A Dynamical Model of Communities and a New Species-Abundance Distribution

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Abstract. It is known to many field biologists that bio-surveys of natural communities tend to produce a J-shaped curve when the numbers of species are plotted against abundances. In other words, when the number of species of abundance k is plotted against k (running from 1 to some large number), the resulting distribution peaks at the lowest abundance, then forms a concave ramp as it approaches zero at the far end of the abundance axis. Does this distribution represent a single formula operating behind the scenes, or does it represent several formulas, appropriate for different types of community? Or does it represent no particular formula at all?

The research reported here has three components: (1) The analysis of a new dynamical system that simulates multi-species communities (producing J-curves in the process) and the derivation of the "logistic-J" distribution, as the underlying community equilibrium curve; (2) the summary of a general theory of sampling as a bridge between natural communities and samples of them; (3) the evaluation of extant proposals for species-abundance distributions by application of a general theory of sampling or by cross-comparison *via* 100 biosurveys randomly selected from the literature.

Introduction

A glance at the species/abundance distribution for almost any community of organisms surveyed in the literature reveals a distinct tendency for the community-as-sampled to have more species at lower abundances than at higher ones. In fact the number of species per abundance tends to be highest at the lowest abundance and thereafter to taper somewhat in the manner of the empirical distribution shown

in Figure 1. In biological folklore (if not in the literature), this curve is known as the "J-curve," owing to its resemblance to a backwards letter J.

To speak of "*the* J-curve," however, begs a very large question. Is there a single theoretical distribution that underlies virtually all natural communities? Although it seems almost too much to ask, this may well be the case.

Prior distributions

In spite of the fact that the J-curve is a commonplace observation (Williams, 1964), one of the most popular theoretical distributions, namely the lognormal distribution (Preston, 1948), shows little resemblance to it. As shown in Figure 2 (upper), the lognormal distribution is essentially a normal distribution that has been compressed at the low end and drawn out at the high end, both operations effected by a single logarithmic transformation.

Conspicuously absent from the lognormal distribution is the sharp peak at the low abundance end. To save it from such a discrepancy, its proposer has postulated a "veil line" (See Fig. 2), a vertical line of truncation that has the desired effect, more or less. Preston argued that samples of a natural community do not follow the same distribution as the community itself: all the species below a certain abundance (the veil line) simply fail to show up in samples.

This claim is fundamentally wrong (Dewdney, 1998). Indeed, species that fail to show up in a sample are veiled by a very different line, as shown in Figure 2 (lower). In this figure we use an unrealistic species/abundance distribution to illustrate the difference between the "veil line" and the "veil curve." Far from being a vertical, straight line, the true veil curve is a sloping, sigmoidal one. The species above or to the left of the veil curve will tend to be absent from the sample. As proved in the recently developed general mathematical theory of sampling (Dewdney, 1998), the removal
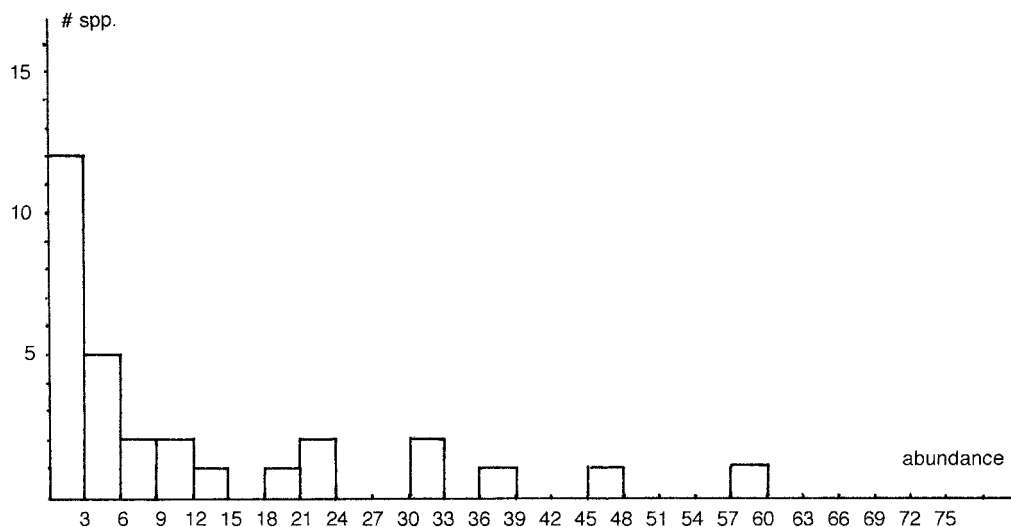
Figure 1. A typical species-abundance distribution (McCabe and Weber, 1994).

of these species cannot change the shape or formula of the distribution, only its parameter values. It follows that when we apply the veil curve to the lognormal distribution, we must get a new, complete lognormal distribution, not a truncated one.

The metastudy reported in this paper compares two theoretical proposals for the distribution of species abundance in natural settings. But it does not even consider the lognormal distribution: if the lognormal were present in nature, the first abundance categories would have to be smaller than succeeding ones. Not one case of this has turned up in the 50 randomly selected biosurveys used in the metastudy. This observation, coupled with the new sampling theory, means that the lognormal distribution, as a descriptor of abundances in natural settings, is effectively dead.

A closely related distribution, the negative binomial (Pielou, 1975), also uses the veil line concept and suffers from the same unrealistic shape when unveiled, so to speak. This distribution is therefore also not considered in the metastudy and for the same reasons. It is no longer usable as
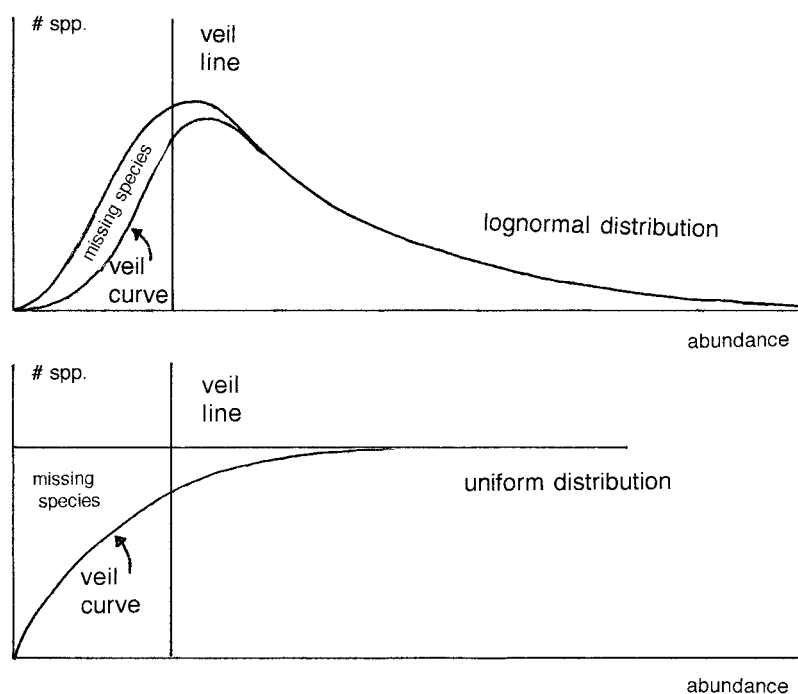

Figure 2. Veil line and veil curve for the lognormal distribution.

a descriptor of natural abundances. One may suspect that a general theory of sampling was not developed until now because of the confusion created by the mistaken concept of the veil line.

The other leading contender for species/abundance distribution of choice has been the log-series distribution developed by C. B. Williams and R. A. Fisher (Fisher *et al.,* 1943). As shown in Figure 3 below, it has the right general shape, being most sharply peaked at the low abundance end and tapering in concave fashion to zero.

