Alternatives to resilience for measuring the response of ecological systems to perturbations

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3-12-2020

Overview

1. Preliminaries: 1.)Basic results from *ODE*.
   2) Define measures of the effects of perturbations; resilience, reactivity, amplification envelope, ρ_{max}, t_{max}.

2. Models: Phosphorous transfer in a lake ecosystem, Predator-prey model.

3. Discussion: The limitations of proposed measures.

Preliminaries

Definition

An **equilibrium point** of the differential equation $(D.E)$

$$\frac{dX}{dt} = f(X) \qquad X(0) = X_0$$

is the value $\tilde{X}$ such that $f(\tilde{X}) = 0$.

- The solution of $D.E$ starting at an equilibrium point remains at that equilibrium point for all times.
- The $D.E$ is linear if $f(X)$ is a linear function of X and it is non linear if $f(X)$ is non linear function of X.

- If the $D.E$ is linear then it is easier to analyze. For a non linear $D.E$ we 'linearize' the $D.E$.

Definition

Linearization of a non linear $D.E$ is the linear system

$$\frac{dX}{dt} = J(f)|_{\tilde{X}}.(X - \tilde{X})$$

$J(f)|_{\tilde{X}} = [\frac{\partial f_i}{\partial x_j}]$ is the jacobian of f evaluated at $\tilde{X}$.

- The Hartman Grobman theorem asserts that the solutions of the linearized system is qualitatively similar to the solutions of the non linear system in the vicinity of the equilibrium point $\tilde{X}$, provided the real part of the eigenvalues of $J(f)|_{\tilde{X}}$ are non zero.

Lemma

The solution of a linear system

$$\frac{dX}{dt} = AX \quad X(0) = X_0$$

for $A \in M_n(\mathbb{R})$ *is given by*

$$X(t) = e^{At}X_0$$

for $0 \leq t < \infty$.

Definition

The equilibrium point $\tilde{X}$ of the $\frac{dX}{dt} = f(X)$ is **asymptotically stable** if the following holds:

1) For a given $\epsilon > 0$ there exists $\delta > 0$, such that $||X(t) - \tilde{X}|| < \epsilon$ for all $t \geq 0$, when $||X(0) - \tilde{X}|| < \delta$.

2) There exists $\gamma > 0$ such that $lim_{t\to\infty}X(t) = \tilde{X}$ when $||X(0) - \tilde{X}|| < \gamma$.

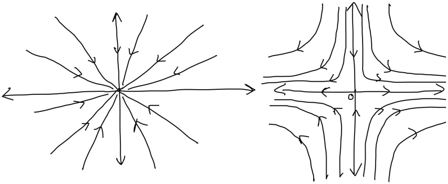

Figure: Equilibrium points

Lemma

The equilibrium point 0 of $\frac{dX}{dt} = AX$ *for* $A \in M_n(\mathbb{R})$ *is asymptotically stable iff the eigenvalues* λ_j *of* A *satisfies* $Re(\lambda_j) < 0$ *for* $j = 1, ...n$.

- Throughout the project the linear systems $\frac{dX}{dt} = AX$ have $A \in M_n(\mathbb{R})$ to be invertible, hence there is a unique equilibrium point 0.

- Throughout the project the focus is on asymptotically stable equilibrium points. Hence the eigenvalues of A for the system $\frac{dX}{dt} = AX$ will satisfy; $Re(\lambda_j) < 0$ for $j = 1, .., n$.

Definition

Perturbation of an ecological system modelled by the $D.E$

$$\frac{dX}{dt} = AX$$

is the initial point X_0 of the solution $X(t)$ such that $X_0 \neq \tilde{X}$, where $\tilde{X}$ is the equilibrium point of the system.

- **Stability** is the qualitative measure of the system to return to the equilibrium point after a perturbation.
- Quantitatively this is measured using **resilience**.

Definition

Resilience is the measure of how rapidly a system returns to equillibrium after a perturbation. For a linear system $\frac{dX}{dt} = AX$ this is measured as

$$-\max_{1 \leq i \leq n} \{Re(\lambda_i(A))\}$$

where $\lambda_i(A)$ are the eigenvalues of A for $i = 1, .., n$.

