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Stability and diversity in mathematical models of ecosystems

B.S. Goh

Department of Mathematics, Nanjing University, Nanjing, Jiangsu, China

ABSTRACT

Questions: Does diversity beget stability in ecosystems? What are the limits of mathematical modelling to understand this question? What is the dynamical behaviour of a model ecosystem that describes the effect of ‘not putting all one’s eggs into one basket’?

Methods: Mathematical models have been used to determine whether diversity begets stability in ecosystems. Experience of the use of mathematics in the management of fisheries helps us to understand the limits in using mathematics to describe biological populations and to answer this ecological question. I use some properties of dynamical systems in control theory to study the effects of ‘not putting all one’s eggs into one basket’ in a model ecosystem.

Conclusions: To better understand the issue of biodiversity and stability more research is required. First, there are many concepts of stability in model ecosystems and they do not define fully the stability of real ecosystems. Second, for a species with very high fecundity, for example the Asian silver carp, the Beverton-Holt approach does not even try to use mathematics to model the first stage of the dynamics of a year-class in the fish population. Thus, conclusions from an analysis of a model ecosystem may have limited applications to real ecosystems. I studied a linear model of a large ecosystem with many null interactions and showed that just a single disturbance can adversely affect each and every species or component of the model ecosystem. Thus to be invulnerable to continuous disturbances, an ecosystem requires subtle patterns of interactions among the species and between the species and the environment.

Keywords: biodiversity, decoupling, ecosystem stability, resilience, non-vulnerability.

INTRODUCTION

At the time of writing, the world is experiencing its worst financial crisis since the Great Depression in the 1930s. One of the interesting features of this financial crisis is the way it affects financial institutions on a worldwide scale. Initially, it was caused by difficulties with sub-prime mortgages in the US housing market. But then the financial crisis began to affect

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Correspondence: B.S. Goh, Department of Mathematics, Nanjing University, Nanjing, Jiangsu 210093, China. e-mail: bsgoh82@gmail.com

many other industries, including manufacturing, automobiles, and air travel. Discussion sites on the Internet have blamed the failures partly on bad mathematical modelling in financial analysis. In some leading newspapers, discussions advocate the need for more *decoupling* between these interconnected economic dynamics. It is thought that decoupling some of these economic interactions will make the economic systems more robust. It is a challenge for control system theorists to define what this decoupling property means and how such dynamic economic systems can be better designed. A common reason why many people expect diversity *per se* to confer stability on a dynamical system is the effect of 'not putting all one's eggs into one basket'. However, they then forget the caveat that a collection of baskets must not be connected by strings, so that when one basket falls off the table the others do not follow. This principle is often applied more or less vaguely to stability in complex dynamical systems in the real world.

A similar debate on diversity versus stability has occurred in ecological theory over the past 50 years (Elton, 1958; Holling, 1973; May, 1973; Beddington *et al.*, 1976; Vincent and Anderson, 1979; DeAngelis, 1980; Goh, 1980; Yodzis, 1981; Pimm, 1984; Levin, 1992; Grimm and Wissel, 1997; McCann, 2000; Justus, 2008). Elton (1958) suggested that, in nature, complex ecosystems like those in tropical rainforests are more stable than the less diverse ecosystems in the Arctic. This question on the relationships between stability and diversity (complexity) in an ecosystem has been reviewed by Pimm (1984) and McCann (2000).

May (1973) showed how, in some mathematical models of ecosystems, the probability of getting a stable system decreases as the number of species increases. May's analysis shook the confidence of ecologists in the principle that diversity begets stability, and it changed dramatically the thinking of ecologists. May then proposed that the parameters of real ecosystems are restricted and special in some manner, thus providing stability for ecosystems. Subsequently, Pimm (1984), Grimm and Wissel (1997), and McCann (2000) have all pointed out that there are many definitions of stability for ecosystems. Furthermore, these varied mathematical definitions of stability may still not fully describe the concepts of stability that are relevant to ecosystems in the real world.

Researchers of control systems (Michel and Miller, 1977; Vincent and Grantham, 1997; Khalil, 2002) study many different types of behaviour and stability of dynamic systems in engineering. It is a challenge to apply their knowledge of dynamic system behaviour to questions of system behaviour and the stability of real ecosystems.

Here I discuss two issues regarding this debate on diversity versus stability of ecosystems. The first issue concerns the effectiveness of mathematical models of biological populations. This is important, as many useful ideas in this debate have had their source in such mathematical models. Second, a key property of dynamical systems that we would like to understand better is the 'decoupling effect', or the effect of 'not putting all one's eggs into one basket', and apply it to the study of the dynamics of ecosystems.

