

ALTERNATIVES TO RESILIENCE FOR MEASURING THE RESPONSE OF THE ECOLOGICAL SYSTEMS TO PERTURBATIONS

Subsection 0.1. Summary. Ecological systems are subject to perturbations. The resilience is a measure of the rate at which the perturbations to an ecological system decay. The most common measure of resilience is using the eigenvalues of the linearized system near the equilibrium point. However, the perturbations can increase in magnitude before decaying. This transient growth is not observed using the eigenvalue analysis. In this review of the paper Neubert and Caswell 1997, new measures of the transient growth that complement resilience are introduced. These are reactivity (the maximum possible growth rate immediately after a perturbation), Maximum amplification ρ_{max} (the largest possible deviation from the equilibrium that can be produced by a perturbation), the maximum time t_{max} required to achieve this maximum amplification. These measures are applied to three models, two linear compartment models (Phosphorous cycling through a lake ecosystem and the flow of matter through a tropical rain forest ecosystem) and a standard predator prey model. These models exhibit the transient growth even though the equilibrium is asymptotically stable. Hence the measures of relative stability which ignores the transient growth can give an incomplete image about the effects of a perturbation to an ecological system.

Subsection 0.2. Introduction. Ecological systems can be modelled by a system of differential equations ($D.E$). The linear differential equations are easier to analyse. If the system of $D.E$ is nonlinear then it can be *linearized* near an equilibrium point[0.6.1]. Qualitatively the solutions of the linearized system and the non linear system are the same in a neighbourhood of the equilibrium point.

A *perturbation* is the change in the initial condition from the equilibrium point or the solution of the corresponding $D.E$ which starts at an initial point different from the equilibrium point.

Stability is a qualitative measure of the ability of an ecological system to return to equilibrium after a perturbation. Quantitatively this is measured using *resilience*. Resilience measures how rapidly a system returns to its equilibrium after a perturbation. Resilience is commonly calculated using the eigenvalues of the n dimensional linear system

$$(1) \quad \frac{dx(t)}{dt} = Ax(t) \quad x(0) = x_0.$$

where $x(t) \in \mathbb{R}^n$ and $A \in M_n(\mathbb{R})$. Let $x^* = 0$ be an asymptotically stable equilibrium of the system[0.6.2]. This system can also be a linearization of a non linear system near the equilibrium $x^* = 0$. Hence the eigenvalue λ_j of the matrix A satisfy; $Re\lambda_j < 0$ for $j = 1, \dots, n$ [0.6.10]. The system (1) has a unique solution

$$(2) \quad x(t) = e^{At}x_0.$$

Let $T : \mathbb{C}^n \rightarrow \mathbb{C}^n$ be any linear transformation. A vector v is called a *generalized eigenvector* of degree p if for some $\lambda \in \mathbb{C}$

$$(3) \quad (T - \lambda I)^p v = 0$$

and

$$(4) \quad (T - \lambda I)^{p-1}v \neq 0.$$

Since $(T - \lambda I)(T - \lambda I)^{p-1}v = 0$ and $(T - \lambda I)^{p-1}v \neq 0$ it follows that λ is an eigenvalue of T . It can be shown that $v, (T - \lambda I)v, (T - \lambda I)^2v, \dots, (T - \lambda I)^{p-1}v$ are linearly independent[0.6.5]. Let $\mathcal{N}(T) = \{v : T(v) = 0\}$ denote the *null space* of T . Hence

$$(5) \quad \{0\} \subset \mathcal{N}(T - \lambda I) \subset \mathcal{N}(T - \lambda I)^2 \subset \dots$$

Since $\mathcal{N}(T - \lambda I)^k$ for $k \geq 1$ are finite dimensional subspaces of \mathbb{C}^n , there exists a smallest number k such that $\mathcal{N}(T - \lambda I)^k = \mathcal{N}(T - \lambda I)^{k+1}$. Denote this number by $r(\lambda)$.

The *generalized eigenspace* for λ is defined as $M(\lambda) = \mathcal{N}(T - \lambda I)^{r(\lambda)}$. It can be shown[0.6.9] for distinct eigenvalues $\lambda_1, \lambda_2, \dots, \lambda_\rho$ of a linear transformation $T : \mathbb{C}^n \rightarrow \mathbb{C}^n$ with multiplicities m_1, m_2, \dots, m_ρ , and $M(\lambda_1), M(\lambda_2), \dots, M(\lambda_\rho)$ be the corresponding generalized eigenspaces, then the dimension of $M(\lambda_j)$ is m_j and

$$(6) \quad \mathbb{C}^d = M(\lambda_1) \oplus \dots \oplus M(\lambda_\rho).$$

Consider the system (1). Let $\lambda_1, \lambda_2, \dots, \lambda_d$ be the distinct eigenvalues of A arranged in nonincreasing order of their real parts. By (6), $x_0 = v_1 + v_2 + \dots + v_d$, where v_1, v_2, \dots, v_d are some vectors of $M(\lambda_1), M(\lambda_2), \dots, M(\lambda_d)$ respectively. Using (2).

$$(7) \quad x(t) = e^{At}(v_1 + v_2 + \dots + v_d).$$

$$(8) \quad x(t) = e^{\lambda_1 t} e^{(A - \lambda_1 I)t} v_1 + e^{\lambda_2 t} e^{(A - \lambda_2 I)t} v_2 + \dots + e^{\lambda_d t} e^{(A - \lambda_d I)t} v_d.$$

$$\begin{aligned} x(t) = & e^{\lambda_1 t} \left(I + (A - \lambda_1 I)t + \dots + \frac{(A - \lambda_1 I)^{r(\lambda_1)-1} t^{r(\lambda_1)-1}}{(r(\lambda_1) - 1)!} \right) v_1 + \dots \\ & \dots + e^{\lambda_d t} \left(I + (A - \lambda_d I)t + \dots + \frac{(A - \lambda_d I)^{r(\lambda_d)-1} t^{r(\lambda_d)-1}}{(r(\lambda_d) - 1)!} \right) v_d. \end{aligned}$$

The last step follows since, $v_j \in M(\lambda_j)$ implies $(A - \lambda_j I)^k v_j = 0$ for $k \geq r(\lambda_j)$, for $j = 1, 2, \dots, d$ (0.6.6). Let the matrix A be such that, $Re(\lambda_1) > Re(\lambda_j)$ for $j = 2, \dots, d$, hence $e^{(\lambda_j - \lambda_1)t} \rightarrow 0$ as $t \rightarrow \infty$ for $j = 2, \dots, d$. Let the initial point x_0 be such that for the decomposition $x_0 = v_1 + v_2 + \dots + v_d$, the vector $v_1 = w_1$, where w_1 is an eigenvector corresponding to the eigenvalue λ_1 , and v_2, v_3, \dots, v_d are some arbitrary vectors in $M(\lambda_2), M(\lambda_2), \dots, M(\lambda_d)$ respectively. Hence for almost all initial conditions x_0 , $\lim_{t \rightarrow \infty} e^{-\lambda_1 t} x(t) = w_1$. It follows that $x(t) \propto w_1$ and decays like $e^{\lambda_1 t}$ for large values of t . Hence asymptotically the magnitude of $x(t)$ decreases by a factor of $\frac{1}{e}$ in the time interval $\Delta t = \frac{-1}{Re(\lambda_1)}$. Hence $-Re(\lambda_1)$ is a measure of the asymptotic rate of decay. Let the *resilience* of the system (1) be defined as

$$(9) \quad resilience \equiv -Re(\lambda_1) = -\max_i(Re(\lambda_i)).$$

This is an asymptotic approximation of the rate of decay of the perturbation. The larger the resilience the faster the decay. This measure of the asymptotic decay ignores any effect of a perturbation at a short

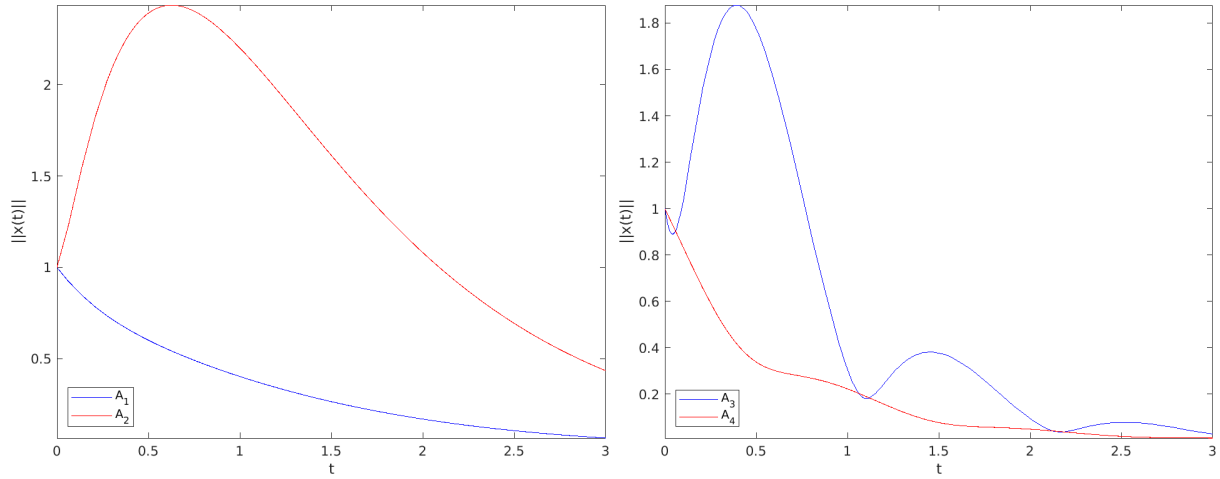


FIGURE 1. The magnitude of the four solutions of linear system (1). (a) The bottom curve represents the solution for A_1 , top curve for the solution of A_2 . For both of the systems the initial condition is $(\frac{1}{2}, \frac{\sqrt{3}}{2})$. (b) The top curve represents the solution for A_3 , the bottom curve for A_4 . The initial conditions are the same $:(\cos(2\pi/5), \sin(2\pi/5))$.

