

TO PERSIST OR NOT TO PERSIST — DIFFERENTIAL EQUATIONS IN ECOLOGY

Josef Hofbauer

*Department of Mathematics, University College London, London WC1E 6BT, U.K.
and Mathematics Faculty, University Vienna, 1090 Wien, Austria.
E-mail: josef.hofbauer@univie.ac.at*

The basic ODE models in mathematical ecology take the form

$$\dot{x}_i = x_i f_i(x_1, \dots, x_n) \quad (i = 1, \dots, n) \quad (1)$$

Here $x_i \geq 0$ denote the densities of n interacting species, and f_i are their per-capita growth rates or interaction functions which are assumed to be C^1 . What makes (1) special compared to general ODEs is that all the faces of the nonnegative orthant \mathbf{R}_+^n are invariant: If $x_i(0) = 0$ then $x_i(t) = 0$ for all t . Such systems are often called *ecological differential equations* on \mathbf{R}_+^n .

A prominent special case are the *Lotka–Volterra equations*

$$\dot{x}_i = x_i \left(r_i + \sum_{j=1}^n a_{ij} x_j \right) \quad (2)$$

Best known are the predator–prey equations $\dot{x} = x(r - by)$, $\dot{y} = y(-s + cx)$. However, this system is somewhat exceptional because of its conservative oscillations. Realistic models have $a_{ii} < 0$. LV equations (2) have several special properties, some of which are mentioned in section 1.2. A detailed understanding of LV equations is also important for dynamical systems: The truncated normal form of an n –fold Hopf bifurcation (without resonances) reduces to the n –dimensional LV equation. However, for $n \geq 3$, a complete classification of dynamic behaviour of LV equations is out of reach, due to many numerical examples of chaotic behaviour.

1. PERMANENCE

From the biological point of view the relevant question is: Will some species die out? Or can all species coexist? This leads to the following concept.

(1) is *permanent* (or uniformly persistent) if there is a compact set $\Lambda \subset \text{int } \mathbf{R}_+^n$ which attracts all positive solutions, or equivalently there are m, M such that

$$0 < m < \liminf_{t \rightarrow \infty} x_i(t) < \limsup_{t \rightarrow \infty} x_i(t) < M$$

holds for all interior solutions $x(t) \in \text{int } \mathbf{R}_+^n$. With other words, the boundary of the nonnegative orthant, $\partial \mathbf{R}_+^n$, together with infinity is a repeller.

(1) is *robustly permanent* if all nearby systems $\dot{x}_i = x_i g_i(x)$ (with g C^k -close to f , for some $k \geq 0$) are permanent.

A simple example of a permanent system that is not robustly permanent is $\dot{x} = x^2(1-x)$.

We assume that all systems considered are dissipative, i.e., there is some M such that $\limsup_{t \rightarrow \infty} x_i(t) \leq M$ holds for all solutions $x(t) \in \mathbf{R}_+^n$. Conditions on the matrix A guaranteeing dissipativity of (2) are given in [10].

1.1. Saturated equilibria

\hat{x} is an equilibrium of (1) if $f_i(\hat{x}) = 0$ whenever $\hat{x}_i > 0$. \hat{x} is a (strictly) *saturated equilibrium*, if additionally

$$\hat{x}_i = 0 \Rightarrow f_i(\hat{x}) \leq 0 \quad (f_i(\hat{x}) < 0).$$

The $f_i(\hat{x})$ are invasion rates of the missing species at \hat{x} . They are eigenvalues of the linearized vectorfield at \hat{x} . Loosely speaking, an equilibrium is saturated iff the missing species cannot invade there. If an interior orbit $x(t) > 0$ converges, $x(t) \rightarrow \hat{x}$ as $t \rightarrow \infty$, then its limit \hat{x} is saturated. On the other hand, a strictly saturated equilibrium attracts interior orbits (by the stable manifold theorem). Every interior equilibrium is saturated.

The following follows from Brouwer's degree theory, as adapted to a manifold with corners.