- $\lambda_1(A)$ is the eigenvalue with the largest real part among all eigenvalues. w_1 is an eigenvector corresponding to $\lambda_1(A)$. For almost all initial points x_0 we get $lim_{t\to\infty} e^{-\lambda_1(A)t} x(t) = w_1$.
- For sufficiently large t, $x(t) \propto w_1$ and decays like $e^{\lambda_1(A)t}$. Hence asymptotically the magnitude of $x(t)$ decreases by a factor of $\frac{1}{e}$ in the time interval $\Delta t = \frac{-1}{Re(\lambda_1(A))}$.
- Hence $-Re(\lambda_1(A))$ is a measure of the asymptotic rate of decay of almost all perturbations. Hence resilience of the system $\equiv -Re(\lambda_1(A)) = -\max_{1 \leq i \leq n}\{Re(\lambda_i(A))\}$.

Drawbacks of the measure of resilience

- Consider the solution of $\frac{dX}{dt} = AX$ with the initial condition $X(0) = (\frac{1}{2}, \frac{\sqrt{3}}{2})$ when A is either

$$A_1 = \begin{bmatrix} -1 & 1 \\ 0 & -2 \end{bmatrix} \qquad or \qquad A_2 = \begin{bmatrix} -1 & 10 \\ 0 & -2 \end{bmatrix} \tag{1}$$

- The eigenvalues of the matrices are -1 and -2.
- Resilience=1, hence the solutions decay at the same rate asymptotically.

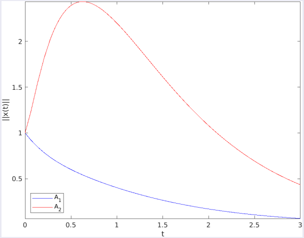

Figure: The magnitude of the solutions of linear system (1).

- Consider the solution of $\frac{dX}{dt} = AX$ with $X(0) = (Cos(\frac{2\pi}{5}), sin(\frac{2\pi}{5}))$ when A is either

$$A_3 = \begin{bmatrix} -1 & -12 \\ 0.75 & -2 \end{bmatrix} \qquad or \qquad A_4 = \begin{bmatrix} -1 & -4 \\ 2.25 & -2 \end{bmatrix} \tag{2}$$

- The matrices have the same eigenvalues $\frac{-3+i\sqrt{35}}{2}$ and $\frac{-3-i\sqrt{35}}{2}$.
- Each of the systems have the same resilience $\frac{3}{2}$.

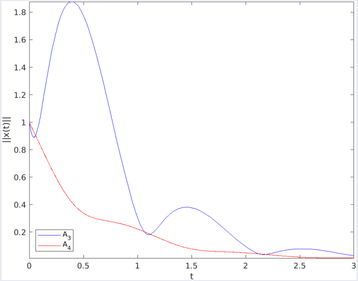

Figure: The magnitude of the solutions of linear system (2)

- The transient growth is not due to the non linearity of the system.
- Knowing the eigenvalues of a system alone is insufficient to predict any transient growth.
- Hence the need for a new measure which can complement resilience.

Definition

The *reactivity* of the equilibrium point is defined as

$$reactivity = max_{||x_0|| \neq 0} \left[\frac{1}{||x_0||} \frac{d||x(t)||}{dt} |_{t=0} \right]. \quad (3)$$

$X(t)$ is the solution of $\frac{dX}{dt} = f(X)$ starting at X_0.

- An equilibrium point which has positive reactivity is reactive.
- For the linear system $\frac{dX}{dt} = AX$ there exists a perturbation which attains this maximum rate of amplification at $t = 0$.

$$\frac{d||x||}{dt} = \frac{d\sqrt{x^T x}}{dt} = \frac{x^T \frac{dx}{dt} + \frac{dx}{dt}^T x}{2||x||} = \frac{x^T(A + A^T)x}{2||x||}. \tag{4}$$

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

$$\frac{1}{||x||}\frac{d||x||}{dt} = \frac{x^T(A + A^T)x}{2||x||^2} = \frac{x^T H(A)x}{x^T x}. \tag{5}$$

$$\frac{1}{||x||}\frac{d||x||}{dt}_{t=0} = \frac{x_0^T H(A)x_0}{x_0^T x_0}. \tag{6}$$

- This ratio is termed as the *Rayleigh quotient*.

