

Structural instability and emergence of biodiversity

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Synopsys

Remarks on population dynamics under splitting of one species into two subspecies (or subpopulations) and small differentiation of them.

Structural instability of the splitting and consequences.

Simple (uniform) and complex (non-uniform) differentiation.

Consequences on preservation of the diversity and emergence of stable (static or dynamic) structures.

Elements of structural stability

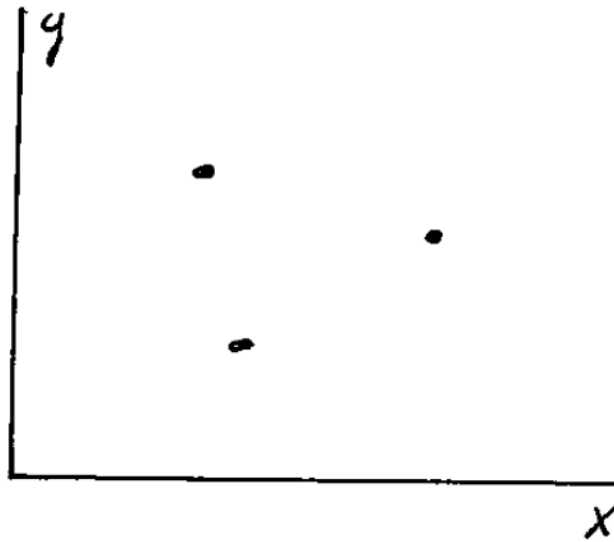
(Dimension 2)

$$\begin{cases} \dot{x} = f(x, y) \\ \dot{y} = g(x, y) \end{cases}$$

Equilibrium
points:

$$\begin{cases} f(x, y) = 0 \\ g(x, y) = 0 \end{cases}$$

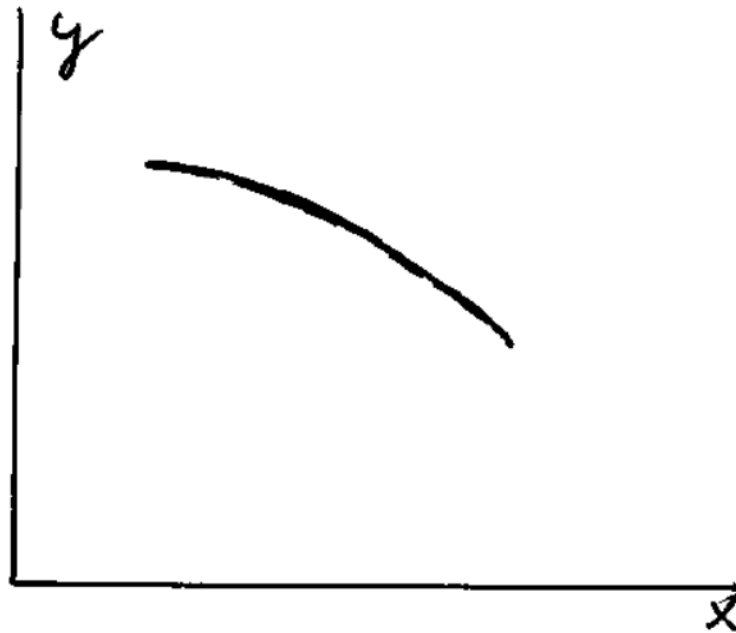
1 - Generic pattern
(structurally
stable)
isolated equilibria



2 - Non-generic pattern
(structurally
unstable)

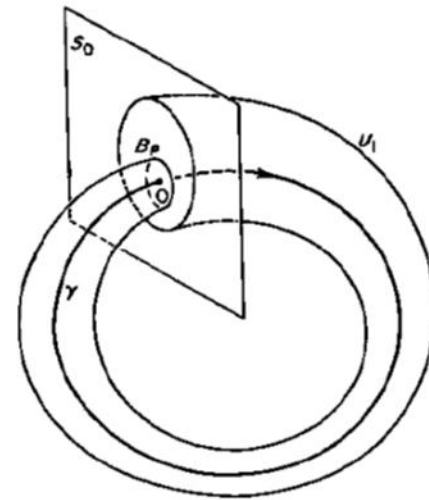
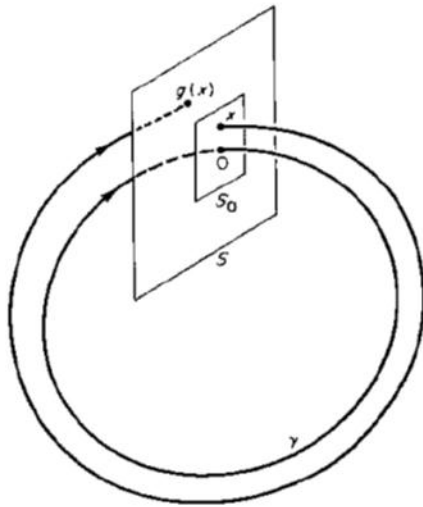


