Stabilizing fluctuating populations: Chaos control methods in ecology

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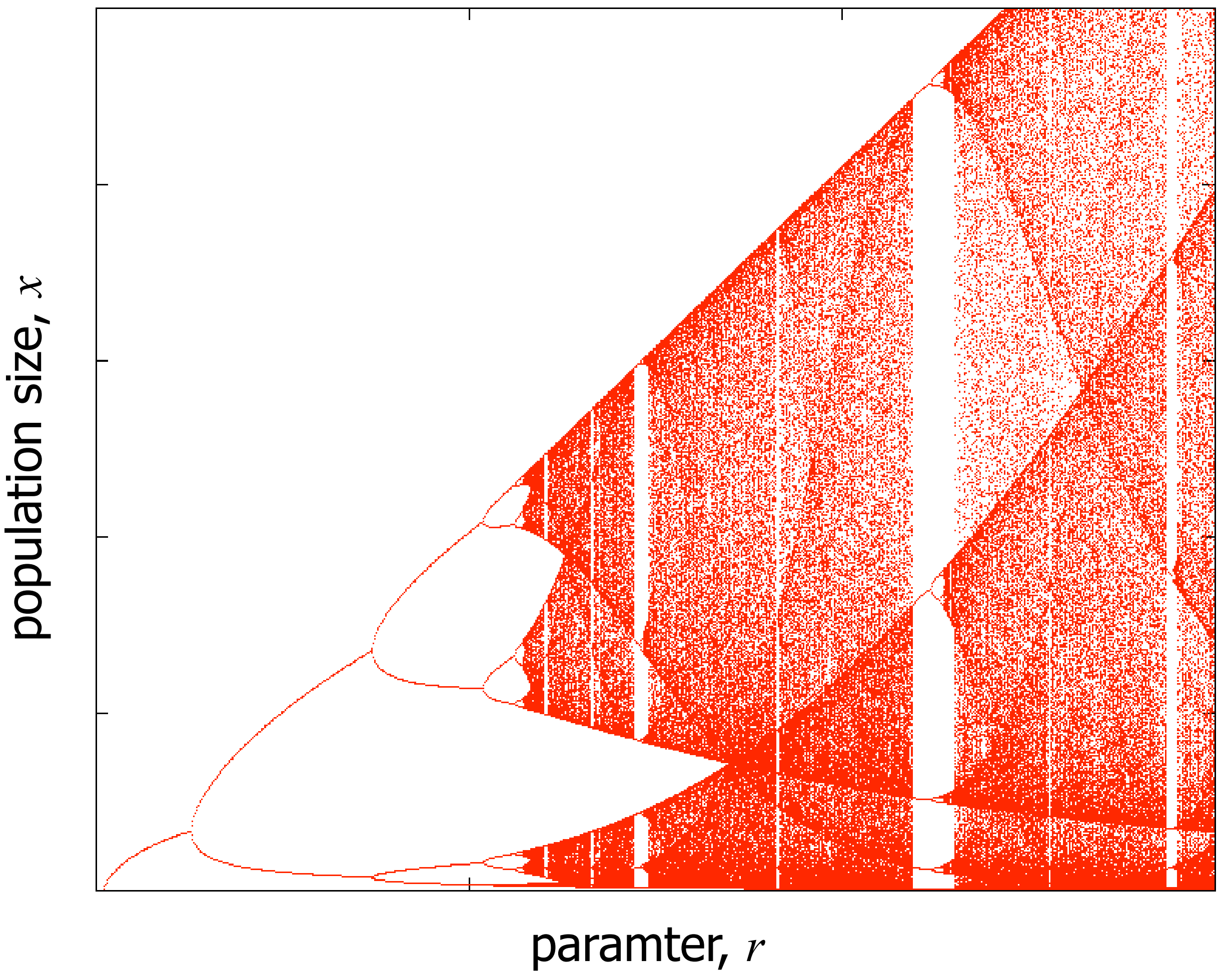
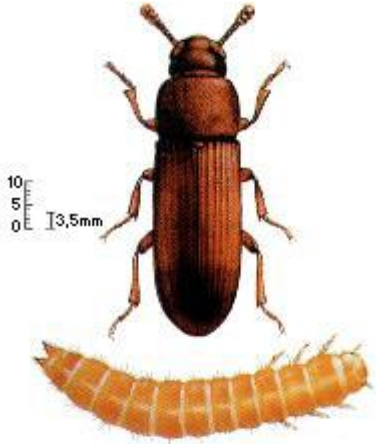
Chaos is ubiquitous in population models

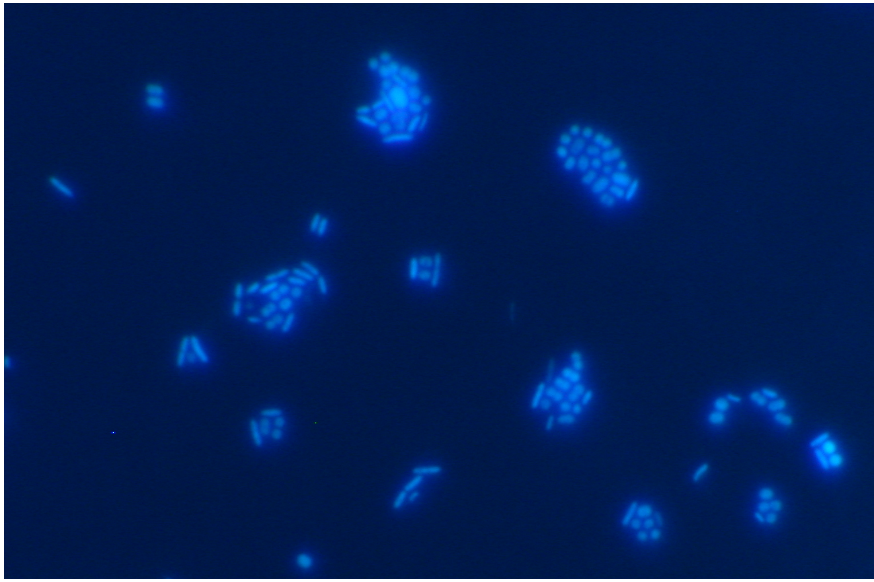


$$x_{t+1} = x_t \, e^{r(1-x_t)}$$ Ricker map

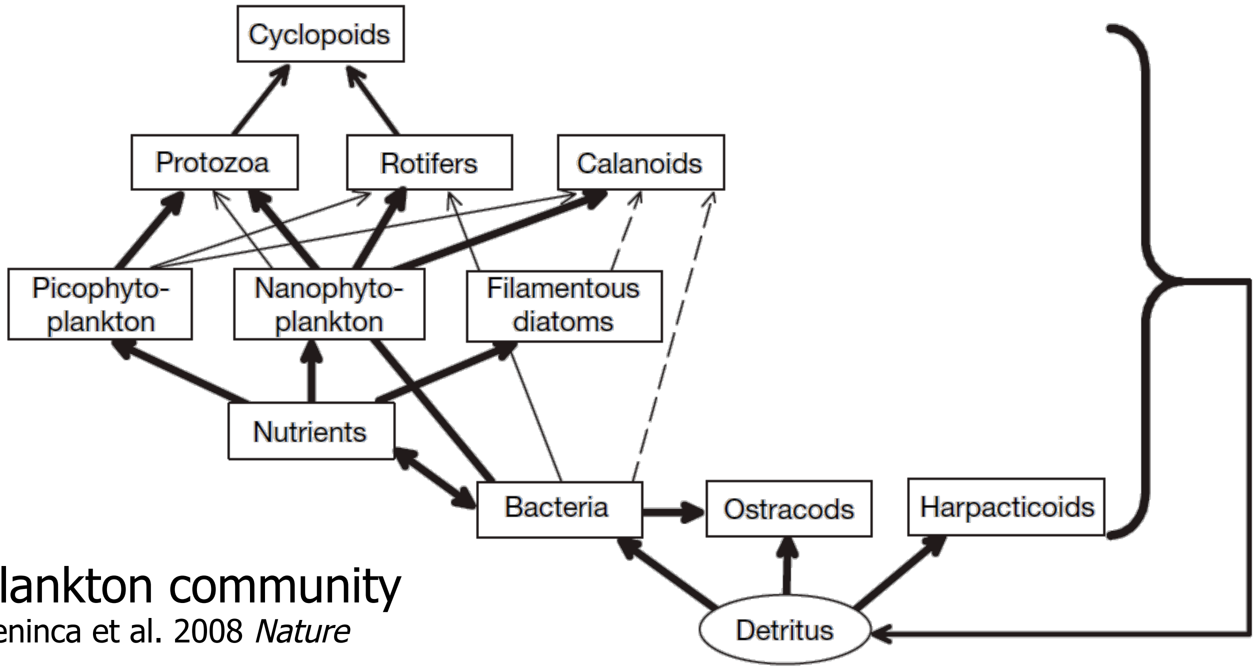
Chaos in population dynamics



Flour beetle *Triboleum castaneum*
Costantino et al. 1997 *Science*



Microbial food web
Becks et al. 2005 *Nature*



Plankton community
Beninca et al. 2008 *Nature*

A three-player solution

Lewi Stone

The seemingly unpredictable 'boom and bust' of insect-pest populations will be better understood with the advent of a deceptively simple model combining field and laboratory data with earlier theories.

Etienne Leopold Trouvelot, an astronomy professor at Harvard in the nineteenth century, had his scientific career "ruined by a moth"[1]. As it turns out, Trouvelot, an obsessive amateur entomologist, could not have chosen a more formidable opponent. In 1868, his experiments with the gypsy moth (*Lymantria dispar*) resulted in disaster after several of the insects escaped from his suburban Boston home. The moth was an alien species. It proceeded to multiply, only slowly at first, but some 20 years later it could be found in its millions, defoliating forests and causing major economic and ecological damage as it went on to invade North America (Fig. 1). Enormously embarrassed, Trouvelot, the classic 'good man gone wrong', returned to France and to obscurity.

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AP

Figure 1 Bare birch — an upshot of the gypsy moth invasion of eastern North America. These grey birch trees would be in leafy splendour had they not been stripped of developing foliage. Inset, a gypsy moth caterpillar, the insect stage that does the damage.

Alas, the same can't be said of the gypsy moth, which remains one of the most devastating forest pests to this day. Pinning down the ecological processes that give rise to outbreaks of this type of insect pest, and modelling their complex dynamics, has troubled

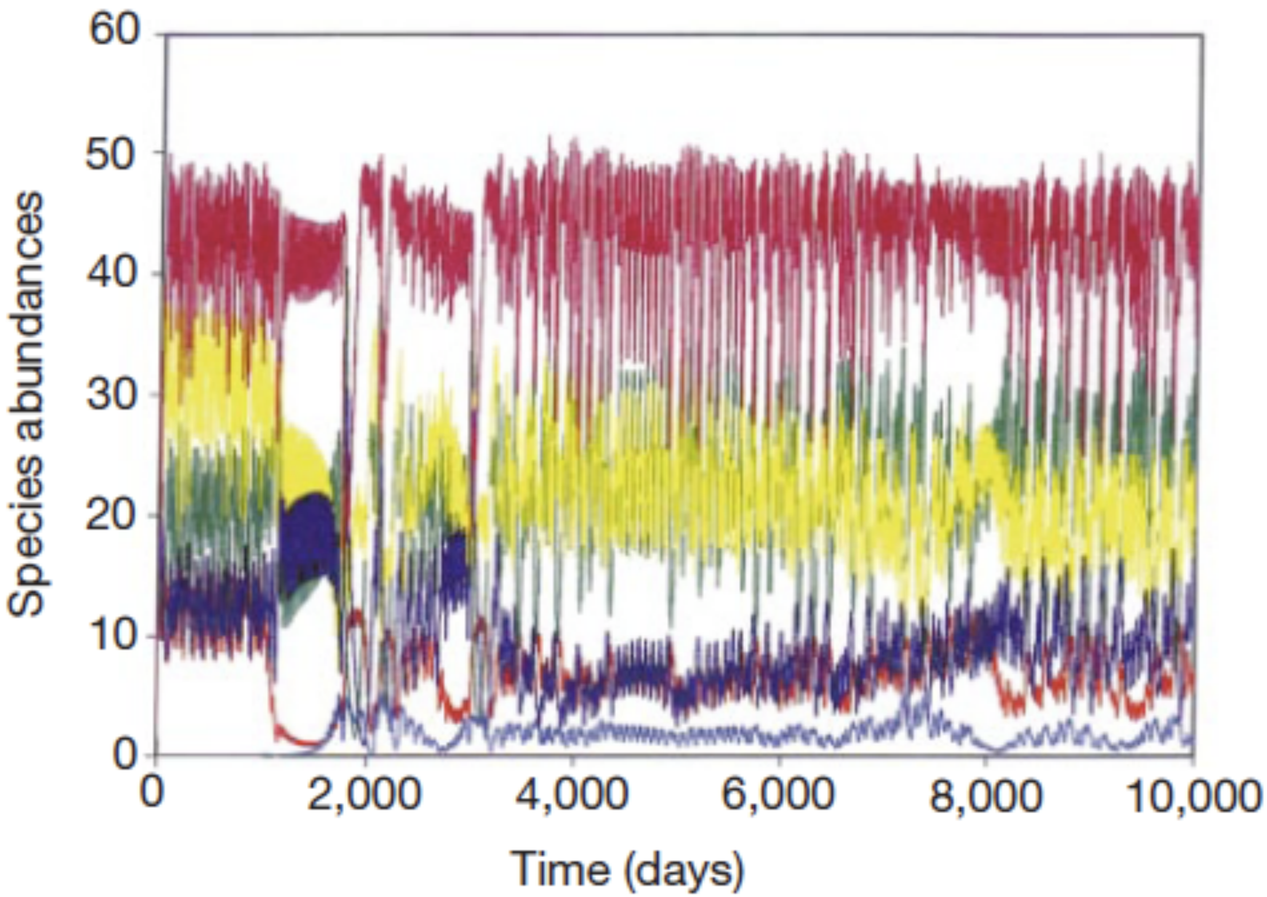
force that drives it. The recurrent patterns, moreover, seem to be highly resilient to perturbation and do not break down

description should also include the so-called induced-defence hypothesis, whereby the deteriorating quality of forest foliage due to defoliation has a negative impact on the gypsy moth population.

Stone (2004, *Nature*)

Chaos in ecology

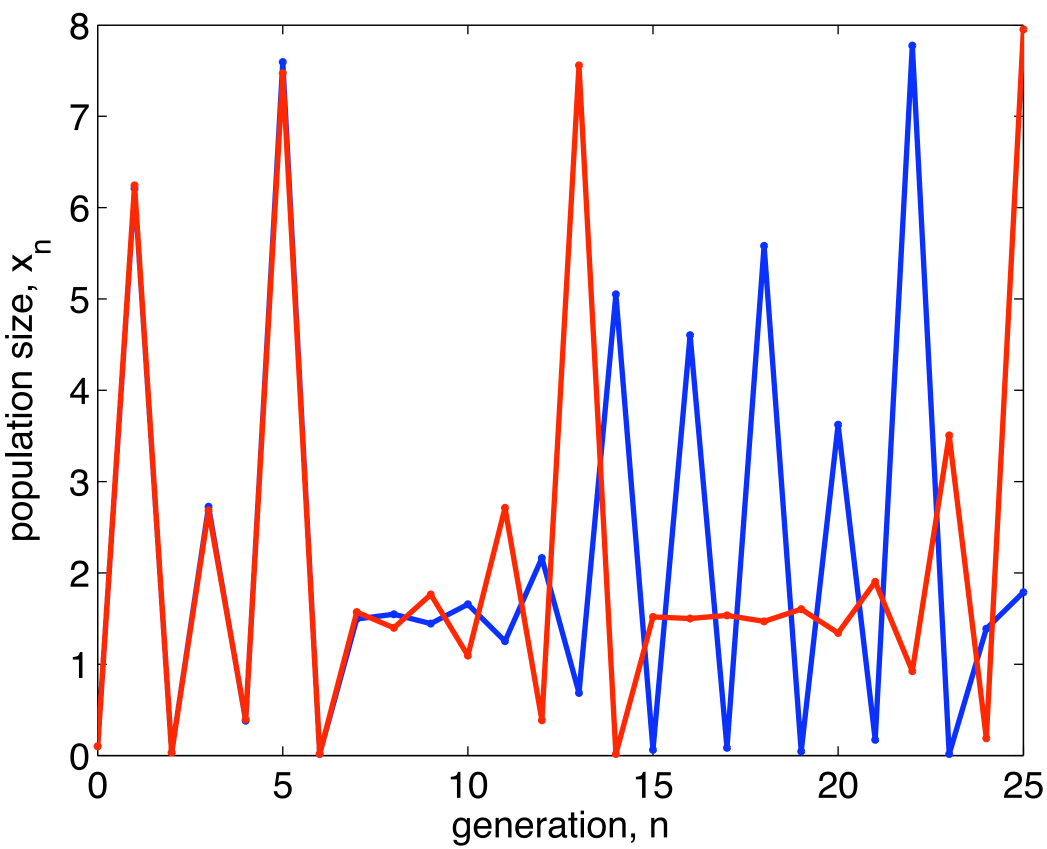
- favours biodiversity (Huisman and Weissing 1999)
- reduces extinction risk (Allen et al 1993, Ruxton 1994)
- optimal from evolutionary perspective (Ferriere and Gatto 1994)



Why control (ecological) chaos?

