TOPOLOGICAL REMARKS AND NEW EXAMPLES OF PERSISTENCE OF DIVERSITY IN BIOLOGICAL DYNAMICS

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ABSTRACT. There are several definitions of persistence of species, which amount to define interactions between them ensuring the survival of all the species initially present in the system. The aim of this paper is to present a wide family of examples in dimension \( n > 2 \) (very natural in biological dynamics) exhibiting convergence towards a cycle when starting from anywhere with the exception of a zero-measure set of “forbidden” initial positions. The forbidden set is a heteroclinic orbit linking two equilibria on the boundary of the domain. Moreover, such systems have no equilibrium point interior to the domain (which is necessary for classical persistence for topological reasons). Such systems do not enjoy persistence in a strict sense, whereas in practice they do. The forbidden initial set does not matter in practice, but it modifies drastically the topological properties.

1. Introduction. In the framework of ecological dynamics, the problem of persistence of species amounts to define interactions between several species (as well as their resources) ensuring the survival of all the species initially present in the system. Obviously, there are many different precise definitions of such a general concept (see for instance [2] chapters 13 and 16, [4], [14], the review paper [3] and the book [15], as well as [7] for the ecological framework), concerning for instance the admissible initial populations (satisfying or not certain conditions), but mostly the very definition of “extinction”, i.e. the proper definition of convergence to zero. As a matter of fact, the elaboration of such definitions was historically linked with the discovery of examples of persistence or extinction, so that this is a naturally open question (See the review paper [3] in this connection).

The aim of this paper is to present a family of examples (with very natural structure in biological dynamics) exhibiting almost-everywhere convergence towards a classical attractor (namely a stable cycle) when starting from any choice of non-zero initial populations with the exception of a zero-measure set of “forbidden” initial values which lead towards the extinction of one of the species. More precisely, in dimension \( n > 2 \) there is a heteroclinic orbit linking (for time tending to \(-\infty\)...)
and $+\infty$) two equilibria on the boundary of the domain. As this boundary is on the coordinate planes (accounting for zero values of one of the species), when starting from points of this orbit (a zero-measure set) the system leads to the extinction of one of the species.

Obviously, this exceptional zero-measure set does not matter from the viewpoint of modelling in biological (or ecological) dynamics. As a matter of fact, any definition of persistence excludes as admissible initial values the boundaries, as they usually are invariant manifolds of the system, accounting for lack of one of the species. Nevertheless, as the heteroclinic orbit is a curve internal to the domain, it drastically modifies the topological properties of the domain of initial values leading to persistence. This point is very important, as certain criteria of non-persistence are based on topological properties of that domain, which is obviously absorbing for the vector field. As a matter of fact, there is a large class of ecological sys-
temes which are persistent when starting from almost everywhere, but not from everywhere in the strict mathematical sense.

Indeed, when persistence is understood in the sense of convergence towards a bounded attractor from any initial point (more explicit comments are given in the conclusion, Section 5), one reduces (after some technical handling to avoid neighbour-
hoods of the coordinate planes and of infinity) to a compact set homeomorphic to a ball, the vector field being non-vanishing and inwards on its boundary. Index theory then implies that the vector field certainly vanishes inside. So, non-existence of an equilibrium point inside the domain of admissible initial values implies that the system is not persistent (see for instance theorem 13.3.1 of p. 158 in [2]). This argument is obviously false (see the explicit examples in the sequel) when persistence only takes place almost everywhere. Note also that [2] excludes heteroclinic orbits (see hypothesis H2 of p. 211).

Moreover, the above situation also furnishes a family of examples of systems (not necessarily in biological dynamics) enjoying endogeneous oscillations without interior rest point. Clearly, in dimension two, the existence of a cycle in a domain homeomorphic to a ball implies by index theory the presence of a rest point interior to the cycle. Moreover, usual examples (Van der Pol-like electronic devices for instance) are concerned with a stable rest point which, under Poincaré-Andronov-Hopf bifurcation induced by modifying some destabilizing parameter, becomes unstable and surrounded by a stable cycle. The analogy with this elementary example makes it difficult to imagine the existence of a stable cycle without a (unstable) rest point. Obviously, this heuristics, though correct in dimension two, is false in higher dimension. Indeed, we shall see (in sections 2, 3 and 4) that the above mentioned examples with a heteroclinic orbit have no rest point (out of the boundary). The global dynamics is some kind of helicoidal flow converging to a cycle.

