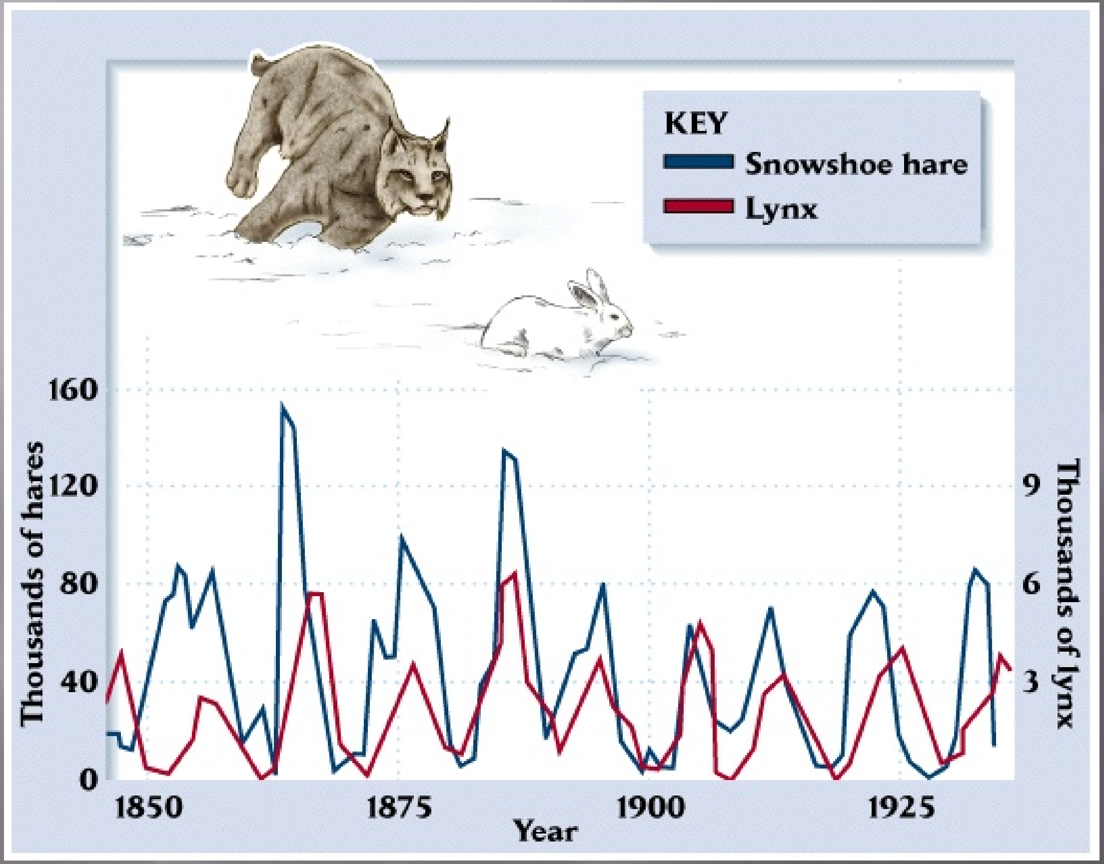
Stabilization of metapopulation cycles: Toward a classification scheme



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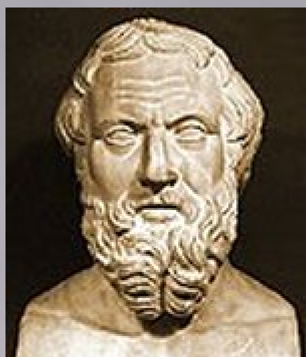
Phys. Rev. E **75**, 051914 (2007)

From Herodotus of Halicarnassus to Lotka and Volterra

Why the wolves do not consume all the sheep? When a wolve consumes a sheep, it becomes happier, healthier, stronger, and is more likely to breed and to produce more little wolves. The prey predator system, thus, is **inherently unstable**.



Fifth century BCE

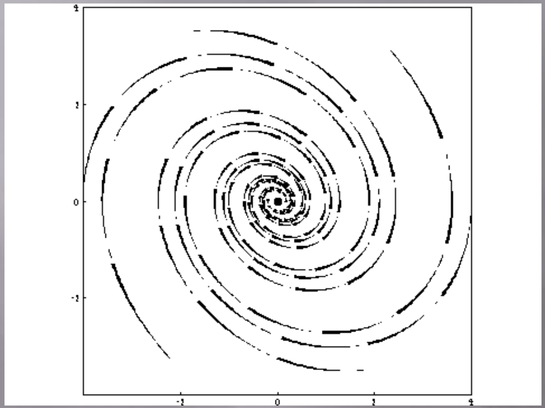
That's where the theory stands for about 2500y

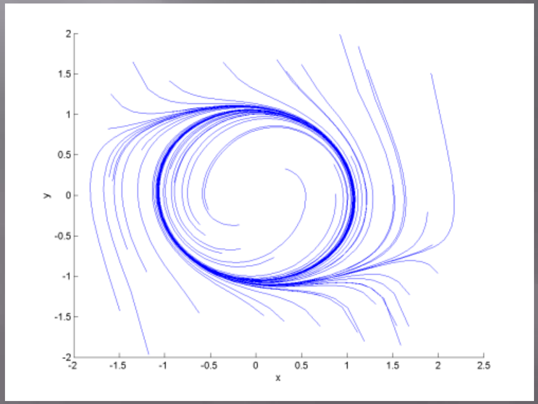
The Arabians say that the whole world would swarm with these [winged] serpents, if they were not kept in check in the way in which I know that vipers are. Of a truth Divine Providence does appear to be, as indeed one might expect beforehand, a wise contriver. For timid animals which are a prey to others are all made to produce young abundantly, so that the species may not be entirely eaten up and lost; while savage and noxious creatures are made very unfruitful. The hare, for instance, which is hunted alike by beasts, birds, and men, breeds so abundantly as even to superfetate, a thing which is true of no other animal. You find in a hare's belly, at one and the same time, some of the young all covered with fur, others quite naked, others again just fully formed in the womb, while the hare perhaps has lately conceived afresh. The lioness, on the other hand, which is one of the strongest and boldest of brutes, brings forth young but once in her lifetime, and then a single cub; she cannot possibly conceive again, since she loses her womb at the same time that she drops her young. The reason of this is that as soon as the cub begins to stir inside the dam, his claws, which are sharper than those of any other animal, scratch the womb; as the time goes on, and he grows bigger, he tears it ever more and more; so that at last, when the birth comes, there is not a morsel in the whole womb that is sound.

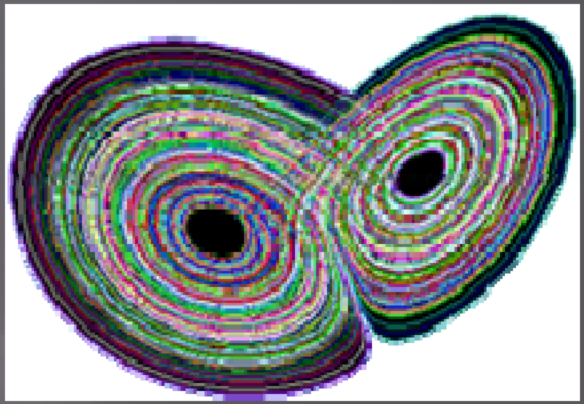
Now with respect to the vipers and the winged snakes of Arabia, if they increased as fast as their nature would allow, impossible were it for man to maintain himself upon the earth. Accordingly it is found that when the male and female come together, at the very moment of impregnation, the female seizes the male by the neck, and having once fastened, cannot be brought to leave go till she has bit the neck entirely through. And so the male perishes; but after a while he is revenged upon the female by means of the young, which, while still unborn, gnaw a passage through the womb, and then through the belly of their mother, and so make their entrance into the world. Contrariwise, other snakes which are harmless, lay eggs, and hatch a vast number of young.[25]

Possible solutions to Herodotus puzzle:

- ***It may happen that the underlying dynamics supports an attractive manifold, like limit cycle, fixed point or strange attractor***







•***Otherwise, it may happen that the system is actually unstable, but migration between spatial patches is the stabilizing factor. This is the possibility considered here. Why?***

The basic models for victim-exploiter system are unstable.
Lotka-Volterra (1920's)

When the sheep population decreases, the wolves have no food anymore

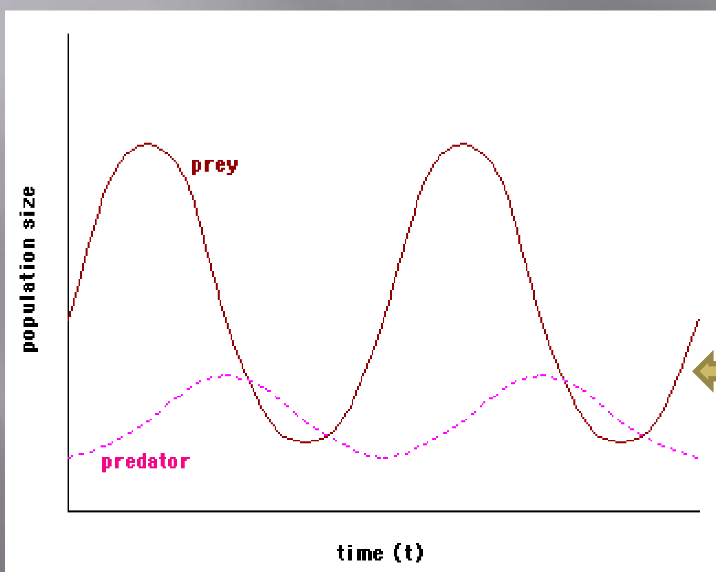
→ ***Population oscillations***

$$\frac{\partial a}{\partial t} = -\mu a + \lambda ab$$

$$\frac{\partial b}{\partial t} = \sigma b - \lambda ab$$

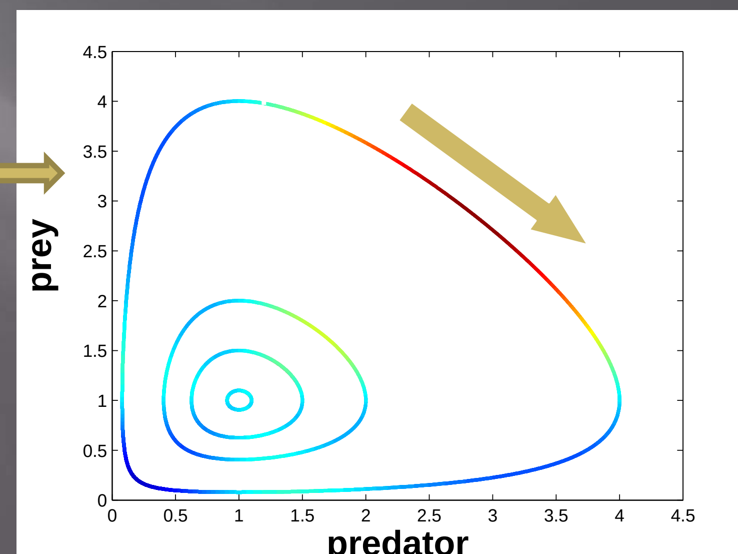
a=predator

b=prey



Phase portrait

Density vs. time



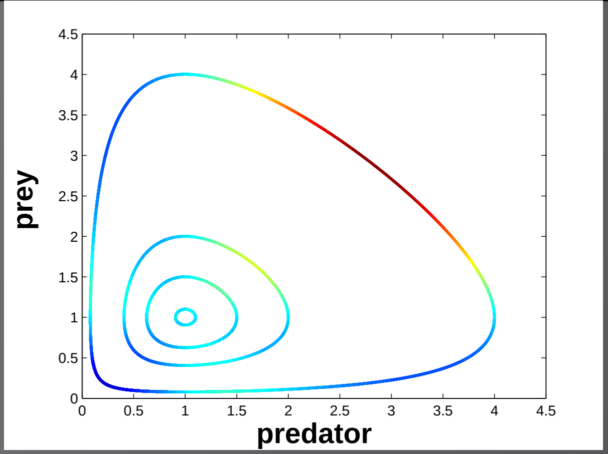
Conserved quantity, $H = \lambda_1 b + \lambda_2 a - \mu \ ln(a) - \sigma \ ln(b).$

$(0,0) \quad (0,\infty) \quad (\sigma/\lambda, \mu/\lambda)$

1d *trajectories* *marginal* stability !!

$\mu = \lambda = \sigma = 1$

Instability: any noise drives a marginally stable system to extinction of (at least) one of the species:

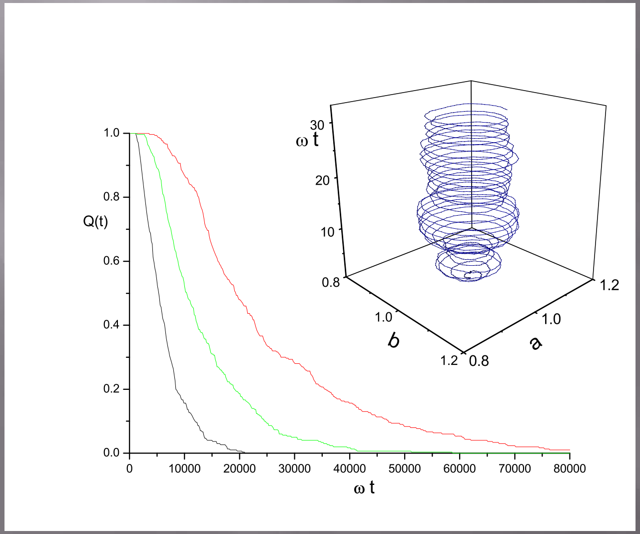


$$\frac{\partial a}{\partial t} = -\mu a + \lambda ab + \eta_1(t)$$

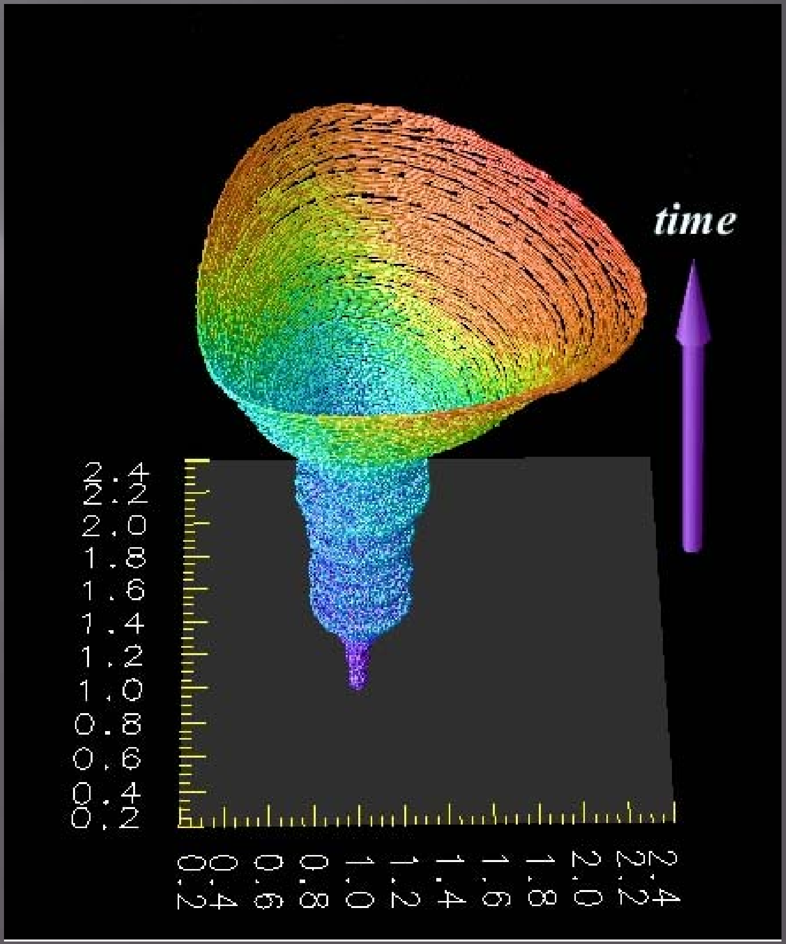
$$\frac{\partial b}{\partial t} = \sigma b - \lambda ab + \eta_2(t)$$

$$\langle \eta_i(t)\eta_j(t') \rangle = \Delta^2 \delta(t-t')\delta_{ij}$$

Random walk to extinction



Q(t) is the chance that the system do not hit the walls until t, and is plotted against t for several noise amplitudes.



