényi's definition of a generalized entropy. A unified concept of diversity is presented, according to which there is a continuum of possible diversity measures. In a sense which becomes apparent, these measures provide estimates of the effective number of species present, and differ only in their tendency to include or to ignore the relatively rarer species. The notion of the diversity of a community as opposed to that of a sample is examined, and is related to the asymptotic form of the species-abundance curve. A new and plausible definition of evenness is derived.

When we say that the humid tropics are more diverse than the tundra, we mean that there are more species there. More precisely, we mean that the species in the humid tropics have on average lower proportional abundances than those in the tundra—a fact which is amply visible to the naked eye and which can be demonstrated by the use of any measure of diversity we care to devise. But there is little point in merely confirming the obvious; the purpose of determining diversity by a numerical index is rather to provide a means of comparison between less clear-cut cases. Unfortunately, when we look for a suitable numerical definition, we find that no particular formula has a pre-eminent advantage, and that different authors have plausibly proposed different indices. In the ensuing confusion, Hurlbert (1971) has despaired, declaring diversity to be a nonconcept. Fortunately his despair is premature, and when carefully defined according to an appropriate notation, diversity can be as unequivocal as any other ecological parameter.

Many of the indices which have been proposed apply only to counts of individuals and not to continuous measures of quantity. There is no obvious intuitive reason why this should be so, and Goodall (1970) observes that in plant communities counts of individuals are often impossible. Ideally, indeed, we should like to compute the diversity of a sample of dry weights or of productivities, as well as that of a sample of counts of individuals. Another point, often noticed and repeatedly ignored, is that whereas it is easy enough to define measures of diversity which apply to a particular sample, very often they will have no meaning when applied to the whole community. Consider, for example, the diversity as measured by the number of species in a sample. As the size of the sample is increased, so also will the "diversity," almost without limit. On this basis MacArthur and Wilson (1967) propose a law of species-area relations: that the number of species encountered is proportional to a power of the area sampled. In symbols,

$$S \propto A^z ,$$

where S is the number of species encountered, A is the area sampled, and z is an empirical constant which usually lies between 0.1 and 0.4. So if we wish to use indices of diversity to characterize some feature of a hypothetically infinite community rather than of a particular sample, then we must allow for an arbitrarily large number of species.

Different indices measure different aspects of the partition of abundance between species. Simpson's index, for example, is sensitive to the abundance only of the more plentiful species in a sample, and can therefore be regarded as a measure of "dominance concentration" (Whittaker 1965). Other statistics, such as the total number of species, are strongly affected by the presence of rarities. Whittaker considers that the partition of abundance cannot be adequately summarized by one statistic, but should be characterized both by the "dominance concentration" and by the total number of species. Other authors (e.g., Lloyd and Ghelardi 1964) have gone further, and have defined a notion of "evenness," which is in effect a comparison between the diversity as measured by the total number of species, and the diversity as measured by some other statistic.

Having developed an appropriate notation, we shall see that the statistics advocated by Whittaker are closely related to Shannon's entropy, and that all three measures are in a sense evaluations of the number of species present in the sample. They differ in their propensity to include or to exclude the relatively rarer species. Evenness is then redefined as the ratio of any two such evaluations, a definition which is shown to satisfy an important intuitive criterion.

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NOTATION

Let

$$p_1, p_2, \ldots, p_n$$

denote the proportional abundances of the n species in a sample. If we are dealing with dry weights, then p_i is the ratio of the mass of the i^{th} species to the total mass of the sample. If we are dealing with counts of individuals, then p_i is the ratio of the count of the i^{th} species to the total number of individuals in the sample. And so on.

Clearly,

$$p_1 + p_2 + \ldots + p_n = 1 \, .$$

Ignoring finite sample considerations, Simpson's index is

$$q = p_1^2 + p_2^2 + \ldots + p_n^2 \, .$$

The formula can be rewritten

$$q = \frac{(p_1p_1 + p_2p_2 + \ldots + p_np_n)}{(p_1 + p_2 + \ldots + p_n)} = \frac{(w_1p_1 + w_2p_2 + \ldots + w_np_n)}{(w_1 + w_2 + \ldots + w_n)} \, ,$$

where

$$w_i = p_i \qquad (i = 1, \ldots, n) \, .$$

It follows that q is a weighted mean of the proportional abundances. Now when only one species has any appreciable abundance

$$q \approx 1 \, ,$$

and when all n species are equally abundant

$$q = 1/n \, .$$

Other cases are intermediate. It follows that the quantity

$$N_2(p_1, p_2, \ldots, p_n) = 1/q$$

is a measure of the degree of polydominance. (This is a loose description of what is measured by N_2, but it does convey an intuitive impression.)

