Chapter 6. The Stochastic Community

Viewing a natural community as a dynamic system, we may readily imagine populations fluctuating over time, some increasing, some decreasing, others retracing their steps. A myriad of physical events and natural interactions influence the ups and downs of every population in a manner that (with a few caveats) appears to be effectively random. In this chapter I describe three abstract systems that provide a framework for the stochastic species hypothesis. I then demonstrate that the ones intended to reflect the behaviour of real communities follow the logistic-J distribution.

I then provide alternative but equivalent formulations of the stochastic species hypotheses by analysing time series of events.

Finally, I state an "isotropic principle" which insists that there is no intrinsic difference between the histograms of samples and those of communities or between samples of different species, for that matter.

6.1 The logistic-J Community

The stochastic species hypothesis forms the centrepiece of this section. Central to the hypothesis is the notion of innate probabilities that cannot be observed or measured directly. The same notion is central to the theory of evolution (probability of survival), so it is not a new concept, in principle. On the other hand, some may question the "reality" of an unseen probability -- and not without reason.

Interestingly, the same notion lies at the heart of the most successful physical theory ever discovered -- quantum mechanics. Photons that pass through a single slit may manifest anywhere on a screen according to the (statistical) dictates of the wave function, a "probability wave" that merely governs the overall distribution of photons on the screen (Rae 1986, p. 10). The reality of the underlying probabilities is inferred from the reality of the pattern so manifested. The

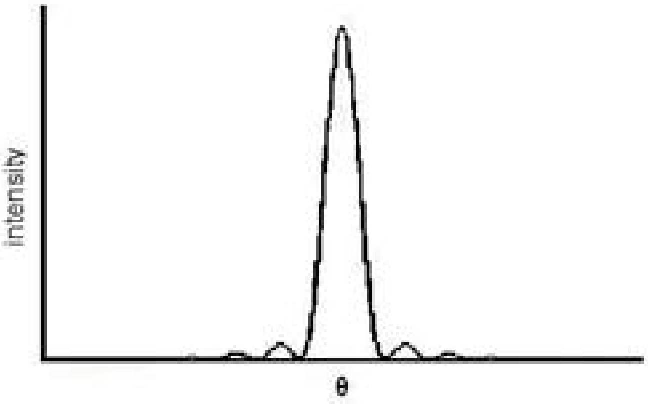

Figure 6.1. Airy Pattern

conversion of a photon in its wave (probability) form to a small flash of light on the screen, its particle form, involves the infamous “collapse of the wave function,” a seemingly random point on the screen where the photon manifests and becomes visible. The placement of all such points nevertheless follows the Airy distribution, as shown in Figure 6.1. The precision with which the manifesting pattern of flashes on the screen “fill out” the Airy distribution cannot be gainsaid; the more photons that arrive at the screen, the more fully and accurately that distribution (and no other) appears.

Such probabilities can only be “measured” after the fact. Only by counting the births and deaths within a population over time can we infer anything about the hidden probabilities. And of course, we may get it wrong. The births and deaths manifest such probabilities only in the long run, as the expression goes.

6.1.1. Stochastic systems

Up to this point I have not been very precise about what the term “stochastic community” actually means. I therefore begin at the most general, entirely abstract level.

A *stochastic system* is a set C of N elements (called *individuals*) that is partitioned into non-empty subsets (called *species* or *populations*, according to context). The species are indexed by the integers 1, 2, 3, . . . , R and the community system obeys the following dynamic that incorporates a clock based on a fundamental time unit, τ. At each tick of the clock (passage of one time unit) an individual is selected at random from C and is either duplicated (a birth), deleted (a death), or left alone, resulting in a new value for N, namely N-1, N or N+1. A stochastic system also has a set of rules that govern the relative probabilities of a birth (p_i) versus those of a death (q_i) for an individual belonging to species i, where $p_i + q_i = 1.0$ The rules may be fixed for the duration or they may vary, depending on the type of system being defined. If the p_i and q_i all have the same value, the system is called *uniform*, otherwise *nonuniform*.

A stochastic system is *strongly stochastic* if at each iteration of the system an individual is chosen at random and reproduces (increase of 1) or dies (decrease of 1) with probability

$$p_i = q_i,$$

where i is the species to which that individual belongs and $p_i \leq 0.5$, allowing for the possibility that a randomly drawn individual will not change at all.

Example: The MSL system is obviously a uniform strongly stochastic community system in which pi = 0.5 for all index values i = 1, 2, 3, . . . R.