time after its start. The question arises whether the resilience is a complete measure of the effects of a perturbation on an ecological system. Consider the solution of (1) when A is either

$$(10) \quad A_1 = \begin{bmatrix} -1 & 1 \\ 0 & -2 \end{bmatrix} \quad or \quad A_2 = \begin{bmatrix} -1 & 10 \\ 0 & -2 \end{bmatrix}$$

Fig(1)(a) is the plot of the magnitude of the solution of (1) for the perturbation $x_0 = (\frac{1}{2}, \frac{\sqrt{3}}{2})$ for $A = A_1$ and $A = A_2$ respectively. The solution for $A = A_2$ exhibit a transient growth and then it decays to the equilibrium point 0. The solution for $A = A_1$ doesn't show any transient growth. A_1 and A_2 have the same eigenvalues -1 and -2. Hence for both of the systems the resilience is the same; resilience=1. Hence in asymptotic limit both of the solutions have the same rate of decay. Consider the solution of (1) when A is either

$$(11) \quad A_3 = \begin{bmatrix} -1 & -12 \\ 0.75 & -2 \end{bmatrix} \quad or \quad A_4 = \begin{bmatrix} -1 & -4 \\ 2.25 & -2 \end{bmatrix}$$

The matrices have the same eigenvalues $\frac{-3+i\sqrt{35}}{2}$ and $\frac{-3-i\sqrt{35}}{2}$. From the fig(1)(b), the solution for $A = A_3$ exhibit a transient growth but the solution for $A = A_4$ does not show any transient growth. Both of the solutions have the same resilience $\frac{3}{2}$. Hence we observe that perturbations to the linear or linearized systems may or may not exhibit a transient growth. The transient growth is not due to the non linearity of the system, although non linearity can enhance the effect of the transient growth as we will see in the predator prey model. Knowing the eigenvalues of a system alone is insufficient to predict any transient growth. Hence the need for a new measure which complement resilience and characterize the transient behaviour of a perturbation.

(Pimm and Lawton 1977) have used $\frac{1}{-\max_i(\text{Re}(\lambda_i))}$ as a measure of the return time of the system after a perturbation. Since (9) is an asymptotic measure and is valid for large values of t , other measures of the return time similar to

$$(12) \quad T_R = \int_0^\infty \frac{\|x(t)\|^2}{\|x_0\|^2} dt.$$

is used for example DeAngelis 1980, Cottingham and Carpenter 1994. T_R varies with different perturbations. Hence one must find the return times for a collection of perturbations and find their average

value. When the dimension of the system is large such computation becomes tedious hence the preference for (9). Three new measures of the transient behaviour of a system following a perturbation will be introduced in the next section. They are *reactivity* (which measures the maximum instantaneous rate at which a perturbation can be amplified at $t = 0$), the maximum possible amplification ρ_{max} that can be achieved by any perturbation, the time t_{max} required to achieve this maximum amplification. Throughout this review it will be assumed that the linear system (1) will be such that the matrix A is invertible. Hence the only equilibrium point for this system is the zero vector. Also the equilibrium point will be assumed to be asymptotically stable. Hence by (0.6.10) all the eigenvalues of A will have negative real part.

Subsection 0.3. Characterizing Transients. Consider the linear system (1). Any perturbation to the system may initially show a transient growth. Hence the *reactivity* of an equilibrium point is defined as

$$(13) \quad reactivity = \max_{||x_0|| \neq 0} \left[\frac{1}{||x_0||} \frac{d||x(t)||}{dt} \right]_{t=0}.$$

For non linear systems reactivity is calculated by linearizing the system near the equilibrium point. An equilibrium point which has positive reactivity value is called reactive. For the linear system (1) there exists a perturbation which attains this maximum instantaneous growth rate at $t = 0$, as the following calculations show

$$(14) \quad \frac{d||x||}{dt} = \frac{d\sqrt{x^T x}}{dt} = \frac{x^T \frac{dx}{dt} + \frac{dx^T}{dt} x}{2||x||} = \frac{x^T (A + A^T)x}{2||x||}.$$

The matrix $\frac{A+A^T}{2}$ is the hermitian part of A and is denoted by $H(A)$.

$$(15) \quad \frac{1}{||x||} \frac{d||x||}{dt} = \frac{x^T (A + A^T)x}{2||x||^2} = \frac{x^T H(A)x}{x^T x}.$$

$$(16) \quad \frac{1}{||x||} \frac{d||x||}{dt} \Big|_{t=0} = \frac{x_0^T H(A)x_0}{x_0^T x_0}.$$

This ratio is termed as the *rayleigh quotient*. This ratio is maximized by the eigenvector u_1 corresponding to the largest eigenvalue $\lambda_1(H(A))$ and the maximum value is $\lambda_1(H(A))$ (Horn and Johnson 2013). Hence the reactivity of an equilibrium point for a linear system is given by

$$(17) \quad reactivity = \lambda_1(H(A))$$

Let the eigenvalue $\lambda_1(A)$ have the largest real part among all the eigenvalues of A . $Re(\lambda_1(A))$ and the reactivity $\lambda_1(H(A))$ may have different signs. if $Re\lambda_1(A) < 0$ and $\lambda_1(H(A)) > 0$ then the equilibrium is asymptotically stable but reactive. For the linear systems (10) and (11), $\lambda_1(H(A_1)) = -0.79$, $\lambda_1(H(A_2)) = 3.52$, $\lambda_1(H(A_3)) = 4.15$ and $\lambda_1(H(A_4)) = -0.49$. Hence the equilibrium point is reactive for the systems A_2 and A_3 .

Subsection 0.4. Amplification Envelope. The reactivity is a measure for $t \rightarrow 0$ and resilience is a measure for $t \rightarrow \infty$. This doesn't give any information on the behaviour of the perturbation between the time interval 0 and ∞ . If the perturbation has an initial transient growth and if it decays towards the equilibrium at large values of time, then there is a maximum amplification of the perturbation and the time required to achieve this maximum amplification. These two quantities are the characteristics of the amplification curve $\rho(t)$

$$(18) \quad \rho(t) = \max_{||x_0|| \neq 0} \left[\frac{||x(t)||}{||x_0||} \right].$$

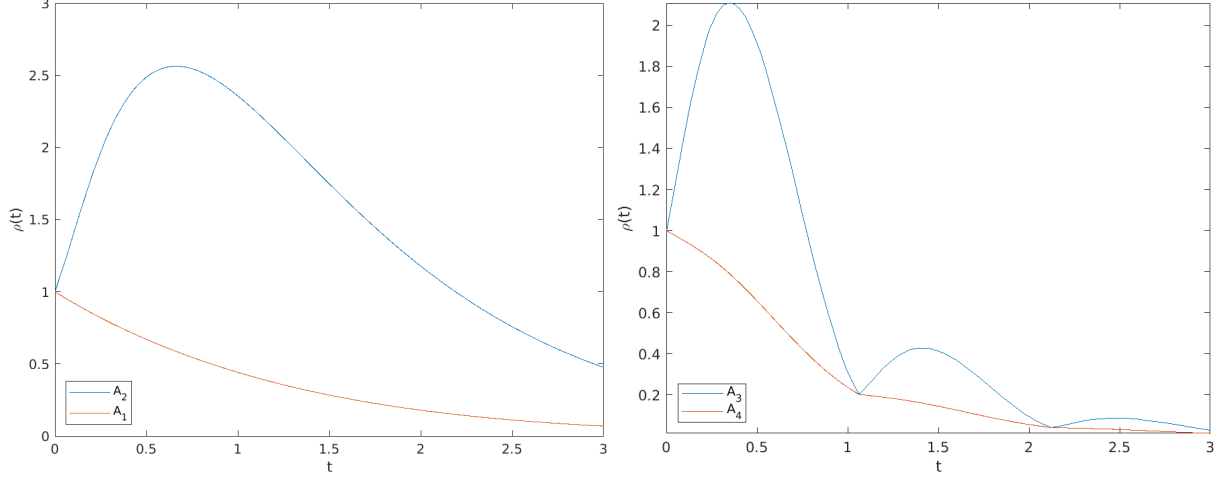


FIGURE 2. The amplification envelopes of example matrices A_1 through A_4 . The envelopes for A_2 and A_3 have an initial growth, indicating that A_2 and A_3 are reactive. The envelopes for A_1 and A_4 have a decay, hence A_1 and A_4 are not reactive.