It is worthwhile to mention that the initial example which we develop here is concerned with a two predators and one prey system, which was first published in [5], also constitutes a counter-example to the “competitive exclusion principle” according to which two different species cannot survive on the same ecological ressource as one of the species should necessarily be more performant than the other, then dis-
placing it. But it is known that such principle is not valid when non-linear relations are involved in the predation process (see for instance [2], [6]). In this connection, it should be noted that the very innovating and deep (but very scarcely quoted in ulterior literature on the subject) paper [8] contains an example which is very close
to ours, as well as very many very interesting considerations on these subjects, in particular the very pertinent concept of attractor block (absorbing compact set with nonempty interior containing an attractor) and comments on the topological properties of that blocks. In particular, an attracting block containing a cycle and no rest point has (according to Poincaré - Hopf theorem for manifolds with boundary, see for instance [9] p. 35, where the vector field is necessarily outward transversal to the boundary and then applies to the present problem after a change of sign) necessarily an Euler characteristic equal to zero (roughly speaking, as the volume limited by a toroidal surface, whereas the Euler characteristic of a ball is equal to 1).

This is not a genuine mathematical paper, but rather a computing one. Mathematics are practically reduced to description and comments on the basis of the numerical examples (done with Mathematica). We did not search to generalize the examples, nor to give a new definition of persistence. Indeed, we mainly focus on the description of certain mechanisms leading (up to a zero-measure exceptional set) to both persistence and some kind of endogenous oscillations; there probably are many others, and in our opinion, the time is not come to construct a general theory of these subjects. For the same reason (in particular in dimension $n > 3$ we did not search to give an explicit and rigorous description of the admissible set of initial values; we only show that it contains a “somewhat large” compact domain of dimension $n$, with the exclusion of a zero-measure heteroclinic orbit (or something analogous). Roughly speaking, all the examples are concerned with “structurally stable” systems (in the sense that equilibria and periodic orbits are hyperbolic), thus admitting (at least small) perturbations of the parameters.

The paper is organized as follows:

Section 2 (mainly taken from [5]) contains a description of the basic example in dimension three (two predators an one prey) in the context of persistence, showing that there is no interior rest point.

In Section 3, using a technique of splitting and perturbation we give analogous examples of (almost everywhere) persistence without interior rest point in dimension $n > 3$, in particular $n = 4$ (two predators and two preys).

In Sect 4 we show that (well-known) systems of one predator and two preys exhibiting persistence (or rather almost everywhere persistence) have not interior rest points for certain domains of the values of the parameters. This shows that this property is rather widespread.

Final comments on persistence and endogenous oscillations are in the conclusion, Section 5.

An appendix gives explanations on the mathematical models of predation.

2. The basic example of two predators and one prey. In this section, we consider the system for the joint evolution of two predators $z_1, z_2$ and one prey $x$ (see the appendix for an explanation on the various terms and coefficients of our model, essentially analogous to the Monod-Rosenzweig-Mc Arthur system):

$$
\begin{align*}
\dot{x} &= bx(1 - x/p) - z_1 d_1 \text{Tanh}(a_1 x/d_1) - z_2 d_2 \text{Tanh}(a_2 x/d_2) \\
\dot{z}_1 &= z_1(-c_1 + d_1 \text{Tanh}(a_1 x/d_1)) \\
\dot{z}_2 &= z_2(-c_2 + d_2 \text{Tanh}(a_2 x/d_2))
\end{align*}
$$

(1)

With the values of the parameters $a_1 = 1, a_2 = 1, b = 1, c_1 = 0.55, c_2 = 0.7, d_1 = 1, d_2 = 2, p = 4$. We note that $c_1 < c_2$, which amounts to saying that the predator $z_2$ has a natural mortality larger than the $z_1$. Moreover, $d_1 < d_2$, i.e.
the limit of satiety of the $z_2$ is larger than that of the $z_1$. This gives an advantage and a disadvantage of the $z_1$ with respect to the $z_2$ of different character, so that we may expect some kind of balance, leading to a coexistence of the two predators.