More generally, we can define

$$N_a = \left[\frac{(w_1p_1^{a-1} + w_2p_2^{a-1} + \ldots + w_np_n^{a-1})}{(w_1 + w_2 + \ldots + w_n)}\right]^{1/(1-a)}$$

which is the reciprocal of the $(a-1)^{\text{th}}$ root of a weighted mean of the $(a-1)^{\text{th}}$ powers of the proportional abundances of the n species. For reasons similar to those given for the special case $a = 2$, N_a can be regarded as an estimate of the effective number of species present in the sample. We shall call it the diversity number of order a. Remembering that the weights w_i are equal to the proportional abundances p_i, we can rewrite our definition as

$$N_a = (p_1^a + p_2^a + \ldots + p_n^a)^{1/(1-a)} \, .$$

N_0 can easily be seen by substitution to be n, the total number of species in the sample. N_1 is as yet undefined. However, N_a is continuous with derivatives of all orders at $a = 1$. (For a proof, see Appendix.) Defining

$$N_1 = \lim_{a \to 1} (N_a) \, ,$$

we find that

$$N_1 = \exp(-\Sigma\, p_i \ln(p_i)) = \exp(H) \, ,$$

where H is Shannon's entropy,

$$-\Sigma\, p_i \ln(p_i) \, .$$

Our notation therefore covers the three most important measures of diversity, Simpson's index $(= 1/N_2)$, the total number of species $(= N_0)$, and Shannon's entropy $(= \ln(N_1))$. It derives from Rényi (1961), who defined

$$H_a = \ln(N_a)$$

to be the generalized entropy of order a, and proved that the quantities H_a satisfy certain axioms which entitled them to be regarded as measures of "information." The information-theoretic analogy is not illuminating in the present context; diversities are better characterized as reciprocals of mean proportional abundances. In particular, $1/N_2$ is an arithmetic mean of the proportional abundances, $1/N_1$ is a geometric mean of the proportional abundances, and $1/N_0$ is a harmonic mean of the proportional

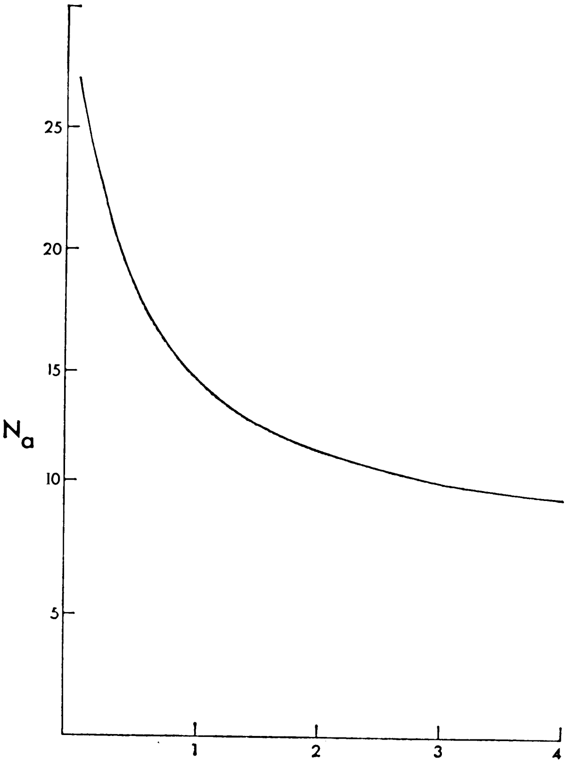

FIG. 1. The relation between the diversity number N_a and its order a for a particular 30 cm × 30 cm dry-weight sample in a pasture.

abundances. (The means in question are, as we have seen, weighted by the proportional abundances themselves.) It is well known that the geometric mean always assumes a value intermediate between the arithmetic mean and the harmonic mean, so that N_1 ($= \exp(H)$) is always sandwiched between N_0 the total number of species and N_2 the reciprocal of Simpson's index. Whittaker's (1965) assertion, therefore, that Simpson's index and the total number of species are between them suitable for characterizing the partition of abundance in a sample, is well borne out. Shannon's entropy, being essentially intermediate, conveys little extra information.

