

國立交通大學

應用數學系
碩士論文

生態系統中恢復率的計算

Computations of Recovery Rates in Some
Ecological Systems

研究生：李柏瑩

指導老師：石至文 教授

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研究生：李柏瑩

Student : Bo-Ying Lee

指導教授：石至文

Advisor : Chih-Wen Shih

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生態系統中恢復率的計算

學生：李柏瑩

指導老師：石至文 教授

國立交通大學應用數學系(研究所)碩士班

摘 要

生態系統中變化的發生往往沒有明顯的徵兆。因而需要一個有效的方式以預測變化的發生。近來眾多研究者提出環境恢復力的下降可提供變化即將來臨的預兆；但是，在實際上環境的恢復力是難以量測的，於是需要一些間接的指標以測量環境的恢復力。最近的一些研究文獻顯示臨界慢化是一個良好的環境恢復力的指標。在這篇報告裡頭我們運用分析以及數值的方法刻劃了幾個關於捕食者與獵物模型，三個物種的食物鏈模型，以及基因控制模型的結果。這些結果將引領我們預測在更多物種的生態學模型或真實世界變化的發生。

Computations of Recovery Rates in Some Ecological Systems

Student : Bo-Ying Lee Advisor : Chih-Wen Shih

Department of Applied Mathematics
National Chiao Tung University
Hsinchu, Taiwan, R.O.C.

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Abstract

Transitions in ecological systems often occur without apparent warning. Thus an effective way of prediction is in strong demand. Recent researchers proposed that decreasing ecological resilience can signal an upcoming transition. Unfortunately, it is very difficult to measure the resilience in practice. Therefore, we need some indicator to measure it. Some recent works in the literatures investigated that critical slowing down is a good indicator of ecological resilience. In this report, we use analytical and numerical methods to characterize several results about two-species generalized predator-prey model, three species food chain model, and generic control system. These results can lead directly to predict more complex systems in ecology or real world.

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1 Introduction

It is very important to predict the transition in ecosystems. However, the transitions are often difficult to predict, because they can originate from a variety of factors. Decreasing ecological resilience has been proposed as a signal of upcoming transitions in complex systems [6, 7]. Ecological resilience is the ability of a system to absorb perturbations and persist at a particular stable equilibrium [3, 5]. In other words, this is a measure of how much that parameter would need to be perturbed to reach the threshold point, and it correlates to the size of the basin of attraction. Unfortunately, ecological resilience can not be measured directly in practice, so there is a need for indirect indicators. One such potential indicator is “critical slowing down”, the decrease in recovery rate that occurs as the basin of attraction around a stable equilibrium contracts and a system approaches a transition [5]. For a variety of ecological models, critical slowing down often occurs far enough from a threshold to be a potentially useful indicator of an upcoming transition [5]. Most importantly, this phenomenon can be proved mathematically to occur as all continuous differential equations approach local bifurcations [4]. Recovery rates are inferred from the amount of time that the system needs to return to equilibrium after a small perturbation [5]. But, it is also not so easily quantified, even in models. Hence, we demand some method to estimate the quantity of recovery rates for any system. Fortunately, the recovery rate can be determined by linearizing at the stable equilibrium and determining the eigenvalues in a model, since the dominant eigenvalue is an approximation of the recovery rate to equilibrium [17, 18].

For each model, we then calculate the recovery rate as the absolute value of the real part of the dominant eigenvalue λ_{dom} of the Jacobian matrix at each stable equilibrium (the dominant eigenvalue is the eigenvalue with greatest real part for a continuous system) [5, 19]. The first step in the analysis of each model is to find its equilibria and the conditions for existence and stability of these equilibria. To find the conditions for stability we linearize each model around its equilibria by constructing the Jacobian matrix and applying the Routh-Hurwitz criteria for two dimensional and three dimensional continuous-time systems. In this report, we estimate the recovery rates by linearizing the models and determining the maximal real part of the eigenvalues of the Jacobian matrix.

However, we are interested in measuring the distance between the point at which the recovery rate starts to decrease K_r and the critical transition K_{crit} . This

distance can be seen as a warning period of the upcoming transition. The utility of critical slowing down as a leading indicator of the transition depends on the length of this warning period. Our method can yield general conclusions about the effects of the various parameters on the usefulness of critical slowing down as an indicator of an upcoming transition in a systems dynamics.

Critical slowing down has been proposed as a leading indicator of transitions in real world [5]. In 2007, Van Nes and Scheffer showed using numerical techniques that critical slowing down occurs far enough from a transition to be a promising indicator of loss of resilience for several ecological models. Van Nes and Scheffer are only the first steps towards establishing when critical slowing down will be a useful leading indicator of transitions in different ecosystems. In the last few years, several articles have been devoted to the study of the relationship between critical slowing down and ecological resilience. In this report, we choose these models because they are the simplest and most studied in biology. Of course, we can extend these insights to more complex, multi-species systems and predict that critical slowing down is still an effective indicator. Here, we just give slight theoretical contributions. Our study in this report is just a stepping stone to understanding more complex ecological models. To understand them, we require more mathematical theories than we have used here.

Moreover, there are various concepts and terminology from dynamical systems that we use in this report. These concepts are usually covered in an undergraduate (or graduate) course in ordinary differential equations. Here, we summarize these basic theory in Section 2. For a more complete treatment and more details, see [1, 2, 8, 9, 10, 11, 12, 13, 14].

2 Some basic definitions and classical theorems

In this section, we collect some basic definitions and classical theorems in ordinary differential equations that we will use in this report. Consider the nonlinear system

$$\dot{\mathbf{x}} = f(\mathbf{x}), \quad f \in C^1(\mathbb{R}^n).$$

Let ϕ_t be the flow map for the system.

Definition 1. An equilibrium \mathbf{x}_0 is said to be **stable** if for all $\varepsilon > 0$ there exists a $\delta > 0$ such that for all $\mathbf{x} \in N_\delta(\mathbf{x}_0)$ and $t \geq 0$ we have $\phi_t(\mathbf{x}) \in N_\varepsilon(\mathbf{x}_0)$, i.e. nearby solutions stay nearby for all future time.

Definition 2. An equilibrium \mathbf{x}_0 is said to be **unstable** if it is not stable. This means that there is a neighborhood U of \mathbf{x}_0 such that for every neighborhood U_1 of \mathbf{x}_0 in U , there is at least one solution $\mathbf{x}(t)$ starting at $\mathbf{x}(0) \in U_1$ that does not lie entirely in U for all $t > 0$.

Definition 3. An equilibrium \mathbf{x}_0 is said to be **asymptotically stable** if it is stable and there exists a $\delta > 0$ such that for all $\mathbf{x} \in N_\delta(\mathbf{x}_0)$, we have

$$\lim_{t \rightarrow \infty} \phi_t(\mathbf{x}) = \mathbf{x}_0.$$

For linear systems, there is a criterion on the eigenvalues that ensures asymptotic stability of the origin. This criterion is summarized in the next theorem.

Theorem 2.1 [2] : Consider the linear differential equation

$$\dot{x} = Ax.$$

(a) If all of the eigenvalues λ of A have negative real parts, then the origin is asymptotically stable. In particular, stable nodes, degenerate stable nodes, and stable foci are all asymptotically stable.

(b) If one of the eigenvalues λ_1 has a positive real part, then the origin is unstable. In particular, saddles, unstable nodes, degenerate unstable nodes, and unstable foci are all unstable. A saddle has some directions that are attracting and others that are expanding, but it still satisfies the condition to be unstable.

(c) In two dimensions, if the eigenvalues are purely imaginary $\pm\beta$ then the origin is

stable but not asymptotically stable.

(d) In two dimensions, if one eigenvalue is 0, then the origin is stable but not asymptotically stable.

In two dimensional case, we can use the determinant and the trace to determine the type of linear system. It is convenient to have these results summarized so we can immediately recognize the stability type from these quantities, which are easy to compute.

Theorem 2.2 [2] : Let A be a 2×2 matrix with determinant Δ and trace τ .

(a) If $\Delta < 0$, then the linear system is a saddle, and therefore unstable.

(b) If $\Delta > 0$ and $\tau > 0$, then the linear system is unstable.

(i) If $\tau^2 - 4\Delta > 0$, then it is an unstable node.

(ii) If $\tau^2 - 4\Delta = 0$, then it is a degenerate unstable node.

(iii) If $\tau^2 - 4\Delta < 0$, then it is an unstable focus.

(c) If $\Delta > 0$ and $\tau < 0$, then the linear system is asymptotically stable.

(i) If $\tau^2 - 4\Delta > 0$, then it is a stable node.

(ii) If $\tau^2 - 4\Delta = 0$, then it is a degenerate stable node.

(iii) If $\tau^2 - 4\Delta < 0$, then it is a stable focus.

(d) If $\Delta = 0$, then one or more of the eigenvalues is zero.

(i) If $\tau > 0$, then the second eigenvalue is positive.

(ii) If $\tau = 0$, then the both eigenvalues are zero.

(iii) If $\tau < 0$, then the second eigenvalue is negative.

If \mathbf{x}_0 is a hyperbolic equilibrium (there is no eigenvalues with zero real parts for the Jacobian matrix at \mathbf{x}_0), then the stability type of the equilibrium for the nonlinear system is the same as that for the linearized system. The following result states this more precisely.

Theorem 2.3 [2] : Consider a differential equation $\dot{\mathbf{x}}=F(\mathbf{x})$ in n variables, with a hyperbolic equilibrium \mathbf{x}_0 . Assume that F , $\frac{\partial F_i}{\partial x_j}(\mathbf{x})$, $\frac{\partial^2 F_i}{\partial x_j \partial x_k}(\mathbf{x})$ are all continuous. Then, the stability type of the equilibrium for the nonlinear system is the same as that for the linearized system at that equilibrium.

(a) If the real parts of all the eigenvalues of $DF(\mathbf{x}_0)$ are negative, then the equilibrium \mathbf{x}_0 is asymptotically stable for the nonlinear system. (i.e., if the origin is asymptotically stable for the linearized system, then \mathbf{x}_0 is asymptotically stable for

the nonlinear system).

(b) If at least one eigenvalue of $DF(\mathbf{x}_0)$ has a positive real part, then the equilibrium \mathbf{x}_0 is unstable for the nonlinear system.

How do we determine whether a non-hyperbolic equilibrium is stable, asymptotically stable, or unstable? The following method, due to Lyapunov, is very helpful for answering this question.

Definition 4. Assume \mathbf{x}_0 is an equilibrium for the differential equation $\dot{\mathbf{x}} = f(\mathbf{x})$. A real-valued function L is called a **weak Lyapunov function** for the differential equation provided there is a neighborhood U of \mathbf{x}_0 on which L is defined and (i) $L(\mathbf{x}) > L(\mathbf{x}_0)$ for all \mathbf{x} in U but distinct from \mathbf{x}_0 , and (ii) $\dot{L}(\mathbf{x}) \leq 0$ for all \mathbf{x} in U . The function L is called a **Lyapunov function** or strict Lyapunov function on an open neighborhood U provided it is a weak Lyapunov function which satisfies which satisfies $\dot{L}(\mathbf{x}) < 0$ for all \mathbf{x} in U but distinct from \mathbf{x}_0 .