Nicholson - Bailey host-parasitoid model (30's)

$$H_{t+1} = \sigma H_t e^{-\lambda P_t}$$

$$P_{t+1} = cH_t(1 - e^{-\lambda P_t})$$

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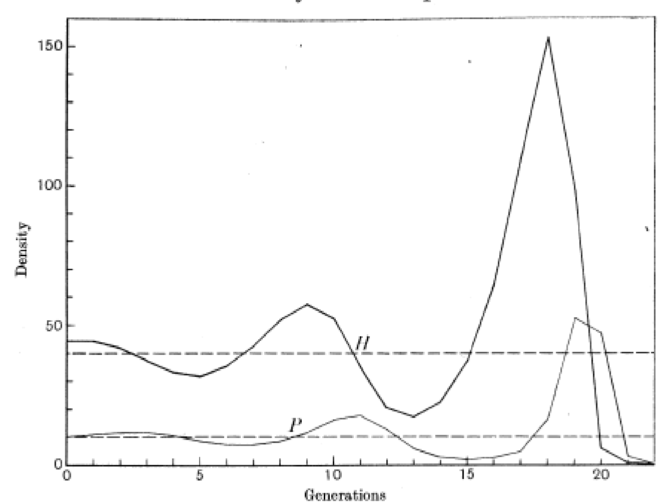
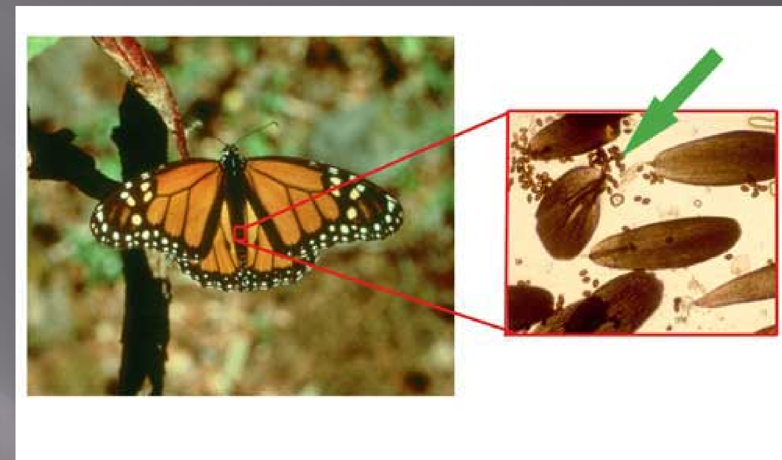


Fig. 6. Interaction of a specific host species (H) and a specific parasite species (P). Power of increase of host 2. Area of discovery of parasite 0·035. Arbitrary initial displacement of host density from 40 to 44. H, host curve; P, parasite curve. The steady densities are represented by dotted lines. Parasite curve drawn to half the vertical scale of host curve.

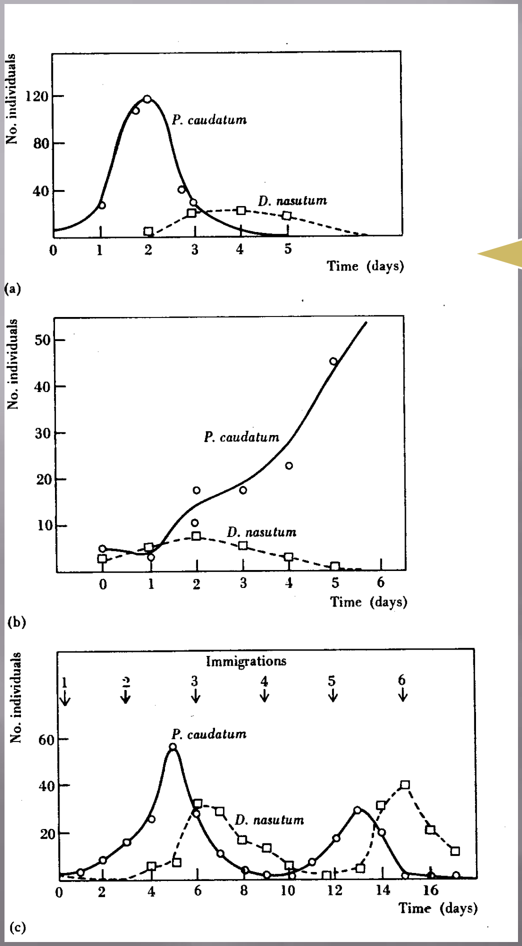


This model is "more" unstable! Even without noise the oscillations grow until one of the species gets extinct.

Bottom line: Both LV and NB models leads to an extinction of (at least) one of the species.

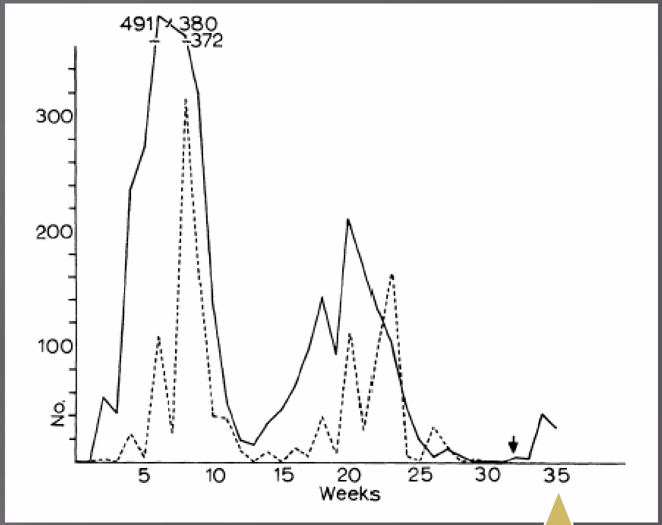
Should it bother us?

(Old) Experimental demonstrations: growing oscillations and extinction

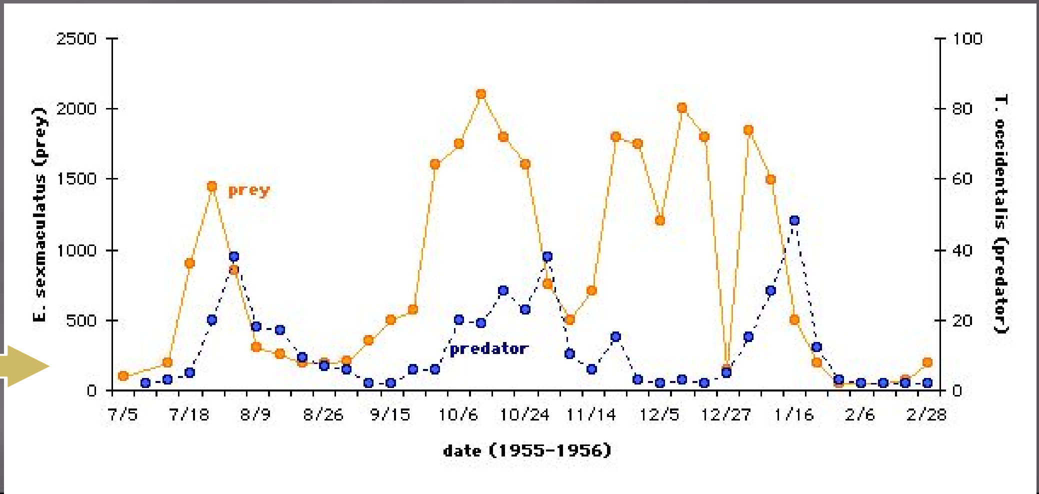


Gause 1935:Two protist species in laboratory culture vials: Paramecium grazes on algae in the vials, Didinium preys on Paramecium

Small systems are actually unstable, one of the species get extinct after a while.



Pimintel flies-wasps



Huffaker's (1958) oranges:

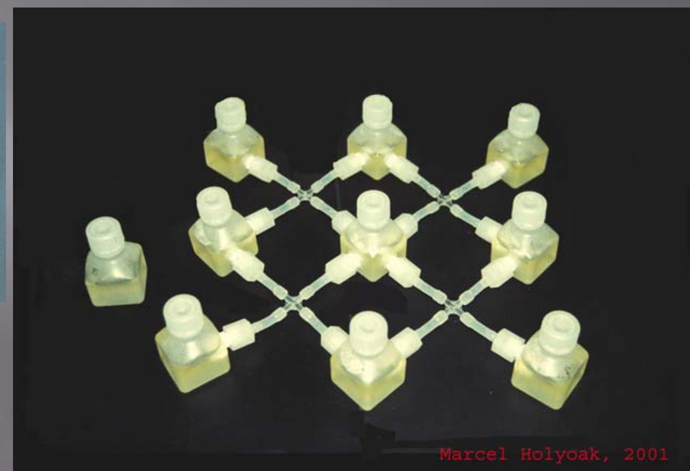
6-spotted mite and *Typhlodromus*

Stable oscillations in large systems: experimental (new)

Holyoak & Lawler (1996)

Predaor

Prey

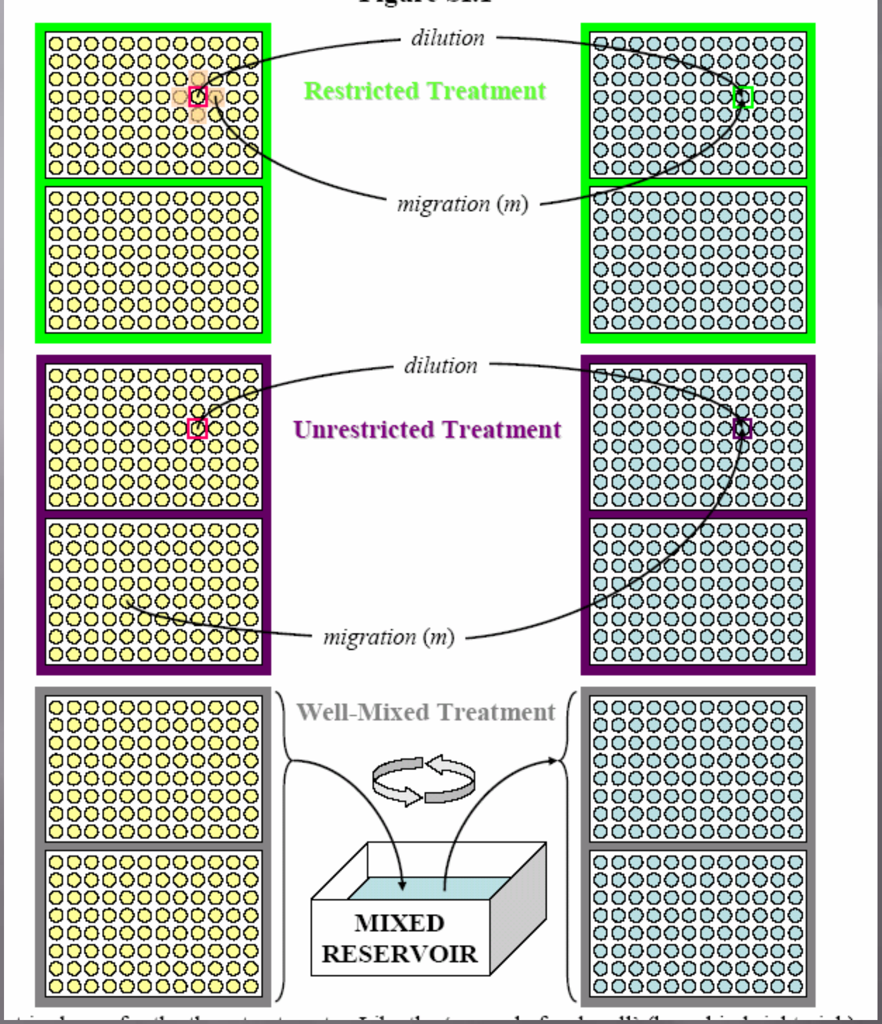


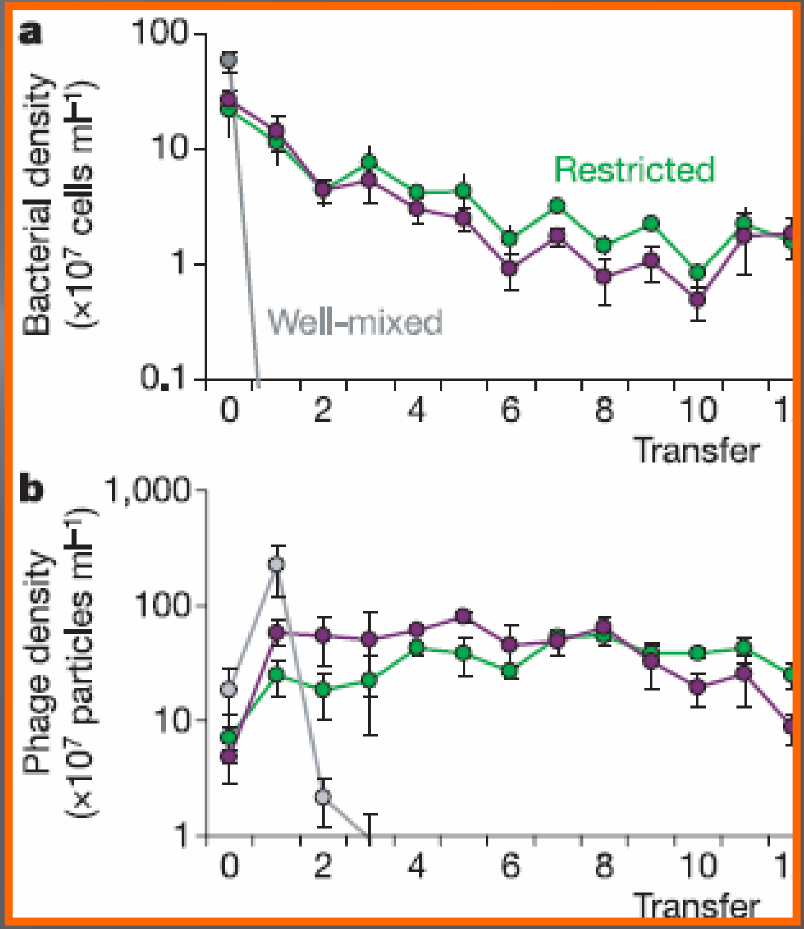
***microcosms typically consist of arrays of interconnected 30-mL bottles, isolated 30-mL bottles, or large undivided bottles of the same total habitat size** (not shown). **The predators and prey both move freely through the interconnecting tubes**.*

volumes: 30, 180, 270, and 750 mL. Subdivided microcosms, or "arrays," were groups of nine or 25 linked 30-mL bottles (270 or 750 mL total volume). In arrays, predators and prey persisted for 130 d (602 prey and 437 predator generations), at which point the experiment ended. Predators went extinct in undivided microcosms of equivalent volumes within a mean of only 70 d. Predators persisted for a mean of just 19 d in isolated 30-mL