A graph of N_a versus a for a particular case is given in Figure 1, and two points should be noticed: that N_a is a strictly decreasing function of a, and that N_1 in no way stands out from the trend. Although exceptional in being related to Shannon's entropy, as a diversity number it is merely one of the N_a.

We may summarize our results as follows.

$N_{-\infty}$ = reciprocal of the proportional abundance of the rarest species
N_0 = total number of species present
N_1 = $\exp(H)$
N_2 = reciprocal of Simpson's index; i.e. $1/(p_1^2 + p_2^2 + \ldots + p_n^2)$
N_∞ = reciprocal of the proportional abundance of the commonest species.

An important consequence is that for the purposes of community description we should express measures of diversity on a uniform scale. That is to say, we should use the reciprocal of Simpson's index N_2 or conceivably the generalized entropy

$$H_2 = \ln(N_2) ,$$

but not

$$1 - \text{Simpson's index} ,$$

which is the measure favored by Whittaker (1965) and Pielou (1969).

There is good reason for favoring diversity numbers over entropies. A diversity number is figuratively a measure of how many species are present if we examine the sample down to a certain depth among its rarities. If we examine superficially (e.g., by using N_2) we shall see only the more abundant species. If we look deeply (e.g., by using N_0) we shall see all the species present. The diversity numbers N_a have therefore a natural intuitive interpretation, albeit rather a vague one. The corresponding generalized entropies H_a, being logarithmic, are harder to visualize.

Information-theoretic notation is now well established in descriptive ecology and systematics. Sibson (1969) has used Rényi's generalized information theory to construct satisfying measures of taxonomic distance. He defined a notion of "information radius," of which the "bird species difference" of MacArthur, Recher and Cody (1966) is the special case of order 1. MacArthur and Wilson (1967, p. 110) assert that in future studies the diversity number N_2 and another index, analogous to a correlation coefficient, may be used to measure diversity and overlap respectively. Following Sibson, their index of overlap should be replaced by the information radius of order 2. But although Sibson's measures are trustworthy, the investigator is advised to be cautious. *Indices non sunt multiplicandi praeter necessitatem;* and the use of diversity numbers of "peculiar" orders such as $N_{1.5}$ or $N_{1.414}$ is strongly to be discouraged. There is almost unlimited scope for mathematical generality in relation to measures of diversity and taxonomic difference. Simple and well-understood indices should be used.

EVENNESS

The concept of evenness can now be thrown into a clearer light. For any particular set of proportional abundances $p_1, p_2, \ldots, p_n$ we have a continuum of possible diversity numbers N_a, corresponding to the possible values of the index a. As a varies from $-\infty$ to ∞, so the diversity number comes to depend more and more on the common species and less and less on the rare. In the "totally even" case,

$$p_1 = p_2 = \ldots = p_n = 1/n ,$$

the diversity numbers of all orders are equal to n; and in general the more even the proportions p_i, the less variable will be N_a over the range of a.

It is open to us to define a double continuum of measures of evenness

$$E_{a,b} = N_a/N_b \;\; . \;\; . \;\; . \;\; . \;\; . \;\; . \;\; . \;\; . \qquad (1)$$

corresponding to all possibles pairs of values a,b. The usual definition is (Pielou 1969, p. 223)

$$J = H/H_{\max} = \ln(N_1)/\ln(N_0) ,$$

which is not a measure of evenness according to the equation (1). At least some of the $E_{a,b}$ have, however, been considered in the literature. For example, Sheldon (1969) remarks briefly that $E_{1,0}$ would be quite suitable for the purpose.

The use of the statistics $E_{a,b}$ is a departure from standard practice and must be justified. Consider a species-abundance relation having the property that each species is matched by a "double" of the same abundance. (One might, for example, take the two sexes of dioecious organisms.) Intuitively, this has the same evenness as the corresponding species-abundance relation in which each species and its "double" are combined to form one super-species. The measures $E_{a,b}$ satisfy this criterion, but J does not. Thus, let our species-abundance relations be

$$S : p_1, p_1, p_2, p_2, \ldots, p_n, p_n$$

and

$$S' : 2p_1, 2p_2, \ldots, 2p_n .$$

Then

$$N_a(S) = (2\Sigma\, p_i^{a})^{1/(1-a)}$$

and

$$N_a(S') = (\Sigma(2p_i)^{a})^{1/(1-a)} ;$$

from which it follows that

$$N_a(S) = 2\, N_a(S') .$$

In other words, S is exactly twice as diverse as S', so that the evennesses $E_{a,b}(S)$ and $E_{a,b}(S')$ are equal for all values of a, b.

