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EXAMPLES OF CREATIVE EXTINCTION IN DYNAMIC ECOLOGY

E. SANCHEZ-PALENCIA AND JEAN–PIERRE FRANÇOISE

Abstract. In problems of ecological dynamics involving bistability (two disjoint attractors A_1 and A_2), we present (with various examples) a natural ecological mechanism allowing the transfer from the attraction basin of A_1 to the other basin, so allowing to reach A_2 from any initial configuration. The mechanism involve an extra species which changes the dimension of the phase space and the topology of the attraction basins. The extra species disappear in a natural way, so that this mechanism keeps some relation with apoptosis, but is different of it.

1. Introduction and basic example

When considering complex ecological communities, it often appears a phenomenon of bi-stability, i. e. there are two different attractors one "trivial" (it means that the asymptotic populations are 0) and another "non-trivial", (obviously with disjoint attraction basins). Starting from an initial state containing small populations (so in the attraction basin of the trivial attractor), it is impossible to reach the non-trivial configuration. The actual presence of a system working at the non-trivial attractor is usually explained by invoking a change of the general conditions in the distant past ; one must imagine that in the early times the system was another, allowing a gradual transition to the present state. This is not very convincing, as the given system is unable to describe the whole process. We show here that it is often possible to overcome this difficulty in another very different way, by taking account of an extra species (then changing the dimension of the space) which changes the topology of the attraction basins and that disappears naturally after a transient period.

Let us see this with a very simple model system in dimension 2:

$$\left\{ \begin{array}{l} \dot{y} = -y(y-2)(y+z-1) \\ \dot{z} = -z(1+z^2+y-3/2) \end{array} \right. \tag{1}$$

The system reduced to the axis y, is one-dimensional, with two stable equilibria, $(0,0)$ (trivial) and $(2,0)$ non-trivial. The attraction basins are separated by a third (unstable) equilibrium $(1,0)$, and it is impossible to go to the non-trivial attractor starting with a very small quantity of $y(0)$ (See 1, axis Y). Nevertheless, taking account of the whole system in dimension 2, the only attractor is the point $(2,0)$, with the whole quadrant (unless the boundary) as attraction basin, allowing to reach the non-trivial attractor from any point out of the axes.

We see that the key point in this mechanism is that the non-trivial attractor $(2,0)$ *is also a two-dimensional attractor (as it is transversally stable), whereas the two*

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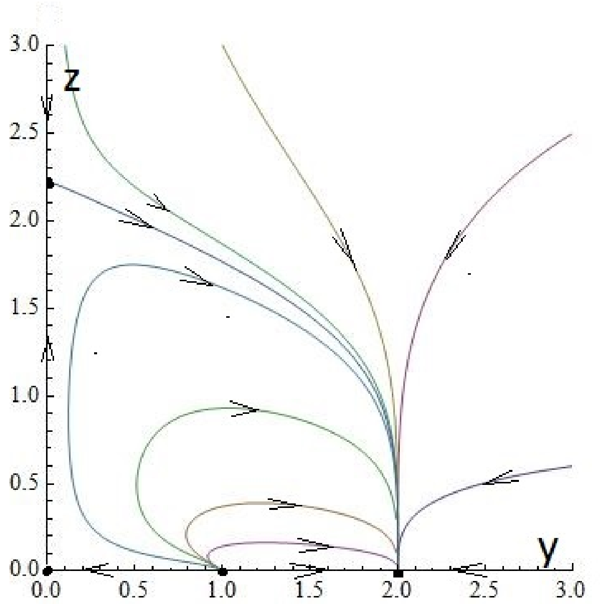

FIGURE 1. The phase portrait of (1)

others equilibria $(0,0)$ *and* $(1,0)$ *are transversally unstable, so repelling the moving point.*

Imagine that y and z are populations of two species. In the strict absence of z, a small quantity of $y(0)$ automatically sends to the trivial attractor $(0,0)$, whereas having in addition a (even very small) quantity of $z(0)$ sends to the non-trivial attractor $(2,0)$; note that *this implies the extinction of* z*, which operates as a starter*: it is necessary to start the process, and its ulterior extinction sends the system to the non-trivial configuration.

Note also that *this is an essentially non-linear process*: in order to start, the species z must be growing for small y ; oppositely, in the region nearby the non-trivial attractor, it is demographically less performant than y, it is decreasing and vanishes for $t \to +\infty$. In more general problems, the attractors are not necessarily points, most of times they are periodic cycles.

The purpose of this paper is to show examples of this mechanism in real situations involving several species. The role of y is played by two or three species submitted to complex interactions. We shall also show examples of the classical explanation involving time-dependent laws.

This mechanism of creative extinction keeps some relation with the apoptosis (programmed cell death) of developmental biology (for instance, the fetus develops webbed hands, the fingers appearing by apoptosis of the cells between the fingers), but is different of it.

This paper is issued from a talk to the Conference on Qualitative Properties of PDEs on occasion of the J. I. Diaz's 70 birthday, on July 15, 2021. For the sake of completeness, we took again (sections 2 and 3) in a succinct way some elements about predation and predation - commensalism systems exhibiting bistability contained in [2]. The new material in the present paper is the above model problem in dimension 2, the end of section 6 and the whole sections 7 and 8.

2. The Predation system (and the efficiency threshold for invasion)

We use a predator – prey system within the large Kolmogorov framework. After normalisation, the system is (1) , with functional response of type Holder II):

$$\left\{\begin{array}{l} \dot{x} = ax(1-(x/P)) - y\tanh(ex) \\ \dot{y} = -cy + y\tanh(ex) \end{array}\right. \tag{2}$$

Where x and y are the populations of the prey and the predator. In the absence of y, the preys x satisfy a logistic equation: a is the population growth for small x and P is the population of equilibrium with the subsistences (i. e. the capacity of the medium). The predators alone cannot subsist ($-c$ is the mortality ratio). The interaction terms in x and y are negative for the preys and positive for the predators ; they are the same (this means that, with suited units, the conversion rate is equal to one). This term is $y\tanh(ex)$, where $\tanh(ex)$ is the "functional response", the number of preys that each predator eats per unit of time. When x is small, it is equal to ex (so proportional to x, according to the number of preys statistically encountered), whereas for large x it is constant, equal to the satiety threshold (the maximum number of preys that each predator can eat (which is equal to one by normalization). The proportionality constant e is a measure of the efficiency of the predation process, and it plays an important role in the sequel. When e is small, such that $\tanh(eP) < c$, there is no invasion of the predator, (this is easily seen from the second equation (2), as $y'/y < 0$ in the vicinity of $(P, 0)$) and the attractor of the two-dimensional system is merely the point $(P, 0)$, the equilibrium of the preys alone, and the predators disappear. It is maybe useful to point out that, as the axis x is an invariant manifold, the jacobian matrix of the system at $(P, 0)$ has an eigenvector along the axis x (with a negative eigenvalue), and $\tanh(eP) - c$ is the other eigenvalue. When e is sufficiently large for $\tanh(eP) > c$, according to the second equation, the population of predators takes off from $(P, 0)$, and it is said that y is an invading species (there is an attractor with y strictly positive). There are then two different patterns of the phase portrait:

-For moderately large values of e, the attractor is a point (2).