Williams originally believed that the curve ought to be hyperbolic (Williams, 1964). Such a curve has the general form of $1/k$, where k represents abundance. But Fisher pointed out that the area under the hyperbolic function was infinite, hardly desirable in a statistical distribution! He suggested altering the hyperbolic function by inserting a convergent series that forced the area under the curve to converge to a finite value. (There is no biological reason for this alteration.) The probability density function (pdf) is therefore

$$x^k/k,$$

where k is an abundance and x^k is the convergent series, x being a parameter that is strictly less than 1 (but usually close to it). When used in the field, the distribution contains an additional factor α that reflects the number of individual organisms in the sample. But α is not a parameter, and the log-series is known as a one-parameter distribution. It has

been noted (May, 1975) that the log-series distribution has points of superiority over the lognormal.

Theory: a new individual-based dynamical model

Independently of concerns about the state of theoretical abundance distributions, the author had constructed an individual-based (Judson, 1994) dynamical system (Dewdney, 1997) that was originally intended as an exploratory tool for probing the abundance distributions of heavily predaceous communities such as stream benthic protists (Dewdney, 1996). In this model, an arbitrary number of species, each with an arbitrary population size, preyed on one another in the following manner: Within each iteration, two individuals (not species) are chosen at random. One individual ingests the other, reproducing in consequence. It is called the multispecies logistic system, or MSL system, for short. The adjective "logistic" was chosen because the total biomass (number of individuals) remained fixed as a simple consequence of the basic trophic act. Thus very abundant species were less likely to ingest other species as they approached the logistic limit.

The MSL system was embedded in a computer program, written in Turbo Pascal and running on a 486 computer. One hundred iterated pair selections (births and deaths) make up one "cycle" (a programming convenience). After each cycle, the program displays a histogram of species *versus* abundances. It permits the user to select any number of
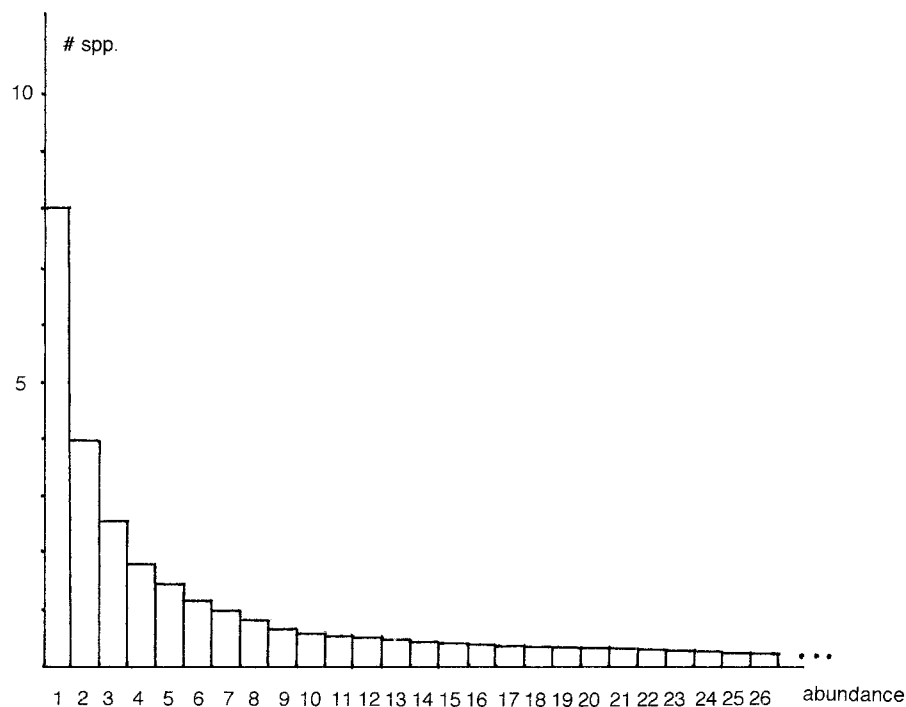

Figure 3.   The log-series distribution.

species, as well as initial abundances for each. The program comes equipped with an "extinction switch," essential to the program's usefulness. With the extinction switch "on," any species having abundance 1 will, when eaten, disappear from the simulation. With the extinction switch "off," species with abundance 1 will not be eaten, although they can (and do) end up preying on other species, with a possibility of subsequent further increase.

With 200 species, each with initial abundance of 20, a 486 computer takes about 10 minutes to drive the MSL system to equilibrium (extinction switch off). Initially, the species appear as a sharp spike at 20, then spread out into a binomial distribution with 20 as mean. However, the species continue to drift in abundance until the shape of the distribution changes radically. A peak forms at the low end, and a long tail appears on the right.

Surprisingly, the process stops when the distribution curve reaches what can only be described as a "J-shape," retaining roughly that shape for as long as the computer is run. The higher the initial average abundance, the shorter

the initial spike. At very high abundances, there are only occasional, small spikes at the lowest abundance.

The appearance of a J-curve invariably surprises those who would predict that a binomial (or normal) distribution must result or that, contrariwise, all but a few of the species will migrate to the low end. In the next section we show how a large metastudy of extant biosurveys has already begun to indicate that distributions produced by the MSL system cannot be distinguished statistically from typical biosurvey species abundance distributions.

The MSL program is capable of calculating the average of the distributions it produces at each cycle. Figure 4 shows such an averaged distribution. The height of each bar in the histogram represents the average number of species that occupied the corresponding abundance category from the onset of equilibrium. Because the behavior of the MSL at the high abundance end has special interest, the frequencies have been inverted in Figure 4, appearing above the bars as a separate plot of isolated points. These will be examined presently.
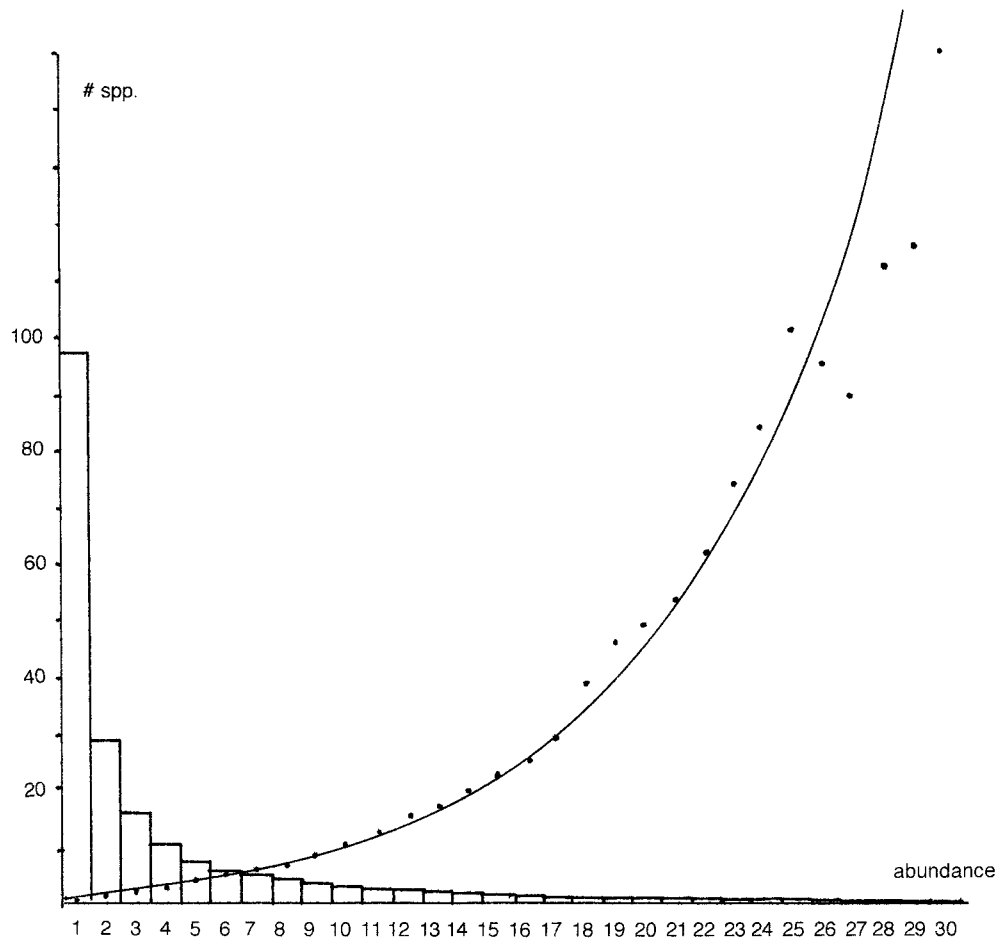

Figure 4. An average distribution produced by the multispecies logistic system, and a plot of inverted average frequencies.

