Resilience and stability of ecological systems

an awesome paper by C.S. Holling

LASTIG Reading Group - summer 2024 - paul

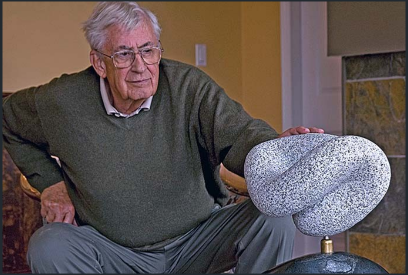
Disclaimer

This talk contains

- no AI
- no GIS
- no maps
- no LASTIG specific topic
- no expertise

The Author

C.S. Holling, the man, the legend



Crawford Stanley "Buzz" Holling, (1930 - 2019)

- PhD in 1957
- worked several years in the Canadian Forestry Departement
- Professor and Director of the Institute of Animal Resource Ecology, Univ. of British Columbia
- Awarded multiple times

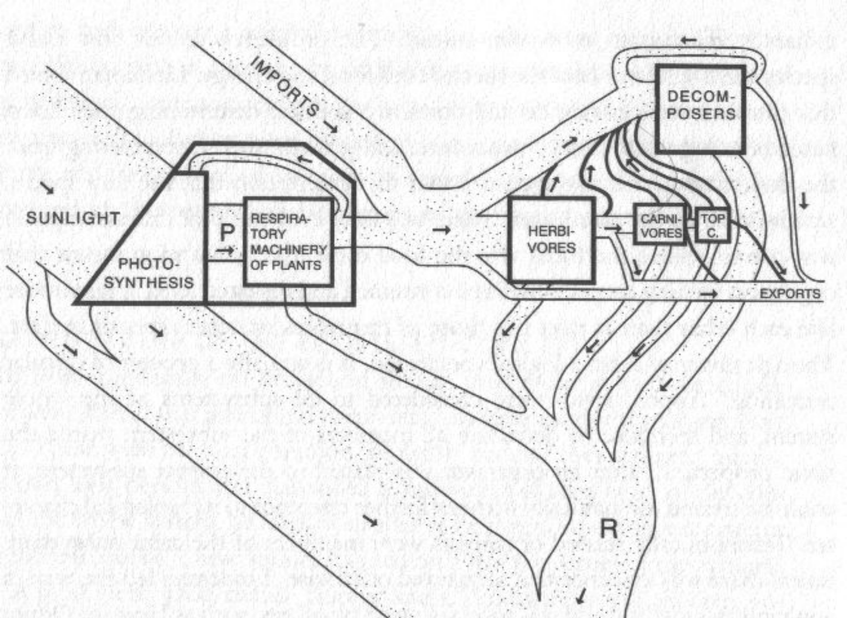
Father of the concept of resilience, adaptive management, adaptive cycle, and panarchy.

Pionneer in interdsciplinary and participatory modeling workshops about natural systems management.

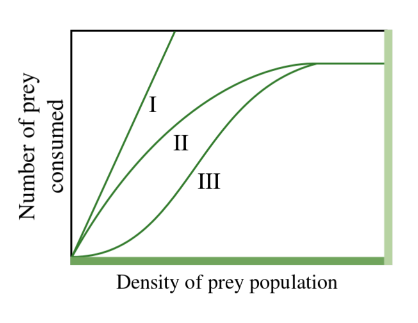
Ecological modeling in three slides

(1) Silver Springs model

Energy flows in a natural system [Odum, 1971]