E Coli (prey) phage (predator)

Kerr et. al., Nature 442 (2006)

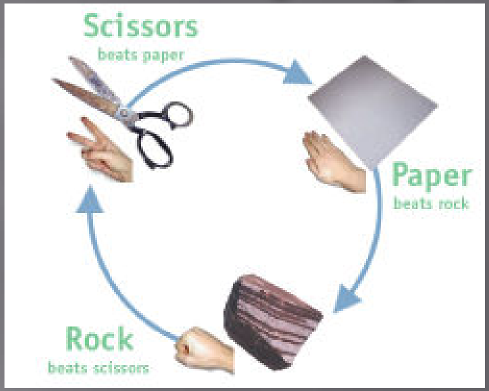


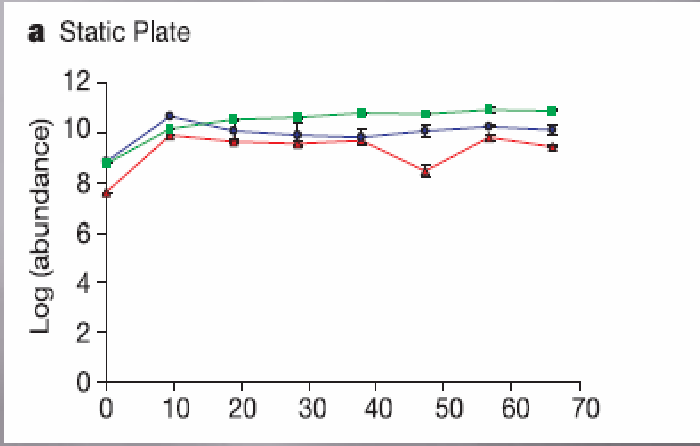


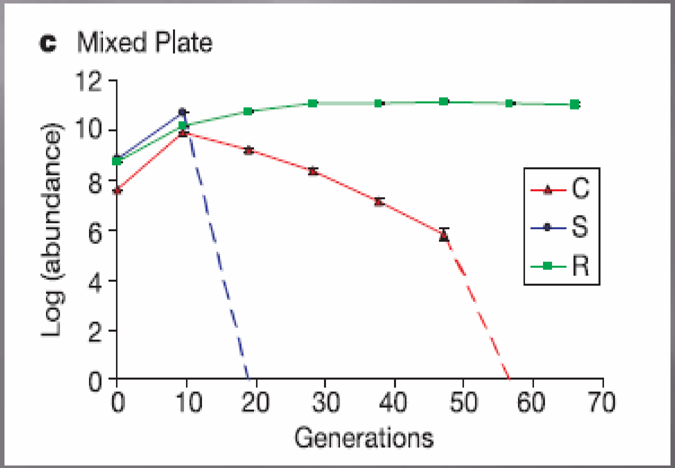
Bacteria playing rock-paper-scissors:

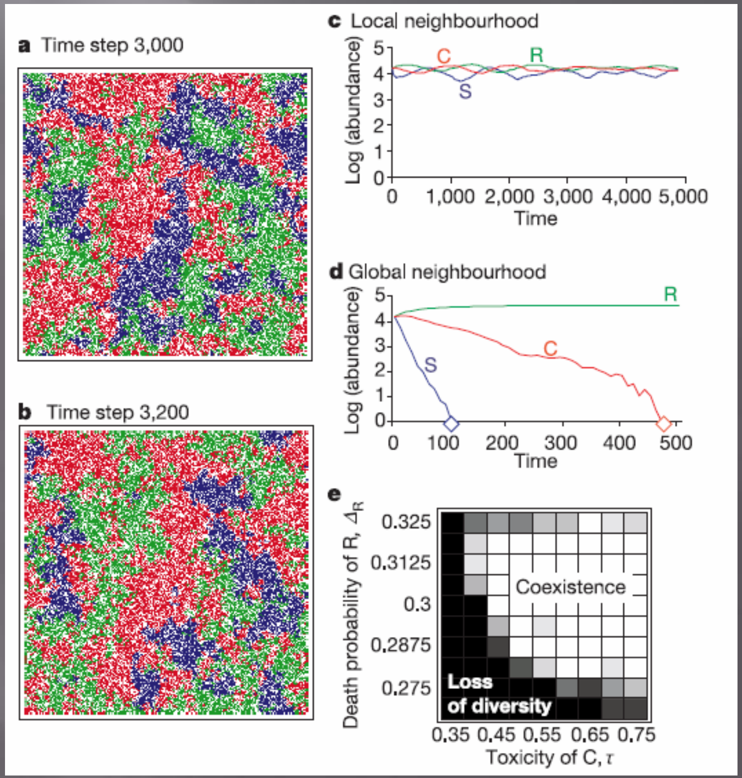
3 strains of E-Coli R,S and C

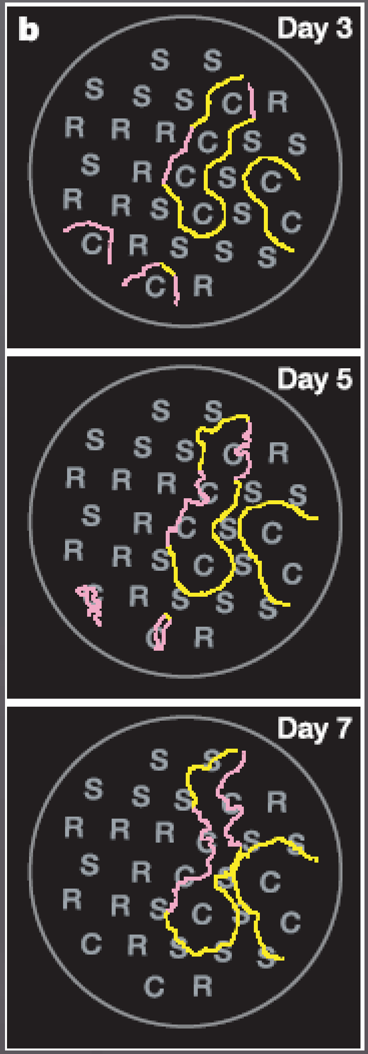
-Kerr et al, Nature 418 171 (2002)





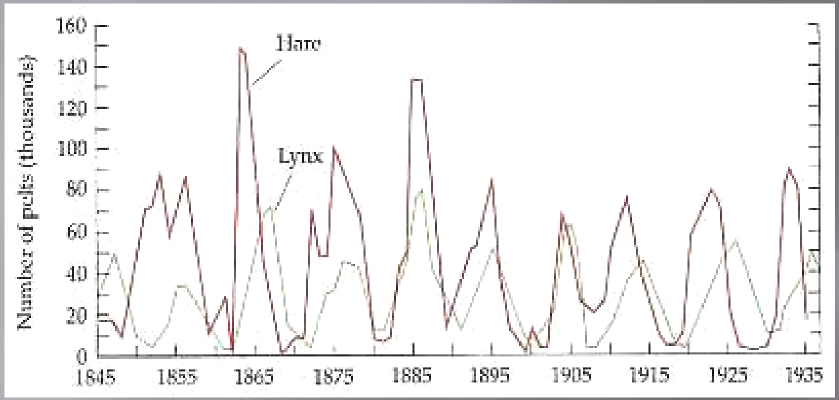






So why there are stable oscillations in large systems ? …

Lynx-Hare (Canada)



Prickly pear cactus – cactoblastis cactorum (eastern Australia)

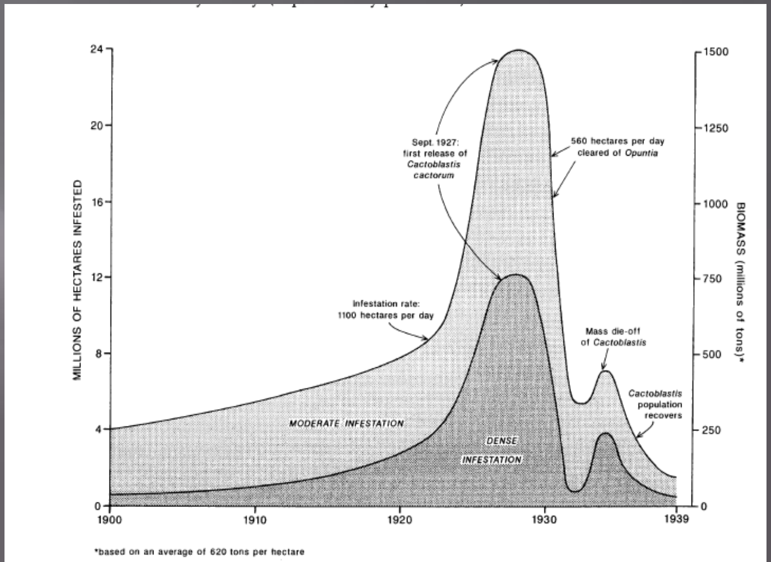
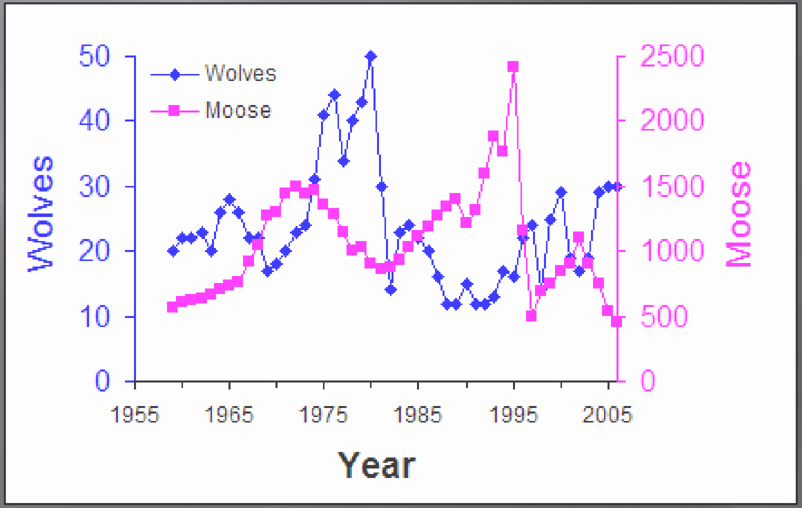


FIG. 4—Growth and collapse of prickly pear infestations 1900–1939. *Sources:* Survey data and estimates from Steele 1923; Dodd 1940; Johnston and Lloyd 1982.

Moose-Wolves (Isle Royal)



Experiments + theory suggest that it has to do with the fact that the population is spatially structured, with patches connected by migration. But how ??

The writing was on the wall… Nicholson 1933:

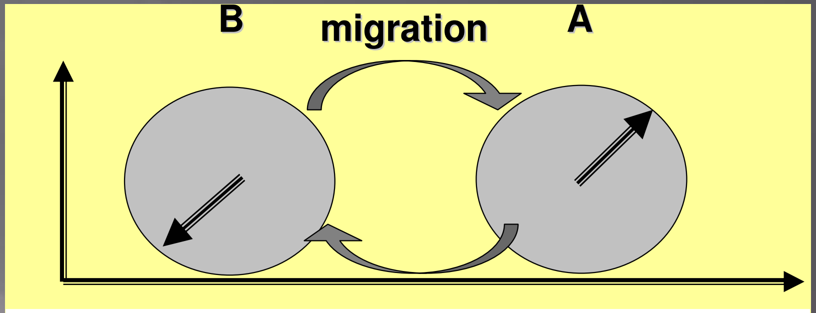
of hosts, some of which have established new groups. Thus, instead of there being a simultaneous oscillation of the animals throughout the whole environment, there are large numbers of independent local systems of oscillation, all phases of oscillation being represented in the environment at any given time. The fact that parasites can develop only in areas in which hosts occur means that such areas are searched more intensively than the rest of the environment. Consequently, the parasites do not have to cover a fraction of the whole environment equal to the fraction of hosts that is surplus, but only need to cover a much smaller fraction in order to find the surplus hosts. Therefore the density of parasites, and consequently the density of hosts, necessary for balance under the given conditions is much below the calculated values of the steady densities of the animals.

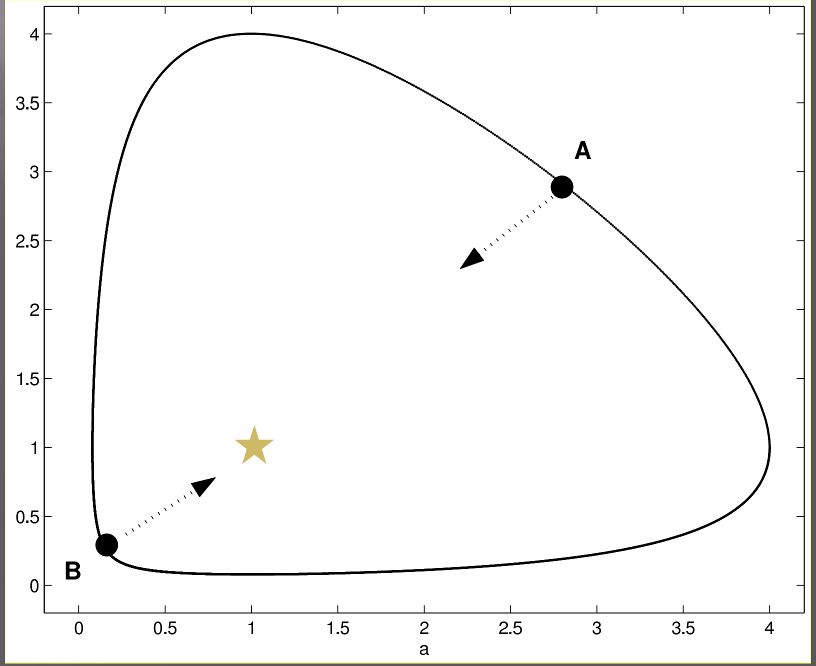
Predator-prey system persist, even under the influence of *noise*, on spatial domains connected by *migration* (diffusion) due to *desynchronization* of different patches.

