PART IV

Chapter VII: May’s Model of Two - species Under Co-operation:
Thermodynamic and Stochastic Approaches

Chapter VIII: Stability of Two - species Competition System:
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CHAPTER - VII

MAY'S MODEL OF TWO SPECIES UNDER CO-OPERATION:

THERMODYNAMIC AND STOCHASTIC APPROACHES
7.1 Introduction

The most interesting and beneficial association between two species is the act of co-operation. Classical examples of co-operation include the algal and fungal components of lichens, the clown fish (Amphiprion perculae) and sea-anemones, the antacacia system and plant-pollinator system. In the absence of interspecific effects, the individual populations are assumed to be governed by logistic equations. May (1976) had proposed a model equation of two-species co-operation by modifying the carrying capacity of logistic equations to reflect dependence upon the density of the complementary populations. The system of equations considered by May (1976) is given by,

\[
\frac{dN_1}{dt} = rN_1 \left[ 1 - \frac{N_1}{K + \alpha N_2} \right]
\]

\[
\frac{dN_2}{dt} = rN_2 \left[ 1 - \frac{N_2}{K_2 + \beta N_1} \right]
\]

The study of stability of higher-dimension co-operative communities is an important part of mathematical analysis of population biology [Hallam and Levin, 1986] and there are different concepts of stability and different approaches to them.
The non-equilibrium thermodynamic modelling of biological communities supplemented by the stochastic theory non-equilibrium fluctuation is in progress [Assimacopoulis, 1987; Chakrabart and Ghosh, 1992]. The object of the present chapter is to study the stability of the stationary state of the system from the thermodynamic and stochastic modelling of the system. The present thermodynamic and stochastic analysis has also strengthened the deterministic analysis of the study of criteria of stability.

7.2. Backgrounds: Basic Equation and Stability

Let us first study the deterministic analysis of the stability of the stationary state of the system governed by the equations (7.1). This is for the proper understanding of the subsequent non-equilibrium thermodynamic and stochastic analysis of the stability of the system under consideration.

Let us consider the system of equation (7.1) namely

\[
\frac{dN_1}{dt} = rN_1 \left[ 1 - \frac{N_1}{K_1 + \alpha N_2} \right]
\]

\[
\frac{dN_2}{dt} = rN_2 \left[ 1 - \frac{N_2}{K_2 + \alpha N_1} \right]
\] .........(7.2)
Setting \( x_1 = \frac{1}{N_1} \), \( x_2 = \frac{1}{N_2} \), we get

\[
\frac{dx_1}{dt} = r \left[ \frac{x_2}{\alpha + k_1 x_2} - x_1 \right]
\]

\[
\frac{dx_2}{dt} = r \left[ \frac{x_1}{\beta + k_2 x_1} - x_2 \right]
\]

For steady state solution

\[
x_1^* = x_1^* , \quad x_2 = x_2^* \quad \frac{dx_1^*}{dt} = 0 , \quad \frac{dx_2^*}{dt} = 0
\]

Therefore

\[
\begin{cases}
x_1^* (\alpha + k_1 x_2^*) - x_1^* = 0 \\
x_2^* (\beta + k_2 x_1^*) - x_2^* = 0
\end{cases}
\]

\[\begin{align*}
x_1^* = \frac{1 - \alpha \beta}{k_1 + \alpha \beta} , \quad x_2^* = \frac{1 - \alpha \beta}{k_2 + k_1 \beta}
\end{align*}\]

\[\text{giving} \quad x_1^* = \frac{1 - \alpha \beta}{1 - \alpha \beta} , \quad x_2^* = \frac{1 - \alpha \beta}{1 - \alpha \beta}
\]

So the steady state population is given by

\[
N_1^* = \frac{1 + \alpha \beta}{1 - \alpha \beta} , \quad N_2^* = \frac{1 + \alpha \beta}{1 - \alpha \beta}
\]
It is evident from (7.5b) that the steady state populations exist provided $\alpha \beta < 1$.

