STABILITY OF ECOSYSTEM MODELS

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CERTIFICATE

The work presented in this dissertation entitled "**STABILITY OF ECOSYSTEM MODELS**" has been carried out in the School of Environmental Sciences, Jawaharlal Nehru Univeristy, New Delhi. The work is original and has not been submitted so far in part or full for any other degree or diploma of any University.

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CHAPTER I

INTRODUCTION

In the prsent dissertation, we have reviewed, to begin with, the data on relative abundance of species within a taxonomic group in various multispecies ecosystems. The most remarkable analysis in this field was done by Preston who fitted the experimental data to lognormal distributions. His work is discussed in detail in chapter II.

In chapter III, we have reviewed the theoretical work of Gunasekaran and Pande who developed the conceptual basis for understanding Preston's lognormal distribution. They took the dynamics of interacting system as given by Gompertz coupled equations for multispecies ecosystems and developed their statistical mechanics, as was done by Kerner for Lotaka-Volterra model. The new Gompertz model led to lognormal distribution of species within a taxanomic group. Though the present analysis is simplistic, it gives the same result, as the more detailed analysis done by Sita Ram, Verma, Pande and Negi.

After reviewing the theoreticl basis for exerimental lognormal distribution, we have developed the stability analysis for our Gompertz model. The stability is then inter-related with some biological parameters of relevance like productivity, biomass and diversity. This analysis is along the lines of Leigh, who developed his interesting approach in the context of the Lotka-Volterra model.

The stability analysis in chapter IV reveals that the stablest food-web structure in the model is that in which every species feeds on all other species which do not feed on it, i.e., the most stable system is also the most connected and therefore the most complex. This result is identical to that of Leigh for the Lotka-Volterra model. The analysis of the model also shows that stability decreases with increasing productivity whereas it varies proportionally with biomass and diversity although the effect of diversity is less pronounced than that of biomass.

The results obtained by us from Gompertz system of equations in chapter IV are basically the same as those of Leigh for the Lotka-Volterra model. This similarity indicates the generality of the results and the results may very well be model independent.

CHAPTER II

A REVIEW OF THE DATA ON THE RELATIVE ABUNDANCE OF SPECIES

The relative abundance of different species within a genera is repeatedly observed by Taxonomists experimentally. Examples are -

i)   Corbet's result on Malayan butterflies.

ii)   William's result on moth species obtained by means of light trap at Rothamsted.

iii)   Saunder's observation on the birds of Quaker Run valley, western New York state.

iv)   Preston and Norris's data on the breeding birds of the Frith (Preston Laboratory grounds).

v)   Dirk's data on Moths in a light trap at Orono, Maine, and

vi)   Seaman's data on moths in a light trap at Lethbridge, Alberta.

In the light of these experimental results several theoretical attempts have been made to describe the distribution of different species. Among these Preston's

distribution is the most satisfactory. He proposed the
distribution,

$$n = n_o \, e^{-(aR)^2} \tag{1}$$

where n_o is the number of species belonging to the so-called
octave, n is the number of species belonging to an octave
distance R octaves from model octave and 'a' is a constant
calculated from experimental data. This distribution, being
the most remarkable hypothesis in this field, deserves a
detailed discussion.

Preston's Analysis

The species abundance data reveal that the
collections in all cases contain many rare species and a few
abundant ones, although, of course, in terms of numbers of
individuals those of few common species far outnumber those
of many rare species. In any case, in view of the large
variation in the numbers of individuals per species, it is
convenient to plot these numbers on a logarithmic scale.
Preston considered the number of species, n_1, n_2, n_3,....,
and in general n_r, represented respectively by one
individual, two individuals,.... and in general by r
individuals, i.e., he considered the different species

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frequencies. He then plotted these n_r against the corresponding r, choosing of course, a logarithmic scale for r. Preston found it convenient to introduce a few other technicalities in his analysis. We note those —

In relative abundance of species, we frequently come across the facts such that one species is twice as abundant as another. This led Preston to graduate the abcissa as equal increments in logarithms of the number of individuals representing a species and he used as such increments as "octave", i.e., the intervals in which the representation is doubled. In other words, the mid point of each octave is double that of the preceeding octave. With this the abcissa became simply a scale of octaves which is equivalent to taking "logarithms to the base 2". The detailed grouping of this is given in Table I.

The table I clearly shows the relationship between airthmatic grouping and corresponding logarithmic grouping. For instance, in case of octave B, the airthmatic groupping is 2 to 4 and corresponding logarithmic groupping is 1 t0 2 [since $\log_2 2 = 1$ and $\log_2 4 = 2$]. The way in which the number of species belonging to each octave is calculated is also shown in table I, column IV. For instance , if a

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species is represented by 5, 6 or 7 individuals, it clearly falls in octave C. If a species is represented by 8 individuals, octave C is credited with the other half. In a similar way all other octave are composed. All species falling in, say, one octave may be thought of as having roughly the same degree of abundance, in comparision with those falling in any other octave.

It is noticeable that below octave A will correspond fractional numbers and will thus not correspond to any physically observable situations.

This is indicated in the plots (see figures 1-6) by drawing the curves in this region by broken lines. Preston calls his Y-axis, to the left of which is this broken line, as the " veil line". It should be remembered, however, that doubling the size of the sample will double the number of species belonging to each octave which results in shifting the curve by one octave to the right. In other words, an octave which was hitherto not observable has become observable now. It is thus clear from here that if this process of doubling is continued, all the species that exist in the system will become observable and the corresponding curve will be a true representative of the

system. Of course, the lognormal nature of this curve does

not change as it shifts to the right, the only change being

in the constant n_o and possibly 'a' (introduced below) which

will obviously have numerical value characterised by the

size of the sample chosen.

In all, Preston grouped six different sets of data

in this manner and plotted with abcissa as the scale of

octaves and the frequency of species (i.e.   the number of

species belonging to a particular octave) as ordinate.   He

observed that each curve exhibits a maximum in some octave

to the   right of the first one and the observed octave

frequencies first increase and then decrease.   The mode of

this set of data is that value which occurs with maximum

frequency.   Therefore, the octave which corresponds to the

maximum number of species is known as <u>model</u> <u>octave</u>.   For

convenience, the plots obtained by Preston are all

reproduced at the end of this chapter in figures 1 to 6.

The main point that emerges from this analysis is

that in all cases the data is well fitted by a symmetrical

normal curve truncated on the left. The general equation of

such a curve is :

$$n(R) = n_o \, e^{-(aR)^2} \tag{1}$$

where, n_o is the number of species in the model octave. $n(R)$ is the number in an octave distance R octaves from the model octave and

$$a^2 = \frac{1}{2\sigma^2} \qquad (2)$$

where, σ is the measure of the mean square diviation of the population from its mean value.