For linear systems (1), $\rho(t)$ is given by

$$(19) \quad \rho(t) = \max_{\|x_0\| \neq 0} \left[\frac{\|e^{At}x_0\|}{\|x_0\|} \right].$$

Hence $\rho(t) = \|e^{At}\|$ is the matrix norm of e^{At} induced by the euclidean norm $\|\cdot\|$. The maximum amplification ρ_{max} is defined as

$$(20) \quad \rho_{max} = \max_{t \geq 0} \rho(t).$$

The t_{max} is such that it satisfies the equation

$$(21) \quad \rho(t_{max}) = \rho_{max}.$$

It can be shown that the derivative of $\ln(\rho(t))$ approaches $\lambda_1(H(A))$ as t tend to 0. This follows

$$\begin{aligned} \text{because } e^{At} &\approx I + At \text{ for a small value of } t. \text{ Hence } \rho(t) = \max_{x_0 \neq 0} \sqrt{\frac{\|e^{At}x_0\|^2}{\|x_0\|^2}} = \max_{x_0 \neq 0} \sqrt{\frac{x_0^T e^{A^T t} e^{At} x_0}{x_0^T x_0}} \approx \\ &\max_{x_0 \neq 0} \sqrt{\frac{x_0^T (I + A^T t)(I + At) x_0}{x_0^T x_0}} \approx \max_{x_0 \neq 0} \sqrt{1 + \frac{x_0^T (A^T + A) x_0 t}{x_0^T x_0}} = \sqrt{1 + 2t\lambda_1(H(A))}. \quad \frac{d\ln(\rho(t))}{dt} \approx \frac{d\ln(\sqrt{1+2t\lambda_1(H(A))})}{dt} = \\ &\frac{\lambda_1(H(A))}{1+2t\lambda_1(H(A))} \approx \lambda_1(H(A)). \end{aligned}$$

It can also be shown that the derivative of $\ln(\rho(t))$ approaches resilience as t tend to ∞ . Hence reactivity and resilience are the characteristics of the amplification envelope. The amplification envelope for the example matrices (10) and (11) are shown in fig(2). The next section will be devoted to applying these measures to various ecological models.

Subsection 0.5. Compartment Models.

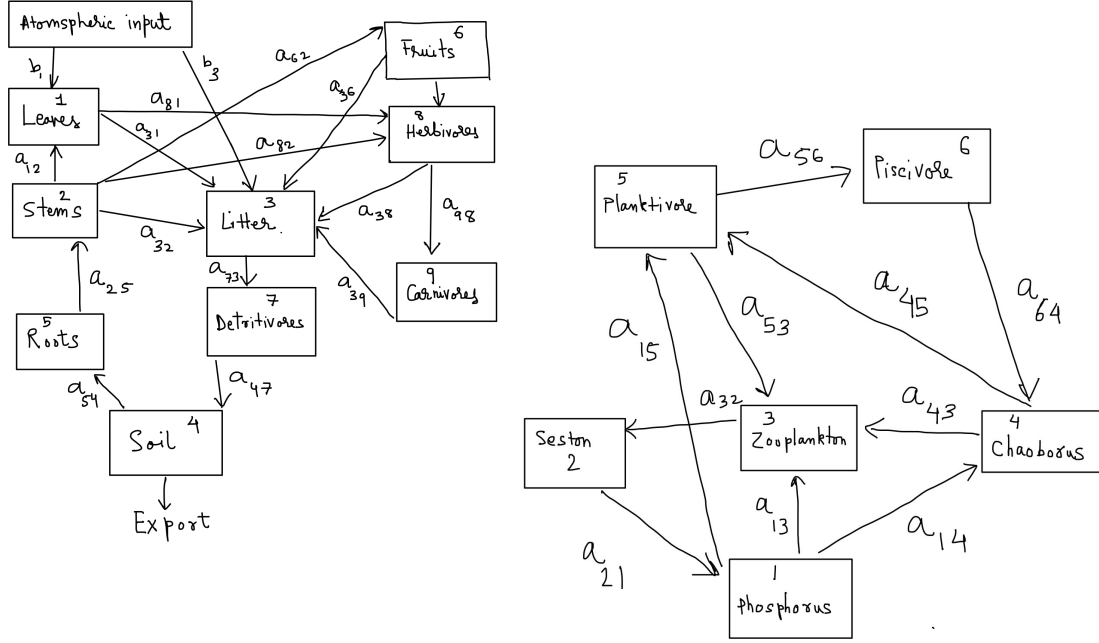


FIGURE 3. (a) The Compartment model of the transfer of matter through the Panamanian tropical rain forest.(b) The compartment model for the transfer of phosphorous in the Tuesday lake ecosystem.

0.5.1. *Tropical rainforest model.* *Compartment models* describes the flow of some quantities such as nutrients, energy from one compartment to another. Neubert and Caswell 1997 used the data of the flow of matter through a tropical rainforest compartment model from McGinnis 1969 to measure the resilience of this ecological system. In this model matter is input to leaves and litter and it flows through herbivores, carnivores, roots, stems and finally leaves the system through soil as shown in fig(3)(a).

In the linear compartment model it is assumed that the flow rate from compartment j to compartment i is proportional to the amount of material in the donor compartment j . The proportionality constant is given by a_{ij} . The rate of input from outside the system is independent of the amount of material in that compartment. Let y_i be the amount of material in the compartment i at time t . b_i is the external input. Hence

$$(22) \quad \frac{dy_i}{dt} = \sum_{j=1}^n a_{ij}y_j + b_i \quad i = 1, 2, \dots, n$$

with initial conditions

$$(23) \quad y_i(0) = y_{0i} \quad i = 1, 2, \dots, n$$

Here a_{ij} is also the fraction of material in component j that flows into component i per unit time. $a_{ij} \geq 0$ if $i \neq j$ and a_{jj} is the fraction of materials flowing out of the j th component per unit time, hence $a_{jj} \leq 0$.

Tropical rainforest										
Compartment and number		1	2	3	4	5	6	7	8	9
Leaves	1	-1.5622	0.6685							
Stems	2		-0.7119			2.5632				
Litter	3	1.4627	0.0364	-6.4091			1.1446		55.8201	17.2972
Soil	4				-0.0222			315.9443		
Roots	5				0.0201	-2.5632				
Fruits and Flowers	6		0.0070				-2.0348			
Detritivores	7			6.4091				-315.9443		
Herbivores	8	0.0995†					0.8902		-62.6458	
Carnivores	9								6.8257	-17.2972

† All entries are in yr^{-1}

TABLE 1. Transfer matrix for elemental dynamics in a Panamanian tropical rain forest (Neubert and Caswell 1997).

The fractional loss from compartment j is equal to its contributions to all other compartments and any loss from the system from compartment j hence

$$(24) \quad a_{jj} \leq -\sum_{i \neq j} a_{ij}$$

Hence (22) can be written in a matrix form

$$(25) \quad \frac{d\mathbf{y}}{dt} = \mathbf{A}\mathbf{y} + \mathbf{b} \quad \mathbf{y}(0) = \mathbf{y}_0$$

where the matrix $\mathbf{A} = [a_{ij}]$ and $\mathbf{b} = (b_i)$. Let \mathbf{A} be an invertible matrix. Hence the equilibrium point for the system is $\bar{\mathbf{y}} = -\mathbf{A}^{-1}\mathbf{b}$. The deviation from the equilibrium point is $\mathbf{x}(t) = \mathbf{y}(t) - \bar{\mathbf{y}}$. Hence the system is given by

$$(26) \quad \frac{d\mathbf{x}(t)}{dt} = \mathbf{A}\mathbf{x}(t) \quad \mathbf{x}(0) = \mathbf{y}(0) - \bar{\mathbf{y}}$$

Table(1) represents the matrix \mathbf{A} of the transfer coefficients of matter through a tropical rain forest ecosystem. The eigenvalues of the matrix \mathbf{A} are -315.9443, -62.6458, -17.2972, -6.4087, -0.002, -0.7718, -1.5051, -2.5817, -2.0341. The eigenvalue with the largest real part is $\lambda_1(\mathbf{A}) = -0.002yr^{-1}$, hence the resilience is $0.002yr^{-1}$. The eigenvalues of the matrix $\mathbf{H}(\mathbf{A}) = \frac{\mathbf{A} + \mathbf{A}^T}{2}$ are -381.4053, -71.1448, -20.6952, -3.2328, -2.0756, -1.6383, -0.0017, 8.5284, 65.4385 hence $\lambda_1(\mathbf{H}(\mathbf{A})) = 65.4yr^{-1}$. Hence the system is clearly reactive. The amplification curve of this model using the data in table(1) is given in the figure(4). It can be observed that $t_{max} \approx 7years$ and $\rho_{max} \approx 280\%$. It is reported in Neubert and Caswell 1997 that this reactive equilibrium is not restricted to tropical rain forest alone, there are various ecological models of real systems which exhibit reactive equilibrium.