Most natural communities of interest do not have the low average abundance used in the computer run for Figure 4. Instead of in the tens, average abundances may easily run into the thousands or even millions. In other words, the overall shape of the distribution shown in Figure 4 would be more typical of a sample than of a community. As mentioned earlier, when the MSL system is run with such high abundances, there is little or no peak at the low abundance end. The distribution resembles instead the idealized pattern shown in Figure 6, as explained later. Nevertheless, when the extinction switch is turned on during such an equilibrium state, species occasionally visit the low end, either to escape again or to become extinct. The time between successive extinctions grows at a modestly exponential rate.

Far from being unrealistic, this is precisely what we expect in natural communities. For example, the island biogeography theory of R. H. MacArthur and E. O. Wilson (1967) recognizes that isolated communities naturally lose a certain percentage of species every year. They estimate that when the island of Krakatoa achieved equilibrium between immigrants and extinction losses in its bird community at roughly 27 species, the turnover rate was about 1.13% of species annually.

Anticipating the discussion at the end of this article, we may imagine for the moment that the MSL describes birds as well as microorganisms. A community of 27 species of "birds" with an average of 200 individuals per species typically loses about 9 species during 1000 cycles of operation. Each cycle involves 100 reproductive events. If half the total bird population (*i.e.,* females), namely 2700 individuals, reproduce in one year, then 27 cycles corresponds to the passage of one year. Thus 1000 cycles corresponds to 37 years and a loss of 33.3% of its species over the period. This corresponds to a rate of at least 0.9% of the species every year. This figure is certainly close enough to the MacArthur and Wilson (1967) figure to make the only claim that is necessary in this context: the rate of species loss in the MSL system appears to be of the right order of magnitude. To explore equilibrium conditions, the MSL system can be run with the extinction switch "off."

Variations of the underlying MSL dynamical system make little difference to the outcome. These have included (1) changing the food web so that predation follows a cyclic order, (2) redefining the food web to include four compartments: plants, herbivores, carnivores, and saprobes, (3) running separate communities in which randomly selected individuals may migrate from one "patch" to another. In all cases the same J-curve apparently re-emerges. This robust character of the J-curve seems to indicate a phenomenon more fundamental than predation or other trophic behavior at work. In fact, the essential feature of the MSL is that each species vibrates stochastically, in effect. In other words, each species in the system performs a constrained random walk in the sense that (a) at each abundance each species

has an equal probability of decrease as increase, and (b) the total abundance of all species remains constant. Typically, species may be said to be in a *stochastic orbit* about the mean abundance, with a majority having less than the mean abundance at any time.

Assuming only this fundamental property and assuming for the moment an infinite number of species, it is easy to prove that, at equilibrium,

$$k \cdot f(k) = (k + 1) \cdot f(k + 1).$$

In other words, at equilibrium the probability of a species of abundance k increasing equals the probability of a species of abundance $k + 1$ decreasing. This equation has essentially only one solution, namely $f(k) = 1/k$.

The foregoing analysis paves the way for the finite case. Since the number N of individuals in the MSL system remains constant during a run, no species can ever have abundance greater than $N - R + 1$. At equilibrium, in the ideal sense of this analysis, there must be a number Δ at (and beyond) which $f(k) = 0$. The number Δ may well be less than the absolute limit just cited. We assume (but cannot prove directly) that the function f is driven to zero in the following manner,

$$p(k) \cdot k \cdot f(k) = p(k + 1) \cdot (k + 1) \cdot f(k + 1)$$

Here we have postulated what dynamicists call a "forcing function," which acts to drive the values of f to zero at the limiting k-value of Δ. This equation can also be solved readily.

$$f(k) = 1/(k \cdot p(k))$$

If $f(\Delta) = 0$ then there is an obvious singularity at $k = \Delta$. The simplest function capable of such behavior is

$$p(k) = (\Delta - k)^{-1}$$

and the function f can therefore be rewritten,

$$f(k) = (\Delta - k)/k$$

or, equivalently,

$$f(k) = (1 - \delta k)/k,$$

where $\delta = 1/\Delta$. Anticipating the addition of a normalizing constant presently, we can multiply f by any constant we like in the process of developing a convenient mathematical expression for the density function.

The logistic-J distribution

The *logistic-J distribution* (discrete version) has the following pdf:

$$f(k) = c(1/k - \delta); \quad k = 1 \ to \ \Delta,$$

where the abundance k runs from 1 to a maximum Δ called

the *outer limit* and δ is the inverse of Δ. The latter parameter is not a hard limit, but an average maximum, as will be made clear later. This particular pdf has one parameter, Δ, the constant c being simply a function of Δ. When the MSL system reaches equilibrium, one finds a species with abundance greater than Δ about half the time.

In a more general setting, where the distribution is to apply equally to real communities and samples of them, it is useful to have the logistic-J distribution in continuous form:

$$f(x) = c(1/x - \delta), \ \varepsilon \le x \le \Delta,$$

$$= o, \text{ elsewhere}$$

In this form an additional parameter, ε, appears. Called the *inner limit,* it represents the average lower limit of abundances in a community or as reflected in a sample of that community. For example, abundances in a sample may be given as density data wherein the lowest abundance might be 0.25. Or sample abundances may start at 5, say. Superficially, the use of epsilon resembles a veil line, but it has nothing to do with sampling. Instead, it represents the average minimum abundance in the community of organisms *per se.*

The constant c is simply shorthand for the standard normalizing constant for pdfs. In this case,

$$c = (\ln(\Delta/\varepsilon) - 1)^{-1}$$

The pdf *f* is defined to be zero outside of the interval (ε, Δ). As a mathematical convenience, we adopt the notation

$L(\varepsilon, \delta)$ for the logistic-J distribution with parameters ε and δ.

In the case of the frequencies generated by the MSL system, as shown in Figure 3, the appropriate logistic-J distribution *f* has been calculated. To demonstrate that the distribution of frequencies produced by the MSL system does indeed appear to follow the logistic-J distribution, we have inverted the theoretical values, plotting them as a smooth curve, for comparison with the (inverted) model-generated values. It will be seen that the agreement is as close as can be expected, bearing in mind that the smallest statistical fluctuations at the high abundance end will, when inverted, produce relatively large fluctuations in the (point) plot shown in the figure. The overall trend is clear. The inverted theoretical curve approximates the inverted MSL points about as well as can be expected. The distribution produced by the MSL appears to be logistic-J.

The parameters ε and δ define a logistic-J distribution completely. A useful visualization of the significance of these parameters is presented in Figure 5, which shows a standard hyperbola ($f(x) = 1/x$) in relation to axes rendered in thick lines. Two other axis systems, rendered in lighter lines, are superimposed on the figure. In the first axis system the hyperbola has the formula $1/x$, and in the other axis systems it has logistic-J formulas, to be explained presently. The logistic-J distribution corresponds to a section of the standard hyperbola, the origin of the section being determined by the parameters ε and δ.

