Chapter 9. Open Problems

Not to treat the present theory as a closed book, it is important to highlight areas where further work is needed and to encourage students of the subject to pursue the lines of research indicated in this chapter. In the first two topics presented below, some progress has already been made.

The first line of research seeks a complete understanding of the relationship between the value of epsilon that appears in a sample and that of the community from which the sample came, the linking factor being the intensity of the sample. A formula or method of determining the relationship has yet to appear. In the second topic, the mathematics of the sampling process dictates a new formula for the accumulation curve that results when the number of species in a sample is plotted as a function of sample size. The formula is exact in the cae of sampling with replacement but only approximate in the case of sampling without replacement.

The third topic describes some of the possibilities open to developing stochastic systems. It includes the dexcriptions of six different versions of the experimental systems spawned by the basic idea of the stochastic species hypothesis.

9.1 The effect of sampling on ε and Δ

When one samples a community with intensity r, the natural question is how the parameters ε' and Δ' of the sample are related to the corresponding parameter values of the community. As far as the parameter Δ' is concerned, the situation is simple. A sample of intensity r will map (in the statistical sense) the maximum abundance Δ in a community into a maximum abundance $\Delta' = r\Delta$ in the sample. In other words, Δ'/r is an unbiased estimator of Δ. The situation with ε is more complicated. In order to develop a theoretical handle on the behaviour of a sample epsilon in relation to its corresponding community epsilon, one needs an equation in which ε occurs along with other parameters for which values (or estimates) are available. Such an equation is readily derivable from equation (iii) in section 1.1.1:

$$F(1) = Rc[\ln((1 + \varepsilon)/((k-1) + \varepsilon) - \delta a],$$

The parameter ε occurs three times in this formula, one of the occurrences being concealed within the constant c. Thus the fully explicit formula for F(1) would be

$$F(1) = R(\ln(\Delta/e) - 1)[\ln((ka+\varepsilon)/((k-1)a+\varepsilon) - \delta a] \qquad \text{(i)}$$

One can replace the estimate for F(1) in equation (i) by evaluating the Pielou transform (Section 2.6, equation (i)) specialized to k = 1:

$$F(1) = \int_0^\infty (e^{-rx}(rx))G(x)dx,$$

Unfortunately, replacing G by the logistic-J distribution for a community hardly makes the problem any easier. In fact, even with a simpler expression in hand, we would probably still be faced with a mixed log/linear equation which has no closed-form solution.

It is nevertheless possible to determine the effect of sampling on ε by carrying out actual experiments on the computer. If we apply the Pielou transform to a variety of community distributions of the form LJ[ε, Δ] x 50, we may compute the expected sample in each case and then apply a best fit procedure in order to obtain estimates for the sample parameter ε'. Tables 9.1a-d portrays the outcome for a variety of intensities. Four rather different logistic-J communities were each sampled at intensities varying from r = 0.020 to r = 0.005. This range of values spans the intensity of many of the samples reported in the metastudy references.

intensity r	**ε'**	**R'**	**chi square**
0.020	1.04	35.8	0.007/4
0.012	0.92	31.0	0.007/3
0.011	0.91	31.0	0.008/3
0.010	0.89	30.2	0.002/2
0.009	0.84	29.4	0.004/2
0.008	0.81	28.5	0.003/2
0.007	0.80	27.4	0.005/2
0.006	0.75	26.1	0.006/2
0.005	0.72	24.7	0.006/1

Table 9.1a Values for ε' derived from samples of LJ[10.0, 4000] x 50

Each table row lists the intensity of the sample, the value of ε that results from a best fit to the logistic-J distribution for that intensity, the number R' of species expected in the sample, and the chi square score of the best fit, the number behind the slash indicating the number of degrees of freedom. Readers will note that the communities so tested have ε-values of 10.0 and 5.0 combined with Δ-values of 3000.0 and 4000.0 in the four possible ways. The experiment is modest, but revealing, as we shall see. In the last table, a slight flaw in the mathematical software allowed samples with intensity no smaller than 0.006.

intensity r	ε’	R’	chi square
0.020	1.04	34.4	0.004/3
0.012	0.88	30.5	0.006/2
0.011	0.89	29.8	0.005/2
0.010	0.86	29.2	0.006/2
0.009	0.86	28.2	0.004/2
0.008	0.85	27.3	0.003/2
0.007	0.80	26.3	0.004/2
0.006	0.77	24.8	0.002/1
0.005	0.72	n/a	0.002/1