-For larger values of the efficiency e, there is a Poincaré-Andronov-Hopf bifurcation and the attractor is a periodic cycle (2) :

3. The predation-commensalism system (bistability)

Commensalism is a relation between two species where one of them takes (demographic) profit of the other, which is (demographically) indifferent to the first. An obvious example appears when a species takes profit of the waste of the other.

We consider a predator – prey system where, in addition to the obvious predator – prey relations, the prey takes benefit of the predator in another way, as the predator increases the "capacity" of the medium. Among the very complex interactions between two species, an example of this is: The preys are herbivores and the predators are insects (parasites of the preys), which also increase the capacity on the medium by pollination. Clearly, the predators have two (opposite, but of different

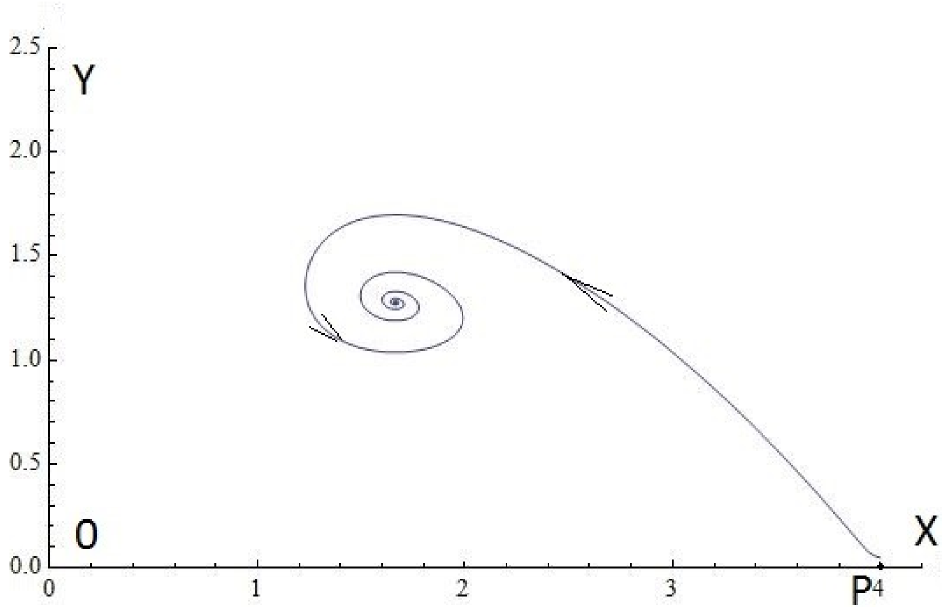

Figure 2. An orbit of system (2) for $a = 1$, $c = 0.716$, $P = 4$, $e = 0.6$ starting from a point nearby the equilibrium of the preys alone, $(P, 0)$. The same attractor is reached from any point out of the axes.

nature) actions on the prey: they eat (or kill in the parasite case) the preys and they improve the capacity of the medium. The equations are the previous ones, but P is no longer constant, it is an increasing function of y ; we shall use either

$$P = P_0 + \lambda y \tag{3}$$

(influence of the predators themselves) or

$$P = P_0 + \lambda y \tanh(ex) \tag{4}$$

(influence of the predation activity); here, λ is a parameter describing the intensity of the influence.

The results are qualitatively analogous for (3) or (4) . We shall give some computations, mainly for (4). There is a threshold for invasion of y from the vicinity of $(P_0, 0)$; it is the same as in the standard predator – prey system, as according to (3) or (4)the new commensalism term vanishes for small y.

The invasive case (i. e. $\tanh(eP_0) > c$*) is qualitatively analogous to the standard predator-prey system).*

In the non - invasive case (i. e. $\tanh(eP_0) < c$) the results are highly dependent on λ. For small λ, the new term has negligible influence and the attractor is obviously the equilibrium of the preys alone, $(P_0, 0)$ (3):

But for larger λ, there is a bifurcation with simultaneous inception of two new equilibria, a (unstable) saddle S and a stable focus A (attractor). But $(P_0, 0)$ is always an attractor, and there is a bi-stability phenomenon (see 3). The unstable

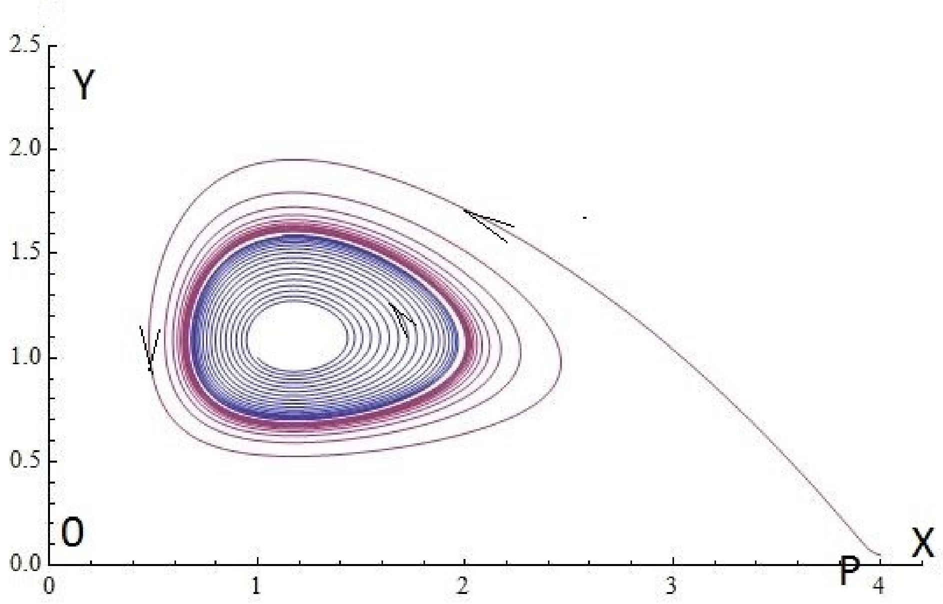

Figure 3. Two orbits of system (2) for $a = 1$, $c = 0.716$, $P = 4$, $e = 0.85$. One starts from a point nearby the equilibrium of the preys alone, $(P, 0)$ and spirals around the limit cycle from the outside. The other starts from a point inside the cycle and wraps on the cycle from the inside. The cycle is reached starting from any point out of the axes.