Let us consider small perturbation $(x, y)$ about $(x^*_1, x^*_2)$ i.e. we put

$$x_1 = x^*_1 + x$$

$$x_2 = x^*_2 + y$$

in equation (7.3). On linearisation, we have

$$\frac{dx}{dt} = -r_x - r \left( \frac{2k}{\alpha^2} x^*_2 - \frac{1}{\alpha} \right) y$$

$$\frac{dy}{dt} = -r \left( \frac{2k}{\beta^2} x^*_1 - \frac{1}{\beta} \right) x - ry$$

The eigenvalue $\lambda$ of this set of linear equation is given by

$$\lambda = r \left[ -1 + \left\{ \frac{2k}{\alpha^2} \left( \frac{1}{\alpha^2} - \frac{1}{\alpha} \right) - \frac{1}{\alpha} \right\} \right]^2$$

$$\left\{ \frac{2k}{\beta^2} \left( \frac{1}{\beta^2} + \frac{1}{\beta} \right) - \frac{1}{\beta} \right\}$$

$$\left\{ \frac{2k}{\beta^2} \left( \frac{1}{\beta^2} + \frac{1}{\beta} \right) - \frac{1}{\beta} \right\}$$

The real part of the eigenvalue is negative, so the steady state is locally stable. So the steady state population exists provided $\alpha \beta < 1$ and it is locally stable.
7.3 Thermodynamic Model and Stability

For the non-equilibrium thermodynamic model of the system governed by the system of equations (7.1), we write it as,

\[
\begin{align*}
\frac{1}{N_1^2} \frac{dN_1}{dt} &= r \left( \frac{1}{N_1} - \frac{1}{N_1^*} \right) - \frac{r}{\alpha} \left( \frac{1}{N_2} - \frac{1}{N_2^*} \right) \\
\frac{1}{N_2^2} \frac{dN_2}{dt} &= r \left( \frac{1}{N_1^*} - \frac{1}{N_1} \right) + \frac{r}{\beta} \left( \frac{1}{N_2^*} - \frac{1}{N_2} \right)
\end{align*}
\]

Where the stationary states \( N_1^* \) and \( N_2^* \) are given by

\[
\frac{dN_i^*}{dt} = 0, \ i = 1, 2
\]

The form of (7.8) is suitable for thermodynamic modelling. We choose the thermodynamic flux \( J_i \) and force \( X_i \) (1=1,2) as

\[
\begin{align*}
J_i &= \frac{1}{N_i^2} \frac{dN_i}{dt}, \ i = 1, 2 \\
X_i &= \left( \frac{1}{N_i} - \frac{1}{N_i^*} \right), \ i = 1, 2
\end{align*}
\]

\[\cdots\cdots(7.9)\]
Thus equations (7.8) reduce to the form

\[ \begin{align*}
J_1 &= L_{11} X_1 + L_{12} X_2 \\
J_2 &= L_{21} X_1 + L_{22} X_2
\end{align*} \]

..........(7.10)

Where

\[ \begin{align*}
L_{11} &= r, & L_{22} &= r, & L_{12} &= -\frac{r}{\alpha}, & L_{21} &= -\frac{r}{\beta}
\end{align*} \]

..........(7.11)

Thus equations (7.10) are the linear phenomenological relations between the thermodynamic fluxes \( J_1, J_2 \) and the forces \( X_1, X_2 \); \( L_{ij} \)'s \((i = 1,2; j = 1,2)\) are the phenomenological coefficients.

The thermodynamic criteria of stability of the stationary state \((N_1^*, N_2^*)\) is given by [Glansdorff and Prigogine, 1971]

\[ \frac{\partial}{\partial t} \left( \frac{1}{2} \delta^2 S \right)_{\text{at}} = \Sigma \delta X_i \delta X_i > 0 \]

..........(7.12)

Where \( S \) is the entropy of the system. Expanding the entropy \( S \) about the stationary state we have

\[ S = S_0 + \delta S \bigg|_{\text{at}} + \frac{1}{2} \left( \frac{\partial^2 S}{\partial X_i \partial X_i} \right)_{\text{at}} \]

..........(7.13)

Now

\[ \Sigma \delta X_i \delta J_i = L_{11} \delta X_1^2 + (L_{12} + L_{21}) \delta X_1 \delta X_2 + L_{22} \delta X_2^2 \]

\[ = r(\delta X_1^2 + \delta X_2^2) - \left( \frac{r}{\alpha} + \frac{r}{\beta} \right) \delta X_1 \delta X_2 \]
So the criteria for stability are given by, [Glansdorff and Prigogine, 1971]

\[ r > 0 \]

and \[ \left( \frac{1}{\alpha} + \frac{1}{\beta} \right)^2 > 4 \] \hspace{1cm} ............(7.14)

Which implies \( \alpha \beta < 1 \), (that \( r \), positive is assumed in the model).