0.5.2. *Aquatic food chain manipulation.* Neubert and Caswell 1997 reported the data of phosphorous cycle in a lake ecosystem from Carpenter 1992 to analyze the transient behaviour of the system. The Tuesday lake ecosystem in Winsconsin, which was dominated by planktivorous minnows in 1984, was altered by Carpenter 1992 by introducing a new trophic level of piscivorous largemouth bass in 1985. Enough minnows were removed from the lake to maintain the total biomass. The rate of transfer of phosphorous from one compartment to another compartment was measured by Carpenter 1992 and is reproduced in Neubert and Caswell 1997. Hence the transfer matrix \mathbf{A} for both the 1984 and 1986 lake ecosystem is reported in table(2). They calculated the resilience of the 1984 ecosystem to be 0.035. The eigenvalues of the 1984 matrix using the program MATLAB are -0.9491, -0.5922, -0.2624, -0.1742, -0.0388. Hence the calculation of resilience turns out to be 0.0388, which is different from the reported value. The eigenvalues of the 1986 transfer matrix are -0.9309, -0.3522, -0.1042, -0.0138, -0.0123, -0.0049. Hence the resilience is 0.0049, which is the reported value by Neubert and Caswell 1997. It can be observed that

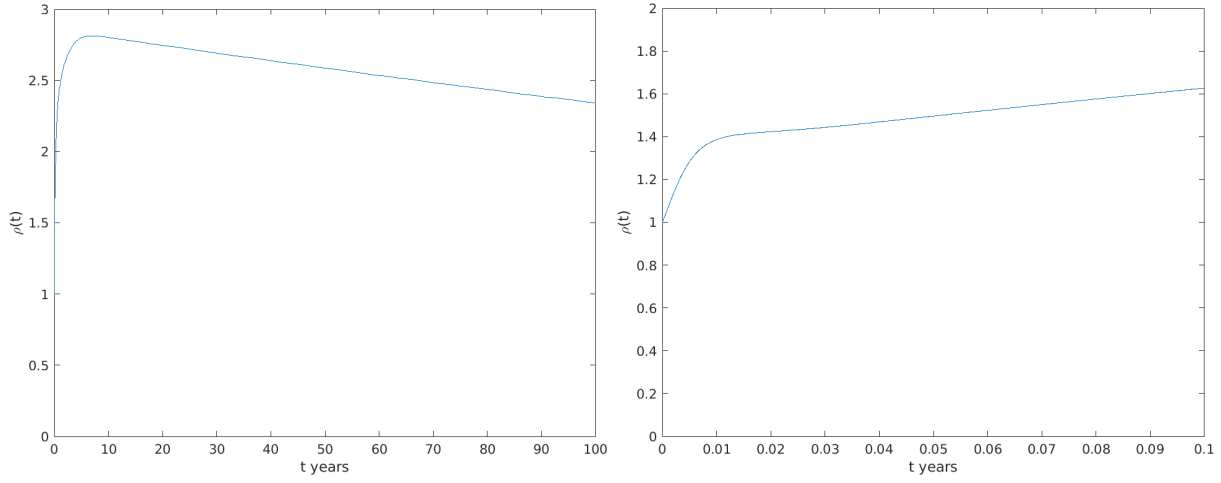


FIGURE 4. The amplification envelope of the tropical rainforest model(table(1)). Here the two graphs depicts the same amplification envelope of the tropical rain forest model; the two graphs are shown to indicate the two phases of transient growth happening in the interval $0 < t < 0.1$ and $0.1 < t < 100$.

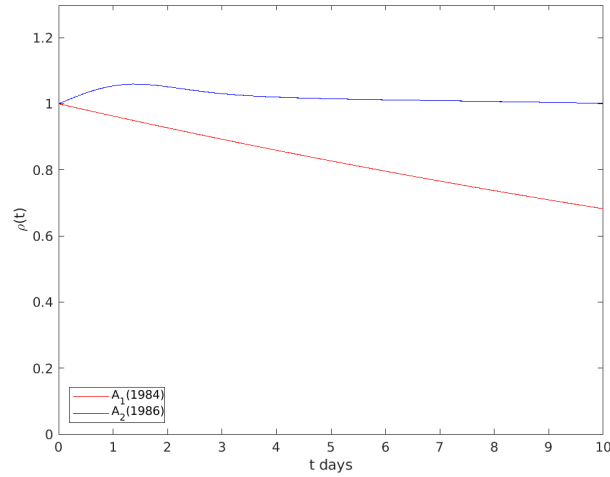


FIGURE 5. The amplification envelope for the 1984 and 1986 phosphorous transfer matrix of the Tuesday lake ecosystem.

resilience decreased by approximately $\frac{1}{7}$ of the value at 1984(using either of the values; 0.0388 or 0.035). This satisfies the hypothesis that increase in food chain length decreases the resilience of the system.

The eigenvalues of the symmetric part of the 1984 transfer matrix \mathbf{A}_1 are -1.2783, -0.3301, -0.2609, -0.1097, -0.0377. Hence the reactivity is $\lambda_1(H(\mathbf{A}_1)) = -0.0377$. The reported value of the reactivity for the 1984 matrix by Neubert and Caswell 1997 is 0.148.

The eigenvalues of the symmetric part of the 1986 transfer matrix \mathbf{A}_2 are -1.1767, -0.2865, -0.0127, -0.0072, -0.0047, 0.0694, hence the reactivity is $\lambda_1(H(\mathbf{A}_2)) = 0.0694$. The figure(5) represents the amplification envelope for the 1984 and 1986 matrices. The amplification envelope of the 1984 matrix is different from what is reported in Neubert and Caswell 1997.

Compartment and number		1	2	3	4	5	6
1984							
Soluble phosphorous	1	-0.9503†	0	0.0130	0.0056	0.0257	-
Seston	2	0.9500	-5.900	0	0	0	-
Zooplankton	3	0	-0.0290	-0.2622	0	0	-
Chaoborus	4	0	0	0.2000	-0.1752	0	-
Planktivore	5	0	0	0.0192	0.0026	-0.0389	-
1986							
Soluble phosphorous	1	-0.9503	0	0.0690	0.0002	0.0027	0.0034
Seston	2	0.9500†	-0.1800	0	0	0	0
Zooplankton	3	0	0.1500	-0.2569	0	0	0
Chaoborus	4	0	0	0.1000	-0.0138	0	0
Planktivore	5	0	0	0.0019	0.0002	-0.0124	0
Piscivore	6	0	0	0	0.0001	0.0028	-0.0049

†All the entries are in d^{-1} .

TABLE 2. Phosphorous transfer matrix of Tuesday lake before and after addition of piscivorous fish (Neubert and Caswell 1997).

Let a transfer matrix \mathbf{A} be such that it has distinct eigenvalues. The matrix of sensitivities of the resilience to changes in the flow rate a_{ij} is given by

$$(27) \quad \left(\frac{dresilience}{da_{ij}} \right) = -Re \left(\frac{vw^T}{v^T w} \right).$$

Where v and w are the respective left and right eigenvectors corresponding to the eigenvalue λ which has the largest real part among all the eigenvalues of \mathbf{A} . This can be derived as follows

Let w be the eigenvector corresponding to the eigenvalue λ hence $\mathbf{A}w = \lambda w$. Perturbing the matrix \mathbf{A} by $\Delta\mathbf{A}$ we get

$$(28) \quad (\mathbf{A} + \Delta\mathbf{A})(w + \Delta w) = (\lambda + \Delta\lambda)(w + \Delta w).$$

Neglecting the terms $\Delta\mathbf{A}\Delta\lambda$ and $\Delta\lambda\Delta w$

$$(29) \quad \mathbf{A}\Delta w + (\Delta\mathbf{A})w = \lambda\Delta w + (\Delta\lambda)w$$

Let v be the left eigenvector of \mathbf{A} hence $v^T \mathbf{A} = v^T \lambda$

$$(30) \quad v^T \mathbf{A}\Delta w + v^T (\Delta\mathbf{A})w = v^T \lambda\Delta w + (\Delta\lambda)v^T w$$

$$(31) \quad v^T \lambda\Delta w + v^T (\Delta\mathbf{A})w = v^T \lambda\Delta w + (\Delta\lambda)v^T w$$

If the change in \mathbf{A} is only in the term a_{ij} then $\Delta\mathbf{A} = \Delta a_{ij}$, hence the above equation

$$(32) \quad v_i(\Delta a_{ij})w_j = (\Delta\lambda)v^T w$$

Hence $\frac{d\lambda}{da_{ij}} = \frac{v_i w_j}{v^T w}$. Hence the matrix of the sensitivities is given by $\left(\frac{d\lambda}{da_{ij}} \right) = \frac{vw^T}{v^T w}$. Since the resilience is $-Re(\lambda)$, the matrix of resilience sensitivities is given by $\left(\frac{dresilience}{da_{ij}} \right) = -Re \left(\frac{vw^T}{v^T w} \right)$.

The matrix of resilience sensitivities for 1984 and 1986 matrix are reported in the table(3). The observed values of the 1984 resilience sensitivities are different from what is reported in Neubert and Caswell 1997.