This pattern
disappears by a
generic small
perturbation,
becoming 1

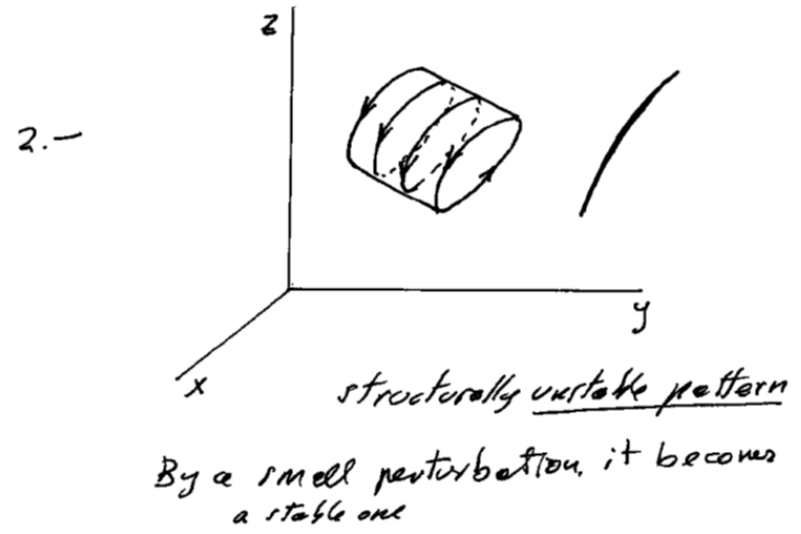
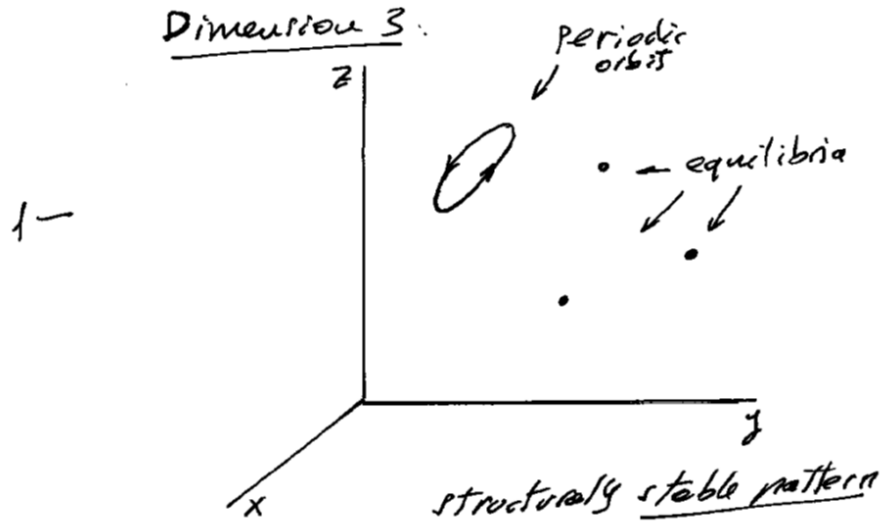


Dimension 3:

The Poincaré map of a
periodic orbit



Periodic orbits are fixed points
of a $n-1 \Rightarrow n-1$ map.



Issues of splitting and differentiation.

- We shall consider a (small) perturbation of the splitted system (differentiation of the subspecies).
- Generically, it destroys the structurally unstable pattern and only a finite number of equilibria persists.
- The crucial question is what of the main possibilities holds true:
 - a) There is only a stable equilibrium with one of the populations = 0 and the other different from 0. (Survival of the best adapted)
 - b) There is one (or several) stable equilibria with both populations different from 0 (preservation of the diversity).