It is easily seen that there is no equilibrium point with the three populations different from zero. Indeed, the rest points are the solutions of the algebraic system in $x$, $z_1$, $z_2$ obtained by equating to zero the right-hand sides of the system (1). For $z_1 \neq 0$, $z_2 \neq 0$, the two last equations give two different equations with the unique unknown $x$, hence the property.

Fig 1 is a plot of orbits on the coordinate planes and of the heteroclinic orbit of system (1). It is apparent that on the plane $z_1 = 0$ (i.e. the system of the prey $x$ with predator $z_2$) there is a stable equilibrium, whereas on the plane $z_2 = 0$ (i.e. the system of the prey $x$ with predator $z_1$) there is a stable cycle (which has an interior unstable equilibrium). On the plane $x = 0$ there are no preys, and the orbits obviously converge to the origin. Moreover, the equilibrium on the plane $z_1 = 0$ (resp. $z_2 = 0$) is transversally unstable (resp. stable). The figure also exhibits the heteroclinic orbit linking the equilibria on the planes $z_1 = 0$ and $z_2 = 0$ (for $t = -\infty$ and $t = +\infty$ respectively, as they are transversally unstable and stable respectively).

Moreover, the attractor is the cycle shown in Figure 2 with the three populations never vanishing (i.e. not touching the coordinate planes). The travel along the cycle as a function of time is apparent in Figure 3, which is a plot of a solution for large values of the time $t$ (then after the transient which depends on the initial values).

It should be emphasized that the attraction basin of this cycle is the whole space with the exception of the coordinate planes (which are invariant manifolds with the corresponding attractors which are apparent in figure 1) and the heteroclinic orbit (whose attractor is the equilibrium point on the plane $z_2 = 0$, which is unstable in this plane but transversally stable, with the heteroclinic orbit as stable manifold).

The attractor obviously surrounds the heteroclinic orbit; the movement around the cycle amounts to turning around the heteroclinic orbit. The convergence of
any orbit towards the limit cycle is some kind of helix-like movement made by the combination of the previous rotation and another one in the family of normal planes to the cycle (this latter rotation shrinks to zero, then leading to the limit cycle). The reader may refer to figure 10 and perhaps 11 and 12 in the conclusion for more clear artist view of the orbit. The structure of any attractor block is then apparent: they are toroidal volumes containing the cycle, whereas the hole is traversed by the heteroclinic orbit. Their Euler characteristic is equal to zero (not to one as in the classical persistence on blocks without hole).

The crucial point in the structure of this flow is the transversal instability of the cycle in the plane $z_2 = 0$ (which is obviously stable in its plane). As the cycle itself is only known by numerical computation, it is clear that this point may only be checked numerically too. The numerical evidence of this fact is apparent by considering...
solutions starting with very small values of $z_2$, as shown in Figure 4, which is a plot of $z_2(t)$; it is apparent that $z_2$ evolves with non small values, oscillating with some kind of double periodicity. The small period one, which remains at the limit, is the movement along the limit cycle, whereas the long period one accounts for the helical approach to the cycle and vanishes slowly.

3. **An example in dimension four: Two predators and two preys.** The suited model for two preys (analogous to (1) is not obvious, as the maximal quantity of food consumed by each specimen of the predators depends simultaneously on both preys (satieties with respect to the two preys are related). We shall derive such model from (1) in two times, splitting and perturbation (but a direct derivation is also possible, see the appendix). Splitting (see [12], [13]) is an automatic algorithm for obtaining the system accounting for two indiscriminated subspecies from the equation for their whole population. Among the vast litterature on these topics, it should be noticed that logic constraints to be satisfied by models of trophic webs where given in ([1]); the article ([11]) should also be cited concerning the long transient in related topics in a chemostat.

Let us consider a generic equation for the evolution of a population $u$:  
\[ \dot{u} = F(u) \]  
(2)

When the population $u$ splits into the populations of two indiscriminated subspecies $u_1$ and $u_2$, they should satisfy:  
\[ \begin{cases} 
  u_1(t) + u_2(t) = u(t), & t \geq 0 \\
  u_i(t)/u(t) = u_i(0)/u(0), & i = 1, 2, & t \geq 0.
\end{cases} \]  
(3)