Compartment and number		1	2	3	4	5	6
1984							
Soluble phosphorous	1	-0.0002	0	0	-0.0001	-0.0057	-
Seston	2	-0.0002	-0.0003	0	0	0	-
Zooplankton	3	0	-0.0050	-0.0007	0	0	-
Chaoborus	4	0	0	-0.0001	-0.0002	0	-
Planktivore	5	0	0	-0.0063	-0.0093	-0.9987	-
1986							
Soluble phosphorous	1	-0.0001	0† †	-0.0002	-0.0021	-0.0001	-0.0120
Seston	2	-0.0001	-0.0003	0	0	0	0
Zooplankton	3	0	-0.0004	-0.0002	0	0	0
Chaoborus	4	0	0	-0.0003	-0.00034	0	0
Planktivore	5	0	0	-0.0058	-0.000644	-0.0032	0
Piscivore	6	0	0	0	-0.1715	-0.0084	-0.9929

† † Calculation of resilience using the formula $-Re\left(\frac{vw^T}{v^Tw}\right)$ yields a non zero value at this entry. This value can be neglected since there is no transfer of phosphorous at the corresponding entry in the phosphorous transfer matrix. This comment applies to all the other 0 entries in this table.

TABLE 3. Sensitivities of resilience to changes in the flow rates of phosphorous in the Tuesday lake ecosystem.

The sensitivity of the reactivity $\lambda_1(H(\mathbf{A}))$ to the changes in the flow rate a_{ij} can be calculated as follows. Let the entries of $H(\mathbf{A})$ be denoted as h_{ij}

$$(33) \quad \frac{d\lambda_1(H(\mathbf{A}))}{da_{ij}} = \frac{\partial\lambda_1(H(\mathbf{A}))}{\partial h_{ij}} \frac{dh_{ij}}{da_{ij}} + \frac{\partial\lambda_1(H(\mathbf{A}))}{\partial h_{ji}} \frac{dh_{ji}}{da_{ij}}.$$

$$(34) \quad = \frac{\partial\lambda_1(H(\mathbf{A}))}{\partial h_{ij}} \frac{1}{2} + \frac{\partial\lambda_1(H(\mathbf{A}))}{\partial h_{ji}} \frac{1}{2}.$$

$$(35)$$

Since the left and right eigenvectors of a symmetric matrix are the same. Let the eigenvector corresponding to the eigenvalue $\lambda_1(H(\mathbf{A}))$ of the matrix $\frac{\mathbf{A}+\mathbf{A}^T}{2}$ be \mathbf{u} . Hence the sensitivity is given by

$$(36) \quad \frac{d\lambda_1(H(\mathbf{A}))}{da_{ij}} = \frac{\mathbf{u}_i \mathbf{u}_j}{\mathbf{u}^T \mathbf{u}} \frac{1}{2} + \frac{\mathbf{u}_j \mathbf{u}_i}{\mathbf{u}^T \mathbf{u}} \frac{1}{2}$$

$$(37) \quad = \frac{\mathbf{u}_j \mathbf{u}_i}{\mathbf{u}^T \mathbf{u}}$$

Hence the matrix of sensitivities of reactivity due to the changes in the flow rate is given by

$$(38) \quad \left(\frac{d\lambda_1(H(\mathbf{A}))}{da_{ij}} \right) = \frac{\mathbf{u} \mathbf{u}^T}{\mathbf{u}^T \mathbf{u}}.$$

The matrix of sensitivities of the reactivity for the 1984 and 1986 lake ecosystem is given in the table(4). The observed values of 1984 reactivity sensitivities are different from what is reported by Neubert and Caswell 1997.

Compartment and number		1	2	3	4	5	6
1984							
Soluble phosphorous	1	0.0008	0	0.0021	0.0018	0.0283	-
Seston	2	0.0008	0.0007	0	0	0	-
Zooplankton	3	0	0.0019	0.0054	0	0	-
Chaoborus	4	0	0	0.0046	0.0040	0	-
Planktivore	5	0	0	0.0729	0.0629	0.9891	-
1986							
Soluble phosphorous	1	0.1672	0† †	0.1084	0.0653	0.0042	0.0039
Seston	2	0.3510	0.7369	0	0	0	0
Zooplankton	3	0	0.2275	0.0702	0	0	0
Chaoborus	4	0	0	0.0423	0.0255	0	0
Planktivore	5	0	0	0.0027	0.0016	0.0001	0
Piscivore	6	0	0	0	0.0015	0.0001	0.0001

† † Calculation of reactivity using the formula $\left(\frac{uu^T}{u^T u}\right)$ yields a non zero value at this entry. This value can be neglected since there is no transfer of phosphorous at the corresponding entry in the phosphorous tranfer matrix. This comment applies to all the other 0 entries in this table.

TABLE 4. Sensitivities of reactivity to changes in the flow rates of phosphorous in the Tuesday lake ecosystem.

0.5.3. *A nonlinear predator prey model.* In this section a non linear predator prey model will be considered to analyse the resilience and reactivity. The prey population follows a logistic growth in the absence of predator. The intake rate of the consumer follows a holling type II response

$$(39) \quad \frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{aNP}{N+b}$$

$$(40) \quad \frac{dP}{dt} = \frac{caNP}{N+b} - dP$$

N and P are the prey and predator densities respectively. r is the intrinsic growth rate of the prey (unit t^{-1}), K is the carrying capacity, a is the saturation level (unit t^{-1}), b is the half saturation constant of the predator's functional response. c is the predator's yield coefficient (dimensionless quantity) and d is the mortality rate (unit t^{-1}).

By using the change of variables

$$(41) \quad y_1 = \frac{N}{b} \quad y_2 = \frac{aP}{rb} \quad \tau = rt \quad k = \frac{K}{b} \quad \alpha = \frac{ac}{r} \quad \beta = \frac{d}{ac}$$

The equation takes a dimensionless form

$$(42) \quad \frac{dy_1}{d\tau} = y_1 \left(1 - \frac{y_1}{k}\right) - \frac{y_1 y_2}{(y_1 + 1)}$$

$$(43) \quad \frac{dy_2}{d\tau} = \alpha \left(\frac{y_1 y_2}{y_1 + 1} - \beta y_2\right)$$

We will consider the equilibrium where prey and predator coexists

$$(44) \quad (y_1^*, y_2^*) = \left(\frac{\beta}{1-\beta}, \frac{1}{1-\beta} \left(1 - \frac{\beta}{k(1-\beta)}\right)\right)$$

The linearization of the system gives us the form

$$(45) \quad \begin{bmatrix} \frac{dy_1}{d\tau} \\ \frac{dy_2}{d\tau} \end{bmatrix} = \begin{bmatrix} \left(1 - 2\frac{\beta}{k(1-\beta)} - \frac{1}{1-\beta} \left(1 - \frac{\beta}{k(1-\beta)}\right)\right) & -\beta \\ \frac{\alpha}{1-\beta} \left(1 - \frac{\beta}{k(1-\beta)}\right) & 0 \end{bmatrix} \begin{bmatrix} y_1 \\ y_2 \end{bmatrix}$$

For an asymptotically stable equilibrium point the trace of the linearized system should be negative. Hence

$$(46) \quad \left(1 - \frac{2\beta}{k(1-\beta)} - \frac{1}{1-\beta} \left(1 - \frac{\beta}{k(1-\beta)}\right)\right) < 0.$$

Further simplification yields the inequality

$$(47) \quad \frac{k-1}{2} < \frac{\beta}{1-\beta}.$$

For the eigenvalues of the matrix to be complex, the matrix should satisfy $trace^2 - 4(determinant) < 0$. Hence

$$(48) \quad \left(1 - \frac{2\beta}{k(1-\beta)} - \frac{1}{1-\beta} \left(1 - \frac{\beta}{k(1-\beta)}\right)\right)^2 - 4 \left(\frac{\alpha\beta}{1-\beta}\right) \left(1 - \frac{\beta}{k(1-\beta)}\right) < 0.$$

(49)

Further simplification yields

$$(50) \quad \left(\frac{\beta}{1-\beta}\right) \left[\frac{\beta}{1-\beta} \left(1 + \frac{1-2\beta}{k(1-\beta)}\right)^2 - 4\alpha \left(1 - \frac{\beta}{k(1-\beta)}\right)\right] < 0.$$

hence the necessary condition for this inequality to be satisfied is

$$(51) \quad \frac{\beta}{1-\beta} < k$$

Using the above results we find that when β and k satisfies

$$(52) \quad \frac{k-1}{2} < \frac{\beta}{1-\beta} < k$$

the eigenvalues have negative real part and hence the equilibrium is asymptotically stable. When the right hand inequality is violated, one of the eigenvalues is real and positive hence the system is unstable. It is noted by Neubert and Caswell 1997 that the violation of left hand inequality leads to a stable predator prey oscillation.

Fig(6) illustrates resilience, reactivity, time to maximum amplification(t_{max}) and maximum amplification ρ_{max} as a function of the predator mortality rate β and maximum predator growth rate α . The values of k and β are chosen so that the inequality (52) is satisfied.

