Mathematical Biology and Dynamical Systems.
Lecture 2.

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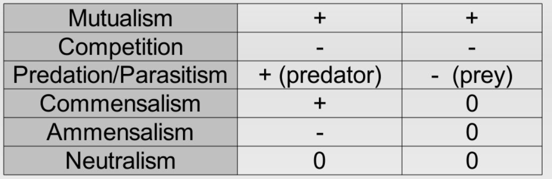
Types of species' interactions

- Interspecific interactions occur when the actions, traits, or density of individuals of one population result in a change in some attribute of another species' population.
- Intraspecific interactions occur when they are between members of the same species' population.

Interaction between two species (so, interspecific) can be classified in different types. A possible classification is the following one:



Mutualism	+	+
Competition	-	-
Predation/Parasitism	+ (predator)	- (prey)
Commensalism	+	0
Ammensalism	-	0
Neutralism	0	0

Mutualism (+/+)

Honey Bee - Dandelion (pollinisation): The honey bee gets to eat the pollen from the flower. The dandelion uses the bee to spread its pollen to another flower.

Clownfish - Sea Anemone: The sea anemone protects the clownfish from predators, as well as providing food through the scraps left from the anemone's meals. In return, the clownfish defends the anemone from its predators, and parasites.

Competition (-/-)

Trees: competition for light in plantations.

Pink coralline algae gets pushed out by **fleshy algae**.

Predation or parasitism (+/-)

Predation: lion on impala.

Dust mites: Feed on dead skin, partially digested food and fecal matter contributes to asthma and allergies.

Commensalism (+ / 0) - *Cum mensa*

Phoresy (transport only): Beetles, flies, bees, ...(arthropods). One organism transports another one of a different species.

Inquilinism (epitiphia): Using a second organism for housing (orchids that grow on trees, ...).

Amensalism (-/0) and Neutralism (0/0)

Examples of amensalism are:

- Penicillium secretes penicillin, which kills some types of bacteria.
- Roots of black walnut release juglone, a toxic material that destroys some herbaceous plants.

Examples of neutralism are:

- A rainbow trout(fish) and dandelion (flower) in a mountain valley.
- Cacti and tarantulas living in the desert.

Kolmogorov systems

The systems we are dealing with are particular cases of the general family of Kolmogorov systems

$$\dot{x}_i = x_i f_i(x), \qquad x = (x_1, x_2, \ldots, x_n) \in \mathbb{R}^n, \qquad \dot{} = \frac{d}{dt}, \tag{1}$$

n being the number of species and with $f_i : \mathbb{R}^n \to \mathbb{R}$, $i = 1, 2, \ldots, n$ being $\mathcal{C}^1$-functions. x_i often corresponds to the population density of the i-th species.

- An important property: if $x_j(0) = 0$ for some $j \in \{1, 2, \ldots, n\}$ then $x_j(t) = 0$ for $t \geq 0$. That is, trajectories starting in $\{x_j = 0\}$ remain there for any positive time and also interior trajectories cannot reach these coordinate planes in finite time.

- They can also be written in the form

  $$\frac{\dot{x}_i}{x_i} = f_i(x), \qquad x = (x_1, x_2, \ldots, x_n) \in \mathbb{R}^n.$$

  The term $\dot{x}_i / x_i$ represents the population growth per individual and time unit of population x_i.

Lotka-Volterra systems

- Kolmogorov systems of the form

$$\frac{\dot{x}_i}{x_i} = r_i + \sum_{j=1}^{n} a_{ij} x_j, \tag{2}$$

  where the constants $r_i, a_{ij} \in \mathbb{R}$, for $i, j = 1, 2, \ldots, n$, are usually called Lotka-Volterra systems.

- Parameter r_i represents the growth rate per individual of the i-th species.

- Parameter a_{ij}, for $i \neq j$, denotes the (interspecific) interaction rate of species j over the species i. Positive corresponds to cooperation whilst negative stands for competition.

- Interaction matrix:

$$A = (a_{ij})_{ij} = \begin{pmatrix} a_{11} & a_{12} & \cdots & a_{1n} \\ a_{21} & a_{22} & & a_{2n} \\ \vdots & & \ddots & \vdots \\ a_{n1} & a_{n2} & \cdots & a_{nn} \end{pmatrix}. \tag{3}$$

Lotka-Volterra systems

- If all the **off-diagonal** terms

$$A = (a_{ij})_{ij} = \begin{pmatrix} \bullet & a_{12} & \cdots & a_{1n} \\ a_{21} & \bullet & & a_{2n} \\ \vdots & & \bullet & \vdots \\ a_{n1} & a_{n2} & \cdots & \bullet \end{pmatrix} \tag{4}$$

are ≥ 0 the system is cooperative. The matrix A is a Z-matrix.
If all of them are ≤ 0 the system is competitive. The matrix A is a Metzler matrix.

A Competition model

A simple model for competition

- Let x_1, x_2 be two population species, each one obeying a logistic model in absence of the other species:

$$\dot{x}_i = r_i x_i \left(1 - \frac{x_i}{K_i}\right), \quad i = 1, 2,$$

  where $x_j = x_j(t)$ and $\dot{} = d/dt$.

- A simple competitive interaction can be modelled as

$$\begin{aligned} \dot{x}_1 &= r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) - c_1 x_1 x_2 \\ \dot{x}_2 &= r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) - c_2 x_1 x_2 \end{aligned} \tag{5}$$

  with $c_i > 0$, $i = 1, 2$. The competition terms $c_{1,2} x_1 x_2$ are assumed to depend on the product of both species' densities.

- Equivalently, in Lotka-Volterra system form (2),

$$\begin{aligned} \frac{\dot{x}_1}{x_1} &= r_1 \left(1 - \frac{x_1}{K_1}\right) - c_1 x_2 \\ \frac{\dot{x}_2}{x_2} &= r_2 \left(1 - \frac{x_2}{K_2}\right) - c_2 x_1, \end{aligned}$$

  or

$$\begin{pmatrix} \dot{x}_1/x_1 \\ \dot{x}_2/x_2 \end{pmatrix} = \begin{pmatrix} r_1 \\ r_2 \end{pmatrix} + \begin{pmatrix} -\frac{r_1}{K_1} & -c_1 \\ -c_2 & -\frac{r_2}{K_2} \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}. \tag{6}$$

Adimensionalising the equations

We seek a simpler form to analyse our model, despite we can loss a direct interpretation in terms of the initial variables x_1, x_2.

To do that, we introduce a "new time" $\tau = r_1 t$ and so

$$x_j' = \frac{dx_j}{d\tau} = \frac{1}{r_1}\dot{x}_j.$$

Hence, defining the new variables

$$u = \frac{x_1}{K_1}, \qquad v = \frac{x_2}{K_2}$$

and the constants

$$\rho = \frac{r_2}{r_1}, \qquad a = \frac{c_1 K_2}{r_1}, \qquad b = \frac{c_2 K_1}{r_2},$$

system (5) becomes

$$\begin{aligned} u' &= u(1 - u - av) \\ v' &= \rho v(1 - v - bu). \end{aligned}$$

Adimensionalising the equations

If we assume $x_j \in [0, K_j]$ (i.e., below their carrying capacity), we can identify $u = x_1/K_1$ and $v = x_2/K_2$ as species' densities. Consequently, the unit square $(u, v) \in I = [0, 1] \times [0, 1]$ is invariant by the dynamics of:

$$\begin{aligned} u' &= u(1 - u - av) \\ v' &= \rho v(1 - v - bu). \end{aligned} \tag{7}$$

This system can be expressed as $(u', v') = f(u, v)$ with $f(u, v) = (u(1 - u - av), \rho v(1 - v - bu))$ its associated vector field.