We thus have:

$$R = [\log_2 i - \log_2 i^*] \qquad (3)$$

where, i are numbers of individuals, the logarithms to the base 2 of which are plotted along the x-axis and i^* is the particular value of i corresponding to the peak of the curve. Preston took for any i corresponding to any octave the mid value of that octave, in the same way i^* is the mid value of model octave. Note that,

$$\overline{R^2} = \overline{[\log_2 i - \log_2 i^*]^2} \qquad (4)$$

which can be simplified as :

$$\overline{R^2} = \frac{\int_{-\infty}^{\infty} n(R)R^2 dR}{\int_{-\infty}^{\infty} n(R) dR}$$

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$$
= \frac{\displaystyle\int_{-\infty}^{\infty} n_o e^{-(aR)^2} R^2 \, dR}{\displaystyle\int_{-\infty}^{\infty} n_o e^{-(aR)^2} \, dR}
$$

$$
= \frac{\dfrac{n_o \sqrt{\pi}}{2a^3}}{\dfrac{n_o \sqrt{\pi}}{a}}
$$

$$
= \frac{1}{2a^2} \tag{5}
$$

$$
= \sigma^2
$$

Next also that the total number of species N for the system is given by :

$$
N = \int_{-\infty}^{\infty} n(R) \, dR
$$

$$
= \int_{-\infty}^{\infty} n_o e^{-(aR)^2} \, dR
$$

$$
N = \frac{n_o \sqrt{\pi}}{a} \tag{6}
$$

This N should be the total number theoretically available for observation. In practice, the presence of the veil line will imply that the actually observed number is

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smaller. Now since the quantities 'a' and 'n_o' can be calculated from the curve fitted to the data, the theoretical value of the total number of species for the system can be calcualted from equation (6).

The difference between this and the observed value will give an estimate of how much was missed out in any particular sample. In table II, we present the calculated values of 'a','n_o', 'N' as well as the observed values (in the given sample) for N, for all the six cases analysed by Preston. Note that the values of 'a' in all these cases is close to about 0.20.

Noting these points, the distribution given by equation (1) can be conveniently written in the form :

$$n(\log_2 i) = \frac{N}{\sigma\sqrt{2\pi}} \exp[\frac{(\log_2 i - \log_2 i^*)^2}{2\sigma^2}] \qquad (7)$$

which aside from the trivial difference of the logarithms taken to the base '2' instead of base 'e' is identical to the standard lognormal distribution, which will be discussed in the next chapter.

Inspired by the result given by Preston many theoreticians tried to form a conceptual basis for understanding the relative abundance distribution of species. They thought of theoretical models from which the distribution followed by the relative abundance of species with in a genera could be derived. Such models will throw much light on multispecies interactions which in turn would enable us to understand ecosystem and their course of evolution on a precise quantitative basis.

An early attempt in this direction was made by Kendall. He considered a simple stochastic model which allowed for birth and death as well as the immigration process for the population. He was able to obtain a probability distribution for the population which was analogous to that of an earlier result of Fisher. This result was, however obtained for a single species model.

The multispecies problem was first tackled by Kerner. He assumed the dynamics of the multispecies system to be given by the coupled Lotka-Voltera equations, under the assumption of a constraint, he was able to develope the statistical mechanics of these equations. This then led to a population distribution for each of the component species

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which was precisely the χ^2 distribution assumed by Fisher for the so called intrinsic abundance of species.

Though Kerner initiated and applied the statistical mechanical approach very well, left some questions unanswered. One is that it does not lead to a full explanation of the experimental result but leads only to an understanding of an intermediate result. The second problem is that, in view of the results of Preston, the distribution which needs to be explained is not χ^2 or the compound poisson distribution of Fisher but the lognormal distribution.

Pande and Gunasekaran took a fresh model with Gompertz interaction terms to explain the experimental Preston curve, i.e., lognormal curve. Models characterised by such interactions have been discussed for two and three species earlier by Pande and Bhat. They developed the statistical mechanics of this model in the way of Kerner. Their analysis is reviewed in next chapter.

Table-I: Preston's scheme for grouping species frequencies according to "Octaves"

Name of the Octave	Arithmatic grouping of the no. of individuals per species	Corresponding logarithmic grouping	Number of species belonging to that Octave		
			Half of +	All	+ Half of
A	1-2	0-1	1	–	2
B	2-4	1-2	2	3	4
C	4-8	2-3	4	5-7	8
D	8-16	3-4	8	9-15	16
E	16-32	4-5	16	17-31	32
F	32-64	5-6	32	33-36	64
G	64-128	6-7	64	65-127	128
H	128-256	7-8	128	129-255	256
– – – – etc – – – – –		– – – – etc – – – – –	– – – – etc – – –		

TABLE II: Calculated values of a, n_o, N and the observed value of the total no. of species for cases analysed by Preston

