ON PERSISTENCE AND INVADING
SPECIES IN ECOLOGICAL DYNAMICS

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Abstract. The general problem of persistence of species, amounts to define interactions between them ensuring the survival of all the species initially present in the system. It appears that several relevant persistence schemes induce "forbidden sets" of zero measure for topological reasons. These peculiarities (without practical consequences) are nevertheless not consistent with certain mathematical definitions of persistence, which are too much restrictive. We come back to definitions of McGehee – Armstrong and their celebrated counter-example to the so-called "competitive exclusion principle". We develop these concepts in relation with invasion properties of the species in a rather practical and computational framework. Several examples of communities exhibiting persistence without internal rest point (which necessarily exists according to strict persistence definitions) are given, with explicit description of the attractors, forbidden sets and invasion properties. Mechanisms of contamination of these properties (based on elementary cartesian product and structural stability) are given, showing the widespreading nature of these schemes.

1. Introduction

The problem of persistence of species in ecological dynamics amounts to define interactions between several species and their resources ensuring the survival of all the species. There are many different precise definitions of such a general concept (see for instance [6] (in particular chapters 13 and 16), [10], [22], the review paper [9] and the book [23], as well as [14] for the ecological context), mostly concerning the very definition of "extinction", i. e. the proper definition of convergence to zero. Historically, the elaboration of such definitions was linked with the discovery of examples of persistence or extinction, so that this is a naturally open question (see the review paper [9] in this connection).

One of the main features in this context is the very controversial "Competitive exclusion principle", according to which two different predators cannot subsist on the same prey. Although the first theoretical results in this connection go back to Volterra [25], the principle was theorized by Gause [4] 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) and of certain experimental (not

general) results. 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 very remarkable and celebrated mathematical paper of McGehee and Armstrong [15], where was proved the existence of an attractor involving both predators. Unfortunately, the proof is more involved, and the attractor and the phase portrait were not very explicit. The next year appeared two papers [7], [8]) with more explicit description and computations on this kind of solutions, and the falsehood of the exclusion principle seemed proven. Moreover, slow-fast asymptotic techniques allowed a further study of the problem under the restrictive assumption of a fast dynamics of the preys with respect to the predators one ([17] and [24])).

Nevertheless, this kind of solution induces topological properties of the attractor and of its attraction basin (which must contain exceptional sets with zero measure not going to the attractor) that are not consistent with very strict and global definitions of persistence (in particular that of [6], and there was a progressive marginalization and oversight of these striking results, so that, for instance, in 2012, [1] considers the principle true (although citing [15]), whereas other authors ([13]) rather think that it is false.

One of the key points in this concern is that when persistence is understood in the sense of convergence towards a bounded attractor from any initial point, one reduces (after some technical handling to avoid neighborhoods 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 [6],). This argument does obviously not hold when persistence only takes place almost everywhere. Note also that persistence according to [6] excludes heteroclinic orbits (see hypothesis H2 of p. 211).

In recent times, explicit models (with very natural structure in biological dynamics) of the two-predator problem, allowed computations and visualization of the attractor [12], [20], [21]. The attractor is merely a periodic cycle, but the main novelty was the explicit visualization of the topological structure of the attraction basin, which is consistent with the non-existence of rest points with non-vanishing populations. Such a situation is classically impossible in two-dimensional patterns by elementary index theory, whereas it is possible in dimension $n > 2$. One of the possible topological patterns may be roughly described by saying that the cycle turns around an axis that is in movement along itself; the axis is an exceptional set (not belonging to the attraction basin) which is sent to the boundary (then violating strict persistence). Such a pattern will be described in Sect 5.

In [20], [21] we exhibited a number of other examples of systems with an attractor and no internal rest point in ecological dynamics (for instance certain cases of the so-called "stabilization by predation" and of a predator with two preys), as well as the corresponding "normal forms" (i.e. model systems allowing explicit computation and description of the phase portrait). The main feature of all of them is the presence of an attractor such that the attraction basin lies around an exceptional set of zero measure which is sent to the boundary. All these situations are examples of systems (not

necessarily in biological dynamics) enjoying endogenous oscillations without interior rest point. In evolution theory, they are examples of pure ESS (Evolutionary Stable Strategies).

The objective of this paper is first to come back to the general definitions and ideas of McGeheee-Amstrong on attractors and persistence, developing them in an explicit way accessible to people (not necessarily professional mathematicians) working in applications of dynamical systems to biological dynamics, mainly by computational methods. In particular, the concept of persistence only makes sense when considering the corresponding attraction basins and the associated invasion properties of the various species from the vicinity of certain domains of the boundary. Both attraction basins and invasion properties usually exclude "forbidden sets", which are often of zero measure, then without practical influence. Second, we develop various examples (in ecological dynamics) of systems with an attractor and no internal rest point. In particular, we revisit the "competitive exclusion principle" from this new (old in fact!) viewpoint exhibiting explicit counter-examples (some new, other taken from previous papers). Third, to show the very wide field of persistent systems without internal rest point, we state the property of "contamination" from a system to others by cartesian product and perturbation (in a classical framework of structural stability), so that we may construct as many of such systems as we wish from a unique example.

In order to improve the practical impact in a computational context, most of the mechanisms of persistence are exposed merely by a numerical example, allowing verification with a personal computer (and a standard Mathematica or Matlab software). Nevertheless, the mechanisms involved in the models are explicit; moreover, all examples are in an obvious structurally stable framework, allowing small (and often large) perturbations of the parameters and other items. In addition, invasion properties of the species is often mentioned allowing verification.

The paper is organized as follows:

Section 2 is taken from pages 34–37 of [15], with the main definitions and general frame of persistence (attractors and attractor blocks).

In Section 3, we give a collection of explanations, remarks and other complements allowing understanding of the previous section by non-professional mathematicians. In particular, the structural stability of attractor blocks, which play a key role (often instead of the attractors themselves) is emphasized.

In Sect 4 we develop the concept of invasion of a species x_n. Special attention is payed to the attraction basins. It is shown that computational checking of the invasion may be limited to the vicinity of the attractor of the dynamics on the manifold $x_n = 0$, as it implies invasion from the rest of the basin (allowing nevertheless non-invasion from a "forbidden set" out of the basin).

Section 5 contains a very elementary and explicit example of system with an attractor and no interior rest point. The "forbidden set" and the invasions are apparent.

The so-called "competitive exclusion principle" is revisited in Section 6, where (not new) counter-examples are given, as well as the invasion properties of the two predators. In Section 7 we give new examples of very plausible communities of three species exhibiting persistence without internal rest point.

Section 8 contains examples in this context of systems in dimension four obtained

by interaction between two subsystems of two species.

In Section 9 we show how a system contaminates by small interaction the property of having persistence without internal rest point. We give an example of synchronisation in this context.

Final comments on persistence and endogenous oscillations are in the conclusion, Section 10.

2. Basic definitions and topological framework according to McGehee-Armstrong

This section is practically a copy of parts of [15], p. 34–37.