It is easily seen that the dynamical system describing the time evolution of $u_1, u_2$ is  
\[ \begin{cases} 
  \dot{u}_1 = \frac{u_1}{u_1 + u_2} F(u_1 + u_2) \\
  \dot{u}_2 = \frac{u_2}{u_1 + u_2} F(u_1 + u_2).
\end{cases} \]  
(4)
Indeed, adding both equations, we see that the sum \( u = u_1 + u_2 \) satisfies (2). Moreover,
\[
u_1/u_2 = \text{const.}
\]
so that (4) is the required dynamical system. Obviously, the dynamics is along the rays \( u_1/u_2 = \text{const} \). An equilibrium \( u = u_c \) of the initial equation implies the segment \( u_1 + u_2 = u_c \) of equilibria of the split system. It is evident that this situation is not structurally stable, so that a small perturbation of the split system usually implies a collapse of this pattern, mostly the condensation into one or several equilibria, either on the boundaries or inside the domain.

Starting from (1), the splitting of the prey into two indiscriminated \( x = x_1 + x_2 \) ones gives:
\[
\begin{align*}
x'_1 &= b_1x_1 \left(1 - \frac{(x_1 + \delta x_2)}{p_1}\right) \\
-d_1z_1 \tanh\left(\frac{a_{11}x_1 + a_{12}x_2}{d_1}\right) \\
-d_2z_2 \tanh\left(\frac{a_{21}x_1 + a_{22}x_2}{d_2}\right) \\
x'_2 &= b_2x_2 \left(1 - \frac{(x_2 + \delta x_1)}{p_2}\right) \\
-d_1z_1 \tanh\left(\frac{a_{11}x_1 + a_{12}x_2}{d_1}\right) \\
-d_2z_2 \tanh\left(\frac{a_{21}x_1 + a_{22}x_2}{d_2}\right) \\
z'_1 &= z_1 \left(-c_1 + d_1 \tanh\left(\frac{a_{11}x_1 + a_{12}x_2}{d_1}\right)\right) \\
z'_2 &= z_2 \left(-c_2 + d_2 \tanh\left(\frac{a_{21}x_1 + a_{22}x_2}{d_2}\right)\right)
\end{align*}
\]

with \( b_1 = b_2 = b, \delta = 1, p_1 = p_2 = p, a_{11} = a_{12} = a_1, a_{21} = a_{22} = a_2 \).

Clearly, the dynamics is along the hyperplanes \( x_1/x_2 = \text{const.} \) and \( x_1 + x_2, z_1, z_2 \) satisfy (1) and displays the limit cycle of Figure 2. This system has a one-parameter family of cycles on these hyperplanes, forming a cylinder with generators parallel to the direction \((1, -1, 0, 0)\). Once again, this pattern is not structurally stable, and a small perturbation of it generically leads to its collapse, mostly the condensation into one or several stable cycles, either on the boundaries or inside the domain.

We then make a perturbation of this system. Instead of taking the above mentioned values of the parameters, we take the next ones, implying some differences between the two preys:
\[
\begin{align*}
\delta &= 0.5, \\
a_{11} &= 1.2, a_{12} = 0.9, a_{21} = 0.7, a_{22} = 1, \\
b_1 &= 1.2, b_2 = 1 \\
c_1 &= 0.55, c_2 = 0.7 \\
d_1 &= 1, d_2 = 1.7 \\
p_1 &= 2.8, p_2 = 5
\end{align*}
\]

This amounts to a somewhat important perturbation with respect to the mere splitting of the prey. In particular, the equilibrium populations of the two preys (with their respective resources), \( p_1 \) and \( p_2 \) are very different. Moreover, the vulnerabilities \( a_{11}, a_{12}, a_{21}, a_{22} \) are also different. Perhaps more important, the parameter \( \delta \), which describes the interdependence of the two preys with respect to their resources, is 0.5, half of the value for indiscriminated preys.

It is not hard to check that this system has no equilibrium point with strictly positive population of each species. Indeed, the equilibria are the solutions of the (algebraic) system obtained equating to zero the right sides of (6), i.e. (after
The two last equations give the two terms in \( \tanh \) and their arguments as functions of the parameters; then replacing this in the two first equations, the system becomes linear, so that (out of the coordinate planes) there is only one solution. Its computation (with the parameters (7) gives values not all positive, hence proving there is no equilibrium with strictly positive population of each species.