- prevent extinctions (or outbreaks)
- stability affects effective population sizes, genetic diversity and population fitness
- long-term predictability

Sensitive dependence on initial conditions

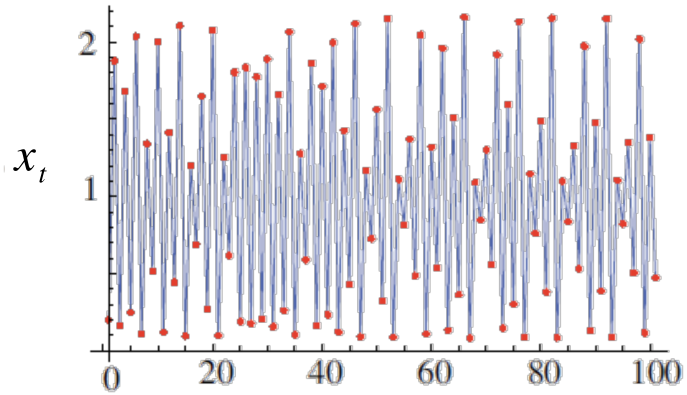


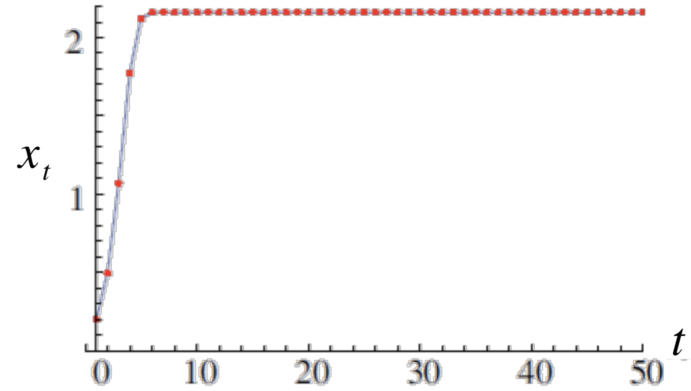
→ short-term predictability

→ long-term predictions worthless

Chaos control in physics

- Aim is to *suppress* chaos
- achieved by stabilizing one of the infinitely many unstable periodic orbits
- perturbations: tiny and instantaneous

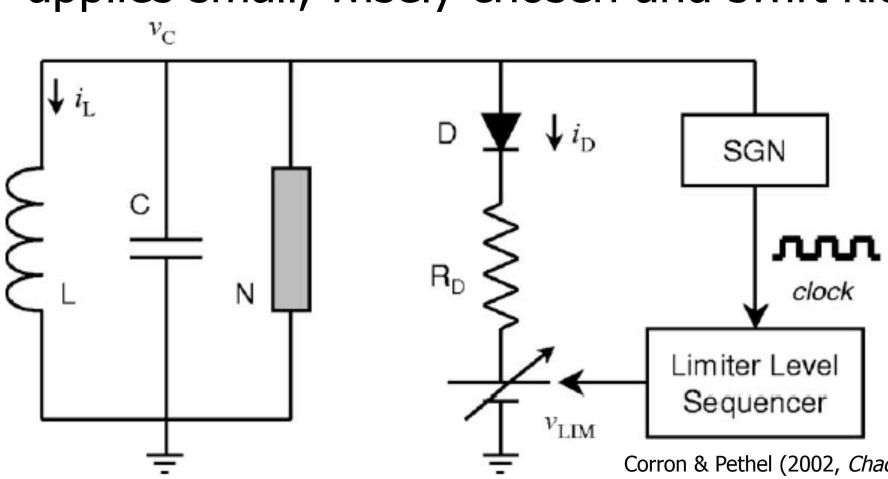




Figures from Liz 2010

Example: OGY method (Ott, Grebogi, Yorke 1990 *Phys. Rev. Lett.*)

- requires previous determination of UPO
- applies small, wisely chosen and swift kicks once per cycle



Corron & Pethel (2002, *Chaos*)

Ecological reality...?

small

swift

regular

continuously

previously determined unstable periodic orbits

wisely chosen

Problems of existing approaches

- Equations need to be known
- Long time series
- Continuous, instantaneous and tiny perturbations
- Robustness in presence of noise?

Outline

- Chaos control methods:
  - Constant feedback (CF)
  - Proportional feedback (PF)
  - Target-oriented control (TOC)
  - Limiter control (LC)
  - Adaptive limiter control (ALC)

- Chaos anti-control (time-series based)

- Conclusions

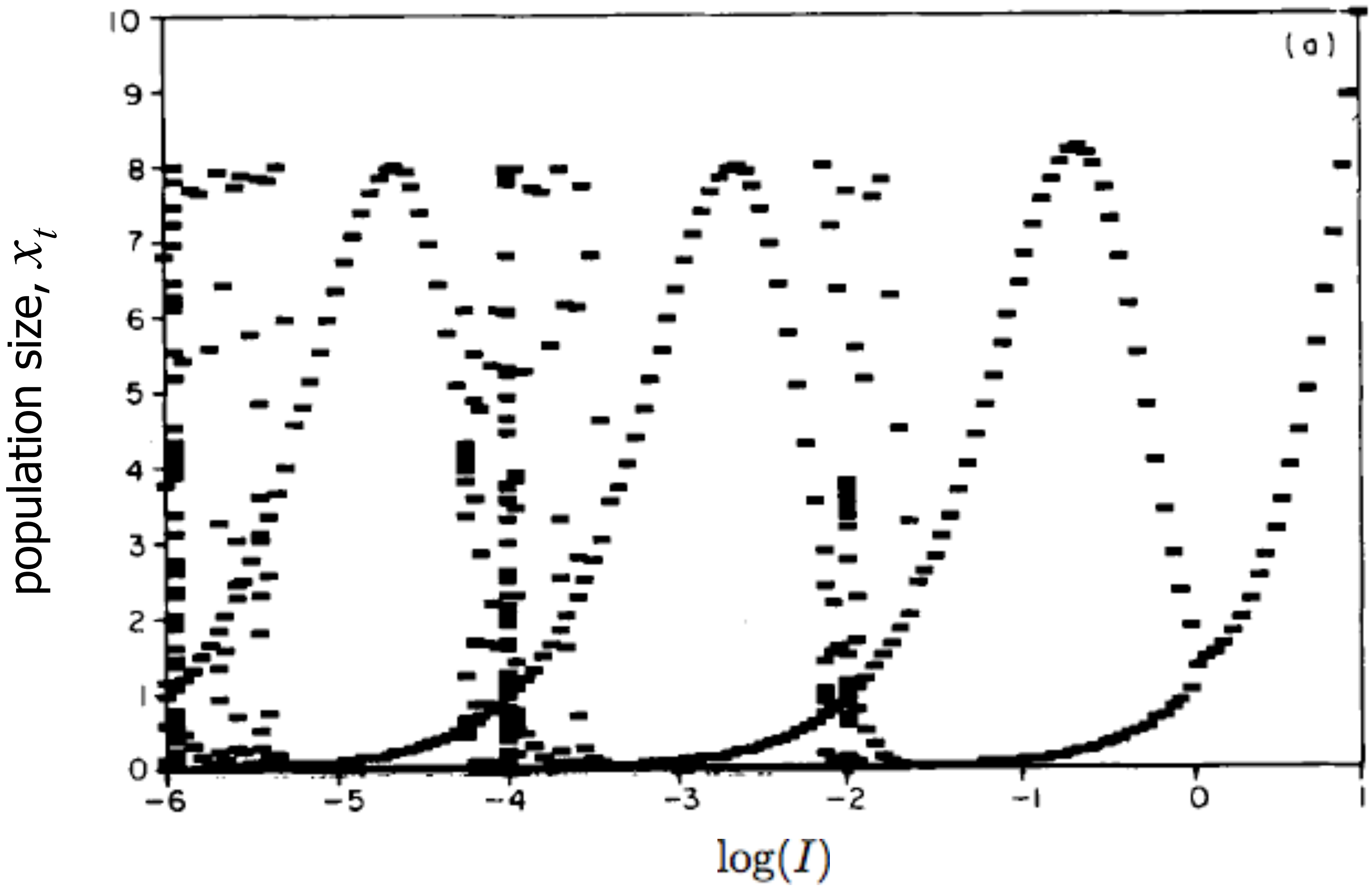
1.) Constant feedback (CF)

$$x_{t+1} = f(x_t) + I$$

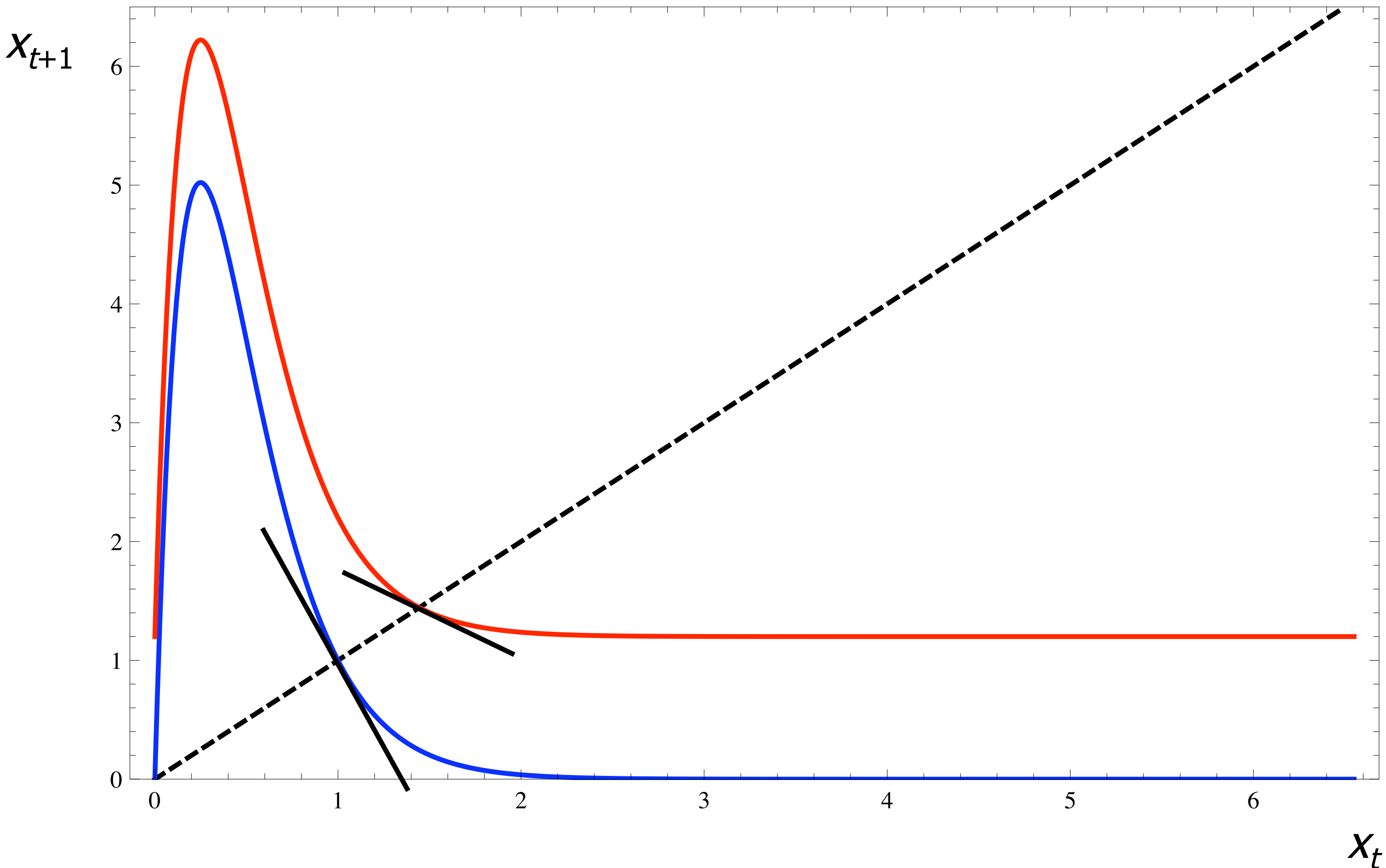
Immigration can stabilize chaotic dynamics

= constant feedback control

Parthasarathy & Sinha (1995, *Phys Rev E*)

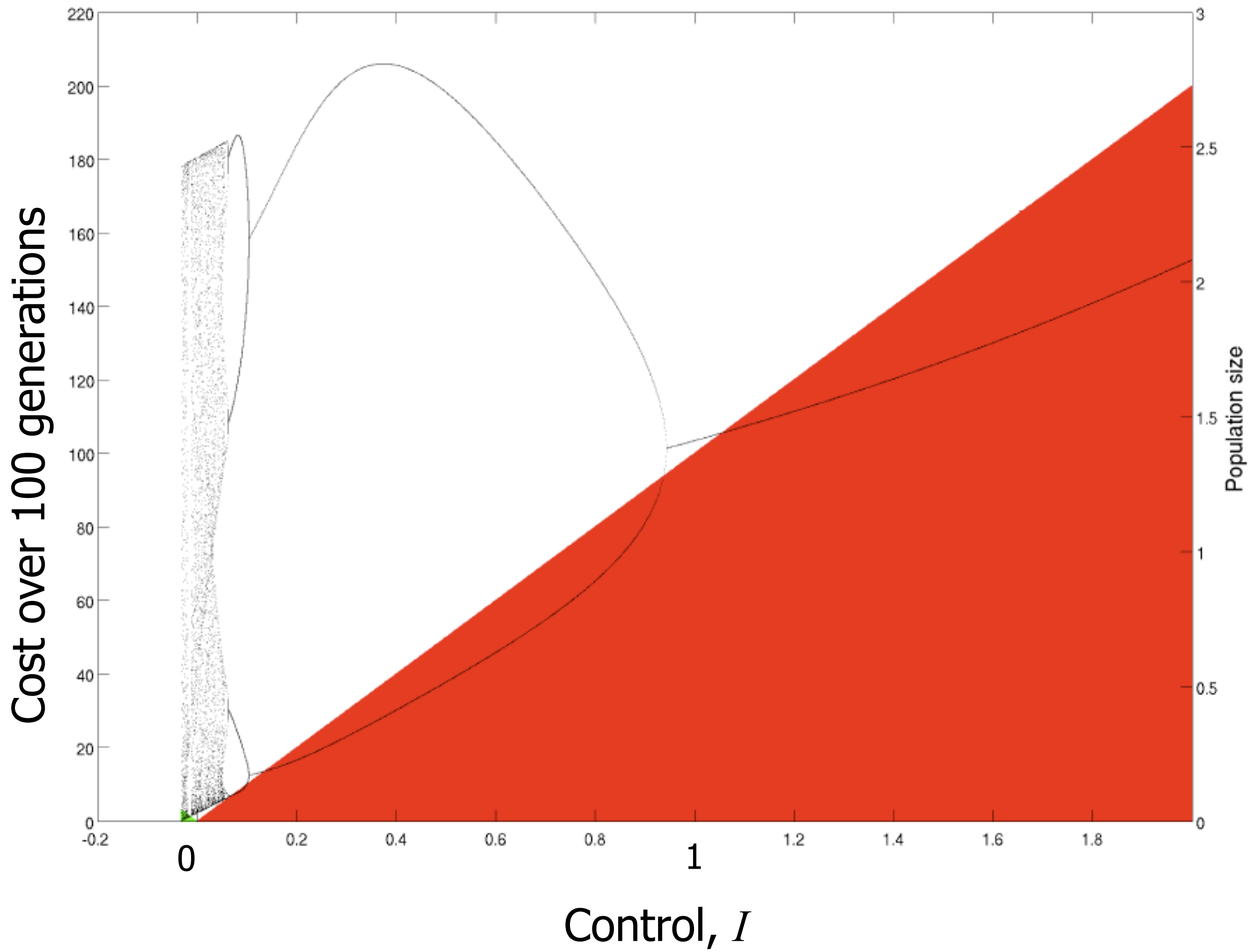


McCallum (1992, *J. Theor. Biol.*)



