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Dynamical Complexity of Multispecies Ecosystems: Analysis of Stability, Periodicity and Bifurcation

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Abstract: The objective of this paper is to introduce a quantitative measure of dynamical complexity of a multispecies ecosystem and to present mathematical characterization of different dynamical behaviors of the ecosystems around the steady-state of the ecosystem. The dynamical complexity based on the local form of generalized Lyapunov-function provides a critical analysis of the dynamical concepts of stability, instability, periodicity and bifurcation, limit-cycle etc. with some illustrative model ecosystems.

Keywords: Ecosystems. Dynamical Model. Lyapunov-function. Dynamical Complexity. Stability. Bifurcation.

1 Introduction

A multispecies ecosystem consisting of many varied interacting species or components connected in a more or less complicated fashion is a complex dynamical system [1,2] Dynamical behaviors exhibited by many species of plants, insects and animals has stimulated great interest in the development of dynamical (both deterministic and stochastic) models of complex ecosystems. The deterministic dynamical models are used to explain system property, for example, stability, instability, bifurcation, catastrophic change of state. In this analysis attentions are focused on the change of state with time, stability of steady states and change of steady state through parametric change (bifurcation) etc. The stability is a vital concept in the study of ecosystems. A variety of ecologically interacting cases can be and have been, attached to the term instability [3]. It plays significant role in the study structure and function of ecosystems. Like stability complexity is an other vital concept of ecosystems. The dynamical complexity is associated with the different dynamical behaviors such as stability, instability, bifurcation, periodicity etc. The complexity is an inseparable part of the world of dynamical system. Henri Poincare, the great mathematician of the twentieth of the century, invented the modern theory of dynamical systems and set as an objective the exploration of the types of behaviors that can be expected from the systems described by coupled non-linear equations [4,5].

The objective of the present paper is to introduce a quantitative measure of dynamical complexity and to present an abstract more or less mathematical characterization of different dynamical behaviors of the ecosystems around a stationary state. The measure of dynamical complexity is based on the local form generalized Lyapunov-function and has similarity with other measures of dynamical entropy or complexity [6,7] and the measure of thermodynamic complexity [8,9]. We have made critical analysis of stability, instability, bifurcation, periodicity etc. in the perspective of this measure of dynamical complexity with some illustrative model ecosystems. In the Appendix we have studied the equivalence between generalized Lyapunov-function and generalized cross-entropy, which plays a significant role in the development of the theory.

2 Multispecies Ecosystem: Dynamical Model and Mathematical Structure

Let us consider a multispecies population ecosystem consisting of n components or species governed by the system of non-linear differential equations [10]

$$\frac{dN_i}{dt} = f_i(N_1, N_2, ...N_n, \alpha), (i = 1, 2, ..., n) \qquad (2.1)$$

where the vector $N(t) = (N_1(t), N_2(t), ..., N_n(t))$ lies in the positive quadrant of the Euclidean space E^n, i.e.,the

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domain of the state-space in which the state-variables $N_i(i = 1,2,....,n)$ are non-negative. This is a general system of equations describing the ecological objects, the state-variables N_i are either biomass or population of the corresponding species $i,(i = 1,2,,...,n)$. α is a parameter (or set of parameters) which describes either the state of environment or characterizes the exchange between the system with its environment. The set of equations (2.1) is in general, non-linear and it is very difficult to solve the equations in closed form. It is customary to study such a system close to stationary(or reference) state. Let $N^* = (N_1^*, N_2^*, ..., N_n^*)$ be a stationary state of the system for a certain value(or a range of values) of the parameter α of the system. Let us consider small deviation

$$\delta N_i(t) = x_i(t) = N_i(t) - N_i^* \tag{2.2}$$

about the stationary state N_i^*. The deviations $\{x_i(t)\}$ are the perturbations or fluctuations acting on the stationary state N_i^*. Linearising the system of equations (2.1) about the stationary state $N^* = (N_1^*, N_2^*, ..., N_n^*)$, we have the system of linear equations

$$\frac{dx_i(t)}{dt} = \sum_{j=1}^{n} \left(\frac{\partial f_i(t)}{\partial N_j}\right)_{N^*} x_j(t), \quad (j = 1,2,...,n) \tag{2.3}$$

or in matrix form

$$\frac{dx(t)}{dt} = Ax(t) \tag{2.4}$$

where the Jacobian A is the community matrix with element

$$a_{ij} = \left(\frac{\partial f_i(t)}{\partial N_j}\right)_{N^*} \quad (i,j = 1,2,..,n) \tag{2.5}$$