Table 9.1b Values for ε’ derived from samples of LJ[10.0, 3000] x 50

intensity r	ε’	R’	chi square
0.020	0.91	32.6	0.009/3
0.012	0.75	28.9	0.004/2
0.011	0.74	28.0	0.009/2
0.010	0.75	27.5	0.004/2
0.009	0.74	26.7	0.003/2
0.008	0.74	25.8	0.002/2
0.007	0.74	24.7	0.002/2
0.006	0.73	23.6	0.003/1
0.005	0.73	n/a	0.001/1

Table 9.1c Values for ε’ derived from samples of LJ[5.0, 4000] x 50

intensity r	ε’	R’	chi square
0.020	0.87	31.7	0.005/3
0.012	0.80	27.8	0.002/2
0.011	0.78	27.1	0.009/2
0.010	0.75	26.3	0.002/2
0.009	0.75	25.5	0.008/2
0.008	0.75	24.6	0.001/1
0.007	0.74	23.6	0.001/1
0.006	0.72	23.3	0.001/1

Table 9.1d Values for ε’ derived from samples of LJ[5.0, 3000] x 50

The foregoing results may be plotted, as in Figure 9.1. The results show high variability, as the best fit response surface is rather shallow and the minimum value is easily influenced by slight changes in parameter values. (See Section 4.3.) But the basic trend is downward as the intensity decreases.

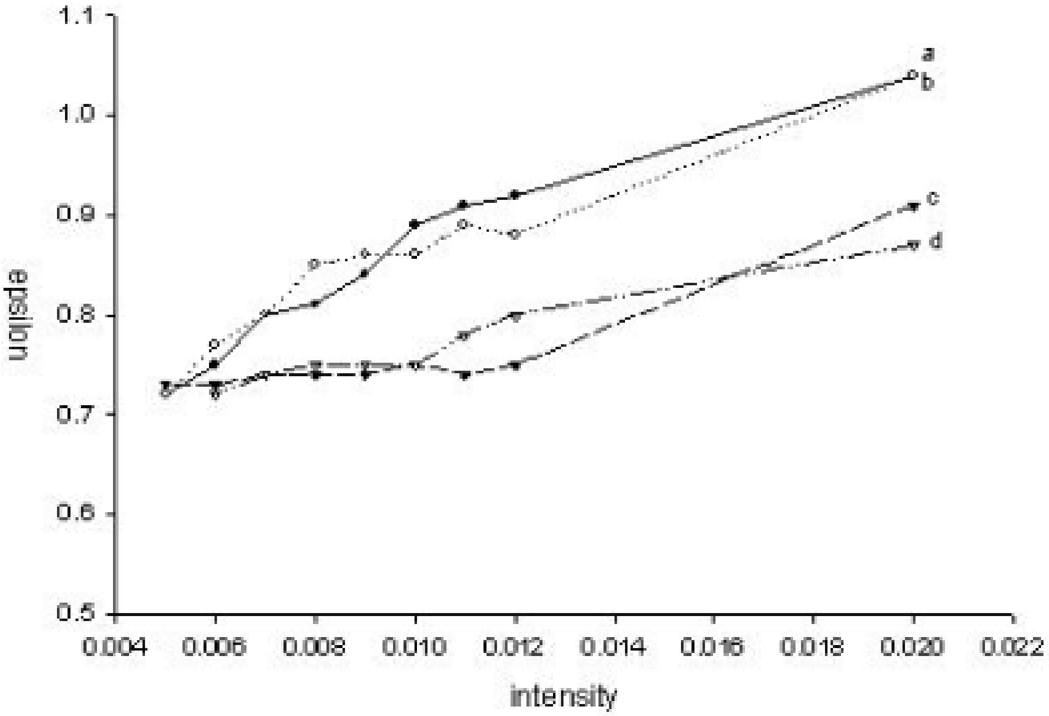

Figure 9.1 Plots of changes in sample ε-values for decreasing r

The plots seem to be more heavily influenced by the choice of values for the community ε than by values of Δ. Plots a and b, for example, share the common value of $\varepsilon = 10.0$, while plots c and d have $\varepsilon = 5.0$. A change from $\Delta = 4000.0$ to 3000.0 makes relatively little difference in either case.