manifold of the saddle S sends on both sides towards the two attractors E and A, whereas the stable manifold of S is the border separating the two attraction basins. In fact, this pattern is very much natural: in the region y small, everything is alike in F, sending to E ; oppositely, for sufficiently large y, the commensalism term increases the effective value of P and there is invasion of the y, but this happens not from E, but from S (= for sufficiently high y), so that the upper part of the pattern is analogous to 3. The pattern is shown in 3:

Moreover, increasing again λ, the previous description remains true, but there is a new Poincaré – Andronov – Hopf bifurcation (somewhat analogous to that from 2 to 2) of the upper attractor, which becomes a periodic cycle, whereas the focus becomes unstable (I in 3).

4. How to reach the upper attractor from the equilibrium of the preys alone?

Let us focus on the case of bi – stability, (3 or 3). It is apparent that it is impossible to reach the upper attractor starting with a small number of predators; in that case, the dynamics leads to the equilibrium of the preys alone, so that the predators disappear at the limit ($t = +\infty$). In principle, the presence of an important population of predators nearby the upper attractor cannot be explained with this scheme.

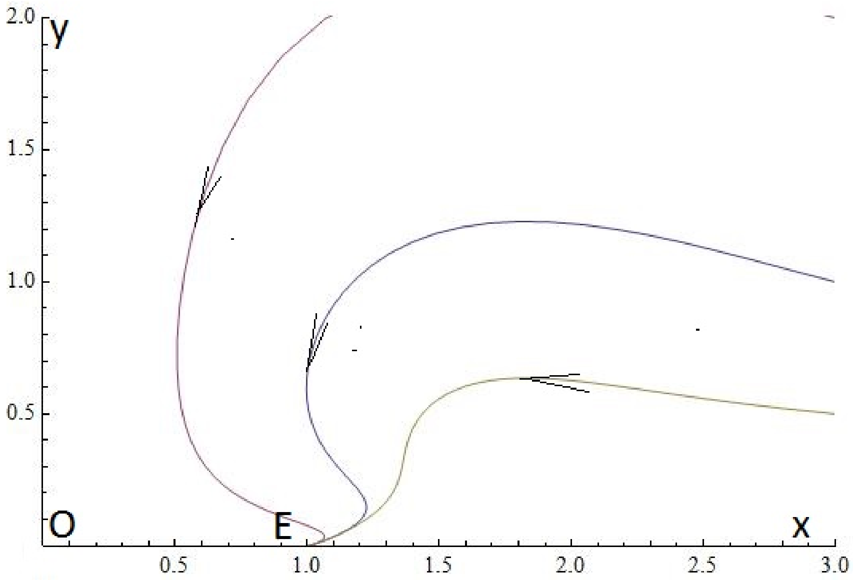

FIGURE 4. The phase portrait of system (2), (4) for small $e = 0.6$ (no invasion) and moderate $\lambda = 3$ (other parameters as in the previous section). The attractor is the equilibrium of the preys alone (E on the figure).

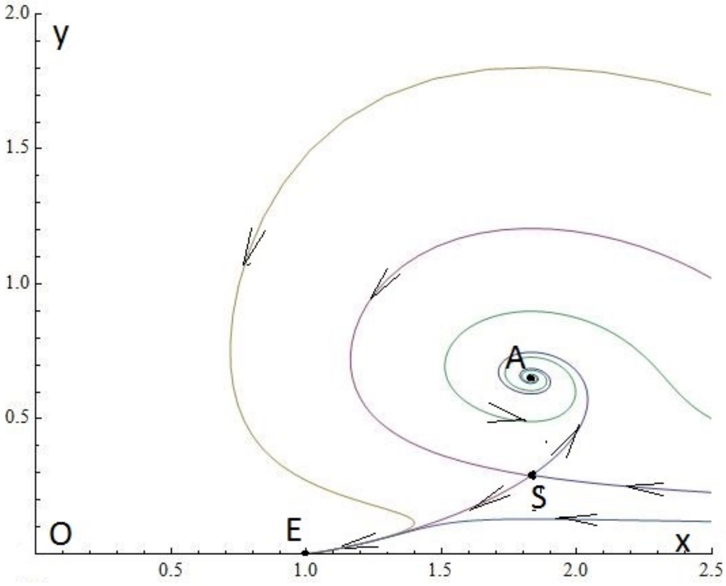

FIGURE 5. The phase portrait with small $e = 0.6$ (no invasion) and larger $\lambda = 5$ (other parameters as in the previous figure). There is a new attractor A in addition to E. The stable manifold of the saddle S is the curve separating the attraction basins of A and E.

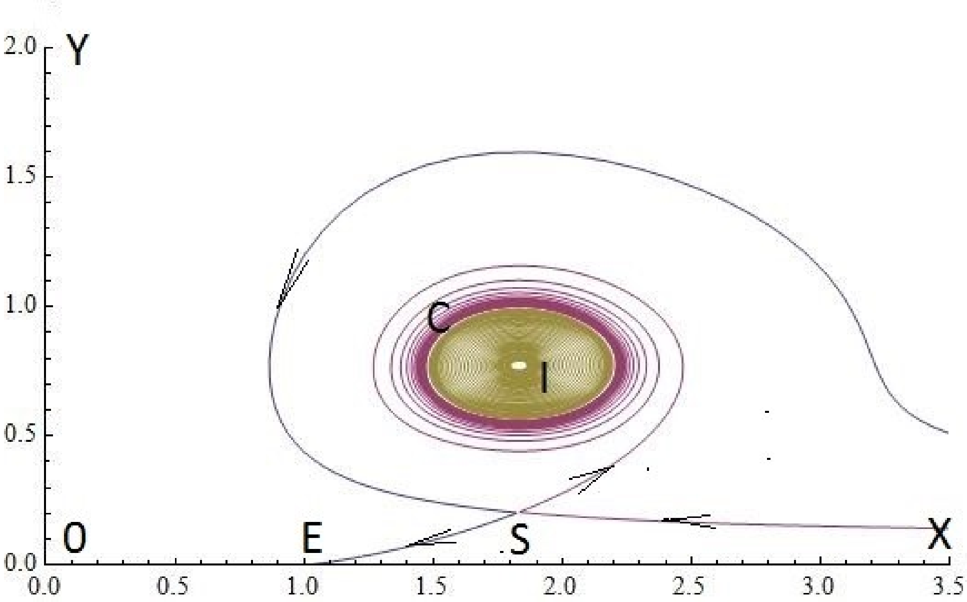

Figure 6. The phase portrait with small $e = 0.6$ (no invasion) and even larger $\lambda = 6$ (other parameters as in the previous figures). The upper attractor becomes a periodic cycle C and the upper equilibrium (I) is unstable. The stable manifold of the saddle S is always the curve separating the attraction basins of C and E.