Theorem 2.4 [13] : Let E be an open subset of \mathbb{R}^n containing \mathbf{x}_0 . Suppose that $f \in C^1(E)$ and $f(\mathbf{x}_0) = 0$. Suppose further that there exists a real valued function $L \in C^1(E)$ satisfying $L(\mathbf{x}_0) = 0$ and $L(x) > 0$ if $x \neq \mathbf{x}_0$. Then (a) if $\dot{L}(x) \leq 0$ for all $x \in E$, \mathbf{x}_0 is stable. (b) if $\dot{L}(x) < 0$ for all $x \in E - \{\mathbf{x}_0\}$, \mathbf{x}_0 is asymptotically stable. (c) if $\dot{L}(x) > 0$ for all $x \in E - \{\mathbf{x}_0\}$, \mathbf{x}_0 is unstable.

The following result is due to **Bendixson** and is called **Bendixson's Negative Criterion**.

Theorem 2.5 [9] : Let $\dot{\mathbf{x}}=f(\mathbf{x})$ be a planar system, where $\mathbf{f}=\begin{pmatrix} f_1 \\ f_2 \end{pmatrix}$, $\mathbf{x} = \begin{pmatrix} x \\ y \end{pmatrix} \in \mathbb{R}^2$. Furthermore $f \in C^1(E)$ where E is a simply connected region in \mathbf{R}^2 . If $\frac{\partial f_1}{\partial x} + \frac{\partial f_2}{\partial y}$ (the divergence of the vector field \mathbf{f} , $\nabla \cdot \mathbf{f}$) is always of the same sign but not identically zero on E , then there are no periodic solution in the region E of the planar system.

3 Generalized predator prey model

The first model we shall study is the generalized predator prey model [20]:

$$\begin{aligned}\frac{dV}{dt} &= rVf(V) - kPh(V) \\ \frac{dP}{dt} &= AkP[h(V) - h(J)]\end{aligned}\tag{3.1}$$

where t is time, V is the prey population size, r is the intrinsic rate of increase in prey, P is predator population size, k is the predation rate, J is the equilibrium prey population size, and A is the predator-prey conversion efficiency. The function $f(V)$ represents the effects of intra-specific competition among the prey: as the prey population increases, the per-capita population growth rate decreases and eventually becomes zero at the carrying capacity K , i.e. (i) $f(V) > 0$, for $0 \leq V < K$, and $f(K) = 0$; (ii) $f'(V) < 0$, for $0 < V < K$. The carrying capacity K is the control parameter. If a family of functions f , i.e. $f = f_K(V)$, are consider, then we further assume that f is an increasing function of K and that the derivative of f_K with respect to V is a non-decreasing function of K , i.e. $\frac{\partial f_K(V)}{\partial K} > 0$, $\frac{\partial f'_K(V)}{\partial K} \geq 0$. The function $h(V)$ represents the per-capita rate at which predators kill prey; the kill-rate increases as the number of available prey increases, but does so at a decreasing rate, i.e. $h(V) > 0$, $h'(V) > 0$, and $h''(V) < 0$. The following Figures 1, 2, 3, 4, depict typical graphs for the functions f and h .

In this section, we summarize the propositions obtained in [20], and provide detailed computations for these results.

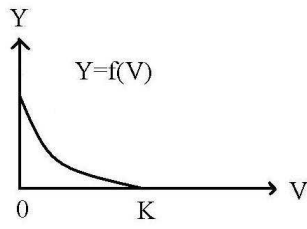


Figure 1: This figure depicts the function f with $f''(V) > 0$.

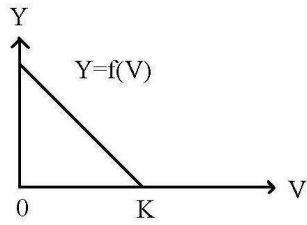


Figure 2: This figure depicts the function f with $f''(V) = 0$.

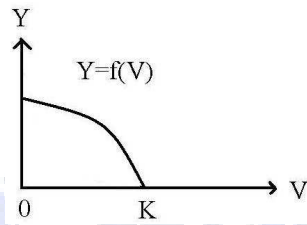


Figure 3: This figure depicts the function f with $f''(V) < 0$.

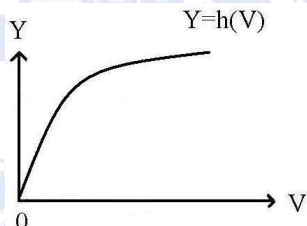


Figure 4: This figure depicts the function h .

It is easy to verify that this model has three equilibria,

$$(V, P) = (0, 0), (K, 0), (J, \frac{rJf(J)}{kh(J)}).$$

At first, let us consider these equilibria of the system (3.1). Existence and local stability conditions of these equilibria of the system (3.1) are summarized in propositions 3.1, 3.2.

Proposition 3.1 [20]: Let K be the carrying capacity and J be the equilibrium prey population size. Then

- (a) the equilibria $(0, 0)$ and $(K, 0)$ exist for all K ;
- (b) the equilibrium $(0, 0)$ is unstable for all K ;
- (c) the equilibrium $(K, 0)$ is stable for $K < J$.

Proof:

- (a) It is easy to see that $(0, 0)$ and $(K, 0)$ exist for all K .
- (b) From the system (3.1), we can compute the Jacobian matrix at (V, P)

$$\begin{pmatrix} r[f(V) + Vf'(V)] - kPh'(V) & -kh(V) \\ AkPh'(V) & Ak[h(V) - h(J)] \end{pmatrix}.$$

Then the Jacobian matrix at the equilibrium $(0, 0)$ is

$$\begin{pmatrix} rf(0) & -kh(0) \\ 0 & Ak[h(0) - h(J)] \end{pmatrix}.$$

Hence, its eigenvalues are given by $\lambda=rf(0)$, $Ak[h(0) - h(J)]$. Since $\lambda=rf(0) > 0$, the equilibrium $(0, 0)$ is unstable for all K .

- (c) Similarly, the Jacobian matrix at the equilibrium $(K, 0)$ is

$$\begin{pmatrix} r[f(K) + Kf'(K)] & -kh(K) \\ 0 & Ak[h(K) - h(J)] \end{pmatrix}.$$

Therefore, its eigenvalues are given by $\lambda=r[f(K) + Kf'(K)]$, $Ak[h(K) - h(J)]$. Both $r[f(K)+Kf'(K)]$ and $Ak[h(K)-h(J)]$ are negative for all $K < J$ by hypothesis of f and h , the equilibrium $(K, 0)$ is stable for all $K < J$. The assertion follows.

Proposition 3.2 [20]: Let K be the carrying capacity and J be the equilibrium prey population size. Then the equilibrium $(J, \frac{rJf(J)}{kh(J)})$ exists for $K > J$, and is stable

for $J < K < K_{crit}$, where K_{crit} is the solution of the equation $\alpha f(J) + Jf'(J) = 0$, where $\alpha = 1 - \frac{Jh'(J)}{h(J)}$. In particular, Hopf bifurcation occurs for $K = K_{crit}$.

Proof:

Since $f(J) > 0$ when $J < K$, the equilibrium $(J, \frac{rJf(J)}{kh(J)})$ exists for $K > J$. From the system (3.1), we can compute the Jacobian matrix at (V, P) is

$$\begin{pmatrix} r[f(V) + Vf'(V)] - kPh'(V) & -kh(V) \\ AkPh'(V) & Ak[h(V) - h(J)] \end{pmatrix}.$$

Then the Jacobian matrix at the equilibrium $(J, \frac{rJf(J)}{kh(J)})$ is

$$\begin{aligned} M &= \begin{pmatrix} r[f(J) + Jf'(J)] - \frac{rJf(J)}{h(J)}h'(J) & -kh(J) \\ Ak\frac{rJf(J)}{kh(J)}h'(J) & 0 \end{pmatrix} \\ &= \begin{pmatrix} r[\alpha f(J) + Jf'(J)] & -kh(J) \\ \frac{r^2\tau f(J)}{kh(J)}h'(J) & 0 \end{pmatrix}, \end{aligned}$$

where

$$\alpha = 1 - \frac{Jh'(J)}{h(J)}, \tau = \frac{AkJ}{r}h'(J).$$

By Mean Value Theorem, we have $h(J) - h(0) = h'(c)$ for some $c \in (0, J)$. Moreover, $h'(c) > h'(J)$ by $h''(V) < 0$. Therefore, $h(J) > h(J) - h(0) = h'(c)J > h'(J)J$, i.e. $\alpha = 1 - \frac{Jh'(J)}{h(J)} > 0$. Since $A, k, J, r, h'(J)$ are positive, $\tau = \frac{AkJ}{r}h'(J) > 0$. In fact, we have the characteristic equation of M is

$$\lambda^2 - r[\alpha f(J) + Jf'(J)]\lambda + r^2\tau f(J) = 0.$$

So, its eigenvalues are given by

$$\lambda = \frac{r[\alpha f(J) + Jf'(J)] \pm \sqrt{r^2[\alpha f(J) + Jf'(J)]^2 - 4r^2\tau f(J)}}{2}.$$

In two dimensional case, we can only use the determinant and the trace to determine the stability of the equilibrium. The determinant and trace of M are $r^2\tau f(J)$ and $r[\alpha f(J) + Jf'(J)]$, respectively. By Theorem 2, the equilibrium $(J, \frac{rJf(J)}{kh(J)})$ is stable when the determinant of M is positive and the trace of M is negative, which occurs at

$$\alpha f(J) + Jf'(J) < 0.$$

Next, let us compute the derivative of $\alpha f(J) + Jf'(J)$ with respect to K .

$$\frac{d[\alpha f(J) + Jf'(J)]}{dK} = \alpha \frac{df(J)}{dK} + J \frac{df'(J)}{dK} > 0.$$

So, as the control parameter K increases, the equilibrium $(J, \frac{rJf(J)}{kh(J)})$ becomes unstable. Furthermore, we have $\lambda = 0 \pm \sqrt{r^2\tau f(J)}$ and $\frac{dRe(\lambda)}{dK} \neq 0$ when $K = K_{crit}$, where

$$\alpha f(J) + Jf'(J) = 0, \quad (3.2)$$

so Hopf bifurcation occurs for $K = K_{crit}$. This completes the proof.

Assume the equilibrium $(J, \frac{rJf(J)}{kh(J)})$ is stable, let us compute the eigenvalues of M and determine the dominant eigenvalue to find the recovery rate. The following proposition will tell us where the maximum recovery rate occurs.

Proposition 3.3 [20]:

Suppose the equilibrium $(J, \frac{rJf(J)}{kh(J)})$ is stable. Then the maximum recovery rate occurs for some value of $K = K_r$ when $\delta^2 + 4\beta\gamma = 0$, which occurs at $\alpha f(J) + Jf'(J) = -2\sqrt{\tau f(J)}$.