x_{t+1}
0
1
2
3
4
5
6
0
1
2
3
4
5
6
x_t

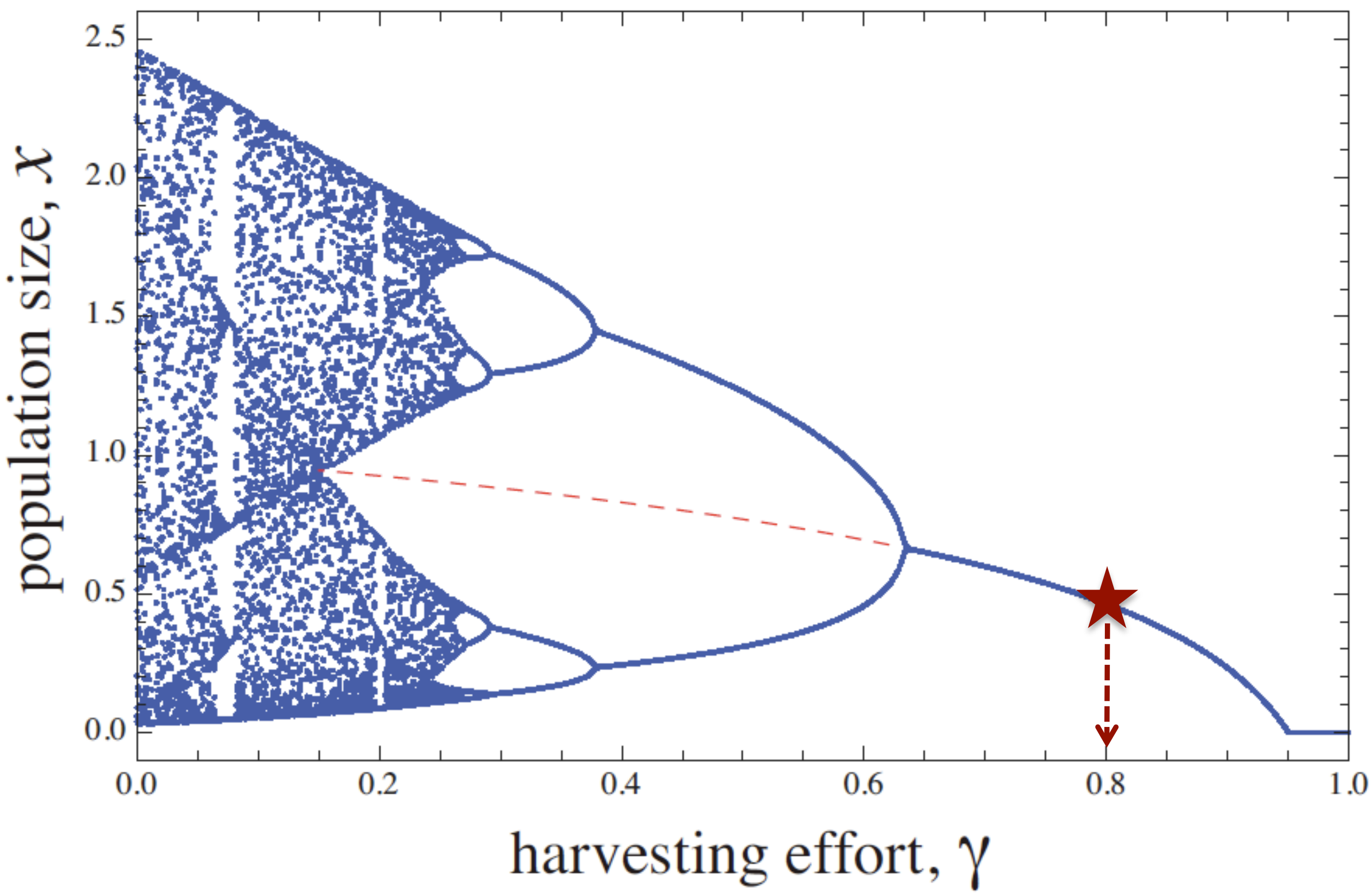
Cost



Constant feedback $x_{t+1} = f(x_t) + I$

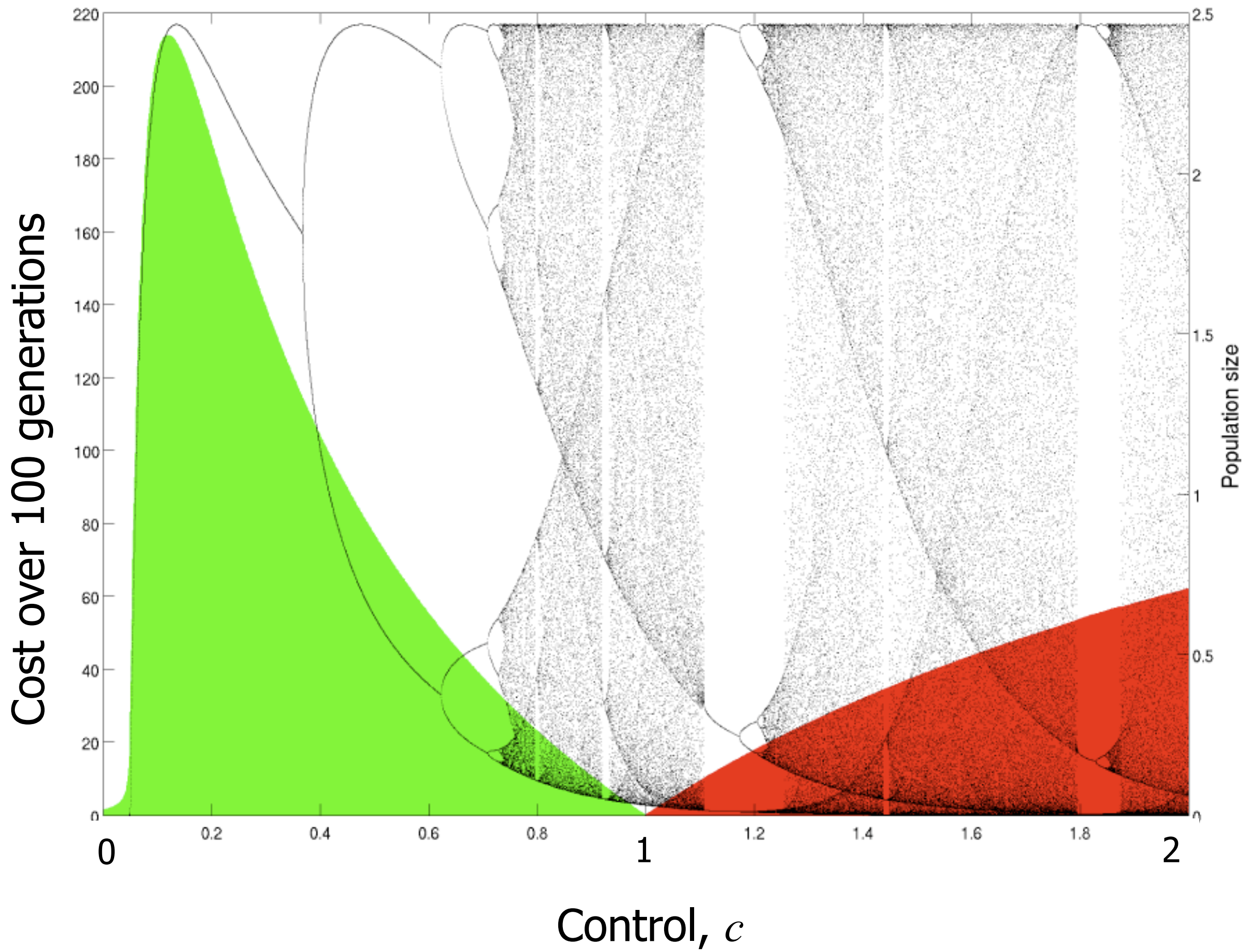
2.) Proportional feedback (CF)

$$x_{t+1} = (1 - \gamma) f(x_t)$$



Liz 2010 *Phys. Lett. A*

Cost



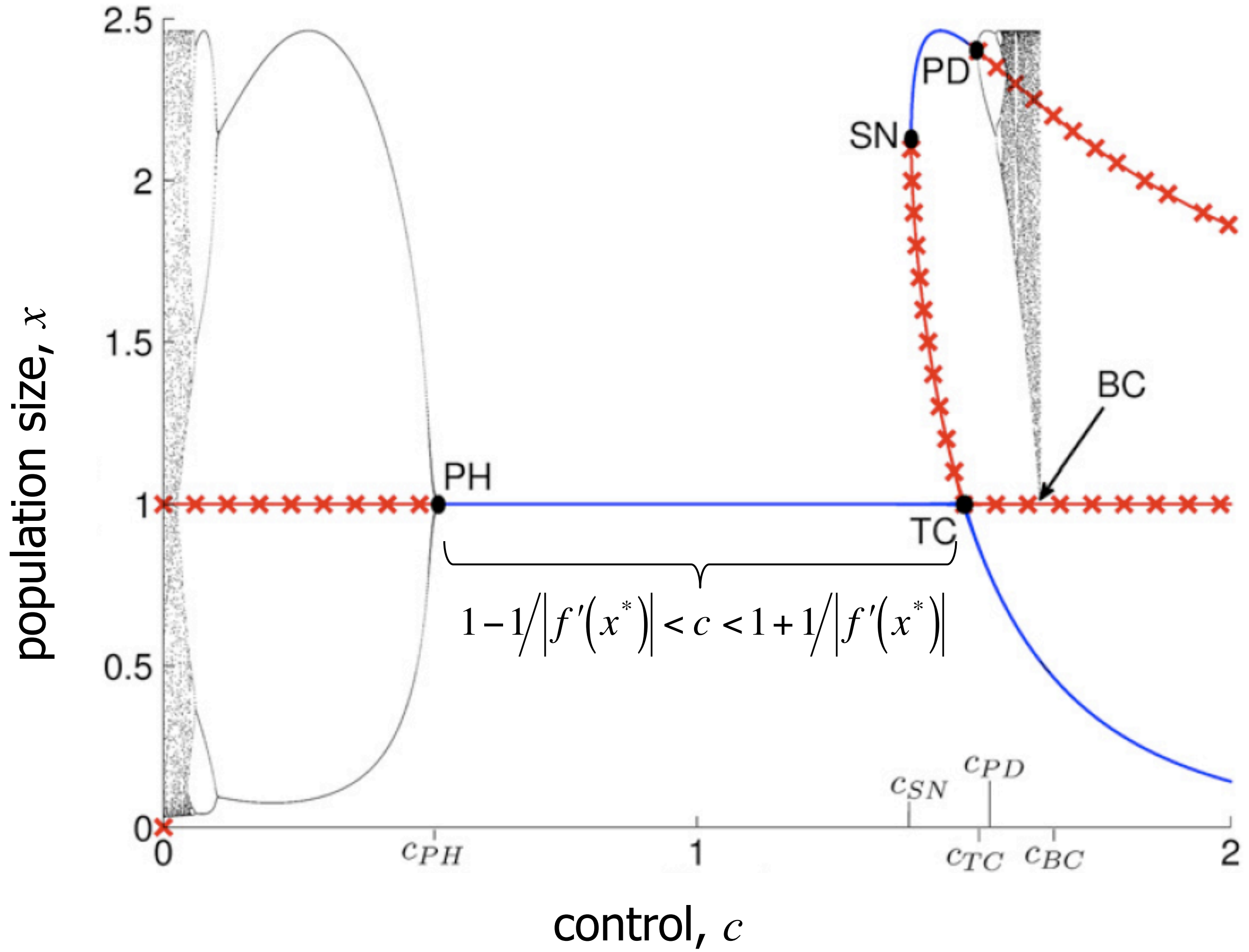
Proportional feedback $x_{t+1} = c\,f(x_t)$

3.) Target-oriented control (TOC)

$$x_{t+1} = f\left(x_t + I(x_t)\right)$$

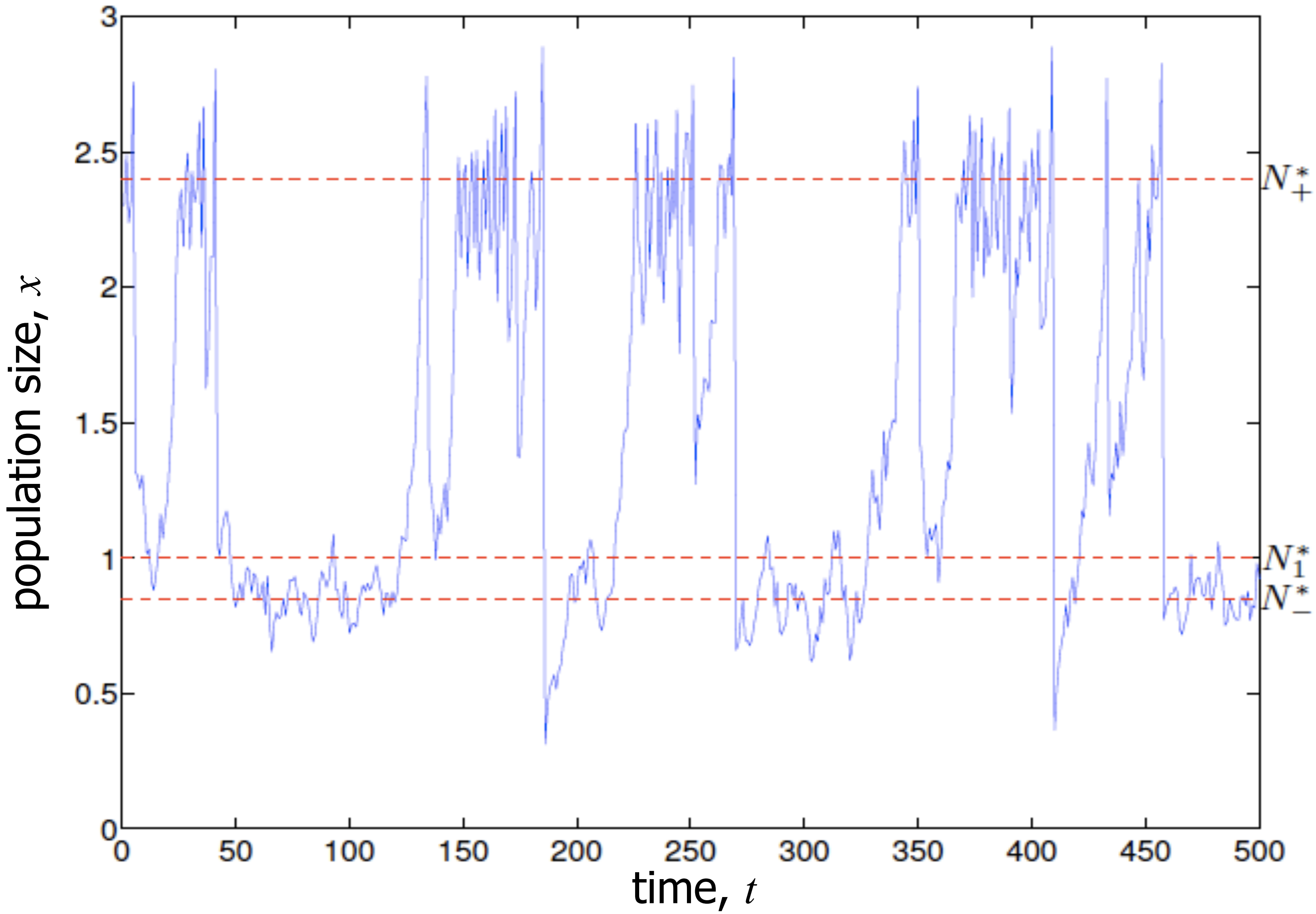
$$I(x) = c\,(T - x)$$

restock population if below target
harvest population if above target



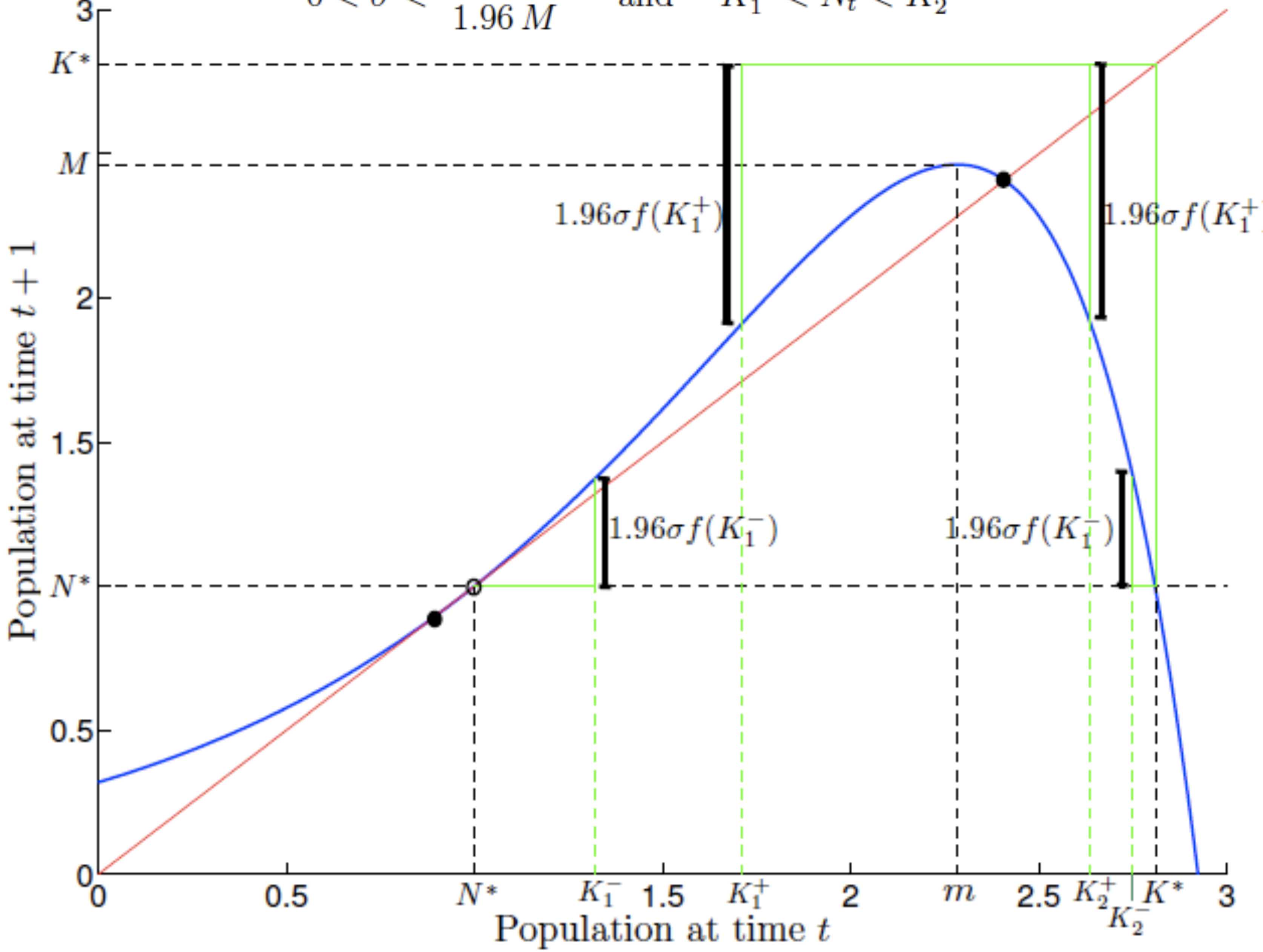
Stochastic attractor switching

$x_{t+1} = (1+\varepsilon_t)\, f\left(x_t + I(x_t)\right)$ ε_t Gaussian noise with zero mean and σ^2 variance