Noise + Migration + **Desynchronization** = stability

Nicholson's proposal - two patches example:

1. ***If*** *the two patches desynchronize,* ***then*** *migration stabilizes the oscillations:*





2. *Diffusion (migration) between desynchronized patches yields a flow towards the fixed point, i.e., stabilization.*

3. *On the other hand, the diffusion itself tend to synchronize the two patches.*

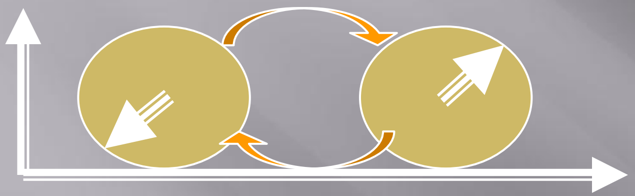
Synchronization:

When oscillating systems are coupled, they tend to synchronize

This happens even for mechanical coupling, not to mention diffusive coupling (density independent migration) that tends to decrease gradients !!

Two coupled LV patches
Migration induced synchronization

$$\frac{\partial a_1}{\partial t} = -\mu a_1 + \lambda a_1 b_1 + D(a_2 - a_1)$$
$$\frac{\partial b_1}{\partial t} = \sigma b_1 - \lambda a_1 b_1 + D(b_2 - b_1)$$



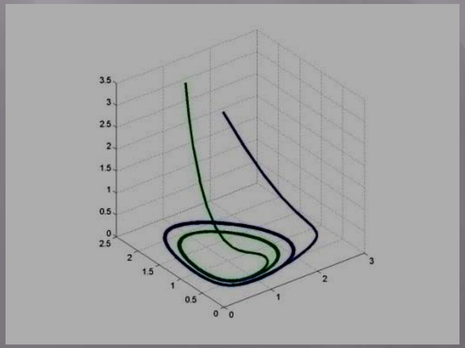
a1(t=0) = 3

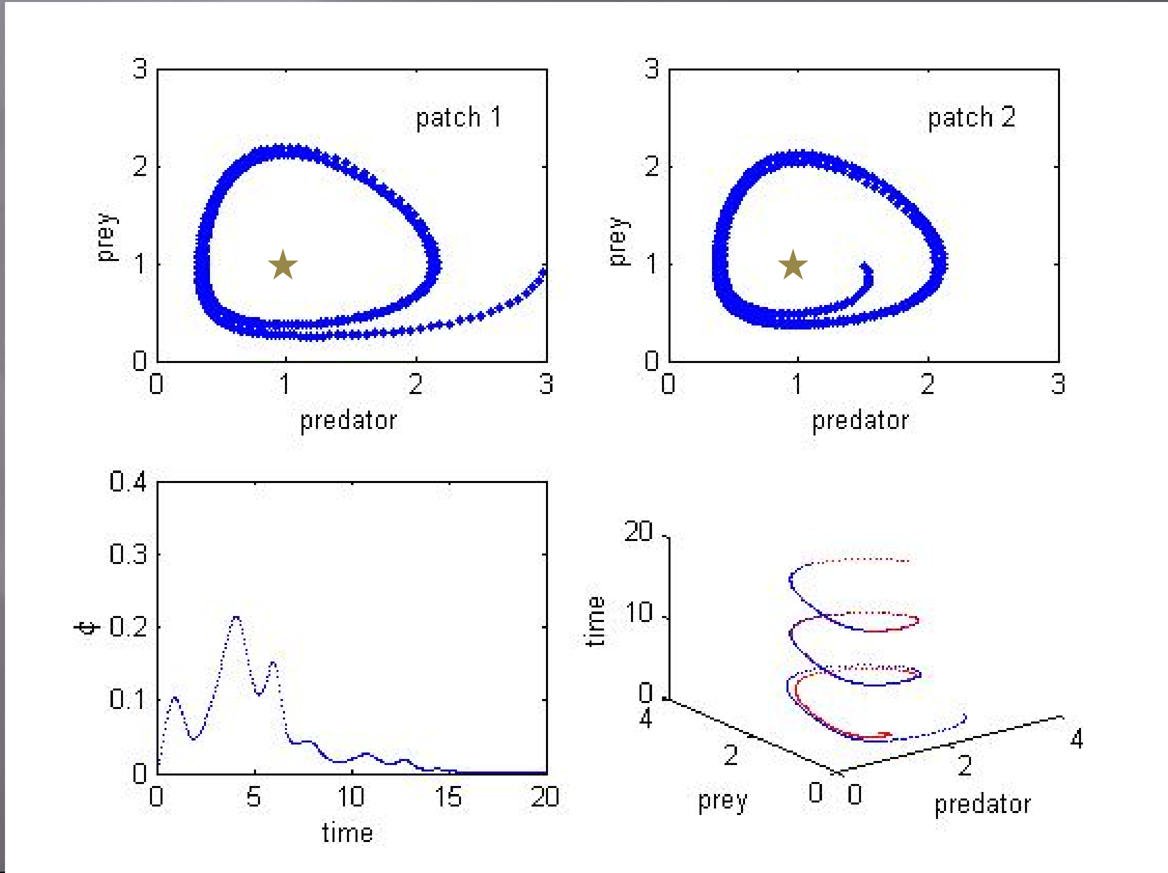
a2(t=0) = 1.5

b1(0)=b2(0) =1

D=0.2

Homogenous (invariant) manifold





The challenge:

find a mechanism that maintains desynchronization in the presence of migration, thus allowing migration to be a stabilizer.

"A unifying explanation or approach has remained elusive …."
[Keeling, Wilson and Pacala, Science 290 1758 (2000)]

The answers:

- *Spatial heterogeneity*
- *Environmental stochasticity*
- *Jansen's mechanism*
- *Noise - nonlinearity induced stability.*

Spatial heterogeneity- LV

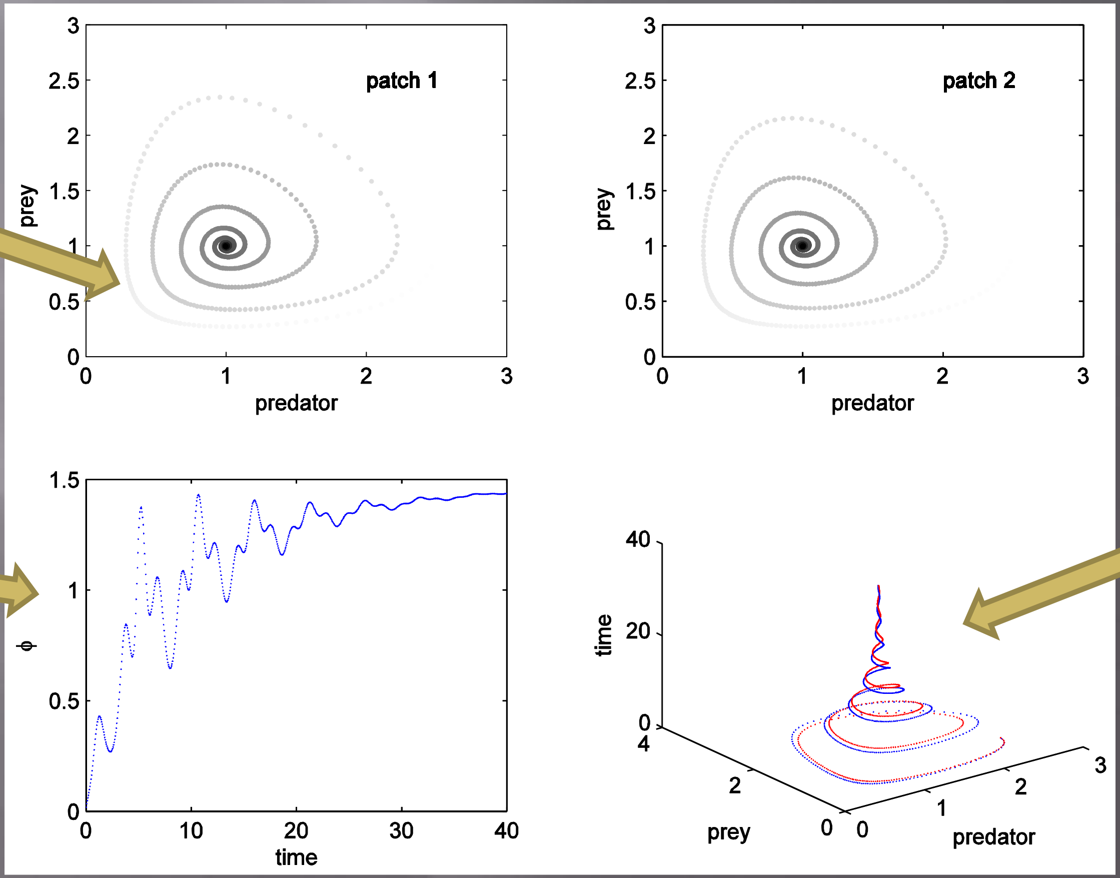
$$\frac{\partial a_1}{\partial t} = -a_1 + a_1 b_1 + D(a_2 - a_1)$$
$$\frac{\partial b_1}{\partial t} = b_1 - a_1 b_1 + D(b_2 - b_1)$$

$$\frac{\partial a_2}{\partial t} = -q a_2 + q a_2 b_2 + D(a_1 - a_2)$$
$$\frac{\partial b_2}{\partial t} = q b_2 - q a_2 b_2 + D(b_1 - b_2)$$

q = 1.4

Gray scale – later times are darker.

Same initial conditions for both patches – system initiated on the invariant manifold



Constant phase Between demoi

Convergence to the fixed point

Environmental stochasticity

$$\frac{\partial a_1}{\partial t} = -a_1 + a_1 b_1 + D(a_2 - a_1)$$

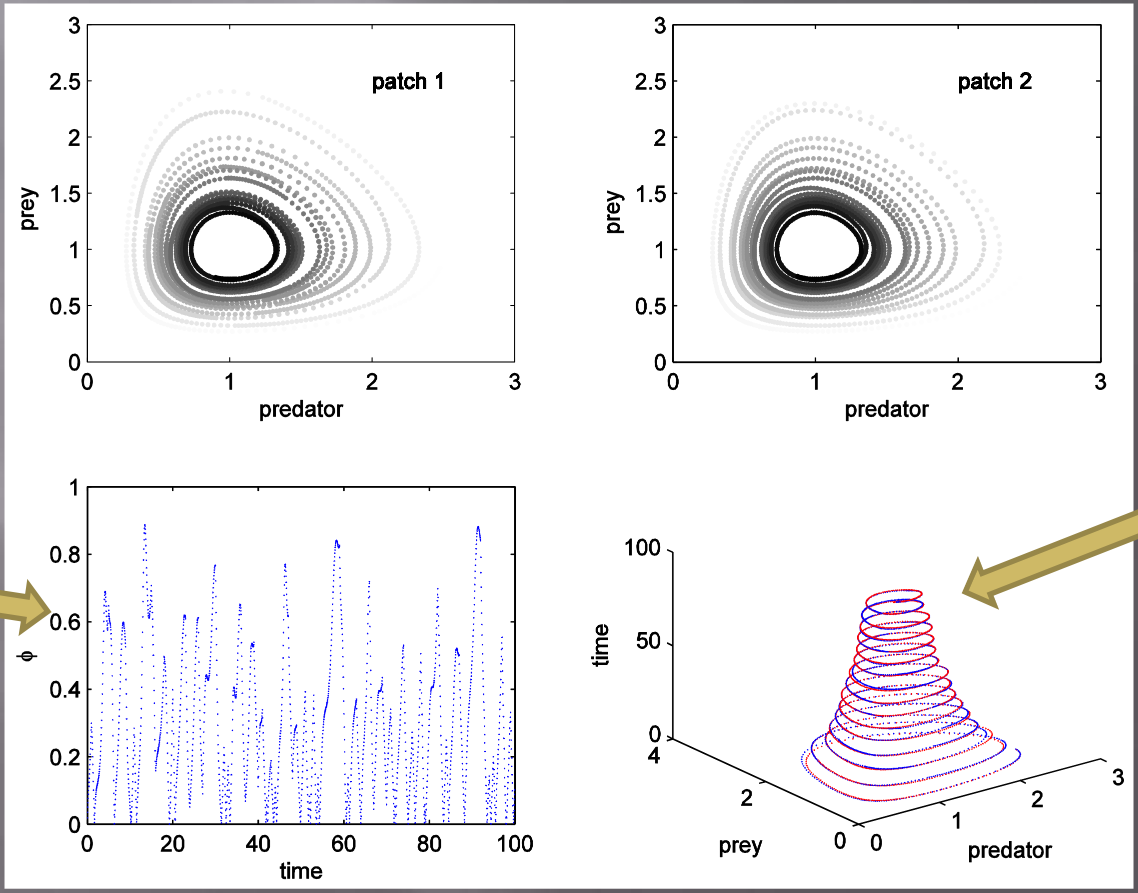
$$\frac{\partial b_1}{\partial t} = b_1 - a_1 b_1 + D(b_2 - b_1)$$

$$\frac{\partial a_2}{\partial t} = -q a_2 + q a_2 b_2 + D(a_1 - a_2)$$

$$\frac{\partial b_2}{\partial t} = q b_2 - q a_2 b_2 + D(b_1 - b_2)$$

***q* jumps randomly between 1.4 and 0.6**

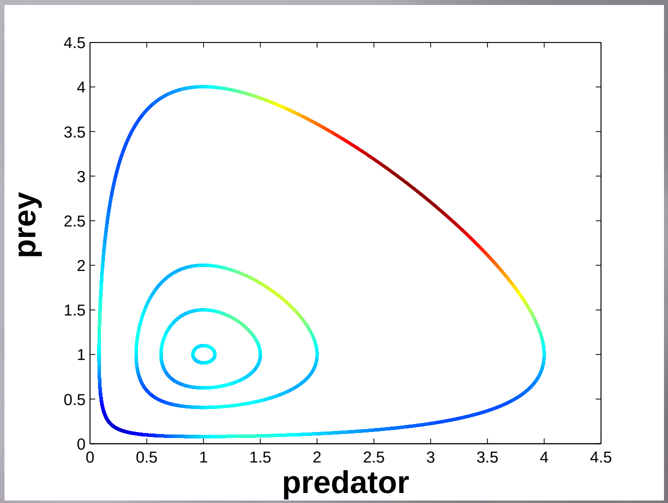
Same initial conditions for both patches – system initiated on the invariant manifold