Before running these tests, I imagined that as the sample intensity declined, the trends in ε-values would be downward and converging to 0. Instead, as the plots in Figure 9.1 show, the trend line aims at a point on the ε-axis at roughly $\varepsilon = 0.5$. (to the left of the axis in Figure 9.1) This puzzled me, especially when a few additional tests revealed a stubborn unwillingness for ε'-values to decline any lower than about 0.5. It occurred to me, however, that the minimum value of r should not be 0, but 1/N, in effect, as it made no sense to have a sample that was devoid of specimens. Thus if $x = 1$ in the formula for the logistic-J distribution, we also have $R = 1$, $\Delta = 1$ and $F(1) =1$, which yields,

$$c(1/(1+\varepsilon) - 1) = 1$$

This equation simplifies to the following,

$$1/(1+\varepsilon) = \ln(1/\varepsilon),$$

and has the unique solution $\varepsilon = 0.51734$, to five places of accuracy.

This explains the mystery of the non-convergent property of ε' as r approaches 0. At $r = 0.005$, a typical value is 0.7, for example, consistent with only a slight further drop by the time $r\Delta$ reaches 1.

Additional experiments on communities with an ε-value less than the critical value arrived at above, abruptly produced samples that were well above the critical value, even for very high sample intensities, such as $r = 0.9$. This implies that if there are any natural communities with an epsilon value below critical, we shall never detect them! As we have already seen however, (Section 6.1.4) such communities would be unstable in the sense that of the several species at abundance 1, at least a few would be gone over a relatively short span of time.

As for the behaviour of ε, the plots of Figure 9.1 may be hinting that Δ plays little or no role in the functional relationship between r and ε. As r declines, however, the value of ε' is unlikely to fall below 0.517. Could the relationship be linear or does the fact that the two sets of curves converge at intensity 0.005 indicate a more complex relationship?

Looking through the other end of the telescope, so to speak, we can next examine the trend in ε'-values as the sample intensity increases. The trend is clearly upward and a brief examination of the slope of the upper pair of curves would allow us to say that for every increment in intensity, the increase in the ε'-values is twenty times greater. For example, an increase in intensity of

0.001 produces, on average, an increase in the ε'-value of 20 x 0.001 or 0.02.

This has proved to be a difficult problem, one supposes, because oscillations in the community involve constantly changing epsilon-values, with no change in biomass, as pointed out in Section 6.1.4.

9.2. Accumulation curves

The accumulation curve is a theoretical shape that one has good reason to believe will be followed by an extended sample of a particular community. As more and more individuals are added to the sample, the rate at which new species are found declines. At first they come in fairly often, but as the sample is extended, new species appear less and less frequently. The resulting curve, giving the number of species found as a function of the number of individuals sampled, appears to be logarithmic in shape but is not. Sometimes called a rarefaction curve (owing to species becoming rarified as the sample process proceeds) the accumulation curve comes in two distinct flavours, depending on whether the associated sampling process is carried out with or without replacement.

For example, if one is sampling without replacement and continues on to the bitter end, one runs out of individuals to sample. The sampling sequence is finite. But if one is sampling a community with replacement, the sampling sequence is potentially infinite, as individuals already sampled may appear again. In this case the curve has a horizontal asymptote that (theoretically) it never quite reaches, the "bitter end" being a long way off. In the case of sampling with replacement, one sees authors claiming the existence of a horizontal asymptote. There might appear to be one, but when the community is embedded in a larger one, the possibility of a continued accumulation of species (however slow) points to an uptrend that was already inherent in the slope of the curve when N was reached -- not quite "asymptotic" to anything.

Although we shall display general formulas for both kinds of sampling process, the formulas themselves are not simple, but involve summations. It remains to be seen whether they can be applied to the problem of determining the richness of a community based on samples of it. To be acceptable, any such application would have to be more efficient than the methods described in Chapter Five. In both cases we use the notation R(n) to stand for the accumulation function. After n drawings have been made, what is the expected number of species? Here, as elsewhere, N will represent the total population size of the community as a whole and R will represent the total number of species occurring there.

