Is Dynamic Complexity of Ecological Systems Quantifiable?

VIKAS RAI1 AND MADHUR ANAND2
1Department of Applied Mathematics, Delhi College of Engineering, Bawana Road, Delhi 110042, India
2Department of Biology, Laurentian University, Ramsey Lake Road, Sudbury, Ontario, Canada P3E 2C6

ABSTRACT

Ecological Systems (natural populations, predator-prey communities, landscapes, etc.) are dynamic. The state of these systems changes with time in a complicated manner. Understanding and quantifying dynamic complexity of an ecological system is vital for designing strategies for restoration and recovery of damaged ecosystems. In this paper, we present a theory for the dynamic complexity of the biotic part of real world ecological systems. Simulation studies of two model ecosystems suggest that food chains with generalist predators at the bottom of the food chain would change their states in time in a quantifiable manner. On the other hand, those dominated by specialist predators will evolve in a manner, which does not allow any quantification. The dynamics of these systems are dictated by exogenous stochastic influences.

Key Words: Food-webs, Deterministic chaos, Predator-prey interactions, Specialist predator, Generalist predator, Environmental stochasticity, Dynamic complexity, Recovery.

INTRODUCTION

Simple ecological models have been designed and studied since the pioneering work of Sir Robert May (May 1976, May 2001). The dynamics of these model systems depend on values of system parameters. Beyond a critical value of a crucial parameter, the system displays a peculiar behaviour, which sensitively depends on initial conditions. This is known as ‘deterministic chaos’. The system trajectories meander aimlessly on a bounded phase space. The characteristic feature of this meandering is that initially close trajectories diverge exponentially from each other as time progresses. There are other kinds of dynamics possible. The geometrical objects which represent these in the phase space of the system, are known as stable focus and stable limit cycle. A stable focus depicts the approach of the system to an equilibrium state as $t \to \infty$. On the contrary, the system oscillates between two extreme asymptotic states when the system parameters are locked onto a set of values corresponding to a stable limit cycle. These are three distinct dynamical possibilities for a three-dimensional dissipative dynamical system. A model system’s practical value depends on how these dynamical possibilities are distributed in a relevant two-dimensional parameter space of the system (Upadhyay, Lyengar and Rai 1998).

Quantification of dynamic complexity of ecosystems is an imperative for the development of practical measures of biodiversity, which can be used for policy guidelines for restoration and recovery of damaged ecosystems (Anand and Desrochers 2004). As building blocks of ecological systems are species, which participate in non-linear interactions with others occupying the same or nearby niches, the key question is how an ecological system interacts with fluctuations in environmental conditions which are stochastic. May’s suggestion (May 1976, May 1995) that a set of deterministic rules can explain complex fluctuations in population abundances of animals is still fascinating and the real challenge is to elucidate mechanisms which cover or uncover signals of deterministic chaos (King et al. 2004).

Concerted efforts have been made (Upadhyay and Rai 1997, Upadhyay et al. 1998, Upadhyay and Rai 2001, Rai 2004) to understand why chaos has been successfully evading its capture in nature. It turns out that this dynamical behaviour is not of a familiar type (robust chaos); rather what one should expect in ecological systems is short-term recurrent chaos (struc) (Turchin and Ellner 2000, Rai 2004, Rai and Upadhyay 2004). What we have found is that over ecological time scales, chaotic dynamics does not get the needed amount of time to develop and is taken over by stable limit cycle oscillations. This is caused either by deterministic changes in parameters or by the influence of stochastic environmental fluctuations (Rai and Upadhyay 2004).
This seems to be a characteristic feature of the dynamics of ecological systems. We discuss the implications of this type of dynamical behaviour for designing practical diversity measures, which mark significant improvement over the existing ones. The dynamic complexity of ecosystems is quantifiable when it is decided by smooth (predictable) changes in system parameters. In the event that exogenous stochastic influences govern the dynamical behaviour of ecosystems, any effort to quantify the dynamic complexity will lead to failure. The paper is organized as follows. The next section discusses the two model ecosystems studied in this paper. The third section presents the rich dynamical repertoire of these systems. The fourth section discusses its implications for development of biodiversity measures and fifth one records some important conclusions of the present study.