Proof:

We know that the characteristic equation of the Jacobian matrix at the equilibrium $(J, \frac{rJf(J)}{kh(J)})$ is

$$\lambda^2 - r[\alpha f(J) + Jf'(J)]\lambda + r^2\tau f(J) = 0$$

and its eigenvalues are given by

$$\lambda = \frac{r[\alpha f(J) + Jf'(J)] \pm \sqrt{r^2[\alpha f(J) + Jf'(J)]^2 - 4r^2\tau f(J)}}{2} = \frac{\delta \pm \sqrt{\delta^2 + 4\beta\gamma}}{2}$$

where

$$\beta = -kh(J) < 0, \quad \gamma = \frac{r^2\tau f(J)}{kh(J)} > 0, \quad \delta = r[\alpha f(J) + Jf'(J)] < 0.$$

Let $\lambda_+ \equiv \frac{\delta + \sqrt{\delta^2 + 4\beta\gamma}}{2}$, $\lambda_- \equiv \frac{\delta - \sqrt{\delta^2 + 4\beta\gamma}}{2}$. Then we can compute the dominant eigenvalue λ_{dom} . First, we divide the situation into two kinds according to $\delta^2 + 4\beta\gamma$. If $\delta^2 + 4\beta\gamma > 0$ then $\lambda_+ = \frac{\delta + \sqrt{\delta^2 + 4\beta\gamma}}{2} > \frac{\delta - \sqrt{\delta^2 + 4\beta\gamma}}{2} = \lambda_-$. Hence, $Re(\lambda_+) > Re(\lambda_-)$, i.e. $\lambda_{dom} = \lambda_+ = \frac{\delta + \sqrt{\delta^2 + 4\beta\gamma}}{2}$. If $\delta^2 + 4\beta\gamma \leq 0$ then $Re(\lambda_+) = Re(\lambda_-) = \frac{\delta}{2}$, i.e. $\lambda_{dom} = \lambda_+ = \lambda_- = \frac{\delta}{2}$. Thus, the recovery rate $\rho \equiv |Re(\lambda_{dom})|$ is

$$\begin{cases} \frac{-\delta - \sqrt{\delta^2 + 4\beta\gamma}}{2} & \text{if } \alpha^2 + 4\beta\gamma > 0, \\ \frac{-\delta}{2} & \text{if } \alpha^2 + 4\beta\gamma \leq 0. \end{cases}$$

Finally, let us compute the derivative of ρ with respect to K . Consider $\alpha^2 + 4\beta\gamma > 0$ and let $\delta' = \frac{d\delta}{dK}$. Then

$$\begin{aligned}
\frac{d\rho}{dK} &= \frac{d\left(\frac{-\delta - \sqrt{\delta^2 + 4\beta\gamma}}{2}\right)}{dK} \\
&= -\frac{1}{2} \cdot \frac{d(\delta + \sqrt{\delta^2 + 4\beta\gamma})}{dK} \\
&= \frac{-\delta'}{2} - \frac{1}{4\sqrt{\delta^2 + 4\beta\gamma}} \cdot \frac{d[\delta^2 + 4(-r^2\tau f(J))]}{dK} \\
&= \frac{-\delta'}{2} - \frac{1}{4\sqrt{\delta^2 + 4\beta\gamma}} \cdot (2\delta\delta' - 4r^2\tau \frac{df(J)}{dK}) \\
&= \frac{-\delta'}{2} \left(1 + \frac{\delta}{\sqrt{\delta^2 + 4\beta\gamma}}\right) + r^2\tau \frac{df(J)}{dK} \\
&> 0
\end{aligned}$$

since $(1 + \frac{\delta}{\sqrt{\delta^2 + 4\beta\gamma}}) < 1 + \frac{\delta}{\sqrt{\delta^2}} = 1 + \frac{\delta}{(-\delta)} = 0$. When $\alpha^2 + 4\beta\gamma < 0$, we have

$$\begin{aligned}
\frac{d\rho}{dK} &= \frac{d\left(-\frac{\delta}{2}\right)}{dK} \\
&= -\frac{r}{2} \cdot \frac{d[\alpha f(J) + Jf'(J)]}{dK} \\
&< 0
\end{aligned}$$

because $\frac{d[\alpha f(J) + Jf'(J)]}{dK} > 0$. Therefore, the maximum recovery rate occurs for some value of $K = K_r$ when $\delta^2 + 4\beta\gamma = 0$, which occurs when

$$\alpha f(J) + Jf'(J) = -2\sqrt{\tau f(J)}. \quad (3.3)$$

To sum up, if we are using the recovery rate as an indicator of the system (3.1), we will have more warning of the upcoming transition when K_r is far enough from K_{crit} . From equations (3.2) and (3.3), we see that K_r is far away from K_{crit} when the right-hand side of (3.3) tends to minus infinity:

$$\tau f(J) = \frac{AkJ}{r} h'(J) f(J) \rightarrow \infty.$$

This occurs as $A \rightarrow \infty$ (predator-prey biomass conversion is efficient), $r \rightarrow 0$ (the intrinsic rate of increase in the prey population is low), or $k \rightarrow \infty$ (predation rate being high). K_r is also far enough from K_{crit} when $h'(J) \rightarrow \infty$, meaning that the predation rate increases quickly with increasing prey population size, which is equivalent to the predation rate being high.

4 Three species food chain model

In this section, let us discuss the Lotka-Volterra equation for a food chain of three species [22]. Consider the system of differential equations are given by

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(r_1 - a_{11}N_1 - a_{12}N_2), \\ \frac{dN_2}{dt} &= N_2(r_2 + a_{21}N_1 - a_{22}N_2 - a_{23}N_3), \\ \frac{dN_3}{dt} &= N_3(r_3 + a_{32}N_2 - a_{33}N_3).\end{aligned}\tag{4.1}$$

where $r_i > 0$ and $a_{ij} > 0, \forall 1 \leq i, j \leq 3$.

In this model, t is time, N_i is the population of species i , r_i is the intrinsic growth rate of the species i , and a_{ij} is the competitive impact of species j on species i . Moreover, N_1 and N_2 have a negative effect on the growth rate of N_1 ; N_1 has a positive effect and N_2 and N_3 have a negative effect on the growth rate of N_2 ; N_2 has a positive effect and N_3 have a negative effect on the growth rate of N_3 . That is why this model is said to be a food chain.

In order to give a manageable exposition, we henceforth reduce the number of parameters in this three species food chain model by making the symmetry assumptions that (i) $r_1 = r_2 = r_3 = 1$; (ii) with respect to species, 2 affects 1 as 3 affects 2, i.e. $a_{12} = a_{23} = \alpha$; (iii) with respect to species, 1 affects 2 as 2 affects 3, i.e. $a_{21} = a_{32} = \beta$; (iv) $a_{11} = a_{22} = a_{33} = 1$, to arrive at

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(1 - N_1 - \alpha N_2), \\ \frac{dN_2}{dt} &= N_2(1 + \beta N_1 - N_2 - \alpha N_3), \\ \frac{dN_3}{dt} &= N_3(1 + \beta N_2 - N_3).\end{aligned}\tag{4.2}$$

The study of equilibria plays a central role in ordinary differential equations and their application. At first, let us find the conditions for existence of the equilibria of this system. It can be computed that there exist eight nonnegative equilibria for this model:

- (i) no-species equilibrium: $E_0 = (0, 0, 0)$.
- (ii) single species equilibrium: $E_1 = (1, 0, 0)$, $\hat{E}_1 = (0, 1, 0)$, $\check{E}_1 = (0, 0, 1)$.
- (iii) two-species equilibrium: $E_2 = (1, 0, 1)$, $\hat{E}_2 = (0, \frac{1-\alpha}{1+\alpha\beta}, \frac{1+\beta}{1+\alpha\beta})$, $\check{E}_2 = (\frac{1-\alpha}{1+\alpha\beta}, \frac{1+\beta}{1+\alpha\beta}, 0)$.
- (iv) three species equilibrium: $E_3 = (\frac{1+\alpha\beta-\alpha+\alpha^2}{1+2\alpha\beta}, \frac{1+\beta-\alpha}{1+2\alpha\beta}, \frac{1+\alpha\beta+\beta+\beta^2}{1+2\alpha\beta})$.

Existence conditions of these equilibria of this model are summarized in proposition 4.1.

Proposition 4.1:

- (a) $E_0, E_1, \hat{E}_1, \check{E}_1$, and E_2 exist and for all values of $\alpha, \beta > 0$.
- (b) \hat{E}_2 and \check{E}_2 exist for $0 < \alpha < 1$ and $\beta > 0$.
- (c) E_3 exists for $\alpha - \beta < 1$.

Proof:

(a) We know that

$E_0 = (0, 0, 0)$, $E_1 = (1, 0, 0)$, $\hat{E}_1 = (0, 1, 0)$, $\check{E}_1 = (0, 0, 1)$, $E_2 = (1, 0, 1)$. Hence, no-species equilibrium E_0 , single species equilibria $E_1, \hat{E}_1, \check{E}_1$, and two-species equilibrium E_2 exist for all values of $\alpha, \beta > 0$.

(b) Since

$$\hat{E}_2 = \left(0, \frac{1 - \alpha}{1 + \alpha\beta}, \frac{1 + \beta}{1 + \alpha\beta}\right),$$

$\check{E}_2 = \left(\frac{1 - \alpha}{1 + \alpha\beta}, \frac{1 + \beta}{1 + \alpha\beta}, 0\right)$, two-species equilibria \hat{E}_2, \check{E}_2 exist for $0 < \alpha < 1$ and $\beta > 0$.

(c) We know that the three species equilibrium

$$E_3 = \left(\frac{1 + \alpha\beta - \alpha + \alpha^2}{1 + 2\alpha\beta}, \frac{1 + \beta - \alpha}{1 + 2\alpha\beta}, \frac{1 + \alpha\beta + \beta + \beta^2}{1 + 2\alpha\beta}\right),$$

so there is the three species equilibrium E_3 when $1 + \beta - \alpha > 0$ and $1 + \alpha\beta - \alpha + \alpha^2 > 0$. Since $1 + \alpha\beta - \alpha + \alpha^2 = (\alpha - 1/2)^2 + \alpha\beta + 3/4 > 0$, for all $\alpha, \beta > 0$, therefore, the three species equilibrium E_3 exists for $\alpha - \beta < 1$.

It is in general a routine, although often algebraically messy, matter to study the stability of such equilibria. For convenience, at first we only verify the local stability of the equilibria of this system when $\beta = 1$. Afterward we focus on stability of the three species equilibrium E_3 for various parameters. Local stability conditions of these equilibria of this model when $\beta = 1$ are summarized in proposition 4.2.

Proposition 4.2: Let $\beta = 1$.