Phase oscillates

Convergence to the fixed point

Jansen's Mechanism

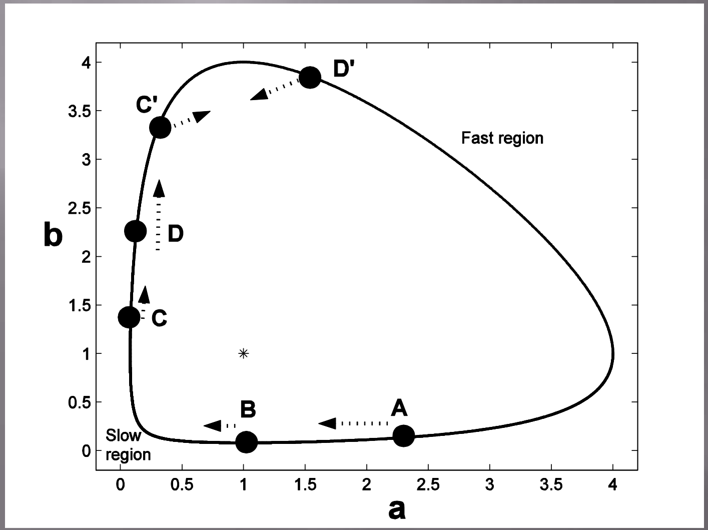


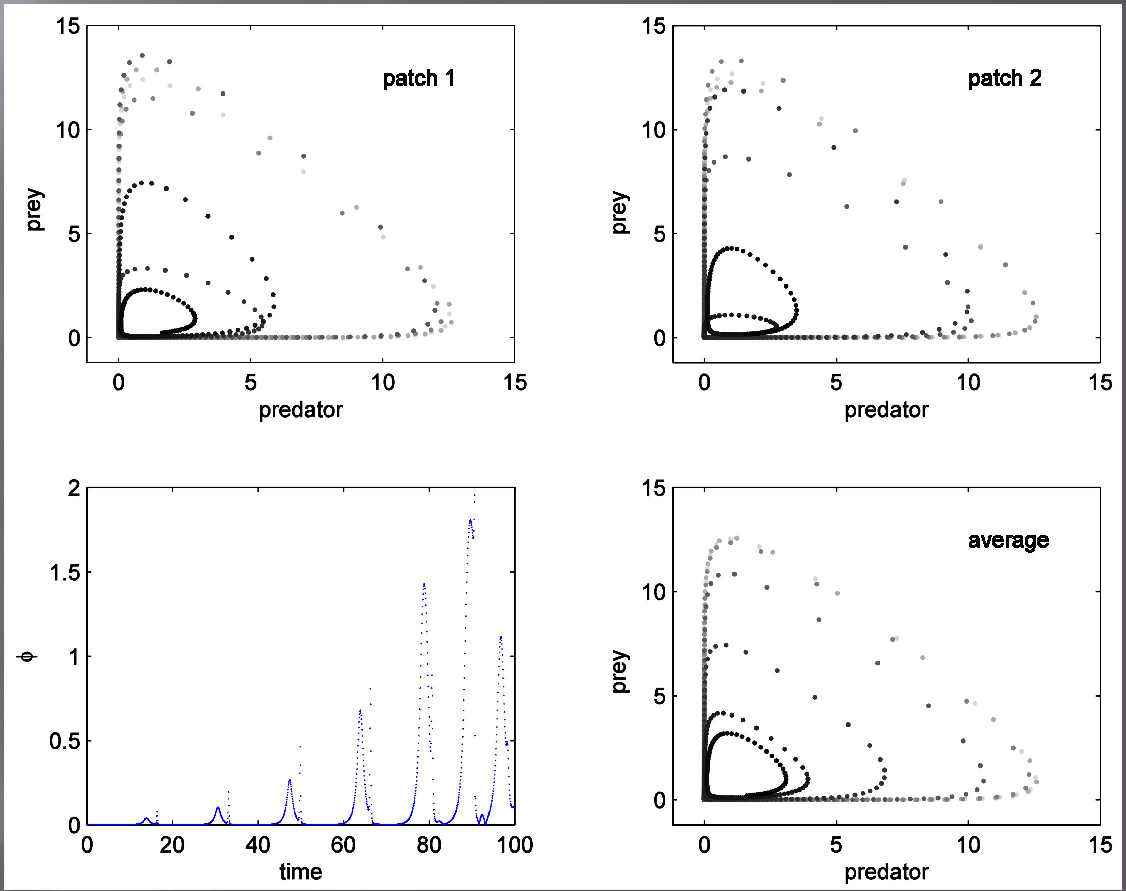
$$\frac{\partial a_1}{\partial t} = -a_1 + a_1 b_1 + D(a_2 - a_1)$$

$$\frac{\partial b_1}{\partial t} = b_1 - a_1 b_1$$

$$\frac{\partial a_2}{\partial t} = -a_2 + a_2 b_2 + D(a_1 - a_2)$$

$$\frac{\partial b_2}{\partial t} = b_2 - a_2 b_2$$

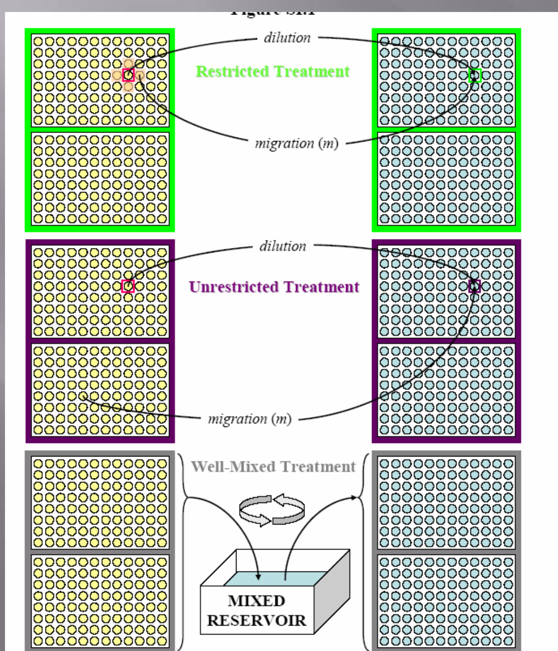


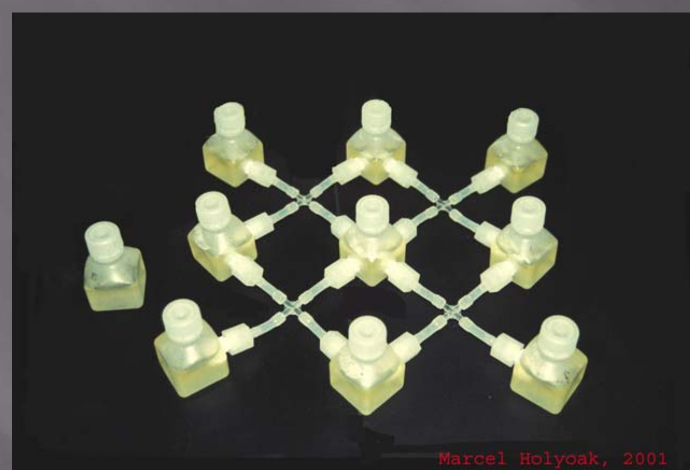


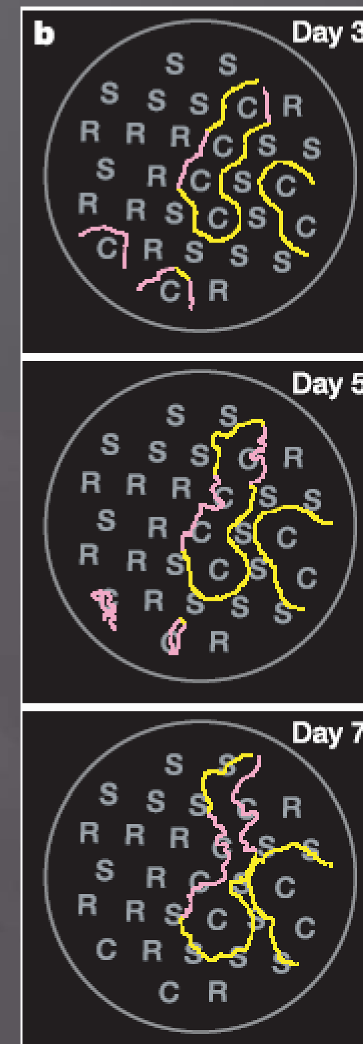
Is that enough ?

Is the stability of these systems relays on one of these mechanisms?

- *Systems seems to admit neither spatial heterogeneity nor environmental stochasticity.*
- *Migration rates are more or less equal for the exploiter and the victim.*

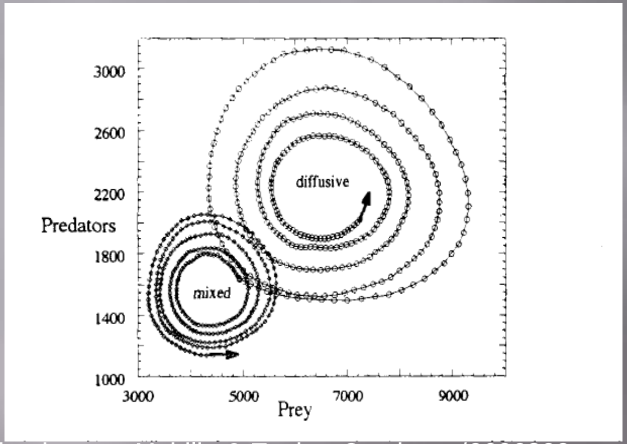






Results from individual-based simulations of predator-prey model. 100% free of any environmental differences, same migration rates, still, it seems that even demographic stochasticity may stabilize the system.

Wilson, de Roos, McCauley, Theor. Pop. Bio. 43, 91 1993



Bettelheim, Agam, Shnerb Physica E 9, 600 (2001)

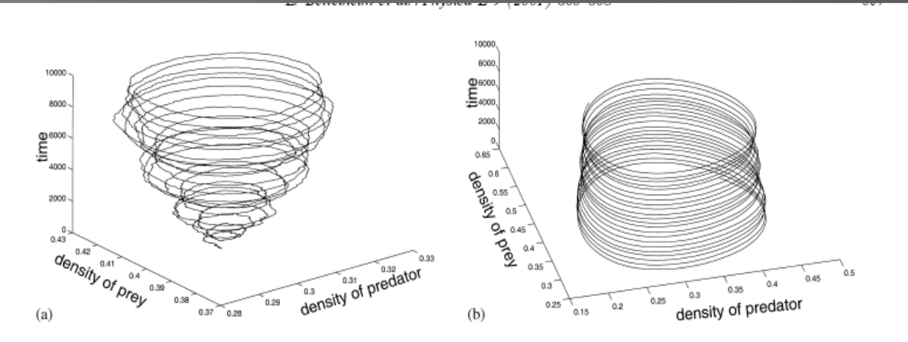


Fig. 2. Plot of prey and predator densities as a function of time for $\lambda = 0.02, \sigma = 0.006, \mu = 0.008$. Upper panel shows simulations with initial conditions near the fixed point. Here the system flows away from the fixed point. The lower panel shows the flow when the initial conditions are set to be far from the fixed point. The converging behavior of the trajectories signals that the dynamics is attracted to a limit cycle.

Washenberger, Mobilia & Tauber Cond-mat/0606809

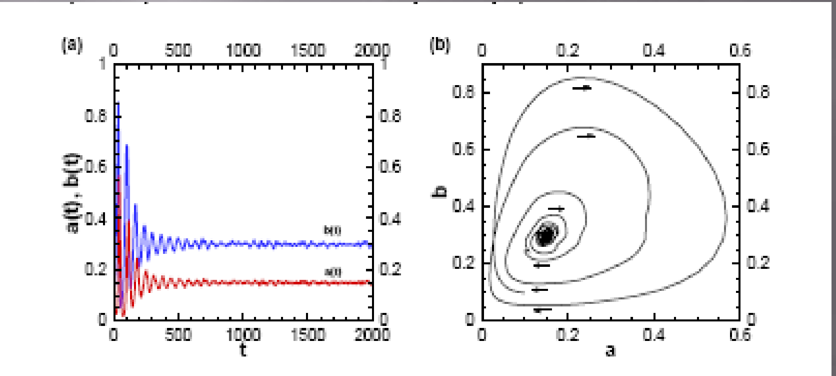
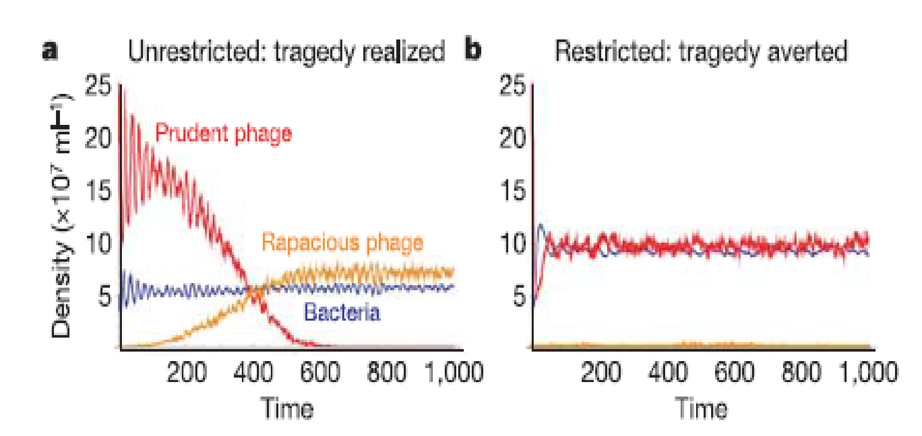


Figure 5. (a) Predators $a(t)$ (red) and prey $b(t)$ (blue) densities vs. time in a simulation run on a 1024×1024 lattice, with random initial distribution, and rates $\sigma = 0.1$, $\mu = 0.2$, $\lambda = 1.0$, and initial densities $a(0) = b(0) = 0.1$. (b) Trajectory in the a-b plane from the simulation data shown in (a), up to $t = 1000$. (Colour online.)