The set of real numbers is denoted R. By a *flow* on a locally compact metric space X we mean a continuous map $\phi: \quad X \times R \longmapsto X$ such that $\phi(x,0) = x$ and $\phi(\phi(x,t_1),t_2) = \phi(x,t_1+t_2)$. For $K \subset X$ and $I \subset R$, we write:

$$\phi(K,I) = \{\phi(x,t) : x \in K, t \in I\} \tag{2.1}$$

A point $x \in X$ will be called a *rest point* if $\phi(x,R) = x$. For flows generated by vector fields, a rest point corresponds to a *critical point*, or *zero*, of the vector field. In such cases, the rest point x will be called *degenerate* if the jacobian matrix of the vector field at x has a zero eigenvalue.

If $K \subset X$ satisfies $\phi(K,R) = K$, then K will be called *invariant*. Note that a rest point is an invariant set. For $U \subset X$ we define the *omega-limit set* of U as

$$\omega(U) = \bigcap\{cl(\phi(U,[t,\infty))) : t > 0\} \tag{2.2}$$

here cl denotes topological closure.

DEFINITION 1. A compact invariant set K will be called an attractor if there is an open $U \supset K$ such that $\omega(U) = K$. By an *attractor block B* we mean a compact set with nonempty interior such that, for each $x \in \partial B$, $\phi(x,(0,\infty)) \in int(B)$.

Here, ∂ denotes the boundary and *int* denotes the interior. It is a standard result that every attractor block contains an attractor and that every attractor is the maximal invariant set inside some attractor block (see refs 1, 2, 12 of [15]). For smooth flows an attractor block can be chosen with smooth boundary and with ϕ transverse to the boundary (see ref 2 of [15]).

A *repeller* is an attractor for the time reverse flow $\phi(x,-t)$. Similarly, a repeller block is an attractor block for the reverse flow.

The concept of an attractor block is particularly well suited for our purposes because it combines two different notions of stability. First, the attractor itself is "asymptotically stable" in the sense that orbits starting close to it approach it asymptotically. Second, the attractor block is "stable under perturbation" in the sense that nearby flows have nearby attractor blocks. Indeed, for smooth flows, an attractor block with ϕ transverse to its boundary remains an attractor block under C^1 perturbations. The attractor

itself may change considerably after a perturbation, but the existence of an attractor remains.

We now turn to the general n-species model

$$\dot{x}_i = f_i(x_1,\ldots,x_n) = x_i g_i(x_1,\ldots,x_n) \quad i = 1,\ldots,n. \tag{2.3}$$

Here $x_i \geqslant 0$ is the population density and $g_i(x_1,\ldots,x_n)$ is the specific grow rate of species i. This system determines a vector field f (and the reduced vector field g) on the closed positive cone

$$E^n = \{(x_1,\ldots,x_n) \in R^n : x_i \geqslant 0, \quad (i = 1,\ldots,n).\} \tag{2.4}$$

All functions in this paper will be assumed infinitely differentiable. A function $f = (f_1,\ldots,x_n) = (x_1 g_1,\ldots,x_n g_n)$ can be thought as the n-species ecological community whose dynamics are given by equations (2.3).

We denote by $\phi(x,t)$ the solution of (2.3) starting at $x \in E^n$ at time $t = 0$. Standard theorems of differential equations imply that ϕ satisfies all the properties of a flow except possibly that solutions may not be defined for all time. This difficulty may be overcome in several ways. In order to streamline our presentation, we choose the easiest way and simply assume that ϕ is a flow. This assumption places restrictions only on the behavior of f near infinity. Such assumptions are of no biological importance.

We are now ready to define "persistence" and "exclusion", at least in the context of equation (2.3).

DEFINITION 2. An ecological community f (or g) will be called *persistent* if ϕ has an attractor in $int(E^n)$. We shall say that f exhibits *exclusion* if it is not persistent.

THEOREM 1. *Suppose that $K \subset int(E^n)$ is an attractor for ϕ and that there is no rest point in $int(E^n)$. Then the Euler characteristic of K is 0.*

The attractor K is not necessarily a manifold. However, it can always be surrounded by an attractor block which is a manifold. We define the Euler characteristic of K to be the Euler characteristic of B, where B is an attractor block containing K as the maximal invariant set in B. This number is well defined and reduces to the ordinary Euler characteristic of K if K is a manifold (see ref 2 of [15]]. The theorem then follows, as $-f$ is a vector field not vanishing on B and outwards transversal on its boundary.

3. Complements and remarks

The main information of the previous section is that persistence is not impossible when there are no rest points in $int(E^n)$, (and persistence will be explicitly proved by various examples). When the dimension of the space n is at least 3, this only implies that the attractors (or the attractor blocks containing them) have Euler characteristic 0. These attractor blocks (and the corresponding attraction basins) are certainly not

homeomorphic to balls, they are traversed by exceptional regions (usually of zero mea-
sure) mostly formed by heteroclinic orbits or families of them, which do not lead to
the attractor, but to the boundaries of E^n. Another important issue is that (often en-
tangled) attractors are not mostly handled themselves, but by attractor blocks around
them, which are manifolds with boundary. Moreover, attractors are not necessarily
unique, and the corresponding attraction basins should be taken in consideration. In
this section we give explanations to understand and handle these issues.

Let us first recall some general features on topology of manifolds, which are
widely known for manifolds without boundary, but a little less for manifolds with
boundary, which are mainly concerned here because of the role of attractor blocks.

Manifolds without boundary have an Euler characteristic, a number χ which is a
topological invariant of the manifold and is defined as follows. Let v be a vector field
defined on the manifold. The rest points of v are in finite number. Each rest point has
an index, equal to $+1$ or -1 according to the sign ($+$ or $-$) of the determinant of the
matrix A which linearizes the vector field at the rest point. This amounts to saying that
the index is $+1$ (resp. -1) when the matrix A preserves (resp. reverse) the orientation
of the space. Obviously, the previous assertion only makes sense when there are no
degenerate rest points, but this case is (very technically) avoided using the property that
a small perturbation of v eliminates the degeneration. The celebrated Poincaré-Hopf
theorem asserts that the sum of the indices of the rest points is independent of the vector
field, then a topological property of the manifold, called its Euler characteristic χ.

It follows that, in order to compute the Euler characteristic of manifold, it suffices
to have a vector field on it, and to perform the computation on it. Moreover, if there
exists a vector field without rest point, χ is equal to 0, and any other vector field will
have rest points with "balanced" indices (i. e., with sum 0).

The Poincaré-Hopf theorem may appear at first glance as a little magic, but in fact,
it is only concerned with changes of the orientations of the local tangent space induced
by the vector field at the singularities. In fact, it furnishes a topological property of
the manifold from topological properties of the field and in particular it asserts that the
vector fields on the manifold cannot have arbitrary singularities.

The elementary example of (smooth) vectors fields on a cycle (torus of dimension
1, noted T^1), which is easily handled using either a drawing or evident properties of
periodic functions, shows that the Euler characteristic of a cycle is 0, and that any rest
point preserving (resp., inverting) the local orientation must be balanced by another one
inverting (resp. preserving) it. The tore of dimension n, noted T^n has also $\chi = 0$; you
may see T^2 either as a manifold in itself or as surface in R^3 (the surface of a tire).