MATHEMATICAL MODEL ECOSYSTEM

In 2006, about 140 million tons of fish were harvested globally. Because of this very valuable product, models of fish populations were among the earliest successful applications of mathematical models to biological populations. Thus, it is worthwhile to examine the nature of these models, and to determine any limitations in their usefulness. We can distinguish between four groups of mathematical models for single-species populations of fish.

The logistic equation provides the simplest model. Let N be the number of animals or plants and r and K be two positive parameters. The logistic model is

$$dN/dt = rN(K - N)/K. \tag{1}$$

This model has been used to separate species into two groups, called the r and K strategists (MacArthur and Wilson, 1967). The r strategists typically have a high fecundity or a short generation time. Examples of these strategists are some fish, weeds, bacteria, and insect pests. The K strategists are animals with low fecundity and large investment in the production and rearing of their offspring. Examples of these strategists include elephants, kangaroos, and whales.

A set of interacting biological populations is often described by the Lotka-Volterra model:

$$dN_i/dt = N_i(b_i + \textstyle\sum a_{ij}N_j) \qquad \text{where } i = 1, 2, \ldots, n. \tag{2}$$

These equations have been used to study predator–prey, competitive, and mutualistic interactions among species and multi-species fish populations.

The Ricker model (Ricker, 1954) was developed for salmon populations in North America. If N is the number of fish and the unit time is 4 years we have

$$N(t + 1) = N(t) \exp[r(K - N(t))/K]. \tag{3}$$

This is also called a stock-recruitment model. The stock is the parent population and the recruitment is the offspring population at a later time when the salmon cohort returns to its rivers. This model has been used successfully to study salmon populations. However, strong fluctuations in recruitments do occur in practice.

The logistic model (1) has been used widely in bioeconomc models of single-species fish populations. Typically, however, many fish populations have high fecundity. Some female fish, such as Asian silver carp females, can lay more than a million eggs. There is no evidence that such fish populations with extremely high fecundities can be described by the logistic model (equation 1), the Lotka-Volterra model (equation 2) or the Ricker model (equation 3). It is unrealistic to expect species with very high fecundity to be described by such mathematical models. Empirical studies by Touzeau and Gouzé (1998) have shown that there is no deterministic relationship between stock and recruitment in a number of fish populations. What can fisheries managers do to develop some realistic quantitative models to manage fish populations with high fecundity? The answer was developed by Beverton and Holt (1957). In this approach, we accept the biological reality and abandon the hope of developing a complete mathematical model relating to stock and recruitment.

In the Beverton-Holt approach, we do not model the year-class during the first stage of its life. A year-class or cohort includes the fish born in a particular year. There are likely high and variable mortalities in the initial stages of the year-class. However, when the year-class reaches some juvenile age, its mortality rate stabilizes and thereafter it can be modelled at a constant rate, M. The age when this happens is called the ‘age of recruitment’. The number of fish in a year-class that survives to the age of recruitment is called the ‘recruitment’. Thus we only attempt to model a year-class from the age of recruitment. We have,

$$dN/dt = -MN(t) \qquad \text{for } T \geq t \geq t_R \tag{4}$$

Here T is the lifespan of a fish under study, t_R is the time from birth to recruitment, and

$$N(t_R) = R. \tag{5}$$

Equation (4) describes the exponential decay in the number of individuals from the recruitment (equation 5). The rate of decline increases for an exploited fish population according to

$$dN/dt = -[M + u]N(t), \tag{6}$$

where $u(t)$ is the fishing effort, which can be subjected to the constraint

$$u_{\max} \geq u \geq 0. \tag{7}$$

The optimal control problem is to choose the control variable $u(t)$ that maximizes the total yield in biomass from the year-class. Let $W(t)$ be the weight of a fish at age t. We maximize,

$$Y = \int_{t_R}^{T} u(t)N(t)W(t)dt. \tag{8}$$

The integral is over the useful time interval, $T \geq t \geq t_R$. The optimal control analysis is described in Goh (1977, 1980). The optimal policy is to catch at a maximum rate all of the fish above a certain age, t_L. The length of an average fish at age t_L is called the 'optimal size limit'. For all $t \geq t_L$, we have

$$W(t) = \int_{t}^{T} u_{\max} W(s) \exp[-(M + u_{\max})(s - t)]ds. \tag{9}$$

This inequality can be used to determine the value of t_L and the optimal size limit.

The important lesson from the Beverton-Holt approach is that we should abandon a full mathematical model of a population in the face of biological reality when the fecundity of a species is extremely high, as in many fish populations.

Whale populations are among the best studied animal populations. Many of these studies are available in the International Whaling Commission publications. Its website is http://www.iwcoffice.org.

