Pre-extinction Dynamics in Stochastic Populations

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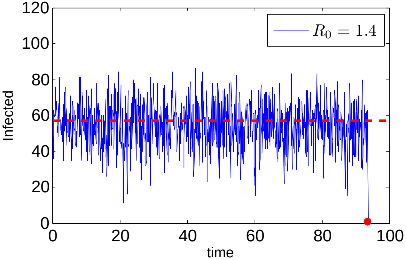
The Problem

There has been a significant amount of work to understand extinction in simple epidemiological systems. (Doering, et al., Multiscale Model. Simul. (2005); Dykman et al, PRL 101 (2008); Schwartz et al, J Stat Mech, P01005 (2009).)



Extinction by escape from a potential well.

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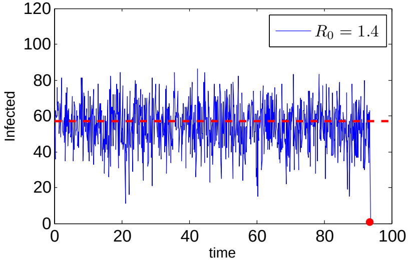

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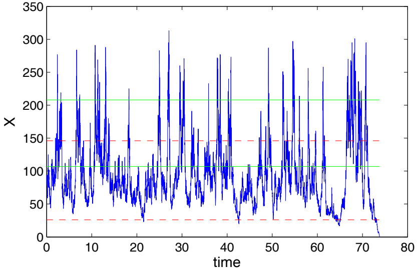

Switching/cycling before extinction...

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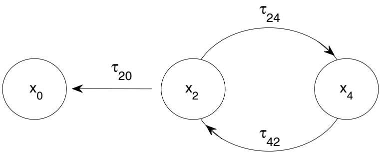
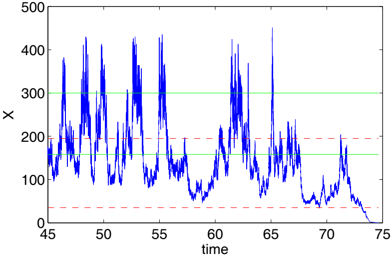


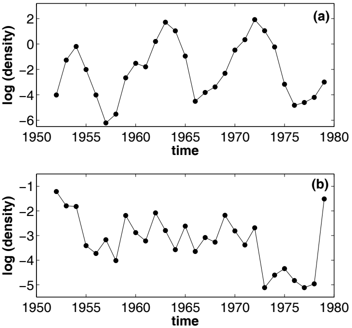
Simple cycling before extinction (x_0)



Switching/cycling before extinction...

Goal: We want to extend this understanding of extinction to stochastic dynamics on a network and develop optimal control methods.

An example of switching from ecology



Berryman, "What causes population cycles of forest lepidoptera," *Trends in Ecology & Evolution* (1996)

Population density fluctuations of Lepidoptera feeding on larch foliage in the Oberengadin Valley of Switzerland.

(a) Exapate duratella (Tortricidae), the fluctuations may be regular, but not seasonal.

(b) Teleia saltuum (Gelechidae), there is a switch between two steady states, with an activation time approximately an order of magnitude larger than the relaxation time.

The drastic population shifts are attributed to a mix of parasitoids, viral outbreak among the moths, and the quality of the available foliage.

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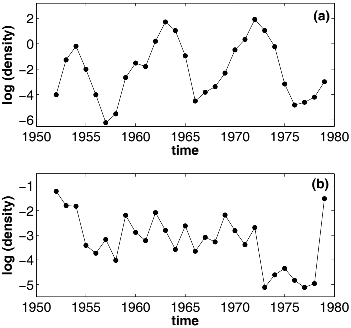

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Can we predict extinction in cycling systems?