9.2.1 Accumulation with replacement

The formula developed in Appendix A.9 yields the exact expected number of species to show up after k samplings of the univoltine distribution. We merely repeat the analysis that appears there, this time taking the context of N individuals into account.

Let $R_j(k)$ denote the number of species of abundance j (in the community) observed by the kth drawing . Then the number of individuals in species of abundance j not yet sampled must be

$$j(F(j) - R_j(k))$$

and the proportion of such individuals must be

$$(j/N)(F(j) - R_j(k))$$

This is the number of new species expected to come from the jth abundance category, actually just the probability that a new species will appear on the next drawing. Adding this number to Rj(k) yields the recurrence,

$$R_j(k+1) = R_j(k) + (j/N)(F(j) - R_j(k))$$

$$= (1 - j/N)R_j(k) + jF(j)/N$$

Back-solving for three levels reveals the emergent formula:

$$R_j(k) = (1 - j/N)^{k-1}Rj(1) + (jF(j)/N)(1 - j/N)^{k-2} + . . + (jF(j)/N)(1 - j/N)^1 + jF(j)/N(1 - j/N)^0$$

With $R_j(1) = jF(j)/N$. we have,

$$R_j(k) = (jF(j)/N) \sum_{i=0}^{k-1} (1 - j/N)^i$$

The full formula for R(k) consists simply of the terms Rj(k) added together, so that

$$R(k) = \sum_{j=1}^{\Delta} Rj(k)$$

$$= \sum_{j=1}^{\Delta} mj \sum_{i=0}^{k-1} (1 - j/N)^i, \qquad \text{(ii)}$$

where $m_j = jF(j)/N$.

Note that the order of summation may be changed, if necessary, for convenience in calculating R(k). Also note that the second summation is a finite power series in x = (1-j/N). As shown in

Appendix A.1.2, the corresponding infinite series sums to 1/(1-x), which becomes simply N/j in cases where x is small enough to converge quickly. In order to split the sum of equation (ii) into convregent and non-convergent parts, a convergence approximation may be used. How large must k be, for example, in order that the following inequality be satisfied?

$$x^k \leq 0.01$$

After a bit of algebra, one obtains the following inequality”

$$j \geq N(1 - (0.01)^{1/k})$$

Denoting the quantity on the right hand side by k’, we can now rerwrite equation (ii) as

$$R(k) = \sum_{j=1}^{\Delta} m_j \sum_{i=0}^{k-1} (1 - j/N)^i$$

$$= \sum_{j=1}^{k'} m_j \sum_{i=0}^{k-1} (1- j/N)^i + \sum_{j = k'+1}^{\Delta} mj \sum_{i=0}^{k-1} (1- j/N)^i$$

Since $\sum(1 - j/N)i \approx N/j$

and $mj = jF(j)/N$,

we have $$R(k) \approx \sum_{j=1}^{k'-1} m_j \sum_{i=0}^{k-1} (1- j/N)^i + \sum_{j=k'}^{\Delta} jF(j)/N \, (N/j)$$

we have $$= (1/N) \sum_{j=1}^{k'-1} jF(j) \sum_{i=0}^{k-1} (1- j/N)^i + \sum_{j=k'}^{\Delta} F(j) \qquad \text{(iii)}$$

In other words, all species with abundances k’ or greater are certain to contribute to the richness of the sample by the kth observation in the community. Contributions by species of lower abundance are conditioned by other factors in the first summation. As k becomes larger, the quantity k’ becomes smaller and the second summation increasingly dominates R(k). It is not clear whether the formula as a whole can be encapslated by a simple function of logarithmic or any other form.

We demonstrate the accumulation formula embodied by equation (iii) on a very simple distribution consisting of 10 species of abundance 2 and five species of abundance 6. A program called *Accum* was written to perform the calculation of R(k) for any value of k. The next table, 9.4, summarizes the results when the values of R(k) are compared with the corresponding output of the program *SampleSim*, with ten trials per case.

k	5	10	15	20	25
r	0.1	0.2	0.3	0.4	0.5
S	4.25	7.15	8.50	10.25	11.20
R(k)	4.21	6.96	8.84	10.19	11.19
error	0.04	0.19	0.34	0.06	0.01

Table 9.4. Comparison of theoretical (R) and sample (S) richness estimates

The relative errors in this example begin at 8.0% and decline to 0.04% in the last case.
The formula for R(k) is not of much practical use because one has to know the values F(j) of the community distribution in order to use it. However, it shows clearly how the number of species expected to show up by the kth sampling step depends on F. This amounts to yet another demonstration of the importance of knowing the distribution that prevails in the community.