It is a highly remarkable (and hitherto unsuspected) fact that a strongly stochastic community does not produce what ecologists call “regulated” populations. Quite the contrary. A large number of populations will drift toward low abundance, while a few populations will drift, with equal certainty, to high abundances. As the system progresses, some of the low abundance populations become numerous again, while one or more of the high-abundance populations will decline in number. All of this happens without the probabilities ever failing to be exactly equal! This result has been demonstrated by extensive experiments and the proof is explained below.

A stochastic system is *weakly stochastic* if the differences in the probabilities p_i and q_i are normally distributed with mean zero and subject to the constraint that $p_i + q_i \leq 1.0$. I will use the following table to illustrate this notion.

probability p_i	**probability <u>of</u> p_i**
0.1	0.0000
0.2	0.0156
0.3	0.0938
0.4	0.2344
0.5	0.3125
0.6	0.2344
0.7	0.0938
0.8	0.0156
0.9	0.0000

Table 6.1. Table of (birth) probabilities

At each iteration of the system an individual is selected at random from the community and the nature of the event (birth or death) is decided first as an equiprobable outcome. If a birth is selected, the probability of a birth is determined according to the distribution in the second column. Most likely, the probability 0.5 will be selected, next most likely 0.4 or 0.6, and so on. The probability of a death is determined in the same way.

Example: The StoComm system (See appendix A.7) uses Table 6.1 to govern probabilities of births and deaths. Figure 6.2 shows an example of the distribution produced by the weakly stochastic system. The distribution records the long-term (average) behaviour of this system.

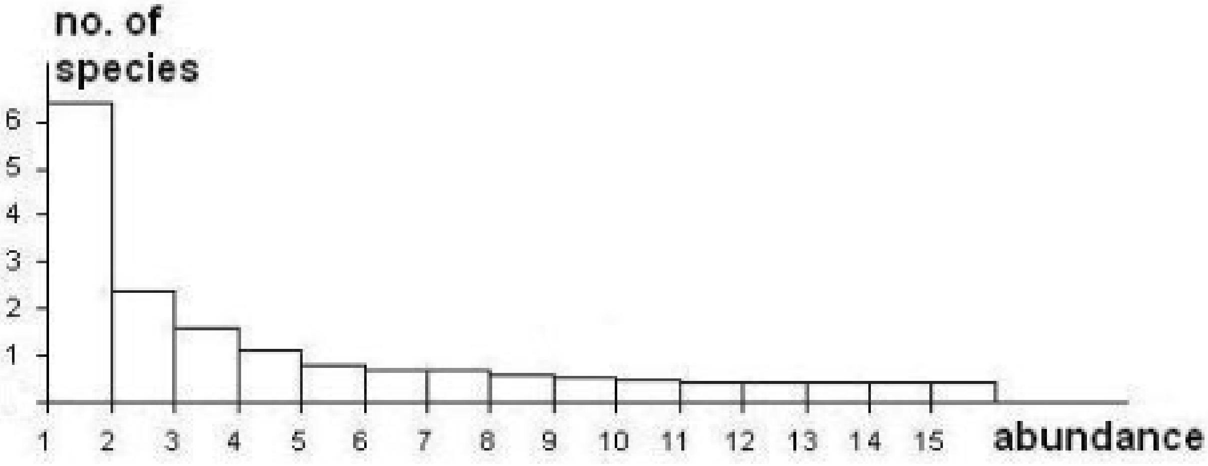

Figure 6.2. Average distribution of abundances produced by StoComm.PAS

The distribution shown represents a weakly stochastic system with 50 species. The species abundance histograms so produced have been averaged over 500 cycles, each cycle consisting of 100 iterations of the basic procedure.

The chi square score for this particular distribution, when compared to the logistic-J distribution, is 2.489 at 5 degrees of freedom. This is a relatively close fit (5.000 being the average under the null hypothesis) but proves nothing. An indication of the actual presence of the distribution in these data comes from further experiments in which the number of cycles is increased to 1000, then 1500, and so on. A continuing decline in chi square scores toward zero implies the logistic-J distribution -- up to a certain point. For example, in the case at hand the 1000 cycle average yielded a chi-square score of 0.611 at 5 degrees of freedom. This fit is very good indeed but in the next section it will be shown that chi square scores may not improve much beyond this order of magnitude, owing to the smearing-out effect of oscillations inherent in strongly stochastic systems and almost certainly present in weakly stochastic communities as well.