Outline

- Simple model demonstrating the methods (Allee effect)
  - Stochastic master equation, optimal path
  - Analytical approximation for mean extinction time
- Pre-extinction cycling dynamics in a single population
  - Extinction prediction
  - Quantifying control measures
- Extinction in multiple interconnected populations
  - Using the optimal path for mean extinction time
  - Pre-extinction dynamics in metapopulations: cycling?
- Conclusions

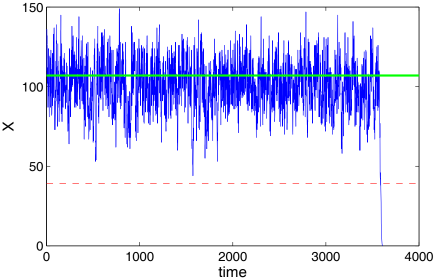
Stochastic modeling

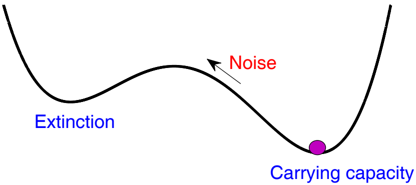
We assume a finite population.

Internal noise: randomness in the demography, birth-death interactions in the system

Analogous to arbitrarily small noise inducing escape of a particle from a potential well.

Other effects can be captured by different stochastic sources such as external noise.





Master Equation Approach

Often used in biological and chemical kinetics and population dynamics.

Consider a well-mixed finite population of size N

- Discrete state vector $\mathbf{X} = (x_1, x_2, \ldots, x_n)$.
- Random state transition rates: $W(\mathbf{X}, \mathbf{r})$.
- Probability $\rho(\mathbf{X}, t)$ of finding the system in state $\mathbf{X}$ at time t:

The master equation definition

$$\frac{\partial \rho(\mathbf{X}, t)}{\partial t} = \sum_{\mathbf{r}} [\underbrace{W(\mathbf{X} - \mathbf{r}; \mathbf{r})\rho(\mathbf{X} - \mathbf{r}, t)}_{\substack{\text{the gain to state } \mathbf{X} \\ \text{from state } \mathbf{X}\text{-}\mathbf{r}}} - \underbrace{W(\mathbf{X}; \mathbf{r})\rho(\mathbf{X}, t)}_{\substack{\text{the loss of state } \mathbf{X} \\ \text{to other states}}}].$$

It is the gain-loss equation for the probabilities of the separate states **X**.

Van Kampen, N.G., Stochastic processes in physics and chemistry, Elsevier (1992).

Approximating switching/extinction events

The master equation

$$\frac{\partial \rho(\mathbf{X},t)}{\partial t} = \sum_{\mathbf{r}} [W(\mathbf{X}-\mathbf{r};\mathbf{r})\rho(\mathbf{X}-\mathbf{r},t) - W(\mathbf{X};\mathbf{r})\rho(\mathbf{X},t)].$$

Assume the Eikonal approximation:

$$\rho(\mathbf{X},t) = \exp(-N\mathcal{S}(\mathbf{q})), \text{ for } \mathbf{q} = \mathbf{X}/N.$$

Since $\mathcal{S}$ satisfies the PDE of Hamilton-Jacobi form:

$$\frac{\partial \mathcal{S}}{\partial t} + H\left(\mathbf{q}, \frac{\partial \mathcal{S}}{\partial \mathbf{q}}\right) = 0,$$

$\mathcal{S}$ is known as the action, and the Hamiltonian is given by

$$H(\mathbf{q};\mathbf{p}) = \sum_{\mathbf{r}} w(\mathbf{q};\mathbf{r})[\exp(\mathbf{p}\cdot\mathbf{r}) - 1]$$

Define the conjugate momenta $\mathbf{p} = \partial\mathcal{S}/\partial\mathbf{q}$.

We assume the distribution is **quasi-stationary**, $\frac{\partial \mathcal{S}}{\partial t} = 0$. (Rare event)

Kubo, et al., J. Stat. Phys. 9 (1973); Gang, PRA, 36 (1987); Dykman, et al., J. Chem Phys, 100 (1994); Elgart, et al., PRE, 70 (2004); and many others.

