Extinction of established populations:
An interplay of physics and mathematics

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This talk is about evaluating probabilities of rare events in non-equilibrium stochastic systems.

Why should one care about rare event?

Practical reasons:

Rare events may have dramatic or even devastating consequences

Earthquakes, volcano eruptions, market crashes, population extinction, …

A more fundamental reason touches the foundations of statistical physics:

Thermal equilibrium : macroscopic fluctuations are fully described, by the Boltzmann-Gibbs distribution, in terms of the free energy of the system

Non-equilibrium fluctuations, especially large ones: we poorly understand their statistics, even for "simple" systems

Dodo. Extinct since the 17th century

Passenger pigeon. Extinct since the beginning of the 20th century

Extinction of an isolated population after maintaining a thriving long-lived state is a dramatic phenomenon. It ultimately occurs, even in the absence of detrimental environmental variations, because of a large fluctuation: an unusual chain of random events when population losses dominate over gains

Tasmanian wolf. Extinct since the 20th century

Outline

- ✓ 1. Extinction of well-mixed populations due to demographic noise
- ✓ 2. Interplay of demographic and environmental noise
- ✓ 3. Extinction in two-population systems
- ✓ 4. Extinction of spatially distributed populations (very briefly)
- ✓ 5. Summary

A simple model of population extinction due to intrinsic (demographic) noise:

A single population of $n(t)$ individuals who multiply and die, as described by a Markov jump process

A.A. Markov 1856-1922

Markov process: random process where future depends only on the present but not on the past

jump process: discrete state space

Extinction of a single population due to demographic noise

Example: SIS model

Nasell 1996,1999; Andersson and Djechiche 1998, Ovaskainen 2001, …

Birth and death rates

$$\lambda(n) = \lambda_0 n(K-n), \quad \mu(n) = \mu_0 n$$

Deterministic rate equation

$$dn/dt = \lambda(n) - \mu(n), \quad \text{or}$$

$$\frac{dq(t)}{dt} = \mu_0 q(R_0 - 1 - R_0 q), \qquad q = n/K, \;\; R_0 = \lambda_0 K/\mu_0$$

reproduction fuctor

$$R_0 > 1: \quad q = 0 \qquad \text{unstable fixed point}$$

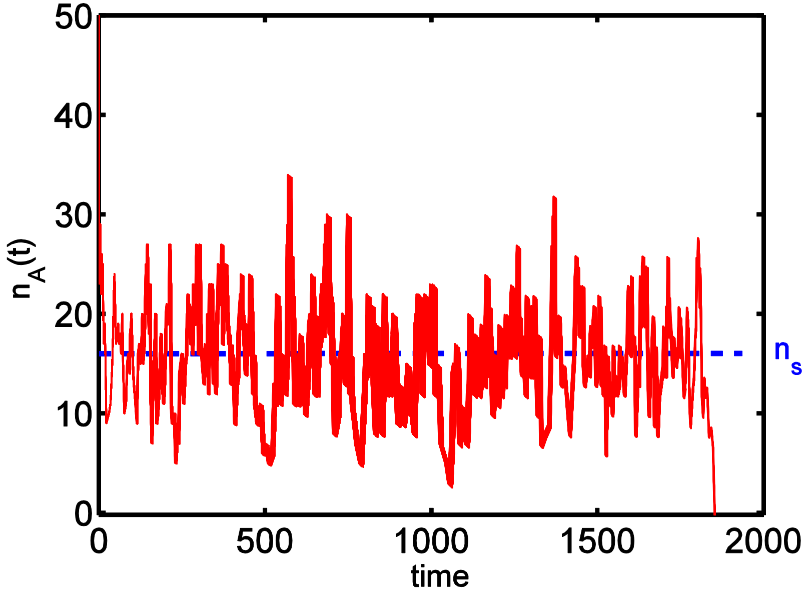
$$q_1 = 1 - \frac{1}{R_0} \text{ stable fixed point, } \; \mathrm{t_r} = \frac{1}{\mu_0(R_0 - 1)}$$

relaxation time

$$n_1 = K(1 - 1/R_0) >> 1$$

Discreteness of individuals and stochastic character of birth-death processes make a big difference!

a stochastic simulation of SIS model



Population ultimately goes extinct:

A large fluctuation brings it into *absorbing state* n=0

Interesting to predict:

- Mean time to extinction (MTE)
- Extinction time statistics
- Quasi-stationary probability distribution of population sizes

Master equation for the Markov jump process

$P_n(t)$: probability to find n individuals at time t

$P_0(t)$: probability of population extinction at time t

$$\begin{cases} \dfrac{dP_n}{dt} = \underbrace{\lambda_o\left[(n-1)(K-n+1)P_{n-1} - n(K-n)P_n\right]}_{\text{birth}} + \underbrace{\mu_0\left[(n+1)P_{n+1} - nP_n\right]}_{\text{death}}, \quad n = 1,2,3,\ldots \\ \dfrac{dP_0}{dt} = \mu_0 P_1 \end{cases}$$

Previous analytical methods for the MTE:

- single-step processes: exact solution, then asymptotics
- Fokker-Planck approximation (aka diffusion approximation): leads to exponentially large errors in the MTE

Until about 10 years ago no satisfactory general methods existed for multi-step processes

At $t \gg t_r$ extinction of established population proceeds as exponential decay of a long-lived *quasi-stationary* state

$$P_n(t) \cong \pi_n \exp(-t/\tau),$$
$$\mathrm{P}_0(t) \cong 1 - \exp(-t/\tau).$$