The point in the present paper is that all the above properties of manifolds without
boundary also hold true for manifolds with boundary, under the condition that the vector
fields are transversally outgoing on the boundary. Proofs and general theory may be
seen for instance in [16] chapter 6, in particular pages 35–37]. The outgoing condition
is chosen by convention, and this is the reason why we usually deal with the vector field
$-f$ instead of f itself in attractor blocks.

Usual examples are the solid torus (the interior of a tire) and the ball, which have
$\chi = 0$ and $\chi = 1$ respectively.

REMARK 1. It may happen that an attractor block contains several attractors, and several attractor blocks. Let us consider, for instance the equation $\dot{x} = -x(1-x)(1+x)$ on R. there are three rest points, -1 and $+1$ are attractors and 0 is a repeller. We may take as attractor blocks small closed segments containing -1 and $+1$, but a large segment as $[-2, +2]$ is also an attractor block, and its maximal attractor is the set of the two attractors -1 and $+1$. Note also that the attraction basin of an attractor block may differ from that of its maximal attractor. Indeed, in the previous example, the attraction basin of the large segment $[-2, +2]$ is the whole line, but the attraction basin of its maximal attractor is the line with the exception of the origin. In practice, we shall mainly deal with attractor blocks and their attraction basins.

REMARK 2. The existence of an attractor A contained in $int(E^n)$ (i. e., persistence) is equivalent to the existence of an attractor block contained in $int(E^n)$. Indeed, as A is compact, it remains at distance > 0 from the boundary, and it has an attractor block K, which cannot touch the boundary, otherwise the solution issued from such a contact point (which remain on the boundary) should not satisfy the condition of going inside K.

We are now in position to understand (and almost prove) Theorem 1. Indeed, if K is an attractor in $int(E^n)$, let S be an attractor block contained in $int(E^n)$ and having K as maximal attractor (i. e. not containing other attractors). Then S is a manifold with boundary, and $-f$ is a vector field transverse and outgoing on the boundary; as there is no rest point in S, the Euler characteristic of S is $\chi(S) = 0$. This number is independent of the choice of S, provided of course that it contains K and no other attractor, so that it is well defined by K, it is a number associated to K, which (by definition) is called the Euler characteristic $\chi(K)$ of K (which is not a manifold). Note, by the way, that the hypothesis that there is no rest point in $int(E^n)$ may be replaced by the non-existence of rest point in a neighborhood of K. It also appears that the (somewhat entangled) property that $\chi(K) = 0$ amounts merely to $\chi(S) = 0$ for any attractor block S having K as maximal attractor.

Another point which deserves explanation is the concept of smooth boundary of a compact with non empty interior. When the compact set K has a non-empty intersection with ∂E^n (i. e. when it contains points of the coordinate planes or edges), only piecewise smoothness is supposed. More precisely, it suffices to assume that the domain is the intersection with E^n of a compact of R^n with smooth boundary. This is allowed by the special form of the field f, which has the boundary as invariant manifold. Note that, without this remark, only boundaries tangent to the coordinate planes and edges should be allowed.

In the previous section it was mentioned the fact that, provided the vector field is smooth, the attractor blocks may be taken themselves smooth. The construction of attracting blocks (and even the larger concept of isolating blocks) may be seen in [2] (in particular Sect 5, p. 53–60). This construction holds inside any open set U of the definition of the attractor. It then follows that, if a (non-smooth) attractor block K is known, it is possible to construct a smooth one $\tilde{K}$ inside K.

Moreover, as the attractors are not necessarily unique and it may happen that there

is one in $int(E^n)$ and others not, an essential complement to the previous considerations is the definition of the attraction basins.

DEFINITION 3. The attaction basin of an attractor A is the maximal open set satisfying $U \supset A$ such that $\omega(U) = A$.

Nevertheless, as we shall mainly deal with attractor blocks, it is even more useful to define their attraction basin:

DEFINITION 4. Let K be an attractor block. Its attraction basin is the set of points x such that $\phi(x,t)$ is in K for sufficiently large t. Obviously, this amounts to the union of the complete orbits (i. e. for $t \in R$) of the points of K. It is also equivalent to the union of K and the negative half-orbits issued from the boundary of K.

4. Invading species

One of the main applications of the concept of persistence is the study of invading species. Roughly speaking, a species is said invading in an ecological pattern if a small insemination of it leads to a new pattern involving the new species. In our framework, this involves the attraction basin of the new attractor and its proximity with the subspace where the new species vanishes. Moreover (specially if there are several attractors) a species may be invading from a region and not from another.

We note

$$x = (\tilde{x}, x_n) \tag{4.1}$$

Obviously, the system on E^n induces automatically a dynamics on E^{n-1} of the $\tilde{x}$ components, which is an invariant manifold. For the same reason, if there is an attractor (or an attractor block) A disjoint of E^{n-1}, its (open) attraction basin $B(A)$ is also disjoint of E^{n-1}. We then define:

DEFINITION 5. Let k be a compact in E^{n-1}. The species x_n is said to be uniformly invading from the vicinity of k if the system has an attractor (or an attractor block) A disjoint of E^{n-1} and there exists $\delta_k > 0$ such that $k \times (0, \delta_k)$ is contained in the attraction basin $B(A)$. Moreover, if σ is a set in E^{n-1} which is a union of compacts, the species x_n is said to be invading from the vicinity of σ if the system has an attractor (or an attractor block) A disjoint of E^{n-1} and x_n is uniformly invading from the vicinity of each compact (then allowing non-uniformity in δ).

It should be noticed that in the previous definition, the attractor A is not necessarily in the interior of E^n, it may happen that it be on a boundary disjoint of $x_n = 0$; in that case, the species x_n displaces others. For the same reason, a system with all the variables invading is not necessarily persistent. The next more strict definition is often useful:

DEFINITION 6. The slightly different concepts of "strictly uniform invading" and "strictly invading" species are defined as the non-strict ones replacing A disjoint of E^{n-1} by $A \subset int(E^n)$.

We are now developing the main property of invasion. It consists in the fact that, roughly speaking, as the dynamics for small x_n is close to a surface dynamics on E^{n-1}, invasion from the vicinity of the attractor of the dynamics on this surface implies invasion from the vicinity of the whole attraction basin of the surface dynamics. More precisely:

THEOREM 2. *In the dynamics on E^{n-1}, let a be an attractor block with smooth boundary, and k a compact contained in the attraction basin $B(a)$. Then, if x_n is uniformly invading (strictly or not) from the vicinity of a, it also does on the vicinity of k.*

LEMMA 1. *In the dynamics on E^{n-1}, the entry time of points in a is bounded on k.*

Proof. Under a local diffeomorphism, which preserves transversality, the boundary of a becomes $x_1 = 0$, and the time of entry t is given by the equation $\phi_1(x,t) = 0$. This equation defines localy t as a smooth function of x by the implicit function theorem, as, by transversality, $\partial \phi_1 / \partial t = f_1 \neq 0$. The entry time is then a well defined smooth function, so bounded on the compact k.   □

REMARK 3. The previous proof is general and works as well for the entry time from any compact in a smooth attractor block. Moreover, (joint to standard perturbation theory) it proves that the property "the compact K is in the attraction basin of a smooth attractor block A" is preserved by small perturbation of the vector field.