Analysis of the system: invariance of the domain.

- The lines $u = 0$ and $v = 0$ are invariant by the flow. The flow goes from $(0, 0)$ towards $(1, 0)$ and $(0, 1)$, respectively.
- We compute the vector field on the line $v = 1$:

$$(u', v') = (u(1 - u - a), -\rho bu) \Rightarrow v' < 0.$$

- And similarly on the line $u = 1$:

$$(u', v') = (-av, \rho v(1 - b - v)) \Rightarrow u' < 0.$$

In both cases it points inwards, so joint to the invariance on $u = 0$, $v = 0$ it follows that the square I is forward invariant by the flow. Poincaré-Bendixson theorem ensures that the ω-limit of any orbit starting at the interior will be or a fixed point, a periodic orbit or a connection of saddles.

Analysis of the system: nullclines.

They are determined by $u' = 0$ and $v' = 0$. They determine regions of increasing/decreasing of the variables u, v. Particularly useful in planar systems.

In our case:

- The u-nullcline:
$$u' = 0 \Leftrightarrow u = 0 \qquad \text{or} \qquad u + av = 1.$$
- The v-nullcline:
$$v' = 0 \Leftrightarrow v = 0 \qquad \text{or} \qquad bu + v = 1.$$

In our case they are the axes and a couple of lines. Depending on the relative position of the two latter, we can know *grosso modo* the evolution of the trajectories.

Analysis of the system: equilibrium points

- They correspond to invariant points by the dynamics, "steady state" solutions, i.e., (u, v) such that
$$u' = 0, \qquad v' = 0.$$
They correspond to the intersections of the u and v-nullclines.

- The equilibrium points at the border of the domain are $(0, 0)$, $(1, 0)$, $(0, 1)$.

- The other (possibly) interior equilibrium point (u^*, v^*) is
$$u^* = \frac{1-a}{1-ab}, \quad v^* = \frac{1-b}{1-ab}$$
if $ab \neq 1$ (in that case we have the line $u + av = 1$ filled with equilibrium points). This point falls inside $[0, 1] \times [0, 1]$ (and so, biologically meaningful) provided
$$0 \leq \frac{1-a}{1-ab} \leq 1, \quad 0 \leq \frac{1-b}{1-ab} \leq 1$$
It is referred, usually, as the coexistence equilibrium.

Analysis of the system: local stability and bifurcations

Let us study the stability of the fixed points. The Jacobian (differential) matrix is:

$$Df(u,v) = \begin{pmatrix} 1-2u-av & -au \\ -b\rho v & \rho(1-bu-2v) \end{pmatrix}$$

We do the analysis for each equilibrium point. We do it here for the “border” equilibria. Certainly, the most interesting case will be the estudy for the coexistence one.

The point $(0,0)$ is a repeller (a source) since it has positive real eigenvalues $\lambda_1 = 1$ and $\lambda_2 = \rho$ (recall $\rho > 0$):

$$Df(0,0) = \begin{pmatrix} 1 & 0 \\ 0 & \rho \end{pmatrix}$$

The corresponding eigenvectors are (as expected) $e_1 = (1,0)$ and $e_2 = (0,1)$, respectively.

Analysis of the system: local stability and bifurcations

At the point $(1, 0)$ the Jacobian matrix is

$$Df(1,0) = \begin{pmatrix} -1 & -a \\ 0 & \rho(1-b) \end{pmatrix}$$

and the eigenvalues are $\lambda_1 = -1$ (stable direction) and $\lambda_2 = \rho(1-b)$.
e_1 is an eigenvector of the eigenvalue $\lambda_1 = -1$ as it was already known from the previous computations.

Depending on the value of b we can have several cases:

- If $b > 1$ then $(1, 0)$ is an attractor (a sink).
- If $b < 1$ it is a saddle point. The unstable invariant curve is tangent to the vector $(\alpha, 1)$, for some $\alpha < 0$. It points inside the square.
- If $b = 1$ then we have eigenvalue $\lambda_2 = 0$ which implies a neutral behaviour in the direction of the eigenvector $(-a, 1)$.

This is an example of a bifurcation. **Could you determine which one? What is undergoing the coexistence equilibrium for this particular value of b?**

Analysis of the system: local stability and bifurcations

At the point $(0,1)$ the Jacobian matrix is

$$Df(0,1) = \begin{pmatrix} 1-a & 0 \\ -b\rho & -\rho \end{pmatrix}$$

and so, with eigenvalues are $\lambda_1 = 1-a$ i $\lambda_2 = -\rho < 0$. As before, depending on the value of $a > 0$ we have several cases:

- If $a > 1$ the point $(0,1)$ is an attractor (a sink).
- If $a < 1$ it is a saddle point, with unstable invariant curve tangent to the vector $(1,\beta)$ for $\beta < 0$. It points inwards the square.

Like for the point $(1,0)$, at $a = 1$ the point $(0,1)$ undergoes a transcritical bifurcation.

Analysis of the system: local stability and bifurcations

The Jacobian at the coexistence equilibrium point (u^*, v^*) is:

$$Df(u^*, v^*) = \begin{pmatrix} 1 - 2u^* - av^* & -au^* \\ -b\rho v^* & \rho(1 - bu^* - 2v^*) \end{pmatrix}.$$

It is easy to check (**do it!**) that:

- If $a < 1$ and $b < 1$ it is an attractor.
- If $a > 1$ and $b > 1$ it is a repeller.

Moreover, one has to take into account if it is biologically meaningful.

If you draw an schematic phase portrait of this model, **what would you observe?**

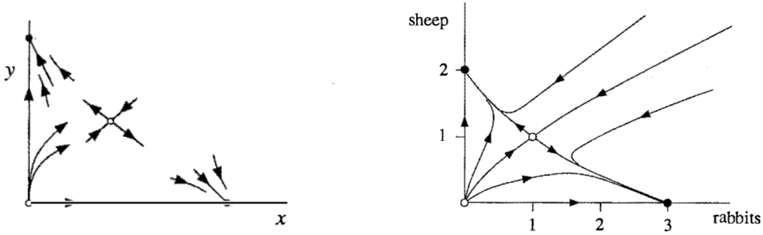
An academic example

(Strogatz, section 6.4). See also (Pianka (1981), Pielou (1969), Edelstein-Keshet (1988), or Murray (1989) for biological discussion.