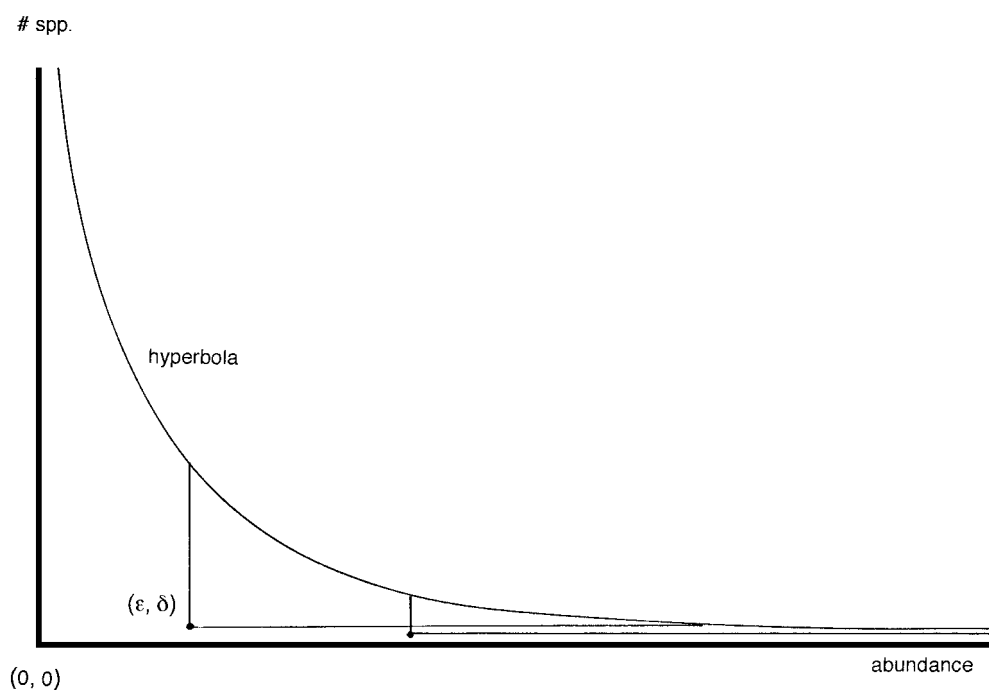According to the sampling theory derived by the author

Figure 5. Logistic-J probability density functions based on the standard hyperbola.

(Dewdney, 1998), it is possible to draw a direct relationship between a sample distribution and the distribution prevailing in the community from which the sample was drawn. The theory applies to all candidate distributions, including the logistic-J, where it has a particularly simple form. Suppose a field biologist samples a community of organisms with intensity r, that is, observes/collects $100r\%$ of the individuals in each species (to within the usual statistical fluctuations). If the distributions are logistic-J and the biologist finds the sample abundances following $L(\varepsilon, \delta)$, then the community abundances follow the distribution $L(\varepsilon/r, r\delta)$. Thus if $r = 0.05$ and the biologist finds $L(0.3, 0.004)$, then he or she may reasonably estimate the community sample as following the distribution $L(6.0, 0.0002)$ (in which the outer limit is therefore 5000).

The sample distribution may be thought of as the left-hand hyperbolic section in Figure 5, while the community distribution may be thought of as the one on the right. In this context, however, continuous figures are a little misleading. Since the community distribution is actually discrete and the abundances are normally much larger than those in a corresponding sample, we may represent the distribution of abundances in a community somewhat in the manner of the idealized diagram in Figure 6, in which individual species appear as small squares separated by spaces that increase in a modestly exponential manner from left to right. The very modest peak in the right-hand logistic-J distribution of Figure 5 would correspond to the relatively small space between the first two species in Figure 6.

The actual spacings shown above derive from the logistic-J distribution and are based on the hypothesis that communities actually follow the logistic-J distribution. As such, the actual distribution would hardly appear so nicely arranged. Clumps and gaps would abound, just as they do in the MSL system when it is operated with parameters that correspond to communities rather than samples of communities. However, even if they follow some other kind of distribution, it must be a J-curve (according to Dewdney, 1998) and the actual distribution would not be noticeably different from a perturbed version of the one shown in Figure 6.

The biosurvey metastudy

For the past few years the author has been gathering abundance surveys from the literature. Called "biosurveys" here, they cover four kingdoms of life (there being apparently few biosurveys of Bacteria or Archaea, if any). They were taken in polar, boreal, temperate, and tropical biomes of every type: terrestrial, freshwater, and marine. The intention is to include, ultimately, 100 "randomly selected" biosurveys in the study. Biosurveys selected for the study have three criteria to fulfill: They must (a) include at least 30 species, (b) not exclude uncommon or low abundance species, (c) not use numbers that are anecdotal or order-of-magnitude figures. So far, out of about 70 biosurveys selected at random, 50 have passed these criteria (and these criteria alone), to be included in the study.

Ideally, a "random selection" of biosurveys would require (a) a list of all the biosurveys ever taken and (b) a random number generator to select items from the list. Unfortunately, no such grand list exists. However, in the context of the metastudy reported here, "random" only needs to mean "not prejudicing the outcome." In other words, it makes no difference how biosurveys are selected from the literature, provided that nothing in the selection process tends to turn up surveys that favor the logistic-J distribution in some way. It is impossible, in any case, even by visual examination of abundance data in a typical biosurvey, to decide whether it would fit one distribution better than another. Even so, the research assistants who did most of the selecting were instructed to scan through *Biological Abstracts* and other databases and to note every biosurvey encountered. If the journal happened to be in our library, the assistant then went to the article in question and, if the total number of species was 30 or more, made a copy of the paper. The author then applied the remaining criteria, rejecting papers that failed to meet conditions (b) or (c), as stated in the previous paragraph, but *accepting all others without prejudice*.

Occasionally, in this process, the author would note that one kingdom of life or another was under-represented. The assistants were occasionally instructed to find more biosurveys on fungi, protists, plants, or what have you. Besides the papers selected by assistants, the metastudy includes a biosurvey by the author (#1) and two papers by biological colleagues (#19, 20) who had heard of the study and volunteered their findings without knowing exactly what I expected to find.

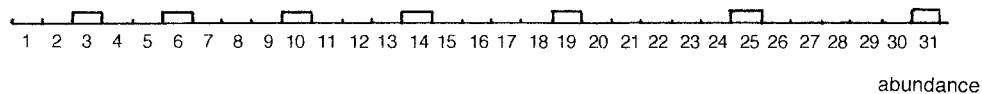At the present point, halfway through the study, the emphasis has been very much on the animal kingdom:

Figure 6. Idealized distribution of species in a large community.

Fungi/Lichens	6
Protista	3
Plantae	5
Animalia	36

The Animalia set includes 10 fish surveys, 7 of birds, 1 of herptiles, 10 of insects, 2 of crustaceans, 1 of molluscs, 4 of "invertebrates," and 1 of "macrofauna." The Plantae set has 3 herbaceous plant surveys, 1 of trees and 1 of mosses. In various combinations, the surveys were conducted in 27 temperate, 16 tropical/subtropical, and 7 boreal/polar locations. General habitat types included 27 terrestrial, 11 freshwater, and 12 marine.

For each biosurvey selected for the study, a species-abundance histogram was created, as outlined in the foregoing section. Some biosurveys gave raw counts for a specific community of organisms, others gave density data. In all cases, the continuous version of the logistic distribution was used, illustrating its great flexibility. The log-series was also applied to both kinds of survey data, according to the method outlined in Magurran (1988). Its normal range had to be extended (in a mathematically defensible way) to handle density and percentage data, however. This extension did not detract from its ability to fit natural communities.

The chi-square test (Hays and Winkler, 1971) is normally used in goodness-of-fit applications to produce a statistic that describes how closely the theoretical distribution fits empirical data. In this study, however, the test was used in comparative mode, a legitimate practice that involved a direct comparison of chi-square scores to determine which theoretical distribution best fit the 50 biosurveys overall.

Figure 7 shows a portion of two consecutive lines from a chi-square table. When the statistic has been computed for both the logistic-J and the log-series distributions in relation to a specific biosurvey, it might well be that one statistic had 5 degrees of freedom and the other had 6.