π_n: QSD

τ : MTE, very large at $K \gg 1$

π_n and τ are the lowest non-trivial eigenstate and inverse eigenvalue of linear eigenvalue problem

$$\lambda_o\left[(n-1)(K-n+1)\pi_{n-1} - n(K-n)\pi_n\right] + \mu_0\left[(n+1)\pi_{n+1} - n\pi_n\right] = -\frac{1}{\tau}\pi_n\ , \quad n = 1,2,3,\ldots$$

$$\frac{1}{\tau} = \mu_0 \pi_1$$

π_n can be found in WKB approximation

WKB (**Wentzel–Kramers–Brillouin)** approximation appears in physics as the semi-classical approximation to quantum mechanics or, more generally, as a ray-equations approximation to wave equations.
WKB is valid in the limit of short wavelengths

A similar-in-spirit approximation works, in the limit of weak noise, or $K \gg 1$
for continuous Markov processes
Freidlin and Wentzel, Graham, Dykman et al., Maier and Stein,…,
and for jump Markov processes
Kubo, Dykman et al, Elgart and Kamenev, Assaf and M, Kessler and Shnerb,…

Recent review: Assaf and M, J. Phys. A: Math. Theor. **50**, 263001 (2017).

The WKB ansatz

$$\pi_n = \exp[-KS(q)], \qquad q = n/K, \quad K >> 1$$

$$S(q) = S_0(q) + \frac{1}{K} S_1(q) + \frac{1}{K^2} S_2(q) + \ldots$$

where, for n>>1, we treat S(q) as a smooth function

$$\pi_{n-1} = \exp[-KS(\tfrac{n-1}{K})] = \exp[-KS_0(q) + S_0{}'(q) + \ldots]$$

$$\pi_{n+1} = \exp[-KS(\tfrac{n+1}{K})] = \exp[-KS_0(q) - S_0{}'(q) + \ldots]$$

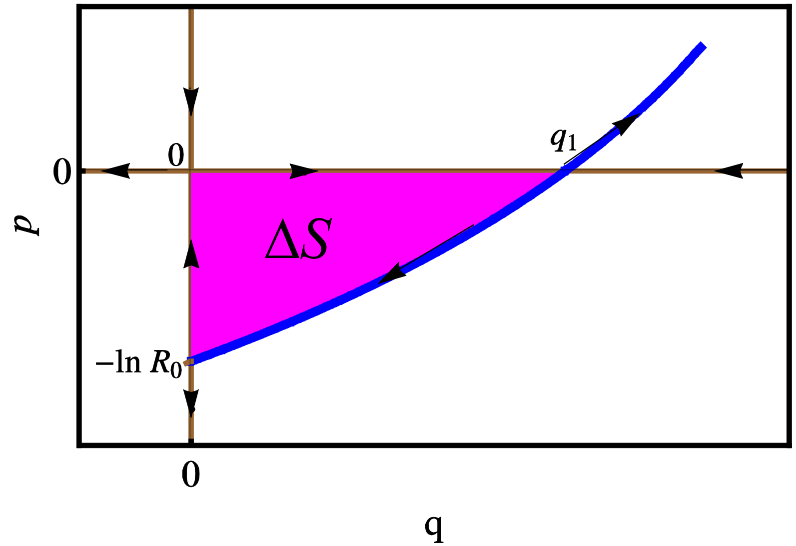
In the leading order in 1/K one arrives at a Hamilton-Jacobi equation

$$H_0\left(q, \frac{dS_0}{dq}\right) \cong 0$$

with Hamilton's function

$$H_0(q,p) = \mu_0 q\left[R_0(1-q)\left(e^{p}-1\right)+e^{-p}-1\right], \qquad p = \partial_q S$$

Solution boils down to finding a zero-energy trajectory of effective "mechanical system"



Downhill trajectory: p=0, deterministic rate equation

Most probable path to extinction (uphill trajectory): separatrix connecting fixed points ($q=q_1$, $p=0$) and ($q=0$, $p=-\ln R_0$)

extinction action

$$p(q) = \ln\left[\frac{1}{R_0(1-q)}\right], \qquad \Delta S = \int_{q_1}^{0} p(q)\,dq = \ln R_0 + \frac{1}{R_0} - 1$$

Mean time to extinction is, up to a pre-factor,

$$\tau \sim \exp(K\Delta S) = \exp\left[K\left(\ln R_0 + \frac{1}{R_0} - 1\right)\right], \qquad K\Delta S >> 1$$