Case	a	no.	N	Observed total no. of species in the particular sample analysed
1	0.194	10	91	80
2	0.207	48	410	349
3	0.205	42	363	226
4	0.227	35	273	240
5	0.152	33	384	277
6	0.160	30	332	291
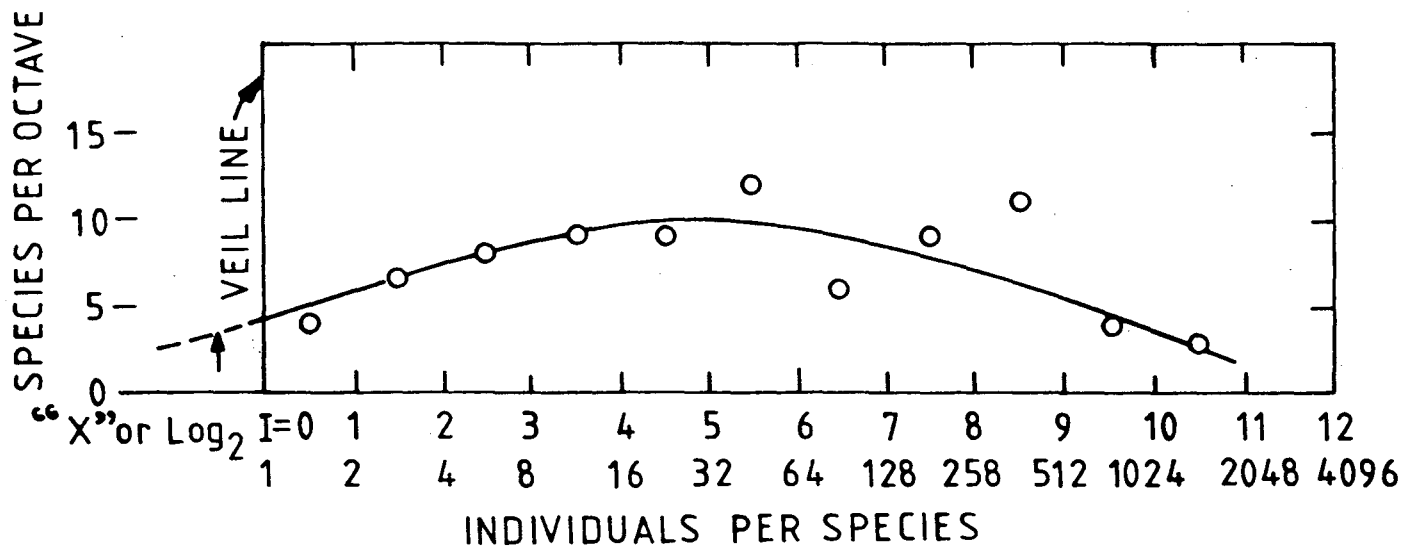
Fig. 1 Species abundances in a collection of birds of Quaker Run Velley, Western New York State. Data from Saunders[3] (1936).
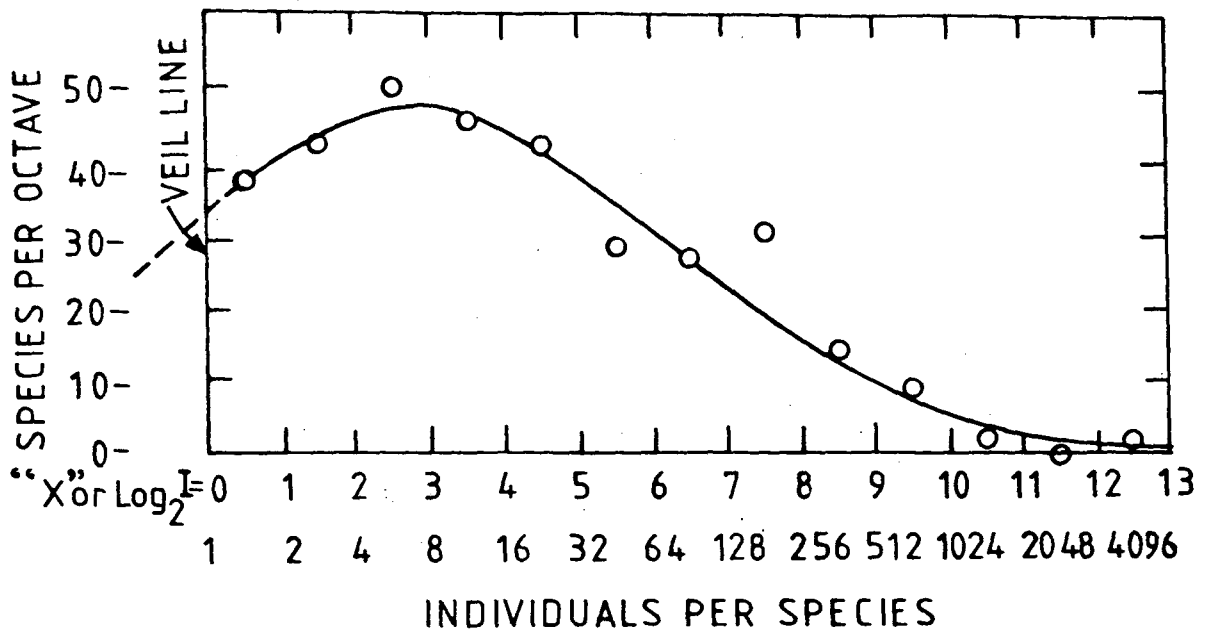
Fig. 2 Species abundance in a collection of moths caught in a light trap at Orono, Maine. Data from Dirks[5] (1937).
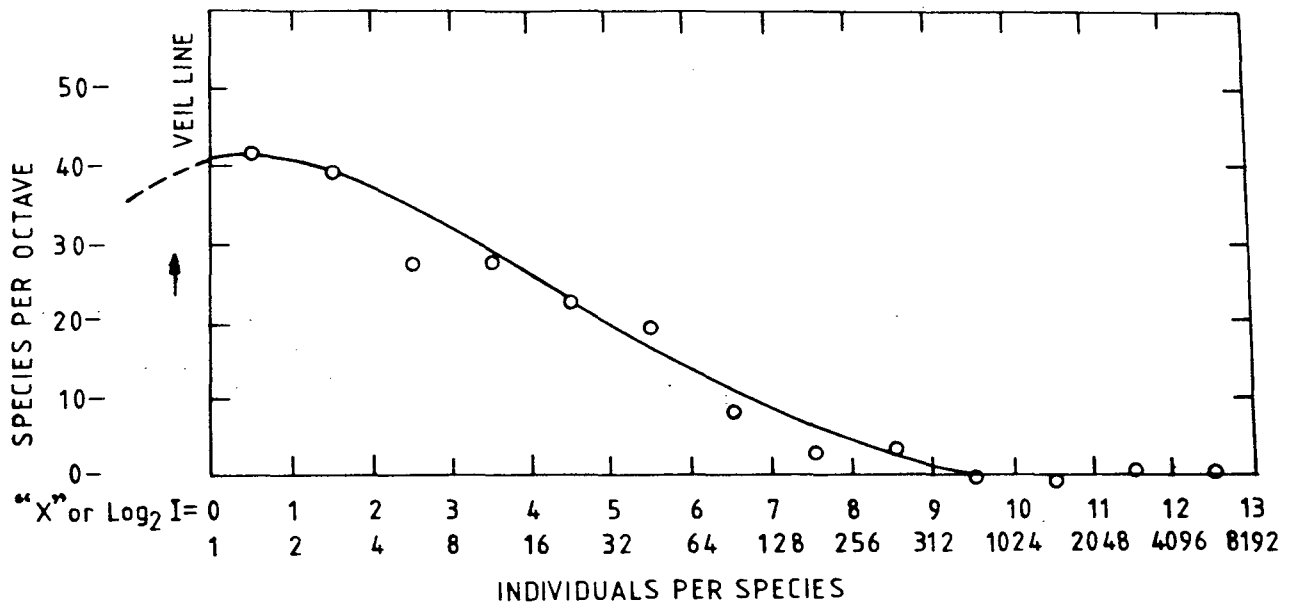
Fig. 3 Species abundances in a collection of female
moths in a light trap at Orono, Maine.
Data from Dirks[5] (1937).
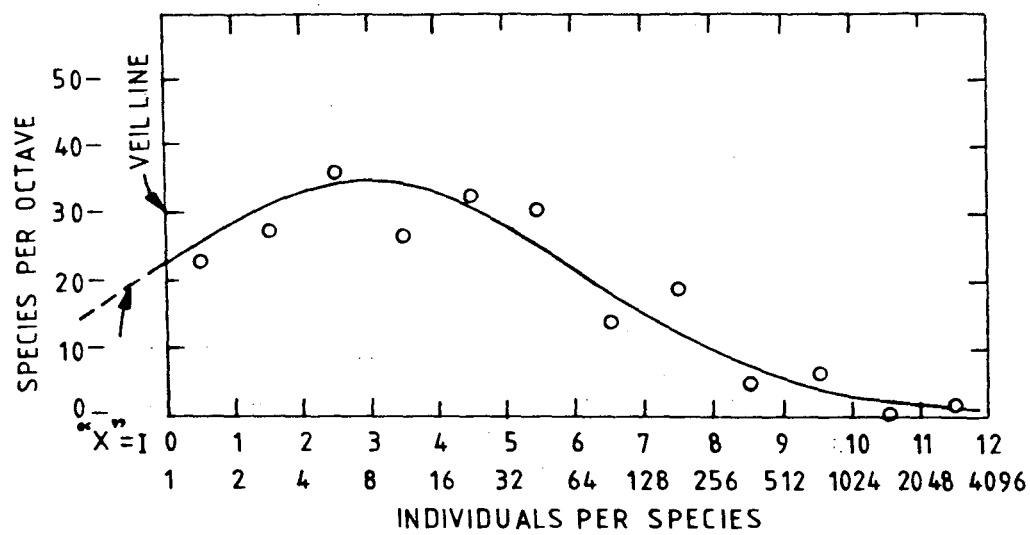
Fig. 4 Species abundances in a collection of moths, in a light trap at Rothamsted, England. Data from Williams[2] (1943).
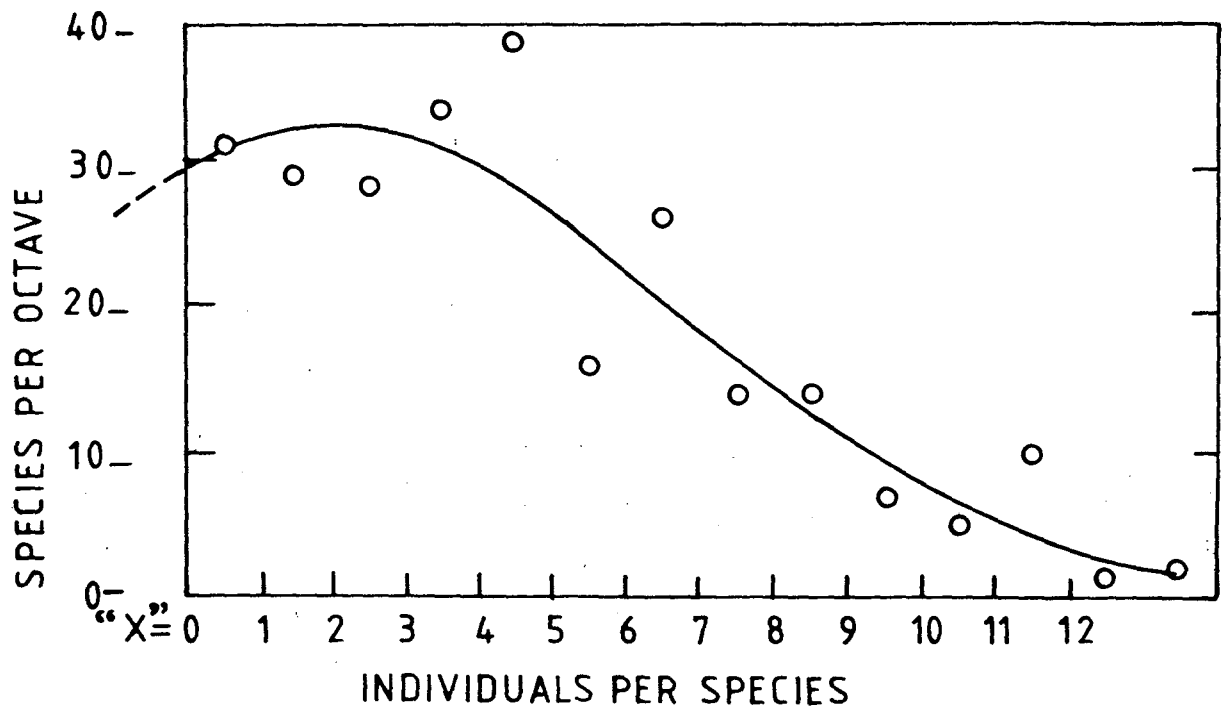
Fig. 5 Species abundances in a collection of moths caught in a light trap at Saskatoon, Saskatchewan. Data from King.
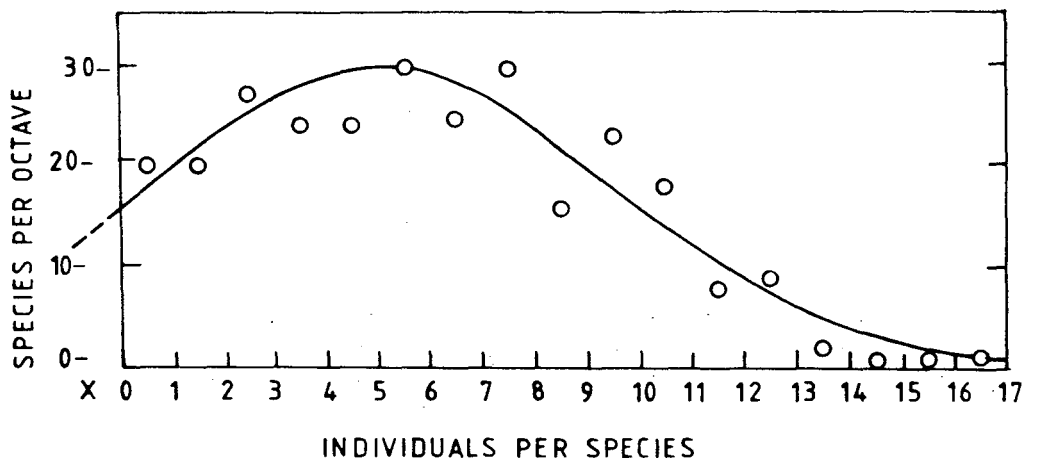
Fig. 6. Species abundances in a collection of moths caught in a light trap at Lethbridge, Alberta. Data from Seamans[6].