The most likely observed paths to extinction

The shape of the distribution is described by Hamilton's eqns:

$$\begin{aligned} \dot{\mathbf{q}} &= \partial_{\mathbf{p}} H(\mathbf{q}, \mathbf{p}; t), \\ \dot{\mathbf{p}} &= -\partial_{\mathbf{q}} H(\mathbf{q}, \mathbf{p}; t), \end{aligned}$$

We study this **deterministic** system to describe the dynamics of the **stochastic** system.

Cost: it doubles the dimension of the system

Benefit: Heteroclinic trajectories connect the saddle steady states

Call the manifold connected to the desired state the optimal path, $p_{opt}(q)$, where the action is minimized so that the probability (ρ) is maximized.

Find the action along the path

$$\mathcal{S}_{opt} = \int_{q_2}^{q_1} p_{opt}(q) dq$$

to approximate the mean time to extinction (MTE):

$$MTE = B\, e^{N\mathcal{S}_{opt}}$$

Basic model for Allee effect

The Allee effect describes the dynamics of populations that benefit from conspecific cooperation. (Allee, Animal aggregations (1931))

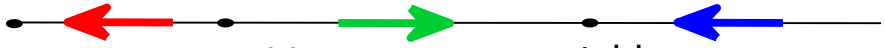
The population performs better in larger numbers because they are more capable of avoiding predation, can reproduce faster, and are able to resist toxic environmental conditions. The growth rate is negative for low densities.

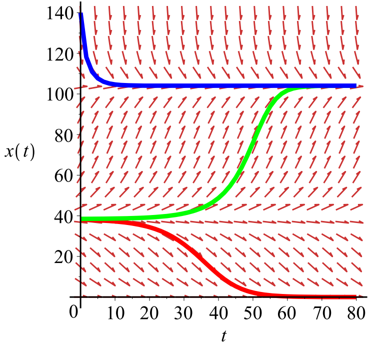
Parameters

μ - death rate of a low-density population
λ - growth rate of a large population
σ - death rate when overcrowded
K - carrying capacity

Basic model: (deterministic)

$\dot{x} = -\frac{\sigma}{6}x^3 + \frac{\lambda}{2}x^2 - \mu x.$

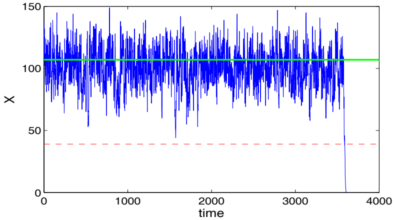




$\mu = 0.2$, $\sigma = 3.0$, $\lambda = 1.425$

The stochastic Allee model - Topology

Transition	W(X;r)
$X \xrightarrow{\mu} \varnothing$	μX
$2X \xrightarrow{\lambda/K} 3X$	$\lambda\frac{X(X-1)}{2K}$
$3X \xrightarrow{\sigma/K^2} 2X$	$\sigma\frac{X(X-1)(X-2)}{6K^2}$



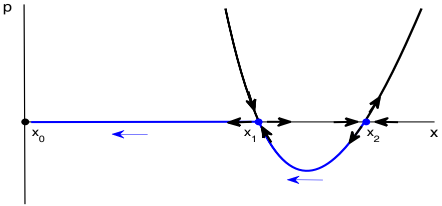
Find the Hamiltonian. Scale the system by K, so $X = Kx$.

$$\mathcal{H}(x,p) = \frac{\lambda x^2}{2}(e^p - 1) + \left(\mu x + \frac{\sigma x^3}{6}\right)(e^{-p} - 1)$$