9.2.2 Accumulation without replacement

The without-replacement accumulation curve found by Hurlburt (1971) certainly belongs in the area of "exact methods." It relies heavily on the combinatorial choice function which will be represented here by the notation,

$$C(n, k) = n!/(n-k)!k!$$

This function C denotes the number of ways of choosing k things from among n. The formula also employs the notation a_i to represent the abundance of the ith species in the community, the exact order of species being arbitrary but fixed. As in the previous section, the function R(n) will denote the number of species to have appeared by the nth observation.

$$R(n) = R - C(N, n)^{-1} \sum_{i=1}^{R} C((N-a_i), n) \qquad \text{(iii)}$$

We may give a brief demonstration of the accuracy of this formula in the univoltine case, U[10] x 20

Here, $N = 200$, $R = 20$ and $a_i = 10$ for all values of i. The formula (iii) becomes

$$R(n) = 20 - C(200, n)^{-1} \sum_{i=1}^{20} C(190, n)$$

$$= 20[1 - C(200, n)^{-1}C(190, n)]$$

Using a hand calculator, it will absorb many busy minutes to discover that

$$R(1) = 1.0$$

and that $R(5) = 4.66$

Running the program *SampleSim* on the distribution U[10] x 20 at intensity $r = 0.025$ (sample size 5), we find an average value of R(5) over twenty samples to be 4.64, about as close as one can reasonably expect. Finally, one might expect that in the case of sampling without replacement,

$$R(200) = 20$$

This result emerges trivially from the fact that C(190, 200) = 0. After all, the number of ways of drawing more balls from an urn than it contains is zero, the feat being impossible. Of course, to apply Hurlburt's formula, one needs to know the species richness of the community beforehand.

It must be remarked, in closing this particular topic, that the accumulation formulas given here can be made fully explicit when used in conjunction with the richness estimation methods developed in Chapter 5. Once one has a logistic-J formula for the community, one can then compute and plot the accumulation curve as far as one likes to see, among other things, the kind of results that further sampling would produce.

9.3 Biogeography: the species area relationship

The problem addressed in the previous section, that of determining how many species might be found in a sample without replacement is obviously related to the problem of determining the number of species that remain in a community after such a sample is taken. Bearing in mind the warning of Ugland et al. (2003) that species accumulation curves and speciea-area curves are not obviously equivalent, one might nevetheless treat the removal of individuals as equivalent to the removal of their habitat, piecemeal or otherwise. Such an approach is not without hope of succeeding. The general problem of describing species-area relationships has occupied many researchers over the years, with no clear consensus and many hurdles to leap. (Drakare et al., 2006) At the risk of muddying the waters further, but without making any claims for the approach taken here, I will present an untested formula simply as an indication of a possible avenue of research.

In the following analysis I will ignore the smearing-out effect of sampling on specific abundance categories in a community. By this I mean that when species of abundance k are sampled at intensity r, the species that appear in the sample do not all show up with abundance rk, so to speak. Their abundances will be smeared out in that some species will show up with abundances less than rk and some with more. Failure to take this phenomenon into account may produce incorrect formulae, as when Preston (1947) assumed that all species below a certain abundance in the community would fail to show up in a sample at all. (See Sections 3.6 and 3.6.1). Whether the following development will suffer the same fate remains to be seen.

Let C be a community that occupies an area A in a random uniform manner. The following transformation of the logistic-J density function f approximates the effect of removing individuals from C. On average, the effect of removing a proportion r of individuals from a species of abundance x is to map that species into one of abundance (1-r)x. This implies the transformation,

$$f(x) \dashrightarrow g(x), \text{ where } g(x) = f(x/(1-r))$$

To discover the number R' of species that remain after the removal of a given number of individuals, one may must add up all the contributions to R' from 0 to Δ. This may be done via the following integral, pretending for the moment that f and g are continuous functions. Some basic algebra applied to the function f(x/(1-r)) yields the integrand that appears here.