The elements $\{a_{ij}\}$ of the community matrix A plays significant role in the dynamical behaviors of the ecosystem. The community matrix A comprising of the elements $\{a_{ij}(N^*)\}$ represents the mathematical structure of the system near the stationary state N^*. It represents the pattern of species interaction independently of the rate of growth or decay [9]. May [3] in his discussion on the stability verses complexity, has studied the properties of the community matrix $A = [\{a_{ij}\}(N^*)]$ for the study of the stability of the ecosystem. It plays significant role in the study of interrelation between stability and complexity of the multispecies ecosystem to be discussed next. To find the solution of the matrix equation (2.4), we assume that A is diagonalizable as almost always turns out to be the case in ecology[10]. Let $\{v_i, i = 1,2,...,n\}$ be n linearly independent column vectors corresponding to the eigenvalues$(\lambda_1, \lambda_2, ..., \lambda_n)$ of the community matrix A, then the solution of the matrix equation(2.4) can be written as [11,12]

$$\delta N(t) = x(t) = \sum_i c_i e^{\lambda_i t} v_i \tag{2.6}$$

$$\textit{or more explicitly}, \quad \delta N_i(t) = \delta N_i(0) e^{\lambda_i t} \quad (i = 1,2,...n) \tag{2.7}$$

where c_i are constants of integration and v_i are constant column vectors.

Let us now investigate the stability of the stationary state on the basis of the solution (2.6). The stability is one of the fundamental concepts of the dynamical systems. It is the response of the system to the perturbation or fluctuation acting on the stationary (or reference) state. A basic result of stability theory states that the asymptotic stability or instability of the stationary state of the system (2.1) are identical to those obtained from the linearized version (2.3) or its solution (2.6). The stability of the system in this way reduces to a linear problem. This is the principle of linearized stability [4]. The criteria of stability of the stationary state can be investigated from the nature of the eigenvalues λ_i appearing in the solution (2.6). It follows from (2.6) that if $Re(\lambda_i) < 0 \; \forall \; i$, then x is an exponentially decreasing function(with or without oscillatory modulation according to whether λ_i (i=1,2,...,n) is non-vanishing or vanishing). Hence the solution $x = 0$ is reached in the limit $t \to \infty$, in other words, $x = 0$ is asymptotically stable. If on the other hand if $Re(\lambda_i) > 0$, the perturbations are growing exponentially and therefore the stationary state $x = 0$ (or $N = N^*$) is unstable. These two regions, for which the principle of linearized stability applies and are separated by the regions where $Re(\lambda_i) = 0$ applies are separated by the regions where $Re(\lambda_i) = 0$. We call the broadline case between asymptotic stability and instability as the marginal stability which signals the threshold of instability of the stationary state $x = 0$ (or $N(t) = N^*$). This analysis is, however, restrictive in the sense that the determination of the eigenvalues is possible only if the ecosystem consists of few number of species. For a community of arbitrary number of n species, we may resort to the method of Lyapunov-function. In the next section we shall illustrate the general form of Lyapunov-function for the model system(2.1) along with its physical significance for the further development of the theory.

Let us now consider the importance of the concept of the environmental parameter α. Indeed, a variation of α induces a variation of the community matrix $A(\alpha)$ and through it, of the eigenvalues $(\lambda_1, \lambda_2, ..., \lambda_n)$. The existence of a transition between two qualitatively different regions will then be reflected by the fact that at least one of the eigenvalues λ_i $(i = 1,2,...,n)$ will change as a function of α in the form depicted in the Fig-1. The value α_c of α at which $Re(\lambda)$ will change sign is the critical value beyond which an instability is beyond to occur [4,5]. The importance of the linear stability analysis is to show that a qualitative change of behavior may occur within a single, well-defined dynamical system beyond the critical value α_c of the environmental parameter α at which the system switches from asymptotic stability to instability. However, as soon as one enters the domain of instability, the linearized

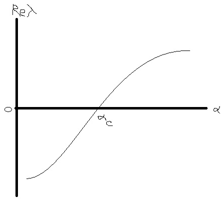

Fig. 1: Dependence of the real part of the stability exponent λ on the environmental parameter α. The value of $\alpha = \alpha_c$ makes the transition from asymptotic stability $(\alpha < \alpha_c)$ to instability ($\alpha > \alpha_c$).

equations become inadequate, as they predict run away to infinity. In order to investigate the existence of new physically acceptable solution, which emerge beyond the threshold of instability, non-linear equations will have to be analyzed [5]. This is a difficult problem. We are however, interested in the study of the behaviors of non-linear equations (2.1) for values of the environmental parameter α in a certain neighborhood of α_c. In the case of a simple eigenvalue under the assumptions that $Re(\lambda)_{\alpha=\alpha_c} = 0$ and the transversibility condition $\frac{dRe(\lambda)}{d\alpha}\ |_{\alpha=\alpha_c} \neq 0$, the Hopf-bifurcation theorem and the existence of limit-cycle at the critical point α_c provides significant information for values of the environmental parameter α in a certain neighborhood of α_c [4,5].