We shall see that in general, a) only appears with very elementary and uniform differentiation. Otherwise, complex differentiation involving advantages and disadvantages rather leads to preservation of the diversity. Often, this property is linked with non-linearity.

Splitting of a population

$u' = f(u)$; $u = \text{population of a species}$

Splitting into two subpopulations $u = x + y$; the parts are distinct but absolutely equivalent concerning time evolution. At any t , the proportions of u and v are the same as the initial time:

$$\begin{cases} x' = f(x + y)x / (x + y) \\ y' = f(x + y)y / (x + y) \end{cases}$$

The system has the first integral $x/y = \text{const.}$

If a is an equilibrium of the primitive equation, the segment $(0, a)$ $(a, 0)$ is a continuum of equilibriums of the split system. Dynamics is along radiuses passing by O .

One species dynamics with limited food supply + splitting and differentiation

$$u' = u - u^2$$

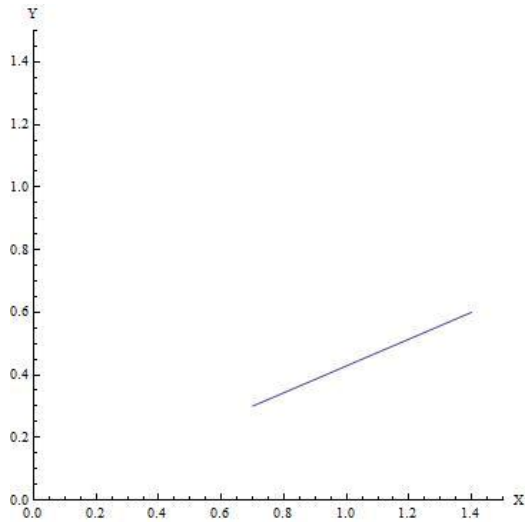
(the linear term is the natural growth and the quadratic one, the logistic term of limitation of the supply)

There is an equilibrium at $u=1$.

Splitting:

$$\begin{cases} x' = x - x^2 - xy \\ y' = y - y^2 - xy \end{cases}$$

The dynamics is by radial segments



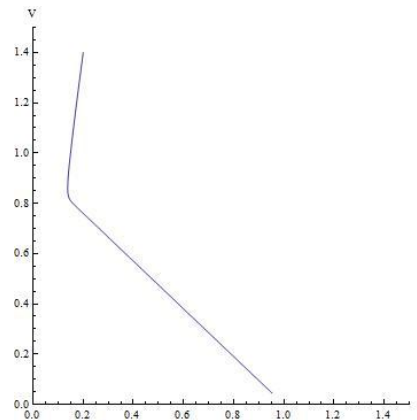
The segment from $(0,1)$ to $(1,0)$ is formed by equilibriums. The system is structurally unstable and very small perturbations modify it drastically.

1st example: The subspecies v diminishes its born rate (coefficient 0.95 instead of 1). The differenciated system is :

$$\begin{cases} x' = x - x^2 - xy \\ y' = 0.95y - y^2 - xy \end{cases}$$

The subspecies y is disadvantaged and it disappear (for any initial position, even if $y(0) \gg x(0)$). There is a fast dynamics going to the line of unperturbed equilibria, then a

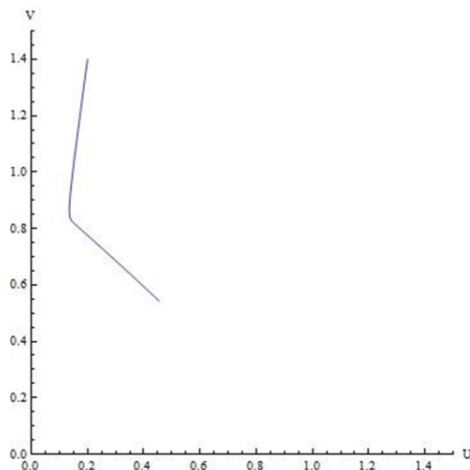
slow dynamics towards extinction of y:



2nd example: The subspecies v take benefit of u (utilisation of denses of u , for instance; coefficient -0.9 instead of 1) and simultaneously it diminishes its born rate (coefficient 0.95 instead of 1). The perturbed system is:

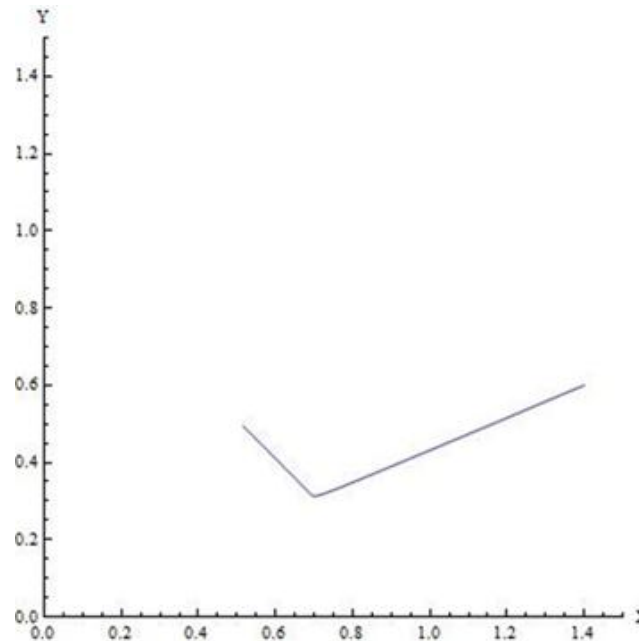
$$\begin{cases} x' = x - x^2 - xy \\ y' = 0.95y - y^2 - 0.9xy \end{cases}$$

Then, there is a unique stable equilibrium nearby $(0.5, 0.5)$. The slow dynamics has a (Liapunov) stable equilibrium nearby the line of equilibriums of the unperturbed system. There is preservation of the diversity.



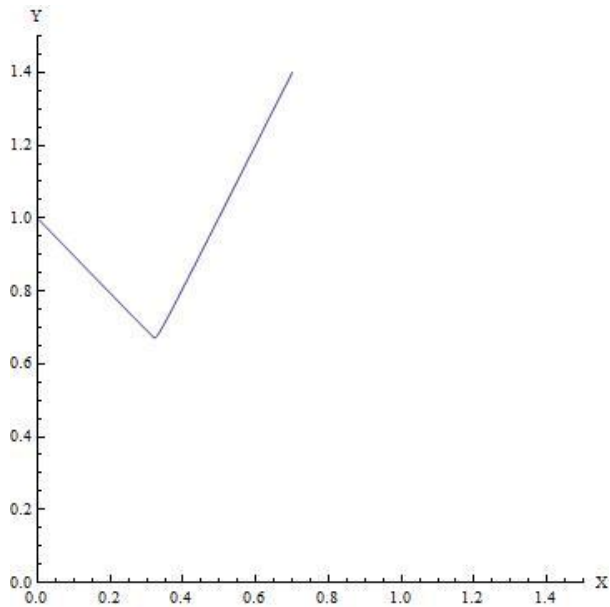
3rd example: The (small) perturbation is a symbiosis between the subspecies:
Stable equilibrium

$$\begin{cases} x' = x - x^2 - 0.98xy \\ y' = y - y^2 - 0.98xy \end{cases}$$



4th example: Oppositely, when the perturbation is a mutual nuisance between the subspecies, there is an unstable equilibrium

$$\begin{cases} x' = x - x^2 - 1.02xy \\ y' = y - y^2 - 1.02xy \end{cases}$$



The fast/slow dynamics

Instead of the x, y unknowns, we take the total population u and $p=x/u$ (total population and proportion of x).

$$\begin{cases} x' = x/(x+y) f(x+y) + \varepsilon \varphi \\ v' = y/(x+y) f(x+y) + \varepsilon \psi \end{cases}$$

Becomes with $p=x/(x+y)$

$$\begin{cases} u' = f(u) + \varepsilon(\varphi + \psi) \\ p' = \varepsilon (q\varphi - p\psi)u \quad (q = 1 - p) \end{cases}$$

Which is a (more or less) classical fast/slow dynamics. p changes slowly.

In most cases, $p=0$ and $p=1$ are equilibriums of the slow dynamics.