Find the zero-energy phase trajectories ($\mathcal{H} = 0$):

$$x = 0, \quad p = 0,$$

$$p_{opt}(x) = \ln\left(\frac{6\mu + \sigma x^2}{3\lambda x}\right)$$



The stochastic Allee model - MTE

Hamilton's equations:

$$\dot{x} = \frac{\lambda x^2}{2} e^p - \left(\mu x + \frac{\sigma x^3}{6} \right) e^{-p}$$

$$\dot{p} = -\lambda x (e^p - 1) - \left(\mu + \frac{\sigma x^2}{2} \right) (e^{-p} - 1)$$

The Hamiltonian system has three steady states on the line $p = 0$:

$$x_0 = 0, \quad x_{1,2} = \frac{3\lambda \mp \sqrt{9\lambda^2 - 24\sigma\mu}}{2\sigma}$$

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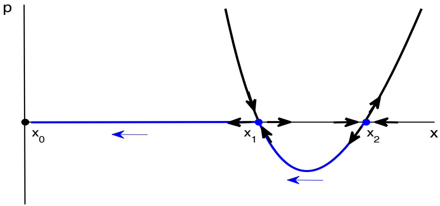

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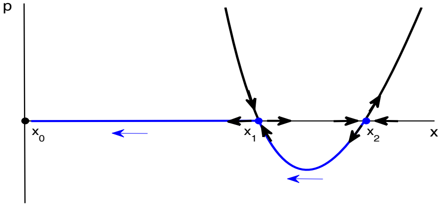
$$\mathcal{S}_{opt} = \int_{x_2}^{x_1} \ln\left(\frac{6\mu + \sigma x^2}{3\lambda x}\right) dx$$

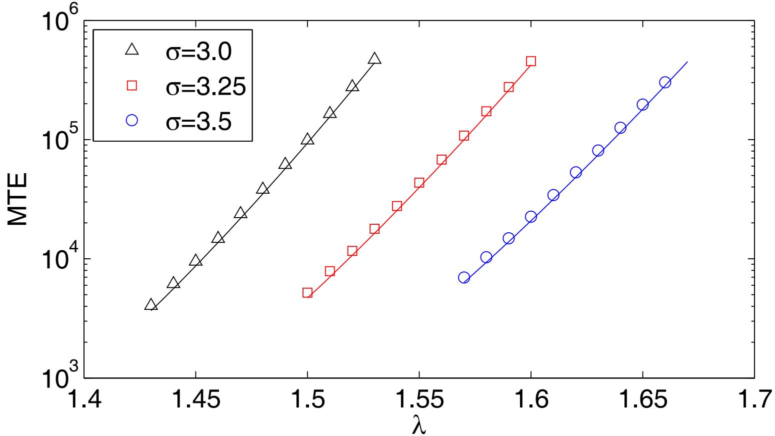
Mean time to extinction*:

$$MTE = B\, e^{K \mathcal{S}_{opt}}$$



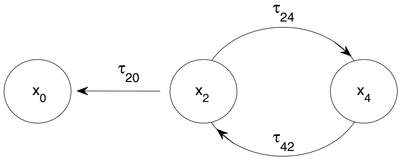
*Assaf and Meerson, Extinction of metastable stochastic populations. Phys. Rev. E (2010)

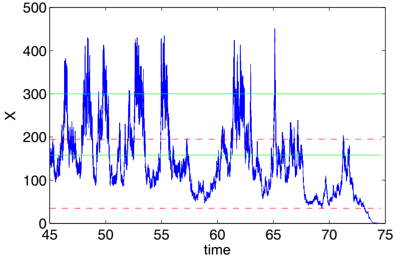
Allee model: analytical prediction vs. numerical simulation



Mean time to extinction for an initial population of X_2.
The curves are the analytical approximation
The symbols represent numerical simulation results (10,000 realizations)
Parameters: $\mu = 0.2$ and $K = 100$, σ and λ are varied.