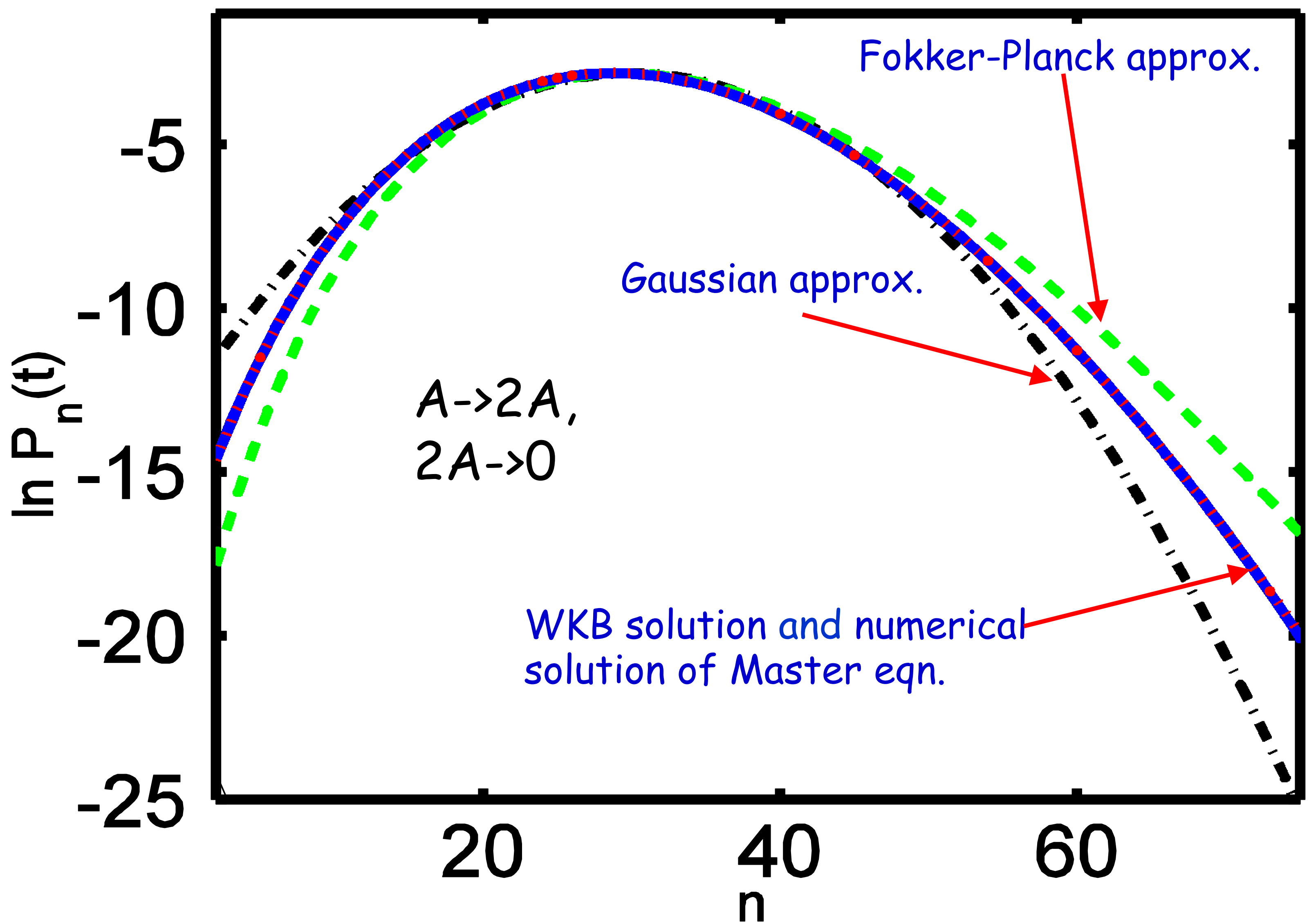
exponentially long in K

Close to the transcritical bifurcation, $\delta = R_0 - 1 << 1$, the result is universal for a whole class of models:

$$\tau \sim \exp\left(\frac{1}{2}K\delta^2\right), \qquad K\delta^2 >> 1$$

Pre-exponential factor can be also calculated, by matching the subleading-order WKB solution with the recursive solution at for small n

Assaf and M 2007,2010, Kessler and Shnerb 2007



FP approximation: good for “typical fluctuations”, fails in tails

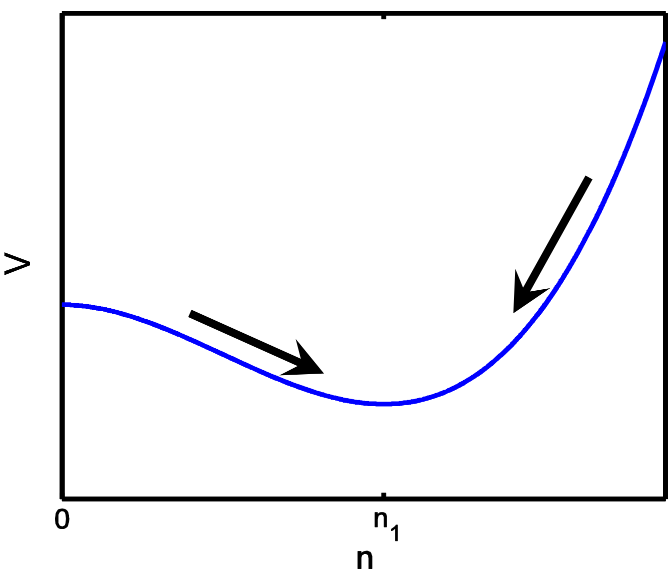
Gaveau, Moreau, and Toth 1996, Elgart and Kamenev 2005, Doering, Sargsyan, and Sander 2005, Assaf and M 2007, Kessler and Shnerb 2007, …

Now let’s go back to the deterministic rate equation and rewrite it as

$$\frac{dq}{dt} = -\frac{d}{dq} V(q),$$

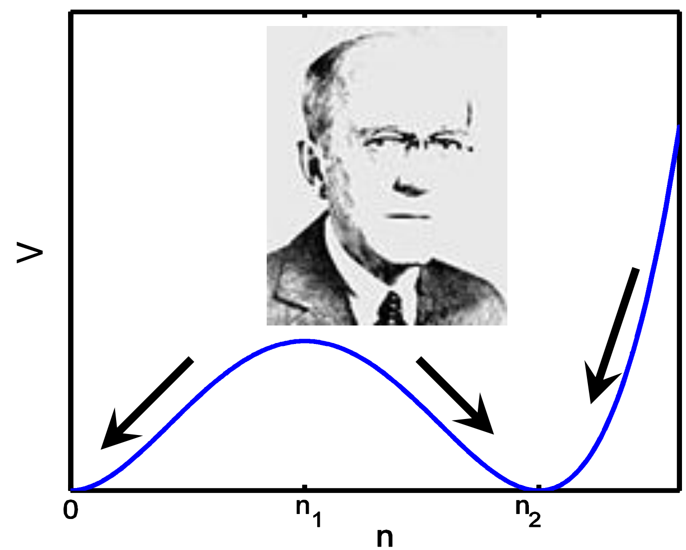
an over-damped particle motion in a potential