As the predator mortality rate β is increased from 0 to 0.25 the long term stability of the system increases (faster rate of decay for any perturbation to the system). The reactivity of the equilibrium also increases. Hence the increase in the stability of the system is compromised by the increased transient growth. As β changes from 0.25 to 0.5 the resilience of the system decreases hence the long term stability decreases but the reactivity remains the same.

When the maximum predator growth rate $\alpha > 1$, the reactivity becomes a constant. This is due to the fact that when $\alpha > 1$ the eigenvalues of the linearized matrix are complex. Hence the real part of the

eigenvalues are independent of α and hence the resilience is independent of α . In contrast the reactivity keeps increasing for $\alpha > 1$, since the eigenvalues of $H(A)$, where A is the linearized matrix, depends on α .

0.5.4. *Discussion.* Most of the ecological theories deals with asymptotic behavior. This is due to the fact that asymptotic behavior can be easily described by the dominant eigenvalues of the matrix. It is also the case that the solutions of the linearization of a non linear system is valid for a small neighbourhood around the equilibrium point. Hence, the solution of this linearized system is closer to the actual solution when it is evaluated near to the equilibrium point. Hence the desire to find the asymptotic behavior of solutions. In this review of Neubert and Caswell 1997, their ideas of new measures of transient behavior is presented with as much mathematical details as possible. The drawbacks of the eigenvalue analysis is presented. The new measures of transient behavior is able to give a better idea of the effects of perturbations on an ecological system.

It can be observed that calculations on the 1984 matrix of the aquatic food chain model is not in agreement with what is reported by Neubert and Caswell 1997. This could be because the reported 1984 matrix may not be the one used for the calculations of the measures of transient behaviour.

Non linearities in a system can enhance the transient behavior. Neubert and Caswell 1997 demonstrated this by comparing the maximum amplification observed in the non linear predator prey model and its linearization for perturbations in different directions in the x-y plane. This observation of the difference in the effects of perturbations in the actual non linear model and its linearization suggests a possible drawback of the new transient measures. It is also the case that the maximum amplification ρ_{max} is achieved by one of the possible perturbations and this may not be the perturbation that corresponds to the one that gives maximum instantaneous growth rate at $t = 0$ (reactivity). It may happen that majority of the perturbations may actually decay to equilibrium. This suggests that instead of (12) one can use

$$(53) \quad T_R = \int_0^{\infty} \rho(t) dt$$

as the measure of return time and this is also a 'worst case measure' as quoted by Neubert and Caswell 1997.

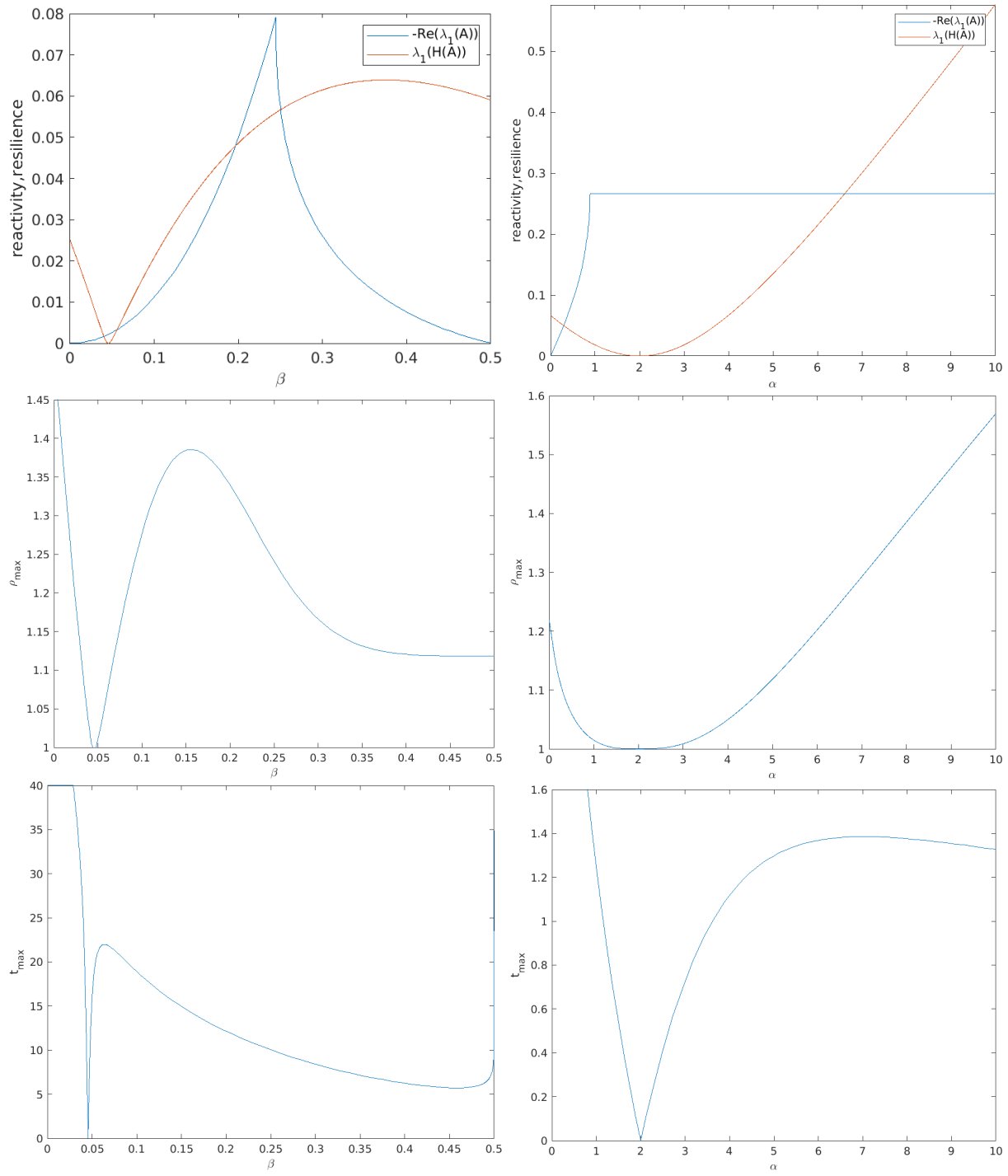


FIGURE 6. The figures in the first column depicts the variation of resilience, reactivity, t_{max} and ρ_{max} as a function of predator mortality rate β . The figures in the second column depicts the variation as a function of α . For the figures in the first column α is fixed and $\alpha = 0.05$ and for the second column β is fixed and $\beta = 0.4$. $k = 1$ is a constant.

Subsection 0.6. Appendix.

0.6.1. *Linearization.* Consider the $D.E$

$$(54) \quad \frac{d\mathbf{x}}{dt} = \mathbf{f}(\mathbf{x}).$$

$\mathbf{f}(\mathbf{x}) = (f_1(\mathbf{x}), f_2(\mathbf{x}), \dots, f_n(\mathbf{x}))^T$ is a non linear function in \mathbf{x} . Let $\mathbf{f}(\bar{\mathbf{x}}) = 0$. Hence $\bar{\mathbf{x}}$ is an equilibrium point of the $D.E$. Using the taylor series of $f_i(\bar{\mathbf{x}})$ about the point $\bar{\mathbf{x}}$

$$(55) \quad f_i(\mathbf{x}) = f_i(\bar{\mathbf{x}}) + D(f_i)|_{\bar{\mathbf{x}}}(\mathbf{x} - \bar{\mathbf{x}})^T + (\mathbf{x} - \bar{\mathbf{x}})D^2(f_i)|_{\bar{\mathbf{x}}}(\mathbf{x} - \bar{\mathbf{x}})^T + \dots$$

Neglecting the non linear terms and using the fact that $f_i(\bar{\mathbf{x}}) = 0$ we get

$$(56) \quad f_i(\mathbf{x}) = D(f_i)|_{\bar{\mathbf{x}}}(\mathbf{x} - \bar{\mathbf{x}})^T.$$

Hence the $D.E$ is linearized at the equilibrium $\bar{\mathbf{x}}$ as follows

$$(57) \quad \frac{d\mathbf{x}}{dt} = J(\mathbf{f})|_{\bar{\mathbf{x}}}(\mathbf{x} - \bar{\mathbf{x}})^T.$$

Where $J(\mathbf{f})|_{\bar{\mathbf{x}}}$ is the jacobian of \mathbf{f} at $\bar{\mathbf{x}}$.

0.6.2. *Asymptotically stable equilibrium.* Consider the $D.E$

$$(58) \quad \frac{d\mathbf{x}}{dt} = \mathbf{f}(\mathbf{x}).$$

The equilibrium point $\bar{\mathbf{x}}$ is *positively stable*, if the following holds

1. For a given $\epsilon > 0$ there exists $\delta > 0$ such that $\|\mathbf{x}(t, \zeta) - \bar{\mathbf{x}}\| < \epsilon$ for all $t \geq 0$ when $\|\zeta - \bar{\mathbf{x}}\| < \delta$, where $\mathbf{x}(t, \zeta)$ is the solution of the $D.E$ starting at the point ζ .