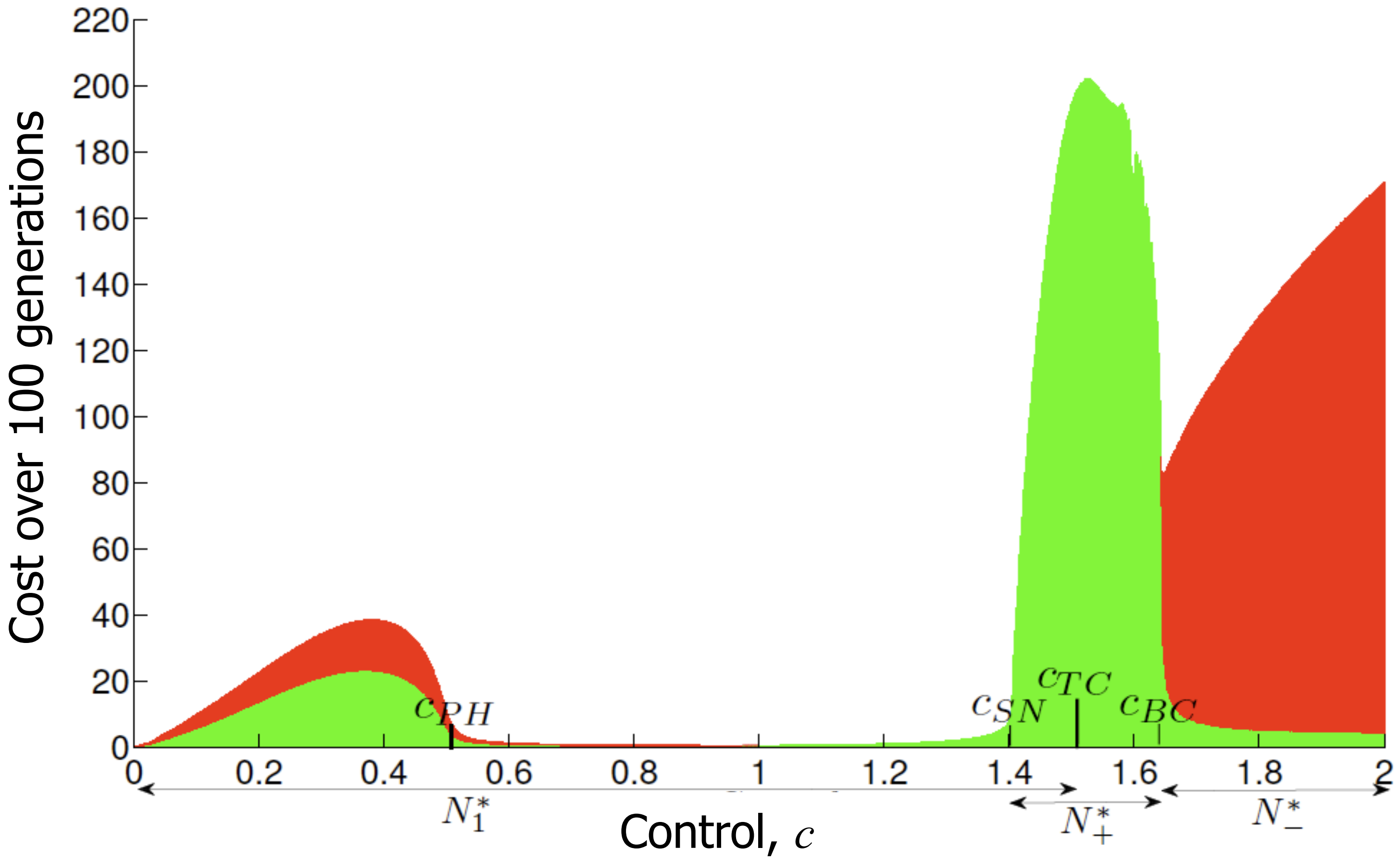


Condition for 95% chance of population size being in basin of attraction for N^*_+

$$0 < \sigma < \frac{M - N^*}{1.96\,M} \quad \text{and} \quad K_1^- < N_t < K_2^-$$

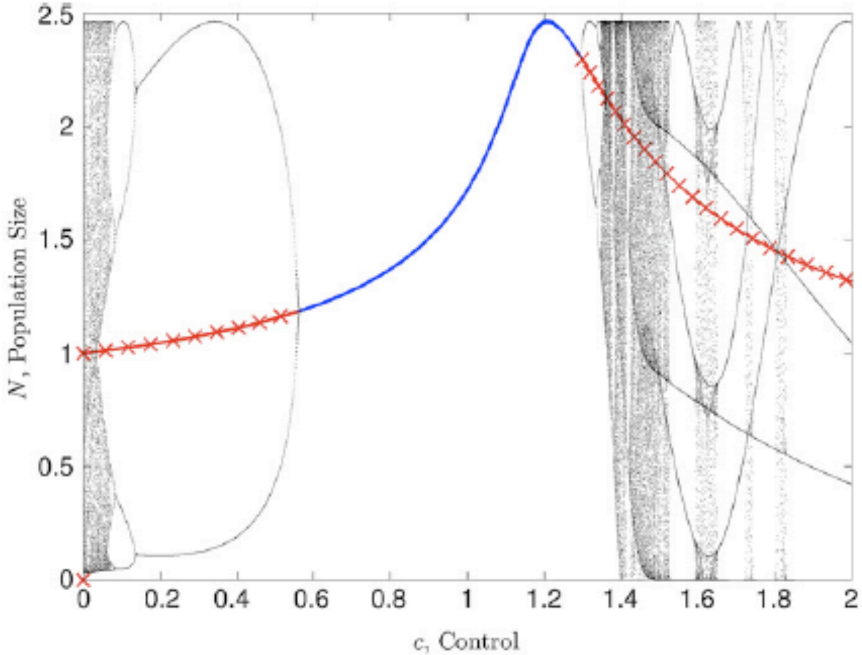


Cost



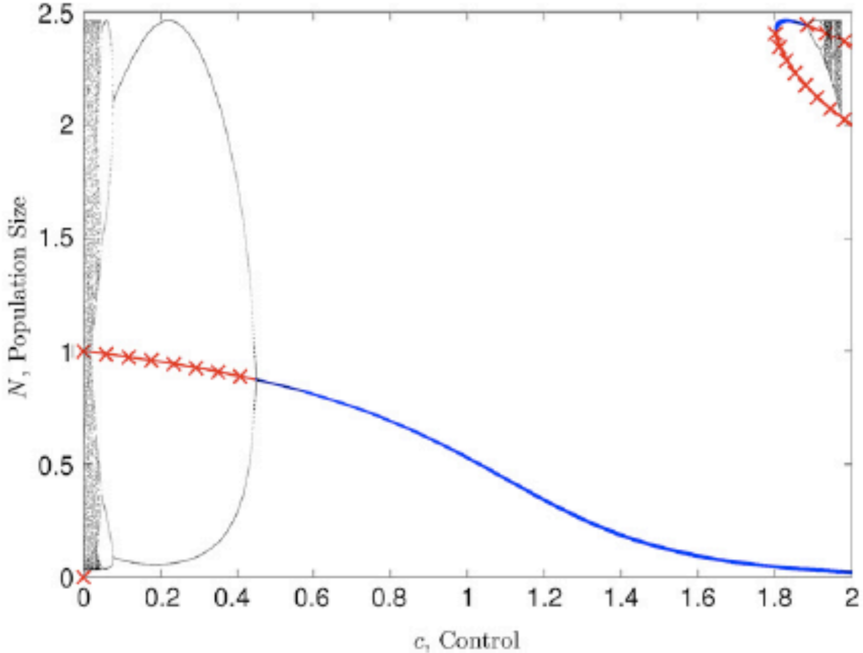
Target-oriented control $x_{t+1} = f\left(\left(1-c\right)x_t + cT\right)$

If we don't target the unstable fixed point, $T \neq x^*$



$T < x^*$

increases population size

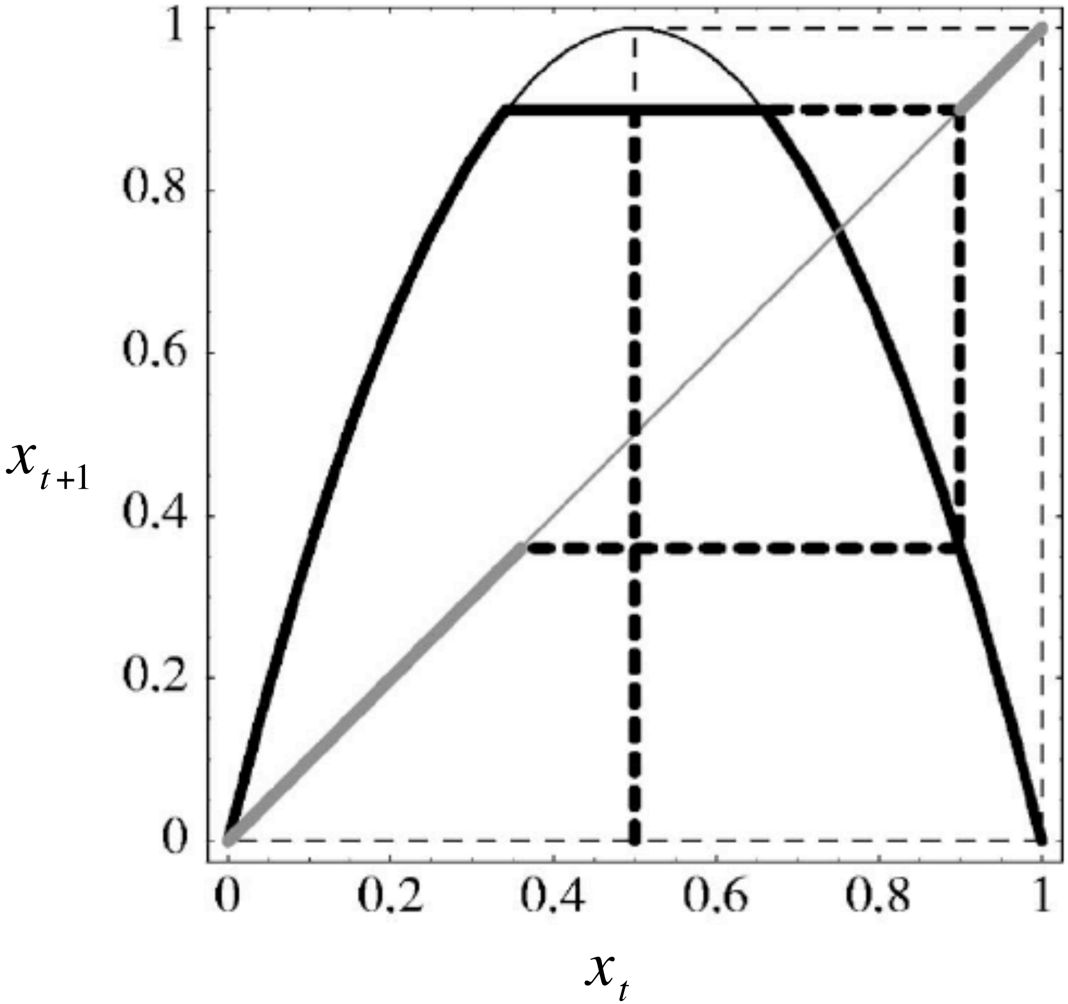


$T > x^*$

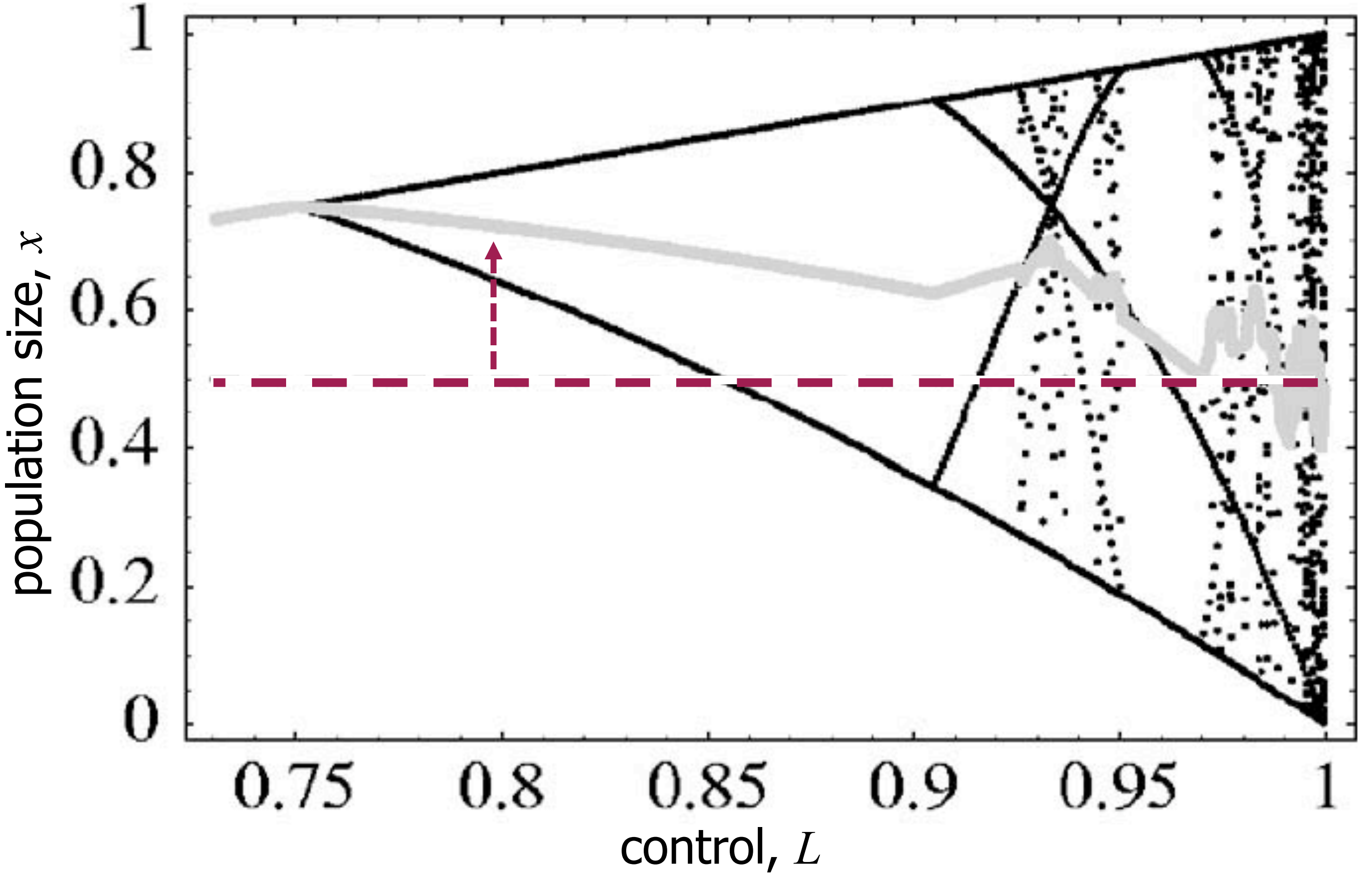
decreases population size

4.) Limiter control (LC)

$$x_{t+1} = \begin{cases} f(x_t) & \text{if } x_t \geq \text{L} \\ L & \text{else} \end{cases}$$



Avoid outbreaks



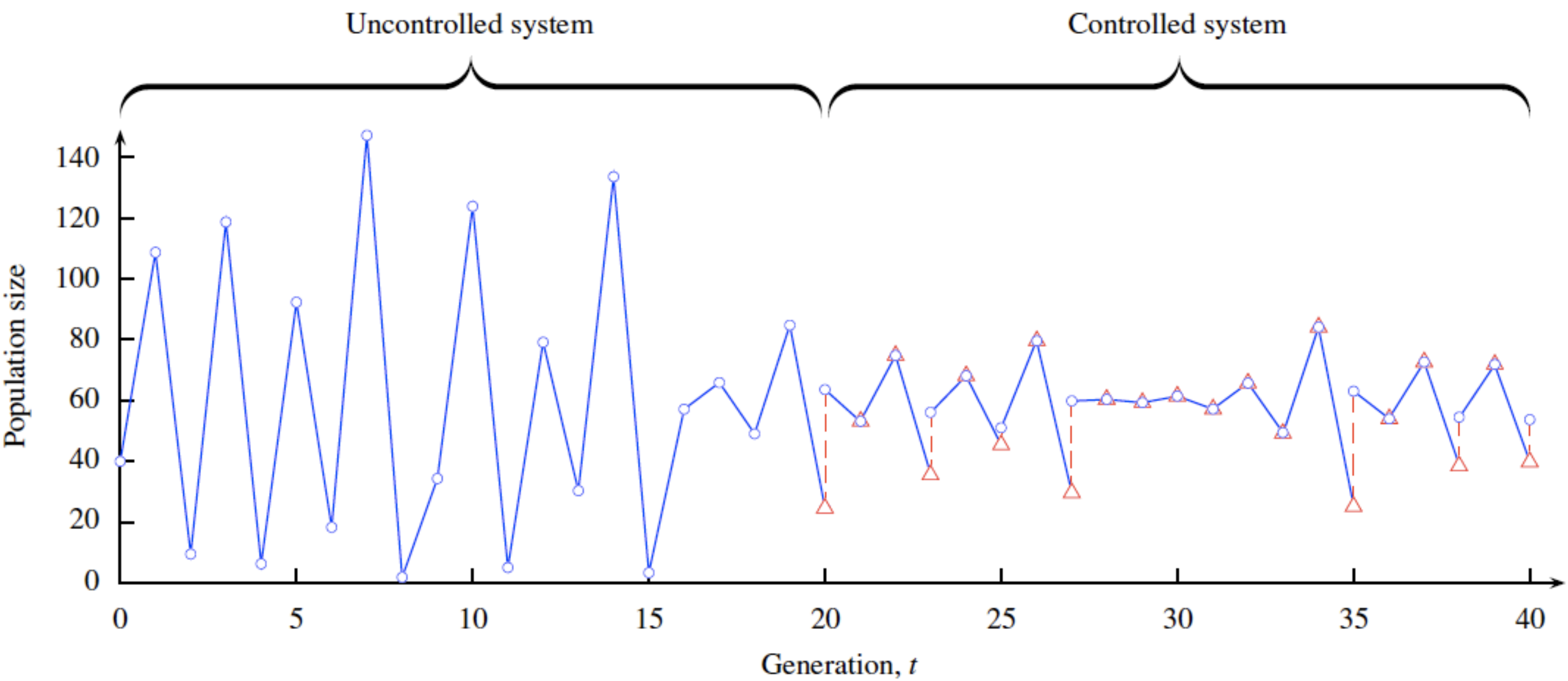
- **Culling increases mean population size (hydra effect)**
- **Culling increases mean population size above equilibrium value (paradox of limiter control)**

5.) Adaptive limiter control (ALC)