We are ready for the proof of Theorem 2.

Proof. Let δ_a be the δ involved in the definition of the invasion from the vicinity of a, and let T be a bound of the entry time from k into a. We consider the continuous mapping $x \mapsto \phi(x, 2T)$. It then suffices to prove that there exists $\delta_k > 0$ such that the mapping maps

$$k \times [0, \delta_k) \quad \mapsto \quad int(a) \times [0, \delta_a) \tag{4.2}$$

We note that the right hand side is an open set of the topology induced by the restriction to E^n (alternatively we may replace in the right hand side $[0, \delta_a)$ by the open set $(-\delta_a, \delta_a)$). Moreover, the mapping sends $k \times \{0\}$ (and so also does a neighborhood of it) into that open set. The conclusion then follows.   □

REMARK 4. As a consequence of the previous theorem, invasion is mainly ruled by the behavior of the vector field in the vicinity of the (even very small) attractor blocks of the dynamics on $x_n = 0$.

REMARK 5. It should be noticed that the very concept "invading" was not defined, but only invading from the vicinity of some set. Often in practice the set is obvious; moreover, according to Theorem 2, invasion of x_n may be understood from the vicinity of the attraction basin of the dynamics on $x_n = 0$, and there is ambiguity only in the case of several attractors.

In practical problems, the question of the structural stability of invasion from the vicinity of a compact k arises in a natural way. We shall prove such a property under suited hypotheses, usual in structural stability theory.

DEFINITION 7. A rest point is said to be hyperbolic when the eigenvalues of the matrix that linearizes the system at that point has no eigenvalues with vanishing real part. A cycle is said to be hyperbolic when the matrix that linearizes the (discrete) system at a Poincaré section has no eigenvalues with vanishing real part (this property is independent of the section).

REMARK 6. The classical construction of the stable and unstable manifolds takes a very simple form under the hypothesis of hyperbolicity, as the two manifolds are locally complementary. The local flow in a neighborhood of the point or cycle then takes the classical "hyperbolic form". In particular, with the sole exception of the stable manifold, each point goes out of the neighbourhood in sufficiently large positive time; this property will be a key point of the proof of the next stability theorem. See any classical treatise of ODE for these questions, for instance [5] sect. 3.3, Saddles for rest points in the plane, [3] sect. 2.4 for cycles.

THEOREM 3. *Let f be a vector field in E^n and a an attractor block of the dynamics on $x_n = 0$, and k a compact of $x_n = 0$ such that $k \supset a$. Let the maximal attractor of a be either a hyperbolic rest point or a hyperbolic cycle (note that then it is a rest point or a cycle of the whole dynamics on E^n as well).*

Then the property "x_n is invading from the vicinity of k" is preserved by small perturbation of the vector field.

Proof. We first note that it is sufficient to prove the invasion from the vicinity of a, or even from any other smaller smooth attractor block.

It follows from the hypotheses that the stable manifold of the attractor is $x_n = 0$, whereas the unstable manifold is (in the two cases of a point and a cycle) either a smooth curve transversal to $x_n = 0$ or a smooth two-dimensional manifold containing the cycle, transversal to $x_n = 0$ along the cycle. We then choose the smooth attractor block inside the neighborhood of the attractor mentioned in Remark 4.

Let ∂a be the boundary of a (in $x_n = 0$). The vector field f enters transversaly to it and has vanishing x_n component. Then, for sufficiently small δ, f enters transversaly to $\partial a \times [0, \delta]$ too. By Remark 6, all the points of $a \times (0, \delta]$ (note that $(0, \delta]$ is open on the left) go out of it in the future, and they go out necessarily by the upper face $a \times \{\delta\}$. We then note that all these properties are classically preserved under small perturbation of the field, so that, after small perturbation, all the points of $a \times (0, \delta]$ go in the future to $a \times \{\delta\}$; this is the key point of the proof, which allows to replace a non-compact domain by a compact one (note, nevertheless, that the previous times of displacement of the points are unbounded, but this is irrelevant). The ulterior movement of the points to a global smooth attractor block disjoint of $x_n = 0$ is trivial according to Remark 3, then achieving the proof.   □

5. A first example of system without interior equilibrium and a cyclic attractor

We are giving here a very simple (academic) example allowing explicit computation and understanding of the topological structure of attractors and invasions. This example will be developed in three versions; the first one is two-dimensional, very close to a predator-prey system, the second is three-dimensional; obtained from the previous one by revolution around an axis, and the third is a diffeomorphic deformation of the second.

We first consider the system

$$\begin{cases} \dot{r} = r(1 - r^2 - z) \\ \dot{z} = z(-c + r) \end{cases} \tag{5.1}$$

with $c = 0.4$, in the positive cone of the plane (r, z). It is easily seen that there is a unique interior rest point $(c, 1 - c^2)$ which is an attractor. The coordinate axes are invariant manifolds; there are two other equilibria, the origin $(0,0)$ and $(1,0)$, which are saddles. The global phase portrait is shown in Fig. 1. Note in particular that along the z-axis there is a dynamics towards the origin. It then appears that there is an attractor in $int(E^2)$, the attraction basin being the whole interior of E^2. Moreover, the species z is uniformly invading from the vicinity of any compact of the r axis, whereas r is uniformly invading from the vicinity of any compact of the z axis without the origin.
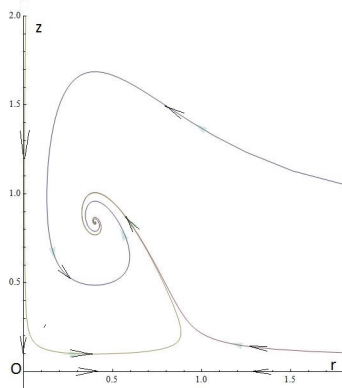

Figure 1: *Two orbits of system (7). The dynamics on the z axis is towards the origin.*

Moreover, we consider r and z as cylindrical coordinates, and we add a rotation with unit angular velocity, i. e. we add the equation $\dot{\theta} = 1$. We then have

$$\begin{cases} \dot{r} = r(1 - r^2 - z) \\ \dot{\theta} = 1 \\ \dot{z} = z(-c + r) \end{cases} \tag{5.2}$$

in the half space $z \geqslant 0$. This is equivalent to the system

$$\begin{cases} \dot{x} = -y + x(1 - x^2 - y^2 - z) \\ \dot{y} = x + y(1 - x^2 - y^2 - z) \\ \dot{z} = z(-c + r) \end{cases} \tag{5.3}$$

in the half space $z \geqslant 0$ of the cartesian frame (x, y, z). The interior equilibrium $(c, 1 - c^2)$ of (7) becomes the attractor cycle $r = 1 - c^2$, $z = c$, whereas the dynamics on the z axis is not modified (dynamics along the axis, towards the origin), Fig. 2. It may be said that the half-space turns around the axis z, which is itself in movement along itself towards the origin. This axis is then an exceptional set of zero measure which leads to the boundary, not to the global cyclic attractor. Moreover, the variable z is uniformly invading from the vicinity of any compact of the plane $z = 0$ without the origin.
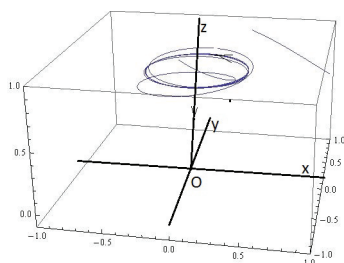
Figure 2: *An orbit and the limit (circular) cycle of system (9) in the half space $z \geqslant 0$ of R^3. The dynamics derives from that of Fig. 1 by rotation around the z axis with constant angular speed. The axis z is always an orbit going to the boundary $z = 0$.*