SIS model: no Allee effect



monostability: $q=q_1$

Allee effect

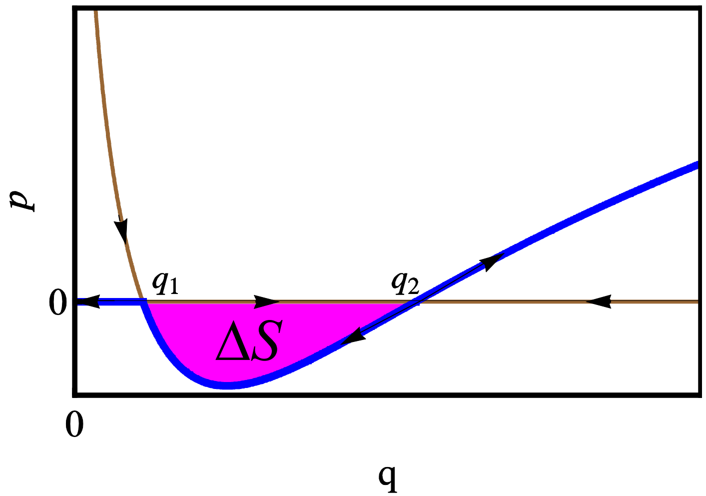


bistability: $q=0$ and $q=q_2$

Warder C. Allee (1885-1955)

Mean time to extinction with account of Allee effect

Using WKB approximation



Again, a separatrix in q,p plane

Mean time to extinction is, up to pre-exponent,

$$\tau \sim \exp(K\Delta S)$$

Elgart and Kamenev 2006

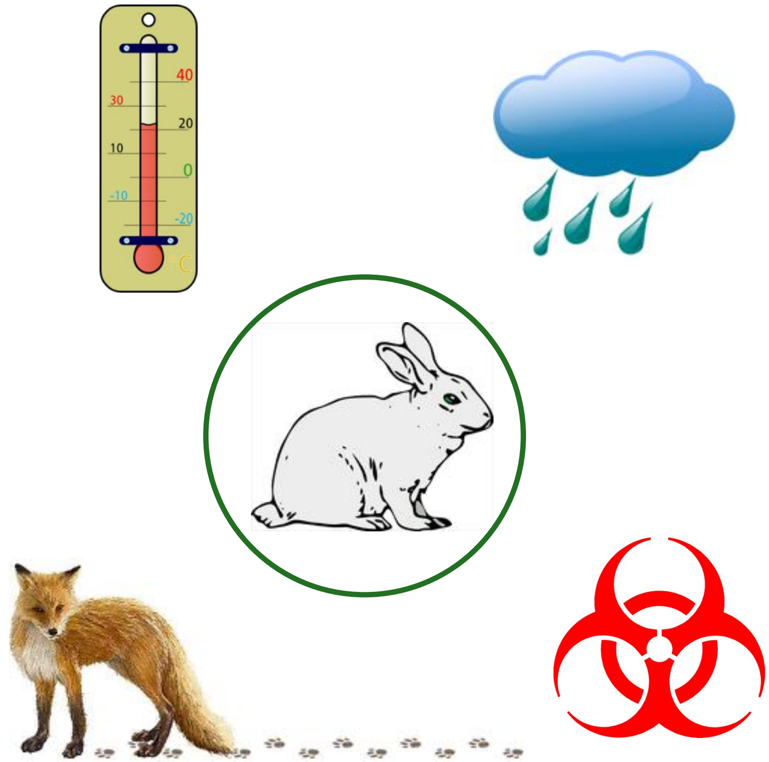
Close to the saddle-node bifurcation, $\delta \ll 1$, the result is universal for a whole class of models with strong Allee effect:

$$\tau \sim \exp\left(\alpha K \delta^3\right), \quad \alpha = O(1), \qquad K\delta^3 >> 1$$

Prefactor has been also found

M and Sasorov 2009, Escudero and Kamenev 2009, Assaf and M 2010

What if, in addition to demographic noise, there are also environmental variations?



Model: Environmental noise modulates birth and/or death rates,

$r \to r - \xi(t)$

A noise-modulated variant of SIS model

$$n \to n+1 \quad \lambda_n = \frac{n}{2}(\mu + r - an)$$

$$n \to n-1 \quad \mu_n = \frac{n}{2}(\mu - r + an)$$

$K=r/a$ carrying capacity

$r \to r-\xi(t)$

Colored gaussian noise, defined by correlation function

$$\langle \xi(t)\xi(t') \rangle = \mathrm{v}\, e^{-|t-t'|/t_c}$$

Ornstein-Uhlenbeck noise

v: variance, t_c: correlation time

How do two noises - demographic and environmental – conspire to kill the population? What is effect of noise color?

It is debated in ecology "whether and under which conditions red noise increases or decreases extinction risk compared with uncorrelated (white) noise" (Schwager et al. 2006)

Method of solution: WKB

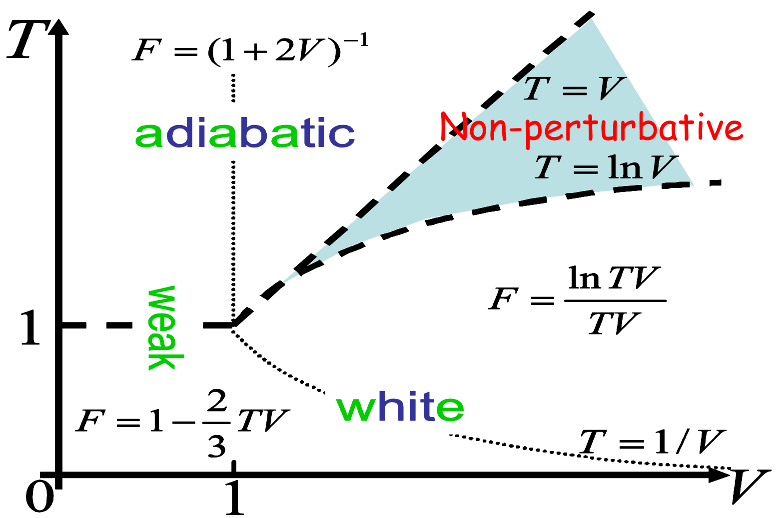
Presence of noise color leads to a 4d phase space:

The problem is not soluble analytically
unless there is additional small parameter

$$\ln(\tau_\varsigma) = \ln(\tau)\, F(V,T)$$

$$V = \mathrm{v}K/(r\mu), \quad T = rt_c$$

Kamenev, M and Shklovskii 2008



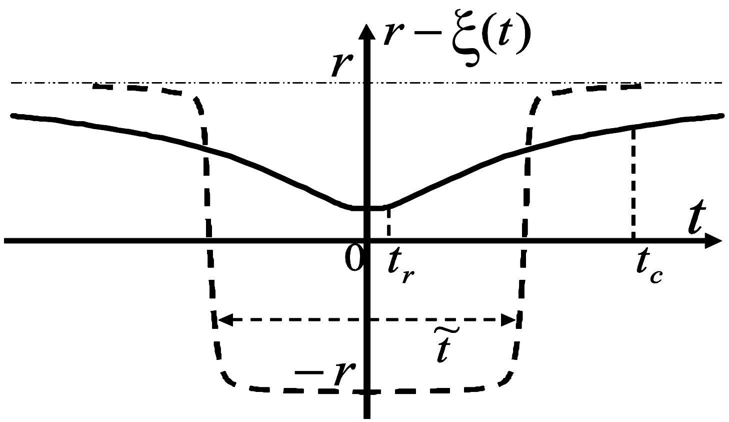
Joint action of demographic and environmental noises:

- Environmental noise causes *exponential* reduction of the MTE

- At fixed variance, positive correlations of the environmental noise quicken extinction

- The population-size dependence of the MTE changes from *exponential* without noise to a *power law* for strong short-correlated noise and to almost *no dependence* for long-correlated noise

- WKB theory yields *most probable path to extinction*, along with *most probable realization* of environmental noise



Extinction in two-population systems: fixed point

Example: SI (Susceptible-Infected) model with population turnover

Captures essence of most common childhood diseases that confer long-lasting immunity: measles, mumps and rubella

Event	Type of transition	Rate
Infection	$S \to S-1,\ I \to I+1$	$(\beta/N)SI$
Renewal of susceptible	$S \to S+1$	μN
Removal of infected	$I \to I-1$	ΓI
Removal of susceptible	$S \to S-1$	μS

Deterministic rate equations

$$\frac{dS}{dt} = \mu N - \mu S - \frac{\beta}{N} SI,$$

$$\frac{dI}{dt} = \frac{\beta}{N} SI - \Gamma I.$$

$$\frac{dS}{dt} = \mu N - \mu S - \frac{\beta}{N} SI,$$
$$\frac{dI}{dt} = \frac{\beta}{N} SI - \Gamma I.$$

$\beta < \Gamma$: only infection-free steady state: attracting fixed point S=N, I=0

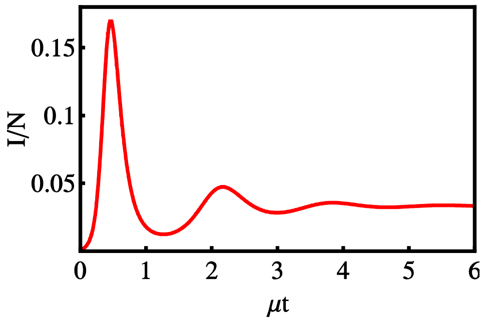
$\beta > \Gamma$: point S=N, I=0 is repelling, attracting *endemic* point appears:

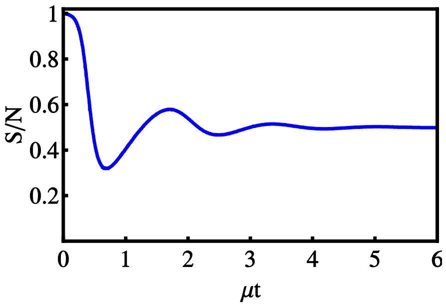
$$\bar{S} = \frac{\Gamma}{\beta} N, \qquad \bar{I} = \left(\frac{1}{\Gamma} - \frac{1}{\beta}\right) N \qquad N \gg 1$$

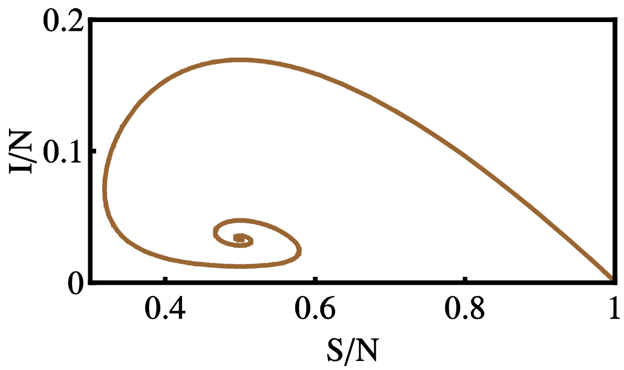
$$\mu < 4(\beta - \Gamma)(\Gamma / \beta)^2$$