6.1.2. Oscillations in stochastic systems

A remarkable feature of equation (ii) in Section 2.1.2 is that for any fixed value of μ it yields a function of ε with two branches. For a given value of Δ it has either no solutions, one solution or two solutions in e, as shown in Figure 6.3.

$$\mu = c((\Delta^2 - \varepsilon^2)/2\Delta - \varepsilon\ln(\Delta/\varepsilon))$$

Expanding the equation in question and transposing terms, we obtain

$$\varepsilon\cdot\ln(\Delta/\varepsilon) = = \Delta/2 - \mu\cdot(\ln(\Delta/\varepsilon) - 1)$$

or $$(\varepsilon + \mu)\cdot\ln(\Delta/\varepsilon) = \Delta/2 - \mu$$

Figure 6.3 shows a plot of the implicit function, with ε treated as the independent variable. For any value of Δ below the minimum of this function, there is no value of ε that will satisfy the equation. At the critical point (ε_c, Δ_c), there is exactly one solution, and for values of Δ above Δ_c, there are always two solutions, as illustrated by the dashed lines. A glance at the diagram reveals that the logistic-J community may occupy either of the two branches of the solution curve. The left branch is asymptotic to the line ε = 0.0, while the right branch is asymptotic to a line having the form Δ = aε - b, where a and b are positive constants. [note: axes to be labeled]

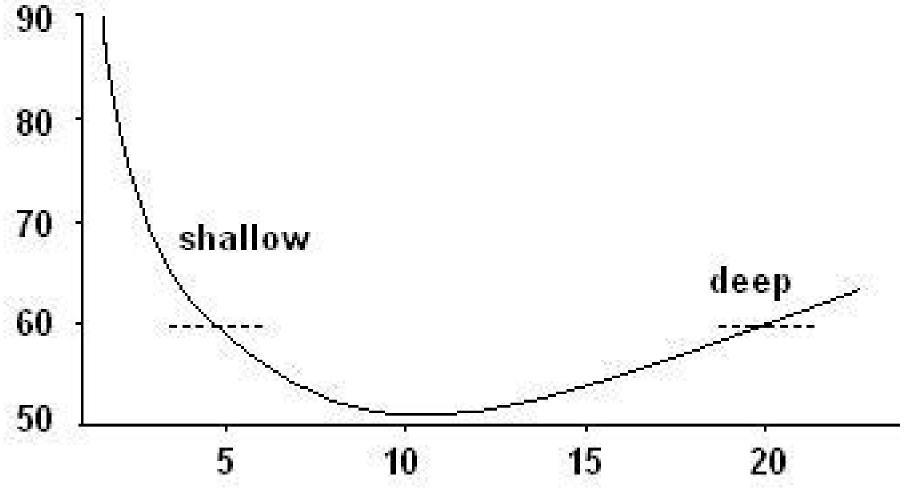

Figure 6.3. Δ as a function of ε, with μ fixed (at 10.0)

The two branches will be called the *shallow* and *deep branches*, respectively. A community having parameter values that place it on the shallow branch will be called *shallow, while* a community occupying the deep branch will be called *deep*. A shallow community may have a great many species of low abundance, while a deep one tends to have relatively few. Figure 6.4 illustrates the two types of community. I remind readers that no references can be supplied with these assertions since we have no complete surveys of any community, per se. However, because these oscillations occur in systems based on the logistic-J theory, they undoubtedly occur in any system that is weakly stochastic.

No particular relationship between richness and either the deep or shallow community types is imposed by the formula for m, since it is independent of richness. Thus, sight unseen, one could have two communities sharing the same value of Δ and having the same number of species, yet one will be shallow (with a rather small values of ε) while the other is deep (with a relatively large value of ε).

The vertical scale of the two logistic-J density functions has been greatly exaggerated so as to make plain the contrasting shapes.