New example starting from a predator – prey dynamics + splitting and differentiation of the prey

Initial system in u, v .

$$u' = u - 0.25 u^2 - \tanh(1.3 u) v$$

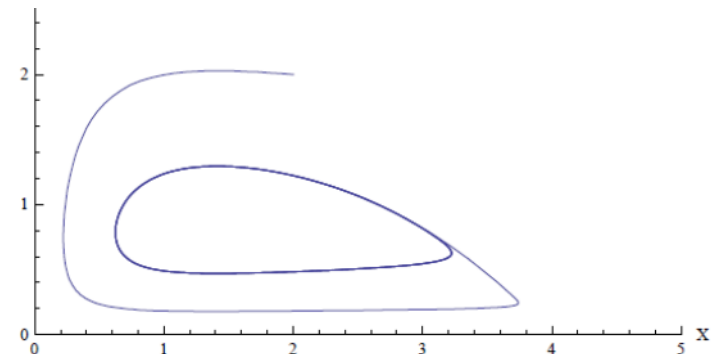
$$v' = -0.95 v + \tanh(1.3 u) v$$

The splitting $u=x, v=y+z$ gives:

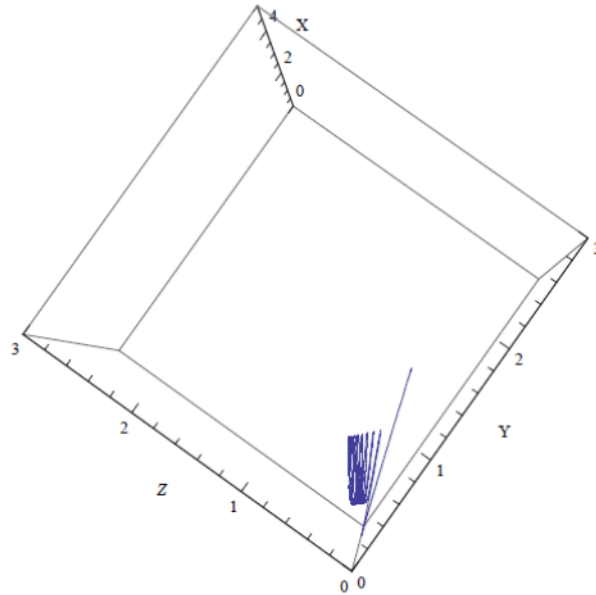
$$x' = x - 0.25 x^2 - \tanh(1.3 x) (y + z)$$

$$y' = -0.95 y + \tanh(1.3 x) y$$

$$z' = -0.95 z + \tanh(1.3 x) z$$



We then consider (somewhat analogous to symbiosis) a differentiation depending on the ratio of populations of the two subspecies: z has a disadvantage (resp advantage) on v when $z > y$ (resp $z < y$). The coefficient of \tanh in z' changes from 1 to $1 - 0.01(z^2 - y^2)/(z^2 + y^2)$



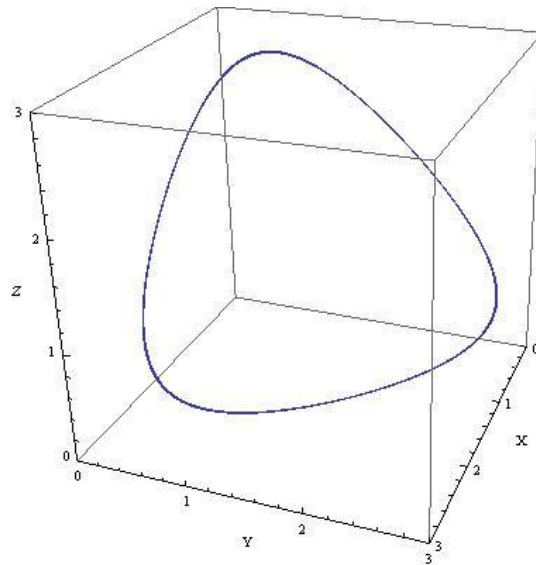
There is a stable cycle with $y = z$. The three species are preserved.

“Trophic cycle – like systems”

We may construct systems analogous to the trophic chains but in closed circuit (the last prey is a predator of the first predator):