3 Generalized Lyapunov-function :Measure of Dynamical Complexity

A powerful method in the stability theory for differential equation is the direct method of Lyapunov-function. A function with particular properties known as Lyapunov-function is constructed to prove stability, asymptotic stability and instability in a given region. The method based on Lyapunov-function can be applied to both autonomous and non-autonomous system of differential equations. It is an energy-like function that increases or decreases along the trajectories. For the system of non-linear differential equations (2.1) a generalized Lyapunov-function is given by [10]

$$V(N|N^*) = \sum_{i=1}^{n} N_i^* \phi(\frac{N_i}{N_i^*}) \qquad (3.1)$$

where $\phi(\frac{N_i}{N_i^*})$ is a continuously twice-differentiable convex function of the argument satisfying the conditions[12]:

$$\phi(1) = \phi^{'}(1) = 0\ ,\ \frac{d^2\phi}{d\xi_i^2} > 0\ \ ,for\ \xi_i = \frac{N_i}{N_i^*} \geqslant 0 \qquad (3.2)$$

The expression of Lyapunov-function (3.1) has important entropic significance. It can, infact, be considered as a measure of generalized cross-entropy-function $S(N|N^*)$ (say) defined over the non-probabilistic positive-additive distribution (PAD) $N = (N_1, N_2, ..., N_n)$ [9,13] (See the Appendix). The entropic character of the generalized Lyapunov-function would be of significant importance for the generalized Lyapunov-function to provide a measure of dynamical complexity. Before we go to the measure of dynamical complexity we need to explain the concept of complexity in ecology. The complexity in ecological context is connected with the total number of participating species and the connectances that is, the number of non-zero elements $\{a_{ij}\}(N^*) \neq 0$ in the community matrix [3] stated otherwise, the complexity of the ecosystem is characterized by the interaction pattern (which involves both the number of participating species and the connectances) that is, by the community or interaction matrix A describing the internal structure of the system [3]. How to measure the complexity? There are different approaches to the concept of complexity. The entropy which is at the heart of the statistical mechanics and information theory plays a significant role in the characterization of complexity [14,15]. For the ecosystem the entropic measure of complexity should be associated with the community matrix A of the ecosystem. This can be based on the measure of entropy of non-probabilistic matrix A consistent with Von-Neumann quantum-entropy. Jumarie [6] was the first to provide such an entropy measure of a non-probabilistic matrix for dynamical system. Chakrabarti and Ghosh [7] have developed the theory for the study of interrelation between the concept of stability and complexity of an ecosystem. Here we shall present a different approach on the basis of the generalized Lyapunov-function (3.1). For this, generalized Lyapunov-function (3.1) must satisfy two basic characteristic properties:

(i) The first is that the generalized Lyapunov-function must be an entropy-function which is a measure of complexity. It is, infact, true as we have studied earlier and proved in an earlier paper [9].

(ii) The second characteristic property is that the Lyapunov-function should be associated with the community matrix A which characterizes the dynamical behaviors of the system in the neighborhood of the stationary point N^*.

Both the above characteristic properties are satisfied by the local form of the Lyapunov-function (3.1) in the vicinity of the stationary point N^*. In view of the above observations we consider the second-variation of the Lyapunov-function $\delta^2 V(N)$ as the basis for the measure of dynamical complexity.