This is a classical situation in biology: the ecological consistency of the present state is understood, but it does not allow to explain the evolution from a natural initial state. The classical explanation in this kind of situation consists in evoking different conditions in the distant past, allowing a gradual transition towards the present state. This will be illustrated in the next section 5. But we shall see that there is another possibility, which consists in the presence of another predator (able to invade), playing the role of a starter; if, in the subsequent process (with both predators) it is less performant than the first predator, it disappears in the limit, whereas the first remains at the upper attractor. This will be illustrated in section 6.

5. Classical explanation with a non-autonomous system

As an example, we consider the system (2), (3) with the parameters depending on time (then it is a non-autonomous system, out of the previous framework), namely :

$$\left\{\begin{array}{l} c = 0.8 - 0.3e^{-\mu t}, \\ e = 0.6 + 1.2e^{-\mu t} \\ a = 0.5, \quad b = 1, \quad \mu = 0.01, \\ P = 1 + \lambda y, \\ \lambda = 5 - e^{-\mu t}. \end{array}\right. \tag{5}$$

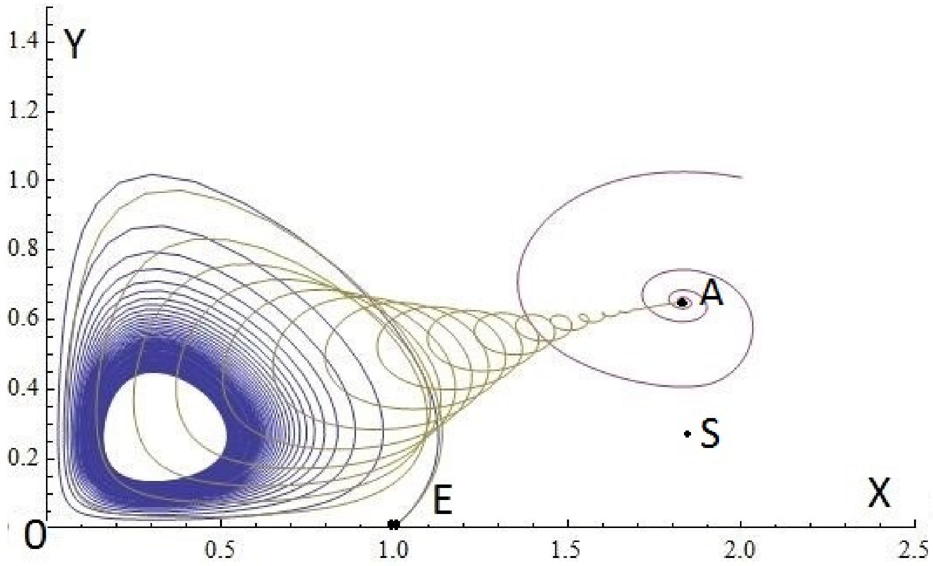

FIGURE 7. A trajectory of the non-autonomous system (2), (5) starting nearby $E = (1, 0)$ evolves slowly to the point attractor $A = (1.82, 0.64)$ on the right. The saddle S=(1.82,0.29) is also represented

We observe that these parameters are slowly dependent of t (note that μ is very small). It is easily seen that the final values correspond to an autonomous system in the framework of 3, with bi –stability and a point upper attractor, impossible to reach starting with small $y(0)$. But, the (variable) parameters are chosen initially with larger efficiency e and smaller death ratio c, allowing invasion.

The next fig 7 is a superposition of three orbits: the first one corresponds to the limit parameters ($t = +\infty$) and converges to the point attractor (starting from a near point). The second orbit is for the constant initial values of the parameters; it starts from a point nearby the equilibrium of the preys alone and converges to the corresponding attractor (a cycle, on the left). The third one is for the very non-autonomous system, starting nearby the equilibrium of the preys alone; it first behaves as the initial autonomous system, then evolves slowly approaching the point attractor on the right.

Obviously, there are very many variants of this. In Fig 8 we have an analogous example where the final attractor is a periodic cycle (as in Fig 6), obtained with a non-autonomous system (2), (5) with

$$a = 1, \quad e = 0.2 + 1.5e^{-\mu t}, \\ \mu = 0.03, \quad P = 4 + 2.9y \tanh(ex), \quad c = 0.8 \tag{6}$$

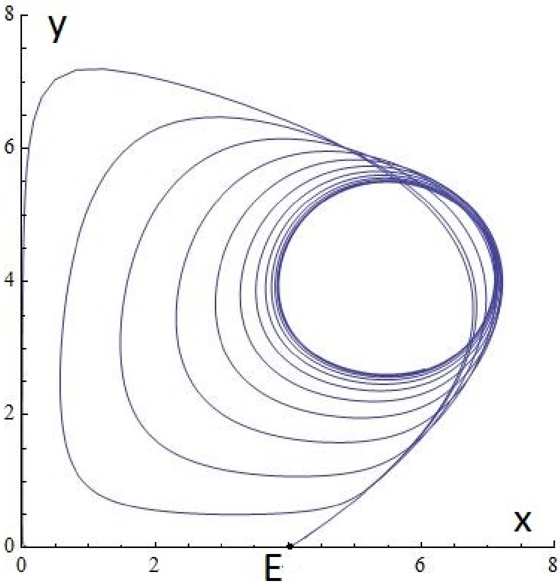

FIGURE 8. A trajectory of the non-autonomous system (2), (5) starting nearby E evolves slowly to the point attractor on the right.