Theorem 1.1 (Index Theorem) [10] *Every dissipative ecological system (1) has a saturated equilibrium. If all saturated equilibria are regular then the sum of their indices equals 1.*

Here the index $i(\hat{x}) = \text{sgn } \det(-DF(\hat{x})) = \pm 1$ is the sign of the Jacobian suitably normalized so that every stable equilibrium has index +1. An equilibrium is regular if $\det(-DF(\hat{x})) \neq 0$.

1.2. Necessary conditions for permanence

Obviously a permanent system cannot have strictly saturated equilibria on $\partial\mathbf{R}_+^n$, and a robustly permanent system has no saturated equilibria on $\partial\mathbf{R}_+^n$. The index theorem then implies the existence of an interior equilibrium. This can also be shown directly for each permanent system, see [10]. For Lotka–Volterra equations permanence implies existence and uniqueness of an interior equilibrium \hat{x} , and since its index is 1, we get $\det(-A) > 0$. For many special classes of low dimensional LV systems these two conditions characterize permanence, e.g. for two predator one prey systems. Furthermore, in a permanent LV system, the time average of every interior solution converges to the equilibrium:

$$\lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T x(t) dt = \hat{x}. \quad (3)$$

On the other hand, if the LV equation (2) has no interior equilibrium then every orbit converges to the boundary of \mathbf{R}_+^n (*exclusion principle*).

1.3. Average Liapunov Functions

In order to prove permanence one could try to find a Liapunov function. As this rarely works I devised an alternative method. A function $P : \mathbf{R}_+^n \rightarrow \mathbf{R}$ is an *average Liapunov function* (ALF) if $P(x) = 0$ for $x \in \partial\mathbf{R}_+^n$, $P(x) > 0$ for $x \in \text{int } \mathbf{R}_+^n$, $\frac{\dot{P}}{P} = \psi(x)$ is continuous on \mathbf{R}_+^n , and

$$\forall x(0) \in \partial\mathbf{R}_+^n : \exists T > 0 : \int_0^T \psi(x(t)) dt > 0. \quad (4)$$

The standard ansatz for an ALF is $P(x) = \prod_{i=1}^n x_i^{p_i}$, for suitably chosen $p_i > 0$. Here $\psi(x) = \sum_i p_i f_i(x)$. The crucial condition (4) implies that for $x(0)$ interior but close to the boundary, $P(x(T)) > P(x(0))$ after some time T , which means, that the ‘distance’ to the boundary increases ‘on the average’. Actually, (4) is equivalent to

$$\forall x(0) \in \partial\mathbf{R}_+^n : \liminf_{T \rightarrow \infty} \frac{1}{T} \int_0^T \psi(x(t)) dt > 0$$

Via the ergodic theorem and the Krylov-Bogoliubov theorem, we can replace time averages with space averages to get the equivalent condition: For all invariant probability measures μ supported on $\partial\mathbf{R}_+^n$,

$$\int_{\partial\mathbf{R}_+^n} \psi(x) d\mu(x) > 0. \quad (5)$$

It is not hard to show that the existence of an ALF implies permanence, see [10]. For the standard ALF, more can be shown.

Theorem 1.2 [2] *Consider the following three conditions.*

(A) *There exist $p_i > 0$ such that $\prod_{i=1}^n x_i^{p_i}$ is an ALF.*

(B) There exist $p_i > 0$, $k > 0$ and a continuous function $Q : \mathbf{R}_+^n \rightarrow (0, \infty)$ (and C^1 if f is C^1) such that $V(x) = \prod_{i=1}^n x_i^{p_i} Q(x)$ is a Liapunov function near $\partial\mathbf{R}_+^n$ which satisfies $\dot{V}(x) \geq kV(x)$ for x in a neighbourhood of $\partial\mathbf{R}_+^n$.

(C) Every invariant probability measure μ supported on $\partial\mathbf{R}_+^n$ is unsaturated:

$$\forall \mu \quad \exists i : \int_{\partial\mathbf{R}_+^n} f_i d\mu > 0. \quad (6)$$

Then $(A) \Leftrightarrow (B) \Leftrightarrow (C) \implies$ robust permanence of (1).