The first variation of $V(N|N^*)$ in the vicinity of the stationary point N^* is given by

$$\delta V = \sum_{i=1}^{n} \frac{\partial V}{\partial N_i} \delta N_i \qquad (3.3)$$

then $\delta V(N_*) = 0$ for any arbitrary variation δN_i. The second variation is then given by

$$\delta^2 V(N) = \frac{1}{2}\sum_{i=1}^{n}\sum_{j=1}^{n}\frac{\partial^2 V}{\partial N_i N_j}\delta N_i \delta N_j = \frac{1}{2}\sum_{i=1}^{n}\phi''(\xi')\frac{(\delta N_i)^2}{N_i^*} > 0 \tag{3.4}$$

for any non-zero variation δN_i. Using (2.6) the second-order variation $\delta^2 V(N)$ reduces to the form

$$\delta^2 V(N) = \frac{1}{2}\sum_{i=1}^{n}\phi''(\xi')\frac{(\delta N_i(0))^2}{N_i^*}e^{2\lambda_i t}$$
$$= \frac{1}{2}\sum_{i=1}^{n} k_i e^{2\lambda_i t} \tag{3.5}$$

where $k_i = \phi''(\xi')\frac{(\delta N_i(0))^2}{N_i^*}$ is a positive constant.

We now proceed to measure the complexity associated with the evolution of the system. The complexity which we shall call dynamical complexity is a property of evolution of a state and not of the state itself[8,14]. We therefore define the dynamical complexity as the rate of change of the entropy that is, of the second-order variation $\delta^2 V(N)$

$$H(\lambda_1, \lambda_2, ..., \lambda_n; t) = \frac{d}{dt}\{\delta^2 V(N)\} = \sum_{i=1}^{n} k_i \lambda_i e^{2\lambda_i t} \tag{3.6}$$

The expression (3.6) has similarity with other measures of dynamical and thermodynamic complexity [7,8]. On the basis of dynamical complexity(3.6) the criteria of stability and instability are given by

$$H(\lambda_1, \lambda_2, ..., \lambda_n; t) = \frac{d}{dt}\{\delta^2 V(N)\} = \sum_{i=1}^{n} k_i \lambda_i e^{2\lambda_i t}$$
$$< 0 \quad for\ asymptotic\ stability$$
$$> 0 \quad for\ instability \tag{3.7}$$

Besides there is a state of marginal stability, the frontier between the asymptotic stability and instability [4,5], which we shall explain later on. The expression(3.6) of dynamical complexity depending on the eigenvalues $(\lambda_1, \lambda_2, ..., \lambda_n)$ of the community matrix A is very suitable for study of stability and instability of the system. The critical analysis of measure of dynamical complexity(3.6) leads to the following conclusions:

C_1 The dynamical complexity (3.6) increases with time t when at least one of the eigenvalues has positive real part. This is the case of instability implying the repelling nature of the stationary state.

C_2 The dynamical complexity (3.6) increases with time t and the system tends to the stationary state if and only if all the eigenvalues have negative real parts. This implies the asymptotic stability and attractive nature of the stationary state.

C_3 The complication arises when all the eigenvalues $(\lambda_1, \lambda_2, ..., \lambda_n)$ are purely imaginary i.e., $\lambda_j = \pm i b_j$, $b_j > 0$, $(j = 1, 2, ..., m | 2m = n)$. The system is then periodic. The application of the Lyapunov function to this fails in this case. If a Lyapunov function exists, then closed orbits are forbidden[7,16]. The criteria of closed orbit of the system the reduces to the vanishing of the time-average (over a period $(0, 2\pi)$) of the dynamical complexity [7]:

$$\bar{H} = \tfrac{1}{2\pi}\int_0^{2\pi}\tfrac{d}{dt}\{\delta^2 V(N)\}dt = \tfrac{1}{2\pi}\int_0^{2\pi}H(\lambda_1, \lambda_2, ..., \lambda_n; t)dt = \tfrac{1}{2\pi}\int_0^{2\pi}\textstyle\sum_{i=0}^{n} k_i \lambda_i e^{2\lambda_i t}dt = 0 \tag{3.8}$$

C_4 The positive value of the dynamical complexity $(H > 0)$ implies the instability of the system. By complexity we mean only the instability, the zero complexity $(H = 0)$ implies the asymptotic stable approaches to the stationary or fixed point N^* and finally the vanishing of the time-average of the dynamical complexity $(H = 0)$ implies the existence of closed orbits of the periodic system.

4 Applications: Illustrative Model Ecosystems

In this section we shall study the role of the measure of dynamical complexity (3.6) in the characterization of different dynamical behaviors such as stability, instability, periodicity, bifurcation and limit-cycle of some model ecosystems.