The cycling model

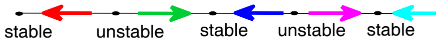


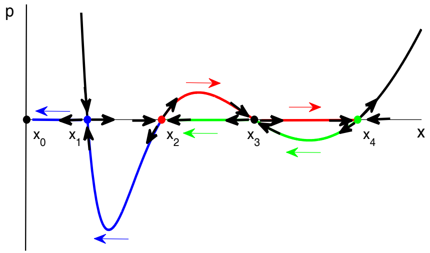


Add another steady state x_4 (builds on the previous model)

Deterministic model:

$$\dot{x} = -\frac{\beta}{120}x^5 + \frac{\alpha}{24}x^4 - \frac{\sigma}{6}x^3 + \frac{\lambda}{2}x^2 - \mu x$$





The cycling model - Topology

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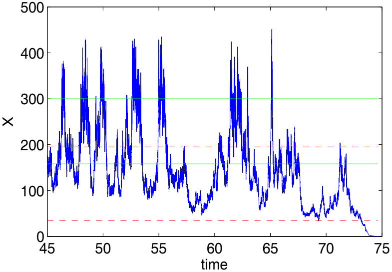
$X \xrightarrow{\mu} \varnothing$	$\mu X,$
$2X \xrightarrow{\lambda/K} 3X$	$\lambda \frac{X(X-1)}{2K}$
$3X \xrightarrow{\sigma/K^2} 2X$	$\sigma \frac{X(X-1)(X-2)}{6K^2}$
$4X \xrightarrow{\alpha/K^3} 5X$	$\alpha \frac{X(X-1)(X-2)(X-3)}{24K^3}$
$5X \xrightarrow{\beta/K^4} 4X$	$\beta \frac{X(X-1)(X-2)(X-3)(X-4)}{120K^4}$

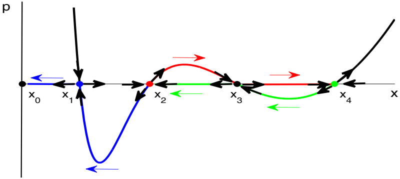


Find the Hamiltonian ($X = Kx$):

$$\mathcal{H}(x,p) = \left(\frac{\lambda x^2}{2} + \frac{\alpha x^4}{24}\right)(e^p - 1) + \left(\mu x + \frac{\sigma x^3}{6} + \frac{\beta x^5}{120}\right)(e^{-p} - 1)$$

Zero-energy phase trajectories ($\mathcal{H} = 0$):
$x = 0, p = 0$, and

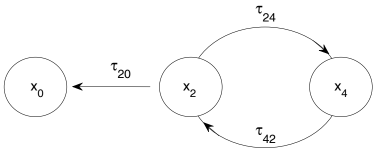
$$p_{opt}(x) = \ln\left(\frac{120\mu + 20\sigma x^2 + \beta x^4}{5x\,(\alpha x^2 + 12\lambda)}\right),$$



The cycling model - MTE

The probability of the population switching from x_2 to x_0 before switching from x_2 to x_4

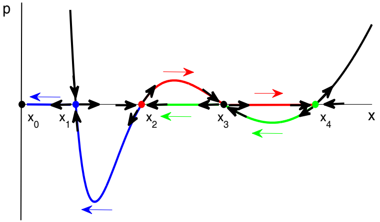
$$\mathcal{P}_{20} = \frac{\frac{1}{\tau_{20}}}{\frac{1}{\tau_{20}} + \frac{1}{\tau_{24}}} = \frac{\tau_{24}}{\tau_{20} + \tau_{24}}.$$



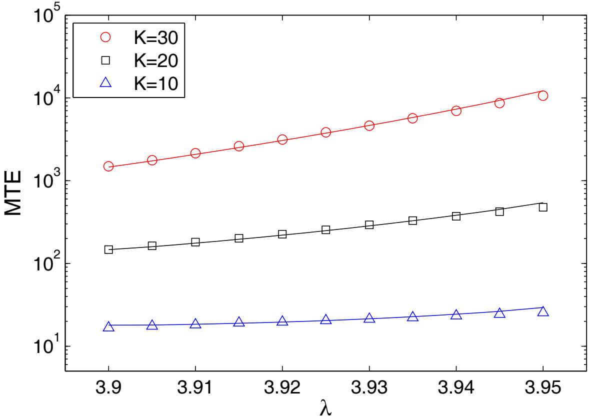
Also, $\mathcal{P}_{24} = 1 - \mathcal{P}_{20}$.