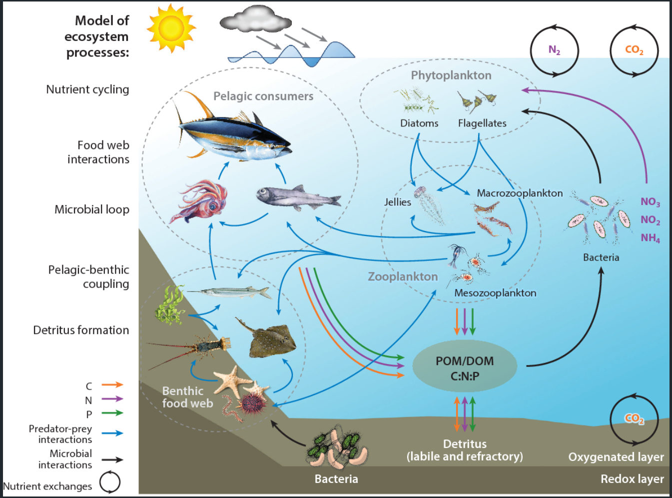
(2) Functional responses



- early work of Holling
- Model the relationships between preys density and consumption
- Type I models instant consumption (no chase, no boundaries)
- Type II models saturation for high prey densities (short chase, early satitation)
- Type III models a learning phase in chasing preys and selection of preys (rare)

$\rightarrow$ real predators feed on several preys, combining Type II and Type III

(3) Ecosystem modeling



An ecosystem model represent the system formed by a bunch of species interacting with and within an environment

Each arrow has to be modelled e.g. Functional responses model the evolution of thuna pop. regarding its preys

Image from : Pethybridge, Heidi R. et al. "Improving Marine Ecosystem Models with Biochemical Tracers." Annual review of marine science 10 (2018): 199-228.

The Paper

"Individuals die, population disappear and species become extinct. That is one view of the world."

(the first two lines of the paper)

Two perspectives on system

Holling distinguishes two perspectives :

- when a system is designed to perform a specific task under a narrow range of predictable external conditions
- consistant non-variable performance and the amplitude and frequency of oscillations (if any) are important
- Quantitative view is preferred : how much more ? how long ?

- when a system is profoundly affected by external changes (i.e. sensitive)
- when confronted to unexpected variations consistancy of behavior $<<$ persistence of properties, relationships
- Qualitative view is preferred : does it exist? would it disappear or come back ?

Quantitative Tradition

Tradition of analysis is quantitative : e.g. physics

- Equilibrium centered view are static
- Transient behaviors (far from equilibrium) are unknown

Some limitations :

- Species populations in equilibrium states won't inform on conditions of persistence
- Human exploitation shifts natural systems away from their equilibrium

Purpose of the article :

Holling delivers a review of ecological theory mixed with real natural system behaviors

$\Longrightarrow$ Would different perspectives yield different useful insights?

Natural systems are dynamic, subject to perturbations (often human).

Persistance, resistance, adaption are properties of interest

Predators and preys

Theoretical (simple) model of two populations :

$x(t)$ are preys , $y(t)$ are predators (population over time)

$$\begin{cases} \frac{\mathrm{d}x(t)}{\mathrm{d}t} & = & \alpha x(t) - \beta x(t) y(t) \\ \frac{\mathrm{d}y(t)}{\mathrm{d}t} & = & \delta x(t) y(t) - \gamma y(t) \end{cases}$$

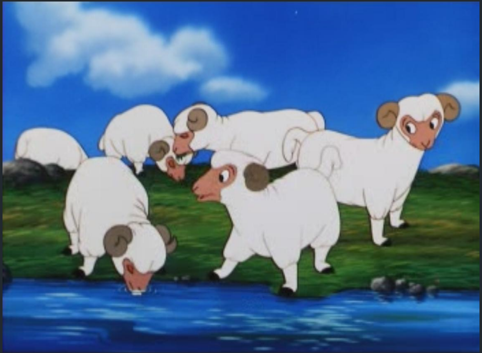
with :

- $\alpha > 0$ is prey intrinsic growth rate
- $\beta > 0$ is prey death (by predation) rate
- $\gamma > 0$ is predator intrinsic death rate
- $\delta > 0$ is predator growth (by eating preys) rate

Patterns of this system :