CHAPTER III

STATISTICAL MECHANICAL APPROACH TO GOMPERTZ MODEL

In this chapter, we shall develop the statistical mechanics of a multi species ecosytem, the dynamics of which is given by Gompertz model. The species interactions in this model are of the form $N_i \log N_j$ in place of $N_i N_j$ as in the Lotaka-Volterra case.

This model is discussed by several workers. See for instance Bhat and Pande (1980), who gave a detailed discussion on 2 and 3 species ecosystems with in such a model.

For applying this model to a large number of species, it is useful to invoke statistical mechanics, as was done by Kerner and others for the Lotka-Volterra model.

First of all we shall show with the set of coupled equations that the model, under a constraint, possesses a constant of motion. We then construct a phase space such that our system belongs to an ensemble in this space on a surface characterised by this constant of motion. The requisite Liouville theorem and the condition for the

ensemble to be in statistical equilibrium can then be established. Following this, microcanonical ensemble is constructed. The possiblility of there being a 'temperature' for the system suggests the way to construct the Gibb's canonical ensemble for any subsystem of the system. As an application, the probability distribution for the number of individulas in any species can then be worked out. The resulting distribution is seen to be of lognormal form in keeping with the well-known results of Preston.

1. STATISTICAL MECHANICS OF THE GOMPERTZ MODEL

We now consider the model of n interacting species where the interaction term appearing in the equation for the time derivative of Nr, is for the interaction between species r and s. The form of interaction term is Nr log Ns. The complete equation is -

$$\frac{dN_r}{dt} = \epsilon_r N_r + \sum_s \alpha_{sr} N_r \log N_s \tag{1}$$

where r,s = 1,2,3,...,n.

and α_{sr} are now assumed to be antisymmetric i.e.,

$$\alpha_{sr} = - \alpha_{rs}$$

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This implies that self interacting terms are absent, i.e.,

$$\alpha_{rr} = 0, \text{ for all } r.$$

The constant ε_r gives the idea how the species N_r progresses if left to itself in a given environment.

For getting the stationary state of equation (1) dN_r/dt must vanish and let the population number N_r have the steady value q_r given by –

$$\varepsilon_r q_r + \sum_s \alpha_{sr} q_r \log(q_s) = 0 \tag{2}$$

Using the variable X_r given by:

$$x_r = \log N_r \tag{3}$$

We can write Eq. (1) as:

$$dx_r/dt = \varepsilon_r + \sum_s \alpha_{sr} (x)_s \tag{4}$$

and by expressing ε_r through equation (2) we have,

$$\dot{x}_r = \sum_s \alpha_{sr} (x_s - x_s{}^*) \tag{5}$$

where $x_s{}^* = \log q_s.$

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Multiplying both sides of equation (5) by $(x_r - x_r^*)$ and summing over r, we get :

$$\dot{x}_r \ (x_r - x_r^*) = \sum_{s,r} \alpha_{sr} \ (x_r - x_r^*) \ (x_r - x_r^*) \qquad (6)$$

Due to antisymmetry of α_{sr}, the right hand side of Eq. (6) vanishes and it yields a constant of motion or a conserved quantity. We have

$$\sum_r \dot{x}_r \ (x_r - x_r^*) \ = \ 0$$

or

$$\frac{d}{dt} \ [\ \sum_r (1/2 \ x_r^2 - x_r x_r^*)] \ = \ 0$$

or, $\sum_r (1/2x_r^2 - x_r x_r^*)] \ =$ constant.

Let const. of motion be G, then :

$$G \ = \ \sum_r (1/2x_r^2 - x_r x_r^*) \ = \ \sum_r G_r \qquad (7)$$

We now construct a Gibb's ensemble for the system governed by equation (4) and (7), in the same way as done by Kerner, by taking all possible copies of the system, each copy corresponding to one set of values for x_r. The

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phase space for the system can be taken as the cartesian system with x_r axes in which a point represents a copy at a particular stage and the ensemble of points represent the whole ensemble.