Theorem

Let $M \in M_n(\mathbb{R})$ be a Hermitian matrix, the ratio $\frac{x^T Mx}{x^T x}$ for $x \neq 0$ is maximized by the eigenvector u_1 corresponding to the largest eigenvalue $\lambda_1(M)$ and the maximum value is $\lambda_1(M)$.

- Hence the reactivity for $\frac{dX}{dt} = AX$ is defined as $\lambda_1(H(A))$ the largest eigenvalue of $H(A)$ which is the Hermitian part of A.
- For the linear systems (1) and (2), $\lambda_1(H(A_1)) = -0.79$, $\lambda_1(H(A_2)) = 3.52$, $\lambda_1(H(A_3)) = 4.15$ and $\lambda_1(H(A_4)) = -0.49$.
- Hence the equilibrium 0 is reactive for the linear system $\frac{dX}{dt} = AX$ with $A = A_2$ or A_3. It is not reactive for $A = A_1$ or A_4.
- The reactivity is a measure for $t = 0$ and resilience is a measure for $t \to \infty$.
- This doesn't give any information on the behaviour of the perturbation between the time interval 0 and ∞.

Definition

The **amplification envelope** is defined as

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

$X(t)$ is the solution of $\frac{dX}{dt} = f(X)$ with $X(0) = X_0$.

For the linear system $\frac{dX}{dt} = AX$, $\rho(t)$ is given by

$$\rho(t) = max_{||x_0||\neq 0}\left[\frac{||e^{At}x_0||}{||x_0||}\right] = \left|\left|\left|e^{At}\right|\right|\right|. \tag{7}$$

- The maximum amplification ρ_{max} is defined as

$$\rho_{max} = max_{t\geq 0}\rho(t). \tag{8}$$

- The t_{max} is the time at which maximum amplification is attained

$$\rho(t_{max}) = \rho_{max}. \tag{9}$$

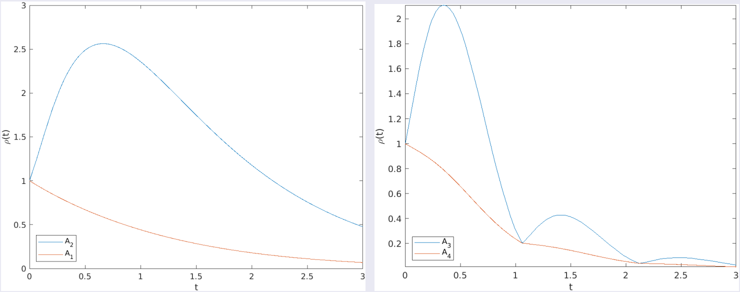

Figure: The amplification envelopes of the linear system $\frac{dX}{dt} = AX$ for A is the matrix A_1 through A_4. A_2 and A_3 have an initial growth, indicating that A_2 ($reactivity = 3.52$) and A_3($reactivity = 4.15$) are reactive. The envelopes for A_1 and A_4 have a decay, hence A_1($reactivity = -0.79$) and A_4 ($reactivity = -0.49$) are not reactive.

Compartment model: Aquatic food chain model

- Compartment model describes the flow of some quantity eg: nutrients, matter or energy from one compartment to another.
- The flow rate from compartment j to compartment i is proportional to the amount of material in the donor compartment j and the proportionality constant is given by a_{ij}.
- The Tuesday lake ecosystem in Winsconsin, dominated by planktivorous minnows in 1984, was altered by Carpenter et. al by introducing a new trophic level of piscivorous largemouth bass in 1985.
- The rate of transfer of phosphorous from one compartment to another compartment was measured by Carpenter et. al(1992) for both 1984 and 1986.