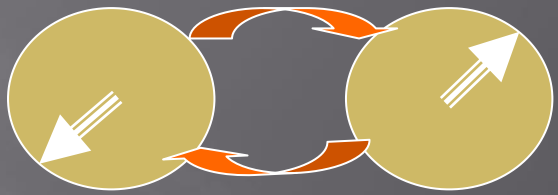
Kerr et. Al. , Nature 2006

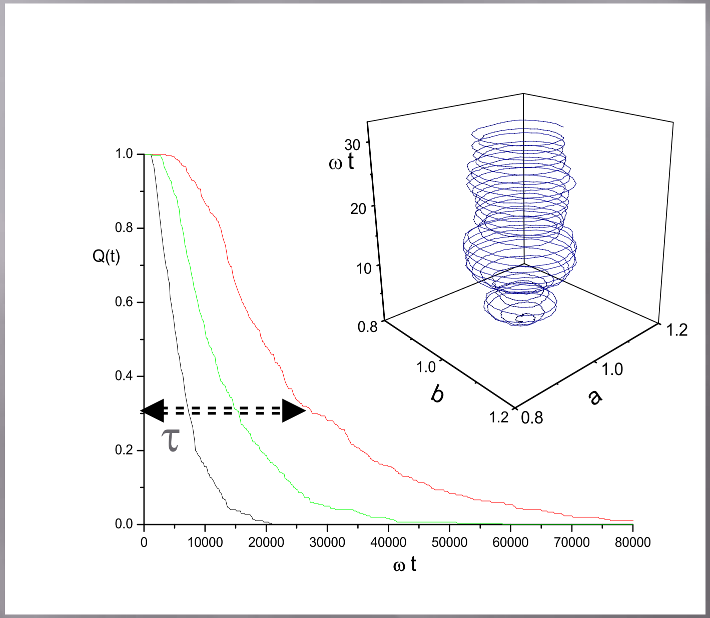


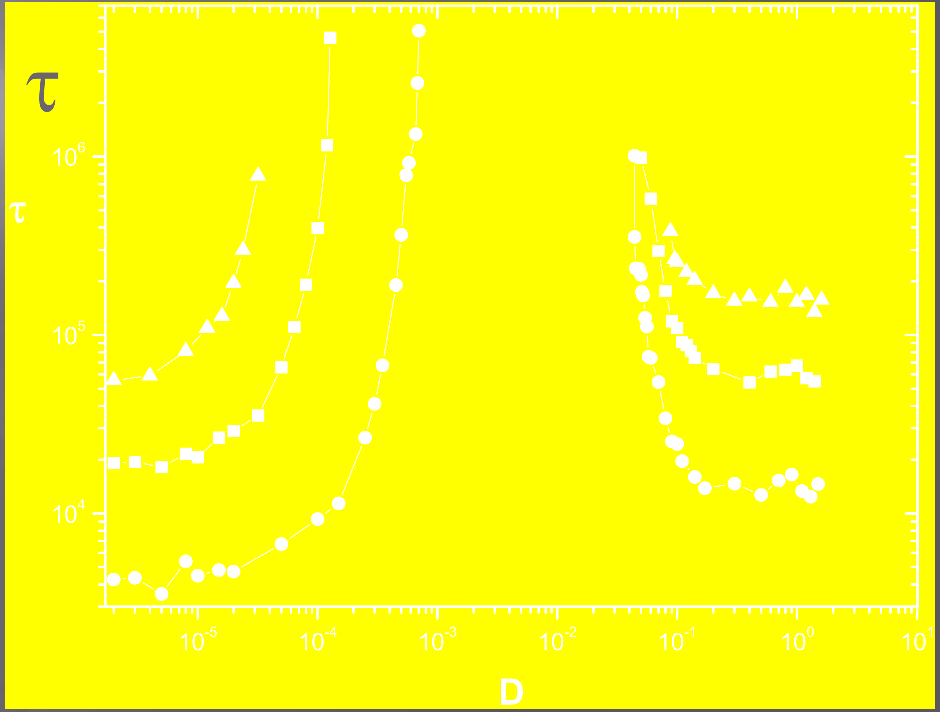
What is going on ?

Two LV patches

Single patch: servival probability Q(t) for few noise amplitudes







Lifetime grows with diffusion -> appearance of an attractive manifold.

What is going on ???

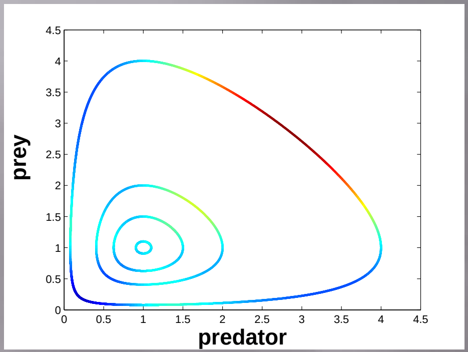
Noise and nonlinearity: Amplitude dependent angular velocity

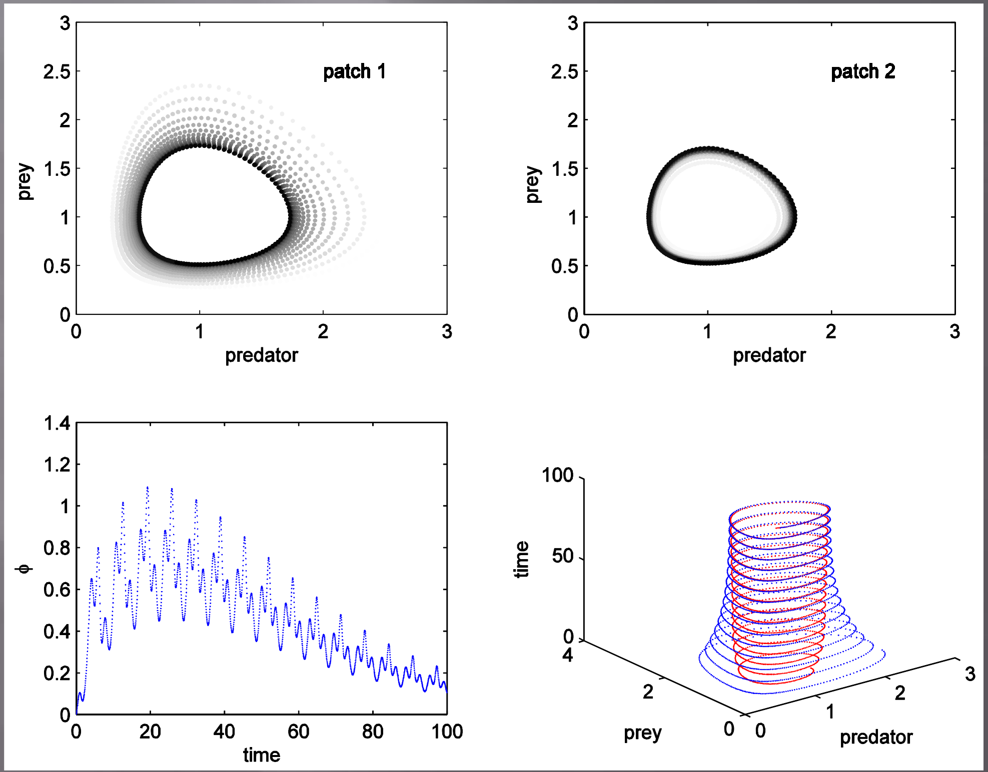
$$\frac{\partial a_1}{\partial t} = -a_1 + a_1 b_1 + D(a_2 - a_1) + noise$$

$$\frac{\partial b_1}{\partial t} = b_1 - a_1 b_1 + D(b_2 - b_1) + noise$$

$$\frac{\partial a_2}{\partial t} = -a_2 + a_2 b_2 + D(a_1 - a_2) + noise$$

$$\frac{\partial b_2}{\partial t} = b_2 - a_2 b_2 + D(b_1 - b_2) + noise$$

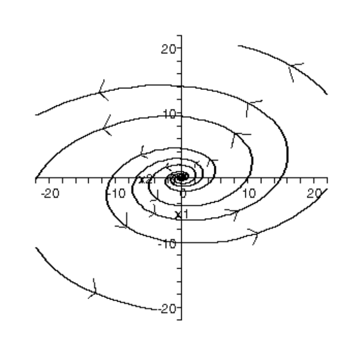


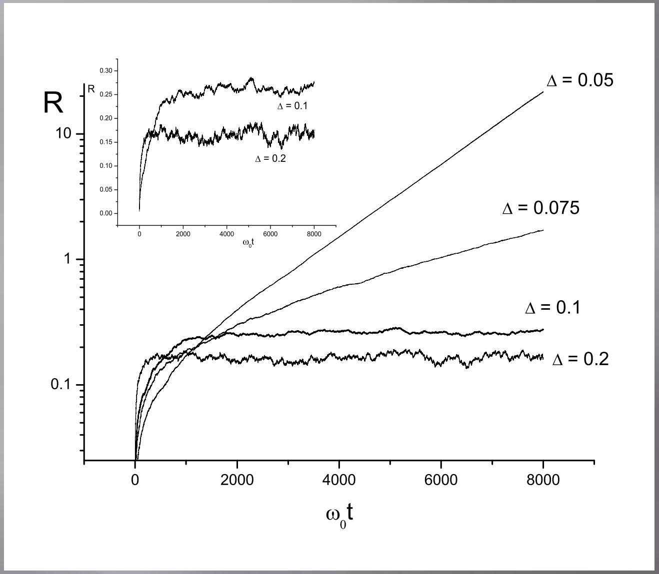


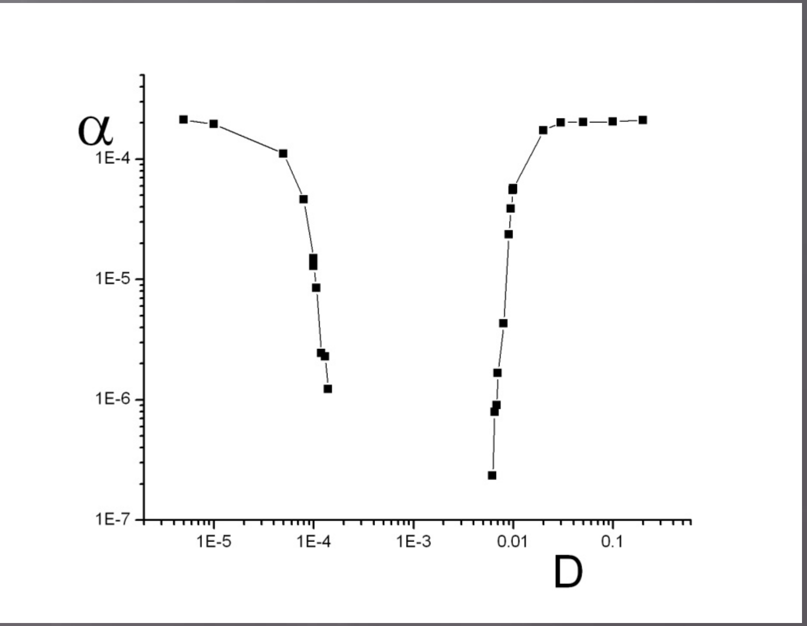
Noise induces amplitude differences.
+
Angular velocity depends on amplitude
=
desynchronization

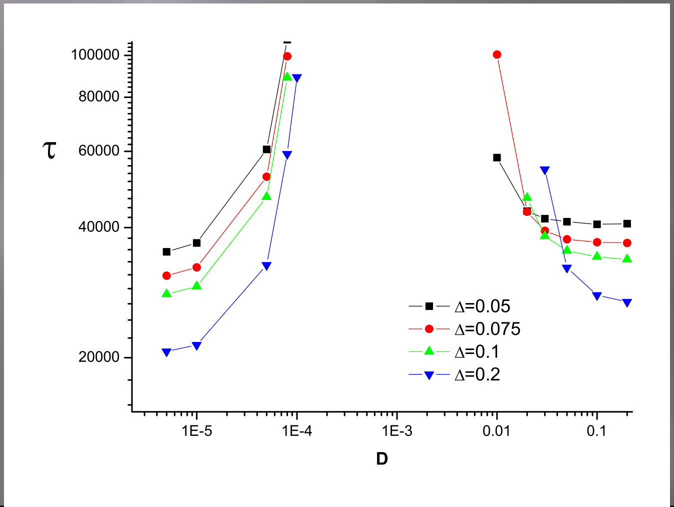
Phys. Rev. Lett. **98**, 098104 (2007).

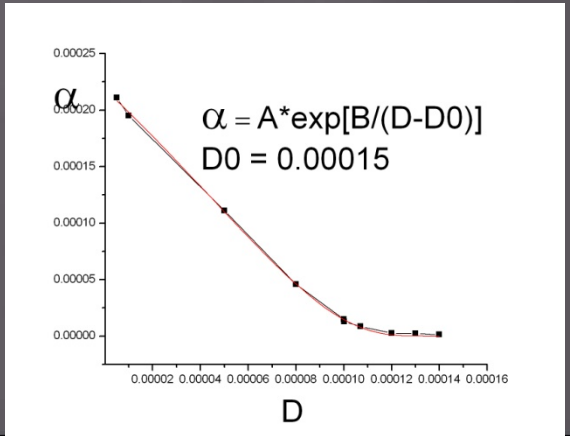
Unstable (NB) case: phase transition at finite noise









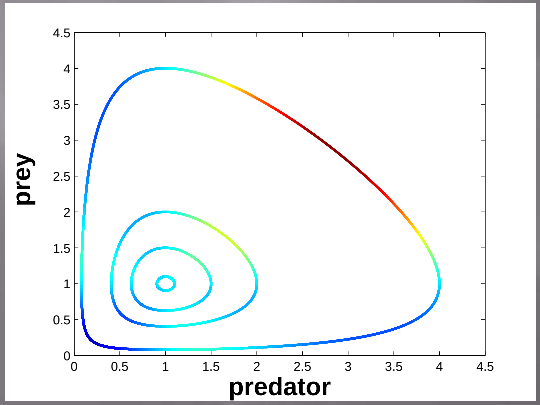


Coupled oscillators model for ADAV

$$\frac{\partial a_1}{\partial t} = D(a_2 - a_1) + \omega(r_1)b_1 + \eta_1(t)$$
$$\frac{\partial a_2}{\partial t} = D(a_1 - a_2) + \omega(r_2)b_2 + \eta_2(t)$$
$$\frac{\partial b_1}{\partial t} = D(b_2 - b_1) - \omega(r_1)a_1 + \eta_3(t)$$
$$\frac{\partial b_2}{\partial t} = D(b_1 - b_2) - \omega(r_2)a_2 + \eta_4(t)$$
$$\eta \in \Delta^2 \cdot \left[-\frac{1}{2}, \frac{1}{2}\right]$$

Noise yields finite distribution of r, NOW this implies different angular velocities along different trajectories. Thus <θ^2> acquires finite expectation value, so does the "restoring force" on the invariant manifold R.

This model supports all the 4 stability mechanisms. May be used to classify the underlying stabilizer using a-priory knowledge of model parameters or aposteriori measurements of species abundance.