4.1 Lotka-Volterra prey-predator model

The model equations are[18]

$$\frac{dx_1}{dt} = ax_1 - bx_1x_2$$
$$\frac{dx_2}{dt} = -cx_2 + dx_1x_2 \tag{4.1}$$

where x_1 and x_2 are the prey and predator populations respectively. Two stationary states are $(0, 0)$ and $(\frac{c}{d}, \frac{a}{b})$

(i) Stationary point: $(0, 0)$; Eigenvalues: $\{a, -c\}$

The dynamical complexity is given by

$$H(t) = k_1 a e^{2at} - k_2 c e^{-2ct} \tag{4.2}$$

The dynamical complexity (4.2) whose results from (3.6) by using the eigenvalues $\lambda_1 = a$,$\lambda_2 = -c$, may be positive or negative. This implies the solution (or trajectory) may approach the stationary point $(0, 0)$ along one direction and recedes from it along another direction. This implies that the stationary state $(0, 0)$ is a saddle point.

(ii) Stationary point: $(\frac{c}{d},\frac{a}{b})$; Eigenvalues: $\lambda_{1,2} = \pm i\sqrt{ac}$
The dynamical complexity is given by

$$H(t) = k[i\sqrt{ac}e^{i2\sqrt{act}} - i\sqrt{ac}e^{-2i\sqrt{act}}] = k\sqrt{ac}\sin(2\sqrt{act})$$

The purely imaginary eigenvalues implies periodic orbit. According to the criteria C_3 of closed orbit we have to consider the time-average of the dynamical complexity over a complete cycle from $t = 0$ to $t = 2\pi$
We have then

$$\bar{H} = \frac{1}{2\pi}\int_0^{2\pi} H(t)dt = \frac{k}{2\pi}\int_0^{2\pi}[i\sqrt{ac}e^{2i\sqrt{act}} - i\sqrt{ac}e^{-2i\sqrt{act}}]dt = \frac{k\sqrt{ac}}{2\pi}\int_0^{2\pi}\sin(2\sqrt{ac})tdt = 0 \tag{4.3}$$

This is a important characteristic behavior of the phenomena for which the time-average of the dynamical complexity along a closed orbit is zero. The same result also holds good for the thermodynamic entropy production rate or thermodynamic complexity [9]. This is a significant result characterizing the analogy between the dynamical and thermodynamical complexity [7,17].

4.2 Damped Lotka-Volterra prey-predator Model

Let us consider the damped Lotka-Volterra system[18]

$$\frac{dN_1}{dt} = N_1(1-N_1) - N_1N_2$$
$$\frac{dN_1}{dt} = -\gamma N_2 + kN_1N_2 \tag{4.4}$$

where $N_1(t)$ and $N_2(t)$ are the populations of prey and predator respectively at any time t.

(a) The non-trivial stationary-states(or points) are $A(\frac{\gamma}{k}, 1-\frac{\gamma}{k})$ for $\frac{\gamma}{k} < 1$ inside the first quadrant and $B(1,0)$ on the abscissa.
(i) Stationary point: $A(\frac{\gamma}{k}, 1 - \frac{\gamma}{k})$;
Eigenvalues:$\{\lambda_{1,2} = \frac{-\frac{\gamma}{k} \pm \sqrt{(\frac{\gamma}{k})^2 - 4\frac{\gamma}{k}(k-\gamma)}}{2}\}$
The dynamical complexity is given by

$$H_1 = k_1\lambda_1 e^{2\lambda_1 t} + k_2\lambda_2 e^{2\lambda_2 t} \tag{4.5}$$

which tends to zero as $t \to \infty$ since $\lambda_1, \lambda_2 < 0$. The stationary point A is thus stable.
(ii) Stationary point:$B(1,0)$;
Eigenvalues:$\lambda_{1,2} = \{-1, k-\gamma\}$
Since $\frac{\gamma}{k} < 1$ i.e.,$k-\gamma > 0$, the eigenvalues of B are of opposite signs. So the stationary point B is a saddle point. The dynamical complexity is given by

$$H_2 = -k_1 e^{-2t} + k_2(k-\gamma)e^{2(k-\gamma)t} \tag{4.6}$$

which tends to infinity as $t \to \infty$. This corresponds to the unstable saddle point B.

(b) If $\frac{\gamma}{k}$ increases the stationary points A and B approach each other, and merge at $\frac{\gamma}{k} = 1$ or $\gamma = k$ to form a saddle node. In this case the eigenvalues of the point B become $(\lambda_1 = -1, \lambda_2 = 0)$ and the measure of dynamical complexity becomes.

$$H_3 = -k_1 e^{-2t} \tag{4.7}$$

which tends to zero as $t \to \infty$. This corresponds to the stable saddle point B. Again for $\frac{\gamma}{k} = 1$ the stationary point $A(\frac{\gamma}{k}, 1-\frac{\gamma}{k})$ reduces to the form $A(1,0)$ which is the same as the stationary point $B(1,0)$ as it should be.