We thus see that the ecosystem governed by (7.10) is thermodynamically stable about the stationary state if \( \alpha \beta < 1 \) which is also the same condition by dynamical analysis.

7.4 Stochastic Model and stability

In stochastic version of our model we consider small fluctuations in the population size caused by random disturbance of the environment.

We add small fluctuation \( \phi(t) \) to both the equations of the linearised form (7.6) of the basic model in order to consider the effect of variable environment.

So we have,

\[
\begin{align*}
\frac{dx}{dt} &= -rx -ray + \phi(t) \\
\frac{dy}{dt} &= -rbx -ry + \phi(t)
\end{align*}
\] \hspace{1cm} ............(7.15)
Taking the Fourier transform of (7.15), we get [Nisbet and Gurney, 1982]

\[
\begin{align*}
- (r + iw) \tilde{x}(w) - ra \tilde{y}(w) + \tilde{\phi}(w) &= 0 \\
- rb \tilde{x}(w) - (r + iw) \tilde{y}(w) + \tilde{\phi}(w) &= 0
\end{align*}
\]

(7.17)

where \( \tilde{x}(w), \tilde{y}(w) \) and \( \tilde{\phi}(w) \) are respectively the Fourier transforms of \( x(t), y(t) \) and \( \phi(t) \). (7.17) gives the transfer functions \( T_1(w) \), \( T_2(w) \) for two populations as,

\[
T_1(w) = \frac{\tilde{x}(w)}{\tilde{\phi}(w)} = \frac{r(1-a) + iw}{r^2(1-ab) - w^2 + 1.2rw} \quad \text{(7.18a)}
\]

\[
T_2(w) = \frac{\tilde{y}(w)}{\tilde{\phi}(w)} = \frac{r(1-b) + iw}{r^2(1-ab) - w^2 + 1.2rw} \quad \text{(7.18b)}
\]

We, now, calculate the fluctuation intensities and auto correlation function (ACF) for different type of species assuming the 'driving' variable \( \Phi(t) \) to be a white noise with spectral density \( D \).
Fluctuation intensities and ACF of the two population are then given by [Nisbet and Gurney, 1982]

\[
\begin{align*}
\sigma^2_i &= \frac{1}{2\pi} \int_{-\alpha}^{\alpha} s(w) \, dw, \quad i = 1,2 \\
\rho(\tau) &= \frac{1}{2\pi} \int_{-\alpha}^{\alpha} s(w) \cos w\tau \, dw
\end{align*}
\]  

(7.19)

where

\[ S(w) = |T_i(w)|^2D \]

Using (7.18a) and (7.18b) we have

\[
\sigma^2_1 = \left[ \frac{r^2(1-a)^2 + r^4(1-ab)^2}{4r^5(1-ab)^2} \right]D 
\]  

(7.20a)

\[
\sigma^2_2 = \left[ \frac{r^2(1-b)^2 + r^4(1-ab)^2}{4r^5(1-ab)^2} \right]D 
\]  

(7.20b)

\[
\rho(\tau) = B e^{-\lambda_1|\tau|} + C e^{-\lambda_2|\tau|} 
\]  

(7.21)

where

\[
\lambda_{1,2} = \frac{1}{2} \beta \pm \frac{1}{2} (\beta^2 - 4w_0^2)^{1/2} 
\]

\[
\beta = 2r, \quad w_0^2 = r^2 (1 - ab)
\]
In (7.20) the dispersions or variances of the population sizes $N_1$ and $N_2$ remains finite.

The condition for stability in the steady state is $\alpha \beta < 1$ which implies $ab < 1$.

Since $ab < 1$, $r > r \sqrt{1 - ab}$.

Again (7.21) shows that the expression for ACF $\rho(r)$ implies that as $r$ increases the co-operation between the two species decreases with time and it tends to zero after an infinitely large time.

7.5. Conclusion: The present chapter is an attempt in the direction of non-equilibrium thermodynamic modelling of a two-species co-operative biological community and the study of stability of the system. The non-equilibrium thermodynamic model has been supplemented by stochastic model and the subsequent analysis of stability. They have strengthened the deterministic method of analysis of stability. The criteria of stability of the stationary state $(N_1^*, N_2^*)$ in each case is $\alpha \beta < 1$. 