It then appears that there is a stable cycle (figure 5). There is computational evidence that this cycle is attained from almost any initial position, i.e. starting from any point with the exception of the coordinate hyperplanes (and certainly a zero-measure internal set issued from the splitting and perturbation of the heteroclinic orbit of the stem system (6). To check this, one may for instance proceed as follows. Taking initial values with \( x_1 = 0 \), we obviously obtain the corresponding solution in this invariant hyperplane of the stem system (with the appropriate values of the parameters), converging to a three-dimensional cycle. We then take an initial position with a very small value of \( x_1 \) and values of \( x_2, z_1, z_2 \) nearby the previous cycle, and it appears that the solution quickly takes off \( x_1 = 0 \) and tends to the four-dimensional stable cycle of figure 5. This amounts to saying that the three-dimensional cycle in the hyperplane \( x_1 = 0 \) is an attractor only in its invariant plane, but it is transversally unstable. The same holds true for \( x_2 = 0 \).
Otherwise, it is not easy to see what becomes, after splitting and an arbitrary perturbation, the heteroclinic orbit of the stem system. The sole splitting is trivial: each one of the equilibria of the stem system becomes a segment of equilibria, and there is a family of heteroclinic orbits in the planes $x_1/x_2 = \text{const.}$ binding them. But the perturbation seems very difficult to catch in dimension four. There is only computational evidence that the exceptional points not belonging to the attraction basin of the four-dimensional cycle (which certainly exist according to the topological argument) form a set with small measure (i.e. are impossible to find by numerical sampling).

We are here in a case where the definition of persistence is by no means trivial: there is evidence of persistence of the four species starting from any initial state, which is topologically impossible as there is no interior equilibrium point. Obviously there is an exceptional set with very small measure, issued from the heteroclinic orbit of the stem system, perfectly negligible in practice.

It should be emphasized that the previous assertions are only concerned with the specific values of the parameters (7). Obviously, other very different patterns may appear under other perturbations of the splitting. Taking the new values (note in particular the drastic difference between the equilibrium populations $p_1$ and $p_2$):

\[
\begin{align*}
\delta &= 0.4, \\
a_{11} &= 1.5, a_{12} = 0.6, a_{21} = 0.6, a_{22} = 0.6, \\
b_1 &= 1.2, b_2 = 0.6 \\
c_1 &= 0.7, c_2 = 1.3 \\
d_1 &= 1.3, d_2 = 2.6 \\
p_1 &= 0.666, p_2 = 4
\end{align*}
\]

the pattern is very interesting, there are two attraction basins: when starting from $(1.5,1,0.7,1.5)$, the solution converges towards the stable four-dimensional cycle shown in figure 6, whereas starting from $(1.5,0.6,0.6,0.8)$ the attractor is an equilibrium with extinction of $x_2$ and $z_1$ (see figure 7). The non-existence of equilibrium points with all strictly positive populations is proved as in the previous example.

4. **Another example in dimension three: One predator and two preys.** The objective of this section is to show that the very fact of having persistence (with the exception of a zero-measure set of forbidden initial positions) is very common, and holds true (within certain domains of the parameters) even in systems such as one predator $z$ and two preys $x_1$, $x_2$ (which are considered as very simple as not
concerned with the competitive exclusion principle). The model is easily derived from the previous one, namely:

\[
\begin{align*}
    x_1' &= b_1 x_1 \left( 1 - (x_1 + \delta x_2)/p_1 \right) - dz \tanh \left( \frac{a_1 x_1 + a_2 x_2}{d} \right) \frac{(a_1 x_1)}{a_1 x_1 + a_2 x_2} \\
    x_2' &= b_2 x_2 \left( 1 - (x_2 + \delta x_1)/p_2 \right) - dz \tanh \left( \frac{a_1 x_1 + a_2 x_2}{d} \right) \frac{(a_2 x_2)}{a_1 x_1 + a_2 x_2} \\
    z' &= z \left( -c + d \tanh \left( \frac{a_1 x_1 + a_2 x_2}{d} \right) \right)
\end{align*}
\]  

(10)

Taking for instance the values of the parameters $b_1 = 1.0$, $b_2 = 0.9$, $d = 1$, $c = 0.65$, $p_1 = 4.0$, $p_2 = 5.0$, $a_1 = 1.0$, $a_2 = 1.05$, it appears that for $\delta$ in the interval $(0.39, 0.82)$, there is a cyclic attractor, whereas there is no equilibrium with positive values of the three populations (this last point is proved as in the two previous sections). Figures 8 and 9 are plots of the limit cycle and of the corresponding periodic solution for $\delta = 0.6$. 