- (a) E_0, E_1, \hat{E}_1 , and \check{E}_1 are unstable for all values of α .
- (b) E_2 is stable for $\alpha > 2$ and is unstable for $\alpha < 2$.
- (c) \hat{E}_2 and \check{E}_2 are unstable for $\alpha < 1$.
- (d) E_3 is stable for $\alpha < 2$.

Proof:

First, we compute the Jacobian matrix at (N_1, N_2, N_3)

$$\begin{pmatrix} 1 - 2N_1 - \alpha N_2 & -\alpha N_1 & 0 \\ N_2 & 1 + N_1 - 2N_2 - \alpha N_3 & -\alpha N_2 \\ 0 & N_3 & 1 + N_2 - 2N_3 \end{pmatrix}.$$

Thus, we obtain the Jacobian matrix for each equilibrium of this system.

(a) (i) At E_0 , the Jacobian matrix is

$$\begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}.$$

Hence, its eigenvalues are given by

$$\lambda = 1, 1, 1.$$

Thus, E_0 is always unstable.

(ii) At E_1 , the Jacobian matrix is

$$\begin{pmatrix} -1 & -\alpha & 0 \\ 0 & 2 & 0 \\ 0 & 0 & 1 \end{pmatrix}.$$

Therefore, its eigenvalues are given by

$$\lambda = -1, 2, 1.$$

Therefore, E_1 is always unstable.

(iii) At \hat{E}_1 , the Jacobian matrix is

$$\begin{pmatrix} 1 - \alpha & 0 & 0 \\ 1 & -1 & -\alpha \\ 0 & 0 & 2 \end{pmatrix}.$$

Thus, its eigenvalues are

$$\lambda = 1 - \alpha, -1, 2.$$

Therefore, \hat{E}_1 is always unstable.

(iv) At \check{E}_1 , the Jacobian matrix is

$$\begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 - \alpha & 0 \\ 0 & 1 & -1 \end{pmatrix}.$$

So, its eigenvalues are

$$\lambda = 1, 1 - \alpha, -1.$$

Thus, \check{E}_1 is always unstable.

(b) At E_2 , the Jacobian matrix is

$$\begin{pmatrix} -1 & -\alpha & 0 \\ 0 & 2 - \alpha & 0 \\ 0 & 1 & -1 \end{pmatrix}.$$

So, one eigenvalue is positive when $\alpha < 2$ and all of its eigenvalues are negative when $\alpha > 2$. Therefore, E_2 is stable for $\alpha > 2$ and is unstable for $\alpha < 2$.

(c) (i) At \hat{E}_2 , the Jacobian matrix is

$$\begin{pmatrix} 1 - \alpha \frac{1-\alpha}{1+\alpha} & 0 & 0 \\ \frac{1-\alpha}{1+\alpha} & 1 - 2\frac{1-\alpha}{1+\alpha} - \alpha \frac{2}{1+\alpha} & -\alpha \frac{1-\alpha}{1+\alpha} \\ 0 & \frac{1-\alpha}{1+\alpha} & 1 + \frac{1-\alpha}{1+\alpha} - 2\frac{1-\alpha}{1+\alpha} \end{pmatrix}.$$

So, there is an eigenvalue

$$\lambda = 1 - \alpha \frac{1-\alpha}{1+\alpha} = \frac{1+\alpha^2}{1+\alpha} > 0.$$

Therefore, \hat{E}_2 is unstable for $\alpha < 1$.

(ii) At \check{E}_2 , the Jacobian matrix is

$$\begin{pmatrix} 1 - 2\frac{1-\alpha}{1+\alpha} - \alpha \frac{2}{1+\alpha} & -\alpha \frac{1-\alpha}{1+\alpha} & 0 \\ \frac{2}{1+\alpha} & 1 + \frac{1-\alpha}{1+\alpha} - 2\frac{2}{1+\alpha} & -\alpha \frac{2}{1+\alpha} \\ 0 & 0 & 1 + \frac{2}{1+\alpha} \end{pmatrix}.$$

So, there is an eigenvalue

$$\lambda = 1 + \frac{2}{1+\alpha} > 0.$$

Therefore, \check{E}_2 is unstable for $\alpha < 1$.

(d) At E_3 , the Jacobian matrix is

$$\begin{pmatrix} -\frac{1+\alpha^2}{1+2\alpha} & 0 & 0 \\ \frac{1-\alpha}{1+\alpha} & -\alpha \frac{1+\alpha^2}{1+2\alpha} & -\alpha \frac{2-\alpha}{1+2\alpha} \\ 0 & \frac{3+\alpha}{1+2\alpha} & -\frac{3+\alpha}{1+2\alpha} \end{pmatrix}.$$

So, we can compute its eigenvalues

$$\lambda = -\frac{1+\alpha^2}{1+2\alpha}, -\alpha \frac{\alpha^2 - \alpha + 3}{1+2\alpha}, -\frac{3+\alpha}{1+2\alpha}.$$

Since all of its eigenvalues are negative, E_3 is stable for $\alpha < 2$.

From now on, we concentrate our attention on the stability of the three species equilibrium E_3 for various parameters. Here, we introduce an useful method to determine the stability of the three species equilibrium E_3 for various parameters. The method is as follows. Given $A \in R^{n \times n}$, $Re\lambda(A) \equiv \max\{Re\lambda : \lambda \text{ is an eigenvalue of } A\}$. How do we verify analytically A is a stable matrix, i.e. $Re\lambda(A) < 0$? Suppose that the characteristic polynomial of A is

$$g(z) = \det(zI - A) = a_0z^n + a_1z^{n-1} + \dots + a_n(a_0 > 0).$$

The **Routh-Hurwitz Criterion** provides a necessary and sufficient condition for a real polynomial to have all roots with negative real parts. We list the conditions for $n = 2, 3$ which are frequently used in applications.

- (i) Assume that $n = 2$. Then $g(z) = a_0z^2 + a_1z + a_2$ with $a_1 > 0$ and $a_2 > 0$ if and only if A is a stable matrix.
- (ii) Assume that $n = 3$. Then $g(z) = a_0z^3 + a_1z^2 + a_2z + a_3$ with $a_1 > 0$, $a_3 > 0$, and $a_1a_2 > a_0a_3$ if and only if A is a stable matrix.

A more thorough treatment are given in [10, 21].

By Routh-Hurwitz Criterion, we will analyze the stability of the three species equilibrium E_3 for various parameters. The result is as follows.

Proposition 4.3: If there exists the three-species equilibrium E_3 , then E_3 is always an asymptotically stable equilibrium.

Proof:

We will apply Routh-Hurwitz Criterion to prove stability of the three-species equilibrium E_3 . Hence, we desire to acquire the coefficients a_0, a_1, a_2, a_3 of the characteristic polynomial of the Jacobian matrix at E_3 . From the system (4.2), we have the Jacobian matrix at $E_3=(\bar{N}_1, \bar{N}_2, \bar{N}_3)$

$$A = \begin{pmatrix} 1 - 2\bar{N}_1 - \alpha\bar{N}_2 & -\alpha\bar{N}_1 & 0 \\ \beta\bar{N}_2 & 1 + \beta\bar{N}_1 - 2\bar{N}_2 - \alpha\bar{N}_3 & -\alpha\bar{N}_2 \\ 0 & \beta\bar{N}_3 & 1 + \beta\bar{N}_2 - 2\bar{N}_3 \end{pmatrix} \\ = \begin{pmatrix} -\bar{N}_1 & -\alpha\bar{N}_1 & 0 \\ \beta\bar{N}_2 & -\bar{N}_2 & -\alpha\bar{N}_2 \\ 0 & \beta\bar{N}_3 & -\bar{N}_3 \end{pmatrix}.$$

Since

$$\begin{aligned}
1 - 2\bar{N}_1 - \alpha\bar{N}_2 &= 1 - 2 \cdot \frac{1 + \alpha\beta - \alpha + \alpha^2}{1 + 2\alpha\beta} - \alpha \cdot \frac{1 + \beta - \alpha}{1 + 2\alpha\beta} \\
&= -\frac{1 + \alpha\beta - \alpha + \alpha^2}{1 + 2\alpha\beta} \\
&= -\bar{N}_1, \\
1 + \beta\bar{N}_1 - 2\bar{N}_2 - \alpha\bar{N}_3 &= 1 + \beta \cdot \frac{1 + \alpha\beta - \alpha + \alpha^2}{1 + 2\alpha\beta} - 2 \cdot \frac{1 + \beta - \alpha}{1 + 2\alpha\beta} - \alpha \cdot \frac{1 + \alpha\beta + \beta + \beta^2}{1 + 2\alpha\beta} \\
&= -\frac{1 + \beta - \alpha}{1 + 2\alpha\beta} \\
&= -\bar{N}_2, \\
1 + \beta\bar{N}_2 - 2\bar{N}_3 &= 1 + \beta \cdot \frac{1 + \beta - \alpha}{1 + 2\alpha\beta} - 2 \cdot \frac{1 + \alpha\beta + \beta + \beta^2}{1 + 2\alpha\beta} \\
&= -\frac{1 + \alpha\beta + \beta + \beta^2}{1 + 2\alpha\beta} \\
&= -\bar{N}_3,
\end{aligned}$$

So, the characteristic polynomial of the Jacobian matrix at E_3 is

$$\begin{aligned}
\det(\lambda I - A) &= \prod_{i=1}^{i=3} (\lambda + N_i) + \alpha\beta N_1 N_2 (\lambda + N_3) + \alpha\beta N_2 N_3 (\lambda + N_1) \\
&= \lambda^3 + (\bar{N}_1 + \bar{N}_2 + \bar{N}_3)\lambda^2 + [(1 + \alpha\beta)\bar{N}_1\bar{N}_2 + (1 + \alpha\beta)\bar{N}_2\bar{N}_3 + \bar{N}_3\bar{N}_1]\lambda \\
&\quad + (1 + 2\alpha\beta)\bar{N}_1\bar{N}_2\bar{N}_3.
\end{aligned}$$

It is easy to see the coefficients a_0, a_1, a_2, a_3 of the characteristic polynomial of the Jacobian matrix at E_3 are

$$\begin{aligned}
a_0 &= 1, \\
a_1 &= \bar{N}_1 + \bar{N}_2 + \bar{N}_3 > 0, \\
a_2 &= (1 + \alpha\beta)\bar{N}_1\bar{N}_2 + (1 + \alpha\beta)\bar{N}_2\bar{N}_3 + \bar{N}_3\bar{N}_1, \\
a_3 &= (1 + 2\alpha\beta)\bar{N}_1\bar{N}_2\bar{N}_3 > 0.
\end{aligned}$$

Therefore, we have

$$\begin{aligned}
a_1 a_2 - a_0 a_3 &= (\bar{N}_1 + \bar{N}_2 + \bar{N}_3)[(1 + \alpha\beta)\bar{N}_1\bar{N}_2 + (1 + \alpha\beta)\bar{N}_2\bar{N}_3 + \bar{N}_3\bar{N}_1] - (1 + 2\alpha\beta)\bar{N}_1\bar{N}_2\bar{N}_3 \\
&= \bar{N}_1^2(\bar{N}_2 + \bar{N}_3) + \bar{N}_2(\bar{N}_3 + \bar{N}_1) + \bar{N}_3^2(\bar{N}_1 + \bar{N}_2) + 3\bar{N}_1\bar{N}_2\bar{N}_3 + 2\alpha\beta\bar{N}_1\bar{N}_2\bar{N}_3 \\
&\quad + \alpha\beta(\bar{N}_1^2\bar{N}_2 + \bar{N}_1\bar{N}_2^2 + \bar{N}_2^2\bar{N}_3 + \bar{N}_2\bar{N}_3^2) - \bar{N}_1\bar{N}_2\bar{N}_3 - 2\alpha\beta\bar{N}_1\bar{N}_2\bar{N}_3 \\
&= \bar{N}_1^2(\bar{N}_2 + \bar{N}_3) + \bar{N}_2^2(\bar{N}_3 + \bar{N}_1) + \bar{N}_3^2(\bar{N}_1 + \bar{N}_2) + 2\bar{N}_1\bar{N}_2\bar{N}_3 \\
&\quad + \alpha\beta(\bar{N}_1^2\bar{N}_2 + \bar{N}_1\bar{N}_2^2 + \bar{N}_2^2\bar{N}_3 + \bar{N}_2\bar{N}_3^2) \\
&> 0.
\end{aligned}$$

By Routh-Hurwitz Criterion, the assertion follows.