$$R' = Rc\int_0^{\Delta} (1-r)(1/(x + \varepsilon') - \delta)\, dx,$$

where $\varepsilon' = (1-r)\varepsilon$. Evaluating the integral, one obtains,

$$R' = Rc(1-r)[\ln(x + \varepsilon') - \delta x)]\Big|_0^{\Delta}$$

$$= (1-r)(c/c')R,$$

where $c' = 1/(\ln((\Delta+\varepsilon')/\varepsilon') - 1) = 1/(\ln(D/e'+1) - 1)\ \alpha\ C(1-r)\ln(D/(1-r))$, with C, D constants

The ratio c/c' is not a very pleasant expression to deal with, but for present purposes it is enough to recognize that if ε and Δ are fixed, so is the denominator in the resulting expression,

$$c/c' = (\ln(\Delta+\varepsilon')/\varepsilon') - 1) / (\ln(\Delta+\varepsilon)/\varepsilon) - 1)$$

r	**(1 - r)**	**c/c'**	**x (1-r)**	**R'**
0.1	0.9	1.02	0.92	46.0
0.2	0.8	1.05	0.84	42.0
0.3	0.7	1.08	0.76	38.0
0.4	0.6	1.11	0.67	33.5
0.5	0.5	1.15	0.58	29.0
0.6	0.4	1.20	0.48	24.0
0.7	0.3	1.27	0.38	19.0
0.8	0.2	1.36	0.27	13.5
0.9	0.1	1.51	0.15	7.5

Table 9.5 Numbers of species that remain following removal of rN individuals

For example, suppose that R = 50, Δ = 1000, ε = 4.0 and that r varies from 0.1 to 0.9 in steps of 0.1. In this case, the denominator has the fixed value 4.525 and the ratio c/c' may readily be calculated, as shown in Table 9.5.

It will be noted that the ratio c/c', combined with the factor (1-r), amounts to the proportion of species that remain. The last column of the table lists the results of applying this proportion to yield the number R' of species that remain The figures so obtained suggest that R' declines somewhat less rapidly than the proportion (1 - r).

If this approach bears the scrutiny that would result from experimental computer testing, it would have obvious applications to habitat loss. For example if the community in question happened to represent the mosses in a 2-hectare wetland and half the wetland were bulldozed to make way for a housing development, the number of species present would drop from 50 to about about 29 or nearly two-thirds, on average.

Not surprisingly, the mathematical machinery just developed runs equally well in reverse gear.

$$f(x) \dashrightarrow g(x), \text{ where } g(x) = f(x(1-r))$$

This results in the parallel integral,

$$\Delta$$

$$R' = Rc/(1+r)\int_{0} (1/(x + \varepsilon') - \delta)\, dx,$$

where $\varepsilon' = \varepsilon/(1+r)$. Cutting to the chase, one arrives in the end at the following expression.

$$R' = (1+r)(c/c')R,$$

where $c' = 1/(\ln(\Delta+\varepsilon')/\varepsilon') - 1$. It is now possible to produce a new table on this basis. The number R' of species in an expanded (similar) area would result from the increase in the number of individuals by a factor $(1 + r)$. The same initial community LJ[4.0, 1000] x 50 is used here.

Other things being equal, the growth in R' is proportional to the quantity,

$$(1+r) \ln(D/(1+r)) ,$$

where D is a constant that has absorbed the other two parameters for simplicity of expression. The essential ingredients of the resulting formula for R' include a factor that increases linearly with r and the logarithm of a factor that decreases inverse linearly with r. The first factor "wins out" in the sense that the quantity R' increases without limit. At the same time, the slope of the resulting curve tends to zero, although not quickly enough for an asymptote to exist. As with so many of the formulae that arise from logistic-J theory, this one is also mixed log/linear in form.

r	**(1+r)**	**c/c'**	x **(1+r)**	**R'**
1.0	2.0	0.84	1.68	84.0
2.0	3.0	0.79	2.28	113.9
3.0	4.0	0.70	2.79	139.3
4.0	5.0	0.65	3.24	162.0
5.0	6.0	0.61	3.65	182.6
6.0	7.0	0.58	4.03	201.3
7.0	8.0	0.55	4.37	218.7
8.0	9.0	0.52	4.69	234.7
9.0	10.0	0.50	4.99	249.5

Table 9.6. Numbers of species that result from the addition of rN individuals

This approach to species area relationships awaits confirmation by further analysis and computer experiments.