Clark (1976) developed a useful and simple model for a single-species Baleen whale population. Let N be the number of breeding females. We have

$$N(t + 1) = sN(T) + R[N(t - m)]. \tag{10}$$

The first term represents the surviving females and those that remain reproductive. The second term represents the females born m years ago and which are now sexually mature. This provides a realistic model of a Baleen whale population. Whales are K-strategists as they invest a lot into bringing up their offspring. Such populations are in sharp contrast to the fish populations with high fecundity.

In the Southern Ocean, the Minke whale population has increased several-fold. Part of this increase is likely due to the depletion of Blue whales through previous heavy commercial harvesting. It is estimated that there are more than 500,000 Minke whales and only about 1150–4500 Blue whales. Whale population estimates are available at the International Whaling Commission's website. The most important food species for the Minke and Blue whales are krill. Unfortunately, in a recent study Atkinson *et al.* (2004) showed that the krill population has declined by about 80% since the 1970s. This may be the result of global climate warming.

Here we have a relatively simple three-species interaction: krill, Minke whales, and Blue whales. Yet there is no mathematical model of this three-species system that is accepted by the many parties interested in the conservation of these whale species in the Southern Ocean. This demonstrates the difficulties in practice in the use of mathematical models of biological populations. Krill have high fecundity and using the Beverton-Holt approach there are difficulties in the mathematical modelling of the krill population. A mature female krill may have several thousand eggs and multiple broods each year. An interesting management question is whether culling the Minke whales would assist in the recovery of the Blue whale populations. Many people oppose the culling of Minke whales in the Southern Ocean without considering whether such culling may be vital to preventing the extinction of the Blue whale. Furthermore, if culled carefully, the harvesting of Minke whales would not pose an extinction risk to these whales.

This whale conservation problem in the Southern Ocean is a challenge for scientists developing management strategies in the face of inadequate or incomplete mathematical models.

RESILIENCE, NON-VULNERABILITY OF ECOSYSTEMS

Holling (1973), an eminent ecologist, has proposed the concept of resilience for biological populations. He used the idea that a dynamic ecosystem has multiple regions of stability. With a sufficiently large disturbance, an ecosystem may shift from one region to another. In this way, the system can survive large disturbances of its initial states, but it does not necessarily return to its original state.

Beddington *et al.* (1976) used the return time of a dynamical system to provide a measure of the resilience of an ecosystem. Vincent and Anderson (1979) showed that a lower bound on the return time is directly proportional to the number of trophic levels.

We can use the Beverton-Holt approach to provide another interpretation for why some biological populations are resilient. With very high fecundity, a population needs only a small number of surviving members to form a viable breeding stock and for the total population to survive and rebound. This is a characteristic of many pest populations. This is the case for several Asian carp fish species that were introduced to the USA to control weeds in aquaculture ponds (Conner *et al.*, 2007). However, some carp escaped into the Mississippi River following flooding. These introduced carp populations have been very difficult to eliminate, presumably because these pests are very resilient with their high fecundities.

Goh (1980) used control theory concepts to define non-vulnerability of a model ecosystem that is continually disturbed by large but bounded perturbations. We have a model ecosystem,

$$\hat{N}_i = N_i F_i[N_1, N_2, \ldots, N_m, u_1, u_2, \ldots, u_p]. \tag{11}$$

The elements of a definition of non-vulnerability are (i) a specified time interval $[0, T]$, (ii) a set $S(0)$ that contains possible initial states of the system, (iii) a set $Z(T)$ that contains undesirable states, and finally (iv) a class of possible disturbances, U. We wish to determine whether admissible disturbances exist that will drive the system from $S(0)$ to $Z(T)$ in the time period $[0, T]$. If so, the system is vulnerable, otherwise it is non-vulnerable. This is a non-linear and a non-local control system problem. In practice, it is very difficult to carry out the analysis.

Vincent and Anderson (1979) studied a special class of stable Lotka-Volterra models that are subjected to a single, large bounded disturbance. They introduced a more qualitative concept of non-vulnerability. They showed that increasing the number of species can reduce the vulnerability of a model ecosystem.

To get some feel for the effects of continual disturbances on a complex ecosystem with many species, we study the time-independent linear control system,

$$\hat{x} = Ax + Bu. \tag{12}$$

Here $x \in R^n$ and $u \in R^m$. As a special case, consider the case when $m = 1$. The question that we now pose is whether a single disturbance represented by a single u variable can cause adverse responses in every single component of x.

To answer this question, we make use of the well-known conditions on complete controllability (Bryson and Ho, 1969). The linear system (12) is completely controllable if the compound matrix

$$CM = [B, AB, A^2B, \ldots, A^{n-1}B] \tag{13}$$

has rank n. This means that a single control variable u can control each and every component of the state vector x.