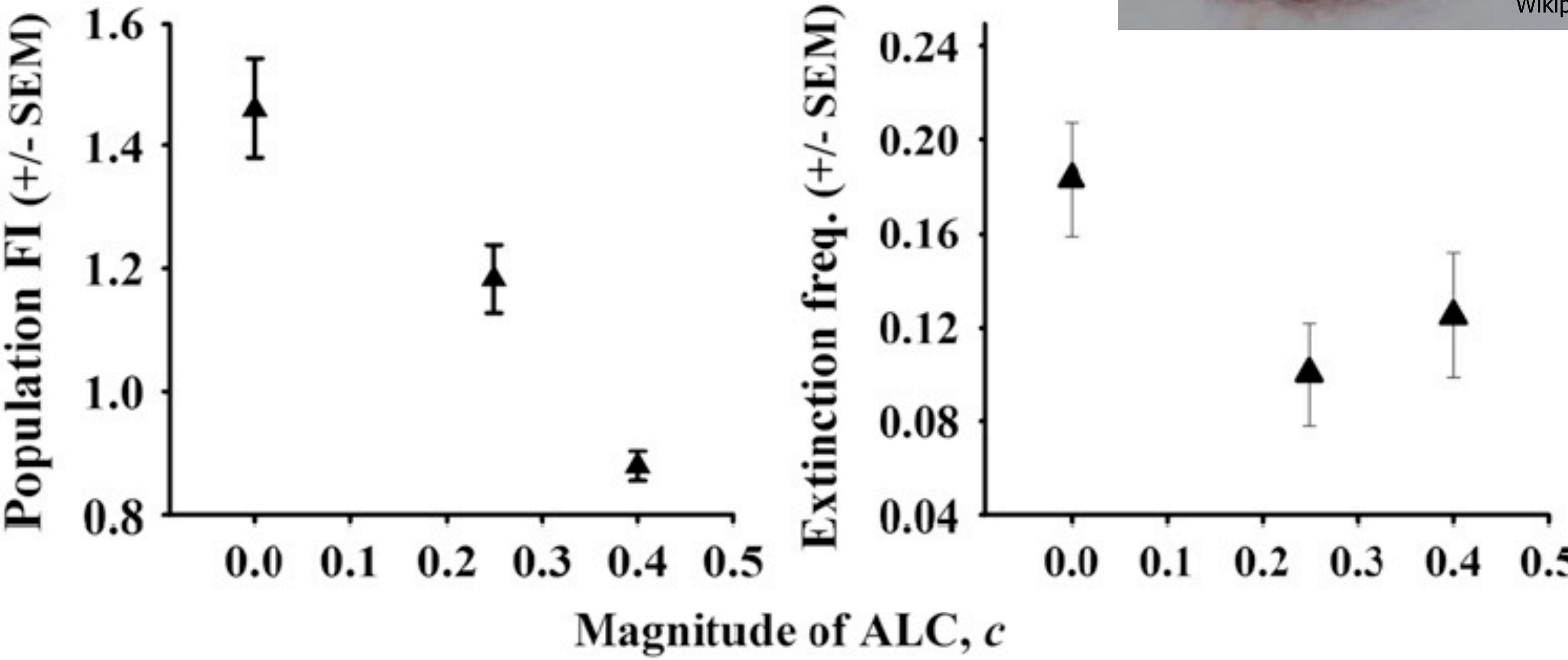
Idea:

If population falls below a fraction of its previous size → restock

(Sah et al. 2013 *J. Theor. Biol.*)



Experimental results with *Drosophila melanogaster*



ALC can reduce fluctuations

ALC can reduce extinction risk

Sah et al. 2013 *J. Theor. Biol.*

Model proposed by Sah et al. (2013)

$$x_{t+1} = f\left(\max\left\{x_t, c \cdot x_{t-1}\right\}\right)$$

Experiments/simulations in Sah et al. (2013)

$$x_{t+1} = \max\left\{f\left(x_t\right), c \cdot x_t\right\}$$

2nd order — not topologically conjugate — 1st order

order of events is important

$$b_{t+1} = f\left(a_t\right) \qquad a_{t+1} = \begin{cases} b_{t+1} & \text{if } b_{t+1} \geq L \\ L & \text{else} \end{cases}$$

b_t : population size *before* control

a_t : population size *after* control

$$L \equiv c \cdot b_t$$

$$b_{t+1} = f\left(a_t\right), \quad a_{t+1} = \begin{cases} b_{t+1} & \text{if } b_{t+1} \geq c \cdot b_t \\ c \cdot b_t & \text{else} \end{cases}$$

$$b_{t+1} = f\left(\max\left\{b_t, c \cdot b_{t-1}\right\}\right)$$

Let $x_t \equiv b_t$ **ALCb**

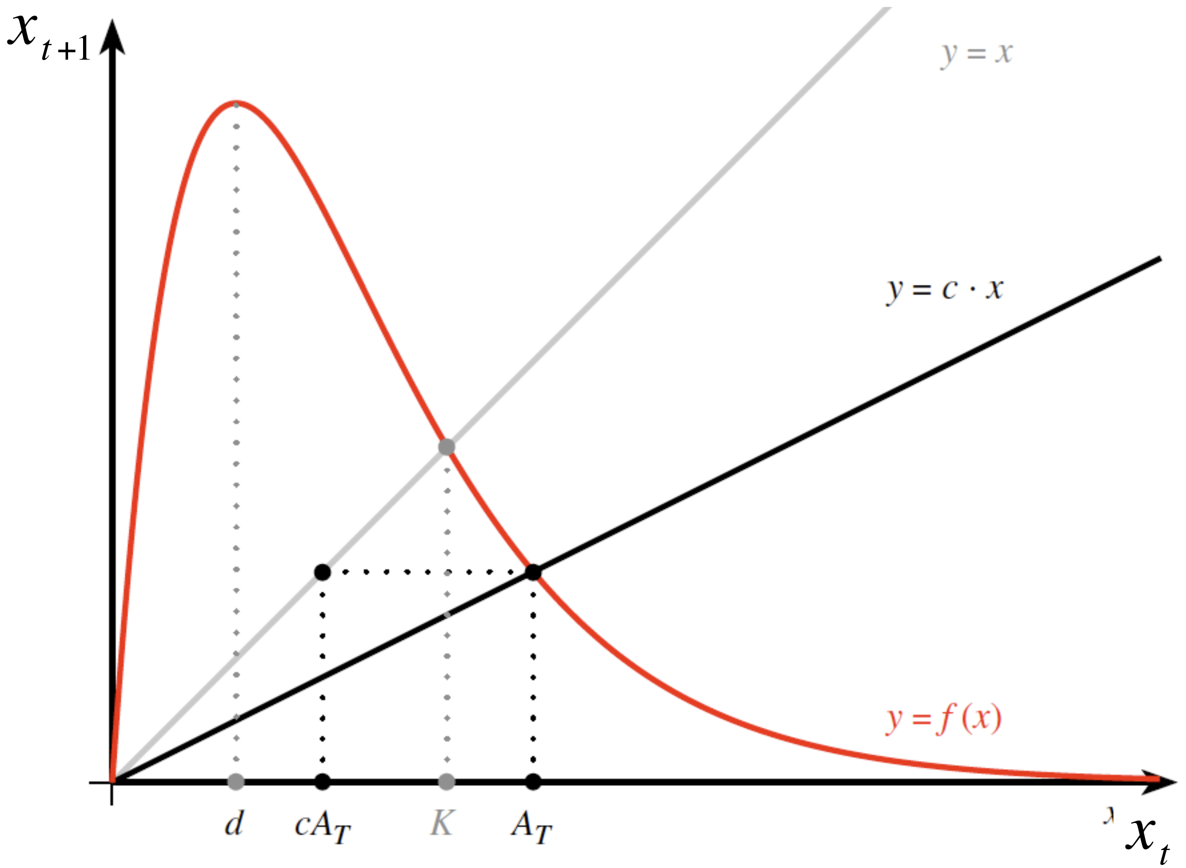
$$L \equiv c \cdot a_t$$

$$a_{t+1} = \begin{cases} f\left(a_t\right) & \text{if } f\left(a_t\right) \geq c \cdot a_t \\ c \cdot a_t & \text{else} \end{cases}$$

$$a_{t+1} = \max\left\{f\left(a_t\right), c \cdot a_t\right\}$$

Let $x_t \equiv a_t$ **ALCa**

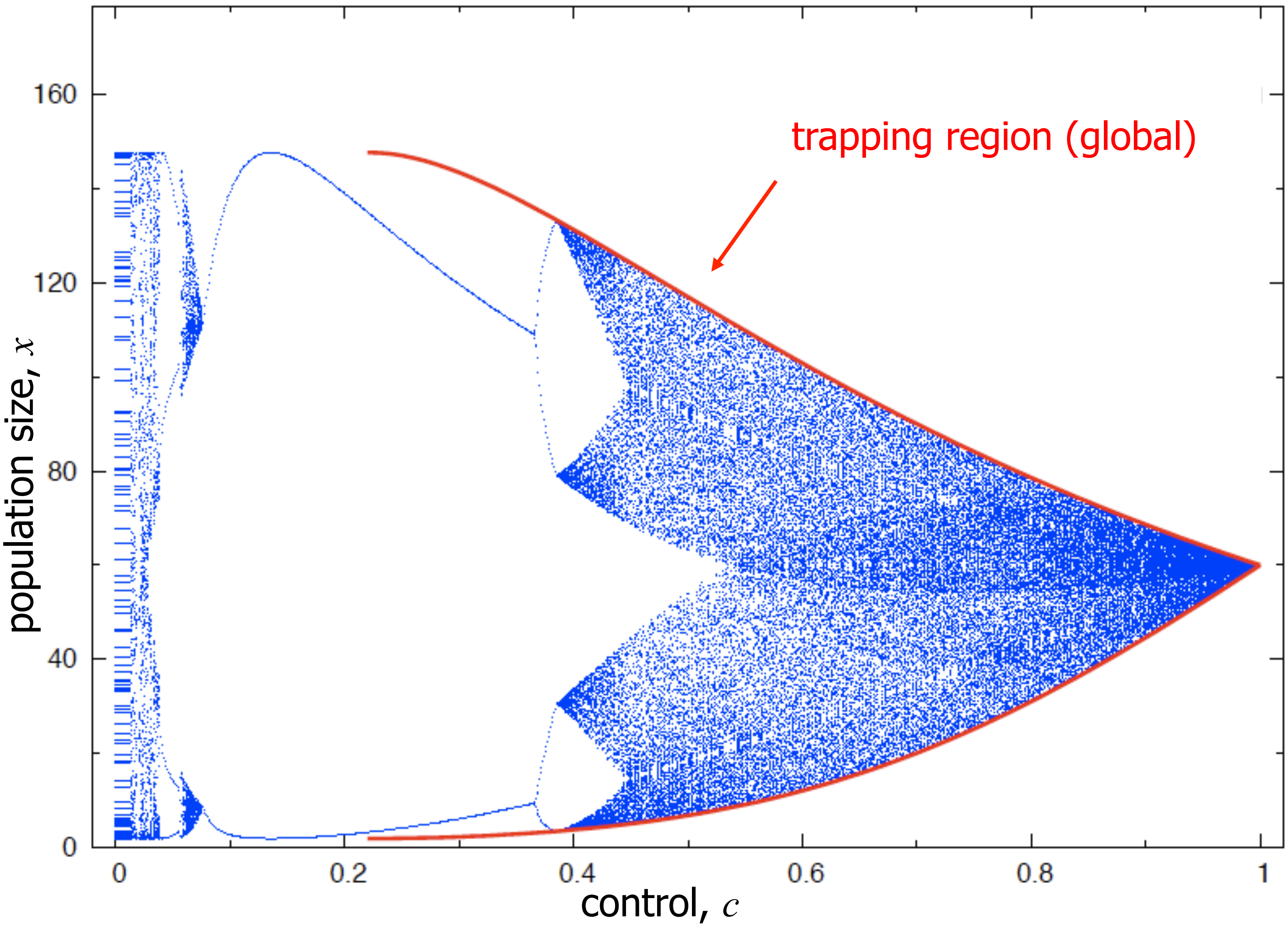
ALCa $x_{t+1} = \max\{f(x_t), c \cdot x_t\}$



Activation threshold A_T

Control is activated if and only if $x_t \geq A_T$

ALCa



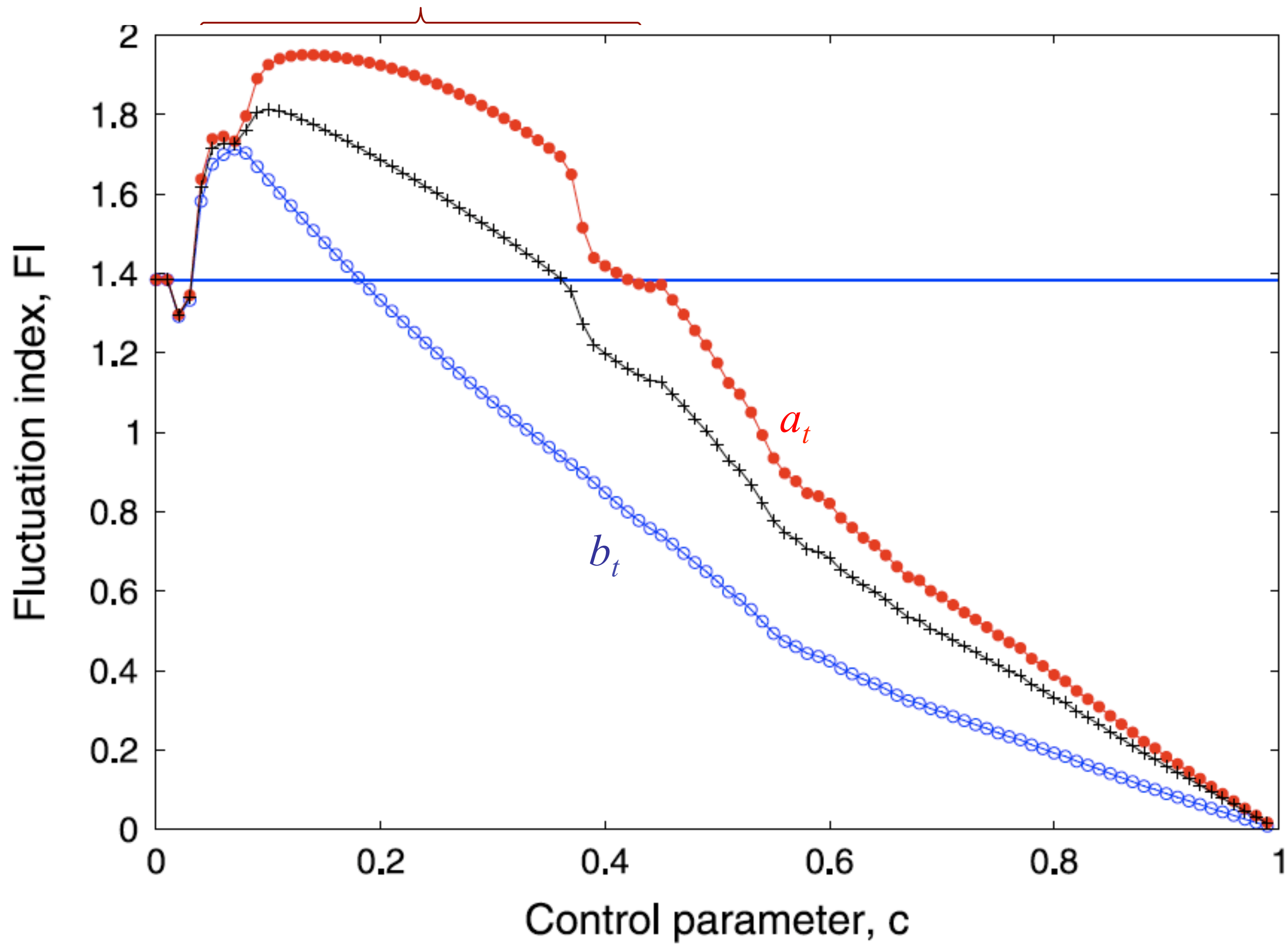
- fluctuation range shrinks
- stabilization to fixed point actually not possible