In the present context, the degrees of freedom to apply in a given instance of the chi-square test is determined by the number of abundance categories into which the data has been divided minus the number of independent parameters in the distribution. Since the log-series distribution has just one parameter, whereas the logistic-J has two, the log-series distribution was typically tested at one higher degree of freedom, an advantage that exactly compensates for the

reduced descriptive power that accompanies fewer parameters.

Suppose for example, that a particular biosurvey matches the logistic-J and the log-series with exactly the same chi-square value, say 5.321. The P value along the top of the table is simply the cutoff probability beyond which the fit would be rejected in normal applications. For example, a chi-square value of 5.321 at 5 degrees of freedom is less than 6.62568, and this means that the fit must be "accepted" at the 0.75 level.

In fact, as normally used, the chi-square test, like all goodness of fit tests, works best as a rejector of fits. If the chi-square statistic were greater than 6.62568, then it could be rejected at the 0.75 level, meaning that one could reject the fit and be 75% positive that no mistake was made in the rejection. However, the test is not symmetrical in relation to "acceptance" and rejection. If accepted, we can say only that the fit was not rejected. Acceptance amounts to nothing like a proof that the accepted theoretical distribution is the actual underlying source of variation. Nor could it. There is an infinity of distribution functions that could be cooked up, all of them quite different from each other, all of them fitting the empirical data equally well.

Although we will not be using the chi-square test in rejection/acceptance mode, the foregoing introduction serves to introduce the P values that are crucial to the metastudy reported here.

Returning to the example where both the logistic-J and log-series happen, by coincidence, to have exactly the same chi-square score of 5.321, we can work out the corresponding P values by a simple process called linear interpolation. The P value gives us a direct comparison between the two scores. Thus at 5 degrees of freedom the chi-square value of 5.321 corresponds to a P value of 0.607, while at 6 degrees of freedom, the chi-square value of 5.321 corresponds to a P value of 0.497. In this case then, the log-series chi-square score (0.497) would be superior to the logistic-J score (0.607).

This example not only illustrates how more degrees of freedom translates, other things being equal, into a lower P value, but how the P values themselves make it possible to translate between chi-square scores at different degrees of freedom. Since the mapping between chi-square scores and their corresponding P values is 1-1, it is reversible. In other

p value:	0.50	0.75	0.90	0.95
df				
.				
.				
5	4.35146	6.62568	9.23635	11.0705 . . .
6	5.34812	7.84080	10.6446	12.5916 . . .
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Figure 7. Two lines from a chi-square table.

words, we can start with a chi-square score at one degree of freedom, map that score into a corresponding P value, then turn around and map the P value into a chi-square score at some other degree of freedom, it being guaranteed (by the definition of the P value) that the scores will be comparable. The chi-square distribution with 10 degrees of freedom was selected as the "currency" of choice, 10 being an intermediate value over all the degrees of freedom that actually occurred in the metastudy. Each chi-square score, whether for the log-series or for the logistic-J distribution, was normalized in this fashion into the corresponding chi-square score at 10 degrees of freedom.

Appendix Table 1 displays the raw chi-square score and the corresponding normalized scores (at 10 degrees of freedom) for both the logistic-J and the log-series distributions, as applied to each biosurvey used so far in the metastudy. All chi-square scores were calculated by a program written in Turbo Pascal by the author and run for both sets of data. The right-hand column of the table displays the difference between the normalized scores.

The average normalized score for the logistic-J distribution over all 50 biosurveys was 10.653, while the average score for the log-series distribution was 12.949. The latter score is significantly higher, as revealed by a paired sample interval estimate (Wonnacott and Wonnacott, 1982). In this technique the paired differences are subjected to a means test specialized for paired data such as we treat in Figure 8. A confidence interval based on these data yields an average difference in normalized scores of 2.296 ± 1.547, which may be interpreted as follows: the probability that the two means differ by less than 2.296 − 1.547 = 0.749 is 5%. Indeed, a better interval at 99% confidence of 2.296 ± 2.063 can also be constructed. Here, with probability of only 1%, the two means differ by no less than 2.296 − 2.063 = 0.233. The difference, though small, is apparently real: With 99% probability, the mean chi-square score for the logistic-J distribution is definitely lower than the mean chi-square score for the log-series distribution on the same data. The logistic-J distribution outperforms the log-series distribution in this sense.

Not only are the test score means apparently different, but the average score of the logistic-J distribution also appears to be optimal or near-optimal, and in two ways.

The mean of the chi-square distribution with n degrees of freedom is exactly n, and the variance is $2n$ (Hays and Winkler, 1971). Thus the chi-square distribution at 10 de-

grees of freedom has a mean of 10.0. The average normalized chi-square score for the logistic-J distribution, 10.653, is obviously not far from optimal, whereas the average normalized chi-square score for the log-series distribution, 12.949, is further away.

Under the null hypothesis, a distribution that was the actual source of variation in the biosurvey data would tend to have a score of around 10. On the other hand, the rather high variance, 20.0 in this case, serves as a warning not to take the closeness too seriously. Even if the logistic-J had achieved an average normalized score of 10.0, it could easily have been as much as one standard deviation (4.47) away from the optimal score, and in either direction.

The median of the chi-square distribution for a given number of degrees of freedom is the score that corresponds to a P value of 0.500. Under the null hypothesis for the chi-square distribution with 10 degrees of freedom, we would expect half the scores to be less than 9.342. As it happens, some 23 of the normalized logistic-J scores have this property, whereas only 17 of the normalized log-series scores are less than 9.342.

Taken together with the near-certain superiority of the logistic-J distribution over the log-series, this evidence may be interpreted as reasonably strong support for the hypothesis that abundances in natural communities follow the logistic-J distribution.

A final result is worth reporting. The version of the logistic-J distribution that appears in this study used an estimate for the parameter Δ based on the mean and lowest category frequency of the empirical distribution. The resulting value of Δ may therefore be interpreted as a prediction of the maximum abundance for every biosurvey in the study. Since the predicted maximum abundance is only an average value, we would expect that if the predictions were accurate in this sense, the average value of the maximum abundances in the biosurveys would be fairly close to the average predicted values.

To test this hypothesis, the ratio (percentage) of actual maximum abundance to that predicted by the logistic-J distribution was calculated for each biosurvey and the results plotted as percentages, as in Figure 8.

As it turns out, the average percentage ratio of maximum abundances is 99.1%. This means that the 50 predicted (average) maximum abundances behaved as would be expected if the communities in question followed the logistic-J distribution. Although highly accurate, this result must
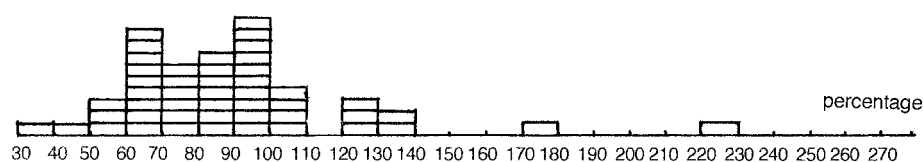

Figure 8.   The distribution of maximum abundances *vs.* outer limits.

again be interpreted with some caution, as the statistic is apt to suffer from a high variance. Nevertheless, this result also supports the hypothesis, and from a quite different direction.

Summary

There are two hypotheses implicit in the foregoing. The first hypothesis is that all natural communities follow the logistic-J distribution. The second hypothesis hinges on what level of interpretation is applied to the MSL system itself.

The first hypothesis has little meaning until the word "community" is defined. We define a *place* as any connected volume within the biosphere, a *time* as the period between two clock/calendar readings, and the *supercommunity* connected with this place and time as the set of all living organisms within the space over the time in question. A "community," as we shall use the word, will be a subset of the supercommunity. Although somewhat too abstract to be very useful, we may restrict the meaning somewhat by allowing as "subsets" only taxonomically related organisms or those related by similar size or by being found in the same habitat type or, in general, any sense of the word habitually used in the field. Although the MSL system models only supercommunities, a compartmentalized version of the model reveals the same distribution obtaining within compartments (*e.g.,* herbivores).