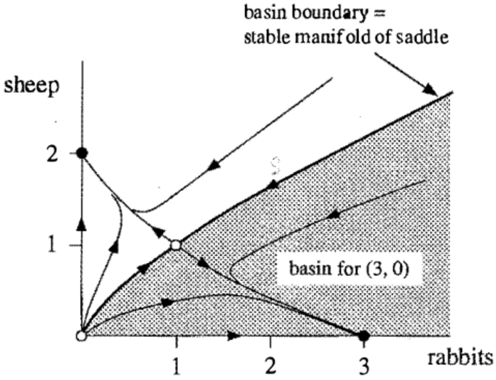
$$\begin{aligned} \dot{x} &= x(3 - x - 2y) \\ \dot{y} &= y(2 - x - y) \end{aligned}$$

where $x(t)$ denotes rabbits population and $y(t)$ corresponds to sheeps population, competing for the same food supply (grass). We assume that this food supply is limited in space and so in quantity.

- Now, variables x, y are not normalised to $[0, 1]$. They belong to the rectangle $[0, 2] \times [3, 0]$.
- Equilibrium points: $(0, 0)$, $(0, 2)$, $(3, 0)$, and $(1, 1)$.



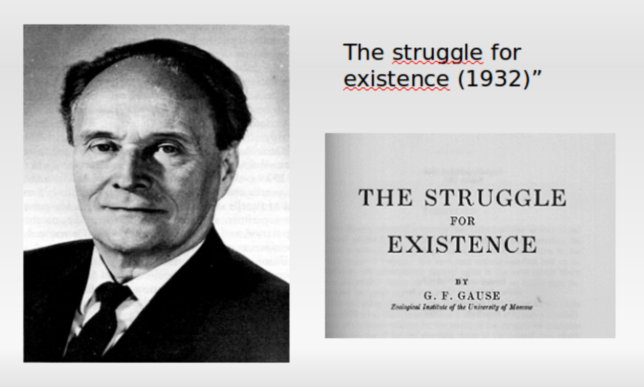
Local behaviour around equilibria and schematic phase portrait.



Basin of attractions of each attractor, bistability and separatrices.

This dichotomy occurs in many models of competition. Biologist call it the principle of competitive exclusion (see references above), which states that two species competing for the same limited resource, typically, cannot coexist.

The Principle of competitive exclusion (Gause)



The struggle for existence (1932)”

THE STRUGGLE
FOR
EXISTENCE
BY
G. F. GAUSE
Zoological Institute of the University of Moscow

Figure: Georgii Frantsevich Gause’ paper in 1932.

Principle of competitive exclusion

- Summary of the experiments: *based on laboratory competition experiments using two species of Paramecium, the Paramecium aurelia and Paramecium caudatum. Following a lag phase, the Paramecium aurelia was able consistently to drive the other to extinction. The conditions was to add fresh water everyday and input a constant flow of food. On the other hand, Gause was able to let the Paramecium caudatum survive by driving differently the environmental parameters (food, water): that explains why the Gause law is valid only if the ecological factors are constant.*
- The principle of competitive exclusion states that two species cannot occupy exactly the same ecological niche. In practice, there is sometimes coexistence.

Predators vs preys:
the Lotka-Volterra model

The model

They both derived, independently, the same model. Volterra proposed it first, in 1926, modelling oscillatory behaviour of certain fish catches in the Adriatic. They both derived, independently, the same model. Volterra proposed it first, in 1926, modelling oscillatory behaviour of certain fish catches in the Adriatic sea.

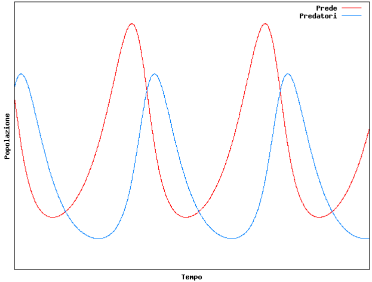


Figure: Alfred J. Lotka (1880-1949) and Vito Volterra (1860-1940). Source: Wikipedia.

If $N(t)$ denotes the prey population and $P(t)$ the predator one, then the model reads

$$\left\{ \begin{array}{ll} \dot{N} & = N(a - bP) \\ \dot{P} & = P(cN - d) \end{array} \right.$$

with positive parameters a, b, c and d. It combines Malthus growth of preys, in absence of predators; decrease of predator population, in the absence of preys; and reduction/contribution proportional to the product of both densities.

It is easy to check that:

- Only non-negative values of N and P have biological sense.
- Lines $N = 0$ and $P = 0$ are invariant.
- This system has two equilibria: $(0, 0)$ and $(N_*, P_*) = (d/c, a/b)$.
- To determine local stability of the system around each equilibrium, we compute the Jacobian matrix:

$$J(x, y) = \left(\begin{array}{cc} a - bP & -bN \\ cP & cN - d \end{array} \right)$$

Stability of equilibria: the linearisation method

Stability of the origin.

- The Jacobian on it is

$$J(0,0) = \begin{pmatrix} a & 0 \\ 0 & -d \end{pmatrix}$$

  so, eigenvalues $a > 0$ and $-d < 0$. This means that $(0,0)$ is a saddle point, unstable. $e_1 = (1,0)$ and $e_2 = (0,1)$ are eigenvectors of eigenvalues a and $-d$, respectively. They are also unstable for the complete nonlinear system.

Stability of the point $(N_*, P_*) = (d/c, a/b)$.

- The Jacobian on it is

$$J(N_*, P_*) = J(d/c, a/b) = \begin{pmatrix} a - bP & -bN \\ cP & cN - P \end{pmatrix}$$

  which has eigenvalues $\pm \mathrm{i}\sqrt{ad}$. This means that (N_*, P_*) is a centre for the linearised system around it but no information about being a centre or not for the complete system $\rightarrow$ Lyapunov method.

The Lyapunov method

Theorem (Lyapunov)

Consider

$$\dot{x} = f(x), \qquad x \in \mathbb{R}^n, \tag{8}$$

which defines a flow in $\mathbb{R}^n$*. Let* x_0 *be a fixed point of* (8) *and let* $V : U \subseteq \mathbb{R}^n \to \mathbb{R}$, $\mathcal{C}^1$, $x_0 \in U$*,* U *open set, such that, in* U*:*

(i) $V(x_0) = 0$ *and* $V(x) > 0$ *if* $x \neq x_0$*.*

(ii) $\dot{V}(x) \leq 0$ *in* $U \setminus \{x_0\}$*.*

Then, x_0 *is (Lyapunov) stable. Moreover,*

(iii) *if* $\dot{V} < 0$ *in* $U \setminus \{x_0\}$

then x_0 *is asymptotically stable.*

Remark

- *Remind that*
$$\dot{V}(x) = \frac{d}{dt}\,(V(x)) = \nabla V(x)\cdot\dot{x} = \nabla V(x)\cdot f(x).$$

- *If $\dot{V}(x) = 0$ in $U\setminus\{x_0\}$ then x_0 is (Lyapunov) stable and V is a first integral of* (8)*. The curves $V = \mathit{constant}$ are invariant by the flow.*

- Instability Theorem: *If $\dot{V}(x) > 0\ \forall x \in U\setminus\{x_0\}$ then x_0 is unstable.*