Actually, [2] show more general results, in particular local versions. Condition (C) was introduced by Schreiber [21] who showed that it implies robust permanence. The equivalence $(A) \Leftrightarrow (C)$ follows from the minmax theorem:

$$\min_{\mu \in \mathcal{M}} \max_{p \in \Delta} \sum_i p_i \int_{\partial\mathbf{R}_+^n} f_i d\mu = \max_{p \in \Delta} \min_{\mu \in \mathcal{M}} \sum_i p_i \int_{\partial\mathbf{R}_+^n} f_i d\mu > 0. \quad (7)$$

where \mathcal{M} is the set of invariant Borel probability measures of (1) on $\partial\mathbf{R}_+^n$ and Δ is the probability simplex in \mathbf{R}^n . Condition (B) means that $\partial\mathbf{R}_+^n$ is an exponential repeller.

In order to apply this result to a concrete system we have to solve the system of linear inequalities in $p_i > 0$:

$$\sum_i p_i \int_{\partial\mathbf{R}_+^n} f_i(x) d\mu(x) > 0, \quad (8)$$

for all ergodic measures $\mu \in \mathcal{M}$. This includes in particular all these inequalities for all boundary equilibria \hat{x} ,

$$\sum_i p_i f_i(\hat{x}) > 0. \quad (9)$$

In two cases, the inequalities (9) suffice for $P = \prod x_i^{p_i}$ to be an ALF: first, if all solutions on the boundary converge to an equilibrium, and second, for Lotka–Volterra equations, because of the averaging property, see [10].

The coefficients $f_i(\hat{x})$ in (9) are the invasion rates at the missing species at the boundary equilibria. They can be nicely arranged in a *characteristic matrix* C with n columns, one for each species, and one row for each boundary equilibrium \hat{x} (or invariant measure μ). Then (9) can be restated as

$$p > 0, \quad Cp > 0. \quad (10)$$

One can also show converse results, see [8].

Theorem 1.3 Let $A \subseteq \partial\mathbf{R}_+^n$ be an attractor of the flow restricted to the boundary $\partial\mathbf{R}_+^n$, and let $p_i > 0$ be such that for all ergodic invariant probability measures μ on A ,

$$\sum_i p_i \int_{\partial\mathbf{R}_+^n} f_i d\mu < 0 \quad (11)$$

then A is an attractor in \mathbf{R}_+^n .

The intuition is that for $P(x) = \prod x_i^{p_i}$, $P(x(t))$ will decrease on average for interior solutions $x(t)$ close to A , and hence $x(t) \rightarrow A$ as $t \rightarrow \infty$. In the next section we give some applications of these results. More on permanence can be found in the survey papers [12, 13].

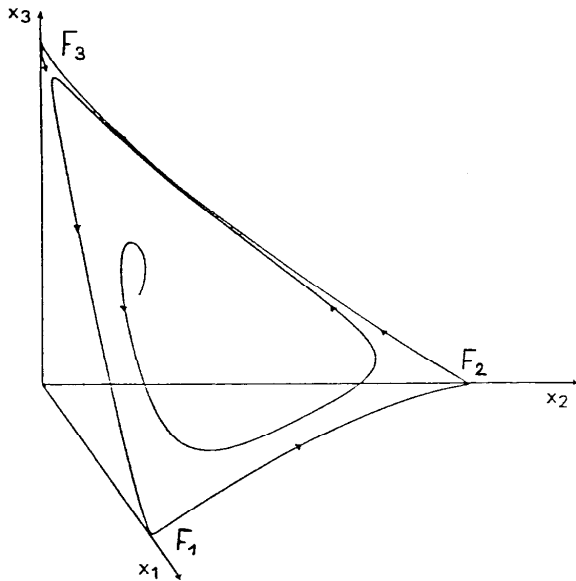
2. HETEROCLINIC CYCLES

2.1. The May-Leonard cycle

This is the simplest example of an ecological system without saturated equilibria on the boundary, and yet not permanent. It is due to May and Leonard [19]. It consists of three competing species, where 1 beats 2, 2 beats 3, 3 beats 1 (in the simplest case with LV dynamics and with cyclic symmetry).