(c) If $\frac{\gamma}{k}$ increases further i.e., if $\frac{\gamma}{k}$ becomes greater than 1 $((\frac{\gamma}{k}) > 1)$, the stationary point $A(\frac{\gamma}{k}, 1-\frac{\gamma}{k})$ disappears into the negative region, since the ordinate of A i.e., $(1-\frac{\gamma}{k}) < 0$. For the stationary point B, the dynamical complexity becomes

$$H_4 = -k_1 e^{-2t} + k_2 e^{2(k-\gamma)t} = -k_1 e^{-2t} + k_2 e^{-2(\gamma-k)t} \tag{4.8}$$

which tends to zero as $t \to \infty$. since $(\gamma > k)$ This implies that the stationary point B remains a stable as before (since both eigenvalues are negative). What is the ecological significance of the 3rd case i.e., $\frac{\gamma}{k} > 1$ or $\gamma > k$? In that case the predator ordinate $(1-\gamma > k)$ becomes negative, implying the extinction of the predator. For the greater value of the mortality rate γ compared to this inter-species competition rate k (i.e., $\gamma > k$) the prey population is unable to feed the predator population implying that the predator population is downed to die out from whatever initial state of the system starts from[19].

4.3 Mutualistic Model population system

Let us consider a mutualistic system[20]

$$\frac{dx}{dt} = \frac{r_1}{k_1}x(k_1 - x + y)$$
$$\frac{dy}{dt} = \frac{r_2}{k_2}y(k_2 - y + bx) \tag{4.9}$$

where k_1 , k_2 are the carrying capacity and r_1 , r_2 are the growth rate of the species $x(t)$ and $y(t)$ respectively. b is the measure of mutualism effect of each and other. In this model each of them benefits from the presence of other species and grows logistically in absence of other species.
(a) The non-trivial stationary-states are $A(x^*, y^*)$, where $x^* = \frac{k_1+k_2}{1-b}$ and $y^* = \frac{k_2+bk_1}{1-b}$ for $b < 1$ inside the first quadrant, $B(k_1, 0)$ and $C(0, k_2)$ on the abscissa and the ordinate respectively.

(i) Stationary point: $A(x^*, y^*)$; Eigenvalues:$\{\lambda_{1,2} = \frac{1}{2}[-(\frac{r_2y^*}{k_2} + \frac{r_1x^*}{k_1}) \pm \sqrt{(\frac{r_2y^*}{k_2} + \frac{r_1x^*}{k_1})^2 - \frac{4r_1r_2(1-b)x^*y^*}{k_1k_2}}]\}$
The dynamical complexity is given by

$$H_1 = p_1\lambda_1 e^{2\lambda_1 t} + p_2\lambda_2 e^{2\lambda_2 t} \tag{4.10}$$

which tends to zero as $t \to \infty$ since $\lambda_1, \lambda_2 < 0$ as $b < 1$. The stationary point A is thus stable.

(ii) Stationary point: $B(k_1, 0)$; Eigenvalues:$\{\lambda_{1,2} = -r_1, \frac{r_2}{k_2}(k_2 + bk_1)\}$
Since $r_1 > 0$, the eigenvalues of B are of opposite signs. So the stationary point is a saddle point.
The dynamical complexity is given by

$$H_2 = -p_1 r_1 e^{-2r_1 t} + p_2 \frac{r_2}{k_2}(k_2 + bk_1) e^{2\frac{r_2}{k_2}(k_2 + bk_1)t} \tag{4.11}$$

which tends to infinity as $t \longrightarrow \infty$. This corresponds to unstable saddle point B.

(iii) Stationary point: $C(0, k_2)$; Eigenvalues:$\{\lambda_{1,2} = \frac{r_1}{k_1}(k_2 + k_1), -r_2\}$
Since $r_2 > 0$, the eigenvalues of C are of opposite signs.So the stationary point is a saddle point.
The dynamical complexity is given by

$$H_2 = p_1 \frac{r_1}{k_1}(k_2 + k_1) e^{2\frac{r_1}{k_1}(k_2 + k_1)t} - p_2 r_2 e^{-2r_2 t} \tag{4.12}$$

which tends to infinity as $t \longrightarrow \infty$. This corresponds to unstable saddle point C.