The first hypothesis, that all natural communities follow the logistic-J distribution, has been supported by three separate outcomes of the metastudy:

First, the logistic-J distribution significantly outperforms the log-series distribution as a descriptor of abundances in communities. As already seen, the lognormal distribution, when truncated properly, has no resemblance at all to empirical data. With the two most commonly used distributions thus eliminated, there remains no serious alternative to the logistic-J distribution;

Second, the logistic-J has a normalized chi-square score that exceeds the median about half the time. Not only does it outperform the log-series distribution in this respect, but its closeness to the expected number of such scores, namely 25, might be interpreted as another hint of optimality.

Third, the scores of the logistic-J distribution on the biosurveys considered as a whole reproduce the chi-square distribution itself. This can happen only if the null hypothesis is always (or almost always) true of the biosurveys in the study. The possibility remains that another theoretical distribution is the proper one, but it will so closely resemble the logistic-J as to be perpetually indistinguishable from it, given the results of the metastudy so far.

Fourth, the average outer limit predicted by the logistic-J distribution matches the average maximum abundance of the biosurveys themselves. This would also be true if all the biosurveys had the logistic-J as their underlying distribution.

The second hypothesis, concerning the mechanism underlying the logistic-J distribution, necessarily involves reflection on the MSL system itself. But the MSL model has three levels of interpretation that are mutually compatible, but successively more general. As originally intended, it was to reflect the high levels of predation to be found in stream benthic micro-environments (Dewdney, 1997).

At the next level of interpretation, individuals are not ingesting each other, but merely trading biomass for reproductive enabling. This view covers not only predation, but competition for sunlight (as when one plant shades out another, taking biomass that would, in effect, have been accumulated by the shaded plant), and saprobic activity of fungi and bacteria. Obviously, this view stretches the MSL system considerably but, as we have already seen, the basic model system is "detail hungry." When altered to employ fractional trophism or when modified to operate on the basis of definite food webs, it still produces J-curves.

At the third level of interpretation, even the trophic activity is irrelevant. All that matters is that a given organism is as likely to reproduce as it is to die before reproducing. Although this may not be true over short periods of time for actual species, a certain long-term birth/death equiprobability surely prevails for every species that has survived to the present day. In other words, regardless of the individuals involved, a species has been as likely to increase, in the long run, as it was to decrease. The ratio, after all, is the number of successful reproductions divided by the number of deaths.

The notions of *a priori* probabilities of death or reproduction are not very useful, unfortunately. There is no way to measure them and no way to predict the outcome even if they turned out to be equal. In direct contradiction to what any theorist (including the author) might have guessed, the seeming stability implied by equal probabilities of decline or abundance is an illusion. Instead of a normal (or even a lognormal) distribution, a J-curve invariably results. This would be just as true of any natural system obeying such an hypothesis as it is of the MSL system. Taken literally, the behavior of the MSL system would predict that most populations will appear to be regulated (Turchin, 1995), at least somewhat, by density over the short run, while appearing increasingly stochastic in the long run.

We shall adopt a hypothesis that is nearly equivalent to this. At any time (seasonal and cyclic effects aside) and in any community, it is unpredictable whether the next change in the population of a given species will be an increase or a decrease. Indeed, we hypothesize that all species in all communities are continually undergoing what may be called "stochastic vibration." In the MSL system, species continually orbit the mean population size. At any time, most have smaller populations, some have larger populations, and a

few have much larger ones. In a purely random manner, some very abundant species decline, ultimately to very small numbers, while others increase dramatically and for no apparent reason. Such an increase in a real community (that followed such a regimen) would usually have many causes that chanced to work together, or sometimes a single cause that happened to dominate all other factors.

Such unpredictability does not amount to a claim of nondeterminism. Perhaps a reasonable analogy will be found in the stock market. Although thousands of investment decisions, each of them deterministic for the individuals concerned, will play a role in the price of a stock over the period of a week, no one can predict the eventual effect of those decisions on the price. No one, after all, knows all the investors and their buying patterns. It is reasonably well understood that stock prices are "random" in this sense (Malkiel, 1985).

Although it would be very difficult to test, the stochastic vibration hypothesis has one important philosophical implication. It amounts to a confession of ignorance about the normal causes of change in abundance of populations, the contributing factors being in most cases beyond observation or calculation. It does not, however, signal a state of despair. It merely injects a note of realism into any project that would ascribe changes in abundance to single factors.

Consider an individual plant, for example. Upon germination and up to reproductive maturity, it may be killed by too much sun or too little, by excess cold or heat, by foraging animals, by fungal or other pathogenic attack, by parasites, by trampling, by overshadowing, by root competition, by excess dryness or humidity, by flooding, by environmental toxins, and so on. Most of these events are completely unpredictable, especially those driven by the weather—which, being chaotic, cannot be predicted with any certainty beyond a day or two. Over a season, some of the plants in a local community will succumb to one of these factors and die.

To reproduce, a plant must first produce seeds. But the flower may not develop properly, the pollinating insect may not visit the plant, the pollinator may not be carrying the right pollen (in the case of cross-pollinating plants), and so on. When ovaries are fertilized, the game gets even rougher. That most plants produce rather large numbers of seed testifies to the fact that most seeds either do not germinate or die after germination. They may land on bad soil, be eaten by animal scavengers, be attacked by fungus, become desicated, and so on.

The logistic-J distribution, including its underlying dynamical system and the stochastic behavior of its species, is here proposed as the major organizing factor present in all natural communities of living things. As such, it would have rather important implications in a number of fields, not least biodiversity assessment and the theory of evolution. Two brief remarks may serve for the time being.

There are many different definitions of biodiversity, no two alike (Magurran, 1988). If it is ultimately concluded that most communities of living organisms follow the logistic-J distribution, then a new and uniform approach to the problem of biodiversity assessment can be developed. One may calculate the "biodiversity" of a community of organisms, not as a single number (a hopeless project [Gaston, 1995]) but as a triplet, (R, ε, Δ). These numbers would be estimates of those parameters for the community as a whole, derived *via* samples that are subjected to the transformations outlined in Dewdney (1998). And the abundances in such communities can be largely reconstructed from these numbers, although our theory says nothing about which species would have which abundances.

In the theory of evolution, it might be asked whether the stochastic vibrations hypothesized here for species might also prevail at the generic and higher taxonomic levels. Williams (1964) observed that the J-curve also emerges if one plots genera against species, not in a community this time, but in standard taxonomic lists. For example, if one counts the number of bird genera that have 1 species, 2 species, and so on, a J-curve emerges. This can be done within families or orders. It may be that genera "vibrate" in the sense that, through evolutionary time, they lose and gain species more or less at random (*i.e.,* unpredictably and with no overall discernible pattern).

Finally, the J-curve, whether one regards it as being logistic-J or not, tells us that within any community of organisms, especially somewhat isolated or patchy ones, there will be many species with relatively small populations—far more than is commonly realized, even by many field biologists. Such populations will be more readily subject to mutational change, since new genes have a much better chance of spreading through them. From this viewpoint, the low abundance end of the J-curve may be identified not only as the grave of evolution, but its cradle, as well.

The research reported in this paper is described in a monograph, draft copies of which can be obtained by contacting the

author. The monograph contains a field manual for the logistic-J distribution which may be requested separately.

Literature Cited

Dewdney, A. K. 1996. *Micro-ecology in a Small Stream.* Monograph, Environmental Science Program, The University of Western Ontario, London, Canada.

Dewdney, A. K. 1997. A dynamical model of abundances in natural communities. *COENOSES* **12(2–3):** 67–76.

Dewdney, A. K. 1998. A general theory of the sampling process with applications to the "veil line." *Theor. Popul. Biol.* **54:** 294–302.

Fisher, R. A., S. A. Corbet, and C. B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* **12:** 42–58.

Gaston, K. J. 1995. Pp. 1–18 in *Population Dynamics: New Approaches and Synthesis.* N. Cappuccino and P. W. Price, eds. Academic Press, San Diego.