Looking at a different stability measure…

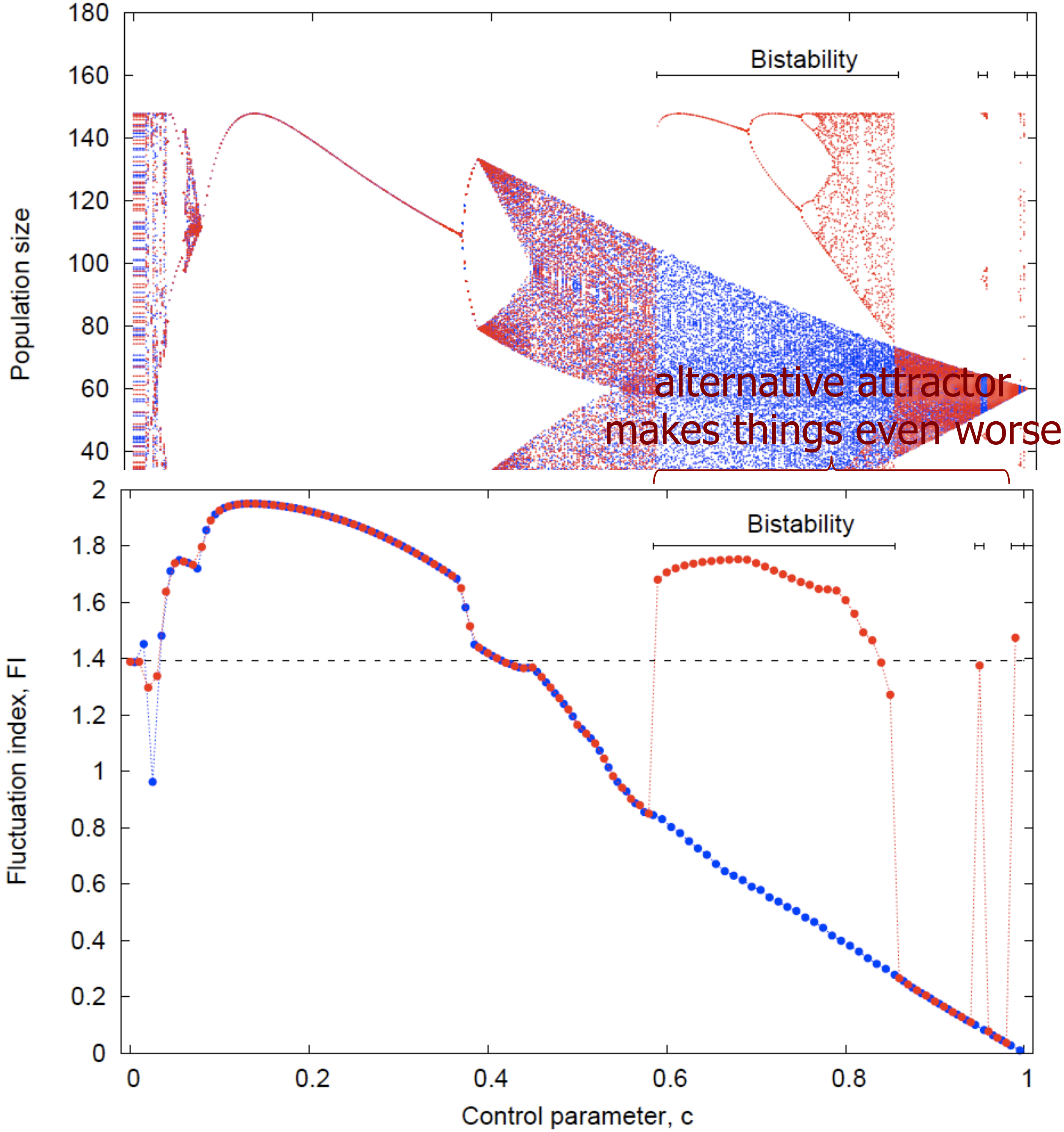
$$FI = \frac{1}{T\,\bar{x}} \sum_{0}^{T-1} \left| x_{t+1} - x_t \right|$$ Fluctuation Index

dimensionless measure of the average one-step variation scaled by the average

control makes things worse



ALCb

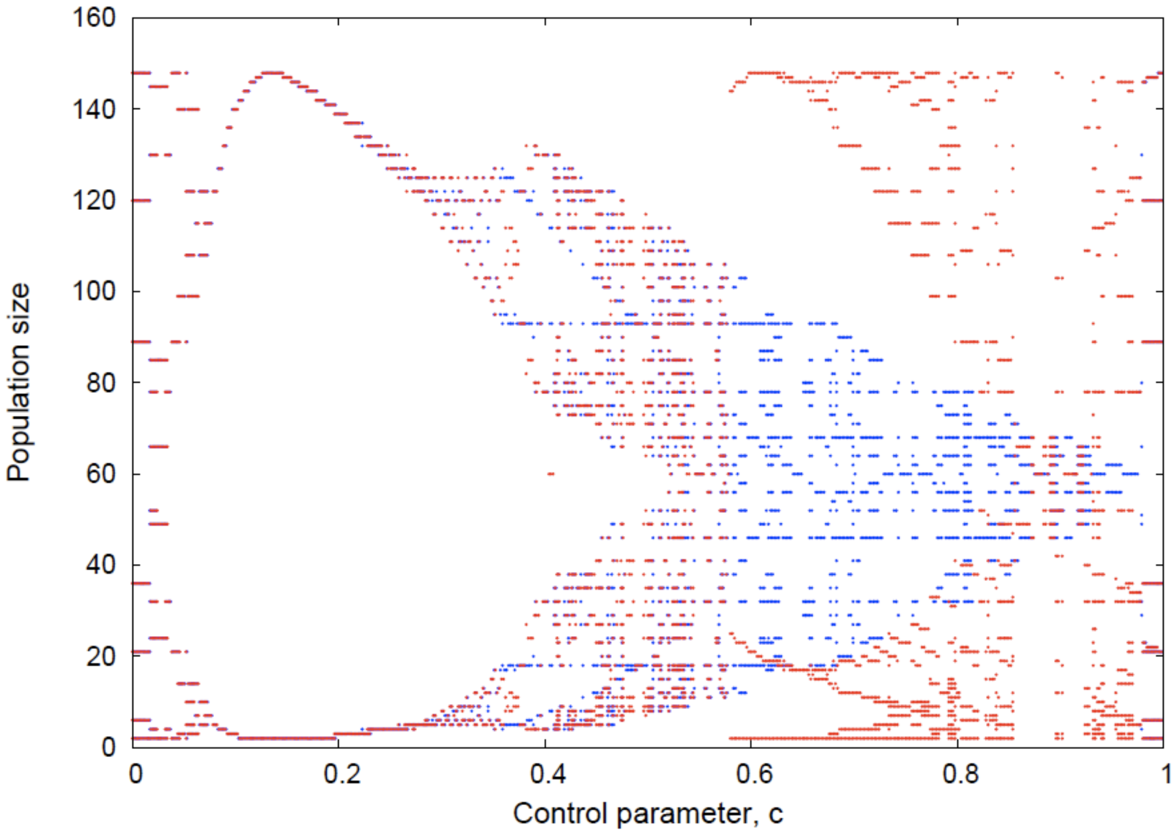


Bistability
Population size
180
160
140
120
100
80
60
40
alternative attractor
makes things even worse
Bistability
Fluctuation index, FI
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
Control parameter, c

ALCb lattice model

discrete-state dynamical system

$$x_{t+1} = \begin{cases} \mathrm{int}\left[f\left(x_t\right)\right] & \text{if } x_t \geq \mathrm{int}\left[c \cdot x_{t-1}\right] \\ \mathrm{int}\left[f\left(\mathrm{int}\left[c \cdot x_{t-1}\right]\right)\right] & \text{else} \end{cases}$$



alternative attractor robust against integerization

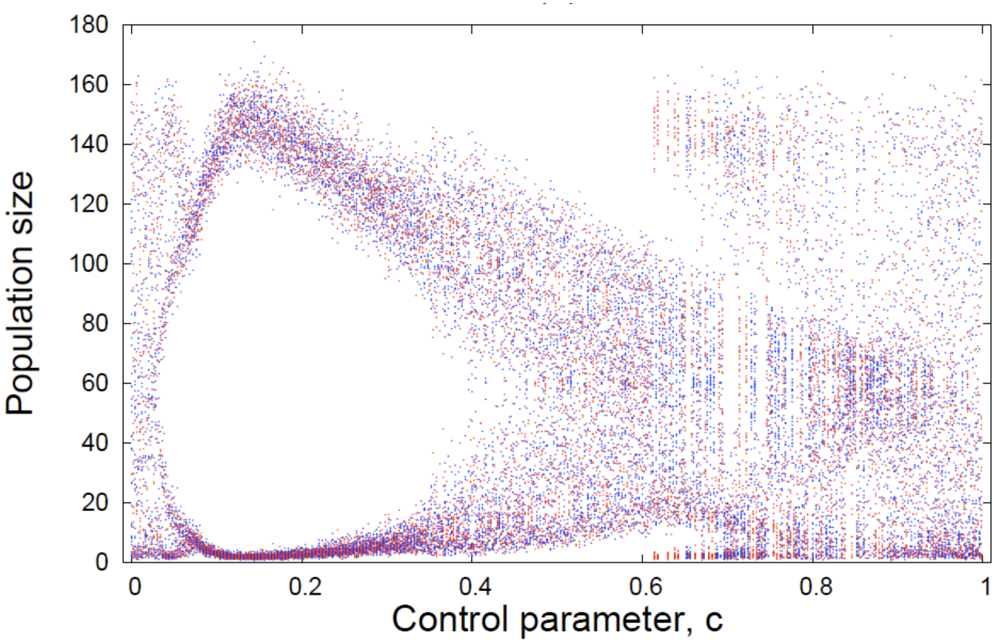
ALCb stochastic models

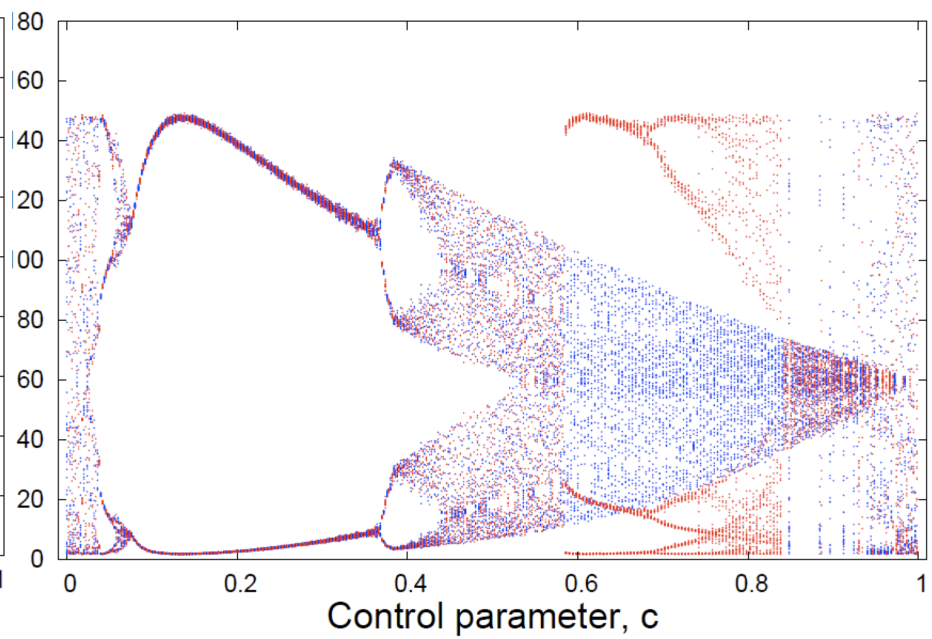
environmental stochasticity

$$x_{t+1} = f(x_t)\exp\left(s\,\varepsilon_t - s^2/2\right)$$

demographic stochasticity

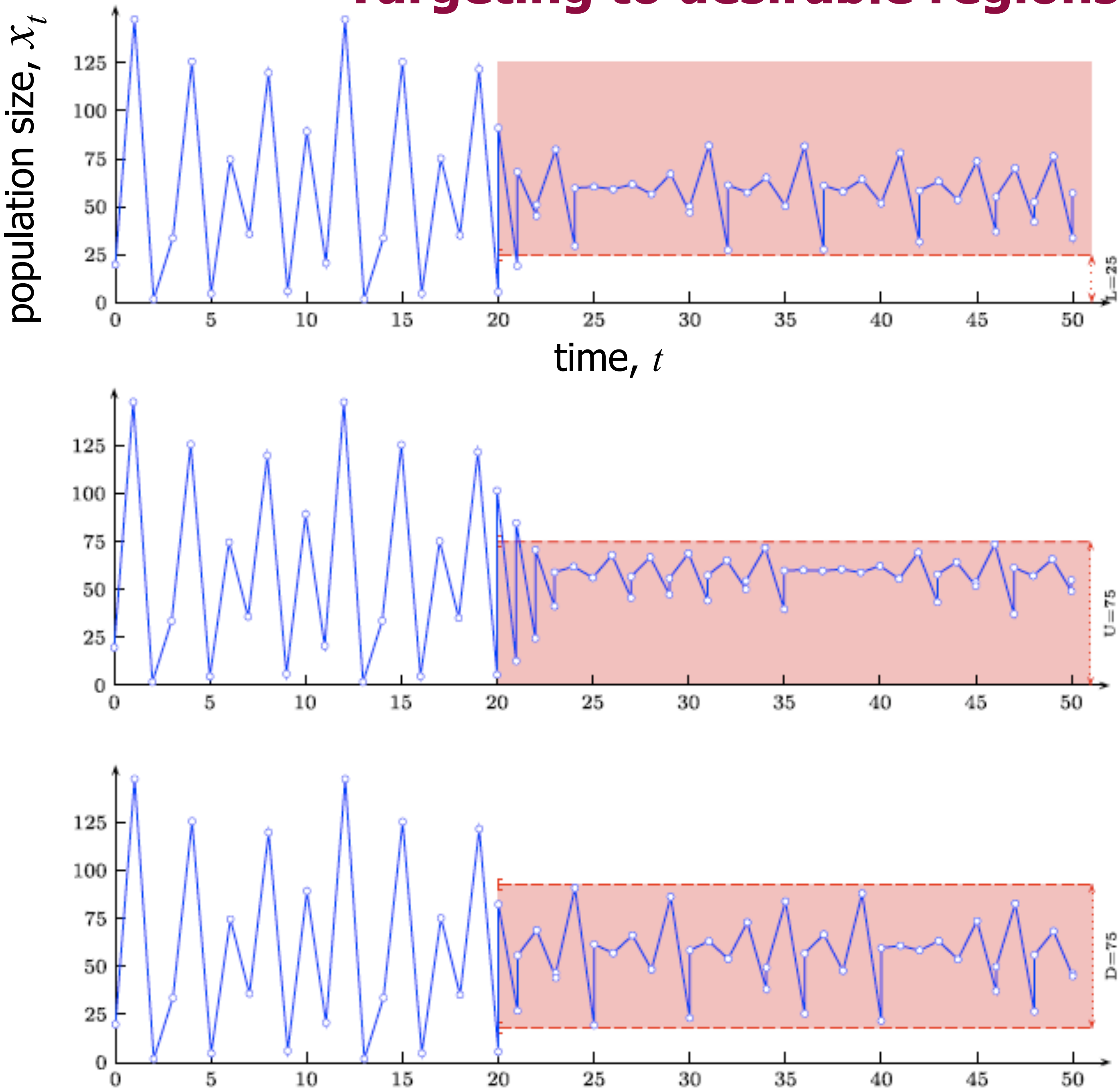
$$x_{t+1} = f(x_t)\exp\left(\sqrt{s^2/f(x_t)}\;\varepsilon_t - \frac{s^2}{2f(x_t)}\right)$$





alternative attractor robust against noise

Targeting to desirable regions

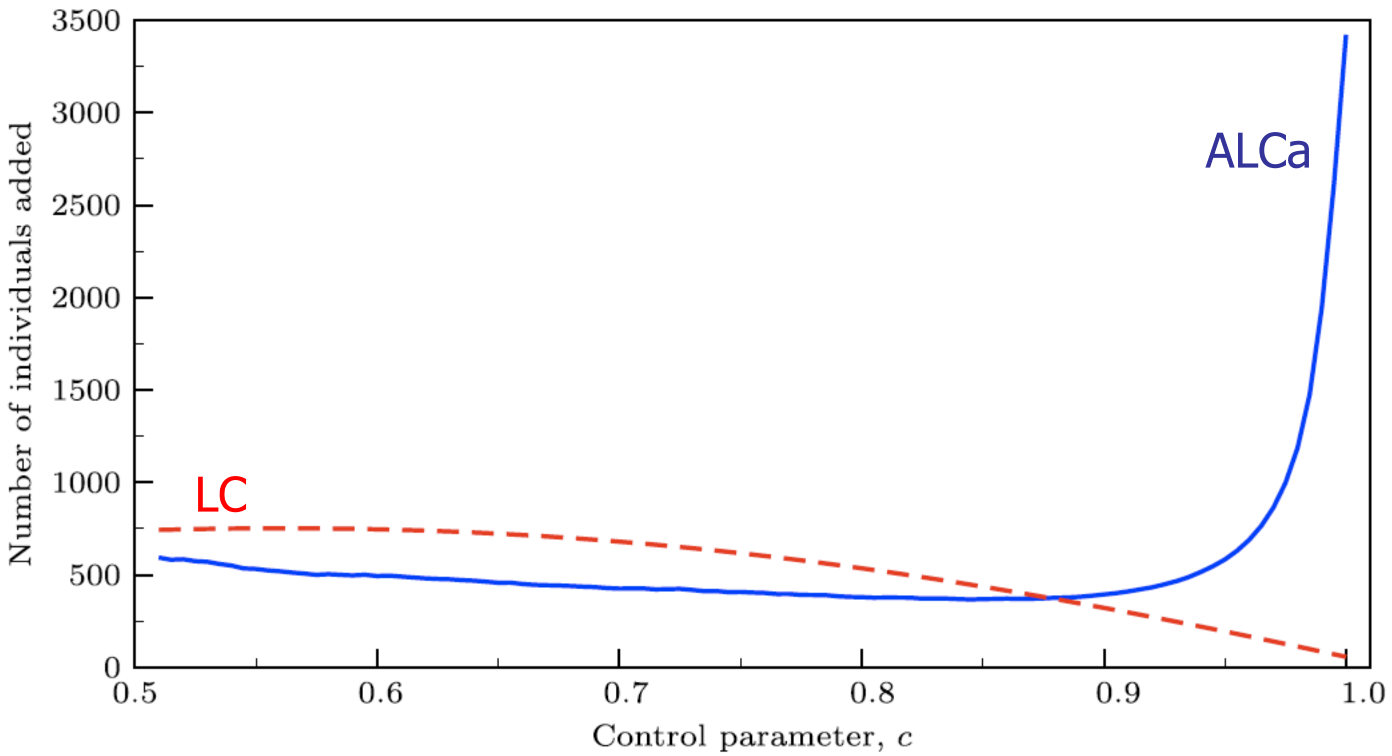


above a lower bound

below an upper bound

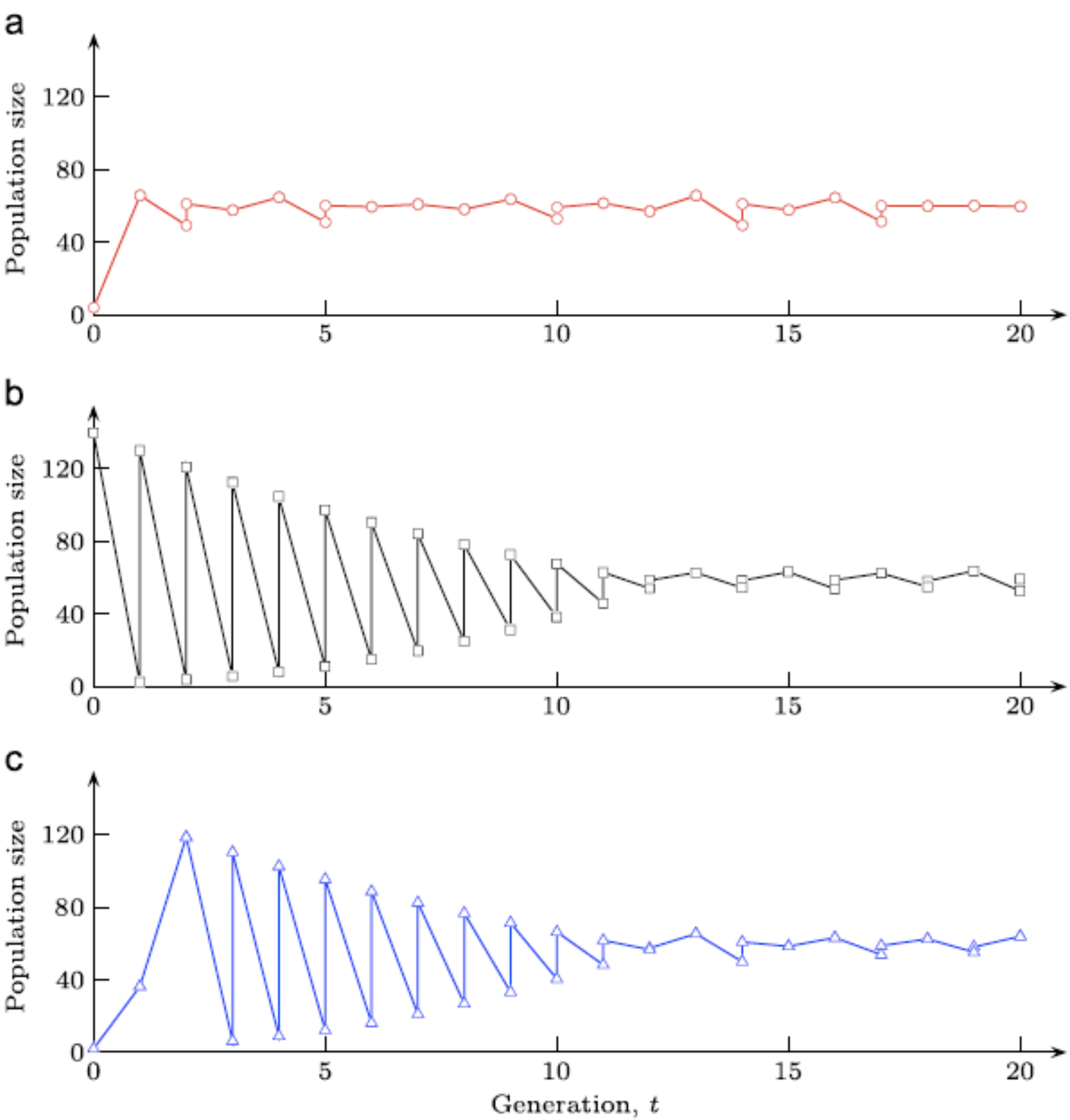
within a certain diameter

Cost



- includes transient
- ALCa without transients becomes more efficient for larger *c*