The constancy of the total number of points in the ensemble along with the dynamics of our model (1) and (4) leads to the requisite Liouville theorem, i.e., the desirable uniformity property of the phase space. Since we define our system over a surface of constant G in the phase space, the condition of statistical equilibrium ($\frac{\partial \rho}{\partial t} = 0$, ρ being ensemble density, being the function of G alone) can also be estiblished.

Now, with uniformity of phase space and in a situation of statistical equilibrium, we define a micro canonical ensemble for our system, the density function ρ for which is characterised by :

$$\rho = \rho_o \, \delta \, (G - G_o) \qquad\qquad (8)$$

where, δ stands for the standard Dirae delta function and ρ_o is a numerical constant .

The ensemble average of any function $f(x_1 \, x_2, \ldots\ldots, x_n)$ of phase co-ordinates is now defined to be:

$$\overline{f} = \frac{\int \rho \, f \, d\tau}{\int \rho \, d\tau} \qquad (9)$$

The integral being over all of the phase space. The element of volume $d\tau$ can be represented as,

$$d\tau = ds.dn = \frac{ds \, dG}{|\nabla G|}$$

where,

    (i)   ds is an element of area on a constant G surface and dn is an increment of length normal to the surface, which can be written as $\frac{dG}{|\nabla G|}$. Where dG is the difference in G values of two neighbouring constant G surface and $\nabla G = \partial G / \partial n$.

So, with this equn. (9) can be written as:

$$\overline{f} = \frac{\int \rho_o \, f \, \delta(G-G_o) \, \dfrac{ds \, dG}{|\nabla G|}}{\int \rho_o \, f \, \delta(G-G_o) \, \dfrac{ds \, dG}{|\nabla G|}}$$

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$$
= \frac{\int_{G_o} f \dfrac{ds}{|\nabla G|}}{\int_{G_o} ds / |\nabla G|} \tag{10}
$$

It is to be noted that these integrals are surface integrals over $G=G_o$.

Let us now choose for f, the function Tr, given by

$$
T_r = x_r \frac{\partial G}{\partial x_r} = [x_2^2 - x_r x_r{}^*]
$$

Now, we know that,

$$
G = \frac{\partial G}{\partial n} \hat{n} = |\nabla G| \hat{n}
$$

and $\qquad \nabla G = \sum_r \dfrac{\partial G}{\partial x_r} \hat{x}_r \qquad$ also.

Where, $\hat{n}$ is the unit vector along the normal to constant G surface and $\hat{x}r$ is the unit vector along x_r direction, the direction cosines of $\hat{n}$ are :

$$
\hat{n} \cdot \hat{x} = \frac{\partial G / \partial x_r}{|\nabla G|}
$$

so that, $\qquad x_r \dfrac{\partial G}{\partial \hat{x}_r} \cdot \dfrac{ds}{|\nabla G|} = x_r (\hat{n} \cdot \hat{x}) d_s$

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Here, $\bar{x}_r$ denotes the vector to the point $(0,0,0,\ldots,x_r,0,0,0,)$. Then if we denote the denominator in equation (10) by :

$$\frac{ds}{|\nabla G|} = \Delta_o$$

the ensemble average of T_r is:

$$\bar{T}_r = \frac{\int_{G_o} (\hat{n} \cdot \bar{x}_r) ds}{\Delta o}$$

$$= \frac{1}{\Delta o} \int_{G_o} \text{div } x_r d\tau$$

$$= \frac{\gamma_o}{\Delta_o} \qquad \text{for all values of r} \qquad (11)$$

Here, we have used Guass's divergence theorem and represent γ_o as the volume enclosed by G_o. The expression (11) is constant for all species r and thus the mean T_r for any species is the same for any other. This result is similar to equipartion, of energy in Physics. The total T of the biological association is equally divided among all the species. This opens up the possibility of defining a temperature, which then enables us to define a Gibbs canonical ensemble for our system. Before doing that,

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however, we show by an example that our system also admits Ergodic Hypothesis.
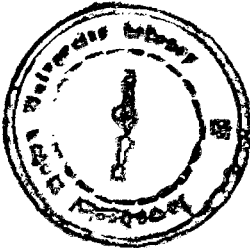
Let us define a function D_r as

$$D_r = \frac{\partial G}{\partial x_r} = (x_r - x_r{}^*) \qquad (12)$$

Let us also calculate the canonical average of D_r, i.e.,

$$\overline{D_r} = \frac{\oint \frac{\partial G}{\partial x_r} \cdot \frac{ds}{|\nabla G|}}{\Delta_o}$$

$$= \frac{\int (\hat{n} \cdot \hat{x}_r) d_s}{\Delta_o}$$

$$= 0$$

i.e., $= \overline{(x_r - x_r{}^*)} = 0$

or

$$\overline{x}_r = x_r{}^* \qquad (13)$$

This shows that the ensemble average of x_r is equal to the steady state value of x_r namely $x_r{}^*$.

Now we can prove that the time average of N is also q_r. We have from equation (1),

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$$\frac{d}{dt} (\log N_r) = \epsilon_r + \sum_s \dot{\alpha}_{sr} \log N_s$$

Integrating with respect to t on both sides, between the limits 0 to T. we get:

$$\frac{1}{T} \log \left[\frac{N_r(T)}{N_r(0)}\right] = \epsilon_r \sum_s \dot{\alpha}_{sr} \left[\frac{1}{T} \int_0^T \log N_s(t)dt\right] \quad (14)$$

Now, since N are bounded, as $T \longrightarrow \bar{\infty}$, the left hand side vanishes, and we know that –

$$\overline{\log N_s} = \lim_{T \to \infty} \frac{1}{T} \int_o^T \log N_s(t)dt]$$

So, we get from equation (14),

$$0 = \epsilon_r + \sum_s \alpha_{sr} \overline{\log N_s}$$

or, $$\sum_s \alpha_{sr} \overline{\log N_s} = -\epsilon_r$$

and by comparing equation (2),

or, $$\overline{x}_s = x_s*$$
$$\overline{x}_r = x_r* \qquad\qquad (15)$$

Thus by combining equations (12) and (13), we see that the time average of x_r is precisely equal to the

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ensemble average of the same. So, we can hope that our biological system is Ergodic.

2.   THE CANONICAL ENSEMBLE

Now, we are in a position to define a subsystem of our general biological system, which would consist of, say, υ number of species, where $1 \leq \upsilon \leq$ n. For this subsystem to be in statistical equilibrium with the rest of the system the subsystem and the rest of the system must have the same 'temprature' θ.