Hays, W. L., and R. L. Winkler. 1971. *Statistics: Probability, Inference, and Decision.* Holt, Rinehart and Winston, New York.

Judson, O. P. 1994. The rise of the individual-based model in ecology. *Trends Ecol. Evol.* **9(1):** 9–14.

MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography.* Princeton University Press, Princeton, NJ.

Magurran, A. E. 1988. *Ecological Diversity and Its Measurement.* Princeton University Press, Princeton, NJ.

Malkiel, B. G. 1985. *A Random Walk Down Wall Street.* W. W. Norton, New York.

May, R. M. 1975. Patterns of species abundance and diversity. Pp. 81–120 in *Ecology and Evolution of Communities.* M. L. Colby and J. M. Diamond, eds. Harvard University Press, Cambridge, MA.

McCabe, T. L., and C. N. Weber. 1994. The robber flies (Diptera: Asilidae) of the Albany Pinebush. *Gt. Lakes Entomol.* **27(3):** 157–159.

Pielou, E. C. 1975. *Ecological Diversity.* John Wiley, New York.

Preston, E. F. 1948. The commonness, and rarity, of species. *Ecology* **29:** 254–283.

Turchin, P. 1995. Pp. 19–39 in *Population Dynamics: New Approaches and Synthesis.* N. Cappuccino and P. W. Price, eds. Academic Press, San Diego.

Williams, C. B. 1964. *Patterns in the Balance of Nature.* Academic Press, London.

Wonnacott, R. J., and T. T. Wonnacott. 1982. *Statistics: Discovering its Power.* John Wiley, New York.

Appendix

Table 1

Chi-square scores and corresponding normalized scores for the logistic-J and log-series distributions on 50 biosurveys

Ref	logistic c2	@ 10 df	log-ser.c2	@ 10 df	difference
1	18.659 @ 18	10.330	26.079 @ 17	17.054	+6.724
2	14.345 @ 8	17.054	18.347 @ 8	20.483	+3.429
3	3.064 @ 3	10.625	2.802 @ 4	8.331	−2.294
4	2.785 @ 5	6.904	7.286 @ 5	13.420	+6.516
5	9.804 @ 12	7.967	15.455 @ 12	12.664	+4.697
6	7.371 @ 4	15.391	5.181 @ 6	9.113	−6.278
7	1.031 @ 3	6.201	4.643 @ 4	11.369	+5.168
8	0.532 @ 3	4.662	3.450 @ 5	7.946	+3.284
9	0.762 @ 4	4.070	3.521 @ 7	5.851	+1.781
10	6.036 @ 6	10.227	4.778 @ 6	8.560	−1.667
11	0.142 @ 3	2.742	4.632 @ 4	9.739	+6.997
12	0.439 @ 5	2.236	2.808 @ 7	4.828	+2.592
13	5.809 @ 9	6.637	11.368 @ 9	12.523	+5.886
14	42.206 @ 27	11.523	46.972 @ 28	14.818	+3.295
15	5.410 @ 3	14.635	3.941 @ 4	10.265	−4.370
16	5.004 @ 3	13.970	4.637 @ 4	11.369	−2.601
17	5.667 @ 8	7.725	2.452 @ 9	2.971	−4.754
18	2.068 @ 3	6.445	5.471 @ 5	10.920	+4.475
19	6.195 @ 5	11.946	10.365 @ 7	14.085	+2.139
20	3.139 @ 4	8.946	12.796 @ 6	18.481	+9.535
21	12.525 @ 13	9.509	17.087 @ 15	11.600	+2.091
22	10.012 @ 9	11.099	10.986 @ 10	10.984	−0.115
23	3.493 @ 8	4.865	7.120 @ 9	8.040	+3.175
24	5.289 @ 6	9.259	5.541 @ 8	7.279	−1.980
25	24.986 @ 17	16.173	18.421 @ 19	9.406	−6.767
26	2.934 @ 5	7.144	11.826 @ 6	17.379	+10.235
27	8.839 @ 9	9.868	30.380 @ 11	29.588	+19.720
28	20.169 @ 18	11.471	33.425 @ 18	22.846	+11.375
29	3.271 @ 6	6.463	3.827 @ 7	6.176	−0.287
30	49.519 @ 41	12.536	57.258 @ 38	23.037	+10.501
31	6.134 @ 5	11.856	4.291 @ 5	9.248	−2.608
32	36.117 @ 20	21.157	36.607 @ 22	19.787	−1.370
33	3.167 @ 4	8.998	3.642 @ 5	8.237	−0.761
34	9.882 @ 9	10.958	13.366 @ 10	13.351	+2.393
35	7.551 @ 3	17.843	7.886 @ 4	16.126	−1.717
36	2.269 @ 3	9.123	2.174 @ 4	7.196	−1.927
37	11.366 @ 5	18.394	13.106 @ 6	18.742	+0.348
38	8.647 @ 4	17.147	13.759 @ 5	20.847	+3.700
39	16.479 @ 10	16.497	15.413 @ 11	14.199	−2.298
40	27.078 @ 15	20.048	59.643 @ 15	19.613	−0.435
41	9.360 @ 12	6.612	13.325 @ 14	9.331	+2.719
42	4.217 @ 6	7.789	8.166 @ 8	10.253	+2.464
43	1.291 @ 4	5.364	1.025 @ 5	3.663	−1.701
44	8.023 @ 4	16.312	8.820 @ 6	13.741	−2.571
45	0.561 @ 4	3.469	3.223 @ 6	6.388	+2.919
46	0.631 @ 4	5.002	1.619 @ 5	4.878	−0.124
47	4.659 @ 4	11.394	55.147 @ 8	29.588	+18.194
48	26.590 @ 10	23.605	75.212 @ 16	29.588	+5.983
49	13.625 @ 11	12.472	12.555 @ 11	11.458	−1.014
50	4.800 @ 5	9.970	6.979 @ 7	10.099	+0.129
Total		532.633		648.058	
Average		10.653		12.961	

The papers used in the metastudy are listed in the order that they appear in this table and are numbered accordingly.

