Transient dynamics in equilibrium and non-equilibrium communities

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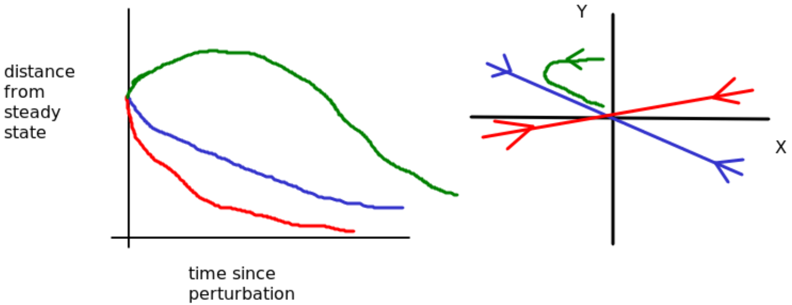
Natural and human disturbances



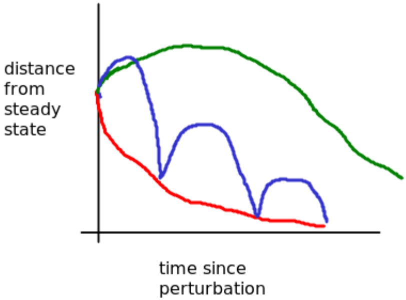

Transients: How does a system respond to a one-time disturbance?

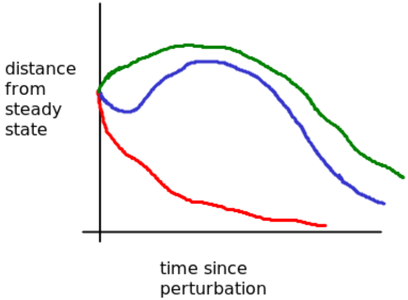
Perturbations from a stable steady state



- How does an equilibrium community respond to a perturbation?
- How long will it take to return to equilibrium?
- How far from equilibrium will it get along the way?

More possibilities





- Eventual decay rate?
- Initial growth or decline?
- Maximal possible deviation?

Concept: Reactivity

- Mathematical set-up: Reactivity
    - Reactivity for steady states in ODEs (Neubert and Caswell 1997) > 300 citations
    - Reactivity for steady states of maps (Caswell and Neubert 2005)
    - Reactivity is necessary for diffusion-driven instability (Neubert et al 2002)
- Reactivity for periodically forced models (Vesipa and Rudolfi 2017) + new results
- Reactivity for intrinsically generated cycles new thoughts



Model set-up

Dynamic equations

$$\frac{\mathrm{d}\mathbf{x}(t)}{\mathrm{d}t} = \mathbf{F}(\mathbf{x}(t)), \qquad \mathbf{x} \in \mathbb{R}^n.$$

Steady state

$$\mathbf{F}(\mathbf{x}^*) = 0.$$

Linearization

$$\frac{\mathrm{d}\mathbf{y}(t)}{\mathrm{d}t} = D\mathbf{F}(\mathbf{x}^*)\mathbf{y}(t) = \mathbf{A}\mathbf{y}(t), \qquad \mathbf{y}(0) = \mathbf{y}_0,$$

Stability assumption:

$$\Re\lambda_1(\mathbf{A}) < 0$$

Resilience and reactivity

Resilience: slowest return rate to steady state (Pimm and Lawton 1977)

$$R := -\Re\lambda_1(\mathbf{A}) > 0$$

Return time $1/R$

Reactivity: maximal instantaneous growth rate (Neubert and Caswell 1997)

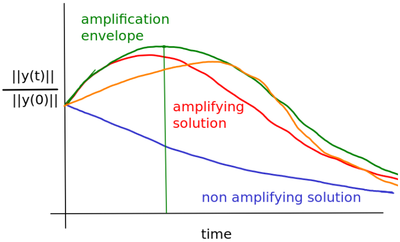
$$\sigma := \max_{\|\mathbf{y}_0\|\neq 0}\left[\left(\frac{1}{\|\mathbf{y}(t)\|}\frac{\mathrm{d}\|\mathbf{y}(t)\|}{\mathrm{d}t}\right)\Bigg|_{t=0}\right]$$