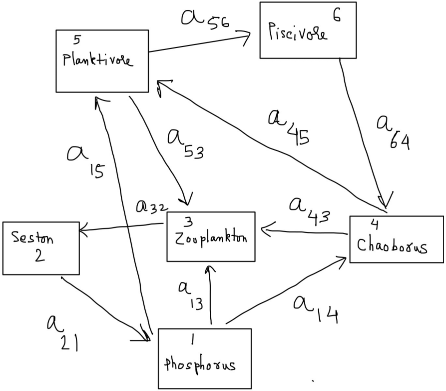

Figure: Phosphorus transfer in aquatic food chain model

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$$\frac{dy_i}{dt} = \sum_{j=1}^{n} a_{ij} y_j \quad i = 1, ..., n \tag{10}$$

with initial conditions

$$y_i(0) = y_{0_i} \quad i = 1, 2..., n \tag{11}$$

The fractional rate of input from other compartments to compartment i is $a_{ij} \geq 0$ and the fractional rate of output from the compartment i is $a_{ii} \leq 0$. In the matrix form

$$\frac{d\boldsymbol{y}}{dt} = \boldsymbol{A}\boldsymbol{y} \quad \boldsymbol{y}(0) = \boldsymbol{y}_0 \tag{12}$$

The matrix $\boldsymbol{A} = (a_{ij})$ is the transfer matrix.

Table: Phosphorous transfer matrix of Tuesday lake before and after addition of piscivorous fish(cf. Caswell and Neubert 1997).

Compartment		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}.

- The eigenvalues of the 1984 matrix are -0.9491, -0.5922, -0.2624, -0.1742, -0.0388. Hence the resilience is 0.0388. The reported value of the resilience by Neubert and Caswell(1997) is 0.035.
- 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.
- The resilience decreased by $\frac{1}{7}$ of the value at 1984. 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 $\boldsymbol{A}_1$ are -1.2783, -0.3301, -0.2609, -0.1097, -0.0377. Hence the reactivity is $\lambda_1(H(\boldsymbol{A}_1)) = -0.0377$. The reported value of reactivity by Neubert and Caswell is 0.148.
- The eigenvalues of the symmetric part of the 1986 transfer matrix $\boldsymbol{A}_2$ are -1.1767, -0.2865, -0.0127, -0.0072, -0.0047, 0.0694, hence the reactivity is $\lambda_1(H(\boldsymbol{A}_2)) = 0.0694$.
- $\boldsymbol{A}_1$ is *not reactive* and $\boldsymbol{A}_2$ is reactive.

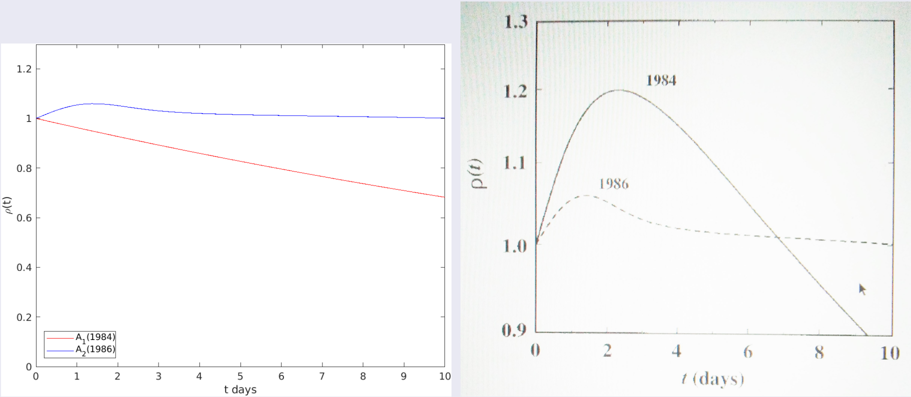

Figure: (a)The amplification envelope for the 1984 and 1986 matrices. (b) The amplification envelopes of 1984 and 1986 matrices from Caswell and Neubert (1997).