Endemic fixed point is a stable focus

epidemic dynamics is oscillatory: multiple outbreaks of disease



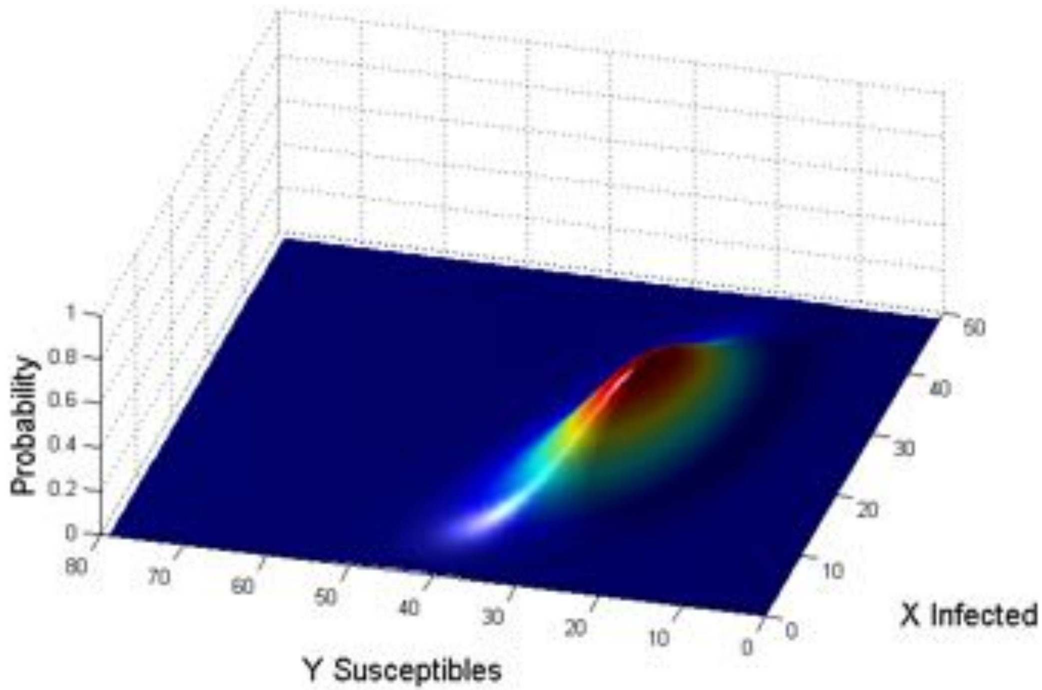




$$\mu > 4(\beta - \Gamma)(\Gamma / \beta)^2$$

fixed point is a stable node

Stochastic dynamics: $P_{nm}(t)$ is "leaking" into disease-free state



$$\tau \approx \left(\Gamma \pi_{n_*,1}\right)^{-1}$$

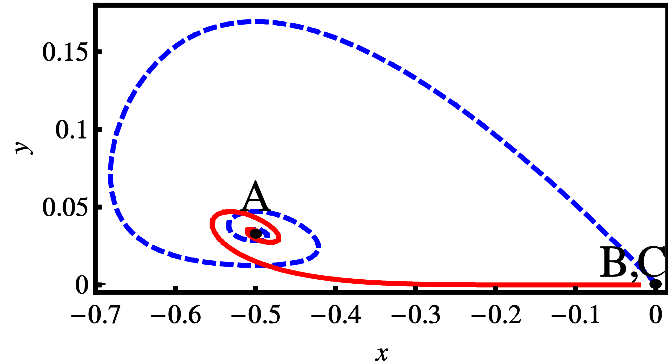
τ: mean time to disease extinction

WKB theory

The most likely disease extinction trajectory is a heteroclinic orbit: it exits from fixed point A and reaches the extinction hyperplane x=0 at fixed point B:

- - - deterministic trajectory

—— most likely path to disease extinction (found numerically)



$$A = [-\delta, (\delta / K)(1-\delta)^{-1}, 0, 0]$$
$$B = [0, 0, 0, \ln(1-\delta)]$$
$$C = [0, 0, 0, 0]$$

Kamenev and M 2008

Related problems

• Extinction in multi-population systems occupying a fixed point: other epidemic models (Dykman, Schwartz and Landsman 2008, …), switching between active and dormant phenotypes (Lohmar and M 2011), minimizing the extinction risk by migration (Khasin, M, Khain, and Sander 2012), extinction of meta-populations (Eriksson, Elias-Wolff and Mehlig 2012), competition between two species (Gabel, Redner and M 2013),…

• Optimization of vaccination protocols
Khasin, Dykman and M 2010

•Immigration-extinction balance
M and Ovaskainen 2013, Be'er, Assaf and M 2015

Extinction of oscillating populations

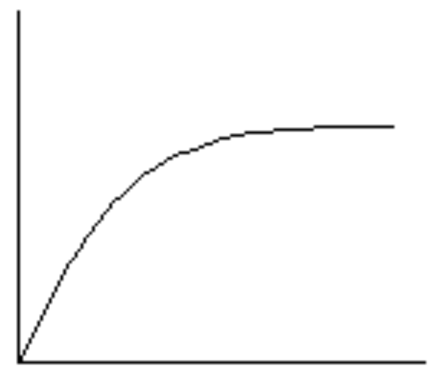
Example: predator-prey model with prey competition and predator satiation (Rosenzweig and MacArthur 1963)