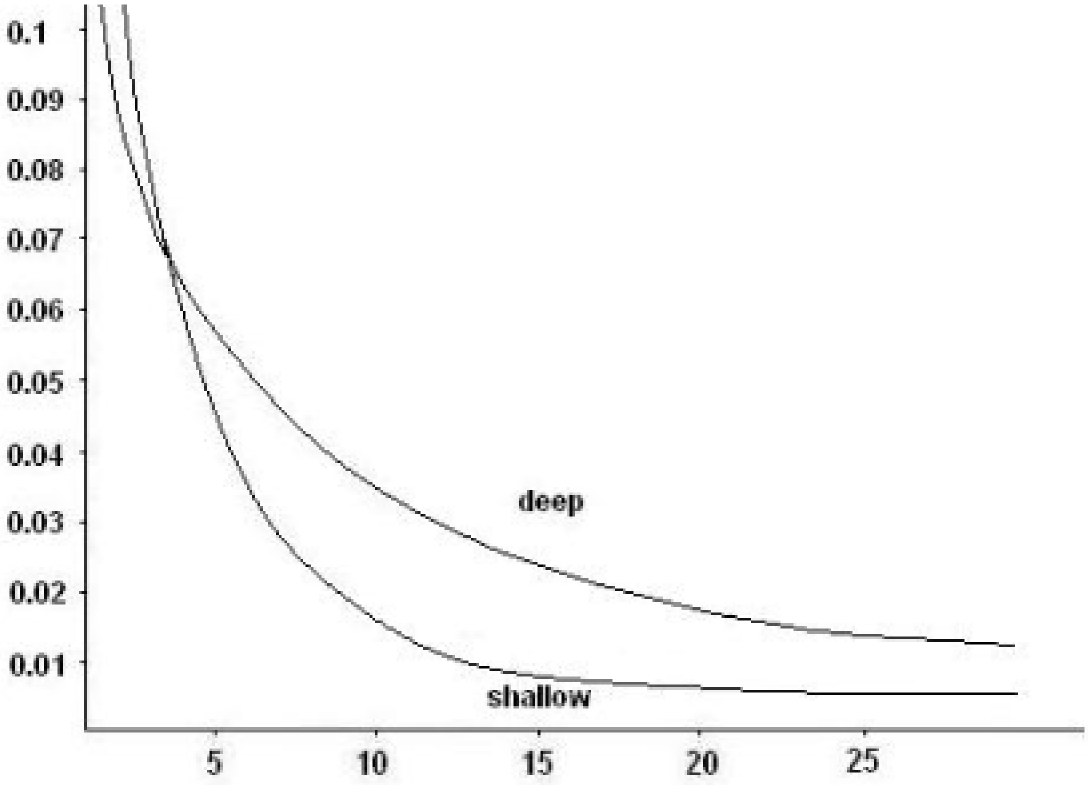

Figure 6.4. Deep (upper) and shallow (lower) communities

Given that ε is typically smaller in a sample than in the community it came from, it might be supposed that all communities are relatively deep, but this remains to be seen. Theoretically, a community of one type can evolve into the other with no change in biomass. However, it must be remarked that a shallow community, particularly with an epsilon-value smaller than, say 0.1 (assuming unit abundance categories) will be rather unstable, losing several (or many, as the case may be) of its species over a relatively short time.

The oscillations described above appear to occur in the simplest MSL system, as embodied in the program Scram1. Since the mean abundance is fixed in this system, the constantly fluctuating histogram always has this mean abundance, whence contractions in delta involve contractions in Fa, the number of species of lowest abundance. The system can then "wander" through various combinations of ε and Δ, the product of these two parameters always being constant. In other words, one can always identify the state of the community by the position it occupies on the "track" of Figure 6.3. Once the MSL system reaches equilibrium, with all trace of the initial conditions (all abundances equal) erased, the parameter values will wander at random. This behaviour can be visualized as a random walk along the track of Figure 6.3.

If the MSL system is run for increasing periods of time, the chi square fits of the resulting average distributions improve up to a point, then become steadily worse. Table 6.3 displays the results of three statistical runs of the MSL program. The statistical part simply compiles the number of species inhabiting each abundance category at each cycle, computing an average when the run is finished. In this experiment the system was run for 2000 cycles to attain equilibrium, then the statistics package was turned on. In each case, the final average histogram was compared to the logistic-J distribution according to the best fit procedure.

No. of cycles	Best fit score
5,000	0.577 @ 8 df
7,000	0.790 @ 8 df
10,000	0.962 @ 8 df

Table 6.3. Scores increase with number of cycles

The reason for the deteriorating fit lies mainly in the tendency of the MSL system to oscillate or wander in terms of its overall shape, as in Figure 6.4 With the passage of time, both Δ and ε vary over wider ranges of values and one is adding somewhat incompatible versions of the distribution together in computing the average. The sum of two histograms having the logistic-J distribution with differing parameter values is not quite a logistic-J distribution, although it may be a close approximation, as the relatively low numbers in the table imply.

A similar two-branched curve results when we plot the quantity F_1, the number of lowest-abundance species as a function of e.

6.1.3 Stochastic systems and the logistic-J distribution

As shown in Appendix A.5, a weakly stochastic system will produce a species abundance graph that follows the logistic-J distribution. The following analogy should make the central idea behind the proof clearer to readers.

Suppose that 100 cars (read species) have joined a most peculiar race. A very long circular track has been divided into 500 m speed zones that range from 10 km/hr to 100 km/hr. Each car in the "race" obeys the speed limits strictly, never driving below or above the speed limit of the zone that it happens to occupy. For example, a car entering the 10 km/hr zone from the 60 km/hr zone abruptly lowers its speed from 60 km/hr to 10 km/hr. Whereas it took only 30 seconds for the car to traverse the 60 km/hr zone, it will take it 180 seconds for it to traverse the 10 km/hr zone. In other words, a car spends more time in the lower speed zones and less time in the higher speed zones. Given that a car leaves the starting line every five seconds,the number of cars occupying the s km/hr zone will be the hyperbolic function, 2500/s.