In order to have an explicit example for a system on the positive cone E^3 we then use the diffeomorphism

$$(x, y, z) \quad \longmapsto \quad (X = e^x, Y = e^y, Z = z). \tag{5.4}$$

The cycle is no longer a circle (it may be parametrized as $X = e^{c \cos(\theta)}$, $Y = e^{c \sin(\theta)}$, $z = 1 - c^2$) and the exceptional orbit becomes $X = 1$, $Y = 1$, $Z \in R_+$ (Fig. 3).
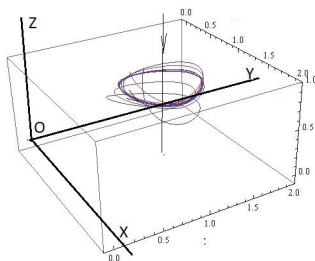

Figure 3: *The same as Fig. 2 under the diffeomorphism (10) in E^3. The attractor is no longer a circle. The straight line $X = Y = 1$ is always an orbit going to the boundary $Z = 0$*

The coordinate planes are invariant manifolds, indeed $\dot{X} = e^x \dot{x}$ tends to 0 as $x \to -\infty$, as the first factor is exponentially small and the second algebraically large. It should be nevertheless noted that it is not smooth in the sense of this article, as the derivative has a slight (logarithmic) singularity; it is obviously possible to avoid it by modifying the initial vector field in order to become bounded at infinity.

6. Two predators and one prey. Various counter-examples to the so-called exclusion principle

As we pointed out in the introduction, even longtime after the (entangled or not very explicit) papers [11], [15], [7], [8], the so called "competitive exclusion principle" was more or less admitted by a part of the scientific community, and a "proof" of it may be seen for instance in [1] sect 5.11, p. 217–218. In fact, their proof relies on the fact that, in their opinion, if the predator y_1 (resp. y_2) is a survivor, then y_1 (resp. y_2) is necessarily invading from the equilibrium of x and y_2 (resp. y_1); and they prove the impossibility of these simultaneous properties. In fact, as we shall show, the invasion of one of the predators takes place on the attractor of the other with the preys, which is a cycle, distinct of the equilibrium.

We consider the system

$$\begin{cases} \dot{x} = ax(1 - x/p) + y_1 b_1 Tanh(e_1 x/b_1) + y_2 b_2 Tanh(e_2 x/b_2) \\ \dot{y}_1 = y_1(-c_1 + b_1 Tanh(e_1 x/b_1)) \\ \dot{y}_2 = y_2(-c_2 + b_2 Tanh(e_2 x/b_2)) \end{cases} \quad (6.1)$$

for a prey x and two predators y_1, y_2. It is immediately seen that there is no interior equilibrium, i. e. a rest point (x^0, y_1^0, y_2^0), all different from 0. Indeed, the corresponding algebraic system has two equations with the unique unknown x^0.
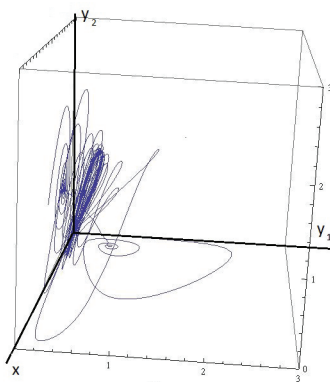

Figure 4: *The attractor of system (11) (parameters $a = 1$, $p = 4$, $b_1 = 1$, $b_2 = 2$, $c_1 = c_2 = 0.7$, $e_1 = 1.8$, $e_2 = 1$) and an orbit starting near the plane $y_1 = 0$ (see text).*

The values of the various parameters are $a = 1$, $p = 4$, $b_1 = 1$, $b_2 = 2$, $c_1 = c_2 = 0.7$, $e_1 = 1.8$, $e_2 = 1$, so that the predation of the y_1 is more efficient than the other ($e_1 > e_2$) but the y_2 have a larger bound of satiety ($b_2 > b_1$). It then appears a three-dimensional cyclic attractor (Fig. 4). The attractors of the surface dynamics on the planes $y_1 = 0$ and $y_2 = 0$ are a point and a cycle respectively; they are both stable in their planes and transversally unstable. The cycle on the plane x, y_1 obviously encloses a rest point, which is unstable in its plane (an unstable focus) but transversally stable. In the three-dimensional dynamics there is a heteroclinic orbit starting from the equilibrium on $y_1 = 0$ and finishing at the equilibrium on $y_2 = 0$; its shape is almost straight. The numerical experience of Figs. 4 and 5 was done starting close to the plane $y_1 = 0$ (from $(2, 0.000001, 1)$) in order to visualize these items. The solution is initially very close to the plane $y_1 = 0$ and it spirals approaching the corresponding attractor point; as it is transversally unstable, the solution then runs close to the heteroclinic orbit approaching the equilibrium on the plane $y_2 = 0$. As this equilibrium is unstable in that plane, the solution then spirals dilatating and then approaches the cycle which is the attractor in that plane. But, approaching to it, as it is transversally unstable, the solution then takes off from the vicinity of the plane and goes towards the tree-dimensional cyclic attractor. Fig. 5 is a plot of y_1 and y_2 exhibiting these various phases, in particular the "exhange" of y_1 and y_2 along the heteroclicic orbit.
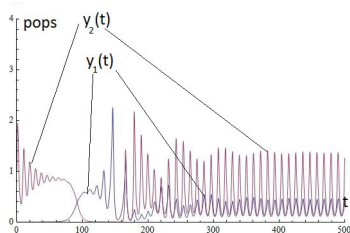

Figure 5: *Plot of $y_1(t)$ and $y_2(t)$ for the same solution. Note the exchange (from the vicinity of $x_1 = 0$ to that of $x_2 = 0$) when passing along the heteroclinic orbit.*

The basin of the attracting cycle is $int(E^3)$ without an exceptional set (the heteroclinic orbit binding the two equilibria on $y_1 = 0$ and $y_2 = 0$). The species y_1 is invading from the vicinity of $int(E^2)$ (in the plane $y_1 = 0$). But y_2 is only invading from the vicinity of $int(E^2)$ (in the plane $y_2 = 0$) without the rest point on $y_2 = 0$.

There are very many variants of this basic scheme. Here we have an example where the advantage of the efficiency of the y_1 is balanced by a greater mortality ratio. We take the same system (11) with the parameters $a = 1$, $p = 4$, $b_1 = b_2 = 1$, $c_1 = 0.60$, $c_2 = 0.55$, $e_1 = 1.5$, $e_2 = 1$. In this case there is again an attractor in $int(E^3)$, but the attractors on the faces $y_1 = 0$ and $y_2 = 0$ are both cycles. The three attractors are simultaneously represented on Fig. 6.