**Figure 7.** Plot of the solution of system (6) with the parameters (9) starting from the point $(1.5, 0.6, 0.6, 0.8)$: there is a stable equilibrium with extinction of $x_2$ and $z_1$.

**Figure 8.** Plot of the limit cycle of system (10) (see text for the values of the parameters) concerned with the competitive exclusion principle). The model is easily derived from the previous one, namely:
5. **Conclusion.** We presented a large class of examples of systems in biological dynamics having an attractor but not an equilibrium point at the interior of the domain of variables. Instead, in these examples, there is a heteroclinic orbit binding two equilibria on the boundaries of the domain, which obviously is not in the attraction basin of the attractor, as it leads towards a point on the boundary. This is certainly incompatible with an attraction basin homeomorphic to a ball, and then with certain definitions of persistence of species (see for instance [2] chapter 13, [3], which (roughly speaking) is understood in the sense of persistence starting from any initial position with strictly positive populations (this domain, after exclusion of a neighbourhood of infinity is homeomorphic to a ball). The definition of persistence of [15] is more general, as it is concerned not with the population themselves, but with a function \( \rho \) of them; theoretically, this function may be taken vanishing on a part of the domain (a heteroclinic orbit, for instance) but this needs the explicit knowledge of the “forbidden” region, so that the practical examples are classical, concerning the populations or a part of them. Coming back to our examples, it is clear that the exclusion of the heteroclinic orbit does not matter in practice, as it is of zero measure. In our opinion, this point is interesting as some of the examples contradict the competitive exclusion principle (which is obviously contoversed, both in practice and theory: their proofs only hold in a very elementary, mostly linear framework, and there is experimental evidence of non-exclusion (see for instance [6]).

On the other hand, there are definitions of permanence that are not concerned with the attraction basin (see essentially [8]); they ammount more or less to the existence of an attractor, not necessarily unique, with all the populations positive. This is obviously compatible with the existence of other attractors on the boundaries, with basins overlapping the region with all positive populations. This situation amounts in practice to some kind of conditional persistence of the species: persistence or not depends on the initial populations. In this context, the concept of persistence is not essentially different from the mere existence of a (non necessarily global) attractor. It should be worth mentioning in this context the “principle of the torus” used in [10] for the existence of a stable cycle in problems of electromagnetic oscillations.

It should be emphasized that most of the examples presented here have no equilibrium point in the interior of the domain; they then have a topological structure.
somewhat different of that of usual two-dimensional examples. For this reason, it seems useful to give an “artist view” of the basic structure of an orbit approaching a limit cycle turning around. Figure 10 is such an “artist view” in the case when the period of the “turning around” is smaller than the period of the limit cycle (the orbit turns around the cycle several times per one turn of the cycle)). An analogous figure in the opposite case when the period of the “turning around” is larger than the period of the limit cycle appears in Figure 11; it is much less clear than the previous one, whereas the structure is the same. Obviously, in practice, orbits do not present in the standard form of the “artist view”, but rather under a diffeomorphism. Figure 12 is a plot of such a deformation of Figure 11: without surprise, it is by no means clear, but it is under this aspect that the phenomenon appears in practical numerical situations. Otherwise, when visualising the solutions as functions of time, the presence of a periodic attractor is apparent, not the structure of the approaching transient.

Appendix. The predation models. Our basic model of predation for one prey $x$ and one predator $z$ is a variant of the Rosenzweig - MacArthur model:

$$
\begin{align*}
\dot{x} &= bx(1 - x/p) - zdTanh(ax/d) \\
\dot{z} &= z(-c + dTanh(ax/d))
\end{align*}
$$

(11)

which may be understood as follows. In the absence of the predator $z$, the population of the preys $x$ is submitted to a “logistic equation” with natural growth $b$ and equilibrium population (with its own ressources) $p$. In the absence of preys, the population of predators $z$ decays at the ratio $c$. The term of interaction $zdTanh(ax/d)$ accounts for the quantity of preys consumed per unit of time; it is proportional to the population of predators. Each predator (each individual) eats (per unit of time) a quantity of preys which is proportional to the number of preys (the coefficient of proportionality is $a$) when the number of preys is small. But when the preys are
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Figure 11. Artist view of an orbit approaching a limit cycle turning around in the case when the period of the “turning around” is larger than the period of the limit cycle.