Three categories of transients



monotonic increase
to the trapping region

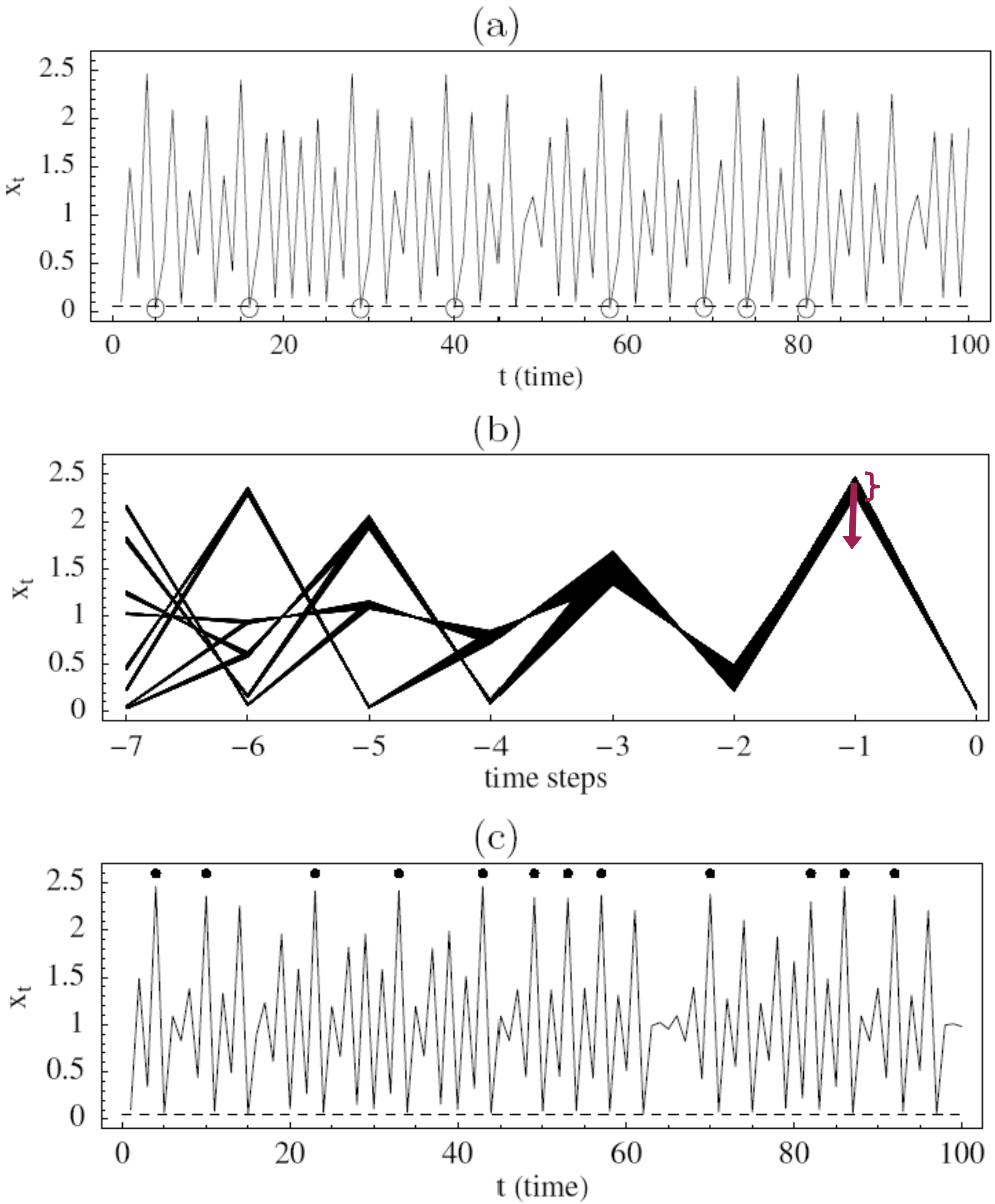
interventions every
other generation
before reaching the
trapping region

mixture of both

Property	CF	PF	TOC	LC	ALC
Stabilization to fixed point	✔	✔	✔	✔	✖
for fixed parameter	✔	✔	✖	✔	✖
for range of parameters	✖	✖	✔	✖	✖
Global behaviour	✖ Gueron 1998	✔ Liz 2010	✔/✖ Franco & Liz 2013 Dattani et al 2011	✔	✔ Franco & H 2013
Can we avoid undesirable population states?	?	?	?	✔/✖	✔
How to choose control?	✔ Gueron 1998 Wieland 2002	✔ Liz 2010	✔ Franco & Liz 2013	?	✔ Franco & H 2013
Do we need to know laws of motion?	Y	Y	Y	Y	Y

Time-series based approach

Chaos anti-control



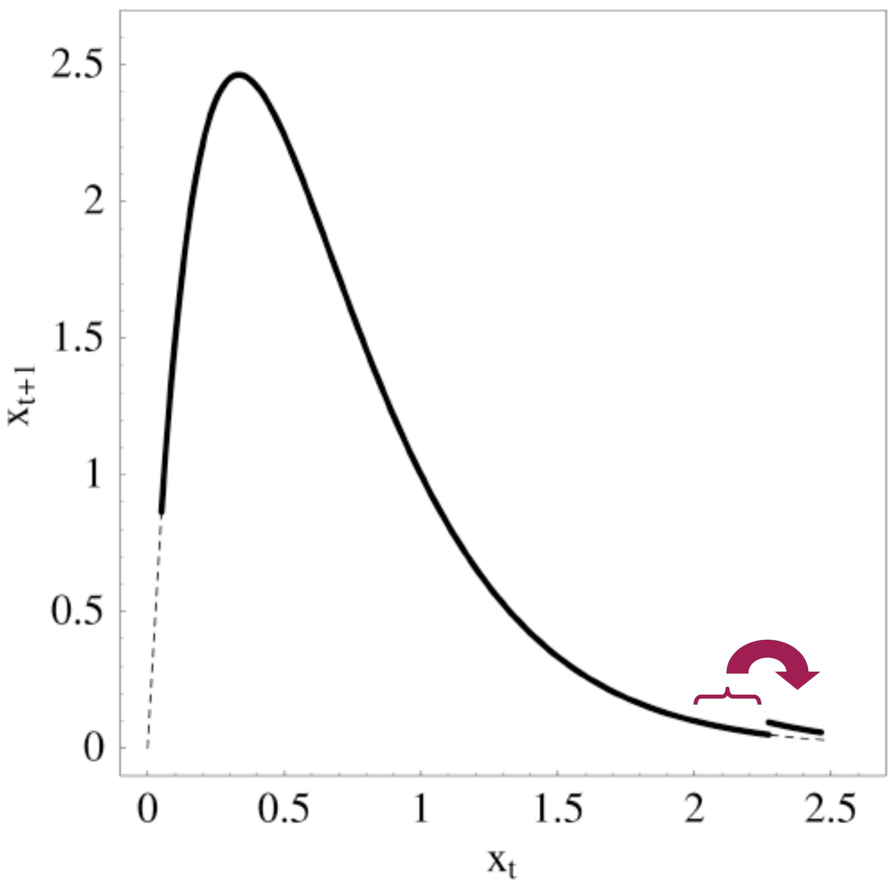
Define undesirable (crash) regions U

"loss region" (Yang et al. 1995 *PRE*)

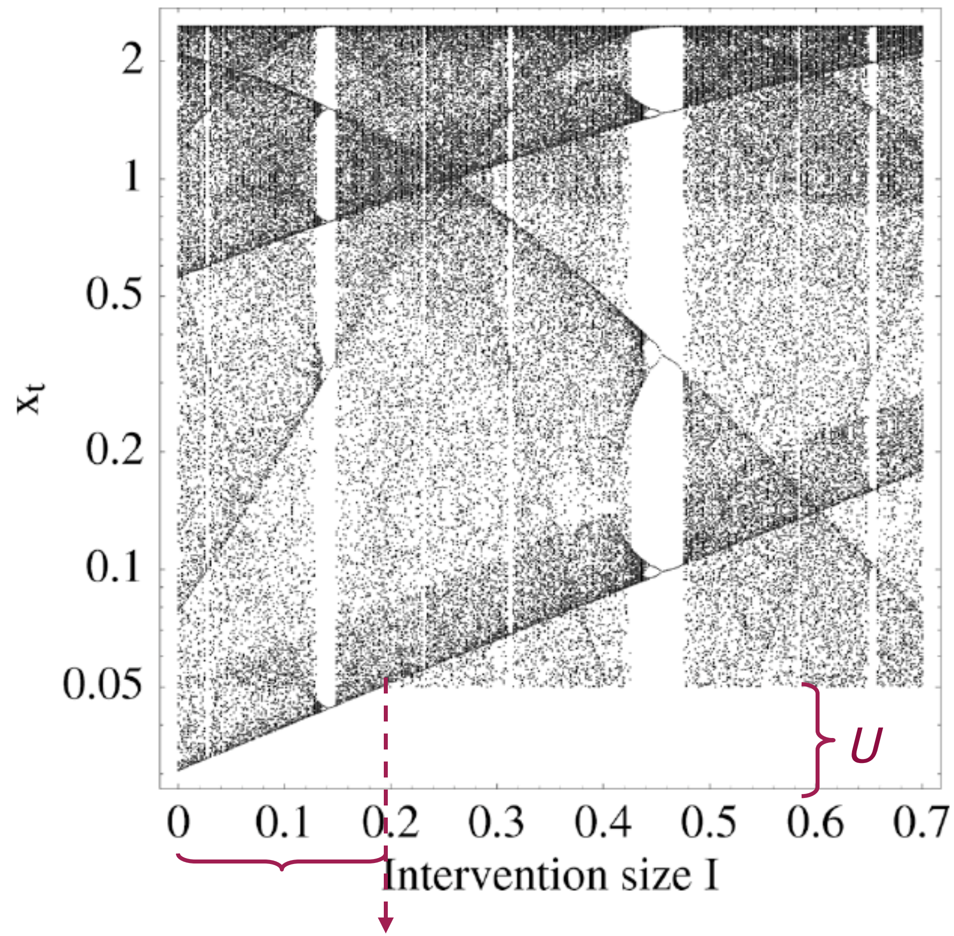
Identify alert zones Z_i

Implement interventions

$$x_{t+1} = \begin{cases} f(x_t - I) & \text{if } x_t \in Z_1 \\ f(x_t) & \text{otherwise} \end{cases}$$

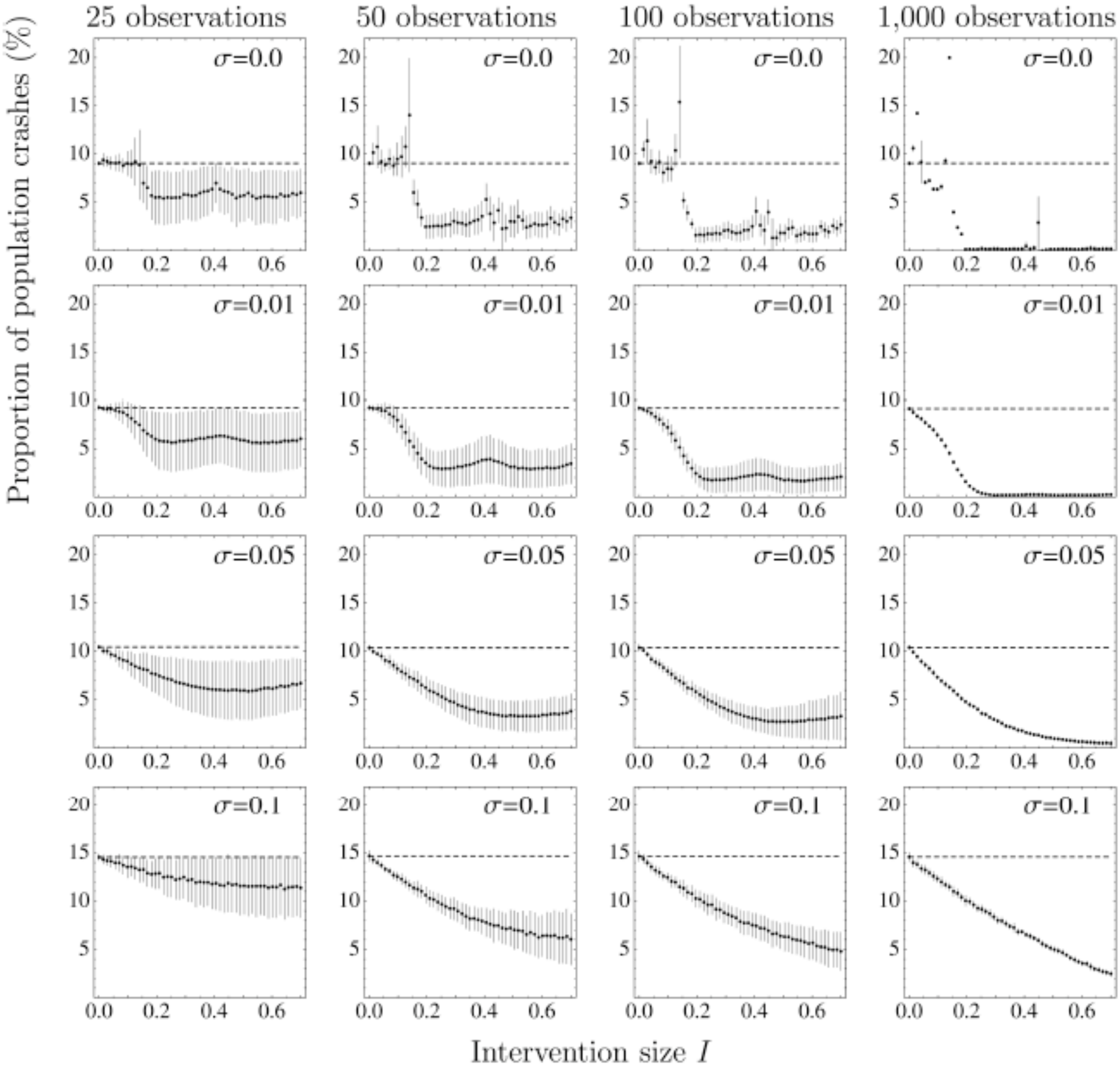


Intervention in the alert zone $Z_1 \approx [2.27, 2.46]$



Critical intervention size

= Width of alert zone Z_1


25 observations
50 observations
100 observations
1,000 observations
σ=0.0
σ=0.01
σ=0.05
σ=0.1
Proportion of population crashes (%)
Intervention size I
0.0
0.2
0.4
0.6
5
10
15
20

Robustness

Approach also tested for

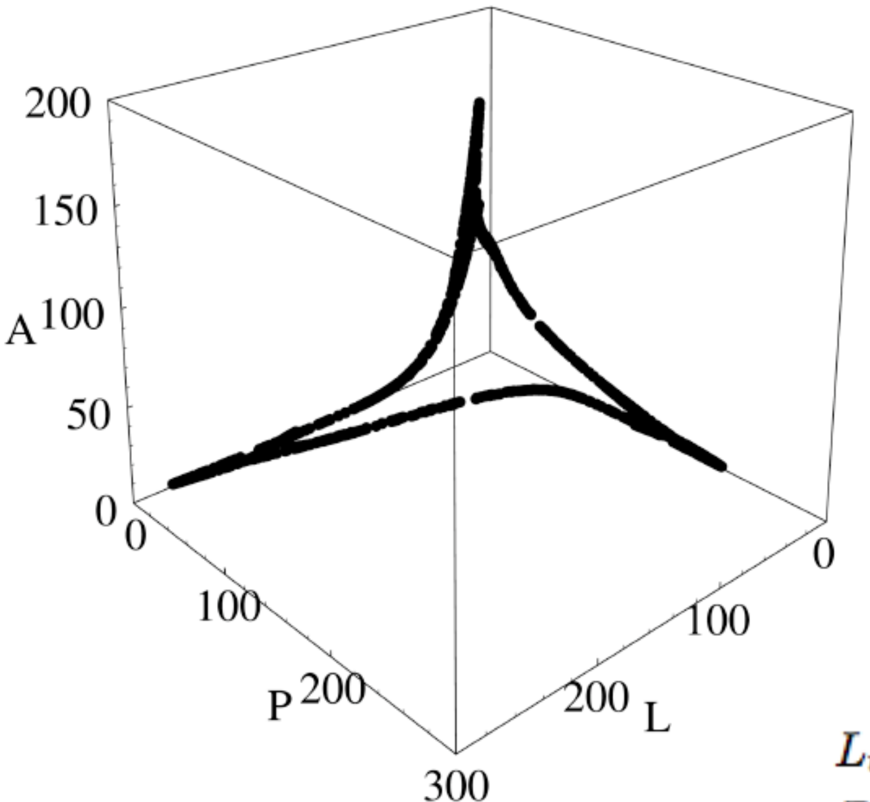
- environmental stochasticity
  (lognormal multiplicative noise)

- alternative interventions (motivated from sustainable harvesting)

$$
\begin{aligned}
x_{t+1} &= f(x_t - E_1 x_t) \quad \text{if } x_t \in Z_1 \ , \\
x_{t+1} &= f(x_t) \exp\left(-E_2 x_t\right) \quad \text{if } x_t \in Z_2 \ , \\
x_{t+1} &= f(x_t) \exp\left(-E_3\right) \quad \text{if } x_t \in Z_2 \ ,
\end{aligned}
$$

The essential thing is to kick the system off the crash path.