Otherwise, it is also possible to get explicit examples of two perfectly analogous predators with a prey provided that the terms $c_1 y_1$ and $c_2 y_2$ accounting for the natural decrease rates of the predators become nonlinear convex functions (the rate of natural deceases decreases with the size of the population). The fact that nonlinear terms inval-
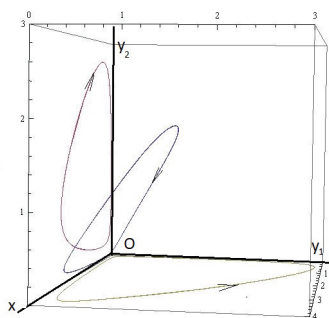
Figure 6: *System (11) with $a = 1$, $p = 4$, $b_1 = b_2 = 1$, $c_1 = 0.60$, $c_2 = 0.55$, $e_1 = 1.5$, $e_2 = 1$. Plot of the three-dimensional cyclic attractor and of the cyclic attractors in the faces $y_1 = 0$ and $y_2 = 0$.*

idate the competitive exclusion principle is known (see for instance [6] or [13]). As a matter of fact, the principle is invalidated by any change in system (11) destroying the peculiarity that the algebraic system for the internal equilibria has two equations with only one unknown; so that obvious modifications send the system into a more classical nonlinear framework. This we proceed to do in the next example, which also exhibits a cyclic attractor. But, because of the symmetry, the plane $y_1 = y_2$ is an invariant manifold, which contains the attractor; by classical index theory in that plane, it has an internal unstable rest point. So, this new counter-example to the exclusion is out of the main focus of this paper, as it satisfies strict persistence.

Specifically, we consider the system

$$\begin{cases} \dot{x} = ax(1 - x/p) + y_1 b_1 Tanh(e_1 x/b_1) + y_2 b_2 Tanh(e_2 x/b_2) \\ \dot{y}_1 = y_1(-c_1 + \delta e^{-\lambda y_1} + b_1 Tanh(e_1 x/b_1)) \\ \dot{y}_2 = y_2(-c_2 + \delta e^{-\lambda y_2} + b_2 Tanh(e_2 x/b_2)) \end{cases} \tag{6.2}$$
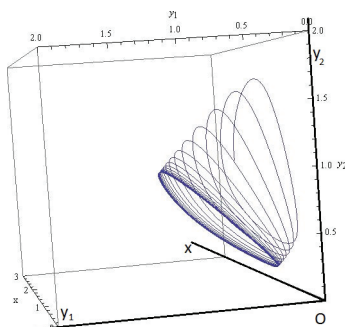

Figure 7: *An orbit and the cyclic attractor in the plane $y_1 = y_2$ for system (12).*

with the values of the parameters: $a = 1$, $p = 4$, $b_1 = b_2 = 1$, $c_1 = c_2 = 0.7$, $e_1 = e_2 = 1$, $\delta = 0.1$, $\lambda = 2$. The attractor is shown in Fig. 7. In addition, this effect of the new nonlinear terms also holds in the case when the attractor is a point instead of a cycle (for instance, taking $e_1 = e_2 = 0.75$ (instead of 1), the attractor becomes a point).

REMARK 7. The effect of the new nonlinear terms is easily understood using the "splitting" procedure (see [19] for the splitting-perturbation method). Indeed, in the case of symmetry in y_1, y_2 without the new terms, it is easily seen that the system is the splitting under $y = y_1 + y_2$ of an analogous system with only one predator y. Such a system has automatically a family of attractors in the family of planes $y_1/y_2 = const$; the extremities of the family being on the planes $y_1 = 0$ and $y_2 = 0$, which obviously have "neutral transversal stability". The new nonlinear terms do not result from a splitting. By comparing them with those obtained by a splitting, it is easily seen that they have a transversally destabilizing effect for $\delta > 0$ (and stabilizing for $\delta < 0$) on the cycles on the planes $y_1 = 0$ and $y_2 = 0$, so sending the attractor towards $int(E^3)$. The opposite holds for $\delta < 0$, which exhibits bi-stability (two three-dimensional attractors on the planes $y_1 = 0$ and $y_2 = 0$).

7. Other examples of persistent communities of three species without internal equilibrium

The examples in the previous section (system (11)) of persistence of two predators on one prey rely on the balance of an advantage and a disadvantage of the predation process itself along the cycle. But there are many other mechanisms of preservation using interactions (commensalism, symbiotic interactions...) between the predators. We are giving here two examples where one of the predators y_1 is less efficient than the other y_2, but it takes a demographic advantage of the presence of the y_2 (commensalism). The two examples differ by the expression (linear and nonlinear) of the commensalism term.

We consider the system

$$\begin{cases} \dot{x} = ax(1 - x/p) + y_1 b_1 Tanh(e_1 x/b_1) + y_2 b_2 Tanh(e_2 x/b_2) \\ \dot{y}_1 = y_1(-c_1 + b_1 Tanh(e_1 x/b_1)) + \varepsilon y_1 y_2 \\ \dot{y}_2 = y_2(-c_2 + b_2 Tanh(e_2 x/b_2)) \end{cases} \tag{7.1}$$

which only differs from (11) by the presence of the term $+\varepsilon y_1 y_2$ in the equation for $\dot{y}_1$. The values of the parameters are $a = 1$, $p = 4$, $b_1 = b_2 = 1$, $c_1 = c_2 = 0.75$, $e_1 = 0.6$, $e_2 = 1.1$, $\varepsilon = 0.2$. This system is persistent, with a cyclic attractor (Fig. 8). This sytem has no rest point in $int(E^3)$. This is easily seen as the algebraic system for the interior rest points reduces to a linear system with the solution $(0.88, -0.62, 1.32)$, then out of $int(E^3)$. The topological structure of the attraction basin and the invasion of the predators are the same as in Fig. 4 (the exceptional set is the heteroclinic orbit binding the equilibria on $y_1 = 0$ and $y_2 = 0$.

An analogous result is obtained when the commensalism term is nonlinear, exhibiting an upper bound analogous to the satiety bound of the predation. Specifically,
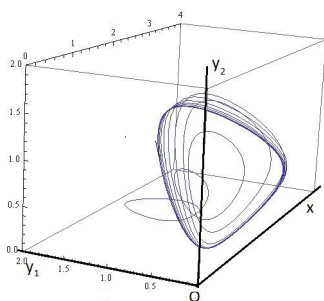
Figure 8: *An orbit and the cyclic attractor for system (13).*

we consider the system

$$\begin{cases} \dot{x} = ax(1 - x/p) + y_1 b_1 Tanh(e_1 x/b_1) + y_2 b_2 Tanh(e_2 x/b_2) \\ \dot{y}_1 = y_1(-c_1 + b_1 Tanh(e_1 x/b_1)) + \varepsilon y_1 b_3 Tanh(e_3 y_2/b_3) \\ \dot{y}_2 = y_2(-c_2 + b_2 Tanh(e_2 x/b_2)). \end{cases} \quad (7.2)$$

with the values of the parameters $a = 1$, $p = 4$, $b_1 = b_2 = b_3 = 1$, $c_1 = c_2 = 0.75$, $e_1 = 0.8$, $e_2 = 1.5$, $e_3 = 1$, $\varepsilon = 0.3$. This system is again persistent, with a cyclic attractor (Fig. 9). Once more, there is no rest point in $int(E^3)$, as the algebraic system reduces to a linear system with the solution $(0.64, -1.27, 1.53)$, then out of $int(E^3)$.
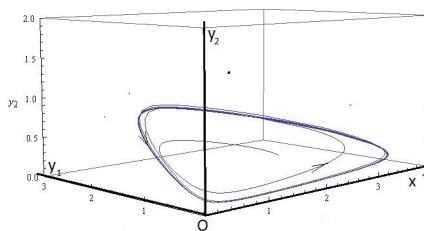