If the stable equilibrium point $\bar{\mathbf{x}}$ in addition satisfies the following

2. There exists $\gamma > 0$ such that $\lim_{t \rightarrow \infty} \mathbf{x}(t, \zeta) = \bar{\mathbf{x}}$ when $\|\zeta - \bar{\mathbf{x}}\| < \gamma$. Then $\bar{\mathbf{x}}$ is *asymptotically stable* equilibrium point.

0.6.3. *Generalized eigenvector of degree p .* v is a generalized eigenvector of degree p if there exists a $\lambda \in \mathbb{C}$ such that $(T - \lambda I)^p v = 0$ and $(T - \lambda I)^{p-1} v \neq 0$. Since $(T - \lambda I)(T - \lambda I)^{p-1} v = 0$ it follows that λ is an eigenvalue of T .

0.6.4. *Generalized eigenspace.* Let λ be an eigenvalue of the linear transformation $T : \mathbb{C}^n \rightarrow \mathbb{C}^n$. Hence the following chain holds

$$(59) \quad \{0\} \subset \mathcal{N}(T - \lambda I) \subset \mathcal{N}(T - \lambda I)^2 \subset \dots$$

$\mathcal{N}(S)$ is the null space of any linear operator $S : \mathbb{C}^n \rightarrow \mathbb{C}^n$. Since the domain of $T - \lambda I$ is finite dimensional, there exists a number k such that $\mathcal{N}(T - \lambda I)^k = \mathcal{N}(T - \lambda I)^{k+1}$. Let $r(\lambda)$ be the minimum of all such numbers. Hence define the generalized eigenspace of λ to be $M(\lambda) = \mathcal{N}(T - \lambda I)^{r(\lambda)}$.

0.6.5. *Proposition.* Let $T : \mathbb{C}^n \rightarrow \mathbb{C}^n$ be a linear transformation. If v is a generalized eigenvector of degree p for the eigenvalue λ then $v, (T - \lambda I)(v), \dots, (T - \lambda I)^{p-1}(v)$ are linearly independent.

Proof. On contrary if the vectors are linearly dependent then there exists k , for $0 \leq k \leq p-2$ and $c_i \in \mathbb{C}$, for $k+1 \leq i \leq p-1$ such that

$$(60) \quad (T - \lambda I)^k(v) = \sum_{i=k+1}^{p-1} c_i (T - \lambda I)^i(v)$$

Applying $(T - \lambda I)^{p-k-1}$ to the above equation

$$(61) \quad 0 \neq (T - \lambda I)^{p-1}(v) = \sum_{i=k+1}^{p-1} c_i (T - \lambda I)^{p-k-1+i}(v) = 0$$

The last equality follows since $p - k - 1 + i \geq p$ for $i \geq k + 1$. This gives a contradiction. Hence $v, (T - \lambda I)(v), \dots, (T - \lambda I)^{p-1}(v)$ are linearly independent.

0.6.6. *Lemma.* The following holds

- (a) The generalized eigenspace $M(\lambda) = \{v : (T - \lambda I)^k v = 0, k \geq r(\lambda)\} = \{v : (T - \lambda I)^k v = 0, k \geq 1\}$.
- (b) $r(\lambda)$ is the maximum degree of the generalized eigenvectors of λ .
- (c) $\text{Dim}[M(\lambda)] \geq r(\lambda)$.

Proof. (a) By the definition of $r(\lambda)$ it follows that $\mathcal{N}(T - \lambda I)^{r(\lambda)} = \mathcal{N}(T - \lambda I)^{r(\lambda)+1}$. Let $\mathcal{N}(T - \lambda I)^k = \mathcal{N}(T - \lambda I)^{k+1}$ for some $k \geq r(\lambda)$. Let $v \in \mathcal{N}(T - \lambda I)^{k+2}$, hence $(T - \lambda I)^{k+1}(T - \lambda I)v = 0$. This implies $(T - \lambda I)v \in \mathcal{N}(T - \lambda I)^{k+1} = \mathcal{N}(T - \lambda I)^k$. Hence $(T - \lambda I)^{k+1}v = (T - \lambda I)^k(T - \lambda I)v = 0$. Therefore $\mathcal{N}(T - \lambda I)^{k+2} = \mathcal{N}(T - \lambda I)^{k+1}$. Hence it follows that $\mathcal{N}(T - \lambda I)^{r(\lambda)} = \mathcal{N}(T - \lambda I)^{r(\lambda)+j}$ for $j \geq 1$. Since the following holds

$$(62) \quad \{0\} \subset \mathcal{N}(T - \lambda I) \subset \dots \subset \mathcal{N}(T - \lambda I)^{r(\lambda)}$$

(a) is proved.

(b) By (a) it follows that every generalized eigenvector belongs to $M(\lambda)$ and the degree of the generalized eigenvectors can't exceed $r(\lambda)$ because $\mathcal{N}(T - \lambda I)^{r(\lambda)} = \mathcal{N}(T - \lambda I)^{r(\lambda)+j}$ for $j \geq 1$. By the definition of $r(\lambda)$, there exists $v \in \mathcal{N}(T - \lambda I)^{r(\lambda)}$ such that $(T - \lambda I)^{r(\lambda)}v = 0$ and $(T - \lambda I)^{r(\lambda)-1}v \neq 0$. Hence the maximal degree of the generalized eigenvectors is $r(\lambda)$.

(c) By (b) there exists a generalized eigenvector of degree $r(\lambda)$, hence by the proposition(0.6.5) there exists $r(\lambda)$ linearly independent vectors in $M(\lambda)$. Hence $\text{Dim}[M(\lambda)] \geq r(\lambda)$.

0.6.7. *Propsoition.* If λ is an eigenvalue of the linear transformation $T : \mathbb{C}^n \rightarrow \mathbb{C}^n$, then the generalized eigenspace $M(\lambda)$ and the range of $(T - \lambda I)^{r(\lambda)}$ denoted by $\mathcal{R}(\lambda)$ are invariant subspaces of \mathbb{C}^n such that

$$(63) \quad \mathbb{C}^n = M(\lambda) \oplus \mathcal{R}(\lambda)$$

Proof. $T(T - \lambda I)^k = (T - \lambda I)^k T$ for $k \geq 1$. Hence it follows that $M(\lambda)$ and $\mathcal{R}(\lambda)$ are invariant subspaces of \mathbb{C}^n . By the rank- nullity theorem $\text{Dim}[\mathcal{R}(\lambda)] + \text{Dim}[M(\lambda)] = n$, hence only need to show that

$$(64) \quad M(\lambda) \cap \mathcal{R}(\lambda) = \{0\}$$

Let u be a vector such that $0 \neq v = (T - \lambda I)^{r(\lambda)}(u) \in \mathcal{R}(\lambda)$ and $(T - \lambda I)^{r(\lambda)}(v) = 0$. Hence u is a generalized eigenvector of degree greater than $r(\lambda)$. This is a contradiction to the lemma(0.6.6). Hence proved.

0.6.8. *Proposition.* Let A be a real $m \times n$ matrix and let e_1, \dots, e_n be the standard basis of \mathbb{R}^n . Let $\|\cdot\|_1$ be the matrix norm induced by the 1-norm $\|\cdot\|_1$, then

$$(65) \quad \|A\|_1 = \max\{\|Ae_j\|_1 : 1 \leq j \leq n\}.$$

Proof. Let $M = \max\{\|Ae_j\|_1 : 1 \leq j \leq n\}$ and note that $M \leq \|A\|_1$. If $\|x\|_1 = 1$ then

$$\begin{aligned}\|Ax\|_1 &= \left\| \sum_{j=1}^n x_j Ae_j \right\|_1 \\ &\leq \sum_{j=1}^n |x_j| \|Ae_j\|_1 \\ &\leq M \sum_{j=1}^n |x_j| = M.\end{aligned}$$

Hence $\|A\|_1 = \max\{\|Ax\|_1 : \|x\|_1 = 1\} \leq M$. Hence $\|A\|_1 = M$.