- Let the transfer matrix $\boldsymbol{A} = (a_{ij})$ have distinct eigenvalues.
- The matrix of the **sensitivity of the resilience** to changes in the flow rate a_{ij} is given by

$$\left(\frac{dresilience}{da_{ij}}\right) = -Re\left(\frac{vw^T}{v^Tw}\right). \tag{13}$$

  v and w are the respective left and right eigenvectors corresponding to the eigenvalue $\lambda_1(\boldsymbol{A})$ which has the largest real part.
- Let $\boldsymbol{A}$ be the transfer matrix. Let w be the right eigenvector corresponding to the eigenvalue $\lambda_1(\boldsymbol{A})$ hence $\boldsymbol{A}w = \lambda_1(\boldsymbol{A})w$.

$$(\boldsymbol{A} + \Delta\boldsymbol{A})(w + \Delta w) = (\lambda_1(\boldsymbol{A}) + \Delta\lambda_1(\boldsymbol{A}))(w + \Delta w). \tag{14}$$

- Neglecting the terms $\Delta\boldsymbol{A}\Delta w$ and $\Delta\lambda_1(\boldsymbol{A})\Delta w$

$$\boldsymbol{A}\Delta w + (\Delta\boldsymbol{A})w = \lambda_1(\boldsymbol{A})\Delta w + (\Delta\lambda_1(\boldsymbol{A}))w. \tag{15}$$

- Let v be the left eigenvector of $\boldsymbol{A}$ hence $v^T\boldsymbol{A} = v^T\lambda_1(\boldsymbol{A})$

$$v^T\boldsymbol{A}\Delta w + v^T(\Delta\boldsymbol{A})w = v^T\lambda_1(\boldsymbol{A})\Delta w + (\Delta\lambda_1(\boldsymbol{A}))v^T w. \quad (16)$$

$$v^T\lambda_1(\boldsymbol{A})\Delta w + v^T(\Delta\boldsymbol{A})w = v^T\lambda_1(\boldsymbol{A})\Delta w + (\Delta\lambda_1(\boldsymbol{A}))v^T w. \quad (17)$$

$$v^T(\Delta\boldsymbol{A})w = (\Delta\lambda_1(\boldsymbol{A}))v^T w. \quad (18)$$

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

$$v_i(\Delta a_{ij})w_j = (\Delta\lambda_1(\boldsymbol{A}))v^T w. \quad (19)$$

- Hence $\frac{d\lambda_1(\boldsymbol{A})}{da_{ij}} = \frac{v_i w_j}{v^T w}$. The matrix of the sensitivities is given by $\left(\frac{d\lambda_1(\boldsymbol{A})}{da_{ij}}\right) = \frac{vw^T}{v^T w}$.
- Since the resilience is $-Re(\lambda_1(\boldsymbol{A}))$, the matrix of resilience sensitivities is given by $\left(\frac{dresilience}{da_{ij}}\right) = -Re\left(\frac{vw^T}{v^T w}\right)$.

Table: Sensitivities of resilience to changes in the flow rates of phosphorous in the Tuesday lake ecosystem.(b) Sensitivities of resilience calculation from 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 $-Re\left(\frac{vw^T}{v^T w}\right)$ 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.

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TABLE 5. Sensitivities of resilience to changes in the elements of the Tuesday Lake phosphorus transfer matrices.

Variable and number		1	2	3	4	5	6
1984							
Soluble phosphorus	1	−0.0038		−0.0194	−0.0278	−0.1199	
Seston	2	−0.0037	−0.1465				
Zooplankton	3		−0.1203	−0.0154			
Chaoborus	4			−0.0033	−0.0047		
Planktivore	5			−0.1345	−0.1921	−0.8296	
1986							
Soluble phosphorus	1	−0.0001		−0.0002	−0.0021	−0.0001	−0.0120
Seston	2	−0.0001	−0.0003				
Zooplankton	3		−0.0004	−0.0002			
Chaoborus	4			−0.0003	−0.0034		
Planktivore	5			−0.0058	−0.0644	−0.0032	
Piscivore	6				−0.1715	−0.0084	−0.9929

Predator Prey model

- The prey population follows a logistic growth in the absence of predator. The intake rate of a consumer follows a holling type II response

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}) - \frac{aNP}{N + b} \tag{20}$$

$$\frac{dP}{dt} = \frac{caNP}{N + b} - dP \tag{21}$$

- 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), d is the mortality rate (unit t^{-1}).