Figure 9: *An orbit and the cyclic attractor for system (14).*

It should be noted that analogous properties of persistence hold true for a symbiotic interaction between y_1 and y_2 instead of commensalism, but in that case, the algebraic system for the rest points is no longer reducible to a linear system, and the non existence of a rest point in $int(E^3)$ cannot be rigorously proved.

8. Examples with four species without interior rest point

In this section we are considering two examples of four-dimensional systems obtained by coupling two systems of two species. The heuristic mechanism to obtain a

cyclic attractor is very easy to understand. We first consider

$$\begin{cases} \dot{x}_1 = a_1 x_1 (1 - (x_1 + \delta x_2)/q_1) + vyx_1 \\ \dot{x}_2 = a_2 x_2 (1 - (x_2 + \delta x_1)/q_2) \end{cases} \tag{8.1}$$

with $v = 0$ for two species x_1, x_2 in competition for resources. They obey to logistic equations with population capacities q_1, q_2 and δ is the parameter of interdependence (see [19] if necessary). The system has the equilibria $(q_1, 0)$ and $(0, q_2)$ as well as another out of the coordinate axes. We may easily choose the parameters (see hereafter) in order to have the third rest point out of E^2 and $(0, q_2)$ as attractor. Moreover, the term $+vyx_1$ with positive v and y (which are taken as parameters for the time being) gives a demographic advantage to x_1, so that, with sufficiently large vy the attractor is on the x_1 axis, specifically $(q_1(vy + a_1)/a_1, 0)$. In other words, for $vy = 0$ (resp. sufficiently large vy) system (8.1) has a point attractor on the x_2 axis (resp. on the x_1 axis).

We then consider an auxiliary system with two species y, z (y is a prey and z a predator) with a cyclic attractor, and we use the $y(t)$ function as parameter y in (15). This amounts to saying that there is an influence of y on x_1 of commensalism nature. System (15) becomes non-autonomous, and clearly the vector field oscillates between a trend towards the attractors on the two axes, so that x_1 and x_2 are incorporated into the oscillation.

Specifically, we consider the system

$$\begin{cases} \dot{x}_1 = a_1 x_1 (1 - (x_1 + \delta x_2)/q_1) + vyx_1 \\ \dot{x}_2 = a_2 x_2 (1 - (x_2 + \delta x_1)/q_2) \\ \dot{y} = by(1 - y/p) - zTanh(y) \\ \dot{z} = z(-c + Tanh(y)) \end{cases} \tag{8.2}$$

with $a_1 = 0.73$, $a_2 = 1$, $b = 1$, $c = 0.7616$, $v = 0.15$, $\delta = 0.9$, $p = 4$, $q_1 = 0.73$, $q_2 = 1$. This system has a cyclic attractor. The established oscillations of the four variables are shown in Fig. 10. A projection of the cycle on the x_1, x_2, y space appears in Fig. 11. Moreover, this system has no internal equilibrium; indeed, the algebraic system for the internal equilibria is reducible to a linear system with the rest point $x_1 = -0.318$, $x_2 = 1.286$, $y = 1$, so out of the positive cone.

The special structure of this system allows an explicit description of the exceptional manifold of dimension $2 = 4 - 2$ formed by the heteroclinic orbits not leading towards the attractor. Indeed, the auxiliary system in y, z obviously has a (unstable) rest point inside the limit cycle; it is $y = y^0 = 1.0$, $z = z^0 = 0.985$. The exceptional manifold is $y = y^0$, $z = z^0$, and the dynamics on it is described by the two first equations of (16) with $y = y^0$.

Concerning the invasion of the various species, it is easily seen by simple inspection of the system that the prey y is invading from the vicinity of the whole (three-dimensional) subspace $y = 0$, and the predator z is invading from the vicinity of the (three-dimensional) subspace $z = 0$ unless the (two-dimensional) subspace $y = 0$.
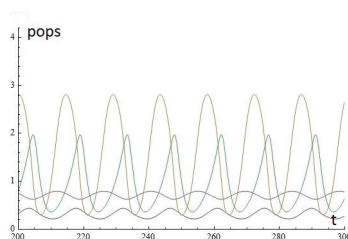
Figure 10: *Plot of the established oscillation of system (16).*

As for the invasion of x_1, we consider the dynamics on the subspace $x_1 = 0$. It is the cartesian product of the dynamics on the axis x_2 and on the plane (y, z), so that there is the attractor $\{q_2\} \times C$, where C denotes the cyclic attractor of the system (y, z). The corresponding attraction basin is the product of the axis x_2 without the origin and the plane (y, z) without the rest point (y^0, z^0) inside this cycle (which necessarily exist according to elementary index theory). This basin is clearly the whole (three-dimensional) manifold $x_1 = 0$ with the exception of a zero-measure set, so that the invasion of x_1 is checked merely by observation of one or several orbits starting with small $x_1(0)$.

The same holds true for the invasion of (x_2); the only difference is the dynamics on the subspace $x_2 = 0$, which is no longer a cartesian product. Nevertheless, for small v the attractor is a cycle as in the previous case; this follows either from structural stability from the cartesian product or directly using classical periodic stable solution theory for x_1 submitted to small periodic forcing coming from (y, z).
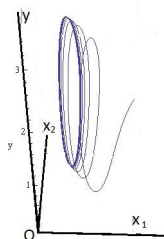

Figure 11: *A projection on the subspace x_1, x_2, y of the attractor of system (16).*

Very many variants of the previous mechanism are easily obtained by perturbation, as the pattern is structurally stable. We are now giving an example where the x_1, x_2 subsystem has in its turn an influence on the y, z, so exhibiting a real interaction between the two subsystems. For instance, we suppose that the presence of x_1 increases the efficiency of the predation of z on y. Specifically, we consider the new system (17) with the new parameter $\beta = 1.1$ and the same values of the other parameters (we note

that this change goes out of small perturbation theory).

$$\begin{cases} \dot{x}_1 = a_1 x_1 (1 - (x_1 + \delta x_2)/q_1) + v y x_1 \\ \dot{x}_2 = a_2 x_2 (1 - (x_2 + \delta x_1)/q_2) \\ \dot{y} = by(1 - y/p) - zTanh((1 + \beta x_1)y) \\ \dot{z} = z[-c + Tanh((1 + \beta x_1)y)] \end{cases} \tag{8.3}$$