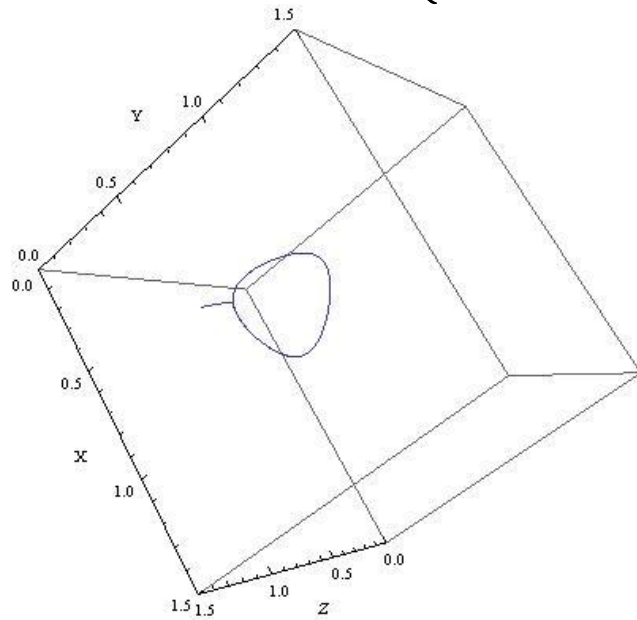
$$\begin{cases} x' = x(z - y) \\ y' = y(x - z) \\ z' = z(y - x) \end{cases}$$

It has the two first integrals $x+y+z=\text{const}$ and $xyz=\text{const}$. All orbits are periodic. (Analogous to Lotka-Volterra but without linear terms).



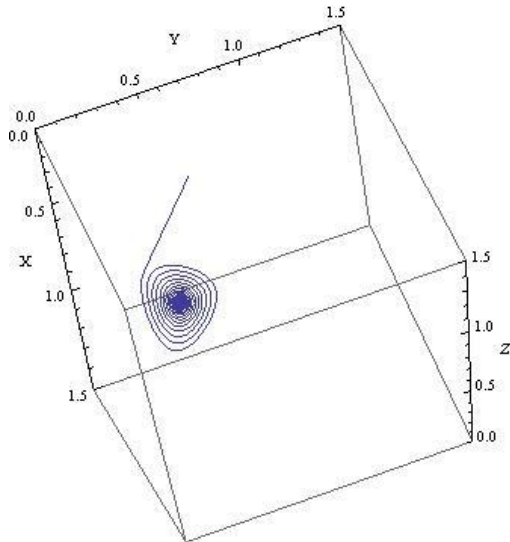
We now take this system as a small perturbation of a splitting of a species into three subspecies (in other words, three subpopulations interact as above; ethologic or functional small change with respect to the standard one-dimensional logistic equation). Obviously, the solutions on $x+y+z=1$ are preserved (periodic cycles in the slow dynamics):

$$\begin{cases} x' = 10x(1 - x - y - z) + x(z - y) \\ y' = 10y(1 - x - y - z) + y(x - z) \\ z' = 10z(1 - x - y - z) + z(y - x) \end{cases}$$



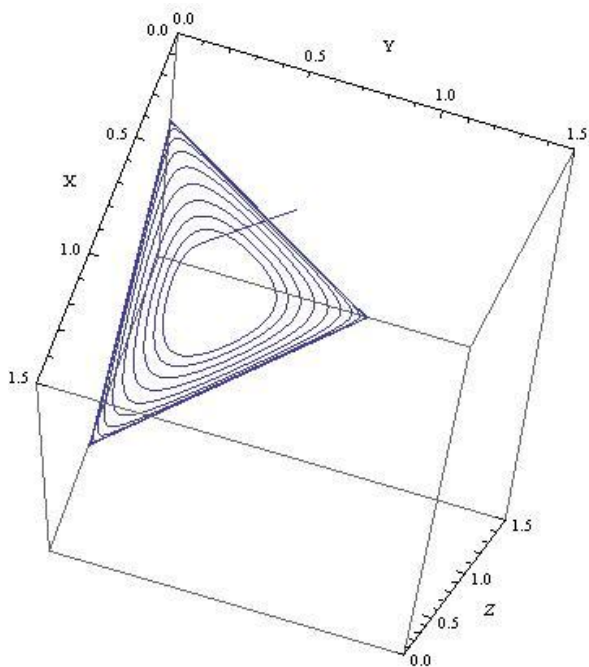
A modification of this perturbation destroys the periodic cycles of the slow dynamics.
When positive terms (=aid terms) are larger than negative ones (=nuisance terms),
orbits converge towards a stable equilibrium (self-organization of a static structure):

$$\begin{cases} x' = 10x(1 - x - y - z) + x(1.02z - y) \\ y' = 10y(1 - x - y - z) + y(1.02x - z) \\ z' = 10z(1 - x - y - z) + z(1.02y - x) \end{cases}$$