The proof of the theorem employs a similar formula (having the same dimensions) that yields the "dwell time" of a particular species in a particular abundance category. The theorem is proved first for uniform communities in which the probability p of increase is the same for all species. In a corollary, I relax this restriction and observe that the theorem also holds for nonuniform communities in which different species have different probabilities of increase (or decrease). The distributions thus derived both turn out to be the discrete logistic-J distribution without the parameter epsilon:

$$f(k) = c(1/k - \delta); \quad k = 1, 2, 3, \ldots \Delta$$

The more general (continuous) form incorporates a second parameter, ε that allows for fractional abundances and turns out to have a symmetrical relationship with δ, both being interpreted as displacements from the axes of a standard hyperbola. The second parameter is certainly essential in capturing the full range of shapes that appear in samples, not to mention natural communities.

6.2 Stochastic communities in nature

Central to the theory presented in this book is the stochastic species hypothesis which posits a long-term equality between the probability of birth and death within all populations of a community. At the far end of this hypothesis, so speak, support is drawn from the simple fact that, for the great majority of populations, every life ends in death. At the near end, the twin probabilities p of birth and q of death may fluctuate about equality and the impact of these fluctuations on the shape of the community is explored. The exploration begins with clear definitions of the stochastic species hypothesis.

6.2.1 Stochastic species hypotheses

Although it may be doubted that real communities obey this hypothesis in its strong form, it is more difficult to doubt that real communities obey its weaker form, now to be introduced. In Section 6.1.1 I introduced definitions of stochastic communities-as-systems. Her I shift the focus to natural communities.

The *strong stochastic species hypothesis* holds for a natural community when, over a certain fixed time unit τ, the probability of a randomly selected individual reproducing equals the probability if it dying. One could rephrase this statement by replacing the word "reproduce" by "increase" and the word "death" by "decrease". The hypothesis would then state that a randomly selected individual would have an equal equal chance of increasing as it does of decreasing. If the probability is p (= q), then the chance of each individual to increase or decrease would be

$$p/N,$$

since the individual must first be selected from a community of size N.

Moving to the level of a species, the statement takes on a new form, but equivalent to the foregoing. Over the period τ, a species of abundance k would have an equal change of increasing as it does of increasing, namely

$$kp/N$$

Finally, over the interval τ, the community as a whole would have an equal chance of increasing as decreasing, namely

$$p,$$

since all populations sum to N and N/N = 1. I will take these three definitions as being equivalent in the context of real communities, even though it is easy to construct highly pathological "communities" that obey the last version, but not the previous one.

The *weak stochastic species* hypothesis holds for a community in which every individual has a "nearly" equal probability of reproducing as it does of dying. By "nearly" is meant that the two probabilities may differ but have the same long-term average, as in Table 6.1.

6.2.2 Natural communities are weakly stochastic

Shown in Figure 6.5 below is a hypothetical time-series in which the variations in a particular population (species) of a natural community are represented by births (1) and deaths (0). The size of the population can be tracked by starting with some initially known figure m, then adding 1 every time a '1' is encountered in the sequence and subtracting 1 every time a '0' is encountered. The axis in Figure 6.5 is not labeled, relative time being indicated by spaces in the diagram. The fundamental time unit τ is assumed in this context.

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--|-----|--|---------|----|-|------|------|----|---------|---|---|--------|----|------|--|-|----|---------|---
  1     0  1         1    1 0      1      1    1         0   1   0        1    1      0  1 0    1         1
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Figure 6.5. A hypothetical time-series for a population

Suppose now that the probabilities of birth and death for the population in question are p_τ and q_τ, respectively, over the time period τ. It may be asked, for each probability, what the long-term average time is between births -- or deaths. It will be convenient to refer to these periods as *time-wavelength*, denoted by λ. One needs a formula for λ births as a function of $p\tau$.