6. A NEW (NON-CLASSICAL) EXPLANATION. AUTONOMOUS SYSTEM IN DIMENSION N+1. FIRST EXAMPLE OF CREATIVE EXTINCTION

The idea is to consider another predator y_2 with parameters different of those of the first one (now denoted by y_1). The new predator is invasive (in particular $e_2 > e_1$), but when the populations are large, y_1 displaces y_2 (in particular, $c_2 > c_1$), so that the attractor is on the plane $y_2 = 0$. (But obviously, the initial values must contain both species). Specifically, we take the system (with constant parameters):

$$\left\{ \begin{array}{l} \dot{x} = ax(1 - x/P) - y_1 \tanh(e_1 x) - y_2 \tanh(e_2 x) \\ \dot{y}_1 = -c_1 y_1 + y_1 \tanh(e_1 x) \\ \dot{y}_2 = -c_2 y_2 + y_2 \tanh(e_2 x) \end{array} \right. \tag{7}$$

with

$$\left\{ \begin{array}{l} a = 0.5, b_1 = 1.7, b_2 = 1 \\ P = 1 + \lambda_1 y_1 b_1 \tanh(e_1 x/b_1) + \lambda_2 y_2 b_2 \tanh(e_2 x/b_2) \\ e_1 = 0.72, \quad e_2 = 1.33, \\ \lambda_1 = 10, \quad \lambda_2 = 6, \\ c_1 = 0.72, \quad c_2 = 0.86. \end{array} \right. \tag{8}$$

It will prove useful to point out that the planes $y_1 = 0$ and $y_2 = 0$ are invariant, so that the equilibrium of the preys alone $(1, 0, 0)$ is non-degenerate, with an eigenvector in the direction of the x axis, and the two other inside the invariant planes, so that the invasion properties are merely those of each predator with the prey.

For $y_2 = 0$, we have a non – invasive predator y_1 in the bi-stability context of Fig 6, with an upper cyclic attractor (so impossible to reach from the vicinity of

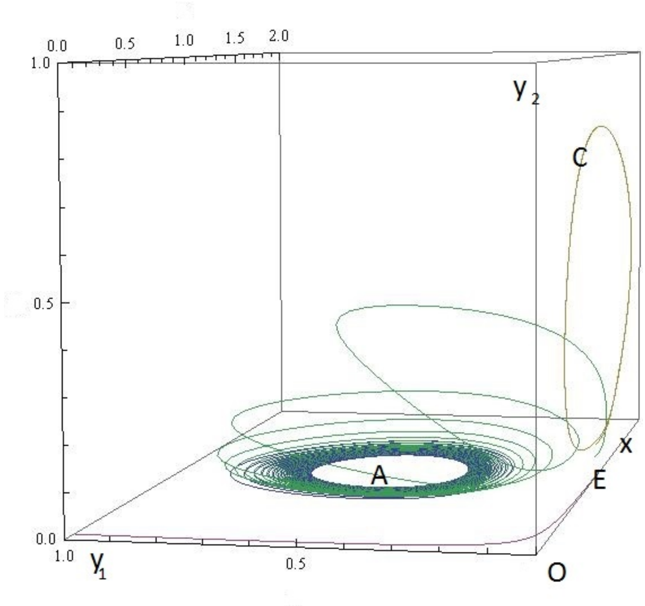

FIGURE 9. An orbit of the system (7) (8) starting nearby E. It first approaches C and then migrates to the attractor A.

E). Oppositely, for $y_1 = 0$, the predator y_2 is invasive, allowing orbits starting near E to grow nearby the attractor of the plane $y_1 = 0$, which is transversally unstable, so that the orbit migrates towards $y_2 = 0$ with significant values of y_1, so on the above attraction basin (Fig 9). The same solution as function of t appears in Fig 10.

There is an interesting property concerning the mechanics just described. We note that the given example is concerned with a case where the final attractor is a periodic cycle. The mechanism does not work in the case where the attractors are points. Indeed, let us denote $h_i(x) = b_i \tanh(e_i x/b_i)$ $(i = 1, 2)$ the functional responses of the two predators. As y_2 is invading and y_1 is not, we have

$$c_1 > h_1(P_0), \tag{9}$$

$$c_2 < h_2(P_0). \tag{10}$$

Let us assume that $(x^*, y_1^*, 0)$ is a global attractor. Then, y_2 cannot be invading from this point, so tat

$$c_2 > h_2(x^*). \tag{11}$$

From (10) and (11), as h_2 is increasing,

$$x^* < P_0. \tag{12}$$

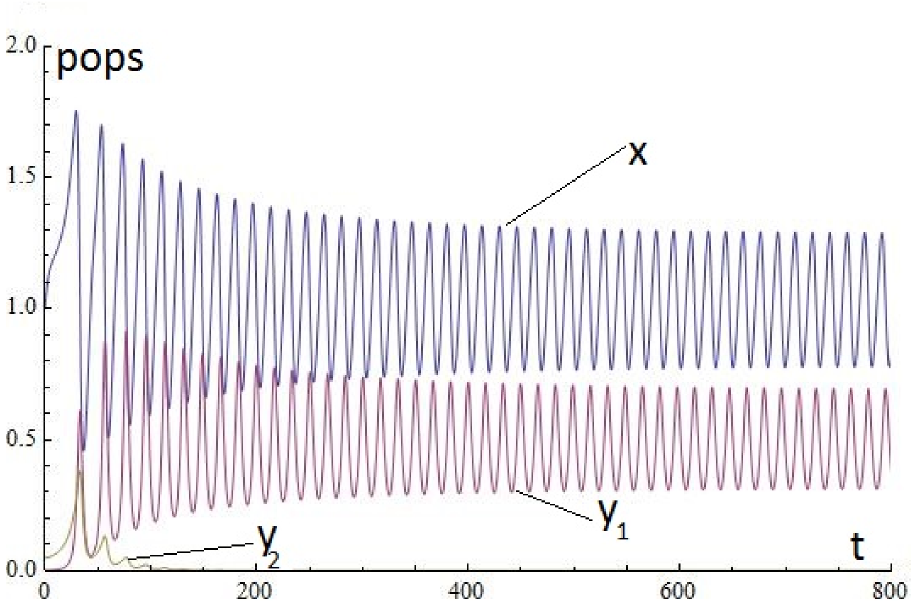

FIGURE 10. The same solution of (7) (8) as a function of t. The starter y_2 first grows and then dies out naturally, whereas y_1 remains.

This is impossible, as in our bi-stability problem, the equilibria have abscissas $> P_0$. Indeed, at the equilibrium, we have

$$h_1(x^*) = c_1 \tag{13}$$

But, from (13) and (9),

$$x^* > P_0 \tag{14}$$

which is in contradiction with (12). Q.E.D.