The MTE becomes the sum of the expected times for all possible number of cycles to occur and the final escape from x_2 to x_0:

$$\begin{aligned} \mathrm{MTE} &= \tau_{20}\mathcal{P}_{20} + \sum_{i=0}^{\infty} i(\tau_{24} + \tau_{42})(\mathcal{P}_{24})^i \mathcal{P}_{20} \\ &= \tau_{20}\mathcal{P}_{20} + \frac{(\tau_{24} + \tau_{42})\mathcal{P}_{24}}{\mathcal{P}_{20}} \\ &= \frac{\tau_{20}\tau_{24}}{\tau_{20} + \tau_{24}} + (\tau_{24} + \tau_{42})\frac{\tau_{20}}{\tau_{24}}. \end{aligned}$$



Cycling model: analytical prediction vs. numerical simulation



Mean time to extinction for an initial population of X_2.
The curves are the analytical approximation
The symbols represent numerical simulation results (5,000 realizations)
Parameters: $\mu = 3.307$, $\alpha = 0.458$, $\beta = 0.047$, and $\sigma = 1.8874$.

The cycling model - Adding control

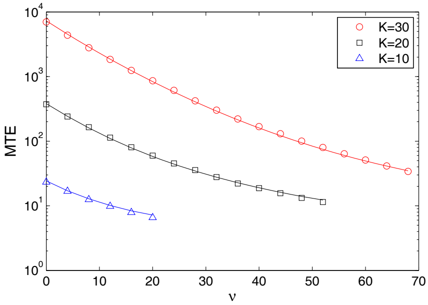
Often the MTE is of interest in the study of population dynamics because either longevity or quick extinction has value. Consider the population as pests and a short MTE is ideal.

The control method we model removes individuals at a particular frequency ν.

Transition	W(X;r)
$X \xrightarrow{\nu} \varnothing$	ν.

The Hamiltonian

$$\mathcal{H}(x,p) = \left(\frac{\alpha x^4}{24} + \frac{\lambda x^2}{2}\right)(e^p - 1) + \left(\mu x + \frac{\sigma x^3}{6} + \frac{\beta x^5}{120} + \frac{\nu}{K}\right)(e^{-p} - 1)$$



$\mu = 3.307$, $\alpha = 0.458$, $\beta = 0.047$, $\sigma = 1.8874$, $\lambda = 3.94$

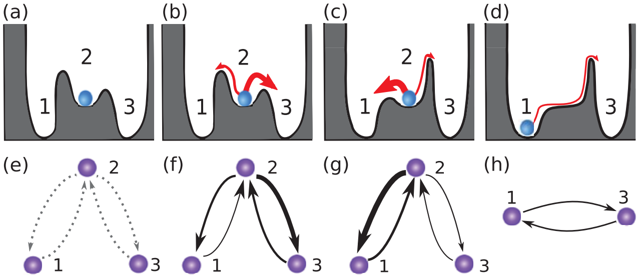
The cycling model - Extensions

The methods can be extended to external noise and Langevin systems:

$$\frac{d\mathbf{X}}{dt} = -F'(\mathbf{X}) + \sqrt{\epsilon}\,\frac{d\mathbf{W}}{dt}$$

$F(\mathbf{X})$ is the effective potential.