MODEL SYSTEMS

Among four basic interactions (predator-prey, competition, interference and mutualism), predator-prey interaction is the most commonly observed and studied (Odum 1971, Pielou 1977). There are two types of predators: (i) specialists and (ii) generalists. A specialist predator dies out exponentially fast when its favourite food is absent or is in short supply. The generalist predators switch over to alternative food options when its most preferred food is in short supply. The Rosenzweig-MacArthur (RM) model (Rosenzweig and MacArthur 1963) is the describes the dynamics of a specialist predator and its prey:

\[
\frac{dX}{dt} = a_1X - b_1X^2 \frac{w_1YX}{(X+D)}, \quad (1a)
\]

\[
\frac{dY}{dt} = -a_2Y + \frac{w_1YX}{(X+D)} \quad (1b)
\]

where X is a prey for specialist predator Y with Holling type II functional response. \(a_1\) is the rate of self-reproduction for the prey. The parameter \(a_2\) measures how fast the predator Y will die when there is no prey to capture, kill and eat. \(b_1\) measures the intensity of competition among individuals of species X for space, food etc. and \(D\) measures the effect of the prey in evading a predator’s attack. It depends on the protection afforded by the environment to the prey. \(D\) has similar meaning as that of \(D_1\).

A model given by Holling and Tanner (HT) (Pielou 1977) describes the dynamics of a generalist predator and its prey:

\[
\frac{dZ}{dt} = AZ \left(1 - \frac{Z}{K}\right) - \frac{w_2UZ}{(Z+D_1)} \quad (2a)
\]

\[
\frac{dU}{dt} = cU - \frac{w_4U^2}{Z} \quad (2b)
\]

where Z is the most favourite food for the generalist predator U. In this model, prey and predator both grow logistically. A and K are respectively the rate of self reproduction and carrying capacity for the prey Z. c is the growth rate of the generalist predator due to sexual reproduction. The last term in Eq. (2b) describes how loss in species U depends on per capita availability of its prey (Z/U). The other parameters have their usual meaning. Eqs. (2a) and (2b) together represent this model. In what follows, we attempt to arrive at a graphical representation of both the RM and HT model dynamics, which gives us an idea about the parameter regimes displaying distinct dynamical possibilities (equilibrium dynamics represented by a stable focus and non-equilibrium dynamics represented by a stable limit cycle in the phase space).

A predator-prey system qualifies as a Kolmogorov (K) system if it can be cast into the following form:

\[
\frac{dX}{dt} = XF (X, Y), \quad (3a)
\]

\[
\frac{dY}{dt} = YG (X, Y), \quad (3b)
\]

where \(F\) and \(G\) are continuous and analytic functions in the domain \(X \geq 0, Y \geq 0\).

It can be easily seen that both the RM and HT models qualify as a K-system. Kolmogorov analysis (May 2001, Yodzis 1989) of RM model yields following conditions:

\[
w_1 > a_2, \quad (3a)
\]

\[
\frac{a_1}{b_1} > \frac{D_1 a_2}{(w_1 - a_2)}. \quad (3b)
\]
The local stability analysis puts the additional constraint

\[ 2b_1 \left( \frac{D_1 a_2}{w_1 - a_2} \right) + b_1 D - a_1 > 0 \]  \hspace{1cm} (4)

One obtains a stable limit cycle in the phase space, if inequality (4) is violated and those from Kolmogorov analysis are honoured while making the choices of the parameter values. The two conditions can be combined to give a straight line with slope \((2D_1/(w_1 - a_2))\). This line is located at a distance \(D\) from the origin of the coordinate system. \(a_1/b_1\) and \(a_2\) are the ordinate and abscissa. The straight line divides the space between two regions: the region above presents parameter values, which correspond to stable limit cycle solutions. The region below the dividing line and the straight line \((a_1/b_1 = D)\) is populated by stable equilibrium solutions (cf. Figure 1a).

The criterion when graphically represented, provides an idea about what parameter values will lead to a stable limit cycle. A graphical representation of the criterion for the case \(A/c = w_3/w_4\) is given in Figure 1b.

![Figure 1(b). Graphical representation of criterion (5). The figure is drawn for \(A/c = w_3/w_4\). Similar stability boundaries exist for other relationships. (adapted from May 2001, page 192, Figure A.1).](image)

The unstable region signifies stable limit cycle solutions, which emanate from stable ones through super critical Hopf bifurcations. The assumed relationship is biologically realistic and was chosen for the shake of simplicity. Similar stability boundaries exist for other relationships. It should be noted that a Kolmogorov analysis of this system does not put any constraint on the parameter values of the system (Eqs. 2a and 2b).