1. **Dewdney, A. K. 1996.** *Ecology in a Small Stream.* Monograph, Environmental Science Program, UWO, London, Ontario, Canada.
2. **Griffiths, R. W., S. Thornley, and T. A. Edsall. 1991.** Limnological aspects of the St. Clair River. *Hydrobiologia* **219:** 97–123.
3. **Griffiths, R. W. 1991.** Environmental quality assessment of the St. Clair River as reflected by the distribution of benthic macroinvertebrates in 1985. *Hydrobiologia* **219:** 143–164.
4. **Hill, J. K., K. C. Hamer, L. A. Lace, and W. M. T. Banham. 1995.** Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *J. Appl. Ecol.* **32:** 754–760.
5. **Hutto, R. L. 1995.** Composition of bird communities following stand-replacement fires in northern Rocky Mountains (U.S.A.) conifer forests. *Conserv. Biol.* **9(5):** 1041–1058.
6. **Al-Safadi, M. M. 1991.** Freshwater macrofauna of stagnant waters in Yemen Arab Republic. *Hydrobiologia* **210:** 203–208.
7. **Novak, R. O., and W. F. Whittingham. 1968.** Soil and litter microfungi of a Maple-Elm-Ash floodplain community. *Mycologia* **60:** 776–787.
8. **McCabe, T. L., and C. N. Weber. 1994.** The robber flies (Diptera Asilidae) of the Albany Pinebush. *Gt. Lakes Entomol.* **27(3):** 157–159.
9. **Harper, F. P., and F. Harper. 1982.** Mayfly communities in a Laurentian watershed (Insecta; Ephemeroptera). *Can. J. Zool.* **60:** 2828–2840.
10. **Gutierrez, D., and R. Menendez. 1995.** Distribution and abundance of butterflies in a mountain area in the northern Iberian peninsula. *Ecography* **18:** 209–216.
11. **Barlocher, F., and B. Kendrick. 1974.** Dynamics of the fungal population on leaves in a stream. *J. Ecol.* **62:** 761–791.
12. **White, D. H., J. S. Hatfield, P. W. Sykes, Jr., and J. T. Seginak. 1996.** Habitat associations of birds in the Georgia Piedmont during winter. *J. Field Ornithol.* **67(1):** 159–166.
13. **Thiollay, J.-M. 1996.** The role of traditional agroforests in the conservation of rainforest bird diversity in Sumatra. *Conserv. Biol.* **9(2):** 335–353.
14. **Varga, S. 1965.** *Vascular Plant Inventory of the Backus Tract.* The Long Point Region Conservation Authority, Simcoe, Ontario, Canada.
15. **Short, T. M., J. A. Black, and W. J. Birge. 1991.** Ecology of a saline stream community responses to spatial gradients of environmental conditions. *Hydrobiologia* **226:** 167.
16. **Colwell, M. A., and S. L. Dodd. 1995.** Waterbird communities and habitat relationships in coastal pastures of northern California. *Conserv. Biol.* **9(4):** 827–834.
17. **Aoki, T., and S. Tokumasu. 1995.** Dominance and diversity of the fungal communities on fir needles. *Mycol. Res. J.* **99(12):** 1439–1449.
18. **Vuori, K.-M., and I. Joensuu. 1996.** Impact of forest drainage on the macroinvertebrates of a small boreal headwater stream: do buffer zones protect lotic biodiversity? *Biol. Conserv.* **77:** 87–95.
19. & 20. **Maycock, P. F., and D. Fahselt. 1992.** Vegetation of stressed calcareous screes and slopes in Sverdrup Pass, Ellesmere Island, Canada. *Can. J. Bot.* **70:** 2359–2377.
21. **Caley, M. J. 1995.** Community dynamics of tropical reef fishes: local patterns between latitudes. *Mar. Ecol. Prog. Ser.* **129:** 7–18.
22. **Lowry, J. K. 1975.** Soft bottom macrobenthic community of Arthur Harbor, Antarctica. Paper 1 in *Biology of the Antarctic Seas V,* D. L. Pawson, ed. *Antarctic Research Series* **23(1):** 1–18.
23. **Haila, Y., O. Jarninen, and R. A. Vaisanen. 1980.** Habitat distribution and species associations of land bird populations on the Aland Islands, SW Finland. *Ann. Zool. Fenn.* **17:** 87–106.
24. **Stein, D. L., B. N. Tissot, M. A. Hixon, and W. Barss. 1992.** Fish-habitat associations on a deep reef at the edge of the Oregon continental shelf. *Fish. Bull. (Wash. DC)* **90:** 540–551.
25. **Winemiller, K. O., and M. A. Leslie. 1992.** Fish assemblages across a complex, tropical freshwater/marine ecotone. *Environ. Biol. Fishes* **34:** 29–50.

26. **Catling, P. M., and L. P. Lefkovitch. 1989.** Associations of vascular epiphytes in a Guatemalan cloud forest. *Biotropica* **21(1):** 35–40.

27. **Janzen, D. H. 1973.** Sweep samples of tropical foliage insects description of study sites, with data on species abundances and size distributions. *Ecology* **54(3):** 659–666.

28. **Lackey, J. B. 1938.** A study of some ecologic factors affecting the distribution of protozoa. *Ecol. Monogr.* **8(4):** 503–527.

29. **Wilson, E. O. 1987.** The arboreal ant fauna of Peruvian Amazon forest: a first assessment. *Biotropica* **19(3):** 245–251.

30. **Williams, C. B. 1964.** (See general Literature Cited.)

31. **Jennings, S., A. S. Brierly, and J. W. Walker. 1994.** The inshore fish assemblies of the Galapagos Archipelago. *Biol. Conserv.* **70:** 49–57.

32. **Bongers, F., J. Popma, J. Meave del Castillo, and J. Carabias. 1988.** Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* **74:** 55–80.

33. **Busby, W. H., and J. R. Parmelee. 1996.** Historical changes in a herpetofaunal assemblage in the Flint Hills of Kansas. *Am. Midl. Nat.* **135:** 81–91.

34. **Bohning-Gaese, K., and H.-G. Bauer. 1996.** Changes in species abundance, distribution, and diversity in a central European bird community. *Conserv. Biol.* **10:** 175–187.

35. **Walters, K. 1991.** Influences of abundance, behavior, species composition, and ontogenetic stage on active emergence of meiobenthic copepods in subtropical habitats. *Mar. Biol.* **108:** 207–215.

36. **Salvado, H., and M. del Pilar Gracia. 1991.** Response of ciliate populations to changing environmental conditions along a freshwater reservoir. *Arch. Hydrobiol.* **123(2):** 239–255.

37. **Niemela, J., Y. Haila, and E. Halme. 1988.** Carabid beetles on isolated islands and on the adjacent Aland mainland variation in colonization success. *Ann. Zool. Fenn.* **25:** 133–143.

38. **Yoklavich, M. M., G. M. Cailliet, J. P. Barry, D. A. Ambrose, and B. S. Antrim. 1991.** Temporal and spatial patterns in abundance and density of fish assemblages in Elkhorn Slough, California. *Estuaries* **14:** 465–480.

39. **Sukumar, R., H. S. Dattaraja, H. S. Suresh, J. Radhakrishnan, R. Vasudeva, S. Nirmala, and N. V. Joshi. 1992.** Long-term monitoring of vegetation in a tropical deciduous forest in Mudumalai, southern India. *Curr. Sci.* **62:** 608–616.

40. **Terborgh, J., S. K. Robinson, T. A. Parker, III, C. Munn, and N. Pierpont. 1990.** Structure and organization of an Amazonian bird community. *Ecol. Monogr.* **60:** 213–238.

41. **Cowx, I. G., W. O. Young, and J. M. Hellawell. 1984.** The influence of drought on the fish and invertebrate populations of an upland stream in Wales. *Freshwater Biol.* **14:** 165–177.

42. **Samways, M. J. 1990.** Species temporal variability: epigaeic ant assemblages and management for abundance and scarcity. *Oecologia* **84:** 482–490.

43. **Kemp, W. P. 1992.** Temporal variation in rangeland grasshopper (Orthoptera Acrididae) communities in the steppe region of Montana, USA. *Can. Entomol.* **124:** 437–450.

44. **Brunner, I., F. Brunner, and G. A. Laursen. 1992.** Characterization and comparison of macrofungal communities in an *Alnus tenuifolia* and an *Alnus crispa* forest in Alaska. *Can. J. Bot.* **70:** 1247–1258.

45. **Spanier, E., S. Pisanty, M. Tom, and G. Almog-Shtayer. 1989.** The fish assemblage on a coralligenous shallow shelf off the Mediterranean coast of northern Israel. *J. Fish Biol.* **35:** 641–649.

46. **Hornbach, D. J., A. C. Miller, and B. S. Payne. 1992.** Species composition of the mussel assemblages in the upper Mississippi River. *Malacol. Rev.* **25:** 119–128.

47. **Holmquist, J. G., G. V. N. Powell, and S. M. Sogard. 1989.** Decapod and stomatopod assemblages on a system of seagrass-covered mud banks in Florida Bay. *Mar. Biol.* **100:** 473–483.

48. **Tzeng, W.-N., and Y.-T. Wang. 1992.** Structure, composition and seasonal dynamics of the larval and juvenile fish community in the mangrove estuary of Tanshui River, Taiwan. *Mar. Biol.* **113:** 481–490.

49. **Butler, L. 1992.** The community of macrolepidopterous larvae at Cooper's Rock State Forest, West Virginia: a baseline study. *Can. Entomol.* **124:** 1149–1156.

50. **Merrett, N. R., R. L. Haedrich, J. D. M. Gordon, and M. Stehmann. 1991.** Deep demersal fish assemblage structure in the Porcupine Seabight (eastern North Atlantic): results of single warp trawling at lower slope to abyssal soundings. *J. Mar. Biol. Assoc. UK* **71:** 359–373.