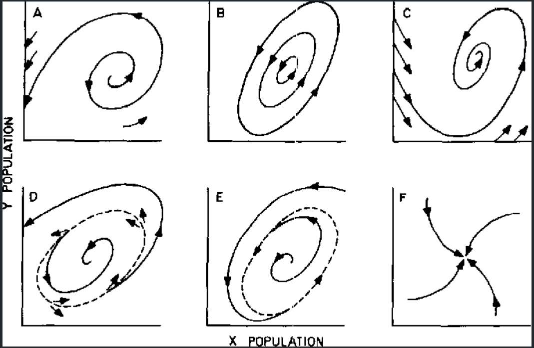
- regulated interactions may lead to oscillations
- some conditions lead to extinction
- system may recover from perturbations : damping

Wolves, sheeps, and grass

Lambert the Sheepish Lion, dir. by Jack Hannah © Disney , 1952

Phase diagram patterns typology



A is unstable equilibrium,
B is neutrally stable cycles,
C is stable equilibrium,
D is domain of attraction,
E is stable limit cycle,
F is stable node

obtained by math. analysis. Roughly : solve derivatives = 0 then apply solutions to the Jacobian matrix, extract the eigen values, real parts signs give (un)stability

"Common" knowledge on these models

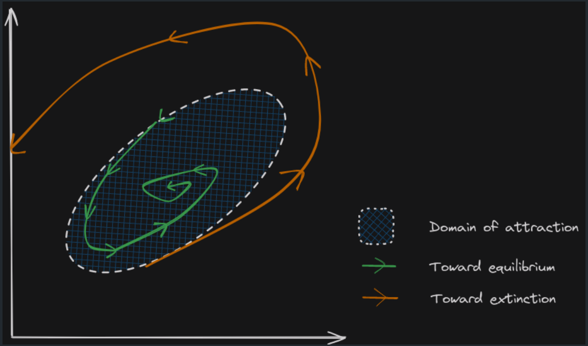
- all these models have either a stable point or a stable limit circle (Kolmogorov theorem)
- a model (given $\alpha, \beta, \gamma, \delta$) is either globally stable or globally unstable
- neutral stability is very unlikely ($\approx$ not attracted by anything)
- when stable, a limit cycle is likely

Model Complexification

$\Longrightarrow$ D-type patterns

Relax simplifying assumptions :

- several species
- add lag in reproduction
- plateau in predators reproduction
- non-random predator attacks
- minimum prey density for reproduction



Domains of attraction

More realistic models have :

- several distinct domains of attraction
- stable nodes,
- stable limit cycles

Size and location of domains $\leftrightarrow$ persistence of the system and probability of extinction of species

Some viability theory should be useful here

Netlogo demo

The Rabbits, Grass, Weeds model in netlogo

What differs from equations ?

Netlogo ABM additions :

- discrete populations & space
- three "species"
- randomness
- spatiality / movement

Real world closed systems

A lake

Garda Lake, Italy (CC)

Nice features :

- almost close (within the watershed)
- fish are mobile inside
- big enough mass of water to buffer the climate changes
- lot of human perturbations documented

Two types of perturbations (controls):

- fish nutrients : human or industrial waste in the lake
- fish harvesting

How real interactions create patterns that differs from the theoretical ones ?

Paleolimnologists exist and are able to monitor a lake state over centuries.

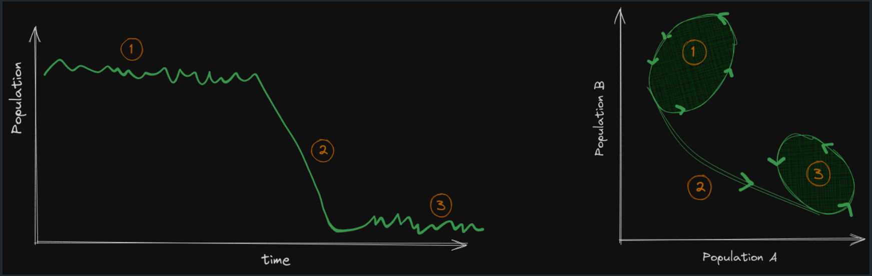
Example of a lake in Italy :