$$\begin{aligned} \dot{x}_1 &= x_1(1 - x_1 - \alpha x_2 - \beta x_3) \\ \dot{x}_2 &= x_2(1 - \beta x_1 - x_2 - \alpha x_3) \\ \dot{x}_3 &= x_3(1 - \alpha x_1 - \beta x_2 - x_3) \end{aligned} \tag{12}$$

If $0 < \beta < 1 < \alpha$, there is a robust heteroclinic cycle Γ connecting the three one-species equilibria $F_1 = (1, 0, 0) \rightarrow F_2 \rightarrow F_3 \rightarrow F_1$.



If $\alpha + \beta > 2$ then Γ is attracting and the system is not permanent. If $\alpha + \beta < 2$ then Γ is repelling, the system is permanent.

This can be seen by looking at the characteristic matrix

	\dot{x}_1/x_1	\dot{x}_2/x_2	\dot{x}_3/x_3
O	1	1	1
F_1	0	$1 - \beta$	$1 - \alpha$
F_2	$1 - \alpha$	0	$1 - \beta$
F_3	$1 - \beta$	$1 - \alpha$	0

Using the criterion (10, 11) and choosing $p = (1, 1, 1)$ gives the above stability condition.

For general cyclic competition, but without cyclic symmetry and with possibly nonlinear interactions, the characteristic matrix of such a heteroclinic cycle reads

	\dot{x}_1/x_1	\dot{x}_2/x_2	\dot{x}_3/x_3
F_1	0	e_2	$-c_3$
F_2	$-c_1$	0	e_3
F_3	e_1	$-c_2$	0

Then Γ is repelling and the system is permanent, if $\exists p > 0, Cp > 0$ iff $e_1e_2e_3 > c_1c_2c_3$, i.e. the product of the outgoing eigenvalues is larger than the product of the incoming eigenvalues. And Γ is attracting if $\exists p > 0, Cp < 0$ iff $e_1e_2e_3 < c_1c_2c_3$.

The detailed dynamics of the general 3d competitive Lotka Volterra equations (2) is not completely understood. Since there is a globally attracting 2d manifold (the *carrying simplex* [7]) Poincaré–Bendixson theory applies, and the open problem concerns the maximal number of limit cycles. [23] found one, [11] found 2, and [17] and [5] found 3 limit cycles. This is the **ecological analog of Hilbert’s 16th problem**.

In the setting of systems with symmetry, essentially the same example as (12) was presented again in [4], see also [3]. An equivalent dynamics occurs in the ‘rock-scissors-paper’ game [10]. Amazingly, real biological systems have been found that display this kind of behaviour. A famous one is *Uta stansburiana*, the side-blotched lizard, that has been followed for decades by Barry Sinervo [22] (google for ‘Lizardland’ to find his beautiful webpages): The males of this species are differentiated by 3 different heritable traits, that govern their behaviour towards females and curiously determine also their throat colour. One type, with orange throats, are strong and control a large territory with many females. This type is easily invaded by a second type, with yellow throats, who sneak up to females to mate with them. A third type with blue throats guard small number of females only, they recognize and drive off the sneakers but loose out against the strong orange males.

2.2. The Kirlinger example

A biologically more plausible example of a heteroclinic cycle was studied by Kirlinger [14]. This is a two-prey two-predator system with Lotka–Volterra dynamics.

$$\begin{aligned}
 \dot{x}_1 &= x_1(r_1 - a_{11}x_1 - a_{12}x_2 - b_1y_1) \\
 \dot{x}_2 &= x_2(r_2 - a_{21}x_1 - a_{22}x_2 - b_2y_2) \\
 \dot{y}_1 &= y_1(-s_1 + q_1x_1) \\
 \dot{y}_2 &= y_2(-s_2 + q_2x_2) .
 \end{aligned} \tag{13}$$