0.6.9. *Theorem.* Let $\lambda_1, \dots, \lambda_\rho$ be the distinct eigenvalues with multiplicities m_1, \dots, m_ρ of the linear transformation $T : \mathbb{C}^n \rightarrow \mathbb{C}^n$, and let $M(\lambda_1), \dots, M(\lambda_\rho)$ be the corresponding generalized eigenspaces. Then the dimension of $M(\lambda_j)$ is m_j and

$$(66) \quad \mathbb{C}^n = M(\lambda_1) \oplus M(\lambda_2) \oplus \dots \oplus M(\lambda_\rho)$$

Proof. Fix j , for $1 \leq j \leq \rho$. By the proposition(0.6.7), there exists a basis u_1, u_2, \dots, u_n of \mathbb{C}^n such that $u_1, u_2, \dots, u_\sigma$ is a basis for $M(\lambda_j)$ and $u_{\sigma+1}, u_{\sigma+2}, \dots, u_n$ is a basis of $\mathcal{R}(\lambda_j)$. $M(\lambda_j)$ and $\mathcal{R}(\lambda_j)$ are T invariant, the matrix of T with respect to this basis has the form

$$(67) \quad \begin{bmatrix} A_1 & 0 \\ 0 & A_2 \end{bmatrix}$$

A_1 is $\sigma \times \sigma$ and A_2 is $n - \sigma \times n - \sigma$. It follows that

$$(68) \quad \text{Det}[A_1 - \lambda I] \text{Det}[A_2 - \lambda I] = \text{Det}[T - \lambda I] = \pm \prod_{k=1}^\rho (\lambda - \lambda_k)^{m_k}.$$

If $\lambda - \lambda_j$ divides $\text{Det}[A_2 - \lambda I]$, then $\mathcal{R}(\lambda_j)$ must contain an eigenvector $v \neq 0$ for λ_j . Since every eigenvector for λ_j lies in $M(\lambda_j)$, it follows that $0 \neq v \in M(\lambda_j) \cap \mathcal{R}(\lambda_j)$, which is impossible by the proposition(0.6.7). Therefore, $\lambda - \lambda_j$ does not divide $\text{Det}[A_2 - \lambda I]$ and $(\lambda - \lambda_j)^{m_j}$ divides $\text{Det}[A_1 - \lambda I]$. If $(\lambda - \lambda_k)$ divides $\text{Det}[A_1 - \lambda I]$ for some $k \neq j$, then $M(\lambda_j)$ contains an eigenvector v for λ_k . Because v would also be a generalized eigenvector of λ_j for some degree p , the following gives a contradiction

$$\begin{aligned}0 &= (T - \lambda_j I)^p(v) \\ &= (T - \lambda_j I)^{p-1}(T - \lambda_j I)(v) \\ &= (T - \lambda_j I)^{p-1}(\lambda_k - \lambda_j)(v) \\ &= (\lambda_k - \lambda_j)(T - \lambda_j I)^{p-1}(v) \\ &\neq 0.\end{aligned}$$

Therefore, $\lambda - \lambda_k$ does not divide $\text{Det}[A_1 - \lambda I]$ and $\text{Det}[A_1 - \lambda I] = \pm(\lambda - \lambda_j)^{m_j}$. It follows that $m_j = \sigma$ and that the dimension of $M(\lambda_j)$ is m_j . Now j was fixed but arbitrary hence $M(\lambda_j) = m_j$ for $j = 1, \dots, \rho$.

Because $m_1 + m_2 + \dots + m_\rho = n$, showing that $\mathbb{C}^n = M(\lambda_1) \oplus M(\lambda_2) \oplus \dots \oplus M(\lambda_\rho)$ is now reduced to showing that $v_1 + v_2 + \dots + v_\rho = 0$, for $v_j \in M(\lambda_j)$, implies $v_j = 0$ for all j .

First, it must be shown that $M(\lambda_j) \cap M(\lambda_k) = \{0\}$ when $j \neq k$. The restriction of T to $M(\lambda_j) \cap M(\lambda_k)$ is a linear transformation of $M(\lambda_j) \cap M(\lambda_k)$ into itself. If $M(\lambda_j) \cap M(\lambda_k) \neq \{0\}$, then $M(\lambda_j) \cap M(\lambda_k)$ must contain an eigenvector for some eigenvalue μ of T restricted to $M(\lambda_j) \cap M(\lambda_k)$ because in complex vector space every eigenvalue has an eigenvector. By the first part of the proof since $\text{Det}[A_1 - \lambda I] = \pm(\lambda - \lambda_j)^{m_j}$, where A_1 is the matrix of T restricted to $M(\lambda_j)$, hence the only eigenvalue of $T|_{M(\lambda_j) \cap M(\lambda_k)}$ is λ_j . It follows that $\lambda_j = \mu = \lambda_k$ and $j = k$. Thus $M(\lambda_j) \cap M(\lambda_k) = \{0\}$ when $j \neq k$.

$M(\lambda_j)$ is also invariant under $T - \lambda_k I$. Consequently, for $0 \neq v \in M(\lambda_j)$ and $k \neq j$,

$$(69) \quad 0 \neq (T - \lambda_k I)^{r(\lambda_k)}(v) \in M(\lambda_j)$$

because $M(\lambda_j) \cap M(\lambda_k) = \{0\}$. Now applying

$$(70) \quad S = (T - \lambda_2 I)^{r(\lambda_2)} \dots (T - \lambda_\rho I)^{r(\lambda_\rho)}$$

to $v_1 + \dots + v_\rho = 0$, we get $S(v_1) = 0$ because $S(v_j) = 0$ for $j = 2, \dots, \rho$. Repeated application of eq(69) for $j = 1$ and $k = 2, \dots, \rho$ implies $S(v_1) \neq 0$, which is a contradiction unless $v_1 = 0$. By the similar method it can be shown that $v_j = 0$ for $j = 2, \dots, \rho$. Hence the theorem is proved.

0.6.10. *Theorem.* consider the system $\frac{dx}{dt} = Ax$. Let $\lambda_1, \lambda_2, \dots, \lambda_d$ be the distinct eigenvalues of the $d \times d$ matrix $A \in \mathcal{M}_n(\mathbb{R})$. The equilibrium point $\mathbf{0}$ is asymptotically stable then $Re(\lambda_j) < 0$ for $j = 1, 2, \dots, d$.

Proof. Suppose $\mathbf{0}$ is positively stable(0.6.2), so there exists $\delta > 0$ such that $\|\mathbf{v}\| < \delta$ implies that $\|x(t, \mathbf{v})\| < 1$ for $t \geq 0$, where $x(t, \mathbf{v})$ is the solution which starts at \mathbf{v} . Since $x(t, \mathbf{v}) = e^{At}\mathbf{v}$, for $\delta' < \delta$ it follows

$$\begin{aligned} \|e^{At}\| &= \sup\{\|e^{At}\mathbf{v}\| : \|\mathbf{v}\| = 1\} \\ &= \frac{1}{\delta'} \sup\{\|e^{At}\mathbf{v}\| : \|\mathbf{v}\| = \delta'\} \\ &\leq \frac{1}{\delta'} \end{aligned}$$

Since δ' is arbitrary it follows

$$(71) \quad \|e^{At}\| \leq \frac{1}{\delta} \quad \text{for } t \geq 0$$

Suppose on contrary for some λ_j , $Re(\lambda_j) > 0$. Let v_j be an eigenvector corresponding to the eigenvalue λ_j with $\|v_j\| = 1$. Then

$$(72) \quad \|e^{At}\| \geq \|e^{At}v\| = e^{Re(\lambda_j)t} \rightarrow \infty$$

Which is not possible since $\|e^{At}\|$ is bounded above by $\frac{1}{\delta}$. Hence $Re(\lambda_j) \leq 0$ for $j = 1, \dots, d$. By the definition of an asymptotically stable equilibrium point there exists a γ such that

$$(73) \quad \lim_{t \rightarrow \infty} \|X(t, v)\| = \lim_{t \rightarrow \infty} \|e^{At}v\| = 0$$

whenever $\|v\| < \gamma$. It follows that $\|e^{At}v\| \rightarrow 0$ as $t \rightarrow \infty$ for all $v \in \mathbb{R}^d$. This is because any $v \in \mathbb{R}^d$ can be re scaled to $\frac{v}{\|v\|}\gamma$. By the proposition(0.6.8) and by the fact that matrix norms are equivalent, there exists constants C and C' such that

$$(74) \quad \|e^{At}\| \leq C \|e^{At}\|_1 = C \max\{\|e^{At}e_j\|_1 : 1 \leq j \leq d\} \leq CC' \max\{\|e^{At}e_j\| : 1 \leq j \leq d\} \rightarrow 0$$

as $t \rightarrow \infty$ hence $\|e^{At}\| \rightarrow 0$ as $t \rightarrow \infty$. If for some λ_j , $Re(\lambda_j) = 0$ and $v \in \mathbb{C}^d$ is an eigenvector for λ_j with $\|v\| = 1$, then

$$(75) \quad \|e^{At}\| \geq \|e^{At}v\| = \|e^{i\beta t}v\| = \|v\| = 1$$

this is a contradiction since $\|e^{At}\| \rightarrow 0$ as $t \rightarrow \infty$. Hence $Re(\lambda_j) < 0$ for $j = 1, \dots, d$.

REFERENCES

- Carpenter, et.al. 1992. "Resilience and Resistance of a lake phosphorous cycle before and after food web manipulation." *The American Naturalist* 140:781–798.
- Cottingham, Katheryn L., and Stephen R. Carpenter. 1994. "Predictive indices of ecosystem resilience in models of north temperate lakes." *The Ecological society of America* 75:2127–2138.
- DeAngelis, D.L. 1980. "Energy flow, Nutrient cycling and ecosystem resilience." *the Ecological society of America* 61:764–771.
- Horn, R., and C. Johnson. 2013. *Matrix Analysis*. 234–235. Second Edition. Cambridge University Press.
- McGinnis, et.al. 1969. "Elemental and hydrological budgets of the Panamian tropical rainforest." *Bio-science* 19:697–700.
- Neubert, M.G, and Hal Caswell. 1997. "Alternatives to resilience for measuring the responses of ecological systems to perturbations." *The Ecological Society of America*, 653–665.
- Pimm, S.L, and J.H Lawton. 1977. "Number of trophic levels in ecological communities." *Nature* 268:329–331.