**Model 1**

RM model displays regular persistent periodic oscillations in a narrow region of the biologically plausible parameter space (cf. Figure 1a). When one adds a super-predator (Z) to this oscillatory predator-prey system, one gets the following model:

\[
\frac{dX}{dt} = a_1 X - b_1 X^2 - \frac{w_1 YX}{(X+D)} 
\]  \hspace{1cm} (7a)

\[
\frac{dY}{dt} = a_2 Y + \frac{w_1 YX}{(X+D_1)} - \frac{w_2 YZ}{(Y+D_2)} 
\]  \hspace{1cm} (7b)

Local stability analysis of HT model (May 2001) provides a criterion

\[
\frac{c}{A} > \frac{2(\alpha - R)}{1 + \alpha + \beta + R} 
\]  \hspace{1cm} (5)

where

\[
\alpha = \frac{w_3 c}{w_4 A}, \quad \beta = \frac{D_3}{K} \text{ and } R = [(1-\alpha - \beta)^2 + 4\beta]\]  \hspace{1cm} (6)
\[
\frac{dZ}{dt} = -cZ + \frac{w_3YZ}{(Y+D_3)}. \tag{7c}
\]

This is model 1 (Hastings and Powell 1991, Rinaldi et al. 2001, Rai and Upadhyay 2004).

**Model 2**

We also study another model ecosystem (Rai and Upadhyay 2004, Rai 2004), which is obtained by coupling RM model with HT model. The resulting model is described by the following system of non-linear ordinary differential equations:

\[
\frac{dX}{dt} = a_1X - b_1X^2 - \frac{w_1YX}{(X+D)}, \tag{8a}
\]

\[
\frac{dY}{dt} = -a_2Y + \frac{w_1YX}{(X+D_1)} - \frac{w_2YZ}{(Y+D_2)}, \tag{8b}
\]

\[
\frac{dZ}{dt} = cZ - \frac{w_3Z^2}{(Y)}. \tag{8c}
\]

Eqs. (8a-8c) describe model 2. The Allee effect (Allee et al. 1949) variant of this model can be written by replacing \(Z\) by \(Z^2\) in the first term of Eq. (8c) and adding an additional constant \(D_3\) in the denominator of the last term of the same equation. In this case, the last equation of the model system is modified to:

\[
\frac{dZ}{dt} = cZ^2 - \frac{w_3Z^2}{(Y+D_3)}. \tag{9}
\]

We study the two 3-dimensional model ecological systems (model 1 and 2) to embrace the most intriguing and interesting dynamical possibility: deterministic chaos. It is well known that minimum three degrees of freedom are needed for a system to support chaos. This is why we construct two model systems with dimensions greater than or equal to three. While model 1 is constituted by three interacting species, model 2 involves at least four. The number of degrees of freedom is the same as the dimensionality (number of participating species) of the system (c.f. Rai 2004 for a more elaborate discussion on this topic). The motivation for studying model 2 is the belief that deterministic chaos is generated in natural ecologies by non-linear coupling of non-linear oscillators (predator-prey interactions).

Predation or competition among different species serves as a coupling instrument.

**DYNAMICAL REPERTOIRE OF THE MODEL SYSTEMS**

A typical set of parameter values at which model 1 supports a stable limit cycle with all the species cycling on it is given as follows:

\[
a_1=1.55, b_1=0.05, c=0.1, w_1=1, D=10, a_2=1, w_2=2, w_2=0.55, D_1=10, D_2=10, D_3=20, w_3=0.25
\]

The parameters \(D\) and \(D_2\) measure the protection afforded by the environment to preys \(X\) and \(Y\). Treating \(a_1, D\) and \(D_2\) as the control parameters, we performed 2-dimensional scan studies in the parameter space. The results are given in Figures 2a and 2b. While Figure 2a presents an 'edge of chaos' phenomenon (EOC) (Kaufmann and Johnsen 1990, Kaufmann 1993, Mitchell et al. 1993), Figure 2b documents evidences in favour of robust chaos (Rai and Upadhyay 2004). Edge of Chaos is a special form of deterministic chaos, which is characterized by the existence of chaos at discrete and isolated points in the parameter space. On the other hand, robust chaos demands the existence of an area in the 2-dimensional parameter space, wherein no other dynamical behavior is found. In addition to this, what is also called for is a basin boundary structure which shows negligible intermixing of basins of different attractors.

![Figure 2a. EOC displayed by model 1. The basal values of the parameters are mentioned in the text. \(a_1\) was varied from 1.55 to 2.0 and \(D\) was varied from 5 to 35.](image-url)
Figure 3 presents results of 2D parameter scan on model 1 for a different set of basal values of the model parameters. It can be seen from this figure that chaos exists in a region (non-zero area) in $a_1$-$w_3$ parameter space. But the chaotic region is intruded by limit cycle attractors. Results of basin boundary calculations at the top-left corner ($a_1=1.75$, $w_3=3.75$), top-right corner ($a_1=3.0$, $w_3=3.75$) and in the middle ($a_1=2.5$, $w_3=3.0$) of the chaotic region of Figure 3 were presented by Rai and Upadhyay (2004). All of these figures convey that the basin of different attractors are intermixed. We reproduce the one (c.f. Figure 4) that was obtained at the middle of the chaotic region for the reader to have a clear idea of the intermixing. In such a case, the dynamics of the system is decided by external stochastic influences and the result is short-term recurrent chaos; a form of chaotic behaviour, wherein it is interrupted by other kind of dynamics at irregular and unpredictable intervals.