$$\dot{R} = aR - \frac{1}{2N}R^2 - \frac{\sigma R F}{N + \sigma\tau R}$$

$$\dot{F} = -F + \frac{\sigma R F}{N + \sigma\tau R}$$

Predation rate

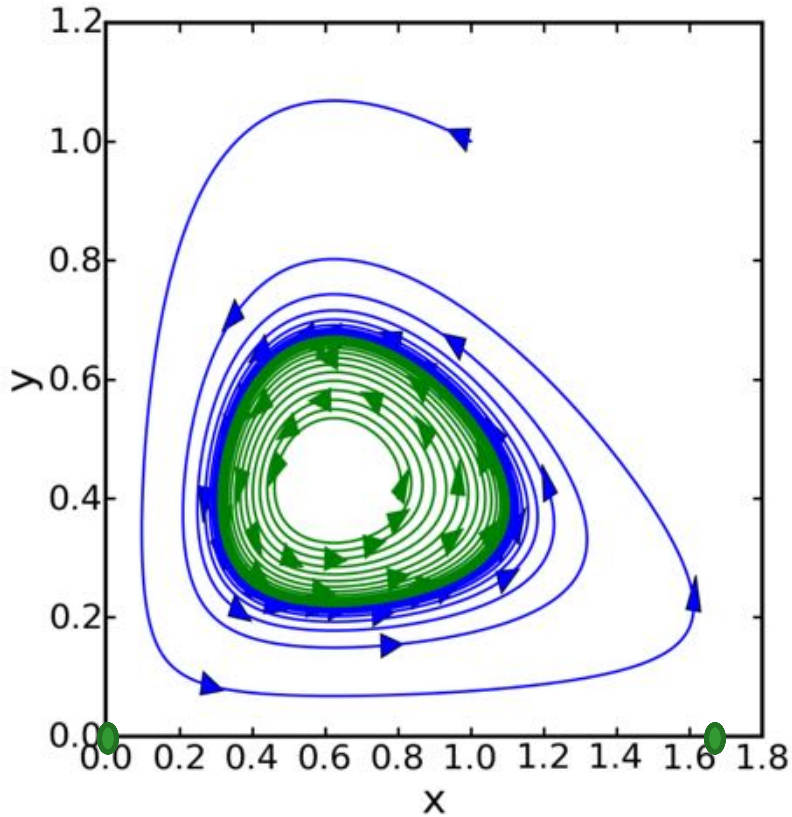
$$\frac{\sigma R}{N + \sigma\tau R}$$



R

Prey density

$\sigma > \sigma^*$ Limit cycle

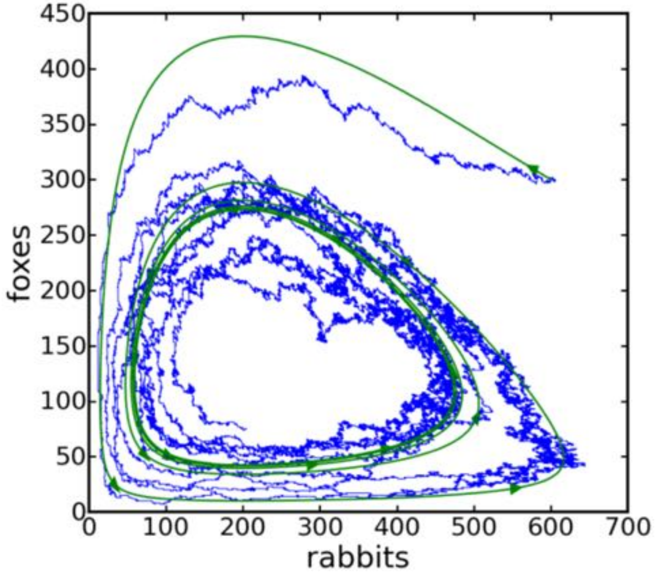


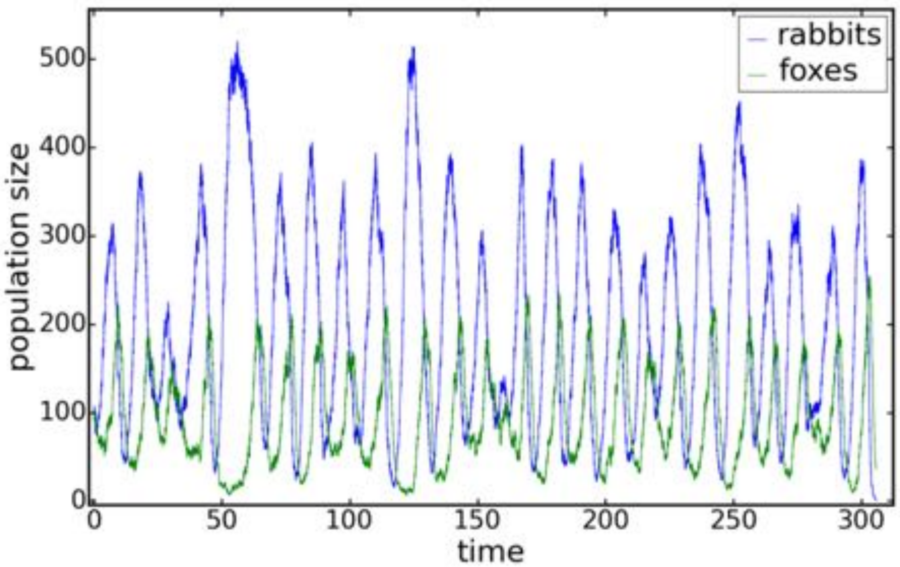
x=R/N
y=F/N

Stochastic version of the RMA model

Smith and M 2016

$$
\begin{aligned}
R &\rightarrow 2R \\
2R &\rightarrow R \\
F + R &\rightarrow 2F \\
F &\rightarrow 0
\end{aligned}
$$