In our case, take the initial system

$$\left\{ \begin{array}{rcl} \dot{N} & = & N(a - bP) \\ \dot{P} & = & P(cN - d) \end{array} \right. \tag{9}$$

and write in the form

$$\begin{array}{rcl} \dfrac{1}{N}\dfrac{dN}{dt} & = & a - bP \\ \dfrac{1}{P}\dfrac{dP}{dt} & = & cN - d \end{array}$$

so

$$\frac{cN-d}{N}\ \frac{dN}{dt} = \frac{a-bP}{P}\ \frac{dP}{dt} \Rightarrow \left(-c + \frac{d}{N}\right)\frac{dN}{dt} + \left(\frac{a}{P} - b\right)\frac{dP}{dt} = 0 \Rightarrow$$

$$\frac{d}{dt}\Bigg(- cN + d\log N + a\log P - bP\Bigg) = 0$$

That is,

$$H(N,P) = d\log N + a\log P - cN - bP \qquad \textit{is a constant of motion.}$$

Let $(N(t),P(t))$ be solution of (9) with i.c. $(N(0),P(0)) \in [0,+\infty)^2$. Then,

- $H(N(t),P(t)) = H(N(0),P(0))\ \forall t \geq 0$.
- H is strictly convex.
- $W = \nabla H \cdot F$ is negative definite so the equilibrium point $\left(\dfrac{d}{c}, \dfrac{a}{b}\right)$ is a centre.
- In fact, introducing the canonical variables

  $$p = \log N, \qquad q = \log P$$

  the function H becomes $h(q,p) = dp - c\mathrm{e}^p + aq - b\mathrm{e}^q$ and system (9) has the following Hamiltonian form

  $$\dot{p} = \frac{\partial h}{\partial q}, \qquad \dot{q} = -\frac{\partial h}{\partial p}.$$

  It can be seen that the centre is global.

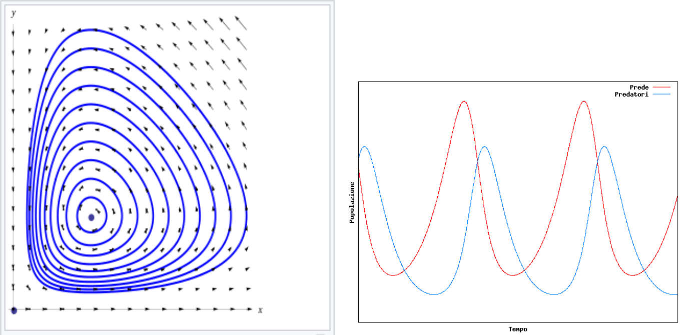


Figure: Orbits of the predator-prey Lotka-Volterra model (left) and evolution of N and P in terms of time t.

Volterra's principle

Take initial conditions $(N(0), P(0)) = (N_0, P_0) \in (0, +\infty)^2$. Denote by T the period of the closed orbit through (N_0, P_0). Then

$$\frac{\dot{N}}{N} = a - bP \Rightarrow \log N(T) - \log N(0) = \int_0^T a - bP(s)\, ds.$$

Since $N(T) = N(0)$ it follows that

$$0 = \int_0^T a - P(s)\, ds = aT - b \int_0^T P(s)\, ds$$

and, finally (Volterra's principle)

$$\frac{1}{T} \int_0^T P(s)\, ds = \frac{a}{b}.$$

In a similar way

$$\frac{1}{T} \int_0^T N(s)\, ds = \frac{d}{c}.$$

LaSalle's Principle [1]

Let us consider

$$\dot{x} = f(x), \qquad f \in \mathcal{C}^r, \quad r \geq 1. \tag{10}$$

Let $\mathcal{M} \subseteq \mathbb{R}^n$ a set satisfying:

- It is a compact set and positively invariant under the flow $\phi_t(\cdot)$ generated by (10).
- It is the closure of some open set (so it has non-empty interior), with boundary at least $\mathcal{C}^1$.

Then $\mathcal{M}$ is a trapping region.

Now in $\mathcal{M}$ we consider the following subsets:

- $E = \{x \in \mathcal{M} \;\Big|\; \dot{V}(x) = 0\}$.

  Notice that, in particular, all the equilibrium points of (10) belong to E.

- And

  $$M = \{\text{the union of all trajectories that start in } E \text{ and remain in } E \text{ for all } t \geq 0\}$$

  Observe that M is the "positively invariant part' of E.

Theorem (LaSalle's Invariance Principle, 1968)

$$\forall x \in \mathcal{M} \quad \textit{one has that} \quad \phi_t(x) \to M \qquad \textit{as } t \to +\infty.$$

Example: (Duffing differential equation)

$$\begin{array}{rcl} \dot{x} & = & y \\ \dot{y} & = & x - x^3 - \delta y \end{array}$$

for $(x, y) \in \mathbb{R}^2$ and $\delta > 0$ a parameter. Define the function

$$V(x, y) = \frac{y^2}{2} - \frac{x^2}{2} + \frac{x^4}{4}$$

(i.e., the Hamiltonian function for $\delta = 0$). Verify that $\dot{V} = -\delta y^2$. Consider the level set $V = c$ for a very large (but finite) c. This curve defines the boundary of a positively invariant compact set $\mathcal{M}$. Then,

- $E = \mathcal{M} \cap \{y = 0\}$.
- $M \subset E$ is formed by the three equilibrium points on $\{y = 0\}$, i.e., $(\pm 1, 0), (0, 0)$.

By LaSalle's Principle, all the trajectories starting in $\mathcal{M}$ will converge to one of these three points.

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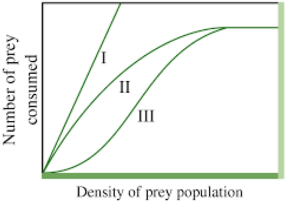
[1] We follow, for instance, [8]

Criticisms to the Lotka-Volterra prey-predator model

- Changes in birth and death rates do not imply rellevant changes in the results but the period of the oscillations.
- No population can dominate and it is also impossible for a population to be driven into extinction. From an ecological point of view this should be expected to happen in nature.
- This model is structurally unstable: small perturbations could break its hamiltonian character and bring the centre into a focus. One would expect models to be structurally stable and non so sensitive to small perturbations.

Predator-prey models: functional and numerical responses



Functional and numerical responses

In 1959, C.S. Holling [3] found that predation rates increased with increasing prey population density.

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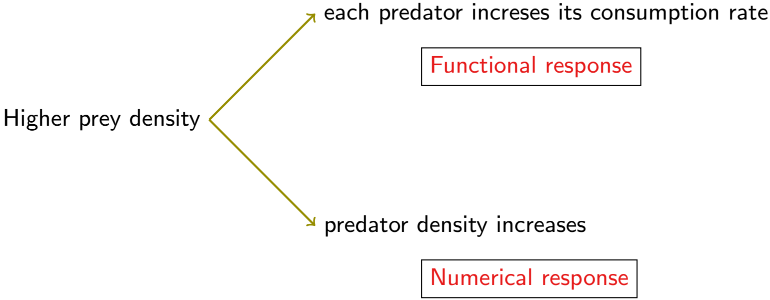


Higher prey density

each predator increses its consumption rate

Functional response

predator density increases

Numerical response

Numerical response

The number of predators increases with higher prey density.
It may result from two mechanisms:

1. Numerical response *per se*: the rate of predator reproduction increases.
2. Aggregational response: attraction of predators to prey aggregations.