The two prey species x_1 and x_2 live in severe competition, i.e. the dynamics of the x_1 – x_2 plane is bistable: There are two stable one-species fixed points F_1 and F_2 . At F_1 predator y_1 , which is specialized on prey 1, is able to invade, leading to a coexistence equilibrium F_1^1 . At this equilibrium, the number x_1 of prey 1 is reduced due to predation so much, that it will be outcompeted by prey 2. There is a heteroclinic orbit in the x_1 – x_2 – y_1 subsystem which connects F_1^1 to F_2 . Assuming a similar behaviour after swapping 1 and 2, there is a heteroclinic cycle Γ on the boundary of \mathbf{R}_+^4 connecting the four equilibria $F_1 \rightarrow F_1^1 \rightarrow F_2 \rightarrow F_2^2 \rightarrow F_1$, for an open set of coefficients in (13). Its characteristic matrix C has the structure

	\dot{x}_1/x_1	\dot{x}_2/x_2	\dot{y}_1/y_1	\dot{y}_2/y_2
F_1	0	$-c_2$	f_1	$-d_2$
F_1^1	0	e_2	0	$-d_2'$
F_2	$-c_1$	0	$-d_1$	f_2
F_2^2	e_1	0	$-d_1'$	0

Here $e_i, f_i > 0$ are the ‘expansion’ rates, $c_i > 0$ describe the competition between the two prey, and $d_i, d_i' > 0$ the death rates of the predators at F_j, F_j^j ($j \neq i$). These eigenvalues can be easily expressed in terms of the parameters of (13). Then $\partial\mathbf{R}_+^4$ is repelling near Γ if (10) has a solution, i.e., if

$$e_1e_2f_1f_2 > (e_1d_1 + c_1d_1')(e_2d_2 + c_2d_2') \tag{14}$$

and Γ is attracting if (11) applies, which is the case if the inequality sign in (14) is reversed. The left hand side is the product of ‘outgoing’ eigenvalues, but the right hand side is an unexpected combination of the entries of C . Note also that the (real part) of the incoming eigenvalues at F_i^i (within the x_i – y_i face) do not enter the stability criterion.

The condition (14) gives the stability criterion beyond the Lotka–Volterra ansatz (13). For nonlinear interaction functions the 2d predator–prey faces could have a limit cycle. Then these periodic orbits replace the equilibria F_1^1, F_2^2 , and the e_i and c_i have then to be replaced by Floquet exponents. The same type of heteroclinic cycle appears also in fluid dynamics, in shearing instability of convection [18].

The condition (14) comes from the determinant of the characteristic matrix C . In general we can use characterizations of M–matrices. First rearrange the rows and/or columns of C such that the positive elements are in the diagonal. For such an $n \times n$ matrix C with $c_{ij} \leq 0$ for $i \neq j$, the following are equivalent:

(1) $\exists p > 0 : Cp > 0$

(2) The leading principal minors are positive: $\det(c_{ij})_{1 \leq i, j \leq k} > 0$ for $k = 1, \dots, n$.

Conversely, if one of the minors is negative (and the others are nonzero) then there is a $p > 0$ such that $Cp < 0$. In this case, Theorem 1.3 can often be used to show that Γ is an attractor, see [8] for further results. There are also situations of heteroclinic networks (several interconnected heteroclinic cycles) where the method gives precise stability criteria, but often there is a gap between the known necessary and sufficient conditions.

For further examples of heteroclinic cycles in ecological differential equations and the use of characteristic matrices see [8, 10]. For more on heteroclinic cycles, with emphasis on systems with symmetry, see [3, 15].

3. ON THE BORDER BETWEEN PERMANENT AND NON-PERMANENT SYSTEMS

In all the examples given above and all explicit examples studied so far, the border between permanent and non-permanent systems is given by a codimension 1 manifold which is piecewise smooth, and given by an algebraic expression in the invasion parameters $\int f_i d\mu$. Is this true in general? The answer is no! Indeed, Sebastian Schreiber and I have shown the following result in [9].