The model system given by Eqs. (8a-8c) does not support chaotic behaviour at all. The Allee variant of this model supports chaotic behaviour at isolated points in the parameter space. These points define the edges of chaotic dynamics displayed by these systems. This is a manifestation of the phenomenon known as EOC (cf. Figure 5). Chaotic dynamics in model 2 was observed only when $a_1$ as fixed at 1. For other values of this parameter, no chaos was found in the model. This suggests that there does not exist a window in parameter space for chaotic dynamics.

Figure 4. Model 1. Basin boundary structure for middle point of chaotic region ($a_1=2.25$, $w_3=3.0$) in Figure 3 for the chaotic attractor. The values of other parameters are $a_1=1.0$, $w_1=1$, $D_1=10$, $b_1=0.05$, $w_2=2$, $D_2=10$, $w_0=1.5$, $D_0=10$, $c=0.7$, $D_3=20$. 
Boundary basin calculations for chaotic attractors supported by model 2 at bottom-left corner \( (a_1=1.92, c=0.03) \), top-right corner \( (a_1=1.975, c=0.045) \) and middle \( (a_1=1.95, c=0.035) \) were presented in Rai and Upadhya (2004) (c.f. Figures 5-7 in their paper). All of them convey the same message; therefore we reproduce on that was obtained at mid-point. This is done in Figure 6. This is the X-Y view of the basin boundary structure \((-100 \leq X \leq 100, -100 \leq Y \leq 100)\) of chaotic attractor (shown in yellow colour). It is clear from Figures 6 that the chaotic attractor is the dominant one. No other attractor with appreciable basin size exists. The encroachment into the basin of chaotic attractor by basin of attractor at infinity (shown in green colour here) can be observed. The basin boundary diagram also shows that there is no intermixing of basins of different attractors. This establishes that strc in this model is generated by deterministic changes in the crucial parameters of the system.

**DISCUSSION**

Although the present simple models are short of being called "ecosystem models", this study points out that the Edge of Chaos phenomenon should be common in ecological systems (cf. Figures 2a and 5). We discover it in both the model systems we study. Even if chaos exists in a region of non-zero area in a 2D parameter space, the corresponding system will not display robust chaos as long as the basin boundary diagram suggests intermixing of basins of different kind of attractors. This does happen in case of model 1. Instead, the system would display strc as it is incessantly acted upon by stochastic influences.

We see that short-term recurrent chaos can be caused either by deterministic changes in system parameters (Allee variant of model 2) or by exogenous stochastic influences (model 1). In the latter, chaotic dynamics is interrupted by smooth changes in system’s parameters where as stochastic influences affect such interruptions in the former one. In both the cases what happens is that the ecological system is not able to lock itself onto a fully developed chaotic state. Since it is constantly influenced by exogenous stochastic fluctuations (Medwinsky et al. 2001), it is forced to leave the chaotic state as initial conditions change.

**CONCLUSION**

There are two types of model systems touched upon in this paper: (a) parameter sensitive and (b) initial condition sensitive (Rai and Upadhya 2004). Under-
understanding and modelling this sensitivity holds the key for applying these models to restoration and recovery of damaged ecosystems. Modelling and quantification of dynamic complexity of natural systems represented by the models in the first category is a smooth task. On the other hand, models of the second type with intermixed basin boundaries or riddled basins deny any quantification of the dynamic complexity that they possess. Actually, this would be an exercise in futility even if one is able to do so as initial conditions are altered by external factors which are beyond our control.

It turns out that food-chains with specialist predators as top-predators will present difficult challenges as far as modelling and quantification of dynamic complexity is concerned. Dynamic complexity of food-chains with generalist predators can be modelled and quantified without much difficulty. These theoretical results should be tested in the laboratory as well as in the field. The design of better diversity measures for use in restoration and recovery programs would depend on the success of these quantification efforts. The other necessity is our knowledge of the relationship between the non-dynamic (structural) (Anand and Orłoci 1996) and dynamic complexities of ecosystems. This relationship would be the focus of our future work.

ACKNOWLEDGEMENTS

M.A. thanks the Natural Science and Engineering Research Council of Canada, the Canada Research Chairs Program and the Premier’s Research Excellence Award (Ontario) for funding.

REFERENCES


Kaufmann, S.A. and Jensen, S. 1990. Coevolution to the edge of chaos: coupled fitness landscapes, poised states, and coevolutionary avalanches. Santa Fe Institute working paper 90-013. Santa Fe Institute, Santa Fe, N.M.


