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.

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 theoretical ecologists for decades in a force that drives it. The recurrent patterns, moreover, seem to be highly resilient to perturbation and do not break down with experimental manipulations; the 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.

In the 1870s, insect outbreak models...
Chaos in ecology

- favours biodiversity (Huisman and Weissing 1999)
- 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

**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
Ecological reality...?

small

swift

continuously

previously determined unstable periodic orbits

regular

wisely chosen

LHRG 2007
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


Cost

Constant feedback

\[ x_{t+1} = f(x_t) + I \]
2.) Proportional feedback (CF)

\[ x_{t+1} = (1 - \gamma) f(x_t) \]
Proportional feedback: \( x_{t+1} = c \cdot f(x_t) \)
3.) Target-oriented control (TOC)

\[ x_{t+1} = f(x_t + I(x_t)) \]

\[ I(x) = c(T - x) \]

\[ \begin{align*}
I(x) & = c(T - x) \\
\text{restock population} & \quad \text{if below target} \\
\text{harvest population} & \quad \text{if above target}
\end{align*} \]
Stochastic attractor switching

\[ x_{t+1} = (1 + \epsilon_t) f(x_t + I(x_t)) \]

\[ \epsilon_t \] Gaussian noise with zero mean and \( \sigma^2 \) variance
Condition for 95% chance of population size being in basin of attraction for $N^*_{+}$

$$0 < \sigma < \frac{M - N^*}{1.96 M} \quad \text{and} \quad K_1^- < N_t < K_2^-$$
Target-oriented control \[ x_{t+1} = f((1 - c)x_t + cT) \]
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)

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

\{ \text{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 $\rightarrow$ restock
(Sah et al. 2013 *J. Theor. Biol.*)

![Graph showing comparison between uncontrolled and controlled systems over generations.](image-url)
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)

Experiments/simulations in Sah et al. (2013)

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

2nd order not topologically conjugate 1st order

order of events is important

\[ b_{t+1} = f(a_t) \quad a_{t+1} = \begin{cases} 
  b_{t+1} & \text{if } b_{t+1} \geq L \\
  L & \text{else}
\end{cases} \]

\[ b_t : \text{population size before control} \]

\[ a_t : \text{population size after control} \]

\[ L \equiv c \cdot b_t \]

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

\[ b_t : \text{population size before control} \]

\[ a_t : \text{population size after control} \]

Let \[ x_t \equiv b_t \] ALCb

Let \[ x_t \equiv a_t \] ALCa

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

\[ a_{t+1} = \max\{f(a_t), c \cdot a_t\} \]
**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 not possible
Looking at a different stability measure…

\[ FI = \frac{1}{T \bar{x}} \sum_{0}^{T-1} |x_{t+1} - x_t| \]  

Fluctuation Index

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

c control makes things worse
alternative attractor makes things even worse
ALCb lattice model

discrete-state dynamical system

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

alternative attractor robust against integerization
ALCb stochastic models

environmental stochasticity

\[ x_{t+1} = f(x_t) \exp(s \epsilon_t - s^2/2) \]

demographic stochasticity

\[ x_{t+1} = f(x_t) \exp\left(\sqrt{s^2/f(x_t)} \epsilon_t - \frac{s^2}{2f(x_t)}\right) \]

alternative attractor robust against noise
Targeting to desirable regions

population size, $x_t$

time, $t$

above a lower bound
below an upper bound
within a certain diameter
• includes transient
• ALCa without transients becomes more efficient for larger $c$
Three categories of transients

a) Monotonic increase to the trapping region

b) Interventions every other generation before reaching the trapping region

c) Mixture of both
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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 $Z_1$
Robustness

Approach also tested for

- environmental stochasticity (lognormal multiplicative noise)
- alternative interventions (motivated from sustainable harvesting)

\[
\begin{align*}
    x_{t+1} &= f(x_t - E_1 x_t) \quad \text{if } x_t \in Z_1, \\
    x_{t+1} &= f(x_t) \exp(-E_2 x_t) \quad \text{if } x_t \in Z_2, \\
    x_{t+1} &= f(x_t) \exp(-E_3) \quad \text{if } x_t \in Z_2,
\end{align*}
\]

The essential thing is to kick the system off the crash path.
Application to a stage-structured insect population (flour beetle)

\[
L_t = bA_{t-1} \exp(-c_{EL}L_{t-1} - c_{EA}A_{t-1}) \\
P_t = L_{t-1} (1 - \mu_L) \\
A_t = P_{t-1} \exp(-c_{PA}A_{t-1}) + A_{t-1} (1 - \mu_A)
\]
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

Idea can also be used for ‘brutal’ targeting

Aim: Generate crashes of a pest species

\[ X_{t+1} = r(X_t + Z_t)(1 - (X_t + Z_t)), \]

where the (time-dependent) interventions \( Z_t \) are

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


Franco D, Hilker FM (submitted) Stabilizing populations with adaptive limiters: prospects and fallacies.