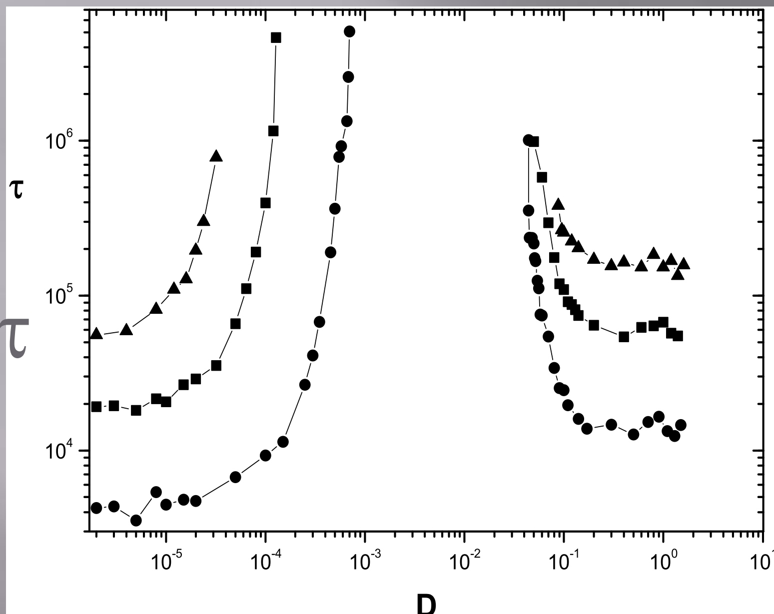


$$r_i \equiv \sqrt{a_i^2 + b_i^2} \qquad tg(\theta_i) \equiv \frac{b_i}{a_i}$$
$$R \equiv r_2 + r_1 \quad r = r_2 - r_1 \quad \varphi \equiv \theta_2 - \theta_1 \quad \Theta \equiv \theta_2 + \theta_1$$
$$\frac{\partial R}{\partial t} = -2DR\sin^2\left(\frac{\varphi}{2}\right) + \eta_R(t)$$
$$\frac{\partial r}{\partial t} = -2Dr\cos^2\left(\frac{\varphi}{2}\right) + \eta_r(t)$$
$$\frac{\partial \varphi}{\partial t} = -2D\left(\frac{R^2 + r^2}{R^2 - r^2}\right)\sin\varphi + \left[\omega(r_2) - \omega(r_1)\right]$$

Lotka Volterra Vs. Coupled oscillators: Lifetime as a function of migration rate

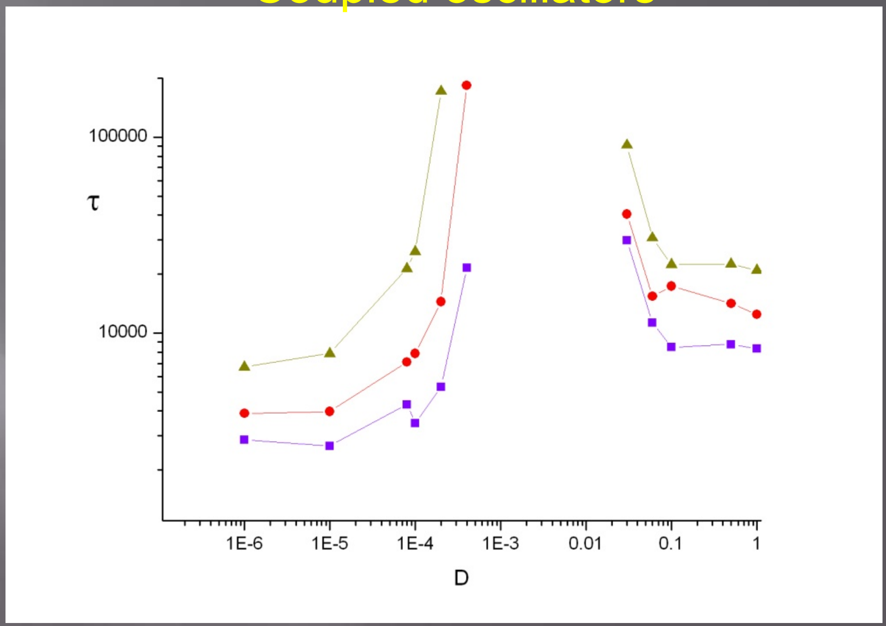
Lotka-Volterra with additive noise

τ

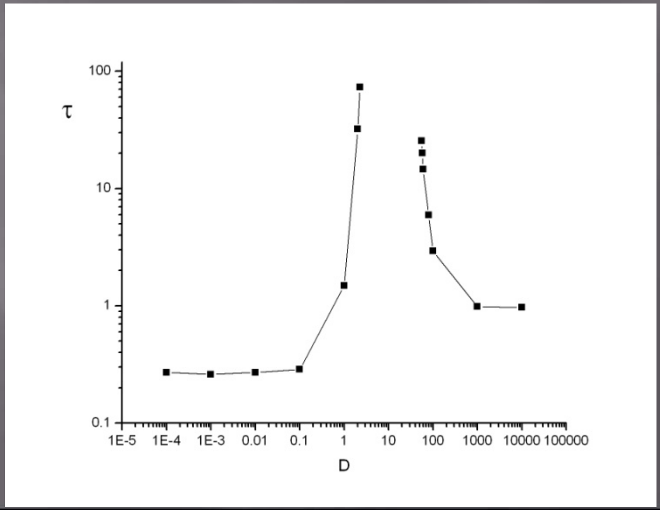


Coupled oscillators

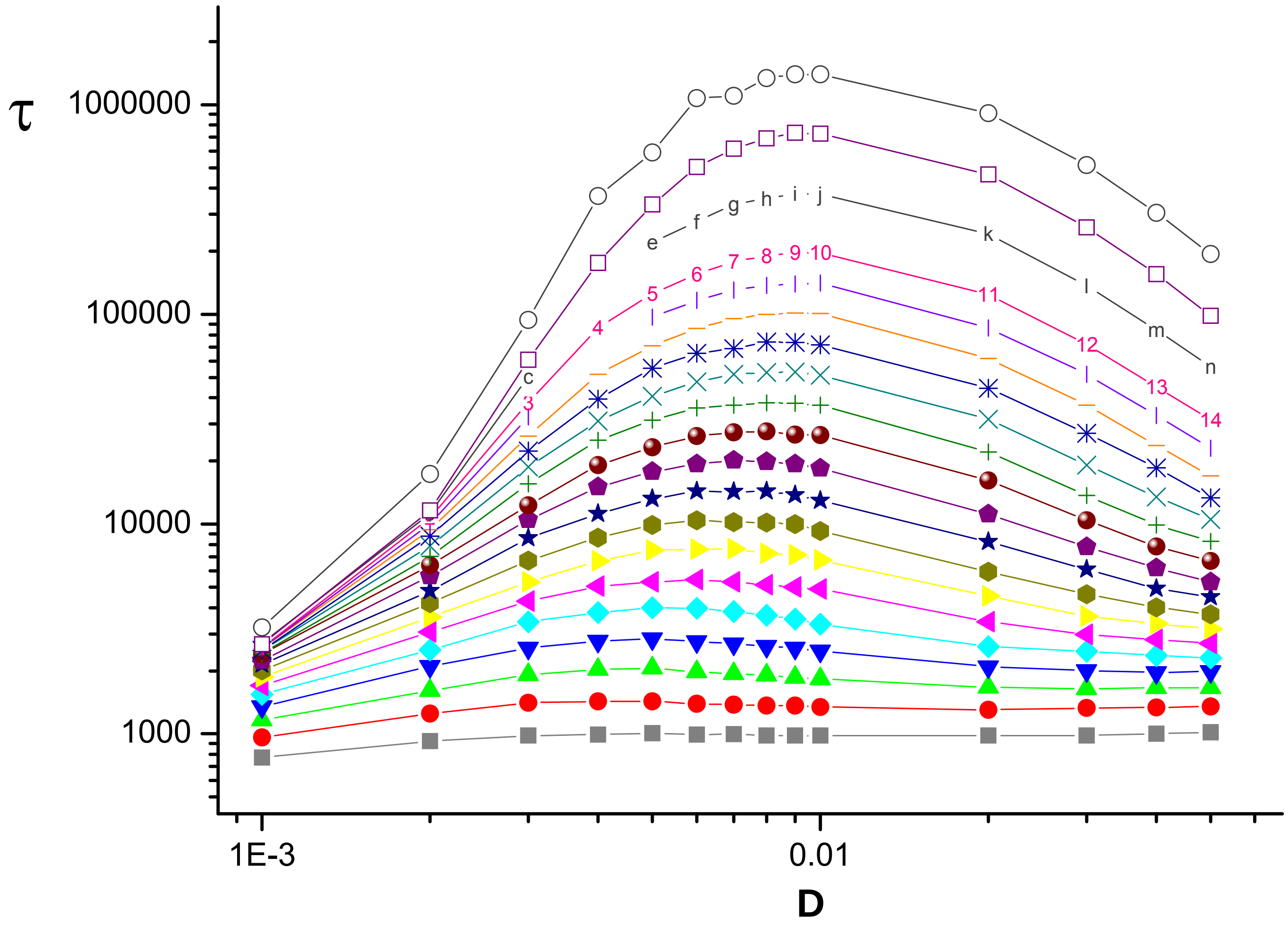
τ



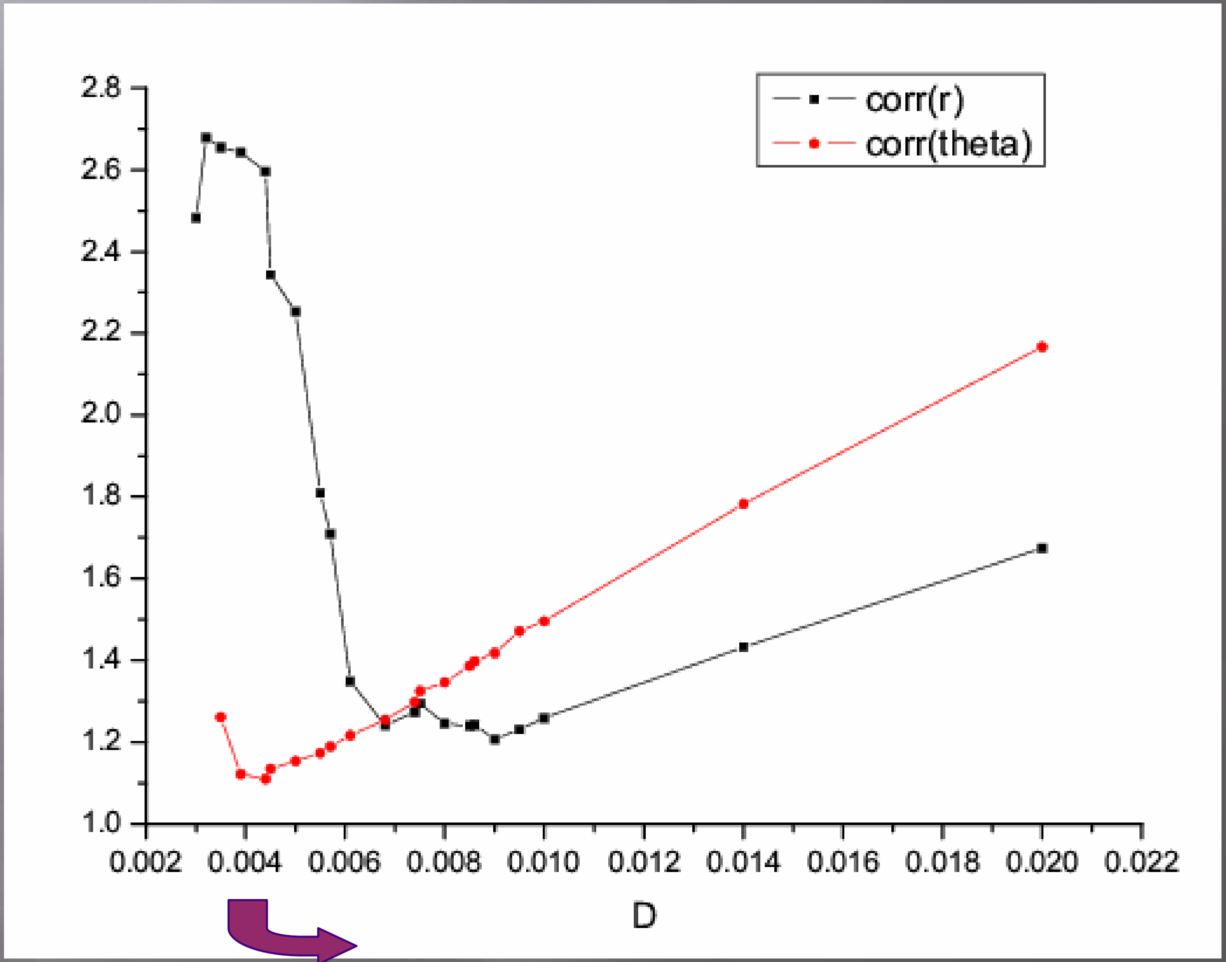
"Demographic stochastisity": LV with discrete agents, using event-driven algorithm. 1000 agents per site.



The skew shape of the average   time to extinction

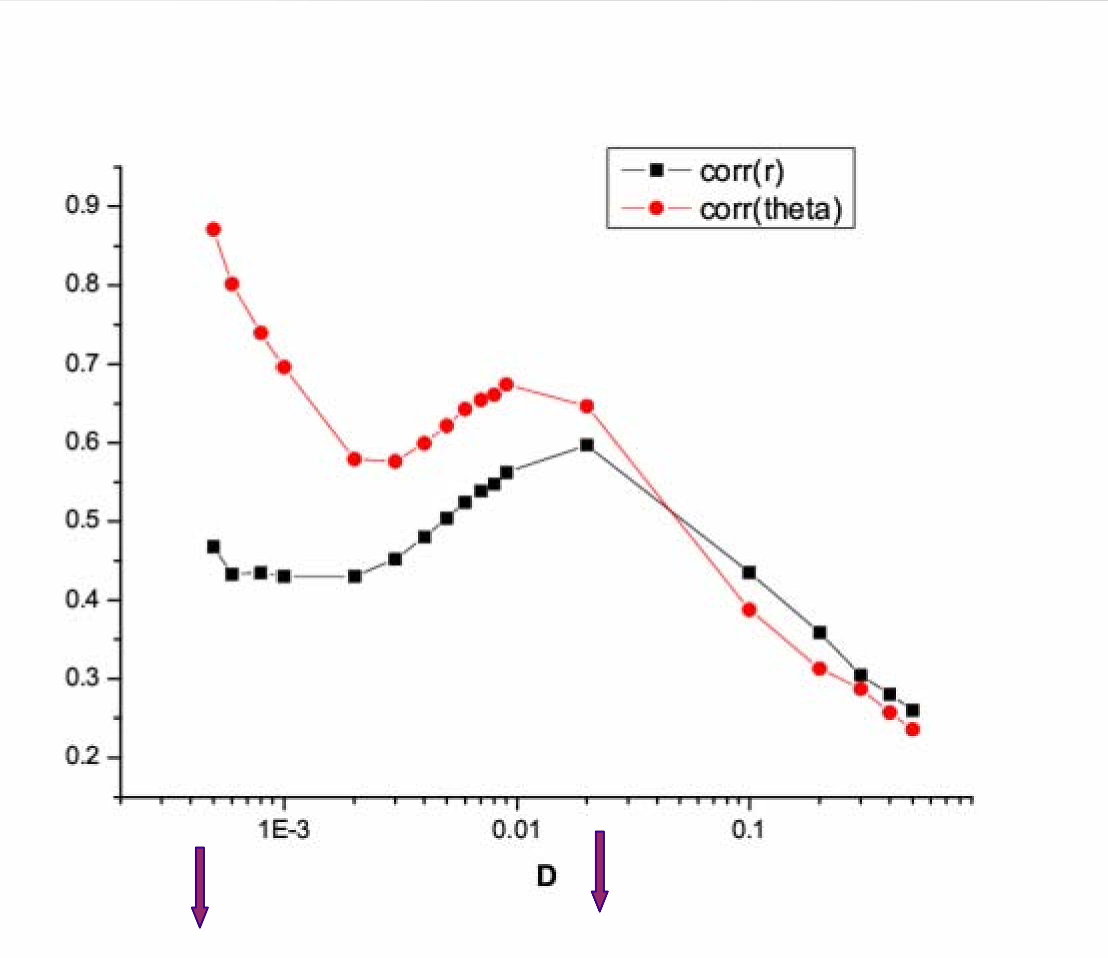


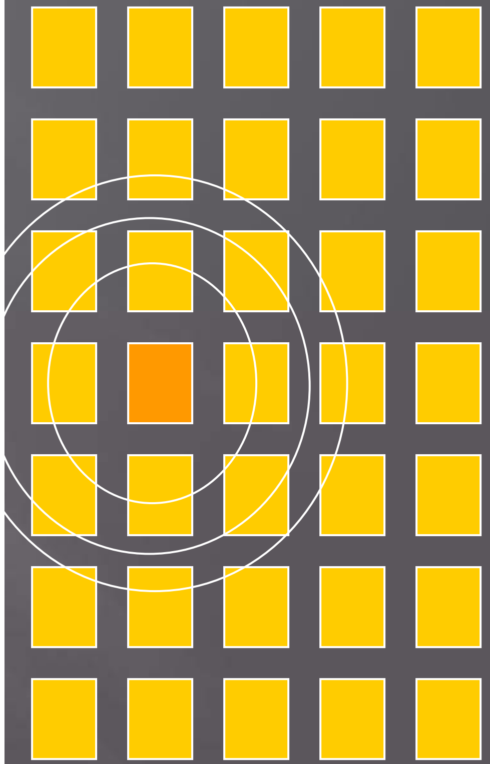
Correlation length: 1D system- 64 patches



DP transition??