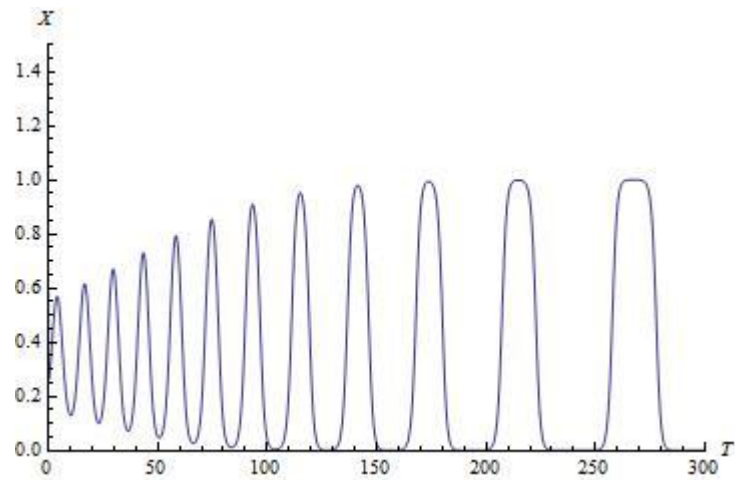


Oppositely, when positive terms (=aid terms) are smaller than negative ones (=nuisance terms), orbits diverge towards a polycycle:

$$\begin{cases} x' = 10x(1 - x - y - z) + x(0.98z - y) \\ y' = 10y(1 - x - y - z) + y(0.98x - z) \\ z' = 10z(1 - x - y - z) + z(0.98y - x) \end{cases}$$

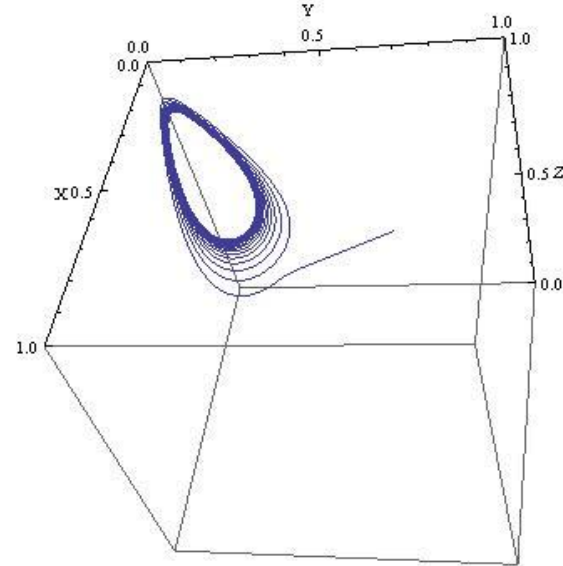


This amounts to some kind of pseudo-extinction: there are periods of increasing length and each one of the subpopulations practically vanishes in a part of the period.



Many variants may be constructed. Suitable non-linear perturbations involving combinations of the two previous cases lead to convergence towards a stable cycle (Self-organization of a dynamic structure):

$$\begin{cases} x' = 50x(1 - x - y - z) + x\{4y - 1.7[0.3333\text{Tanh}(3x)]\} \\ y' = 50y(1 - x - y - z) + y\{z - 6.8[0.3333\text{Tanh}(3x)]\} \\ z' = 50z(1 - x - y - z) + z\{4x - 6.8[0.3333\text{Tanh}(3x)]\} \end{cases}$$



Conclusion and comments

The key point concerning evolution is that mutations (=modification of the genes) should not be confused with modification of the characters. Only in very special cases a character is associated with one gene. The role of a gene is to produce a specific protein (and only that). The usual situation is that a gene has an influence on several characters, and each character depends on several genes. As a consequence, a genetic modification induces in general several modifications of the characters (= differentiations are generically complex). According to previous considerations, population dynamics operates very often rather as a machine preserving diversity than as a machine optimizing species.

In sociology and everyday life, «Darwinian process» is often used in the sense of «random invention and survival of the best». In fact, the very concepts of “advantage” and “disadvantage” are often (near an unstable equilibrium) nonsense, as the surviving species does depend on the initial proportions. Evolution processes do not follow a yes/no logic. For instance, in a «symbiosis» case (=differences are handled as mutual advantages), diversity wins (whatever initial conditions). Oppositely, if differences are handled as nuisances, the process ends by the disparition of the weaker population.