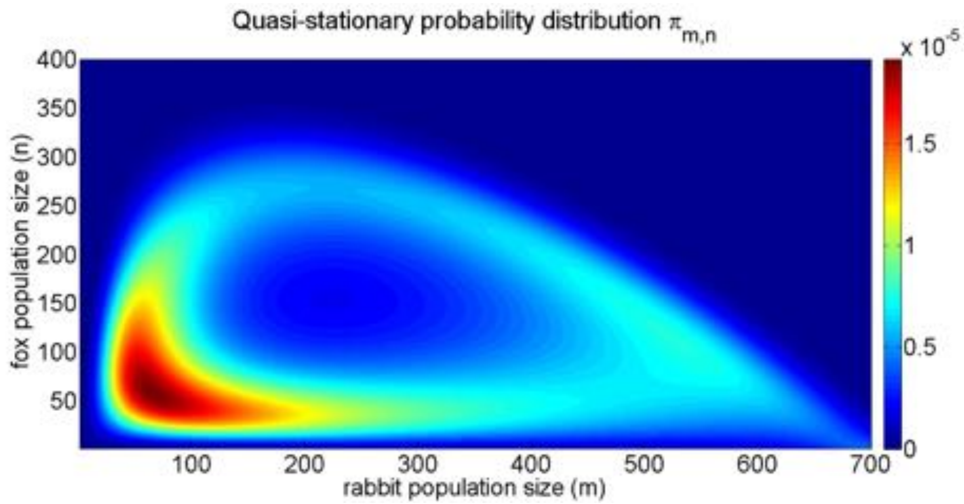




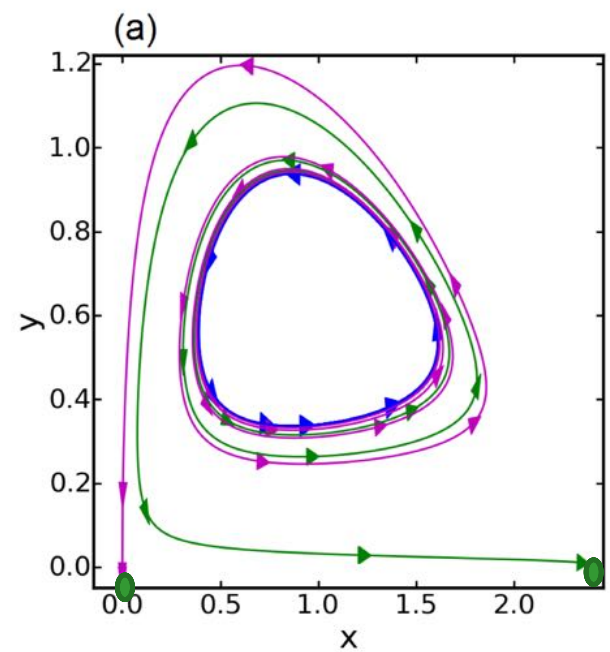
Master equation for the stochastic RMA model

$$
\begin{aligned}
\dot{P}_{m,n} = \; & \underbrace{a\left[(m-1)\,P_{m-1,n} - mP_{m,n}\right]}_{\text{rabbit birth}} + \\
& + \underbrace{\left[\frac{\sigma\,(m+1)\,(n-1)}{N+\sigma\tau\,(m+1)}P_{m+1,n-1} - \frac{\sigma mn}{N+\sigma\tau m}P_{m,n}\right]}_{\text{predation}} + \\
& + \underbrace{(n+1)\,P_{m,n+1} - nP_{m,n}}_{\text{fox death}} + \\
& + \underbrace{\frac{1}{2N}\left[(m+1)\,mP_{m+1,n} - m\,(m-1)\,P_{m,n}\right]}_{\text{rabbit death due to competition}}
\end{aligned}
$$

Smith and M 2016



WKB Hamiltonian



$$H = ax\left(e^{p_x}-1\right)+\frac{\sigma xy}{1+\sigma\tau x}\left(e^{p_y-p_x}-1\right)+ + y\left(e^{-p_y}-1\right)+\frac{1}{2}x^2\left(e^{-p_x}-1\right)=0$$

Numerical solution is based on the Floquet theory

- optimal paths to extinction
- extinction rates/times
- relative probabilities of two extinction routes
- change of these at the Hopf bifurcation of the birth of the limit cycle

Extinction of *spatial* populations

Elgart and Kamenev 2004, M and Sasorov 2011

Model: "Refuge" made of N>>1 identical habitat patches, or sites. On-site births and deaths, random migration between neighboring sites

Deterministic model

$$dq_i/dt = \mu_0[\bar{\lambda}(q_i) - \bar{\mu}(q_i)] + D_0(q_{i-1} + q_{i+1} - 2q_i), \quad q_i = n_i / K$$

When migration is fast this becomes continuous reaction-diffusion equation

$$\partial_t q(x,t) = \mu_0[\bar{\lambda}(q) - \bar{\mu}(q)] + D\,\partial_x^2 q, \quad D = D_0 h^2$$

+ boundary conditions

$x \in [0, L], L = Nh, h$ is the patch size

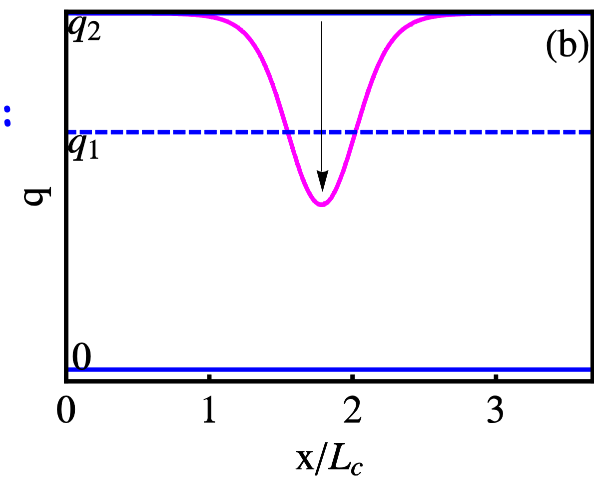
Deterministic steady state

$$\frac{D}{\mu_0}\frac{d^2q}{dx^2}+\bar{\lambda}(q)-\bar{\mu}(q)=0$$

Allee effect: different cases possible depending on which of the states, $q=0$ or $q=q_2$, is “more stable”, on boundary conditions, and on system size

Most interesting example: strong Allee effect ($q=0$ “more stable” deterministically)

Magenta curve: **critical nucleus:** *unstable* x-dependent steady-state solution



Large fluctuations brings population to extinction. Two outgoing extinction fronts.

Solved in WKB approximation, M and Sasorov 2011

Theory similar in spirit to classical nucleation theory of Langer 1967
Finite size effects: Maier and Stein 2001, M and Sasorov 2011

Summary

✓ General take-home message: Weak noise may have dramatic long-time consequences for dynamical systems

✓ Extinction of a long-lived population typically proceeds along an optimal path: a special trajectory of effective "classical mechanics"

✓ Finding these special trajectories, and the mean time to extinction, is both hard work and fun

Thank you