In most applications involving uniform random time series in scientific or industrial simulation, inter-event times are described accurately by the exponential distribution, the continuous cousin of the Poisson distribution. (See Appendix A.4 for the proof.) The following density function incorporates the wavelength λ into its formula.

$$f(t) = (1/\lambda)e^{-t/\lambda} \quad ; t > 0$$

The density function gives the distribution of inter-event times, of which the average is the wavelength λ. For large values of t the function is very small, meaning that the occurrence of interarrival times of such magnitude happens only rarely. In fact the exponential distribution yields an exact value for p_τ. It is simply unity minus the relative f-density of all those instances where the inter-event interval exceeds the time unit τ.

$$p_\tau = 1 - \int_\tau^\infty (1/\lambda)\, e^{-t/\lambda}\, dt$$

$$= 1 - (1 - e^{-t/\lambda}) \Big|_\tau^\infty$$

$$= 1 - e^{-\tau/\lambda}$$

This relationship between τ and λ is invertible and one has,

$$\lambda = - \tau/\ln(1 - p_\tau) \qquad \text{(i)}$$

The quantity so derived is positive in spite of appearances; the natural logarithm of a number less than unity is itself negative. A similar relationship involving the wavelength associated with the probability q_τ may also be derived. If q_τ differs from p_τ, the two wavelengths must also differ.

Now let n(t) denote the number of individuals born over a more lengthy period of time t and let m(t) denote the number of deaths over the same period. The following ratio estimates n(t) with increasing accuracy as t increases:

$$n(t) \approx t/\lambda$$

From equation (i) it follows that

$$n(t) \approx - t\ln(1 - p_\tau)/\tau \qquad \text{(ii)}$$

Similarly, $$m(t) \approx - t\ln(1 - q_\tau)/\tau \qquad \text{(iii)}$$

If one posits a population limit L reflecting ongoing trophic or other conditions, the conclusion of equality of the two probabilities is inevitable. If a population of size P was initially present, the size P(t) after t time units would be

$$P(t) = P + n(t) - m(t),$$

The inequality

$$P(t) \leq L$$

implies that $P + n(t) - m(t) \leq L$

yielding $n(t)/m(t) \leq (L - P)/m(t) + 1$

Since the quantity (L - P) is finite and bounded, while the quantity m(t) increases without limit,

$$\lim_{t \dashrightarrow \infty} n(t)/m(t) \leq 1$$

By invoking a lower limit L' on the population, the opposite inequality appears:

$$\lim_{t \dashrightarrow \infty} n(t)/m(t) \geq 1$$

Under these conditions, the ratio is clearly approaching unity and n(t) and m(t) are asymptotically equal.

$$n(t)/m(t) \approx 1.0$$

so that $n(t) \approx m(t)$

By substituting the expression (ii) and (iii) for n(t) and m(t), respectively, we obtain the asymptotic equality of two otherwise identical expressions containing p_τ and q_τ respectively and sensitive to their values. Since the variable t cancels in the resulting ratio, it follows immediately that

$$p_\tau = q_\tau$$

The equality results from the fact that the two probabilities are fixed. If they vary, as is probably the case in a natural community, they will end up eternally chasing each other, so to speak, with one larger at one time and the other larger at another time. It would then follow that if all the species in a community behave as the one in hand, then the community obeys the weak stochastic hypothesis.

A final remark concerns the distribution of increases and decreases over periods of time that are integer multiples of t. Thus at time t = xt, the probability that a species will have k more individuals is the binomial expression,

$$p(k) = nCk\ p_{\tau}{}^{k}(1-p_{\tau})^{n-k}$$

The binomial distribution characterizes the occurrences of increase and decreases for species in strongly stochastic communities. The same distribution probably characterizes weakly stochastic communities, although the probabilities $p\tau$ will vary over time.

6.3 The stochastic orbit and its variations

Some final remarks concern the motion along the abundance axis of a species through time. I describe this as a *stochastic orbit*. In such an orbit, a species does not progress evenly through its abundances (as a planet progresses evenly through its positions), but erratically, rather in the manner of a random walk, although not quite. Total biomass/energy conservation constrains the orbit statistically at the high abundance end, while species at the low abundance end have slowed to a relative crawl. Indeed, over time and under suitable measurement constraints, a single species will recapture the logistic-J distribution all on its own. The probability of finding a given species at a given position is governed by the logistic-J distribution. It would manifest in a manner similar to that of the Airy distribution in the case of photons passing through a single slit.

In his Robert H. MacArthur Award Lecture, Murdock (1991) illustrated the difficulty of establishing the presence of density dependence in various populations under study. The notion of "regulated populations" was slowly giving way to non-equilibrium population dynamics, an approach that began in the late 1960s, (Den Doer 1968), (Levins 1969), and developed more recently in (Finerty 1980), (Koetsier et al. 1990), and (Murdock 1994). In the non-equilibrium dynamical view, local populations are free to fluctuate randomly, with local extinctions more or less balanced by immigration from neighbouring communities. Indeed, the logistic-J distribution may be regarded as a strong candidate for the "fixed probability distribution" proposed by Murdock. The intermediate notion of "stochastic boundedness" (Chasson 1978) sought to harmonize the two extremes by invoking density dependence as a mechanism only at the extremes of high or low population densities.