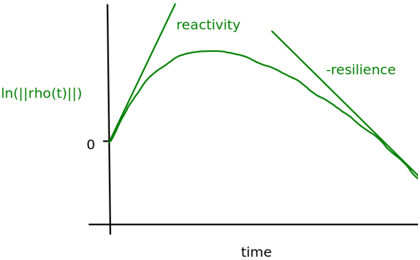
Amplification envelope: maximum growth at time t (Neubert and Caswell 1997)

$$\rho(t) = \max_{\|\mathbf{y}_0\|\neq 0}\frac{\|\mathbf{y}(t)\|}{\|\mathbf{y}_0\|}$$

Illustration

$$\frac{d\mathbf{y}}{dt} = \mathbf{A}\mathbf{y} \qquad \rho(t) = \max_{\|\mathbf{y}_0\| \neq 0} \frac{\|\mathbf{y}(t)\|}{\|\mathbf{y}_0\|}$$





$$\sigma = \frac{d}{dt}\ln(\rho(t))_{|t=0}, \qquad R = -\frac{d}{dt}\ln(\rho(t))_{|t=\infty}.$$

Observations

- Scalar systems cannot be reactive.
- Reactivity and resilience have no correlation.
- Reactivity depends on chosen norm, stability does not.
- Reactivity depends on scaling!
- In the L^2 norm, we have $\sigma = \lambda_1(A + A^\top)/2$.
- We also have $\rho(t) = |||\exp(At)|||$.

Examples

Lotka-Volterra type models

$$\dot{N} = rN(1 - N/K) - g(N)P$$

$$\dot{P} = eg(N)P - mP$$

Leslie model

$$\dot{N} = rN(1 - N/K) - cNP$$

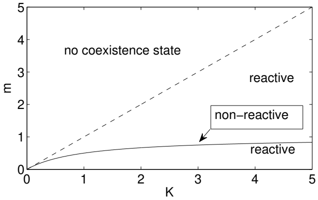
$$\dot{P} = sP(1 - qP/N)$$

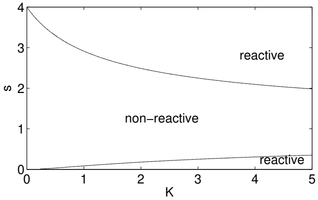
Linearization

$$A = \begin{bmatrix} a_1 & a_2 \\ a_3 & a_4 \end{bmatrix}$$

Reactivity

$$\sigma > 0 \quad \Leftrightarrow \quad 4a_1 a_4 < (a_2 + a_3)^2$$

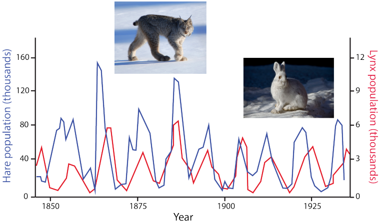




Beyond equilibrium?

- External forcing: seasonality

- Internal generation: predator–prey cycles



Is there a “good" time to perturb an oscillating system?

Seasonally forced systems

Dynamic equations with T-periodic forcing $\mathbf{F}(t,\cdot) = \mathbf{F}(t+T,\cdot)$

$$\frac{\mathrm{d}\mathbf{x}(t)}{\mathrm{d}t} = \mathbf{F}(t,\mathbf{x}(t)), \qquad \mathbf{x} \in \mathbb{R}^n.$$

T-periodic orbit

$$\gamma(t+T) = \gamma(t)$$

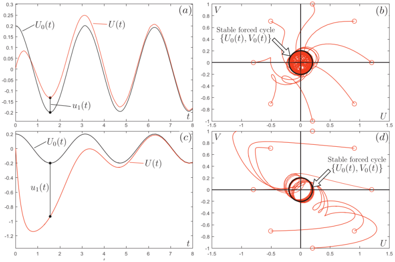
Linearization

$$\frac{\mathrm{d}\mathbf{y}(t)}{\mathrm{d}t} = D\mathbf{F}(\gamma(t))\mathbf{y}(t) = \mathbf{A}(t)\mathbf{y}(t), \qquad \mathbf{y}(t_0) = \mathbf{y}_0, \quad 0 \le t_0 \le T$$

Stability assumption via Poincaré map (independent of t_0)

Transients for seasonally forced systems?