Next, we perform some numerical simulations for various α, β , to explore global dynamics for the system. The numerical computations provide us some observation and motivation to justify more dynamical properties for the three-species equilibrium E_3 .



Example 4.1: If $\alpha = 1$ and $\beta = 2$, i.e., the system is

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(1 - N_1 - N_2) \\ \frac{dN_2}{dt} &= N_2(1 + 2N_1 - N_2 - N_3) \\ \frac{dN_3}{dt} &= N_3(1 + 2N_2 - N_3)\end{aligned}\tag{4.3}$$

then $E_3 = (\frac{3}{5}, \frac{2}{5}, \frac{9}{5})$ is an asymptotically stable equilibrium for the above system. (See Figure 5, Figure 6.)

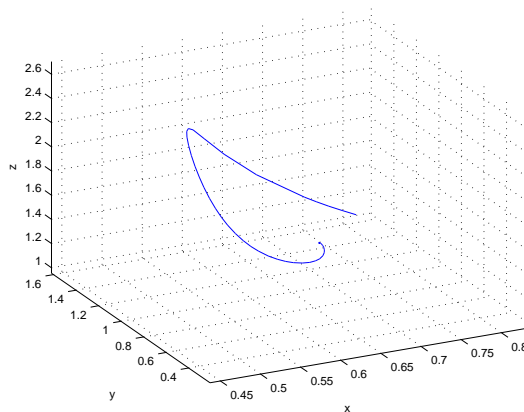


Figure 5: A solution trajectory with initial value (0.8,1.5,1.1) for (4.3).

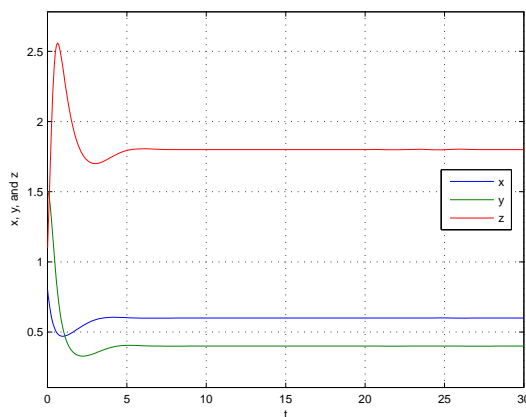


Figure 6: x, y, z components with initial value (0.8,1.5,1.1) for (4.3).

Example 4.2: If $\alpha = 2$ and $\beta = 3$, i.e., the system is

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(1 - N_1 - 2N_2) \\ \frac{dN_2}{dt} &= N_2(1 + 3N_1 - N_2 - 2N_3) \\ \frac{dN_3}{dt} &= N_3(1 + 3N_2 - N_3)\end{aligned}\tag{4.4}$$

then $E_3 = (\frac{9}{13}, \frac{2}{13}, \frac{19}{13})$ is an asymptotically stable equilibrium for the above system. (See Figure 7, Figure 8.)

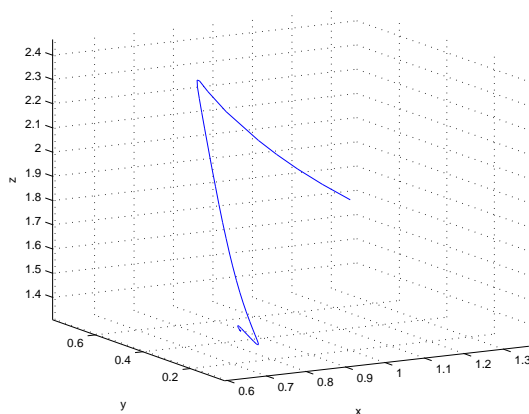


Figure 7: A solution trajectory with initial value $(1.3, 0.7, 1.7)$ for (4.4).

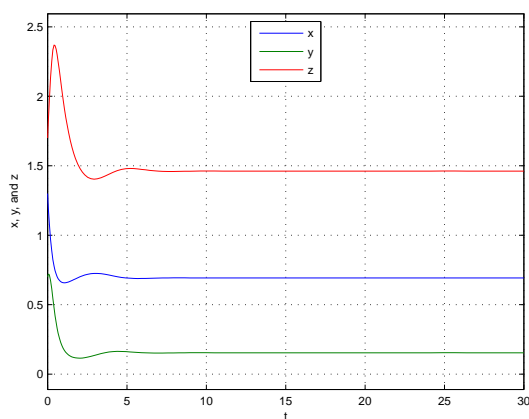


Figure 8: x, y, z components with initial value $(1.3, 0.7, 1.7)$ for (4.4).

Example 4.3: If $\alpha = 3$ and $\beta = 5$, i.e., the system is

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(1 - N_1 - 3N_2) \\ \frac{dN_2}{dt} &= N_2(1 + 5N_1 - N_2 - 3N_3) \\ \frac{dN_3}{dt} &= N_3(1 + 5N_2 - N_3)\end{aligned}\tag{4.5}$$

then $E_3 = (\frac{22}{31}, \frac{3}{31}, \frac{46}{31})$ is an asymptotically stable equilibrium for the above system. (See Figure 9, Figure 10.)

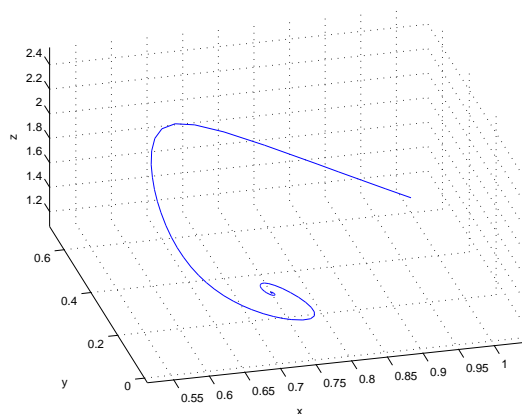


Figure 9: A solution trajectory with initial value (1,0.6,1.2) for (4.5).

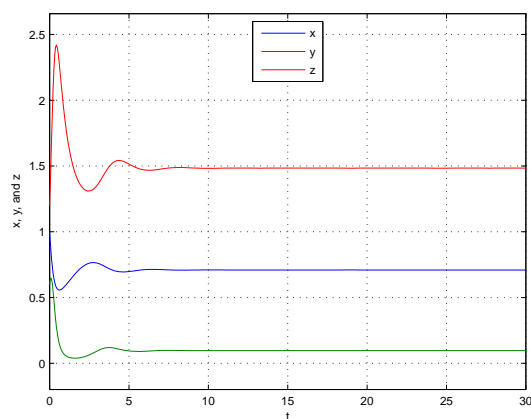


Figure 10: x, y, z components with initial value (1,0.6,1.2) for (4.5).

Example 4.4: If $\alpha = 4$ and $\beta = 6$, i.e., the system is

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(1 - N_1 - 4N_2) \\ \frac{dN_2}{dt} &= N_2(1 + 6N_1 - N_2 - 4N_3) \\ \frac{dN_3}{dt} &= N_3(1 + 6N_2 - N_3)\end{aligned}\tag{4.6}$$

then $E_3 = (\frac{37}{49}, \frac{3}{49}, \frac{67}{49})$ is an asymptotically stable equilibrium for the above system. (See Figure 11, Figure 12.)

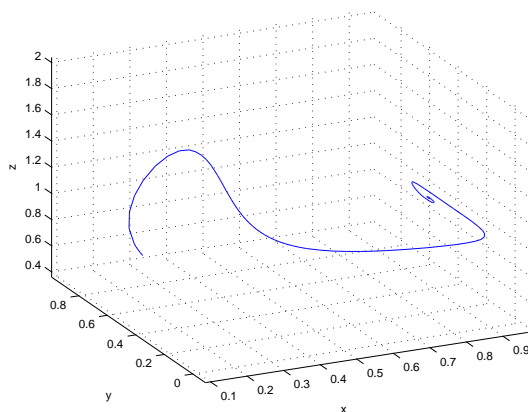


Figure 11: A solution trajectory with initial value $(0.3, 0.9, 0.5)$ for (4.6).

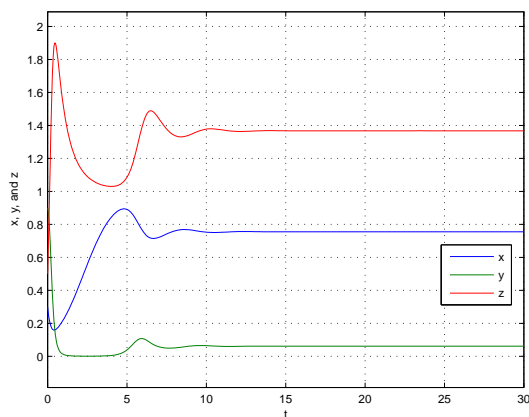


Figure 12: x, y, z components with initial value $(0.3, 0.9, 0.5)$ for (4.6).

Example 4.5: If $\alpha = 1$ and $\beta = 7$, i.e., the system is

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(1 - N_1 - N_2) \\ \frac{dN_2}{dt} &= N_2(1 + 7N_1 - N_2 - N_3) \\ \frac{dN_3}{dt} &= N_3(1 + 7N_2 - N_3)\end{aligned}\tag{4.7}$$

then $E_3 = (\frac{8}{15}, \frac{7}{15}, \frac{64}{15})$ is an asymptotically stable equilibrium for the above system. (See Figure 13, Figure 14.)