Suffice it to say that the most recent approach to population dynamics is entirely consistent with the theory proposed in this book. One might simply add the caveat that the search for equilibrium might appear to be misdirected when aimed at single populations and not whole communities, where true equilibrium is to be found. As we have seen in the foregoing chapters, population sizes may wander more or less randomly, sometimes increasing to dominance and sometimes diminishing to small numbers.

At the same time, one must take account of various cycles in some populations. For example, many insect populations in temperate climates increase dramatically over the warm seasons, only to decline as cold weather approaches. Another example involves predator-prey cycles as described by the Lotka-Volterra equations and apparent in trapping data (Leigh 1968) and from other sources.

Slow seasonal changes in weather or other gradual factors that affect abundance can be viewed as an ocean swell that lifts a pattern of foam up and then down again; the pattern remaining much the same. The J-curve for a community of insects in a temperate biome might well stretch out horizontally as the warm weather intensifies, with many species increasing almost daily in abundance. With the onset of cold weather, the J-curve shrinks back to smaller dimensions. Of course, how one counts the insects under these circumstances may alter the picture considerably. Insects may deal with cold weather in a variety of ways. In North America, among the Lepidoptera alone for example, the Monarch butterfly migrates south to Mexico, the Mourning Cloak overwinters in the adult form, the Black Swallowtail overwinters as a pupa (chrysalis), the Wooly Bear overwinters as a larva,and the Eastern Tent Caterpillar overwinters as an egg.

If one counts only the adults in a given population, the count during the winter months would drop to zero, except for those species that overwinter as adults or migrate away. If one counts different life stages, however, nonzero counts will be maintained. Indeed, if one counted the egg form, the population would appear to surge during the fall, when most of the eggs are laid. Egg mortality would gradually reduce the count until spring, as with other forms. In cases like this, one does not see the typical ups and downs of the stochastic vibration that has been invoked (by implication) for so many other biota. However, a simple alteration of the underlying stochastic system will reproduce the result without changing the logistic-J outcome.

Section 9.3 I describes a variant of the weakly stochastic logistic system in which the probabilities of birth and death, instead of fluctuating in a neighbourhood of equality, follow what might be called a seasonal probability curve. Thus, in the early spring, let us say, the probability of birth, previously less than the probability of death, begins to climb rapidly as eggs begin to hatch, even as the probability of “death” begins an abrupt decline. By the end of the warm season, the two probabilities are approximately equal, following which the probability of birth begins a slow decline. Obviously one may impose any regimen one likes on seasonal changes, as long as the two probabilities come into balance at least once a year.

Predator-prey cycles have little effect on samples of communities since typically only two species are involved and the cycles themselves are somewhat irregular. On the other hand one may implement the MSL system with two species A and B and reinterpret births and deaths as follows. If A is the predator and B is the prey, an increase of A at the expense of B may be given the usual interpretation. However, an increase in B at the expense of A may be interpreted as the failure of A to find B, dying as a result, with a subsequent increase in B’s population. This system does not produce cycles of any regular kind. Indeed, the classic experiments of Gause (1934) with protist predators (*Didinium*) and prey (*Paramecium*) also failed to produce any cycles.

Finally, it may be remarked that the two-species system reproduces the gyrations of the logistic map described in Section 3.4.

One well-known biological phenomenon seems, at first sight, to stand in the way of the views presented here on stochastic populations. In some plant communities, whether of woody or herbaceous type, the well-known phenomenon of succession involves a gradual change in the composition of a plant community, usually following a disturbance. (Riklefs 1990, p. 677) For example in a specific area of Indiana, USA, the woody vegetation that was present 120,000 years ago was erased by the glaciers of the Wisconsinan Period (110,000 BP to 10,000 BP). Post-Wisconsinan, there was a slow succession in that area as woody species invaded from the ice-free lands to the south. First came the conifers, then the mixed hardwood/conifer regime, then the Maple-Basswood forest, followed by the Beech-Maple type. (Braun 1985). Given the relatively stable climate over the area in question during the last few thousand years, Beech-maple forests remained, for the most part, as Beech-maple forest, with American Beech (*Fagus grandifolia*) and Sugar Maple (*Acer Saccharinum*) remaining co-dominants in the canopy. Table 6.4 shows a

species	%
Fagus grandifolia	58.6
Acer saccharum	24.4
Liriodendrom tulipifera	7.9
Fraxinus americana	3.7
Nyssa sylvatica	1.5
Ulmus fulva	1.1
Ulmus americana	0.7
Prunus serotina	0.4
Celtis occidentalis	0.4
Quercus alba	0.4
Carya ovata	0.4
Ostrya virginiana	0.4

Table 6.4. Species composition (%) of a Beech-maple forest (after Braun)

typical survey. Since beeches and maples usually retain dominance in forests of the Beech-maple zone, it may be asked how they can be considered "stochastic" in the sense presented here. Perhaps a closer analysis is called for.