One of the most fundamental questions of ecology is whether or not diversity *per se* confers on an ecological system the property of 'not putting all one's eggs into one basket'. As a starting point, we formulate this as a question: Can a single disturbance adversely affect each and every component of the linear system (12). Furthermore, we ask the question: What happens if the elements of matrices A and B are chosen at random?

The answer to these questions for the linear system (12) is given by a mathematical result of Lee and Markus (1967). The set of all matrices A and B such that the rank CM is n is open and dense in the universe of these matrices. In other words, if we construct matrices A and B in a random manner, the probability that the rank of CM of the chosen matrices A and B is n is one. Then we have complete controllability. Thus a randomly constructed linear system (12) has a probability equal to one that it is completely controllable.

This result is of fundamental significance. It implies that diversity *per se* for the linear system (12) does not confer the desirable property of 'not putting all one's eggs into one basket'. It means that matrices A and B for a model ecosystem must have special structures to have this desirable stability property. We desire the property that a single disturbance (control variable) cannot adversely affect each and every single component of the state vector, where for our purposes this state vector represents the displacements from an equilibrium of the populations of each of the species within the ecological community.

Some ecologists have sought to understand this question by looking at properties of randomly constructed linear dynamical systems,

$$\hat{x} = Ax. \tag{14}$$

They ask the question: What is the probability that the linear unforced system (14) with randomly constructed matrix A is a stable system? The result is stated in terms of the percentage of non-zero elements in A and the average values of the components of A. But such an analysis on the stability of (14) does not provide the answer to the question of whether diversity *per se* confers on a complex dynamical system the property of 'not putting all one's eggs into one basket'.

As a counter example on this issue in the use of the stability analysis of (14), consider the completely controllable system

$$d^n x / dt^n = u. \tag{15}$$

When this system is re-written in the matrix notation (equation 12), most of the elements of A and B matrices are zeros. Yet this is a completely controllable system, which means that a single control variable can affect in any manner each and every component of the state vector x irrespective of the value of n, the number of components of the state vector.

For example, when $n = 3$ we have

$$\begin{pmatrix} \hat{x}_1 \\ \hat{x}_2 \\ \hat{x}_3 \end{pmatrix} = \begin{pmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 0 \end{pmatrix} x + \begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix} u. \tag{16}$$

Clearly, most of the elements of matrices A and B are zeros, but these zero components do not provide the property of *decoupling* in order to confer the dynamical system property of ‘not putting all one’s eggs into one basket’. Thus diversity *per se* does not confer the desirable system property of ‘decoupling’ by our analysis with the controllable matrix (13). Furthermore, many null pairwise interactions in matrix A do not provide the desirable ‘decoupling’ system property.

Thus the interactions among species and the species with the environment must have evolved so that ecosystems are not vulnerable to their normal range of disturbances. Vincent and Anderson (1979) have shown that a Lotka-Volterra model with a special structure can have the property that an increase in the number of species reduces the vulnerability of the system.

For the Asian carp and other fish species with high fecundity, we know it is very hard to eliminate them as pests in the USA (Conner *et al.*, 2007). Thus high fecundity is clearly a way for such a species to adapt to environments where it may be subjected to a wide range of large disturbances. Another way the Asian carp adapted to its native environment is to have more males than females. On the Yangtze River in China, typically a spawning silver carp population would have less than 10% females. In contrast, a dominant male Sperm whale typically maintains a harem of about ten females. The Proboscis male monkey also maintains a harem of about seven females. These are some of the ways biological populations may adapt to cope with uncertainties in their environments.

CONCLUSIONS

In the management of fish populations, the Beverton-Holt model gives up the idea of using complete mathematical models to describe fully a fish population with high fecundity. It accepts the biological reality that the number of fish in a year-class during the initial stage of its life is highly variable and its mortality rates are then unpredictable. It sets out to model the population only from the juvenile stage onwards. Such populations are very resilient, as it needs only a relatively small breeding stock to provide a rebound of the population. Thus the usefulness of mathematical models of real biological populations with high fecundity is limited.

There is a popular expectation that diversity confers in some way the property of ‘not putting all one’s eggs into one basket’. We examine this question for a linear dynamic system with one control variable. We define the control variable as a disturbance. We ask if a single control variable can control each and every state variable in an adverse manner. In the world of randomly assembled linear systems, the probability that a single control variable can adversely affect each and every component of the *n*th order state variable is one. Thus real ecosystems must have special system structures that prevent them from being completely vulnerable to disturbances. It would be interesting to identify how this occurs in an ecosystem in the real world.

One of the most effective ways a plant or animal population is adapted to a wide range of large uncertainties is to have high fecundity. Such a species requires only a small breeding stock to survive and rebound. On the other hand, such an animal species must not produce a recruitment that is too large and which could destroy all its food resources, leading to the collapse of the total population.

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