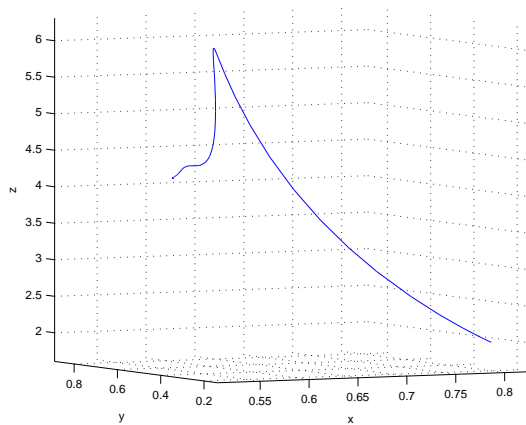


Figure 13: A solution trajectory with initial value $(0.8, 0.2, 2)$ for (4.7).

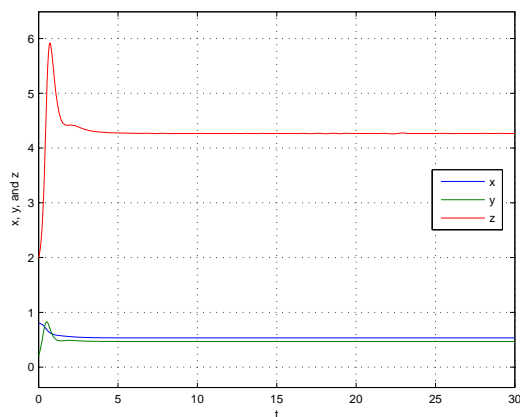


Figure 14: x, y, z components with initial value $(0.8, 0.2, 2)$ for (4.7).

Example 4.6: If $\alpha = 0.5$ and $\beta = 1$, i.e., the system is

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(1 - N_1 - 0.5N_2) \\ \frac{dN_2}{dt} &= N_2(1 + N_1 - N_2 - 0.5N_3) \\ \frac{dN_3}{dt} &= N_3(1 + N_2 - N_3)\end{aligned}\tag{4.8}$$

then $E_3 = (\frac{5}{8}, \frac{3}{4}, \frac{7}{4})$ is an asymptotically stable equilibrium for the above system. (See Figure 15, Figure 16.)

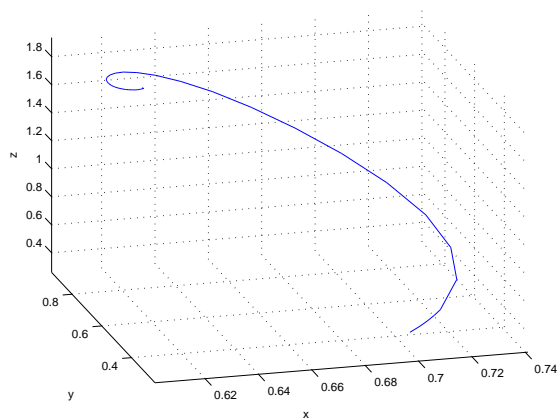


Figure 15: A solution trajectory with initial value $(0.7, 0.3, 0.4)$ for (4.8).

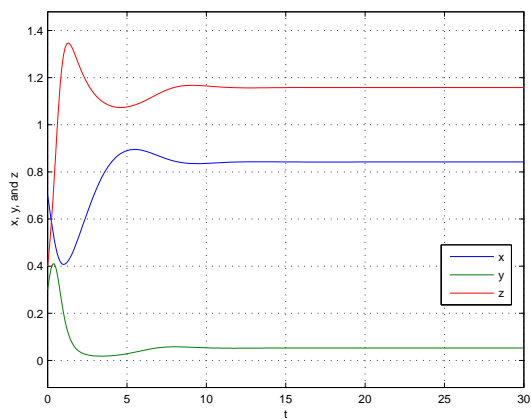


Figure 16: x, y, z components with initial value $(0.7, 0.3, 0.4)$ for (4.8).

Example 4.7: If $\alpha = 3$ and $\beta = 3$, i.e., the system is

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(1 - N_1 - 3N_2) \\ \frac{dN_2}{dt} &= N_2(1 + 3N_1 - N_2 - 3N_3) \\ \frac{dN_3}{dt} &= N_3(1 + 3N_2 - N_3)\end{aligned}\tag{4.9}$$

then $E_3 = (\frac{16}{19}, \frac{1}{19}, \frac{22}{19})$ is an asymptotically stable equilibrium for the above system. (See Figure 17, Figure 18.)

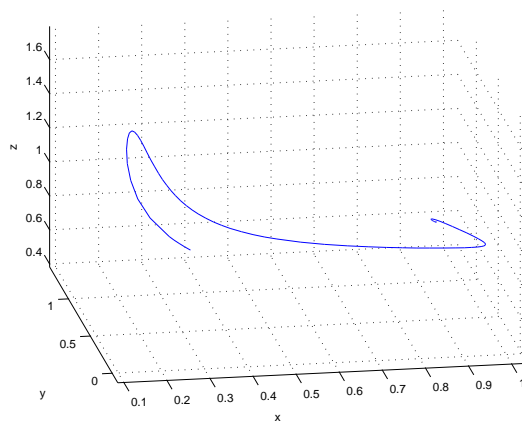


Figure 17: A solution trajectory with initial value (0.4,1.3,0.5) for (4.9).

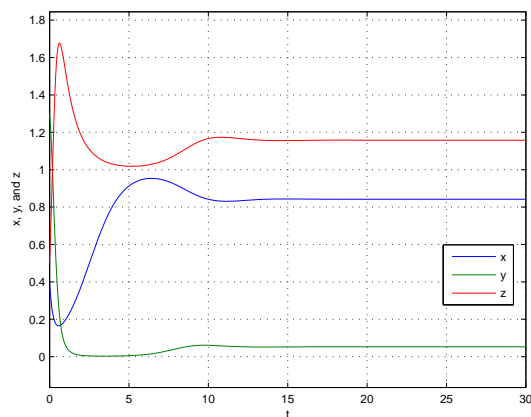


Figure 18: x, y, z components with initial value (0.4,1.3,0.5) for (4.9).

Example 4.8: If $\alpha = 0.3$ and $\beta = 0.000000000000000001$, i.e., the system is

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 (1 - N_1 - 0.3N_2) \\ \frac{dN_2}{dt} &= N_2 (1 + 0.000000000000000001N_1 - N_2 - 0.3N_3) \\ \frac{dN_3}{dt} &= N_3 (1 + 0.000000000000000001N_2 - N_3) \end{aligned} \quad (4.10)$$

then $E_3 \approx (0.79, 0.7, 1)$ is an asymptotically stable equilibrium for the above system. (See Figure 19, Figure 20.)

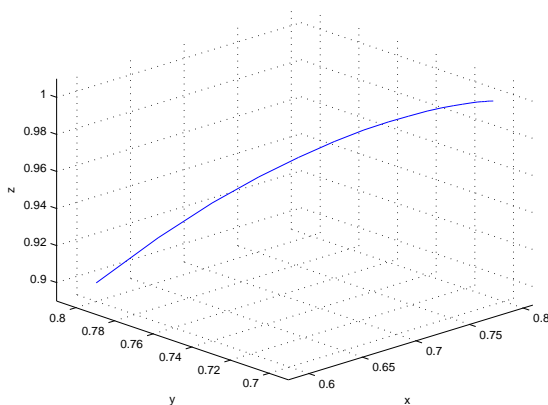


Figure 19: A solution trajectory with initial value $(0.6, 0.8, 0.9)$ for (4.10).

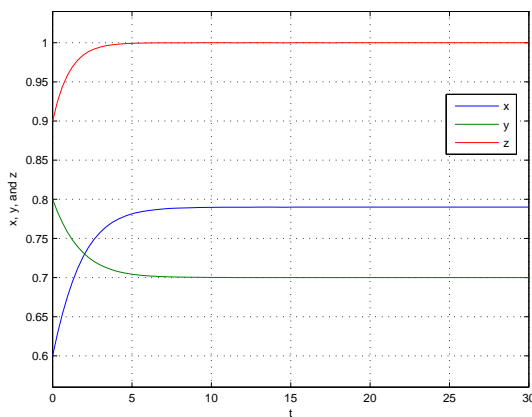


Figure 20: x, y, z components with initial value $(0.6, 0.8, 0.9)$ for (4.10).

Example 4.9: If $\alpha = 0.0000000000000001$ and $\beta = 0.3$, i.e., the system is

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 (1 - N_1 - 0.0000000000000001N_2) \\ \frac{dN_2}{dt} &= N_2 (1 + 0.3N_1 - N_2 - 0.0000000000000001N_3) \\ \frac{dN_3}{dt} &= N_3 (1 + 0.3N_2 - N_3) \end{aligned} \quad (4.11)$$

then $E_3 \approx (1, 1.3, 1.39)$ is an asymptotically stable equilibrium for the above system (see Figure 21, Figure 22.)

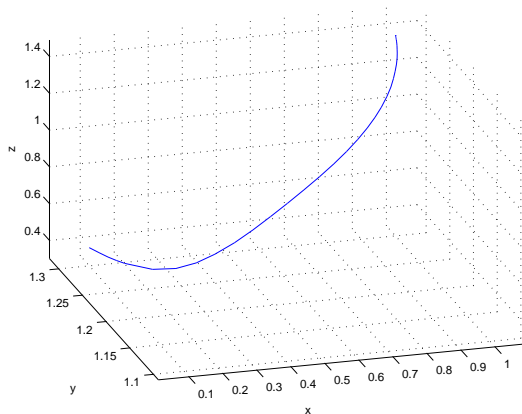


Figure 21: A solution trajectory with initial value $(0.1, 1.3, 0.4)$ for (4.11).

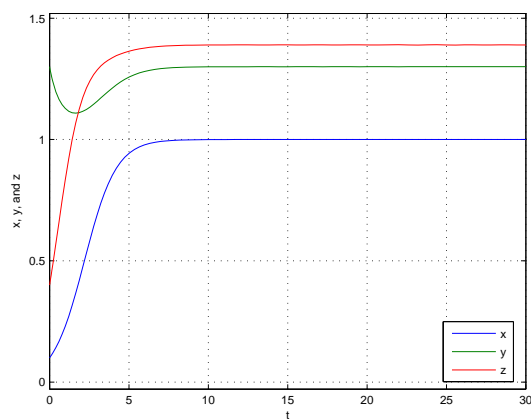


Figure 22: x, y, z components with initial value $(0.1, 1.3, 0.4)$ for (4.11).

According to above proposition and examples, we might apparently observe that the three-species equilibrium is not only asymptotically stable but also globally attracting when it exists. The following result states this more precisely.

Theorem 4.1: Assume there is an equilibrium (p_1, p_2, p_3) for the three-species food chain model (4.1) with $p_i > 0$, $i = 1, 2, 3$. Then the basin of attraction of the equilibrium (p_1, p_2, p_3) includes the first octant $\{(N_1, N_2, N_3) : N_1 > 0, N_2 > 0, N_3 > 0\}$.