1. trophic equilibrium $\approx$ no modification for thousand years (2000 BC to 171 BC), even if surrounding change (steppes $\rightarrow$ grassland $\rightarrow$ forest)
2. Sudden shift due to (external) perturbation : Roman way (Via Cassia) in 171 BC, more people (waste).
3. Eutrophication : the environment becomes rich in nutrients N, P ($\Longrightarrow$ subtle changes in hydrographic regimes : algae , plankton)
4. New dynamics and huge population changes (irreversible)

Common patterns

Same overall patterns in different countries (Italy, Canada, US) and fish species (sturgeon, herring, white fish)

- prolonged high level of harvest
- then sudden drop in populations(up to 4 order of magnitude in few years)
- appearance or disappearance of populations (flies, plancton, worms, fish)
- wide oscillations
- new domain of attraction establish



Empirical Evidences

"It is as is the population had been shifted by fishing pressure from a domain with a high equilibrium to one with a lower one"

- Fishing shifts the age structure of fish population towards younger ages (less opportunity to reproduce)
- Intense fishing pressure + changes in the chemicals of environment $\implies$ apparition of new predators , foreign competitors
- Harvesting at the maximum of sustainable yield + a small mortality is sufficient to cause the collapse

Early Conclusions

- Harvesting progressively reduced the resilience of the fish population
- Lakes have high but limited capacity to absorb perturbation
- Once limits are crossed, the systems shifts to another domain
- Distinct domain of attraction is not uncommon in closed systems

Vocabulary

Driving variables

≈ "things that have an impact on others"

e.g. Land Cover, Rainfall, t in $Pop_{fish}(t)$, Temperature, nutrient concentration, etc.

State variables

≈ observables , measures

e.g. productivity of algae, Net ecosystem exchange of CO_2, Fish population, etc.

Resilience

"a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables"

Other disciplines have different meanings for driving and state variable

Extensions

- Fecundity, mortality , competition and predation : Reproduction curves
- Environnement is not close nor random nor homogeneous : Spatial heterogeneity

Reproduction curves

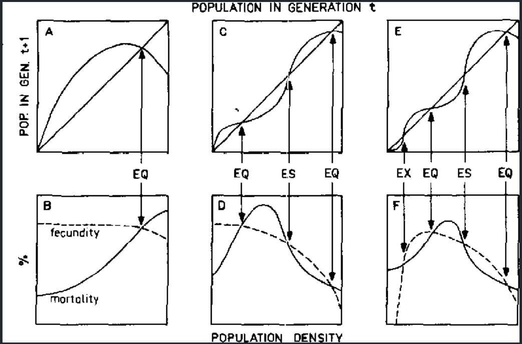
Density of animals is "self regulated" :

- low density : difficulty to mate : density $\searrow$
- high density : competitions for mates, food, nesting sites : density $\searrow$

(also modifies neighbors in the trophic web)

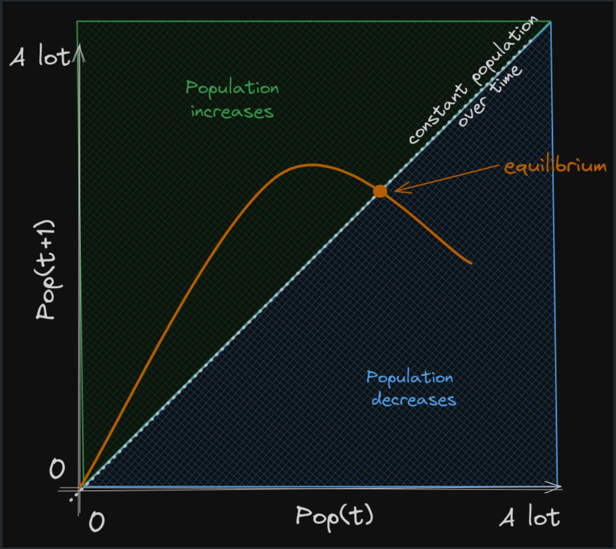
Reproductions curves model that feedback