More sophisticated control methods can be employed, such as optimal least action control (OLAC), which identifies optimal parameter tuning to reshape the quasipotential. [Wells, Kath, and Motter, *Phys Rev X* (2015)]



Cycling in Metapopulations

We now explore extinction dynamics in stochastic, migratory populations. These results can have implications for ecology and public health. For example, understanding what causes local and global disease die out makes infectious populations more manageable.

Consider a 2-population model with birth, annihilation, and immigration.

The deterministic model:

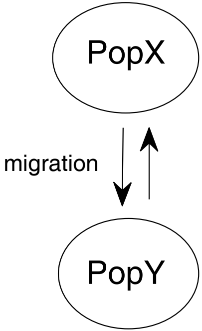
$$\dot{X} = \lambda_1 X - \frac{\sigma_1}{2} X^2 - \mu_{12} X + \mu_{21} Y$$
$$\dot{Y} = \lambda_2 X - \frac{\sigma_2}{2} X^2 + \mu_{12} X - \mu_{21} Y$$

Parameters:

λ - birth

σ - death

μ - migration



Limiting behaviors:

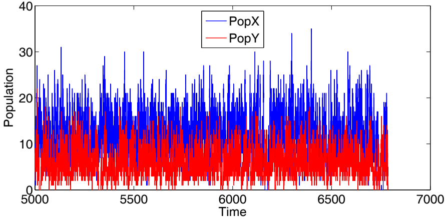
- both populations coexist
- one exists and other dies out
- both populations die out (extinction)

Can we predict the mean time to global extinction?

Metapopulations - Stochastic model

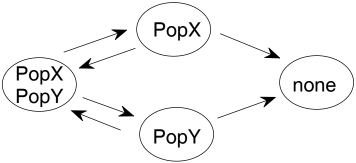
The stochastic model transition rates:

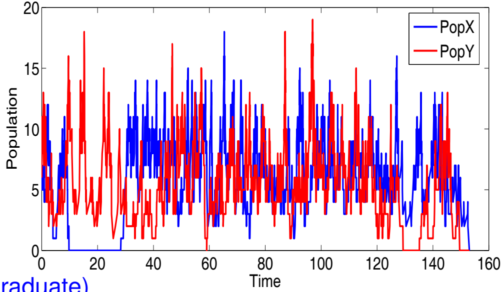
X Event	W(X;r)	Y Event	W(X;r)
$X \xrightarrow{\lambda_1} 2X$	$\lambda_1 X$	$Y \xrightarrow{\lambda_2} 2Y$	$\lambda_2 Y$
$2X \xrightarrow{\sigma_1} \emptyset$	$\sigma_1 \frac{X^2}{2}$	$2Y \xrightarrow{\sigma_2} \emptyset$	$\sigma_2 \frac{Y^2}{2}$
$X \xrightarrow{\mu_{12}} Y$	$\mu_{12} X$	$Y \xrightarrow{\mu_{21}} X$	$\mu_{21} Y$.



The general pre-extinction dynamics follows the cycling ideas from before:

Population Survival





Figures by Alexa Aucoin (MSU undergraduate)

Metapopulations - MTE

The Hamiltonian for the coupled birth-annihilation model

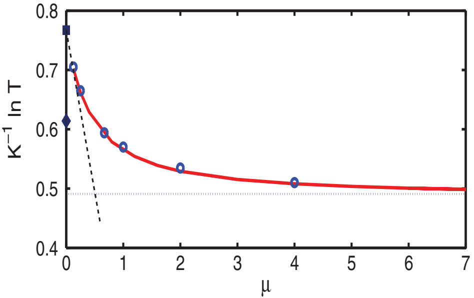
$$\mathcal{H} = x(e^{p_x} - 1) + y(e^{p_y} - 1) + \frac{x^2}{2}(e^{-2p_x} - 1) + \frac{y^2}{2\kappa}(e^{-2p_y} - 1) + \mu x(e^{-p_x + p_y} - 1) + \mu y(e^{p_x - p_y} - 1)$$

Case 1: $\mu = 0$, separable.

$$MTE = \frac{2\sqrt{\pi\sigma}}{\lambda^{\frac{3}{2}}} \exp\left(K \int_{x_1}^{0} p_{opt}(x)dx\right)$$

Case 2: $\mu > 0$, approximate the optimal path numerically (IAMM, etc.)