Thus we justify the statistics $E_{a,b}$ in preference to the established measure J. But whereas J fails by this criterion, the alternative

$$J' = H - H_{\max} = H_1 - H_0 = \ln(N_1/N_0) = \ln(E_{1,0})$$

is entirely unexceptionable.

SPECIES-ABUNDANCE RELATIONS

If we consider a community with a hypothetical infinity of species, then N_0, being infinite, is not properly defined. The slope z of the curve of log (number of species in a sample) versus log(sample size) is a lower bound on the values of a for which the diversity number N_a is finite. (A proof is given in the Appendix.)

We must consequently avoid thinking of evenness statistics such as $E_{1,0}$ as measuring a property of the community: being dependent on N_0 they are too dependent on sample size (Sheldon 1969; Hurlbert 1971). Provided, however, that the conditions of the proof apply—in particular that we can obtain a random sample of the community—the alternative statistic $E_{2,1}$ should stabilize to a true community value as the size of the sample is increased. But with nonrandom sampling (e.g. starting with a small area and working outwards) diversities of all orders will normally show a dependence on sample size.

In practice, diversities, like the frequencies obtained from quadrat sampling, must be regarded as having an essential dependence on sample size. There is therefore no reason to regard the natural statistic N_0 as any less reputable than N_1 or N_2. N_2, however, will usually be more stable than N_0, and may assume a fairly constant value over a wide range of sample sizes.

EXAMPLE

As an example of the sort of relation which can exist between these various measures of diversity, we can consider diversity numbers calculated for dry-weight data in a pasture in North Wales. The pasture was a species-rich community consisting largely of grasses and small sedges, with nowhere any clearly defined dominant. The dry-weight standing crop in August was about 2.6 tons ha^{-1}. A transect was taken, and diversity-numbers of order 0, 0.5, 1, 1.5, 2.0 and ∞ were computed from the dry weights in 30 cm × 30 cm quadrats taken at 1 m intervals along it.

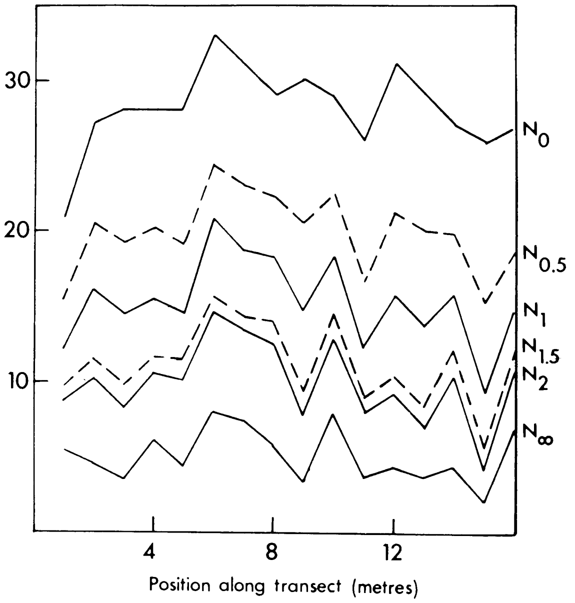

FIG. 2. Diversity numbers of different orders calculated at intervals along a transect.

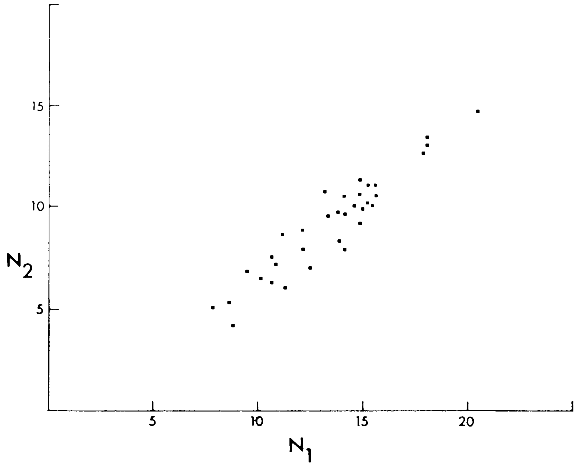

FIG. 3. Scatter diagram of N_1 versus N_2, computed for 30 cm × 30 cm dry-weight samples in a pasture in North Wales.