Reproduction curves

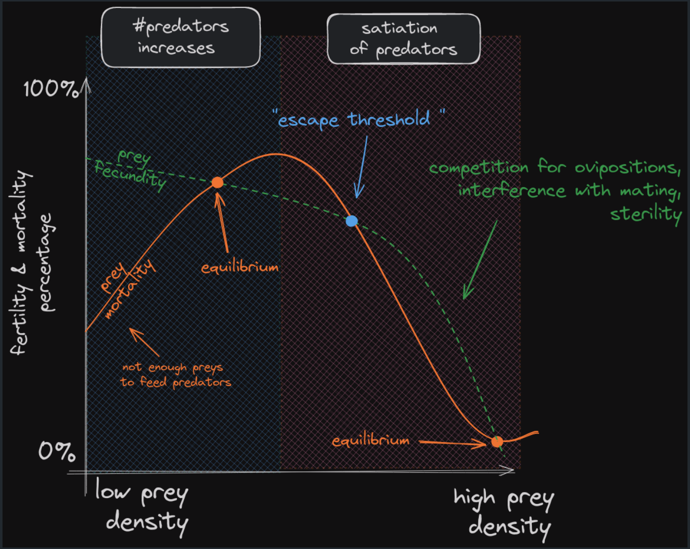


- EQ is equilibrium
- ES is escape threshold
- EX is extinction threshold

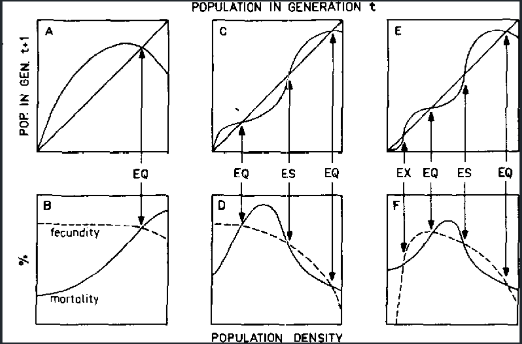
Reproduction curves



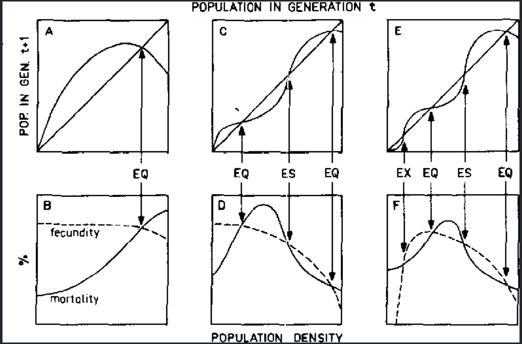
Contributions of fecundity and mortality



Reproduction curves



- B is not realistic, only show negative feedback of overcrowding
- D is called Drosophilia -type curve
- F has been empirically demonstrated for insects



- C/D & E/F are found empirically
- Prey density threshold below which prey become extinct
- Prey density threshold above which prey becomes extinct
- They are domains of attraction ! (no global stability)
- more sinuosity is possible

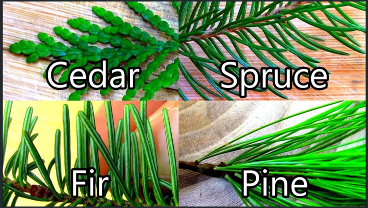
Open real world systems

Grass, trees and worms

Longitudinal study of spruce-fir-birch forest in Canada

Infestation of budworms, parasit of conifers.

Budworm outbreaks appear after several dry years (7 outbreaks since 1700)




Choristoneura is a genus of moths in the family Tortricidae. Several species are serious pests of conifers, such as spruce

Two regimes

During outbreak

Worms population explodes ($\times 10^4$)
Firs collapse
Spruce and birch survive (less prone to worms)

Between outbreaks

Budworms regulated by parasites and predation
Regeneration of fir $\rightarrow$ densification of trees
Spruce and birch suffer from overcrowding, firs dominate

From trees perspective :
stable limit cycle with large amplitude

From budworms perspective :
highly unstable system (population fluctuates widely)
2 distinct basins of attraction : one for standard population, one for outbreaks