Functional response

- Holling (1959) but equivalent to the one of Leonor Michaelis and Maud Menten (1913).
- Very popular among ecologists.
- It assumes a predator invests its time T in two activities:
  1. Searching for a prey.
  2. Prey handling: chasing, killing, eating and digesting.
- Even in the extreme case of high abundance of preys, prey handling time is needed.
- Therefore $T = T_{\text{search}} + T_{\text{handling}}$

Functional response

- H_a= number of preys captured by 1 predator during time T.
- Handling time T_{handling} should be proportional to H_a:

  $$T_{\text{handling}} = H_a T_h$$

  where T_h is the time spent by 1 predator in handling 1 prey.
- "Capturing" is assumed to be a random process: a predator examines an area a per unit time and captures any prey he finds there.
- Parameter a (in units of area/time) is called area of discovery or search rate.
- After spending T_{search} a predator has examined and area aT_{search} and captured aHT_{search} preys, where H is prey density per unit area.

Functional response

- $T_{\text{handling}} = H_a T_h$.
- After spending T_{search} a predator has examined and area aT_{search} and captured aHT_{search} preys, where H is prey density per unit area.
- So:

$$H_a = aHT_{\text{search}} \Rightarrow T_{\text{search}} = \frac{H_a}{aH}.$$

- Therefore

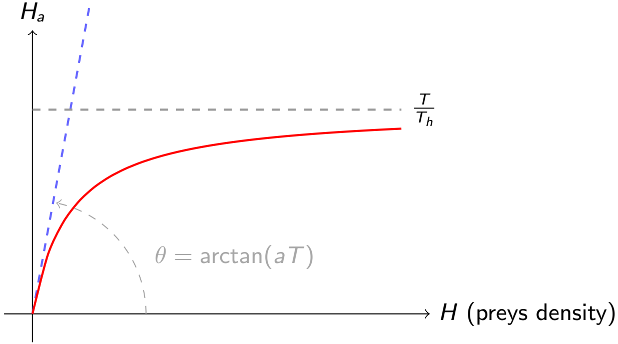
$$T = T_{\text{search}} + T_{\text{handling}} = H_a T_h + \frac{H_a}{aH}$$

  and so

$$H_a = \frac{aHT}{1 + aHT_h} \qquad \text{number of attacked preys by 1 predator in time } T$$

Functional response

$H_a = \dfrac{aHT}{1 + aHT_h}$ number of attacked preys by 1 predator in time T



Functional response

Holling (1959) considered three main types of functional responses H_a:

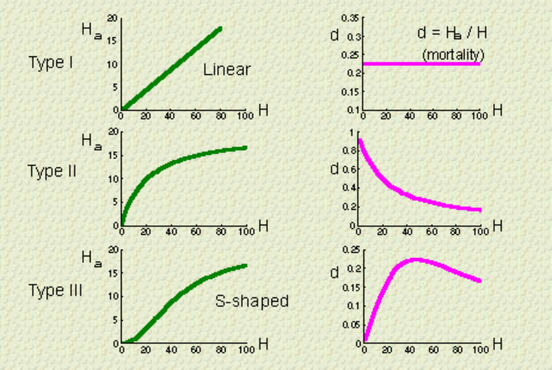
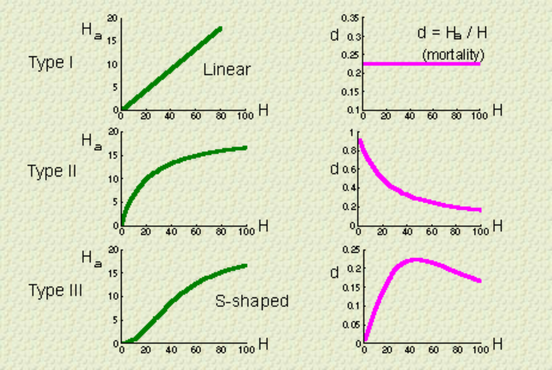


Figure: Source: Quantitative Population Ecology, Alexei Sharov, Department of Entomology, Virginia Tech, Blacksburg, USA

Functional response

Holling (1959) considered three main types of functional responses H_a:



S-shaped → Sigmoidal in Michaelis and Menten (1913).

Predator-prey model with Holling type II response

Prey population

- Functional response: $H_a = \dfrac{aHT}{1 + aHT_h}$.
- Rate of prey consumption by <u>all</u> predators per unit of time:

$$\frac{H_a}{T}\,P = \frac{aHP}{1 + aHT_h}$$

- So

$$\dot{H} = r_H H\left(1 - \frac{H}{K}\right) - \frac{aHP}{1 + aHT_h}$$

Predator-prey model with Holling type II response

Predator population

- It is modeled by

$$\dot{P} = r_P P \left(1 - \frac{P}{KH} \right)$$

- Numerical response of predator population to prey density.
- Logistic model with carrying capacity proportional to number of preys.

The Rosenzweig-MacArthur predator-prey model

Rosenzweig, M.L., and MacArthur, R.H., Graphical representation and stability conditions of predator-prey interaction, American Naturalist 97, 209-223, 1963

$$\begin{aligned}\dot{H} &= r_H\left(1-\frac{H}{K}\right)-\frac{aHP}{1+aHT_h}\\ \dot{P} &= r_P P\left(1-\frac{P}{kH}\right)\end{aligned}$$

- Holling type II functional response.
- Certainly, one of the most popular models for trophic chains among ecologists.

Extensions of Rosenzweig-MacArthur model

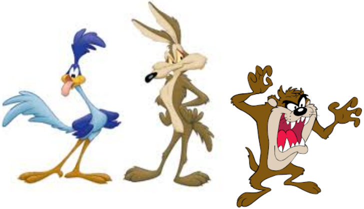
Prey, predator and super-predator.

Extensions of Rosenzweig-MacArthur model

Prey, predator and super-predator.

$$\begin{aligned}
\dot{x} &= x\left(r - \frac{r}{K}x - \frac{p_1 y}{H_1 + x}\right) && \text{(prey)} \\
\dot{y} &= y\left(\frac{c_1 x}{H_1 + x} - d_1 - \frac{p_2 z}{H_2 + y}\right) && \text{(predator, Holling II)} \\
\dot{z} &= z\left(\frac{c_2 y}{H_2 + y} - d_2\right) && \text{(super-predator, Holling II)}
\end{aligned}$$

Extensions of Rosenzweig-MacArthur model

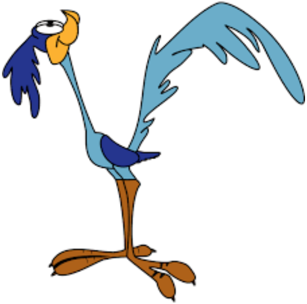


Prey, predator and super-predator.

Routes to chaos:

- Deng and Hines (Chaos 2002, Chaos 2003).
- Strong assumption: drastic time diversification in trophic chain → three time-scales singularly perturbed sistem → homoclinic connection of Shilnikov type (2002).

What about discrete models?