The density function for such a canonical system is given by :

$$\rho_\upsilon \quad = \quad e^{-G_\upsilon / \theta} \tag{16}$$

Where, the suffix υ indicates that we are dealing with the part containing υ number of species. The canonical average of any quantity D_r, where r refers to any of the new species, is given by :

$$\overline{D}_r \;=\; \frac{\int D_r e^{-G_\upsilon/} \, d\tau_\upsilon}{\int e^{-G_\upsilon/} \, d\tau_\upsilon} \tag{17}$$

where,

$$D_r \;=\; \frac{\partial G}{\partial d_r} \;=\; (x_r - x_r^*) \tag{18}$$

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The canonical average of the quantity D_r is given by:

$$\overline{D}_r = \frac{\int \partial G_r / \partial x_r \cdot e^{-G_r/\theta} d\tau}{\int e^{-G_r/\theta} d\tau}$$

$$= \frac{-\theta \frac{\partial}{\partial x_r} [e^{-G_r/\theta}] dx_r}{\int e^{-G_r/\theta} dx_r}$$

$$= 0$$

i.e., $\overline{D}_r = \overline{(x_r - x_r^*)} = 0$

or $\quad \overline{x}_r = x_r^*$ $\hspace{3cm}$ (19)

Let us consider the ensemble average of the quantity D_r^2. We have for this :

$$\overline{D}_r^2 = \frac{\int [\frac{\partial G}{\partial x_r}]^2 e^{-G_r/\theta} d\tau}{\int e^{-G/\theta} d\tau}$$

$$= -\theta \frac{\int [\frac{\partial G}{\partial x_r}]^2 \frac{d}{dx_r} e^{-G_r/\theta} dx_r}{\int e^{-G_r/\theta} dx_r}$$

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$$= \frac{\left[-\theta\left[\left(\dfrac{\partial G}{\partial x_r}\right) e^{-\frac{G_r}{\theta}}\right] + \theta \int e^{-(G_r/\theta)^2} \dfrac{\partial G}{\partial x_r^2} \, dx_r\right]}{\int e^{-G_r/\theta} \, dx_r}$$

$$= \theta$$

(The suffix ν has been dropped as it can be from 1 to n anywhere).

$$\text{So,} \quad \overline{D_r^2} = \theta = \overline{(x_r - x_r^*)^2} \qquad (20)$$

This shows that the temperature in our biological system is a measure of the mean square deviation of x_r from its equilibrium value x_r^*. From here we can also conclude that zero temperature analogue means completely quiet state of our system.

So, we can say that   is a measure of excitation from the stationary state:

Now let us consider the quantity,

$$z = \int e^{-G/\theta} \, dx_1 \, \text{------} \, dx_n$$

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$$= \prod_r \int e^{-G_r/\theta} \, dx_r$$

$$= \prod_{r=1}^{n} Z_r \qquad\qquad (21)$$

where,

$$Z_r = \int e^{-G_r/\theta} \, dx_r$$

$$= \int e^{-[1/2 \, x_r^2 - x_r \, x_r^*]/\theta} \, dx_r$$

$$= \sqrt{(2\pi\theta)} \; e^{(x_r^*)^2/2\theta} \qquad\qquad (22)$$

Z is the well known partition function of canonical ensemble of Gibbs.

Now we are in a situation of calculating the probability $P(x_r) \, dx_r$ of any species r to have its x_r value in the interval x_r and $x_r + dx_r$. For this, we either consider the system with K species or a one component system with species r. In the former case, after a simple integration over all the co-ordinates other than x_r, and in the latter case directly, we get the result:

$$P(x_r) \, dx_r = \frac{e^{-G_r/\theta} \, dx_r}{Z_r}$$

$$= \frac{e^{-1/\theta\, [x_r^2/2 - x_r x_r^*]^2}}{\sqrt{2\pi\theta}\;\; e^{(x_r^*)^2/2\theta}}\; dx_r$$

$$= \frac{1}{\sqrt{2\pi\theta}}\; e^{-1/2\theta\, [x_r - x_r^*]^2}\; dx_r \qquad [23]$$

where, $\qquad \theta = \overline{(x_r - x_r^*)^2}$

By transforming the Eq. from x_r to N_r, we get:

$$P(N_r)\, dN_r = \frac{1}{N_r \sqrt{2\pi\theta}}\; e^{-1/2\theta\, [\log N_r - \log N_r^*]^2}\; dN_r \qquad [24]$$

Where,

$$\theta = \overline{(\log N_r - \log N_r^*)^2} \qquad (25)$$

The expression in equation (24) is a standard lognormal distribution.

3. COMPARISON WITH THE RESULT OF PRESTON

Let us consider the approximation in which the equilibrium value of the number of individuals for any species within the genera is same. Let us multiply the

probability function $P(N_r)$ by the total number of species in the system, say N. We then get

$$NP\ (\log N_r) = n\ (\log i)$$

$$= \frac{N}{\sqrt{(2\pi\theta)}}\ e^{-\ 1/2\theta\ [x_r\ -\ x_r^*]^2} \qquad [26]$$

Where θ has the same meaning as R_2 or σ_2 in Preston's notation, and of course,

$$\log N_r\ =\ x_r\ =\ \log i$$

where i is the number of individual referred to by N_r and the suffix r has been dropped because the distribution is now the same for any r. We have thus established Perston's result for the frequency distribution with in a genera by using Gompertz model in a statistical way.

It is to be noted that in equation (26) logarithms are to the base e, where as in the expression of Perston given in equation (7) of Chapter I, the logarithms are to the base 2. The latter can, however, be converted to the base e without any change in its form, except for an overall factor of constant, i.e., $\log_2 e$.

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The distribution obtained here can be derived from more general considerations which do not need the use of the antisymmetry constraint on the interaction matrix and which eliminate certain drawbacks of the present method (see Varma, Sitaram, Pande and Negi. They are, however, beyond the scope of the present dissertation and will therefore not be discussed here.

We shall now use the results obtained here in the next chapter.

CHAPTER - IV

RELATION BETWEEN STABILITY AND SOME BIOLOGICAL PARAMETERS
OF A COMMUNITY

In the previous chapter, we have applied the statistical mechanical approach to the Gompertz model and got the log normal distribution for the relative abundance of species. In the present chapter we shall use the results of the previous chapter in particular the cononical ensemble density function, to study the stability of the system and the relation between the stability and certain biological parameters of relevance. Such an approach to stability was first used by Leigh in the context of the Lotka-Volterra model.

Here, our ecosystem model is Gompertz model. In this model the interaction term between i and j species is $N_i \log N_J$ type instead of direct proportional interaction $N_i N_J$ of volterra type. This model has been discussed in detail in chapter III.

Following Leigh, we define the stability of our system in terms of the frequency of fluctuations of a species population from a fixed value i.e. from the

equilibrium value. If the fluctuation frequency is large, the system is less stable and the smaller the flactuation frequency gets, the more stable the systems becomes. Once we have calculated the fluctuation frequency, we can relate it to our biological observables like productivity, biomass and diversity. This will enable us to study how the stability of the system changes as we vary these biological parameters.

We start, once again with the equations of the Gompertz model:

$$\frac{dN_i}{dt} = \varepsilon_i N_i + \sum_{s=1}^{n} \alpha_{is} N_i \log N_s \qquad [1]$$

where N_i represents the population of species i of a community of n species. ε_i represents the specific rate of growth of this species in the absence of all other members of the community and is positive only for primary producers. α_{is} is a constant which is a measure of the influence of species s on the rate of growth of species i with $N_i \log N_s$ type interaction. Here we assume the antisymemetry of α_{is} i.e.

$$\alpha_{is} = - \alpha_{si}$$

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Now, in accordance with our model, the rate of flow of mass between species i and s is given by the interaction term which is of the form Ni log Ns. So we define the productivity P of the community as:

$$P = 1/2 \sum_{i,s} |a_{is}| \quad N_i \log N_s \qquad [2]$$

and the community Biomass B as:

$$B = \sum_i N_i \qquad [3]$$

Now, we will find a constant of motion or a conserved quantity and then in terms of that quantity we will rewrite our equations for further analysis of the stability of our system.