Proof:

Suppose there is an equilibrium (p_1, p_2, p_3) for three species food chain model with $p_i > 0$, $i = 1, 2, 3$. Then

$$\begin{cases} p_1(r_1 - a_{11}p_1 - a_{12}p_2) = 0 \\ p_2(r_2 + a_{21}p_1 - a_{22}p_2 - a_{23}p_3) = 0 \\ p_3(r_3 + a_{32}p_2 - a_{33}p_3) = 0 \end{cases}$$

$$\Rightarrow \begin{cases} r_1 = a_{11}p_1 + a_{12}p_2 \\ r_2 = -a_{21}p_1 + a_{22}p_2 + a_{23}p_3 \\ r_3 = -a_{32}p_2 + a_{33}p_3 \end{cases}$$

Let $x_1 = r_1 - a_{11}N_1 - a_{12}N_2$, $x_2 = r_2 + a_{21}N_1 - a_{22}N_2 - a_{23}N_3$, and $x_3 = r_3 + a_{32}N_2 - a_{33}N_3$. Then, we set

$$\begin{aligned} x_1 &:= (a_{11}p_1 + a_{12}p_2) - a_{11}N_1 - a_{12}N_2 \\ &= a_{11}(p_1 - N_1) + a_{12}(p_2 - N_2), \\ x_2 &:= (-a_{21}p_1 + a_{22}p_2 + a_{23}p_3) + a_{21}N_1 - a_{22}N_2 - a_{23}N_3 \\ &= -a_{21}(p_1 - N_1) + a_{22}(p_2 - N_2) + a_{23}(p_3 - N_3), \\ x_3 &:= (-a_{32}p_2 + a_{33}p_3) + a_{32}N_2 - a_{33}N_3 \\ &= -a_{32}(p_2 - N_2) + a_{33}(p_3 - N_3). \end{aligned}$$

Now, we define a function L by

$$\begin{aligned} L(N_1, N_2, N_3) &= c_1[N_1 - p_1 \ln(N_1)] + c_2[N_2 - p_2 \ln(N_2)] + c_3[N_3 - p_3 \ln(N_3)] \\ &= \sum_{i=1}^3 c_i[N_i - p_i \ln(N_i)], \end{aligned}$$

where $\frac{c_2}{c_1} = \frac{a_{12}}{a_{21}}$, $\frac{c_3}{c_2} = \frac{a_{23}}{a_{32}}$ and $c_{ij} > 0$, for $i = 1, 2, 3$. Then $L(N_1, N_2, N_3) > L(p_1, p_2, p_3)$, for all $(N_1, N_2, N_3) \neq (p_1, p_2, p_3)$

and

$$\begin{aligned}
\dot{L}(N_1, N_2, N_3) &= c_1(1 - p_1 \cdot \frac{1}{N_1}) \cdot N_1 x_1 + c_2(1 - p_2 \cdot \frac{1}{N_2}) \cdot N_2 x_2 + c_3(1 - p_3 \cdot \frac{1}{N_3}) \cdot N_3 x_3 \\
&= c_1(N_1 - p_1)x_1 + c_2(N_2 - p_2)x_2 + c_3(N_3 - p_3)x_3 \\
&= c_1(N_1 - p_1)[a_{11}(p_1 - N_1) + a_{12}(p_2 - N_2)] \\
&\quad + c_2(N_2 - p_2)[-a_{21}(p_1 - N_1) + a_{22}(p_2 - N_2) + a_{23}(p_3 - N_3)] \\
&\quad + c_3(N_3 - p_3)[-a_{32}(p_2 - N_2) + a_{33}(p_3 - N_3)] \\
&= -a_{11}c_1(N_1 - p_1)^2 - a_{22}c_2(N_2 - p_2)^2 - a_{33}c_3(N_3 - p_3)^2 \\
&\quad + (-a_{12}c_1 + a_{21}c_2)(N_1 - p_1)(N_2 - p_2) \\
&\quad + (-a_{23}c_2 + a_{32}c_3)(N_2 - p_2)(N_3 - p_3).
\end{aligned}$$

Since $\frac{c_2}{c_1} = \frac{a_{12}}{a_{21}}$ and $\frac{c_3}{c_2} = \frac{a_{23}}{a_{32}}$, $-a_{12}c_1 + a_{21}c_2 = -a_{23}c_2 + a_{32}c_3 = 0$, then

$$\begin{aligned}
\dot{L}(N_1, N_2, N_3) &= -a_{11}c_1(N_1 - p_1)^2 - a_{22}c_2(N_2 - p_2)^2 - a_{33}c_3(N_3 - p_3)^2 \\
&= -\sum_{i=1}^3 a_{ii}c_i(N_i - p_i)^2.
\end{aligned}$$

i.e. for all $(N_1, N_2, N_3) \neq (p_1, p_2, p_3)$, $\dot{L}(N_1, N_2, N_3) < 0$ and $\dot{L}(p_1, p_2, p_3) = 0$. Therefore, L is a Lyapunov function on $\{(N_1, N_2, N_3) : N_1 > 0, N_2 > 0, N_3 > 0\}$. By Theorem 2.4, the assertion holds.

Finally, let us compute the recovery rate at the stable equilibria $E_2 = (1, 0, 1)$ and $E_3 = (\frac{1+\alpha\beta-\alpha+\alpha^2}{1+2\alpha\beta}, \frac{1+\beta-\alpha}{1+2\alpha\beta}, \frac{1+\alpha\beta+\beta+\beta^2}{1+2\alpha\beta})$, respectively. For arithmetical convenience, we only compute the recovery rate of the stable equilibria E_2, E_3 when $\beta = 1$. Of course, we can use similar method to calculate the recovery rate at the stable equilibrium E_3 for the other case. For $\beta = 1$, the recovery rate at the stable equilibria E_2, E_3 are summarized in proposition 4.4.

Proposition 4.4: Let $\beta = 1$. Assume that E_2 and E_3 are stable equilibria. Let α_0 be the solution of the equation $\alpha^3 - 2\alpha^2 + 3\alpha - 1 = 0$.

(a) The recovery rate at the stable equilibrium E_2 is $\alpha - 2$ when $2 < \alpha < 3$. It means the recovery rate at the stable equilibrium E_2 is increasing with respect to α .

(b) The recovery rate at the stable equilibrium E_2 is 1 when $\alpha \geq 3$. It means the recovery rate at the stable equilibrium E_2 is constant.

- (c) The recovery rate at the stable equilibrium E_3 is $\frac{3\alpha - \alpha^2 + \alpha^3}{1 + 2\alpha}$ when $0 < \alpha < \alpha_0$.
(d) The recovery rate at the stable equilibrium E_3 is $\frac{1 + \alpha^2}{1 + 2\alpha}$ when $\alpha_0 < \alpha < 2$.

Proof:

(a)(b) Let $\beta = 1$. By Proposition 4.1, 4.2, we have $E_2 = (1, 0, 1)$ exists and is stable when $\alpha > 2$. At E_2 , the Jacobian matrix is

$$\begin{pmatrix} -1 & -\alpha & 0 \\ 0 & 2 - \alpha & 0 \\ 0 & 1 & -1 \end{pmatrix}$$

and its eigenvalues are $\lambda = -1, 2 - \alpha, -1$. So, the dominant eigenvalue λ_{dom} at E_2 is

$$\begin{cases} 2 - \alpha & \text{if } 2 < \alpha < 3, \\ -1 & \text{if } \alpha \geq 3. \end{cases}$$

Therefore, the recovery rate $\rho \equiv |Re(\lambda_{dom})|$ at E_2 is

$$\begin{cases} \alpha - 2 & \text{if } 2 < \alpha < 3, \\ 1 & \text{if } \alpha \geq 3. \end{cases}$$

(c)(d) Similarly, $E_3 = (\frac{1 + \alpha^2}{1 + 2\alpha}, \frac{2 - \alpha}{1 + 2\alpha}, \frac{3 + \alpha}{1 + 2\alpha})$ exists and is stable when $\alpha < 2$. At E_3 , the Jacobian matrix is

$$\begin{pmatrix} -\frac{1 + \alpha^2}{1 + 2\alpha} & 0 & 0 \\ \frac{1 - \alpha}{1 + \alpha} & -\alpha \frac{1 + \alpha^2}{1 + 2\alpha} & -\alpha \frac{2 - \alpha}{1 + 2\alpha} \\ 0 & \frac{3 + \alpha}{1 + 2\alpha} & -\frac{3 + \alpha}{1 + 2\alpha} \end{pmatrix}$$

and its eigenvalues are

$$\lambda = -\frac{1 + \alpha^2}{1 + 2\alpha}, -\frac{3\alpha - \alpha^2 + \alpha^3}{1 + 2\alpha}, -\frac{3 + \alpha}{1 + 2\alpha}.$$

Since (i) $1 + \alpha^2 < 3 + \alpha$ for $0 < \alpha < 2$; (ii) $3\alpha - \alpha^2 + \alpha^3 < 1 + \alpha^2$ for $0 < \alpha < \alpha_0$; (iii) $3\alpha - \alpha^2 + \alpha^3 > 1 + \alpha^2$ for $\alpha_0 < \alpha < 2$, where α_0 is the solution of the equation $\alpha^3 - \alpha^2 + 3\alpha - 1 = 0$. By Maple, we can compute $\alpha_0 \approx 0.4301597088$. So, the dominant eigenvalue λ_{dom} at E_3 is

$$\begin{cases} -\frac{3\alpha - \alpha^2 + \alpha^3}{1 + 2\alpha} & \text{if } 0 < \alpha < \alpha_0, \\ -\frac{1 + \alpha^2}{1 + 2\alpha} & \text{if } \alpha_0 < \alpha < 2. \end{cases}$$

Therefore, the recovery rate $\rho \equiv |Re(\lambda_{dom})|$ at E_3 is

$$\begin{cases} \frac{3\alpha - \alpha^2 + \alpha^3}{1 + 2\alpha} & \text{if } 0 < \alpha < \alpha_0, \\ \frac{1 + \alpha^2}{1 + 2\alpha} & \text{if } \alpha_0 < \alpha < 2. \end{cases}$$

The result follows.

5 Genetic control system

In this section, we mention a basic model in genetic control system. The following system has been discussed by [16] as a model for a genetic control system. The activity of a certain gene is assumed to be directly induced by two copies of the protein for which it codes. In other words, the gene is stimulated by its own product, potentially leading to an autocatalytic feedback process. In dimensionless form, the equations are

$$\begin{aligned}\frac{dx}{dt} &= -ax + y \\ \frac{dy}{dt} &= \frac{x^2}{1+x^2} - by\end{aligned}\tag{5.1}$$

where x and y are proportional to the concentrations of the protein and messenger RNA from which it is translated, respectively, and $a, b > 0$ are parameters that govern the rate of degradation of x and y .

First, we shall prove a simple result toward the system (5.1). The result is as follows. It can be proved from Bendixson's Negative Criterion.

Proposition 5.1: There does not exist periodic solution in the first quadrant $\{(x, y) : x > 0, y > 0\}$ for the system (5.1).