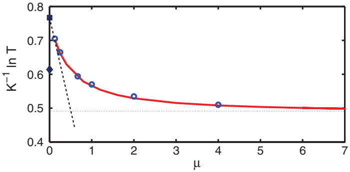
From Khasin, Meerson, Khain, and Sander, PRE (2012).

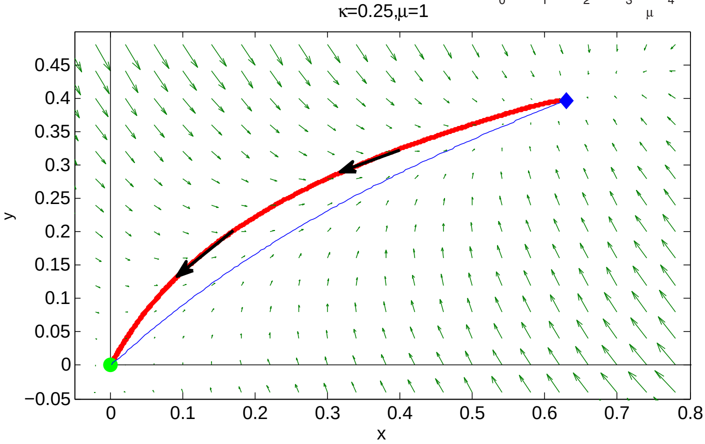


Data: MTE from optimal path, $\kappa = 0.25$.

Curve: MTE from master eqn., $K = 220$.

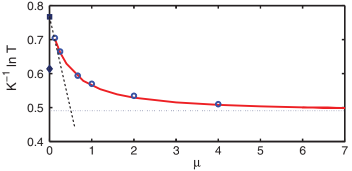
No cycling: $\kappa = 1$

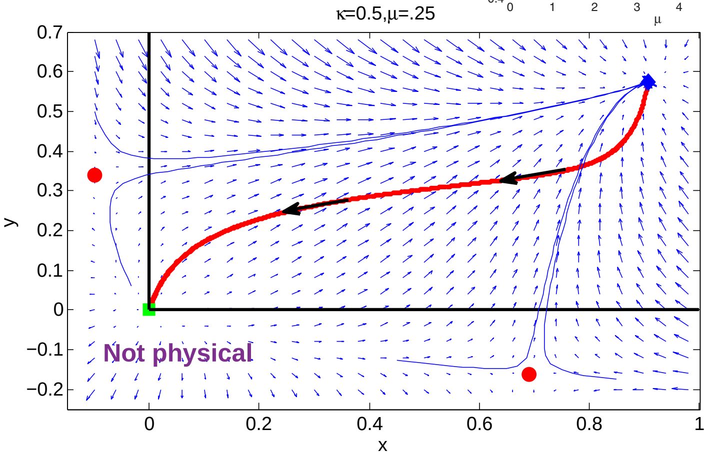




Coupled population with only two steady states

The Puzzle: $\kappa = 0.25$





Coupled population with four steady states

Conclusions

- We explore cycling dynamics within a single population. We develop a general formulation to capture pre-extinction dynamics in a single population with cycling.
- We can quantify the MTE and the effect of control in extinction rates.
- A lot more work to be done:
  - models for more complex models (Ebola)
  - devise and quantify improved control methods (vaccine/treatment)
  - approximation for MTE in higher dimensional systems
  - experimental verification ...

Thank You!

Results from: Nieddu, Billings, and Forgoston, "Analysis and control of pre-extinction dynamics in stochastic populations," Bulletin of Mathematical Biology (2014).