For stationary states of the system (1) dN_i/dt vanishes. Let the population numbers Ni have the steady values q_i given by:

$$\varepsilon_i q_i + \sum_{s=1}^n \alpha_{is} q_i \log q_s = 0$$

or

$$\varepsilon_r + \sum_{s=1}^n \alpha_{is} \log q_s = 0 \qquad [4]$$

Now we use the substitution:

$$x_i = \log N_i/q_i$$

i.e., $\log N_i = x_i + \log q_i$

and

$$\frac{dx_i}{dt} = \frac{1}{N_i} \frac{dN_i}{dt}$$

Eq.(1) can then be written as

$$\frac{1}{N_i} \frac{dN_i}{dt} = \varepsilon_i + \sum_s a_{is} (\log N_s)$$

or

$$\frac{dx_i}{dt} = \varepsilon_i + \sum_s a_{is} (x_s + \log q_s)$$

Now putting the value of ε_i from equation (4) in the above equation, we get:

$$\frac{dx_i}{dt} = \sum_s a_{is} (x_s + \log q_s - \log q_s)$$

or

$$\frac{dx_i}{dt} = \sum_s a_{is} x_s$$

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or,

$$\frac{dx_i}{dt} = \sum_{s=1}^{n} a_{iJ} \frac{\partial H}{\partial x_J} \qquad [5]$$

where,

$$H = \sum_i 1/2 \ x_i^2 \qquad [6]$$

H is our conserved quantity. Next, we define the frequency of fluctuation of population of species from a fixed value as a measure to stability of our system. We evaluate that frequency as the rate of crossing of x_i (t) from a fixed value x_i = c as Kerner and Kac have done:

So the frequency can be written as:

$$\lim_{T \to \infty} \frac{1}{T} \int_0^T \delta [x_i(t) - C] \left| \frac{dx_i}{dt} \right| dt \qquad [7]$$

Where $\delta [x_i(t) - C]$ is the Dirac-delta function which is equal to 1 if $x_i(t)$ = C, otherwise zero.

Following the ideas of statistical machanics, as discussed in the previous chapter, we can replace the time average of a function by an appropriate phase space average. We can thus write:

$$\lim_{T \to \infty} 1/T \int^{T} f[x_i(t), \ldots\ldots, x_n(t)] \, dt$$

$$= \frac{1}{V(c)} \int_{H=c} f[x_i, \ldots\ldots\ldots, x_n] \frac{ds}{|\nabla H|}$$

Where ds is the surface element on H= c and

$$V(c) = \int_{H} \frac{ds}{|\nabla H|}$$

Applying these manipulations we can write our integral (7) as:

$$\lim_{T \to \infty} \frac{1}{T} \int_{o}^{\tau} \delta[x_i(t) - C] \left| \frac{dx_i}{dt} \right| dt$$

$$= \frac{1}{V(c)} \int_{H=C} \delta[x_i(t) - C] \left| \frac{dx_i}{dt} \right| \frac{ds}{|\nabla H|} \qquad [8]$$

Now, for large numbers of species we can think of a subsystem in the system which is in equlibrium with the system at a temperature θ. In this case we can use the canonical ensemble for which the density function ρ is given by:

$$\rho = K \, Exp \left[- \frac{H(x_1, \ldots, x_n)}{\theta} \right]$$

$$= K \, Exp. \left[- \sum_i \frac{(x_i)^2}{2\theta} \right] \qquad [9]$$

where K is a normalization factor.

The fluctuation frequency, say ν , can then be written as:

$$\nu = K \int \delta (x_i - C) \, \mathrm{Exp} \left[-\sum_i \frac{(x_i)^2}{2\theta} \right] dx^n$$

or,

$$\nu = K \int \delta (x_i - C) \, \mathrm{Exp} \left[- \frac{x_i^2}{2\theta} \right] dx_i \cdot$$

$$\cdot \int \mathrm{Exp} \left[-\sum_k \frac{(x_k)^2}{2} \right] dx^{n-1} \cdot \frac{\int \mathrm{Exp} \left[- \frac{(x_i)^2}{2\theta} \right] dx_i}{\int \mathrm{Exp} \left[- \frac{(x_i)^2}{2\theta} \right] dx_i}$$

where the summation over K does not include i = k.

Since we know:

$$\int \delta(x_i - C) \, \mathrm{Exp} \left[- \frac{(x_i)^2}{2\theta} \right] dx_i = \mathrm{Exp} \left[- \frac{c^2}{2\theta} \right]$$

and

$$\int \text{Exp} \left[- \frac{(x_i)^2}{2\theta} \right] dx_i = \sqrt{(2\pi\theta)}$$

So, the above integral can be simplified as:

$$= \frac{K \, \text{Exp} \left[- \frac{c^2}{2\theta} \right]}{\sqrt{2\pi\theta}} \int \left| \frac{dx_i}{dt} \right| \, \text{Exp} \left[- \sum_i \frac{(x^i)^2}{2\theta} \right] \, d^n x$$

or

$$= \frac{K \, \text{Exp} \left[- \frac{c^2}{2\theta} \right]}{\sqrt{2\pi\theta}} \int \left| \sum_J a_{is} x_J \right| \, \text{Exp} \left[- \sum_i \frac{(x_i)^2}{2\theta} \right] \, d^n x$$

Now using the property of complex contour integral we can set in the above integral:

$$\left| \sum_J a_{iJ} x_J \right| = \frac{1}{\pi} \int_{-\infty}^{\infty} \frac{1 - \text{Cos} \left(\sum_J a_{iJ} x_j S \right)}{S^2} \, ds$$

So we get:

$$\nu = \frac{\text{Exp} \left[- \frac{c^2}{2} \right]}{\sqrt{2\pi\theta}} \int_{-\infty}^{\infty} \frac{ds}{\pi S^2} \left[1 - K \int_{\nu} (\text{Cos} \left(\sum a_{iJ} X_J S \right) \right.$$

$$\left. \text{Exp} \left[- \sum_i \frac{(x_i)^2}{2\theta} \right] \, d^n x_i \right)$$

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Since , $\int K \; \text{Exp} \left[- \Sigma \dfrac{(x_i)^2}{2\,\theta} \right] d^n x_i \; = 1$

and now changing,

$$\text{Cos} \left(\underset{J}{\Sigma} \; a_{is} \; x_J S \right) = \text{Real Exp} \; [\; i\Sigma \; a_{is} \; x_J S]$$

We get,

$$\nu = \dfrac{\text{Exp} \left[- \dfrac{c^2}{2\,\theta} \right]}{\sqrt{2}\,\pi\,\theta} \int_{-\infty}^{\infty} \dfrac{ds}{\pi S^2} \left[1 - K \int e^{\; i \; \underset{J}{\Sigma} \cdot} \cdot (a_{iJ} \; x_J S + i \; \dfrac{(x_J)^2}{2\,\theta}) \; d^n x \right]$$

Making the power of exponential as perfect square we get

$$\nu = \dfrac{\text{Exp} \left[- \dfrac{c^2}{2\,\theta} \right]}{\sqrt{2}\,\pi\,\theta} \int_{-\infty}^{\infty} \dfrac{ds}{\pi S^2} \left[1 - \text{Exp} \left[-1/2 \; \underset{J}{\Sigma} \; (a_{iJ})^2 \; S^2 \theta \right] \right]$$

$$\nu = \dfrac{\text{Exp} \left[- \dfrac{c^2}{2\,\theta} \right]}{\sqrt{2\,\pi\,\theta}} \; \dfrac{1}{\pi} - \int \left[\dfrac{\text{Exp} \left[-1/2 \underset{J}{\overset{\Sigma}{}} (a_{iJ})^2 \, \theta \; S^2 \right]}{S^2} \; ds \right]$$

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By doing integral by parts, we get:

$$\nu = \frac{\mathrm{Exp}\left[-\dfrac{c^2}{2\theta}\right]}{\sqrt{2}\,\pi\theta}\;\;\frac{2}{\pi}\;\sqrt{\left(\pi/2\;\sum_{J}\;(a_{iJ})^2\;\theta\right)}$$

$$\simeq\;\mathrm{Exp}\left[-\frac{c^2}{2\theta}\right]\;\frac{1}{\pi}\;\sqrt{\sum_{J}\;(a_{iJ})^2}$$

$$=\;\frac{1}{\pi}\;\sqrt{\left(\sum_{J}\;(a_{iJ})^2\right)}\;\mathrm{Exp}\left[-\frac{c^2}{2\theta}\right]\right)\qquad\qquad [10]$$

So equation (10) gives the frequency of fluctuations of the population x_i around the equilibrium value x_i = C.