Application to a stage-structured insect population (flour beetle)

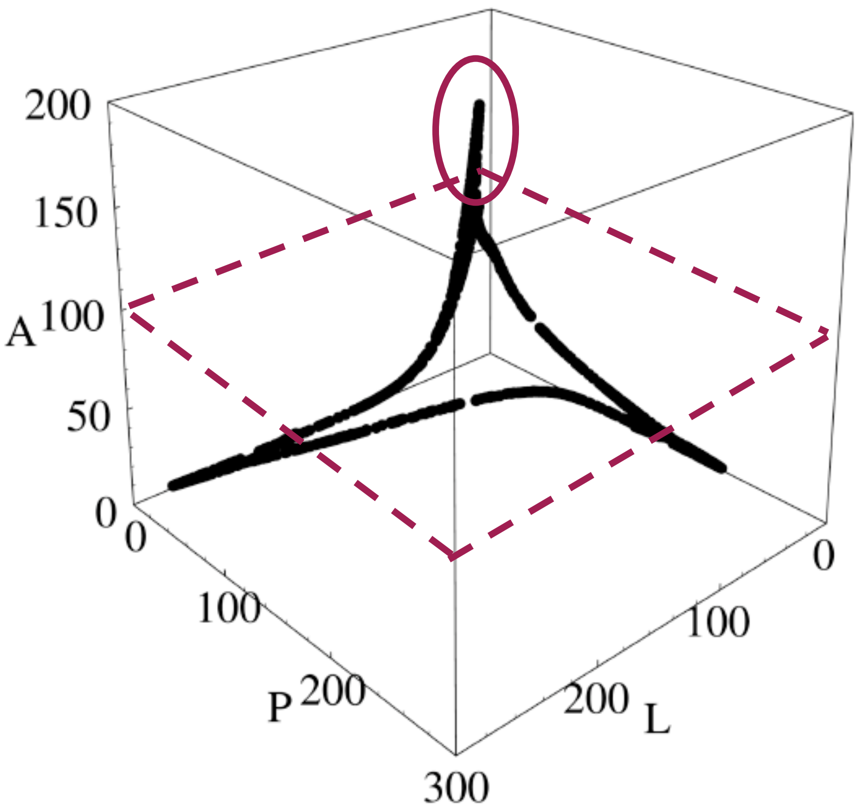


http://caldera.calstatela.edu/nonlin/

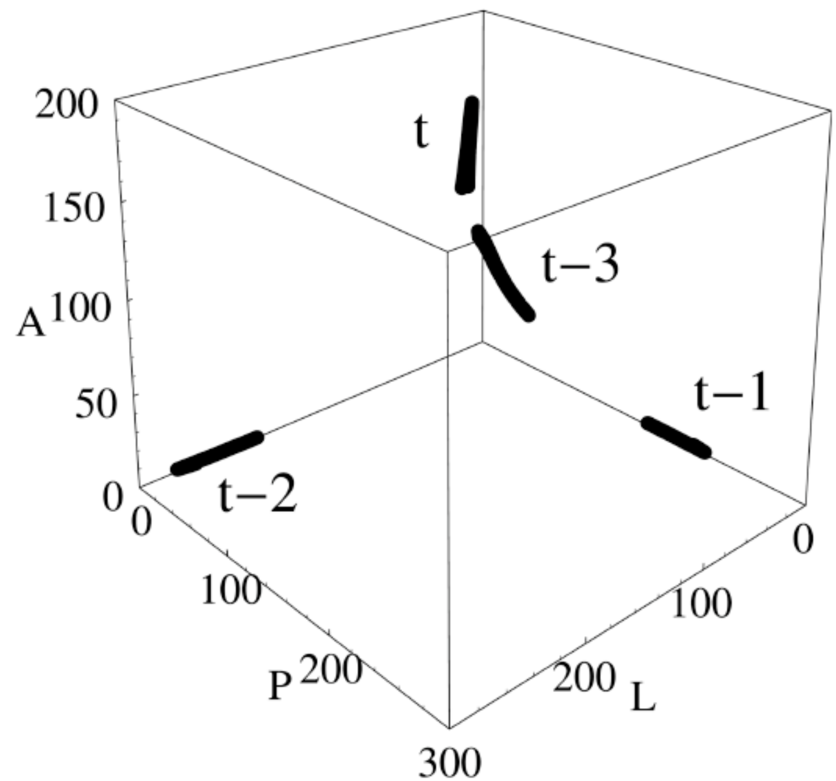
$$
\begin{aligned}
L_t &= bA_{t-1}\exp\left(-c_{EL}L_{t-1} - c_{EA}A_{t-1}\right)\\
P_t &= L_{t-1}\left(1-\mu_L\right)\\
A_t &= P_{t-1}\exp\left(-c_{PA}A_{t-1}\right) + A_{t-1}\left(1-\mu_A\right)
\end{aligned}
$$

Identifying alert zones

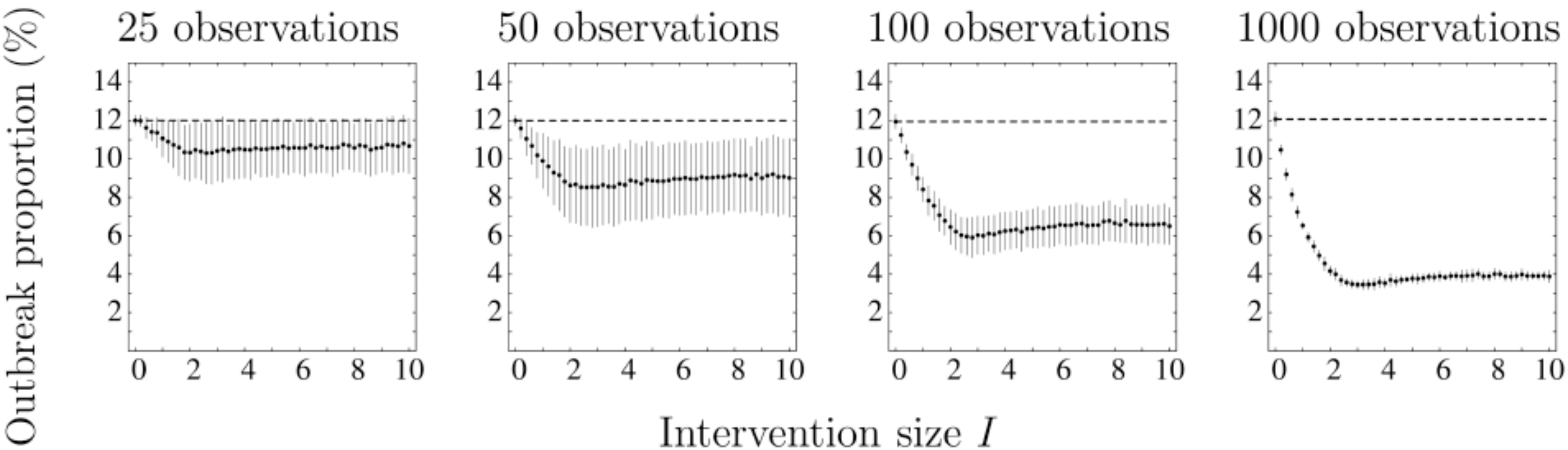
Undesirable region:
A>100 (outbreaks)



Alert zones
(pre-images)



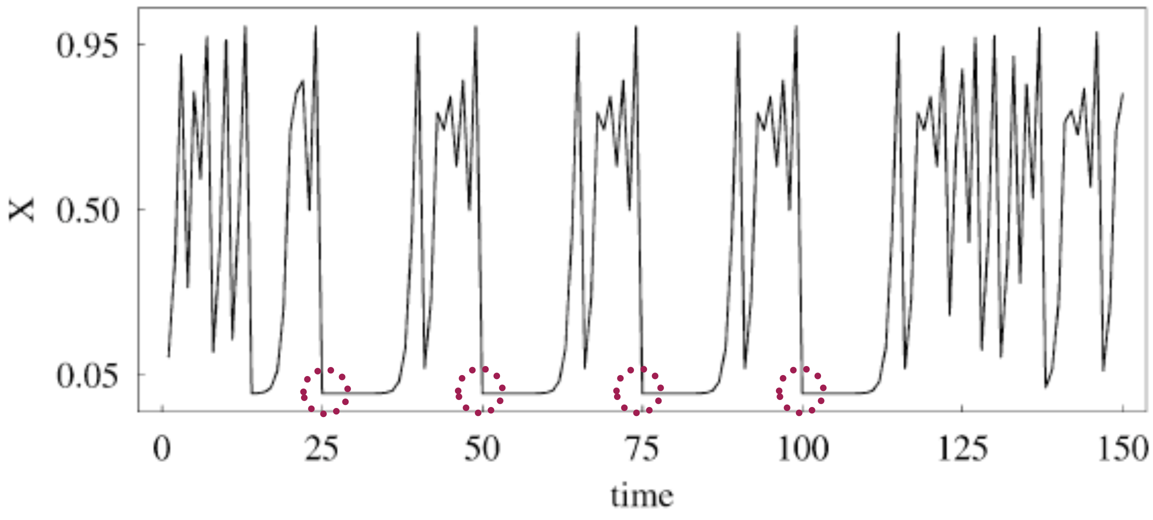
Effectiveness
for LPA model with demographic noise



Intervention at t-1 by adding I adult individuals

Stochastic LPA model from Desharnais et al. (2001, *Ecol Lett*)

Idea can also be used for 'brutal' targeting

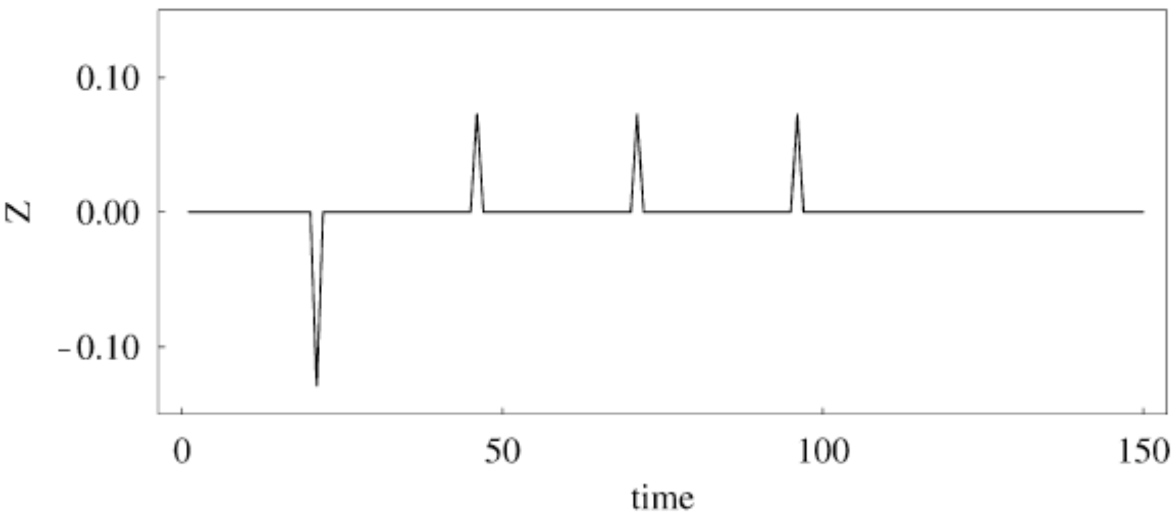


Aim: Generate crashes of a pest species

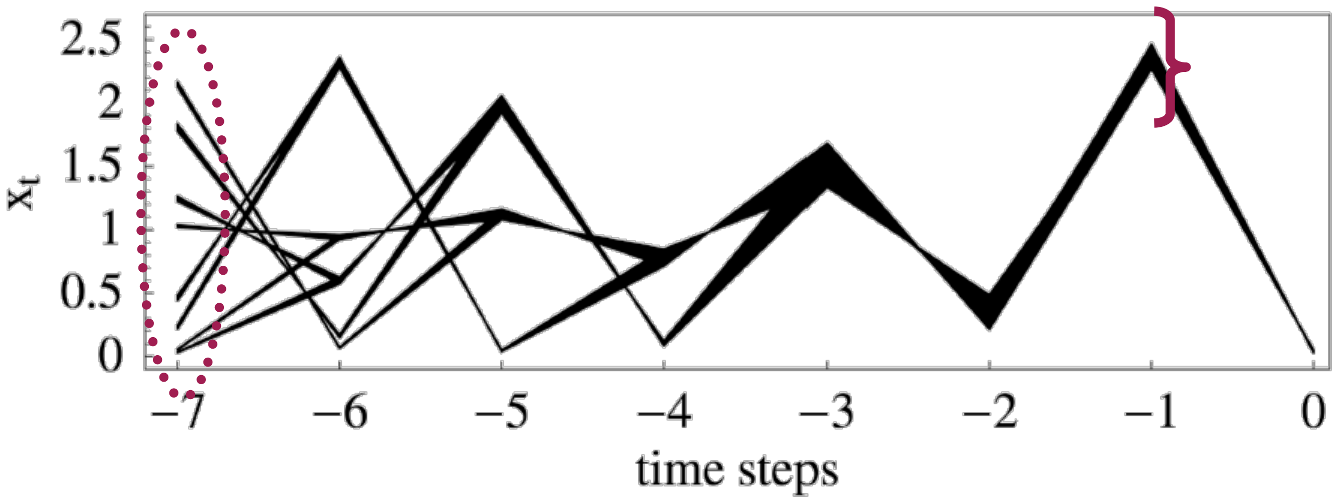
$$X_{t+1} = r(X_t + Z_t)\big(1 - (X_t + Z_t)\big),$$

where the (time-dependent) interventions Z_t are

$$Z_t = \begin{cases} (c_j^{\max} + c_j^{\min})/2 - X_t & \text{for } t = \tilde{t}, \\ 0 & \text{otherwise.} \end{cases}$$



Summary



- There is a critical intervention size corresponding to the ‘width’ of the alert zone.

- Noise widens the alert zones (positive), but also requires larger interventions (negative).

- The earlier we intervene, the smaller the effort (but also more complicated from a management point of view).

Conclusions

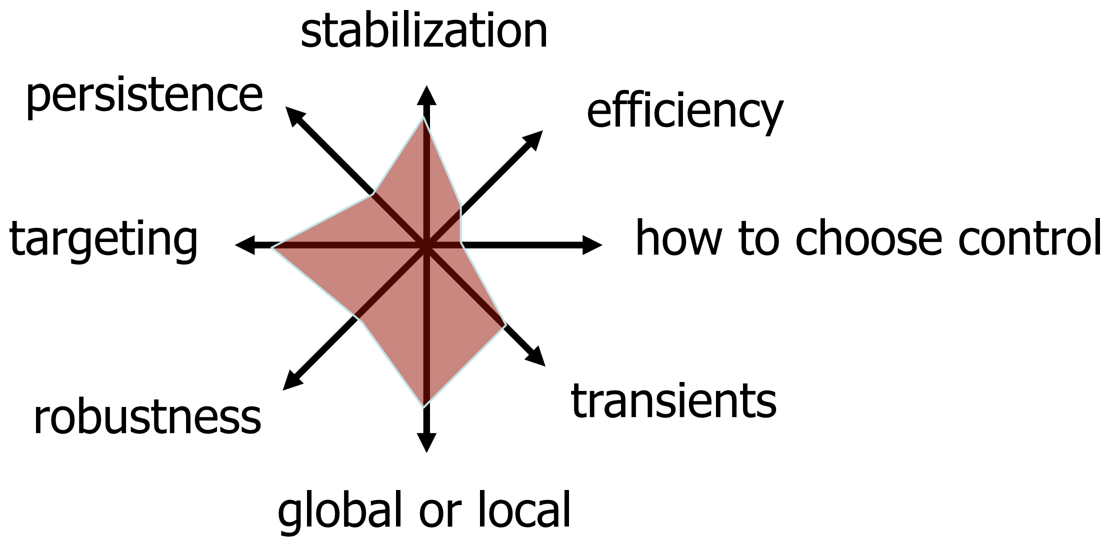
- Chaos *maintenance* while avoiding outbreaks/extinction

- Time series-based approach (no equations needed)

- Utilises short-term predictability

- Works for little available data (typical in ecology)

Future directions



- Spatial structure, synchrony, “pinning” effects
- Higher-dimensional systems
- Different kinds of costs
- Combination of controls

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