Discrete models

- Non-overlaping generations, discrete time evolution (month, year, ...)
- Pionneering works:
  - R.M. May (1974, 1976 Logistic map).
  - J.C. Allen, W.M. Schaffer, and D. Rosko (1993).
  - Chaotic dynamics in insect populations: R.F. Constantino, R.A. Desharnais R.A., J.M. Cushing, and B. Dennis (1997) and B. Dennis B., R.A. Desharnais, J.M. Cushings and Constantino R.F. (1997).
- Prey-predator model (Lauwerier, 1986)

$$T\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} \mu x \left(1 - \frac{x}{K} - y\right) \\ \beta x y \end{pmatrix}$$

with K prey-carrying capacity and intrinsic reproduction rates μ and β, respectively.

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- Prey-predator model (Lauwerier, 1986)

$$T\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} \mu x\,(1-x-y) \\ \beta xy \end{pmatrix}$$

with normalised $K = 1$ prey-carrying capacity and intrinsic reproduction rates μ and β, respectively. x and y are population densities wrt this normalisation.

Discrete models

- Prey-predator model (Lauwerier, 1986)

$$T\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} \mu x\,(1-x-y) \\ \beta xy \end{pmatrix} \tag{11}$$

Discrete models

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$$T\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} \mu x\,(1-x-y) \\ \beta xy \end{pmatrix} \tag{11}$$

- Prey-predator and super-predator model.

$$T\begin{pmatrix} x \\ y \\ z \end{pmatrix} = \begin{pmatrix} \mu x\,(1-x-y) \\ \beta x(y-z) \\ \gamma yz \end{pmatrix} \tag{12}$$

Prey-predator model

- Prey-predator model (Lauwerier, 1986)

$$T\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} \mu x\,(1 - x - y) \\ \beta x y \end{pmatrix} \tag{11}$$

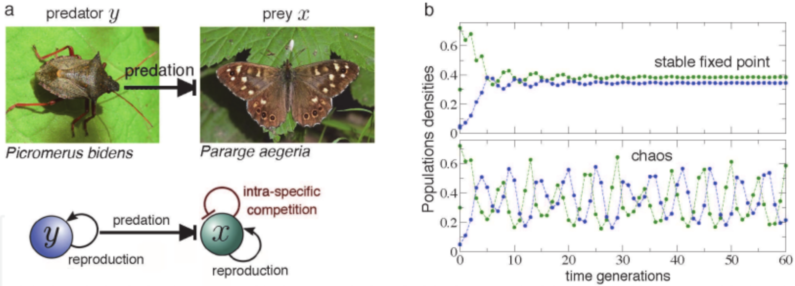


Figure 1.
Two-species predator-prey dynamics can be studied with difference equations or maps when species generations are discrete (univoltine). (a) Here we display two insect species with univoltine generations at the North Hemisphere. The Heteroptera Picromerus bidens predates the butterfly Pararge aegeria by consuming the eggs (photos obtained from the Wikipedia). A simple model for this type of system is given by the map (1). (b) Some typical dynamics arising in discrete-time ecological systems for preys (green dots) and predators (blue dots): (upper panel) period-one fixed point and (lower panel) chaos.

Prey-predator model

Vidiella, L., Alsedà, Sardanyés (2019)

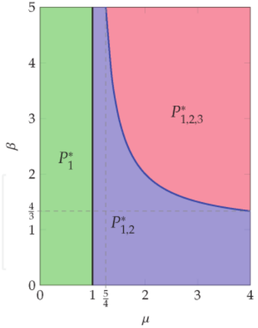
- Lauwerier Map:

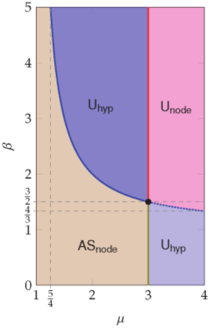
$$T\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} \mu x\,(1-x-y) \\ \beta xy \end{pmatrix} \tag{12}$$

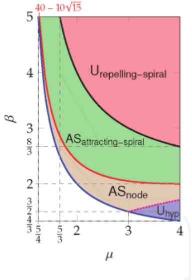
- Parameters domain: $\mu \in (0,4], \beta \in (0,5]$.
- Defined on the simplex $S = \{x, y \geq 0 \text{ and } x + y \leq 1\}$.
- Axis are not barriers anymore.

- Fixed points in S:
  - $P_1^* = (0,0)$ which belongs to the simplex S for every (μ, β).
  - $P_2^* = \left(1 - \dfrac{1}{\mu}, 0\right)$ which belongs to the simplex S for every $(\mu, \beta) \in [1,4] \times (0,5]$.
  - $P_3^* = \left(\dfrac{1}{\beta}, 1 - \dfrac{1}{\mu} - \dfrac{1}{\beta}\right)$ which belongs to the simplex S for every
    $$(\mu, \beta) \in \left[\tfrac{5}{4}, 4\right] \times \left[\tfrac{\mu}{\mu-1}, 5\right].$$

Linear stability:







Invariant set: where dynamics lives and remains

- $T(S) = \left\{ x, y \geq 0 \;\middle|\; \frac{x}{\mu} + \frac{y}{\beta} \leq \frac{1}{4} \right\}.$
- S is T-invariant (i.e. $T(S) \subset S$) $\Leftrightarrow \beta \leq 4$.
- ε: one-step escaping set.

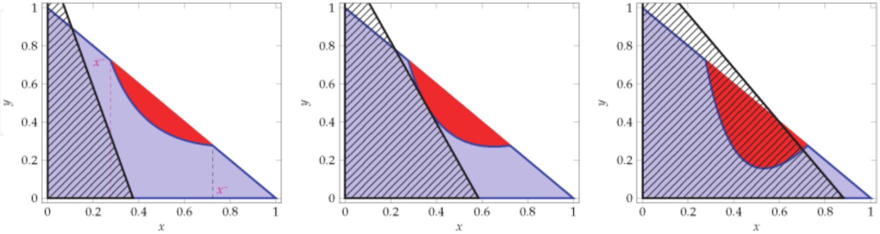


Figure: $\beta = 5$ and $\mu = 1.5$ (left), $\mu = 2.340246528387\ldots$ (centre) and $\mu = 3.525$ (right)

Invariant set: where dynamics live and remain

- Recurrent dynamics takes place in $\Omega(T) \subset \cap_{i=0}^{\infty} T^i(S)$.

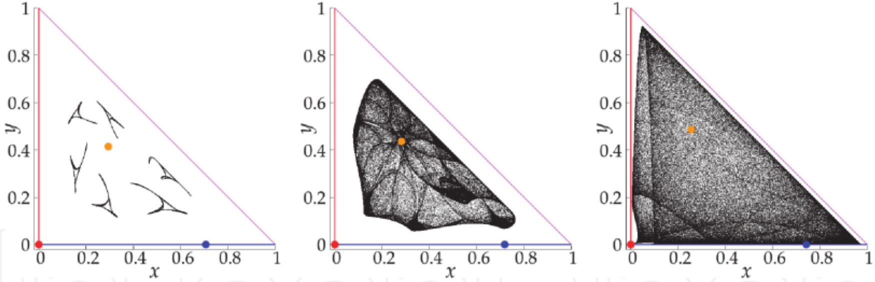
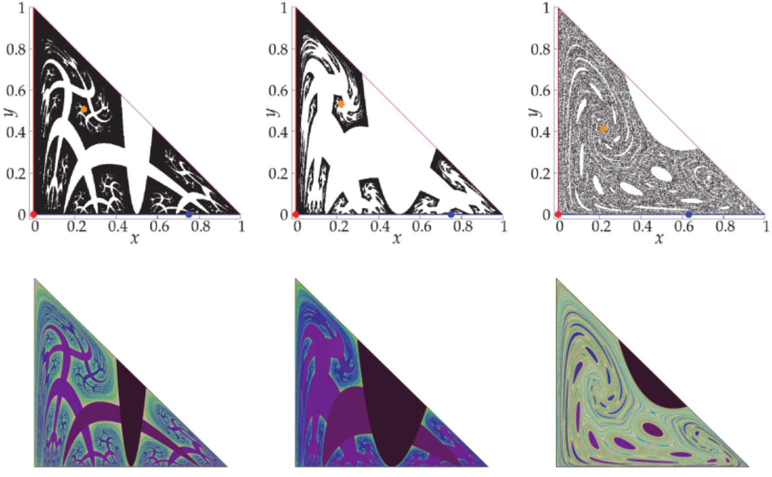