Species survival

- Spruce and birch would be excluded from the forest if no outbreak of budworms
- Fir presist because of its regenerative powers and the interplay of forest growth rates and climatic conditions (that result in outbreak)
- Fluctuations are essential to the maintaining of budworms : successive generations of trees assuring a continued food supply for future generations and persistence of the system $\{budworms, predators, trees\}$

$\{Budworm, forest\}$ system is highly unstable and yet highly resilient

Similar patterns with $\{salmon, predators\}$ and $\{grassland, trees, fires\}$ systems

Some pieces of Ecology to remember / early conclusions

Summary

Stability : the ability to return to an equilibrium after a disturbance
Stability characteristics : degree of fluctuation around the equilibrium states, returning to equilibrium time

Resilience : persistence of relations within the system, ability to absorb changes of state/driving variables and still persist
The result of resilience is the persistence of a species, or a low probability of extinction

The Bowl

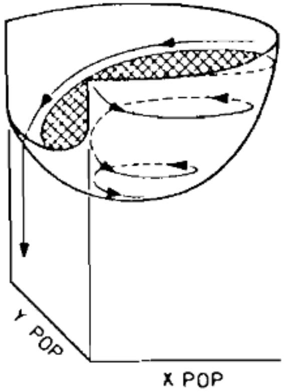


Figure 4 Diagramatic representation showing the feedback forces as a potential field upon which trajectories move. The shaded portion is the domain of attraction.

One can be resilient and unstable (cf. budworms)

One can be stable but not resilient : population in almost constant climatic conditions for a long period can lose the ability to adapt to disturbance (cf . fish in lake)

When systems are open, and the species able to disperse, they tend to be resilient (e.g. pests like locusts)

Complex systems vulgate

Common knowledge is that diversity is linked with stability.
Stability is roughly the number of links in a trophic web

Complex systems tend to fluctuate more than simple ones.

More species $\implies$ more domains of attraction.
Despite higher fluctuation, overall persistence might be increased.

Final words

Take home messages

- Nature is scary (for modelers)
- Everything, everywhere, all at once (has an impact in the ecosystem dynamics)
- Completely quantifying interactions and states is impossible
- Traditional/analytical tools are seldom useful (simulation can help)
- Equilibrium view is not that useful, nor true
- Several basins of attraction, limit cycles, random perturbations.

Engineering resilience : the ability of a system to return to an equilibrium state after a temporary perturbation by measuring how quickly a system's equilibrium is restored (Pimm 1984, Holling 1996).

Socio-technical resilience i.e. common points in a lot of resilience definitions :

- Adaptability and flexibility
- The ability to self-organize
- The ability to build and increase the capacity for learning and adaptation
- The ability to maintain links with other sytems

My POV, chapter I

- domain of attractions are like the algebra they come from : conceptual/imaginary elements and operations
- Sometimes a tiny fraction of the real world can be modelled by combining these elements
- remind me of thermodynamics :
  - only states can be modeled,
  - $\implies$ only Δs can be computed
  - how real transitions occur is untractable/mystery
- Holling's original and iconoclast vision : *There is (almost) no (static) equilibrium in Nature*

My POV, chapter II

- one of the best paper I ever read
- talented writing esp. progressive complexification
- seems to be a must read in the field (similar to Dawkins' Selfish gene paper)

- major impact in a lot of disciplines : resilience is now a buzzword
- easy to learn, hard to master concepts
- Holling proposes a *paradigm* : can be applied to almost everything

Which one is the most resilient ?

Cover by Mark Bagley, © Marvel

The paper : https://pure.iiasa.ac.at/id/eprint/26/1/RP-73-003.pdf

Ecosystem models wikipedia page (a good introduction) :
https://en.wikipedia.org/wiki/Ecosystem_model
Holling's carreer overview
https://www.nature.com/articles/s41893-019-0425-9#ref-CR4

Netlogo Cinematic Universe : https://ccl.northwestern.edu/netlogo/

Thank You

photo from Ecotrust Canada website