Once more, system (17) has a cyclic attractor, shown in Fig. 12 and Fig. 13. This system has no internal equilibrium. In the present case, the algebraic system for the internal equilibria is not reducible to a linear system, but to a quadratic one, with the rest points $x_1 = -0.178$, $x_2 = 1.24$, $y = 1.16$ and $x_1 = -1.626$, $x_2 = -1.27$, $y = 2.46$, so both out of the positive cone.
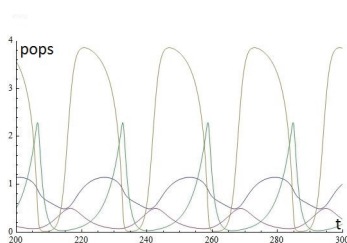

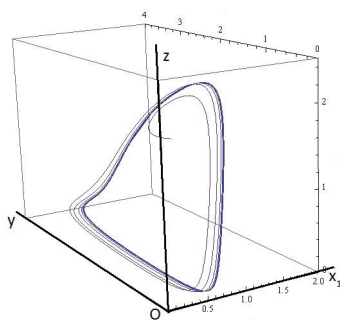Figure 12: *Plot of the established oscillation of system (17).*

Figure 13: *A projection on the subspace x_1, y, z of the attractor of system (17).*

9. Contamination properties by cartesian product of persistent systems with no internal rest point

The cartesian product of dynamical systems with attractors enjoys very simple properties of contamination of the property of not having rest points, which are structuraly stable by ulterior perturbation of the product vector field. They follow immediately from the properties of attractor blocks with smooth boundary. This induces

technical difficulties as the cartesian product of two domains with smooth boundary has not a smooth boundary (think to the square product of two segments), but such difficulties are easily overcame using the properties recalled in Sect 3. In addition, non-existence of rest point is structurally stable on compact domains; its generalization to E^n needs usual hypotheses on the behavior at infinity. For these reasons, the very simple properties hereafter are stated in a slightly entangled way; there are obvious variants of them.

Let f^1, f^2 be two persistent sytems (in the general framework of this paper) on E^n and E^m, with the (internal and with smooth boundary) attractor blocks K^1 and K^2 respectively. Then, the system $F = (f^1, f^2)$ has an attractor K with smooth boundary inside $K^1 \times K^2$. Moreover, this conclusion is structurally stable with respect to perturbations of the reduced field $G = (g^1, g^2)$.

Under the same conditions, if f^1 (or g^1) does not vanish in K^1, then F does not vanish in K, and this conclusion is structurally stable with respect to perturbations of the reduced field $G = (g^1, g^2)$. This property also holds true replacing K^1 by the whole E^n under usual conditions on the behavior of the fields and their perturbations at infinity.

There are obvious corollaries of these properties when f^1 (or g^1) has no rest point and the attractor in K^1 is a cycle. If the attractor in K^2 is a point, then F has a stable cycle in K, (structurally stable) and no rest point. If the attractor in K^2 is a cycle, then F has an invariant torus (which is structurally unstable, whereas the smooth attractor block K is structurally stable) and no rest point. In that case, the perturbations behave according to classical perturbation theory of invariant tori, without rest points.

In this framework, we are now giving an example of product and perturbation exhibiting a synchronisation phenomenon without internal rest point. We consider a system on E^5 which is the cartesian product of two subsystems on E^3 (species x, y_1, y_2) and E^2 (species u, v) respectively. the first subsystem is precisely (13) of section 7; it has an internal attractor without internal rest point. This subsystem has no influence from the second, so that it plays the role of driver. The second subsystem is an independent predator-prey system with an attractor cycle; the parameters were chosen in order to have a cycle with period slightly different of that of the first subsystem. Moreover, there is an extra term $+\eta y_2 v$ on $\dot{v}$ which accounts for an influence of the first (driver) subsystem on the second. The nature of this influence is of the commensalism nature, of v on y_2, with parameter of intensity η.

$$\begin{cases} \dot{x} = x(1 - x/p) + y_1 Tanh(e_1 x) + y_2 b_2 Tanh(e_2 x/b_2) \\ \dot{y}_1 = y_1(-c_1 + Tanh(e_1 x)) + \varepsilon y_1 y_2 \\ \dot{y}_2 = y_2(-c_2 + Tanh(e_2 x)) \\ \dot{u} = u(1 - u/q) + v Tanh(u) \\ \dot{v} = v(-d + Tanh(u)) + \eta y_2 v \end{cases} \quad (9.1)$$

The values of the parameters are $p = 4$, $c_1 = c_2 = 0.75$, $e_1 = 0.6$, $e_2 = 1.1$, $\varepsilon = 0.2$, $d = 0.7$, $q = 4$.

For $\eta = 0$ the two subsystems are independent, and the attractor is the cartesian product of the two cycles with slightly different periods. Fig. 14 is a plot of the projection of this product of cycles on the plane (y_1, u), accounting for a species of the first subsystem and a species of the second, exhibiting the lack of synchronism of the two variables. For $0.045 < \eta < 0.22$ the second subsystem adopts the same period as the first (which is invariable). Fig. 15 is analogous to Fig. 14 with $\eta = 0.1$, showing synchronism. The whole system, with any value of η has no interior rest point.
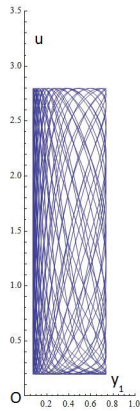

Figure 14: *System (18) with $\eta = 0$. A projection of the attractor on the subspace y_1, u, showing non-synchronism of the two subsystems.*
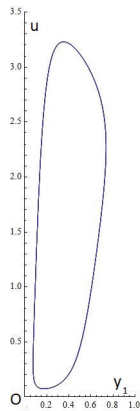

Figure 15: *System (18) with $\eta = 0.1$. A projection of the attractor on the subspace y_1, u, showing synchronisation of the two subsystems.*

10. Conclusion

In dimension $n \geqslant 3$ there are very many dynamical systems (making sense in ecology) with an attractor inside the variables domain and a large attraction basin, often going to the boundaries (so accounting for invasive dynamics) without internal equilibrium point; they are pure ESS (Evolutionary Stable Strategies). In most examples, the attractor itself is very simple, a periodic cycle; the dynamics "turns around an axis" of dimension $n-2$ which is not necessarily at rest, it usually undergoes a movement tangentially to itself (so often sending the axis to the boundary). As a consequence, there is no rest point inside the domain, but obviously the axis itself is not in the attraction basin of the cycle, so that this one excludes exceptional sets with zero n-dimensional measure. A model example of such dynamics is given in Sect 5. This kind of dynamics is (under wide hypotheses) structurally stable. Moreover, it is "contagious" by cartesian product with any other dynamical system, and the product is itself structurally stable, so admitting small interactions between the two subsystems, the whole system becoming itself a pure ESS.

This kind of systems is very wide and includes well established counter examples to the "competitive exclusion principle"; as a matter of fact, two predators may live on a prey in a pure ESS framework without equilibrium point.

This kind of pure ESS are discarded by strict definitions of persistence, which, in our opinion, should be avoided and replaced by the classical one (see for instance [15]) which amounts merely to the existence of an internal attractor. The utilization of this definition in practice is often facilitated using properties of invasion from the boundary (sect 4).

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