Proof:

On $\{(x, y) : x > 0, y > 0\}$, the divergence of the vector field is

$$\frac{\partial}{\partial x}(-ax + y) + \frac{\partial}{\partial y}\left(\frac{x^2}{1+x^2} - by\right) = -a - b = -(a + b) < 0.$$

By Theorem 2.5, the assertion holds.

Next, we will show that the system (5.1) has three equilibria when $a < a_{crit}$, where a_{crit} is to be determined. Moreover, two of these equilibria coalesce in a saddle-node bifurcation when $a = a_{crit}$. Then we will sketch the phase portrait for $a < a_{crit}$, and give a biological interpretation. These results are summarized in proposition 5.2, 5.3.

Proposition 5.2 [15]: The system (5.1) has three equilibria when $a < a_{crit}$, where $a_{crit} = 1/2b$. In particular, two of these equilibria coalesce in a saddle-node bifurcation when $a = a_{crit}$.

Proof:

One of the most useful tools for analyzing nonlinear systems of differential equations (especially planar systems) are nullclines. If we determine all of the nullclines of the system (5.1), then the intersections of the x - and y -nullclines yields the equilibria. From the system (5.1), we have the nullclines are given by the line $y = ax$ and $y = \frac{x^2}{b(1+x^2)}$. To find a_{crit} , we compute the equilibria directly and find where they coalesce. Since the nullclines intersect when $ax = \frac{x^2}{b(1+x^2)}$, the equilibrium $(0, 0)$ always exists for any parameters $a, b > 0$ and there are equilibria $(x^*, y^*) = (\frac{1+\sqrt{1-4a^2b^2}}{2ab}, \frac{1+\sqrt{1-4a^2b^2}}{2b}), (\frac{1-\sqrt{1-4a^2b^2}}{2ab}, \frac{1-\sqrt{1-4a^2b^2}}{2b})$ if $1 - 4a^2b^2 > 0$, i.e. $ab < 1/2$. So, these two equilibria coalesce when $ab = 1/2$ and therefore $a_{crit} = 1/2b$. The assertion follows.

The nullclines also provide a lot of information about the phase portrait for $a < a_{crit}$. The vector field is vertical on the line $y = ax$ and horizontal on the curve $y = \frac{x^2}{b(1+x^2)}$. It appears that the equilibrium $(\frac{1-\sqrt{1-4a^2b^2}}{2ab}, \frac{1-\sqrt{1-4a^2b^2}}{2b})$ is a saddle and the other two are sinks. To confirm this, we turn to classify these equilibria.

Proposition 5.3 [15]: If the system (5.1) has three equilibria, i.e. $a < a_{crit}$ then the equilibria $(0, 0)$ and $(\frac{1+\sqrt{1-4a^2b^2}}{2ab}, \frac{1+\sqrt{1-4a^2b^2}}{2b})$ are stable and $(\frac{1-\sqrt{1-4a^2b^2}}{2ab}, \frac{1-\sqrt{1-4a^2b^2}}{2b})$ is unstable.

Proof:

From the system (5.1), we find the Jacobian matrix at (x, y) is

$$A = \begin{pmatrix} -a & 1 \\ \frac{2x}{(1+x^2)^2} & -b \end{pmatrix}.$$

A has trace $\tau = -(a + b) < 0$, so all equilibria are either sinks or saddles by theorem 2.2. At $(0, 0)$, the determinant $\Delta = ab > 0$, so the origin is always a stable equilibrium. In fact, it is a stable node, since $\tau^2 - 4\Delta = (a - b)^2 > 0$ (except in the degenerate case $a = b$). For the other two fixed points, we can compute that

$$\Delta = ab - \frac{2x}{[1 + (x)^2]^2} = ab[1 - \frac{2}{1 + (x)^2}] = ab[\frac{-1 + (x)^2}{1 + (x)^2}].$$

At $(\frac{1-\sqrt{1-4a^2b^2}}{2ab}, \frac{1-\sqrt{1-4a^2b^2}}{2b})$, the determinant $\Delta < 0$ since $0 < \frac{1-\sqrt{1-4a^2b^2}}{2ab} < 1$. Hence, we have the equilibrium $(\frac{1-\sqrt{1-4a^2b^2}}{2ab}, \frac{1-\sqrt{1-4a^2b^2}}{2b})$ is a saddle. At $(\frac{1+\sqrt{1-4a^2b^2}}{2ab}, \frac{1+\sqrt{1-4a^2b^2}}{2b})$, the determinant $\Delta = ab - \frac{2x}{[1+(x)^2]^2} = ab[1 - \frac{2}{1+(x)^2}] < ab$ since $\frac{1+\sqrt{1-4a^2b^2}}{2ab} > 1$. So,

$\tau^2 - 4\Delta = (a + b)^2 - 4ab - \frac{2x}{[1+(x)^2]^2} = (a - b)^2 + \frac{8x}{[1+(x)^2]^2} > (a - b)^2 > 0$. Thus, the equilibrium $(\frac{1+\sqrt{1-4a^2b^2}}{2ab}, \frac{1+\sqrt{1-4a^2b^2}}{2b})$ is a stable node. This completes the proof.

The phase portrait and the nullclines for the system (5.1) when $a = 0.92$ and $b = 0.5$ are plotted in Figure 23. And we plot the bifurcation diagram for (5.1) when $b = 0.5$ in Figure 24.

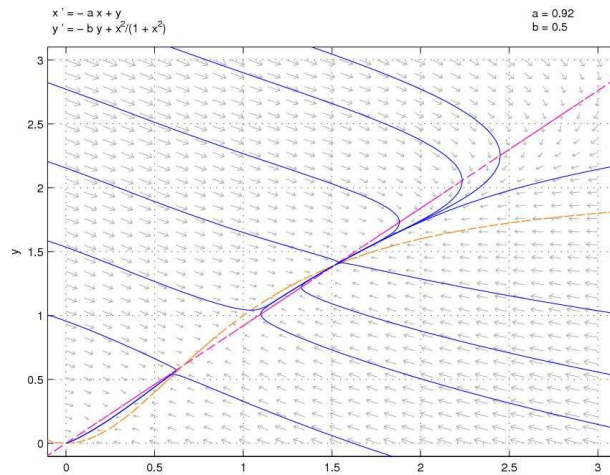


Figure 23: The phase portrait and the nullclines for the system (5.1) when $a = 0.92$ and $b = 0.5$.

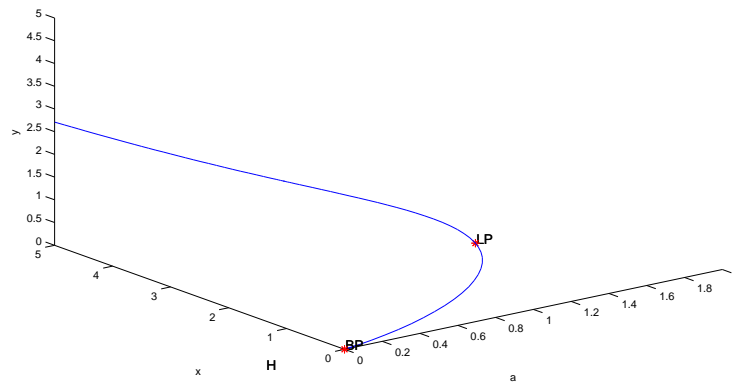


Figure 24: The bifurcation diagram for the system (5.1) when $b = 0.5$.

More importantly, the stable manifold separates the plane into two regions, each a basin of attraction for a sink. The biological interpretation is that the system can act like a biochemical switch, but only if the mRNA and protein degrade slowly enough—specifically, their decay rates must satisfy $ab < 1/2$. In this case, there are two stable steady states: one at the origin, meaning that the gene is silent and there is no protein around to turn it on; and one where x and y are large, i.e. $(x, y) = (\frac{1+\sqrt{1-4a^2b^2}}{2ab}, \frac{1+\sqrt{1-4a^2b^2}}{2b})$, meaning that the gene is active and sustained by the high level of protein. The stable manifold of the saddle acts like a threshold; it determines whether the gene turns on or off, depending on the initial values of x and y . Finally, let us compute the recovery rate at the stable equilibrium $(\frac{1+\sqrt{1-4a^2b^2}}{2ab}, \frac{1+\sqrt{1-4a^2b^2}}{2b})$. For arithmetical convenience we only investigate for $b = 1/2$. Of course, we can use similar method to calculate the recovery rate at the stable equilibrium $(\frac{1+\sqrt{1-4a^2b^2}}{2ab}, \frac{1+\sqrt{1-4a^2b^2}}{2b})$ for the other case. When $b = 1/2$, the characteristic equation of A is

$$\lambda^2 + (a + 1/2)\lambda + \frac{a}{2} \left(\frac{-1 + x^2}{1 + x^2} \right) = 0.$$

So, its eigenvalues are given by

$$\lambda = \frac{-(a + \frac{1}{2}) \pm \sqrt{(a + \frac{1}{2})^2 - 2a \left[\frac{-a^2 + (1 + \sqrt{1-a^2})^2}{a^2 + (1 + \sqrt{1-a^2})^2} \right]}}{2}.$$

Therefore, the dominant eigenvalue

$$\lambda_{dom} = \frac{-(a + \frac{1}{2}) + \sqrt{(a + \frac{1}{2})^2 - 2a \left[\frac{-a^2 + (1 + \sqrt{1-a^2})^2}{a^2 + (1 + \sqrt{1-a^2})^2} \right]}}{2}.$$

At the stable equilibrium $(\frac{1+\sqrt{1-4a^2b^2}}{2ab}, \frac{1+\sqrt{1-4a^2b^2}}{2b})$, the recovery rate

$$\rho \equiv |Re(\lambda_{dom})| = \frac{(a + \frac{1}{2}) - \sqrt{(a + \frac{1}{2})^2 - 2a \left[\frac{-a^2 + (1 + \sqrt{1-a^2})^2}{a^2 + (1 + \sqrt{1-a^2})^2} \right]}}{2}.$$

Let $f'(a) = (a + \frac{1}{2}) - \sqrt{(a + \frac{1}{2})^2 - 2a \left[\frac{-a^2 + (1 + \sqrt{1-a^2})^2}{a^2 + (1 + \sqrt{1-a^2})^2} \right]}$. By Matlab, we calculate $f'(a) = 0$ only when $a = a_r \approx 0.4676$, $f'(a) > 0$ when $a < a_r$, and $f'(a) < 0$ when $a > a_r$. Then f has a local maximum at $a = a_r \approx 0.4676$. Therefore, the maximum recovery rate occurs for $a = a_r \approx 0.4676$. To sum up, if we are using the recovery rate as an indicator of the system (5.1), we will have more warning of the upcoming transition when a_r is far enough from a_{crit} . So far, we have seen that $a_{crit} = 1$ and $a_r \approx 0.4676$ when $b = 1/2$, it will help us judge the dynamics of the system (5.1) when $b = 1/2$.

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