Vesipa and Ridolfi (2017)



- Define σ, ρ as before $\sigma := \max_{\|\mathbf{y}_0\|\neq 0}\left[\left(\frac{1}{\|\mathbf{y}(t)\|}\frac{\mathrm{d}\|\mathbf{y}(t)\|}{\mathrm{d}t}\right)\Big|_{t=0}\right]$
- Numerical scheme for amplification envelope

Dependence on initial time

Local reactivity

$$\sigma_L(t_0) := \max_{\|\mathbf{y}_0\|\neq 0} \left[\left(\frac{1}{\|\mathbf{y}(t)\|} \frac{\mathrm{d}\|\mathbf{y}(t)\|}{\mathrm{d}t} \right) \Bigg|_{t=t_0} \right], \quad 0 \leq t_0 \leq T$$

Local amplification envelope

$$\rho_L(t, t_0) = \max_{\|\mathbf{y}_0\|\neq 0} \frac{\|\mathbf{y}(t)\|}{\|\mathbf{y}_0\|}$$

Relations as before:

$$\sigma_L(t_0) = \lambda_1(H(\mathbf{A}(t_0))), \qquad \sigma_L = \sigma_L(t_0) = \frac{\mathrm{d}}{\mathrm{d}t} \ln(\rho_L(t, t_0))_{|t=t_0}.$$

The periodically forced logistic equation

$$\frac{\mathrm{d}x(t)}{\mathrm{d}t} = rx(t)[1 - x(t)/K(t)]$$

Explicit expression for $\gamma(t)$

Linearization

$$\frac{\mathrm{d}y(t)}{\mathrm{d}t} = r[1 - 2\gamma(t)/K(t)]y(t), \qquad y(t_0) = y_0,$$

Explicit solution

$$y(t) = y(t_0)\exp\left(\int_{t_0}^{t} r[1 - 2\gamma(s)/K(s)]\mathrm{d}s\right).$$

Local amplification envelope

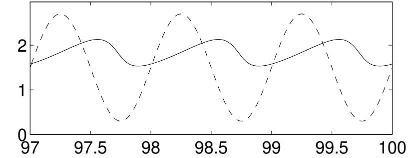
$$\rho_L(t, t_0) = \max_{|y_0| \neq 0} \frac{|y(t)|}{|y_0|} = \exp\left(\int_{t_0}^{t} r[1 - 2\gamma(s)/K(s)]\mathrm{d}s\right)$$

The periodically forced logistic equation II

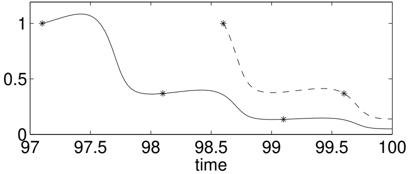
Local reactivity

$$\sigma_L(t_0) = \frac{\mathrm{d}}{\mathrm{d}t} \ln(\rho_L(t, t_0))_{|t=t_0} = r[1 - 2\gamma(t_0)/K(t_0)].$$

$\gamma(t)$ (solid)
$K(t)/2$ (dashed)



Amplification envelope from two initial times



Global quantities?

1. Maximum of local reactivity

$$\sigma_M = \max_{0 \le t \le T} \sigma_L(t)$$

   In the spirit of “worst cases analysis”

2. Period map $\mathbf{z}_n = \mathbf{x}(nT)$

$$\mathbf{z}_{n+1} = \mathbf{P}(\mathbf{z}_n)$$

   Linearize

$$\mathbf{w}_{n+1} = D\mathbf{P}(\gamma(t_0))\mathbf{w}_n = \mathbf{B}(t_0)\mathbf{w}_n$$

   Stability of γ given by eigenvalues of $\mathbf{B}$ (independent of t_0)

Period reactivity

For the period map

$$\mathbf{w}_{n+1} = \mathbf{B}(t_0)\mathbf{w}_n$$

Define the period reactivity (as in Caswell and Neubert 2005)

$$\sigma_P := \ln\left(\max_{\|\mathbf{w}_0\|\neq 0} \frac{\|\mathbf{w}_1\|}{\|\mathbf{w}_0\|}\right) = \ln\left(\max_{\|\mathbf{w}_0\|\neq 0} \frac{\|\mathbf{B}\mathbf{w}_0\|}{\|\mathbf{w}_0\|}\right).$$

With L^2-norm:

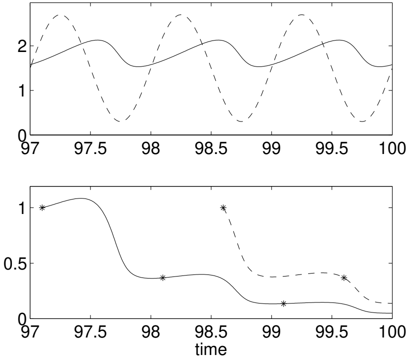
$$\sigma_P : = \sigma_P(t_0) = \ln\left(\sqrt{\lambda_1(\mathbf{B}^T\mathbf{B})}\right).$$

Largest singular value, depends on t_0!