We shall see in the next section that certain modifications of the basic mechanism make it effective even in the previous case.

7. DEVICES FOR IMPROVING THE ROBUSTNESS OF THIS MECHANISM

The success of this process lies on two mechanisms: first, the solution must take off from C (the attractor of y_2 alone) and then it must past to A (the final attractor). It should be noticed that the differences between the two predators give advantages and disadvantages in the various pertinent regions. Obviously, it is not very easy to get values of the parameters allowing the whole process: as a consequence, the intervals of values of the parameters are narrow (out of them, either the starter remains, or y_1 cannot take off from C). But it is possible to add other small terms (with easy ecological meaning) in order to ensure the robustness of this basic mechanism. In particular:

-a) A (even small) term of commensalism of y_1 on y_2 (i. e. y_1 takes benefit from the presence of the starter y_2) helps the orbit to take off from C (the attractor of x, y_2), without modifying essentially the behaviour in the vicinity of $y_2 = 0$.

-b) A (even small) term of negative commensalism of y_2 on y_1 (i. e. the starter y_2 undergoes prejudice from the presence of y_1) helps the orbit to paste to A (the attractor of x, y_1), without modifying essentially the behaviour in the vicinity of $y_1 = 0$.

-c) the two previous properties may be combined to give: A (even small) term of predation of y_1 (predator) on y_2 (prey) helps the orbit to take off from C (the attractor of x, y_2) and to paste to A (the attractor of x, y_1).

These properties follow easily from classical properties of perturbation of the initial conditions in the direction transversal to the coordinate planes. They allow to construct a great variety of examples of creative extinction with very suitable robustness (with respect to the values of the parameters). For simplicity, we shall consider the new terms without satiety threshold, but this is not essential.

We are proving property a; the proofs of the two others are analogous, exchanging y_1 and y_2 with the suited signs. The profs are in the framework of small (linear) perturbation of the cycle C in the plane x, y_2 (of the prey and the starter). For the sake of simplicity in the proof we denote x by y_3, and we write the variables in the order.

$$y = (y_1, y_2, y_3) = (y_1, y_2, x) \tag{15}$$

Let $y^c(t) = (0, y_2^c(t), y_3^c(t))$ be the equation of the cycle C (parametrized by the time t). The complete system of equations writes

$$\begin{cases} \dot{y}_1 = f_1(y_1, y_2, y_3) \\ \dot{y}_2 = f_2(y_1, y_2, y_3)) \\ \dot{y}_3 = f_3(y_1, y_2, y_3)) \end{cases} \tag{16}$$

with

$$f_1(0, y_2, y_3) = 0 \tag{17}$$

as the plane $y_1 = 0$ is an invariant manifold. The linearization amounts to make the change

$$\begin{cases} y_1 = z_1 \\ y_2 = y_2^c(t) + z_2 \\ y_3 = y_3^c(t) + z_3 \end{cases} \tag{18}$$

and linearizing for small z. This gives

$$\dot{z} = J(t)z \tag{19}$$

where $J(t)$ denotes the jacobian matrix at the point $(0, y_2^c(t), y_3^c(t))$. It follows from (17) that $J_{12} = J_{13} = 0$, so that $\dot{z}_1 = J_{11} z_1$ and then

$$z_1(t) = exp(\int_0^t J_{11}(\tau) d\tau) z_1(0). \tag{20}$$

It then follows that the invasion of z_1 from the vicinity of C amounts to

$$exp(\int_0^T J_{11}(\tau)d\tau) > 0. \tag{21}$$

where T is the period of the cycle. On the other hand, a term of commensalism of y_1 on y_2 consist in adding to f_1 a term of the form $\eta y_1 h(y_2)$ where $h(y_2)$ is the functional response (vanishing at the origin and positive for positive y_2), and η denotes a small positive coefficient, allowing linearization). This gives an extra contribution $\eta h(x_2^c(t))$ to $J_{11}(t)$, so proving the first part of property a.

Moreover, the extra term $\eta y_1 h(y_2)$ in f_1 amounts to a perturbation of the vector field in the direction of the y_1 axis, then tangential to the plane $y_1 = 0$. A computation of the perturbation analogous to the previous one gives obviously no contribution to the normal perturbation z_2 of the cycle on $y_2 = 0$. The properties of approaching to the plane $y_2 = 0$ are then not modified, which amounts to the second part of property a.

Here we have an example of the property b. We consider a system analogous to the previous one, but such that the final attractor A is a point instead of a periodic cycle, and we add a small term ($\eta = 0.05$) in the framework of the above property b:

$$\begin{cases} \dot{x} = ax(1 - x/P) - y_1 b_1 \tanh(e_1 x/b_1) - y_2 b_2 \tanh(e_2 x/b_2) \\ \dot{y}_1 = -c_1 y_1 + y_1 b_1 \ \tanh(e_1 x/b_1) \\ \dot{y}_2 = -c_2 y_2 + y_2 b_2 \tanh(e_2 x/b_2) - \eta y_2 y_1 \end{cases} \tag{22}$$

with

$$\begin{cases} P = 1 + \lambda_1 y_1 b_1 \tanh(e_1 x/b_1) + \lambda_2 y_2 b_2 \tanh(e_2 x/b_2) \\ a = 0.5, \quad b_1 = 3.75, \quad b_2 = 1.0, \quad e_1 = 0.70, \quad e_2 = 1.33, \quad \eta = 0.05 \\ \lambda_1 = 10, \quad \lambda_2 = 6, \quad c_1 = 0.72, \quad c_2 = 0.86, \quad c_1 = 0.72, \quad c_2 = 0.86. \end{cases} \tag{23}$$

An orbit starting from the immediate vicinity of the equilibrium of the preys alone is shown in Fig 11 and Fig 12 (which are very much analogous to Fig 9 and Fig 10 unless the attractor A is now a point).

In this example, the role of the small term η (property *b*) is essential: taking $\eta = 0$ the phenomenon disappears (the three species x, y_1, y_2 remain in a cyclic attractor), see fig 13.