Theorem 3.1 *For each $n \geq 5$, there is an open set $\mathcal{F} \subset C^1(\mathbf{R}_+^n, \mathbf{R}^n)$ of interaction functions, together with two subsets, $\mathcal{F}_1, \mathcal{F}_2 \subset \mathcal{F}$, each dense in \mathcal{F} , such that for $f \in \mathcal{F}_1$, the system (1) is permanent, whereas for $f \in \mathcal{F}_2$, the system (1) has an attractor in the boundary $\partial\mathbf{R}_+^n$.*

So the slightest perturbation in the data of the system can change it from permanent to non-permanent, or vice versa. Hence, for all practical purposes, for $f \in \mathcal{F}$, permanence is ‘unpredictable’. In \mathcal{F} , permanent and non-permanent systems are intermingled. The theorem also shows that not every permanent system can be approximated by robustly permanent systems.

In order to construct this open set of systems we consider a ‘resident’ system (species 3, 4, ...) and two potentially invading species 1 and 2. The resident system is assumed to have two attractors, for the start two stable equilibria p and q . At p , species 1 invades, but ‘the resident strikes back’ as in [20]: the invader dies out again, but drives the resident system to the other attractor q . There, similarly, species 2 invades and succeeds only in driving the resident back to p . This situation is robust against perturbations, as is the resulting heteroclinic cycle Γ connecting p to q and back. The stability of Γ depends on the invasion parameters, $f_1(p) > 0$, $f_2(p) < 0$, $f_1(q) < 0$ and $f_2(q) > 0$:

If $f_1(p)f_2(q) < f_1(q)f_2(p)$ then (10) can be used to show that Γ is an attractor, and with the inequality reversed it is a repeller.

Now assume that the resident system is at least two dimensional and q is replaced by an attracting periodic orbit, $q(t + T) = q(t)$, for some $T > 0$, $\forall t$. Then the same stability criterion for γ is given as above, only $f_i(q)$ are replaced by the Floquet exponents $\frac{1}{T} \int_0^T f_i(q(t)) dt$.

Finally assume that the resident system consists of at least three species and replace q by an arbitrary attractor A , and further:

A1 Two attractors (equilibrium p , and an attractor A) in the invariant (resident) subsystem $x_1 = x_2 = 0$,

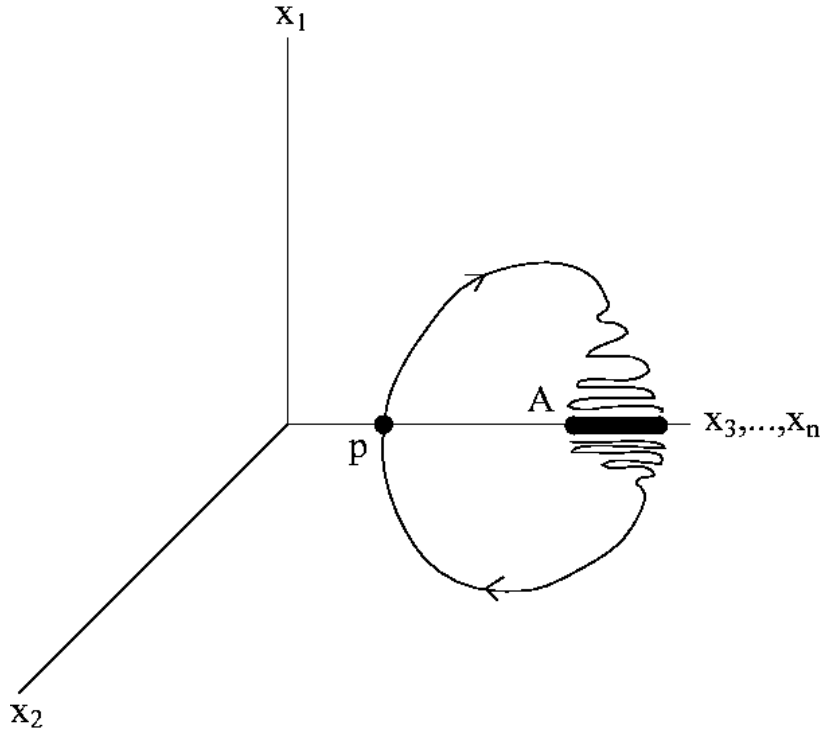
A2 $f_1(p) > 0$ and $f_2(p) < 0$,

A3 $\int_A f_1 d\mu < 0$ and $\int_A f_2 d\mu > 0$ for all (ergodic) invariant probability measures μ with support in A ,