Figure: Plots of $\cap_{i=0}^{\infty} T^i(S)$ for $\beta = \mu = 3.412$ (left), $\beta = \mu = 3.5485$ (centre) and $\beta = \mu = 3.895$ (right).

- Escaping set: $\mathcal{R} = \cup_{n=0}^{\infty}\Big(S \cap T^{-n}(\varepsilon)\Big) = S \cap \Big(\cup_{n=0}^{\infty} T^{-n}(\varepsilon)\Big)$.



$\beta = 4.1$ and $\mu = 4$
$(\mu^* \approx 3.414286583662)$

$\beta = 4.6$ and $\mu = 4$
$(\mu^* \approx 2.681512445211)$

$\beta = 4.6$ and $\mu = 2.72$
$(\mu^* \approx 2.681512445211)$

Figure: Top: invariant set $S \setminus \mathcal{R}$. Bottom: escaping regions in # of iterates to escape: 1 (black), 2 (dark violet), 3 (light violet) to 50 (yellow) (movie1)

Global asymptotic results

1. If $\mu < 1$ then $\lim_{n\to+\infty} T^n(x,y) = (0,0) = P_1^*$.
2. Let us define

$$\varphi(\beta) := \begin{cases} 2 & \text{if } \beta \in [0,2) \\ \dfrac{\beta}{\beta-1} & \text{if } \beta \in [2,5] \end{cases}$$

Then, for any $(\beta,\mu) \in [0,5] \times (1,\varphi(\beta))$ and $(x,y) \in S \setminus \mathcal{R}$

$$T^n(x,y) = (0,0) = P_1^* \quad \text{for some } n \geq 0$$

or

$$\lim_{n\to+\infty} T^n(x,y) = \left(1-\mu^{-1},0\right) = P_2^*.$$

P_1^*, P_2^* are fixed points.

Some chaos indicators: Lyapunov exponents

- We want to determine the rate of divergence between two close trajectories.
- Let x_0 and $x_0 + \delta_0$ be two close initial conditions ($|\delta_0| \ll 1$), and $\delta_n := f^{(n)}(x_0 + \delta_0) - f^{(n)}(x_0)$ the difference between the n-th iterates of the respective orbits ($x_i := f^{(i)}(x_0)$ for $i \geq 0$).
- Assume that $|\delta_n| = |\delta_0| \exp(n\,\lambda)$. Then,

$$\begin{aligned}\lambda &= \tfrac{1}{n} \ln \left| \tfrac{\delta_n}{\delta_0} \right| = \tfrac{1}{n} \ln \left| \tfrac{f^{(n)}(x_0+\delta_0) - f^{(n)}(x_0)}{\delta_0} \right| \\ &\approx \tfrac{1}{n} \ln \left| f^{(n)\prime}(x_0) \right| = \tfrac{1}{n} \ln \left| \prod_{i=0}^{n-1} f'(x_i) \right| = \tfrac{1}{n} \sum_{i=0}^{n-1} \ln |f'(x_i)| \,.\end{aligned}$$

- The Lyapunov exponent is defined as

$$\lambda := \lim_{n \to +\infty} \left\{ \frac{1}{n} \sum_{i=0}^{n-1} \ln \left| f'(x_i) \right| \right\},$$

  assuming that this limit exists (take lim sup instead). Although not strictly correct, $\lambda > 0$ is taken as an indication of chaos[2].
- In higher dimensions, since it depends on the vector δ_0, there arises an spectrum of Lyapunov exponents.

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[2] Although the definition of chaos itself is another controversial issue.

Chaotic behaviour. Example: fixing $\mu = 2.1$,

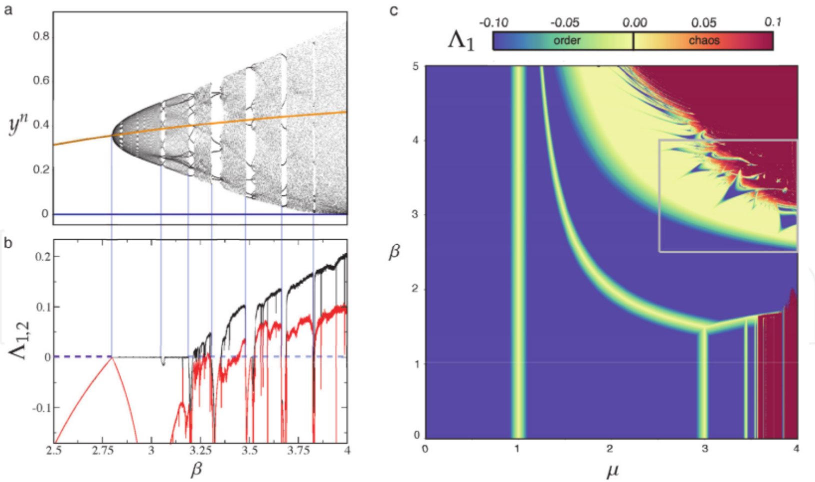


Figure: (a) Dynamics on the attractor for predators. P_2^* (violet), P_3^* (orange).

Chaotic behaviour. Example: fixing $\mu = 2.1$,

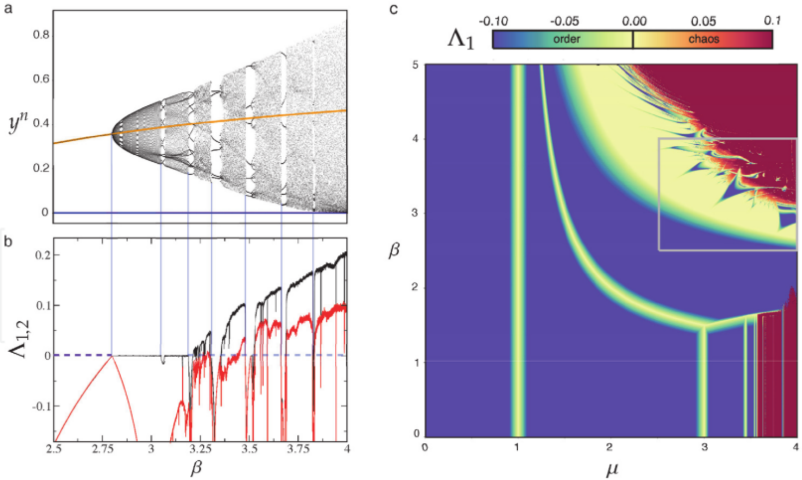


Figure: (b) Lyapunov exponents $\Lambda_{1,2}$. Neimark-Sacker bifurc. → P_3^* becomes unstable. After regular periods it enters into chaos. Hyperchaos.