8. Complements. Example of a purely dynamical community accessible using a species that eventually disappears

The previous mechanism is somewhat general, and it may be applied to overcome a barrier between two attraction basins by adding a new variable which disappears at the limit ($t = +\infty$). We are giving here an example analogous to the previous ones, but with three variables at the limit (x, y_1, y_2, a prey and two predators) plus a starter (y_3, a new predator). The community x, y_1, y_2, exhibits bi-stability: there is an attractor A (a periodic cycle) with an attraction basin which is strictly disjoint of the equilibrium of the preys alone, $(P_0, 0, 0)$. This example is somewhat analogous to the previous one, but with one more predator, which remains in the limit. This limit problem exhibits the particularity that it has no internal equilibrium point (i. e., equilibrium with all the variables different from zero). This is in the framework

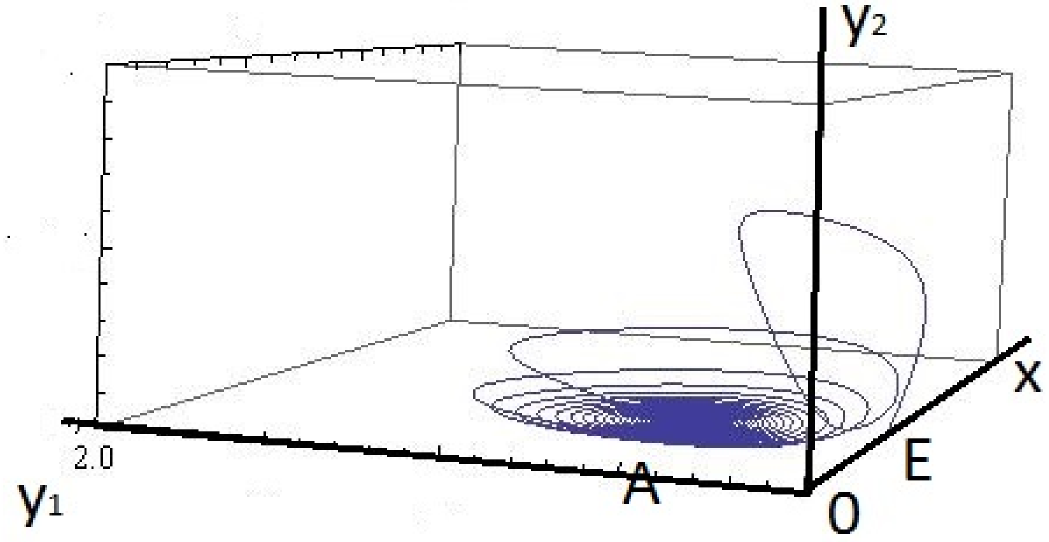

Figure 11. An orbit of the system (22) (23) (with a point attractor) starting nearby $E = (1,0,0)$ first go up and then migrates to the point attractor $A = (1.1, 0.6, 0)$.

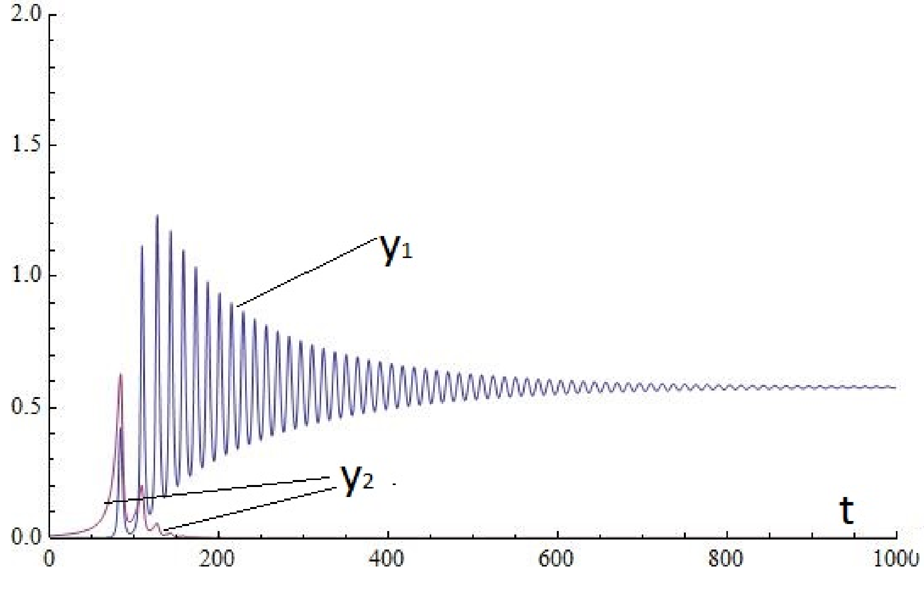

Figure 12. The same solution of (22) (23) as a function of t. The starter y_2 first grows and then dies out naturally, whereas y_1 remains.

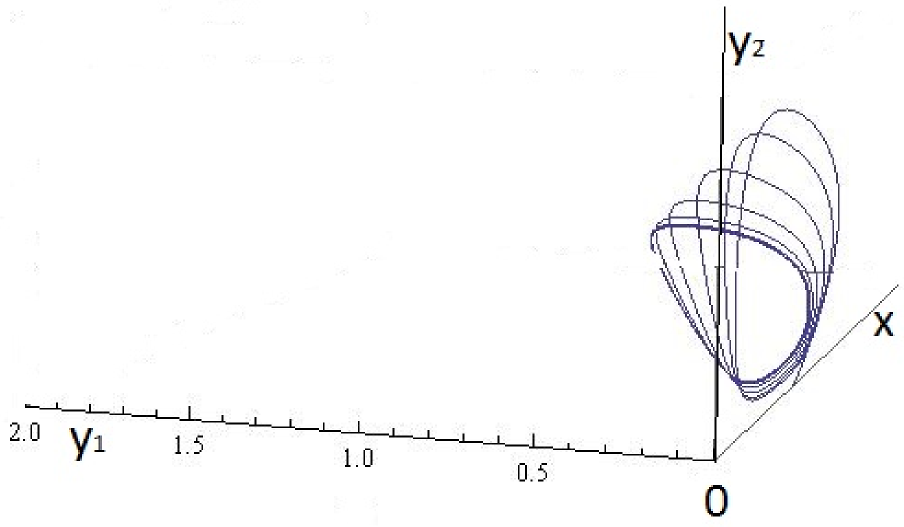

Figure 13. The same without the term η: there is persistence of the three species (the attractor is a periodic cycle disjoint of the coordinate planes).

of the (false, often controverted) competitive exclusion principle; it constitutes a new counter-example, exhibiting, in addition, bi-stability.

Let us recall a little the context of this problem. It is concerned with the general question of the possibility of two predators to subsist in a stable way with one prey.