- By using the change of variables

$$y_1 = \frac{N}{b} \quad y_2 = \frac{aP}{rb} \quad \tau = rt \quad k = \frac{K}{b} \quad \alpha = \frac{ac}{r} \quad \beta = \frac{d}{ac} \tag{22}$$

The equation takes a dimensionless form

$$\frac{dy_1}{d\tau} = y_1\left(1 - \frac{y_1}{k}\right) - \frac{y_1 y_2}{(y_1 + 1)} \tag{23}$$

$$\frac{dy_2}{d\tau} = \alpha\left(\frac{y_1 y_2}{y_1 + 1} - \beta y_2\right) \tag{24}$$

- α is the maximum growth rate of predator and β is the mortality rate of predator.

- We will consider the equillibrium where prey and predator coexists

$$(y_1^*, y_2^*) = \left(\frac{\beta}{1-\beta}, \frac{1}{1-\beta}\left(1 - \frac{\beta}{k(1-\beta)}\right)\right) \tag{25}$$

- The linearization of the system gives us the form

$$\begin{bmatrix} \frac{dy_1}{d\tau} \\ \frac{dy_2}{d\tau} \end{bmatrix} = \begin{bmatrix} \left(1 - 2\frac{\beta}{k(1-\beta)} - \frac{1}{1-\beta}\left(1 - \frac{\beta}{k(1-\beta)}\right)\right) & -\beta \\ \frac{\alpha}{1-\beta}\left(1 - \frac{\beta}{k(1-\beta)}\right) & 0 \end{bmatrix} \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} \tag{26}$$

- For the equilibrium point to be asymptotically stable i.e $Re(\lambda_i) < 0$ for $i = 1, .., n$ it can be deduced that k and β should satisfy

$$\frac{k-1}{2} < \frac{\beta}{1-\beta} < k \tag{27}$$

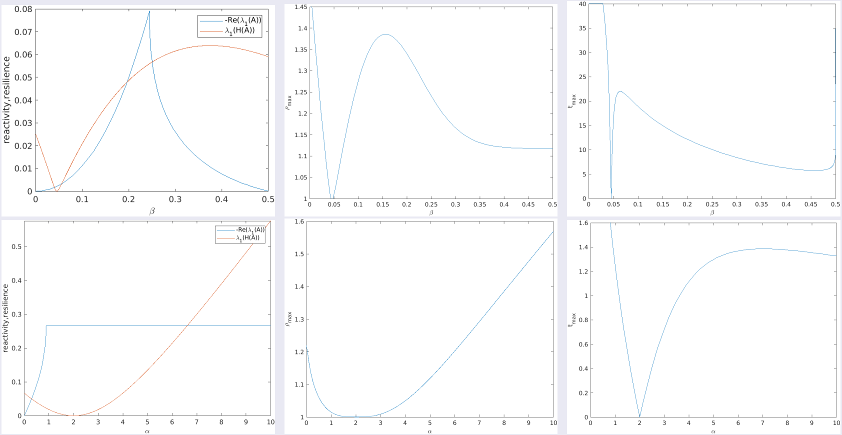

Figure: Figures depicting variation of measures of perturbation as a function of predator mortality rate β and the maximum predator growth rate α. For the figures in first row α is fixed and is equal to 0.05. For the second row β is fixed and $\beta = 0.4$. $k = 1$ is a constant throughout.

Drawbacks of the proposed measures

- Most of the ecological theories deals with asymptotic behavior.
- Asymptotic behavior can be easily described by the dominant eigenvalues of the matrix.
- The solutions of the linearization is valid for a small neighbourhood around the equilibrium point. Hence the desire to find the asymptotic behavior of solutions.
- The proposed measures gives some idea about the transient behaviour of the effects of a perturbation.
- In some reactive systems majority of perturbations may decay monotonically.
- The amplification envelope and its characteristics are the 'worst case measures' of the effects of perturbations.

References

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