The average of this frequency over all the species of the community is given by the expression:

$$\overline{\nu}\;=\;\frac{1}{n}\;\sum_{i}\;\left(\frac{1}{\pi}\;\sqrt{\sum_{J}\;(a_{iJ})^2}\right)\;\mathrm{Exp}\left[-\frac{c^2}{2\theta}\right]\right)\qquad\qquad [11]$$

We will now minimize this frequency with respect to a_{iJ} (or $|a_{iJ}|$), under the constraint that the productivity of the community, i.e.,

$$P = \frac{1}{2} \sum_{i,s} |a_{is}| N_i \log N_s$$

$$\cong \frac{1}{2} \sum_{i,s} |a_{is}| q_i \log q_s \qquad [12]$$

is fixed.

For convenience, we take the simplified expression $\sum_{i,J} (a_{is})^2$ for minimisation, in place of the actual average frequency $\overline{v}$. This does not change the qualitative nature of our discussion. This will also facilitate us in comparing our results with those of Leigh, the since simplication introduced by him are identical to ours.

To minimize a given quantity under a given constraint, we have to use Lagrange's method of undetermined multipliers. In the present case, we can do this by choosing function:

$$Q = \sum_{i,s} (a_{iJ})^2 - \lambda \left[\sum_{i,s} |a_{is}| q_i \log q_s - 2P \right] \qquad [13]$$

and demanding:

$$\frac{\partial Q}{\partial \mid a_{iJ} \mid} = 0 \qquad\qquad [14]$$

This gives us:

$$2 \mid a_{iJ} \mid - \lambda q_i \; \log \; q_J = 0 \qquad\qquad [15]$$

or

$$\lambda = \frac{2 \mid a_{iJ} \mid}{q_i \; \log \; q_J} \qquad\qquad [16]$$

Under the assumption $q_1 = q_2 = \cdots = q_2 \underline{=} q$, (which is implied in the work of Leigh as well), we can see from here that:

$$\mid a_{iJ} \mid = K \qquad\qquad [17]$$

Where K is a constant independent of i and j. This means that for any i, $a_{ij} \ddagger 0$ for all j $\ddagger$ i. The food-web structure of maximum stability in our model is therefore one where every species feeds on all other species which do not feed on it. The structure is thus one of

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maximum connectedness or maximum complexity. The most
stable system according to the present model is therefore
one which is also the most or maximally complex. This result
is identical to that of Leigh for the case of the Lotka-
Volterra model.

To proceed further now, we get, from equations
[12] and [17]

$$P = 1/2 \sum_{i,J} |a_{iJ}| q_i \log q_J$$

$$= K/2 \sum_{i,J} q_i \log q_J \qquad [18]$$

But we have:

$$B = \sum_i N_i$$

$$\simeq \sum_i q_i \qquad [19]$$

and for equal q's, we can write

$$q \simeq B/n \qquad [20]$$

Where n is the number of species in the system.

So we get:

$$P = \frac{K}{2} \; n \, (n-1) \; q \; \log \; q$$

$$\simeq \frac{K}{2} \; n^2 \; q \; \log \; q$$

$$= \frac{K}{2} \; n^2 \; \frac{B}{n} \; \log \left(\frac{B}{n}\right)$$

$$= \frac{K}{2} \; Bn \; \log \left(\frac{B}{n}\right) \qquad\qquad [21]$$

Therefore,

$$K = \frac{2P}{Bn \; \log \; (B/n)} \qquad\qquad [22]$$

Note that this leads to:

$$\lambda = \frac{4P}{B^2 \; \log^2 (B/n)} \qquad\qquad [23]$$

The expression for the frequency ν can not be related to the productivity, biomass and diversity (measured by n) of the system. Since we have:

$$\gamma = \frac{1}{\pi} \quad (\underset{J}{\Sigma} \ ((|\ a_{iJ}\ |)^2) \ \ Exp \ [-\frac{c^2}{2\theta}]$$

$$= \frac{1}{\pi} \int ((n-1)\ _R{}^2) \ \ Exp \ [-\frac{c^2}{2\theta}]$$

$$Where, \quad R = \frac{2P}{n\ B\ \log\ (B/n)}$$

$$\cong \frac{R}{\pi} \quad \sqrt{n} \quad Exp \ [-\frac{c^2}{2\theta}]$$

$$= \frac{1}{\pi} \ \frac{2P \quad \sqrt{n}}{n\ B\ \log\ (B/n)} \quad Exp \ [-\frac{c^2}{2\theta}]$$

$$= \frac{1}{\pi} \ \frac{2P}{B} \ \frac{1}{\sqrt{n}} \ \frac{Exp\ [-\frac{c^2}{2\theta}]}{\log\ (B/n)}$$

$$= \frac{1}{\pi} \ \frac{2P}{B} \ \frac{1}{\sqrt{n}} \ \frac{Exp\ ([-\frac{c^2}{2\theta}]\ -(\log\ \log(B/n)))}{} \qquad [24]$$

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This result shows that:

The frequency ν increases with increase in productivity. A more stable system would thus entail decreased productivity. The relationship between stability and the other biological parameters like biomass B and the species number n (which is a measure of diversity), is also evident from the above formula. Keeping in mind that the factor log (B/n) (or the exponential factor in (24) would be much less important than the factors like B and $\sqrt{n}$, we conclude that the frequency ν could decrease with increase in biomass and it would also decrease with increase in diversity, i.e., increase in the species number but the decrease would be slower, as the factor n appears in (24) only in the square root form. So the stability of our system would increase with increase in its biomass as well as increase in diversity.

We may thus be able to enhance the stability of a system by either increasing the species numbers or by simply increasing the biomass of the existing species, the latter procedure being of course the more effiective one. If, on the other hand,we simply partition the existing biomass among a larger number of species, it will lead, via the productiveity factor, to decreased stability.

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We conclude by noting that when we compare our result with that of Leigh for the Lotka-Volterra model we find that despite various differences we encounter in our intermediate steps, the final result is remarkably alike. The result of Leigh for the frequency ν is:

$$= \frac{1}{\pi} \frac{2P}{B} \frac{1}{\sqrt{n}} \; \mathrm{Exp} - \left(\left[-\frac{c^2}{2\theta} \right] q_i \right)$$

$$= \frac{1}{\pi} \frac{2P}{B} \frac{1}{\sqrt{n}} \; \mathrm{Exp} - \left(\left[-\frac{c^2}{2\theta} \right] B/n \right) \qquad [25]$$

Except for the exponential factors, which are not the major contributing factors as regards the variation in the frequency (or the stability), the expressions (24) and (25) are identical. The basic conclusions drawn by us on the stability of the system are thus the same as those of Leigh. These conclusions may therefore be more universally valid than we may think, i.e., they may basically be model-independent.

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