Correlation Length-2D system

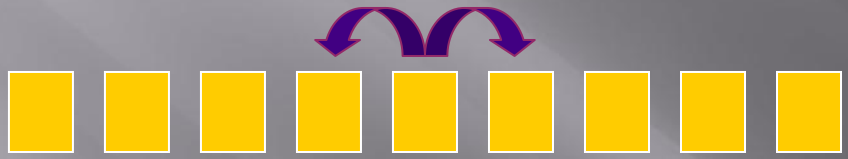




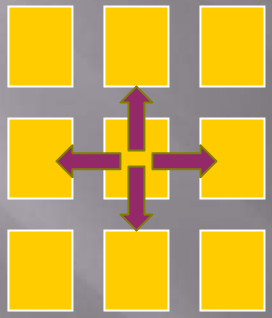
DP transition?

Percolation transition?

Topological effects

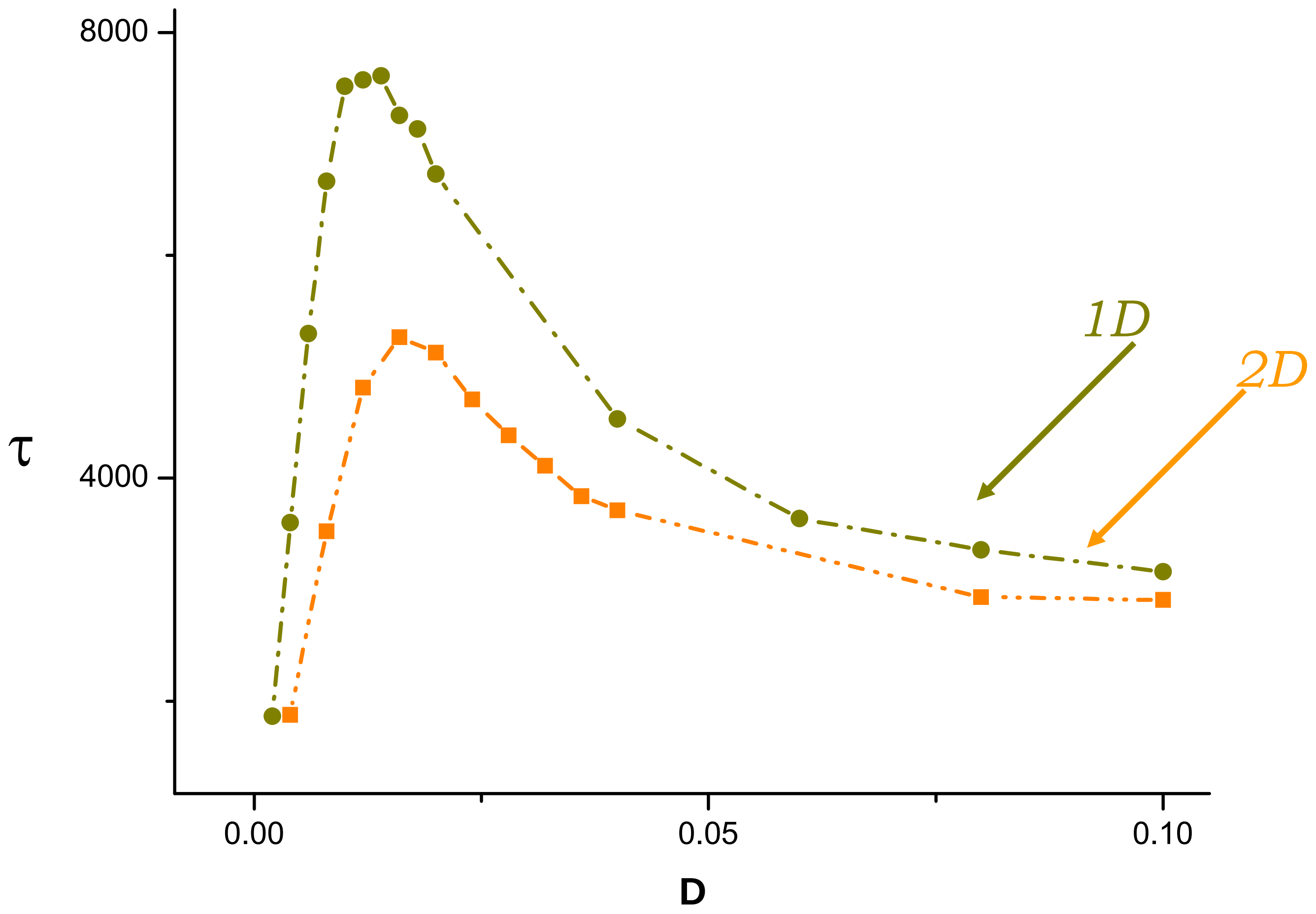


1D

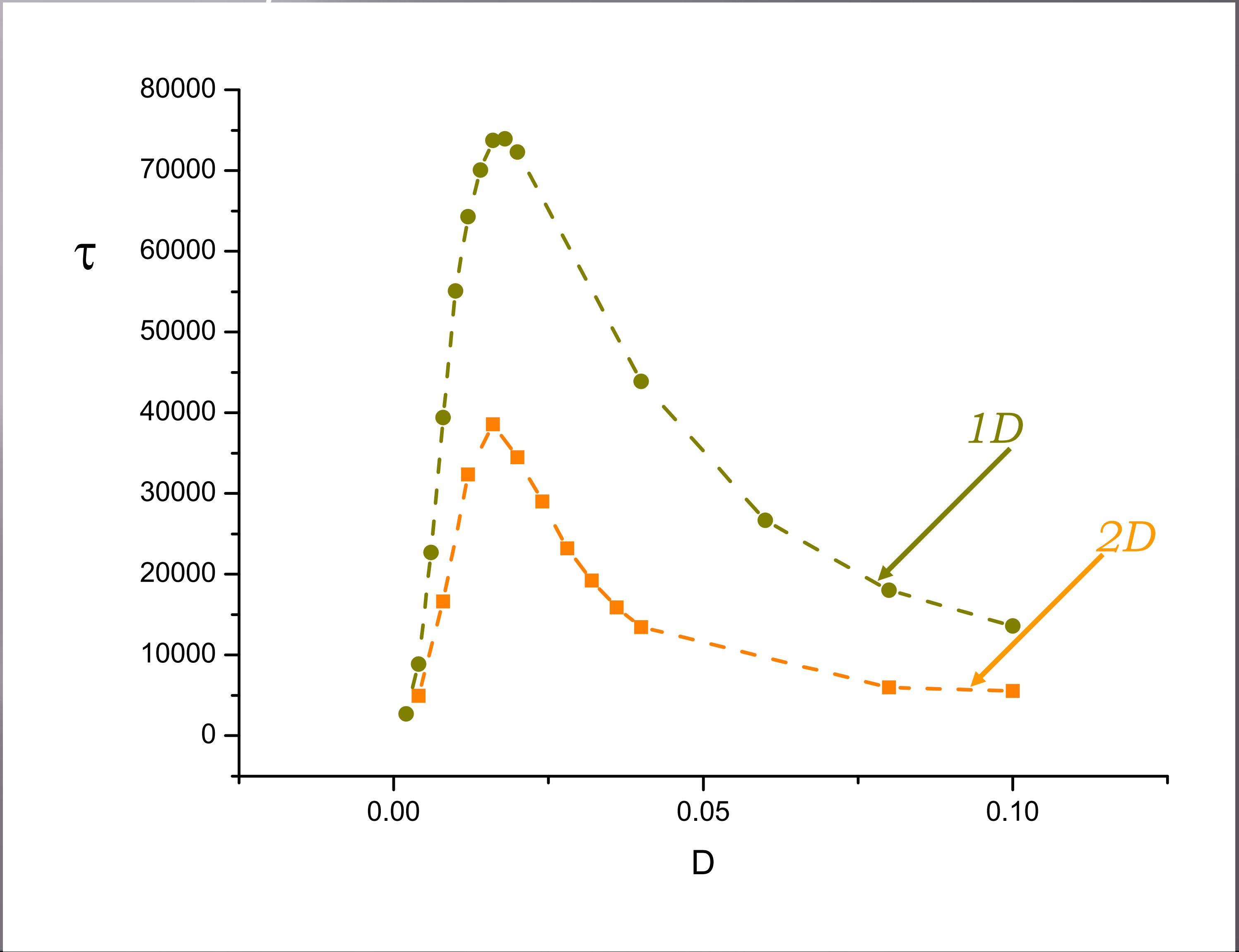


2D

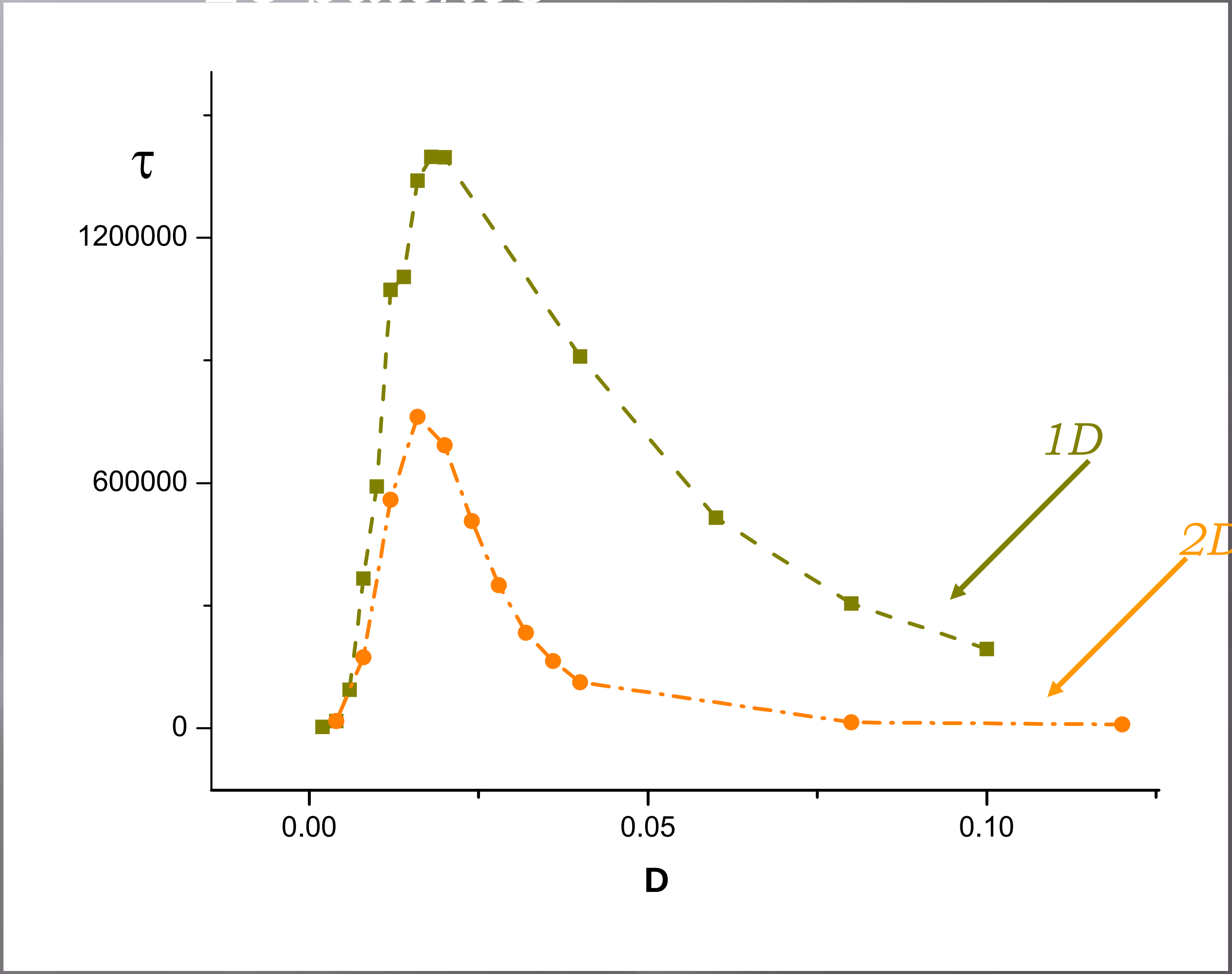
9 patches-



16 patches-


80000
70000
60000
50000
40000
30000
20000
10000
0
τ
0.00
0.05
0.10
D
1D
2D

25 patches-



Conclusions

- *Many experiments suggest that at least some victim-exploiter systems are unstable (extinction-prone) in the well-mixed limit, and gain their stability due to migration between patches.*
- *Migration stabilizes such a system only if it manage to desynchronize. However, migration itself leads to synchronization and stabilize the homogenous manifold.*
- *Mechanisms based on spatial heterogeneity, environmental stochasticity and differences in migration rates fails to explain the apparent stability of some experimental systems and individual-based simulations.*
- *Our mechanism – amplitude dependent angular velocity – does explain these phenomena.*
- *For the NB dynamics (unstable on a single patch) there is critical noise level above which the system becomes stable.*
- *The coupled oscillators system serves very nicely as a toy model for population oscillations.*
- *Jansen's stabilization is explained by the azimuthal dependence of the angular velocity w(q).*
- The wolf also shall dwell with the lamb ? וגר זאב עם כבש ?

Only in a desyncronized, noisy and spatially extended environment, where the angular velocity is amplitude dependent….