The results are presented in Figure 2, and show a rather striking feature. This is that although the diversities of different orders show overall differences, their peaking is arithmetically much of the same size. In other words, N_1 is to a good approximation equal to N_2 plus a constant, rather than to N_2 times a constant. There is therefore the possibility that the difference $N_1 - N_2$ may be more characteristic of the community than is the evenness N_2/N_1 Only a wide-ranging empirical investigation could determine whether this is so. Fairly obviously, however, evennesses should be regarded as secondary, and in routine analyses the original diversity numbers N_2 and N_1, or N_2 and N_0 are to be preferred. These can conveniently be presented in a scatter diagram such as Figure 3.

Discussion and Conclusions

We may summarize our argument by saying that the notion of diversity is little more than the notion of the effective number of species present. Defining a diversity-number to be the reciprocal of a mean proportional abundance, we have followed Rényi (1961) in employing a notation which grades these numbers according to their propensity to include or to exclude the rarer species in the enumeration. Different means—harmonic, geometric and arithmetic—correspond to different well established measures of diversity. Entropies, which are logarithms of diversity numbers, are equivalent, but are less easy to visualize and consequently less suitable for general use.

In view of Goodall's (1970) assertion that future developments in the theory of species diversity will be based on the niche concept, it is embarrassing to observe that we have so far left niches unmentioned. But our argument, which is a presentation of an appropriate notation, should be regarded not so much as a contribution to the theory of species diversity as an essay in nomenclature. It enables us to speak naturally, without being perplexed by apparent lapses into thermodynamics and entropy; it enables us to steer clear of the conceptual muddle occasioned by the use of inappropriate measures of evenness; and it enables us to apply measures of diversity with as much confidence to dry weights as to counts.

But any choice of terminology involves certain, often unstated, theoretical commitments; and it would be disingenuous to claim that the notation is neutral as between different authors' views. Thus Margalef (1968, p. 19) states that "the ecologist sees in any measure of diversity an expression of the possibilities of constructing feedback systems or any sort of links, in a given assemblage of species." Margalef is not always an easy writer to understand; but in this case he clearly means that diversity is essentially a structural concept, and that it cannot be separated from theories of community organization.

Now diversity is of theoretical interest because it can be related to stability, maturity, productivity, evolutionary time, predation pressure, and spatial heterogeneity. It is not necessarily related to feedback. Rather, it should be regarded as a measurable parameter whose observed values may be explained by a variety of theories. Even the connection between cybernetic theories and Shannon's entropy is to some extent historical—ecology is not thermodynamics. Rényi's generalized entropies reduce Shannon's to a special case; and they lead to the conclusion that as a measure of diversity it is in no way exceptional. Diversities are mere numbers and should be distinguished from the theories which they support.

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Appendix

We prove two propositions which are stated without proof in the text.

PROPOSITION 1

Let $p_1, p_2, \ldots, p_n$ be positive numbers such that

$$\Sigma p_i = 1 \; ;$$

and let

$$N_a = (\Sigma p_i^a)^{1/(1-a)} \, .$$

Then N_a is continuous with derivatives of all orders at $a = 1$, and

$$N_1 = \lim_{a\to 1} N_a = \exp(-\Sigma p_i \ln p_i) \, .$$

PROOF

We require three standard results of mathematical analysis.

(a) For small values of x, $\exp(x) \approx 1 + x$.

(b) For small values of x, $ln(1 + x) \approx x$.

(c) Let $A(x)$ and $B(x)$ be functions of x which can be expanded as power series in a neighborhood of

$x = 0$, and let $A(x)$ and $B(x)$ assume the value zero at $x = 0$. Then if the ratio $A(x)/B(x)$ is continuous at $x = 0$, it also has derivatives of all orders, and can itself be expanded as a power series.

We aim to show that

$$\lim_{a\to 1} (\Sigma p_i^a)^{1/(1-a)} = \exp(-\Sigma p_i \ln p_i) .$$

Setting $a = 1 + b$, and taking logarithms of both sides, it will suffice to show that

$$\lim_{b\to 0} \frac{1}{b} \ln(\Sigma p_i^{1+b}) = \Sigma p_i \ln p_i \quad . \quad . \quad . \quad (1)$$

The left side of (1) can be rewritten

$$\lim_{b\to 0} \frac{1}{b} \ln(\Sigma p_i \cdot p_i^b)$$
$$= \lim_{b\to 0} \frac{1}{b} \ln(\Sigma p_i \exp(b \ln p_i))$$
$$= \lim_{b\to 0} \frac{1}{b} \ln(\Sigma p_i + b\, \Sigma p \ln p_i) ,$$

by (a). Observing that

$$\Sigma p_i = 1 ,$$

and using the standard result (b), the left side of equation (1) can be seen to be equal to its right side.