Despite the absence of a complete stochastic orbit for some species in late-successional communities, there is no question that, as far as the 125 biosurveys in the metastudy are concerned, the forest communities that appear in the metastudy followed the same J-shaped pattern as other communities did.

To understand this phenomenon, at least in part, I will invoke a curious feature of the multi-species dynamical system. The feature involves the passage of one species that is declining in abundance, past another that is increasing in abundance. For a period of time, both species have the same abundance. Then they part positions on the abundance axis as the species that is increasing continues to increase and conversely for the declining species. Suppose now that, instead of both species continuing the direction of their changes in abundance, they reverse their former directions. Such an event, as far as pure stochastically is concerned, is equally likely.

The foregoing observation motivates the following definition: The coincidence of two species with index numbers i and j at the same abundance k will be called a *meeting at k*. Suppose that, following a meeting at abundance k, species i increases in abundance, while species j decreases. If the abundance of i was < k formerly, while that of j was > k, the species have evidently crossed paths, so to speak, in their respective orbits. I will call such an event a *crossing*, whereas if both species return to a previous abundance, I will call that a *rebound*.

At any time one may rank the species in the MSL system in order 1, 2, 3, and so on, up to R. For two given fixed ranks, m and m+1, one may seemingly alter the rules governing the system by requiring that any meeting of the two species followed by a separation is a rebound, with each species retaining its former rank. To implement this change, the rules of the MSL system need not be altered at all. One simply interprets the parting of the ways as a rebound! In such a case, the species in the system have been effectively partitioned into two sets, one consisting of the species of rank m or less, the other consisting of rank m+1 or more.

In the MSL system or any of its more general versions, crossings and rebounds at any given position k have exactly the same probability. It follows immediately that one cannot distinguish, from their outward behaviours, a "free" system from one in which a rebound partition has been imposed. Their histograms will be identical. It follows that a full stochastic orbit spanning the entire range of abundances over time is not a fundamental feature of the logistic-J distribution. Indeed, one may partition the entire system, with each species vibrating within a relatively narrow but ever-shifting sub-range of abundances. In such a case the same species would be oscillating about the canonical abundance associated with its rank. Such a possibility remains of theoretical interest only, being highly unlikely in nature.

Returning for a moment to the example of the Beech-maple forest canopy community, we note that the two co-dominant species take up a wide range of relative abundances, with beech more abundant in one forest, while maple predominates in another forest. (Braun 1956) Other species appear to be free to vary in abundances, from zero right up to the the dominant range.

The reason that Beech and Maple so often predominate in this type of forest is that the shade tolerance of younger individuals of these species enables them to survive under a closed canopy, whereas other species tend not to survive this stage unless their is an opening overhead. This theme will be continued in Section 9.3, where it is stated as an open problem. Suffice it to say that further modification of the MSL system is possible, without changing the theoretical shape of its typical histograms.

6.4 The isotropic principle

A useful tool for understanding the relationship between sample and community is the *random sequential representation*. Consider a random sequential arrangement of the N individuals composing a community C of organisms.

$$R_s(C) = (x_1, x_2, x_3, \ldots x_N),$$

For each index value k the set S_k of individuals is defined as follows:

$$S_k = \{x_1, x_2, x_3, \ldots x_k\}$$

This is called the *kth sample relative to Rs(C)*. The samples are not independent, but closely related in an obvious way. As k grows larger, the sample size increases and the corresponding histogram gradually inflates. If one is not allowed to look ahead, but only at the sequence of histograms, there is simply no way to predict when the process will terminate. The present theory will claim that the histograms will simply become larger without ceasing to follow the logistic-J distribution, sometimes closely, sometimes not. This view of the sampling process may be stated as a principle:

There exists no possible test, statistical or otherwise, that will reliably distinguish the histogram of a sample from that of a natural community, nor what organisms have been sampled.

In other words, given a collection of species and abundances (with no other information available), there is simply no way to tell, from the histogram alone, whether it’s a sample of a community or the community itself. With smallish communities, such as all the trees in a one-ha block of deciduous forest, this principle asserts that the histogram of this community could well resemble a sample, say, of fish from a nearby stream..