4.4 Rosenzweig-MacArthur model

Let us now consider the case when the community matrix is a function of the environmental parameters which leads to the eigenvalues dependent on the environmental parameters. We consider a prey-predator model due to Harrison [21] who studied a variety of prey-predator models in order to find which model gives the best quantitative agreement with Luckinbill's data on Didinium and Paramecium [20,21]. Luckinbill's grew Paramecium Aurelia together with its predator Didinium nasutum and, under favorable experimental conditions aimed at reducing the searching effectiveness of the Didinium, he was able to observe oscillations of both populations for 33 days before they become extinct.In terms of scaled variables Harrison model reduces to the form of Rosenzweig-MacArthur model [21]:

$$\begin{aligned} \frac{dx_1}{dt} &= x_1(1 - \frac{x_1}{\kappa}) - \frac{\alpha_1 x_1 x_2}{\beta + x_1} \\ \frac{dx_2}{dt} &= \frac{\alpha_2 x_1 x_2}{\beta + x_1} - \gamma x_2 \end{aligned} \tag{4.13}$$

where

$$\begin{aligned} \alpha_1 &= (1 - \frac{1}{\kappa})(\beta + 1) \\ \alpha_2 &= \gamma(1 + \beta) \end{aligned} \tag{4.14}$$

which predicts the outcome of Luckinbill's experiment. The system of equations (4.13) contains only three independent parameters κ, β, γ. In terms of scaled population, the non-trivial fixed or stationary point is $(1,1)$. The community matrix of the stationary point $(1,1)$ is

$$A = \begin{pmatrix} \frac{(\kappa-2-\beta)}{\kappa(1-\beta)} & (\frac{1}{\kappa} - 1) \\ \frac{\beta\gamma}{1+\beta} & 0 \end{pmatrix} \tag{4.15}$$

The eigenvalues of the community matrix A, given by(4.15) are

$$\lambda_{1,2} = \frac{(\kappa - 2 - \beta) \pm i\sqrt{4(\kappa - 1)\kappa^2\beta\gamma - (\kappa - 2 - \beta)^2}}{2\kappa(1 + \beta)} \tag{4.16}$$

Let us investigate the dynamical behavior of the stationary point $(1,1)$ on the basis of the eigenvalues (4.16). The real part of the eigenvalues characterizes the stability and instability of the stationary point $(1,1)$. The threshold value of the parameter κ is given by $Re(\lambda) = 0$ i.e., by $\kappa = \kappa_c = 2 + \beta$. Below and above the threshold value $\kappa_c = 2 + \beta$, the phase-portrait is qualitatively different. For $\kappa < \kappa_c$ (i.e.,$\kappa < 2 + \beta$) the trajectories converge to the fixed point $(1,1)$, where as for $\kappa > \kappa_c = 2 + \beta$ they converge to a limit cycle. The threshold or critical value $\kappa_c = 2 + \beta$ of the parameter κ where this structural change occurs is called a bifurcation point. This is in view of the criteria of Hopf-bifurcation theorem:$Re(\lambda) = 0$ at $\kappa = \kappa_c$ and $\frac{dRe(\lambda)}{dk}|_{\kappa=\kappa_c} \neq 0$ [17]. For $\kappa_c = 2 + \beta$, the stability point $(1,1)$ is marginal stable, it changes its stability characteristic with slight change of the parameter κ crossing the bifurcation point $\kappa_c = 2 + \beta$ [22].
Let us now investigate the dynamical complexity of the limit-cycle corresponding to the bifurcation value $\kappa = \kappa_c$ i.e. $\kappa_c = 2 + \beta$. For $\kappa = 2 + \beta$, the eigenvalues are purely imaginary given by

$$\lambda_{1,2} = \pm i\frac{\sqrt{(\kappa-1)\kappa^2\beta\gamma}}{\kappa(1+\beta)} = \pm i\sqrt{\frac{\beta}{\gamma}(1 + \beta)(\frac{1}{\kappa} - 1)} = \pm iA(say) \tag{4.17}$$

Thus the dynamical complexity reduces to

$$H(t) = k[iAe^{2iAt} - iAe^{-2iAt}] = k\sin(2At) \tag{4.18}$$

where k is a constant. The time-average of the dynamical complexity (4.13) over a period $(0, 2\pi)$ along the closed orbit is then given by

$$\bar{H} = \frac{k}{2\pi}\int_0^{2\pi} \sin(2At)dt = 0 \tag{4.19}$$

which according to the criterion (3.8)characterizes the closed orbit of the limit cycle.