The negation of such a possibility (known as competitive exclusion principle) comes back to Gause [12], on the basis of heuristic reasons (some difference between the predators should induce a demographic advantage of one of them, which should be the survivor in the competition). Nevertheless, since 1974, certain numerical computations [11] showed in certain cases the presence of stable periodic solutions involving the three species. In 1977 appeared the celebrated mathematical paper of McGehee and Armstrong [4], where was proved the existence of an attractor involving both predators. But the proof was more involved, and the attractor and the phase portrait were not explicit. The next year appeared two papers [5], [6]) with computations on this kind of solutions, and the falsehood of the exclusion principle seemed proven. Nevertheless, because of the involved structure of the solutions and certain topological peculiarities of the attraction basin, the question was often subject to discussion (see for instance [13] and [9]). In recent times, a large variety of new examples, often with explicit description of the topology of the attraction basin was available (see [3], and also [8], [10], [1], [2]).

The next example is then concerned with both this context and creative extinction. The equations are the same as before (with one more predator and the obvious notations) with the parameters (we note that the efficiency e_3 and the natural mortality c_3 are larger than the others):

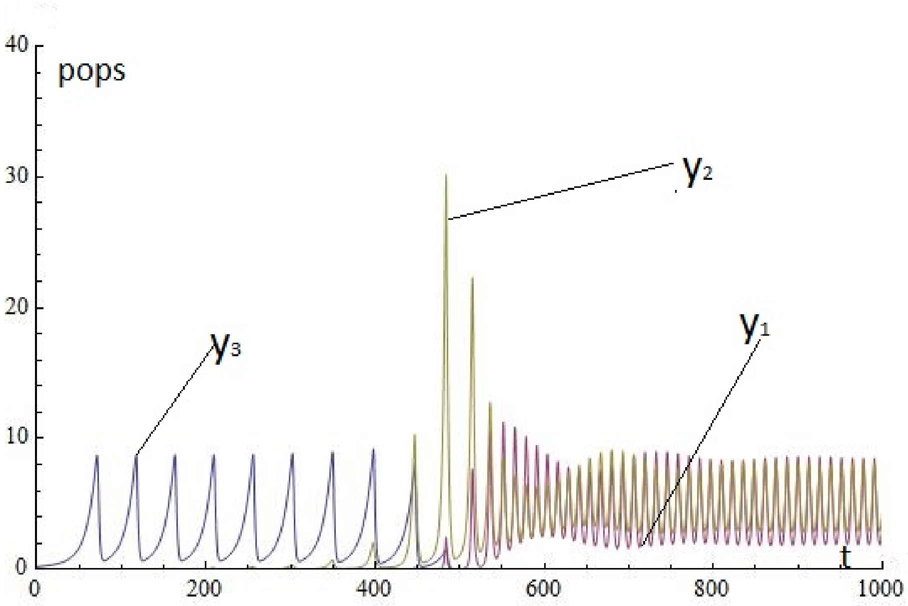

FIGURE 14. A solution of (24). The starter y_3 is initially active and then dies out and the community x, y_1, y_2 remains (the prey x is not represented).

$$(24)\qquad \begin{cases} P = 4 + \lambda_1 y_1 + \lambda_2 y_2 + \lambda_3 y_3 \\ a = 1, \quad b_1 = 1.4, \quad b_2 = 0.75, \quad b_3 = 0.8 \\ e_1 = 0.1, \quad e_2 = 0.1, \quad e_3 = 0.3, \\ \lambda_1 = 3.5, \quad \lambda_2 = 3.5, \lambda_3 = 2.5 \\ c_1 = 0.54, \quad c_2 = 0.45. \quad c_3 = 0.715 \end{cases}$$

Fig 14 is a plot of the three predators (the prey is not represented). The starter y_3 is practically alone in a first phase of the process; it then dies out, replaced by the community y_1, y_2, which remains in the attractor.

This pattern is not very robust; for instance, it holds true only for $0.71 < c_3 < 0.72$ (the other parameters are fixed).

We can make it a little more robust by adding a small predation term of y_2 *on the starter* y_3 (obviously this disappears at the limit). Here we have an example of community in x, y_1, y_2 which is impossible to reach from the equilibrium of the preys alone (because of bi - stability). It is reached with the starter y_3. Fig 15 is a plot of the projection of an orbit on the subspace x, y_1, y_2 (so, the starter is not represented). This pattern is somewhat robust (for instance, fixing the other parameters, we may take $0.52 < c_3 < 0.61$).

$$(25)\qquad \begin{cases} \dot{x} = ... \\ \dot{y_1} = ... \\ \dot{y_2} = ... + \epsilon y_2 y_3 \\ \dot{y_3} = ... - \eta y_2 y_3 \end{cases}$$

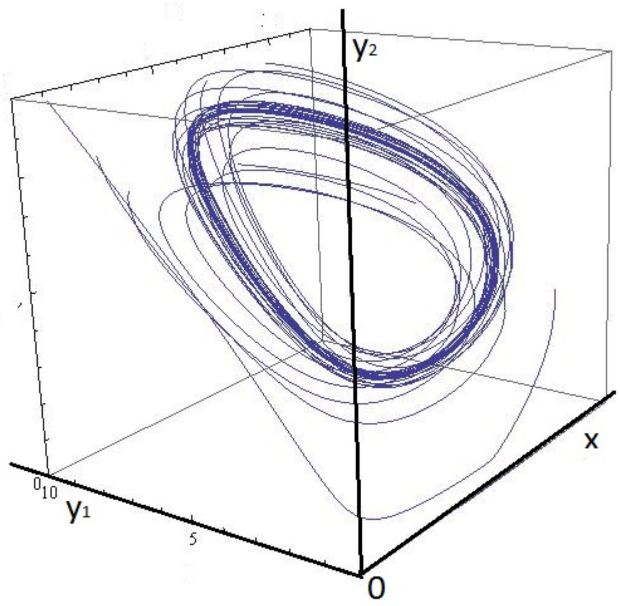

FIGURE 15. A plot of the projection of an orbit of (25) (26) on the space x, y_1, y_2 (so, the starter is not represented). The persistence is apparent.

with

$$\left\{\begin{array}{l} \epsilon = 0, \eta = 0.03 \\ P = 4 + \lambda_1 y_1 + \lambda_2 y_2 + \lambda_3 y_3 \\ a = 1, \quad b_1 = 1.4, \quad b_2 = 0.75, \quad b_3 = 0.8 \\ e_1 = 0.1, \quad e_2 = 0.1, \quad e_3 = 0.3, \\ \lambda_1 = 3.5, \quad \lambda_2 = 3.5, \lambda_3 = 2.5 \\ c_1 = 0.54, \quad c_2 = 0.45. \quad c_3 = 0.715 \end{array}\right. \tag{26}$$

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