Chaotic behaviour. Example: fixing $\mu = 2.1$,

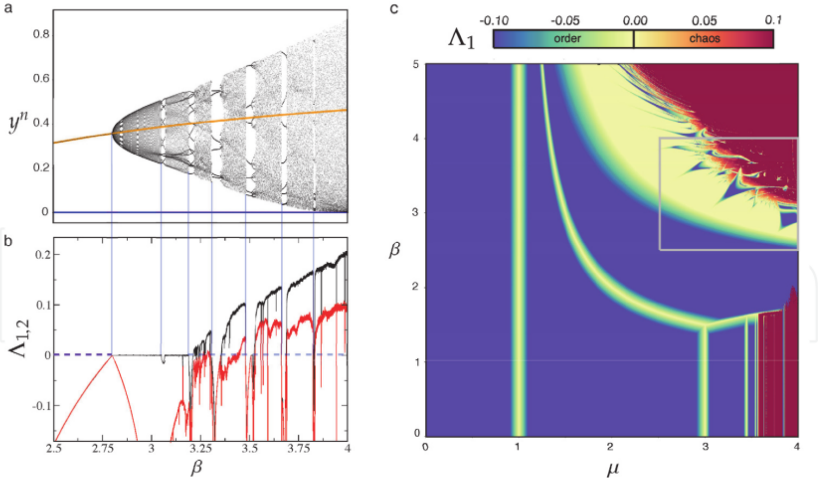


Figure:

(c) Diagram where first Lyapunov exponent Λ_1 is plotted. Red means chaotic zone. (movie2)

Chaotic behaviour: Lyapunov exponents $\Lambda_{1,2}$

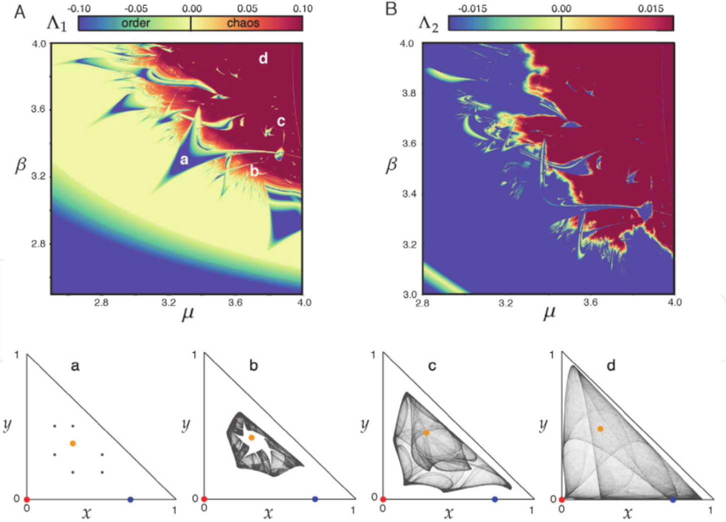


Figure: (A) Enlarged view of square in previous figure (c)

Chaotic behaviour: Lyapunov exponents $\Lambda_{1,2}$

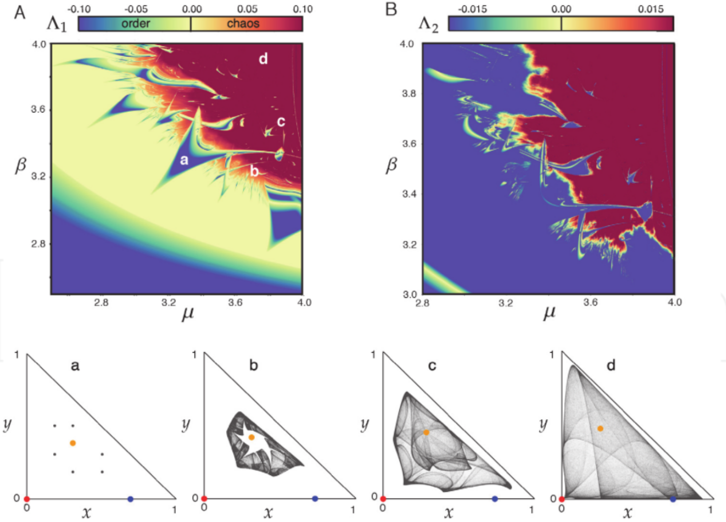


Figure: (B) In orange-red regions $\Lambda_{1,2} > 0 \rightarrow$ Hyperchaos

Chaotic behaviour: Lyapunov exponents $\Lambda_{1,2}$

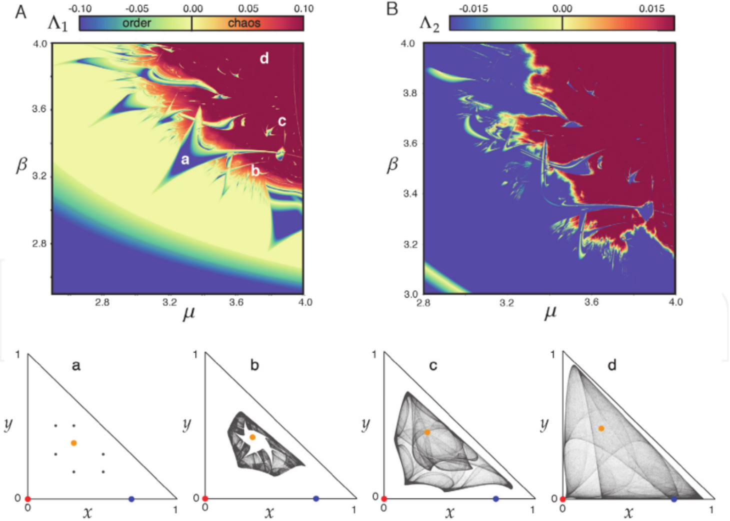
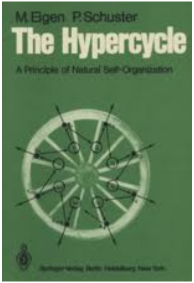


Figure: Bottom: sets $\cap_{i=0}^{\infty} T^i(S)$ in panel (A). Period-6 fixed point (a) and chaotic attractors (b,c,d). Fixed points P_1^* (red), P_2^* (blue), P_3^* (orange) (movie3)

Cooperative models

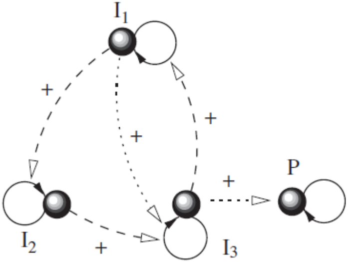
Example: increasing complexity through cooperation, hypercycles.



M. Eigen P. Schuster

The Hypercycle

A Principle of Natural Self-Organization



Hypercycles and quasispecies (Eigen and Schuster, 1971, 1979).

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