5 Conclusion

The objective of the present paper is to introduce a measure of dynamical complexity of a multispecies ecosystem and to study its importance in the characterization of different dynamical behaviors of some model ecosystems. The main results and characteristic features of the paper are as follows:

(i) We have first considered a generalized multispecies ecosystem described by a system of non-linear differential equations. The local analysis of the system around stationary states determines the mathematical structure of the community matrix which is of significant importance in the subsequent analysis.

(ii) The local form (second-order variation) of the generalized Lyapunov-function along with its entropic equivalence has been identified as a measure of complexity of the ecological system around the stationary states characterized by the community matrix A of the ecosystem.

(iii) The dynamical complexity defined to be the rate of change of the local form of generalized Lyapunov-function provides a qualitative measure of complexity associated with concept of stability, instability and periodicity. The dynamical complexity being dependent on the eigenvalues of the community matrix of the ecosystem is thus related to the mathematical structure of the system near the steady state. The states far from the stationary or equilibrium state are outside the domain of the application of the measure of the dynamical complexity defined by (3.6).

(iv) Stability and Complexity are two vital concepts in ecosystems. The relation between the concept of stability and complexity is a long standing well-debated problem of ecology[3,23,24]. A good deal of works on the subject are available in literatures In spite of a great deal of controversies about the unique relationship between the concept of stability and complexity the present analysis based on the Lyapunov-function method of deterministic dynamical model of ecosystem(without consideration of any genomic and environmental stochasticity)gives indication of a fairly important result that the complexity usually results instability rather than stability [3,23,24].

(v) The study of equivalence between generalized Lyapunov-function and generalized cross-entropy plays a significant role in the determination of the measure of dynamical complexity.

Appendix:

Let us now study the significance of the generalized Lyapunov-function(3.1) as a measure of generalized cross-entropy developed in statistical mechanics and information theory. For this, it is first necessary to develop statistical mechanical model of the ecosystem and then to introduce the concept of probability distribution in the context of the statistical model of the ecosystem. Boltzmann's mechanical concept of six-dimensional phase-space composed of a large number of phase-cells (representing the state of the system) can be applied to the macro-structure of the ecosystem. The construction of ecosystem phase-space then consists of developing rules for assigning individuals to different phase-cells or ecological niches, of different metabolic energy-bands $E_i, \ (i=1,2,3,....,n)$. Let w_i be the number of cells or ecological niches of the i^{th} metabolic energy-bands $E_i, \quad (i=1,2,3,....,n)$ [25]. Assuming dilute-gas model of ecosystem we have $N_i << w_{i<}$ where N_i is the population size(the number of individuals) of the i^{th} metabolic energy-bands $E_i, \quad (i=1,2,3,....,n)$ [25]. The ratio $p_i = \frac{N_i}{w_i}, \quad (i=1,2,3,....,n)$ can be considered as the probability of having an individuals in any one of the cells or niches of the i^{th} metabolic energy-bands E_i. $p_i^* = \frac{N_i^*}{w_i}$ is the same for stationary state of the system. The generalized Lyapunov-function(3.1) then can be written as

$$L(N|N^*) = \sum_{i=1}^{n} \phi(\frac{N_i}{N_i^*}) = \sum_{i=1}^{n} p_i^* w_i \phi(\frac{p_i w_i}{p_i^* w_i}) = \sum_{i=1}^{n} p_i^* w_i \phi(\frac{p_i}{p_i^*}) \quad (A1)$$

The r.h.s of $(A1)$ is the generalization of Csizer's directed divergence(or cross-entropy) for a system with non-stationary probability distribution $p^* = (p_1, p_2, ...p_n)$, stationary probability distribution $p^* = (p_1^*, p_2^*, ...p_n^*)$ with weights $w = (w_1, w_2, ..., w_n)$[26]. We call it as the generalized cross-entropy and represent it by $S(N|N^*)$ so that

$$S(N|N^*) = \sum_{i=1}^{n} N_i^* \phi(\frac{N_i}{N_i^*}) \qquad (A2)$$

defined over the positive-additive-distribution(PAD) $N = (N_1, N_2, ..., N_n)$ and $N^* = (N_1^*, N_2^*, ..., N_n^*)$ [13]. The expression $(A1)$ thus provides the probabilistic interpretation of generalized Lyapunov-function and provides the equivalence of the generalized Lyapunov-function $L(N|N^*)$ and the generalized cross-entropy $S(N|N^*)$:

$$L(N|N^*) = S(N|N^*) \qquad (A3)$$

We have thus the entropic significance of the Lyapunov-function for the broader perspective of positive-additive-distribution.

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