Forced logistic equation: continued

$$z_{n+1} = P(z_n) = \frac{z_n \mathrm{e}^{rT}}{1 + z_n a(t_0)}, \qquad a(t_0) = \int_{t_0}^{t_0+T} \frac{r\mathrm{e}^{r(s-t_0)}}{K(s)} \mathrm{d}s.$$

$$\sigma_P = -rT < 0$$



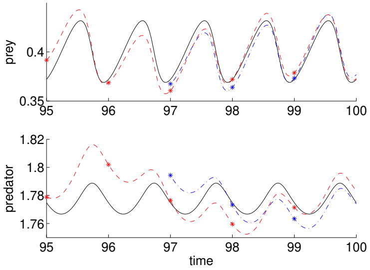
Observation:
A periodic orbit of a scalar periodically forced equation cannot be period reactive.

The forced Lotka–Volterra model

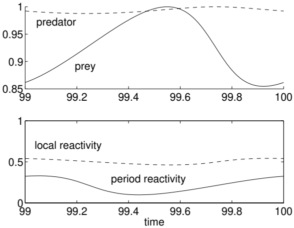
$$\dot{x} = rx[1 - x/K(t)] - cxy$$
$$\dot{y} = ecxy - my$$

with

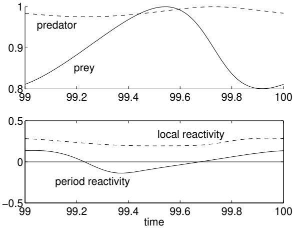
$$K(t) = K_m + K_a \sin(2\pi t).$$



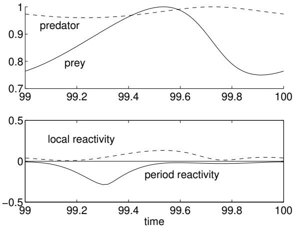
The forced Lotka–Volterra model



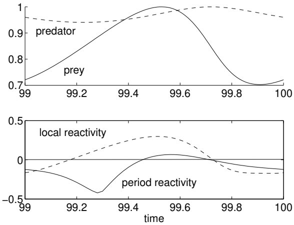
$m = 0.5$



$m = 0.7$



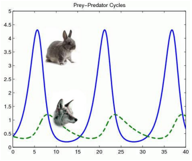
$m = 0.9$



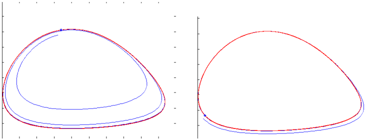
$m = 1.1$

Reactivity of periodic orbits in autonomous systems

- Same as forced cycles ?



Distance from periodic orbit ?



Distance in phase ?

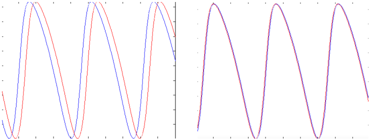
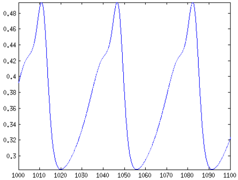


Illustration with Rosenzweig MacArthur model

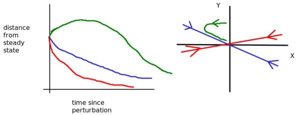
Period-reactive orbit in a food chain model?

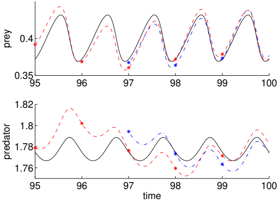


- Locally reactive ! Period reactive ?
- Period reactivity is never negative
- Eliminate the direction of the periodic orbit
- Observation: A planar periodic orbit is not period reactive
- Tri-trophic food chain can be period reactive

Summary

- Reactivity of steady states
  - depends on scaling
  - no relationship to resilience
- Reactivity of forced periodic orbits
  - local and period reactivity
  - requires at least 2D
- Reactivity of autonomous periodic orbits
  - Direction of the periodic orbit?
  - requires at least 3D
  - no simple formulas
  - even numerically not easy





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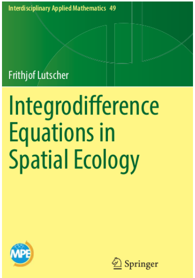
Upcoming book:



Upcoming position:
Tenure-track position in applied mathematics at University of Ottawa

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