The continuity of the derivatives follows immediately from (c) plus the fact that if $A(x)$ is well behaved, so also is $\exp(-A(x))$.

Q.E.D.

PROPOSITION 2

Given random sampling from an infinite community, let z be the asymptotic slope of the curve of log(number of species in a sample) versus log(sample size), and let N_a be the diversity number of order a. Then z is a lower bound on the values of a for which N_a is finite.

PROOF

Define a species-abundance density $f(x)$, such that there are $f(x)\,dx$ species in the proportional abundance range x *to* $x + dx$. (We omit all consideration of the regularity conditions to which f should be subject; attempts to make the argument rigorous would presumably be successful but not very rewarding.) The overall proportional abundance of all species is unity, so that

$$\int_0^1 x f(x)\,dx = 1 \quad . \quad . \quad . \quad . \quad . \quad . \quad (2)$$

We can extend our definition of diversity numbers from finite samples to hypothetically infinite communities by defining

$$N_a = [\int_0^1 x^a f(x)\,dx]^{1/(1-a)} \quad . \quad . \quad . \quad . \quad (3)$$

with suitable modifications for the case $a = 1$. We restrict ourselves, for the sake of argument, to the simplest case, in which abundances are measured by numbers of individuals, and in which samples are taken at random from the infinite community. In a sample of M individuals the chance of getting an individual of a species whose true proportional abundance is x is

$$1 - e^{-Mx} ,$$

so that in a large sample the total number of species is

$$S(M) = \int_0^1 (1 - e^{-Mx}) f(x)\,dx .$$

Following the notation of MacArthur and Wilson (1967, p. 8), let z be such that

$$S(M) \sim M^z \qquad \text{as } M \to \infty .$$

We shall prove as a Lemma that this condition is equivalent to the condition that

$$f(x) \sim x^{-z-1} \qquad \textit{as } x \to 0 \quad . \quad . \quad . \quad (4)$$

Combining (3) and (4) we deduce that whole-community diversity numbers N_a, being of the order of

$$\int_0^1 x^{a-z-1}\,dx$$

are defined only for values of a which are greater than z. We now prove the required lemma.

LEMMA

Under suitable regularity conditions,

$$(1 - e^{-Mx}) f(x)\,dx \sim M^z \qquad \text{as } M \to \infty$$

if and only if

$$f(x) \sim x^{-z-1} \qquad \text{as } x \to 0 .$$

PROOF

Let

$$S(M) = \int_0^1 (1 - e^{-Mx}) f(x)\,dx .$$

We note that

$$\int_0^1 = \int_0^{1/M} + \int_{1/M}^1$$

and that

$$x < 1/M \rightrightarrows (1 - 1/e)Mx < 1 - e^{-Mx} < Mx . \quad (5)$$
$$x > 1/M \rightrightarrows (1 - 1/e) < 1 - e^{-Mx} < 1 \quad . \quad . \quad (6)$$

Now let

$$I(M) = \int_0^{1/M} Mxf(x)\,dx + \int_{1/M}^1 f(x)\,dx .$$

By our inequalities (5) and (6),

$$(1 - 1/e)\, I(M) \leqq S(M) \leqq I(M) .$$

It follows that the asymptotic properties of $I(M)$ are the same as those of $S(M)$. Moreover

$$\frac{d^2}{dM^2} (I(M)) = -f(1/M) / M^3 \quad . \quad . \quad . \quad (7)$$

By (7), if

$$I(M) \sim S(M) \sim M^z \qquad \text{as } M \to \infty ,$$

then

$$M^{-3} f(1/M) \sim M^{z-2} ,$$

so that

$$f(x) \sim x^{-z-1} \qquad \text{as } x \to 0 .$$

The reverse implication follows immediately from the definition of $I(M)$.

Q.E.D.

As becomes apparent in the proof of the lemma, the inference hinges essentially on the assumption that the species in any particular size of sample can be divided into two categories: the rare and the common. The common species are sure to be found, whereas the rare have a chance of being found which is proportional to their true abundance multiplied by the size of the sample.