Figure 12. The same orbit of Fig 11 after a diffeomorphism.

abundant, this number remains lower than an upper bound \(d\) (the satiety of the predator). Indeed, the function \(dTanh(ax/d)\) describes a transition between \(ax\) for \(x\) small and \(d\) for \(x\) large. We note that this term of interaction is the same in the two equations (up to the signs, positive for the predators and negative for the preys); this is general, provided that the units for counting the number of individuals are such that a unit of preys is transformed in a unit of predators.

In theoretical ecology, it is more traditional to use the Monod function \(\mu(x) = \frac{\mu_{max}x}{k+x}\) instead of the function \(dTanh(ax/d)\). As explained above, the qualitative properties are essentially the same and our choice here was motivated by simplifications of numerical simulations.
It should be noticed that taking $b$ and $p$ equal to $+\infty$, (11) becomes the classical Lotka - Volterra model. With respect to this one, the current model (11) incorporates a finite stable equilibrium of the population of preys (instead of infinity, so a disadvantage for the preys) and an upper bound of the quantity of preys eaten per capita by the predators (instead of infinity, so a disadvantage for the predators).

These disadvantages are nonlinear and of different nature, giving a diversity of patterns according to the values of the parameters. It is interesting to follow the evolution of this pattern as a function of $a$ (the vulnerability of the preys). For $dTanh(ap/d) < c$, the predation is not viable (the predation process is unable to balance the natural rate of decay of the population of predators). Increasing $a$ implies viability of the process, which first gives a stable equilibrium with positive values of the two populations. A further increase of $a$ gives a Poincaré - Andronov - Hopf bifurcation, the equilibrium becomes unstable and the stability is transferred to a periodic cycle.

Obviously, the case of two predators and one prey (1) follows from (11) as the two predators are independent of each other.

The case of two preys was derived in sections 3 and 4 by a technique of splitting and perturbation, but it may be derived directly as follows.

Each predator (each individual) eats (per unit of time) a quantity of each species of preys which is proportional to the number of its individuals (the coefficients of proportionality are $a_1$ and $a_2$, which may be assimilated to the respective vulnerabilities) when the number of preys is small. But when the preys are abundant, this total quantity remains lower than an upper bound $d$ (the satiety of the predator, which depends on the total quantity of preys available, not of each one separately). This gives a term of the form $dTanh((a_1x_1 + a_2x_2)/d)$. This function describes a transition between $a_1x_1 + a_2x_2$ for $a_1x_1 + a_2x_2$ small and $d$ for $a_1x_1 + a_2x_2$ large. This total quantity of eaten preys is clearly shared between the two preys proportionally to the populations, ponderated by the corresponding vulnerabilities, i. e.

$$\begin{cases} 
  dTanh((a_1x_1 + a_2x_2)/d) & a_1x_1/a_1x_1 + a_2x_2 \\
  dTanh((a_1x_1 + a_2x_2)/d) & a_1x_1/a_1x_1 + a_2x_2 
\end{cases}$$

We note that the first one (for instance) describes a transition between $a_1x_1$ for $a_1x_1 + a_2x_2$ small and $d$ for $a_1x_1 + a_2x_2$ large. These are the corresponding terms in the equations describing the evolutions of $x_1$ and $x_2$. Moreover, in the absence of predators, in the case of two preys, the terms of natural growth up to the population $p$ of equilibrium with the ressources (logistic terms) take the form $b_1x_1(1 - (x_1 + \delta x_2)/p)$ and $b_2x_2(1 - (x_2 + \delta x_1)/p)$ where $\delta$ denotes a coefficient of interaction between the two preys concerning their ressources. Completely independent preys, rabbits and truits for instance, amounts to $\delta = 0$, whereas two races of rabbits corresponds to $\delta = 1$.

The method of splitting (without perturbation) used in the previous sections gives evidently $\delta = 1$. On the other hand, it should be noted that when $\delta < 1$ (which amounts to partial independence), two different equilibrium populations $p_1$ and $p_2$ may be taken into account.

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