9.4 The multispecies logistical system and its variations

As recounted in Section 1.5, the multispecies logistical system began as a dog-eat-dog interaction among mutually predatory species. If an individual of one species ate an individual of another, the first species would increase by one individual, while the second species would decrease by one individual. Once it dawned on me that the system had another, altogether different interpretation (without altering the underlying dynamic), the way to further generalizations lay open, as described in Section 6.1.1. In what follows, the reader may freely substitute the word "community" for the word "system", since the systems are intended to reflect the behaviour of real communities. Throughout the following development it should be clear that the basic system is capable of endless variation, being what systems developers call "detail hungry".

At the very core of all stochastic systems lies the inner dynamic that guarantees statistically the emergence of the characteristic logistc-J shape. It results simply from the tendency of abundant species to change their abundances more quickly than less abundant species. The analogy with the heated gas explained in Section 2.3 places the phenomenon on a quasi-physical footing akin to statistical thermodynamics.

9.4.1 The basic system

The multispecies logistical (or MSL) system is the name given to the basic stochastic dynamical system, as described in Section 1.5. One may replace the idea that one species is eating another by the interpretation that each death coincides with a birth. One may generalize that notion, in turn, by requiring that births and deaths should maintain a short-term statistical balance, as in the strongly stochastic system, or a long-term statistical balance, as in the weakly stochastic system or the cyclic system to be described. The trophic interpretation, on the other hand, gives rise to a version in which species are divided into trophic compartments. A final version involves abundance partitions, as introduced in Section 6.1.6.

9.4.2 The strongly stochastic system

The strongly stochastic logistical system generalizes the one-for-one replacement scheme of the MSL system by a probabilistic rule that allows births and deaths with equal probabilities. The basic dynamical cycle selects an individual (not a species) at random and either removes it from the system (death) *or* it adds a new individual to the species to which the selected individual belongs (birth). The probabilities of birth and death are fixed and equal.

9.4.3 The weakly stochastic system

The weakly stochastic logistical system generalizes the strongly stochastic one by allowing the probabilities of birth and death to wander from equality, as long as a long-term average equality is maintained. In this system one observes with interest that probabilities themselves may be given probabilities. In both systems the total number of individuals is no longer fixed, but varies more or less normally about a characteristic value. All three systems produce the logistic-J curve when histograms are taken at any post-equilibrium time.

9.4.4 The partitioned system

The partitioned stochastic logistical (or PSL) system is a newer idea based on the phenomenon of climax communities as explored in Section 6.1.5. Although it operates under the rather strange principle of stochastic rebound, it clearly has the same behaviour as the previous systems. This system alone is obviously capable of endless variation. For example one may have more than one rebound partition in one's system.

9.4.5 The cyclic stochastic system

Besides climax communities, the other problem discussed in Section 6.1.5 involved populations undergoing seasonal changes, such as that experienced by temperate zone insects. A time-varying probability curve that extends over an annual cycle may have any shape one likes, steady or varying, but with the death probability preponderant over the cold season and birth preponderant over the warm seasons. The only *sine qua non* would be that both probability curves should have equal integrals annually. The cyclic stochastic logistical system exists at present only in the proposal form and is completely open for experiments by interested parties. In this connection, I should remark that, in adding detail to the system, there is nothing to prevent one from specifying a different probability curve for each species in a community.

9.4.6 The compartmentalized trophic system

In the trophic stochastic logistical system, species are divided into compartments intended to reflect real food webs. A preliminary version of this system has three trophic compartments: producers, consumers, and decomposers, respectively. Individuals are chosen ar random, as in all previous versions of the MSL system. Individuals in the first compartment reproduce with a fixed probability, presumably deriving their energy from an outside source, such as plants absorbing energy from sunlight. When an individual is chosen from the second compartment, it "eats" an individual from the first compartment at random, reproducing in consequence. Finally, every time an individual is chosen from the decomposer compartment, it "eats" an individual from either of the first two compartments at random. Just as producers come into being at random, so decomposers disappear at random. Admittedly a crude reflection of energy flow in nature, this system also appears to produce the characteristic logistic-J shape, although that remains a purely visual assessment, no actual testing having been carried out with this system.