A4 in $\{x_2 = 0\}$: $W^u(p) = \{p\} \cup \gamma$, $\omega(\gamma) \subseteq A$, and

A5 in $\{x_1 = 0\}$: $\forall \gamma' \subseteq W^u(A) \setminus A$: $\omega(\gamma') = \{p\}$.

Let Γ be the union of p , A , and all the connecting orbits γ, γ' described in A4 and A5.



These five assumptions imply (see [9] for two proofs): *If*

$$f_1(p) \int_A f_2 d\mu > f_2(p) \int_A f_1 d\mu \quad \forall \mu \in \mathcal{M}_A^{erg}$$

then $\partial\mathbf{R}_+^n$ is C^r -**robustly repelling** near Γ . If

$$f_1(p) \int_A f_2 d\mu < f_2(p) \int_A f_1 d\mu \quad \forall \mu \in \mathcal{M}_A^{\text{erg}}$$

then $\partial\mathbf{R}_+^n$ is C^r -**robustly attracting** near Γ , i.e. there is an isolating neighborhood U of Γ in $\{x \in \mathbf{R}_+^n : x_1 x_2 = 0\}$ s.t. for every small C^r perturbation of (1), the maximal invariant set in U is an attractor.

If A is uniquely ergodic this covers all generic situations. However, in general, the following is a robust possibility.

A6 There are two ergodic invariant measures $\mu^\pm \in \mathcal{M}_A^{\text{erg}}$ s.t.

$$f_1(p) \int_A f_2 d\mu^+ > f_2(p) \int_A f_1 d\mu^+ \tag{15}$$

$$f_1(p) \int_A f_2 d\mu^- < f_2(p) \int_A f_1 d\mu^- \tag{16}$$

The remaining are technical assumptions that we use in our proof.

A7 A is a transitive, hyperbolic attractor.

A8 normal hyperbolicity at A :

$$\forall \mu \in \mathcal{M}_A^{\text{erg}} : \int_A f_1 d\mu < \lambda^-(\mu) < 0 < \lambda^+(\mu) < \int_A f_2 d\mu$$

where $\lambda^+(\mu)$ (resp. $\lambda^-(\mu)$) denotes the largest (resp. smallest) Lyapunov exponent of (1) within $\{x : x_1 = x_2 = 0\}$

A9 strong internal contraction at p : $\lambda^-(p) < f_2(p) < 0$

For $n \geq 5$, these 9 assumptions define a nonempty open set \mathcal{F} of C^r ecological differential equations (1).

Since in a hyperbolic attractor, periodic orbits are dense in the set of all invariant probability measures, μ^+, μ^- in [A6] can be replaced by periodic orbits q^+, q^- . Since in a transitive hyperbolic attractor, the stable manifold of each periodic orbit is dense, a small perturbation of the vector field along the unstable manifold γ of p in $\{x_2 = 0\}$ can make γ a subset of this stable manifold.

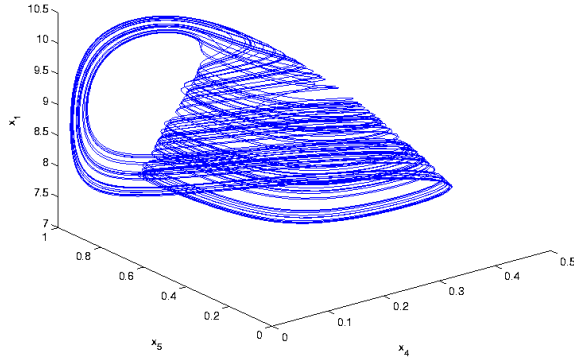
This produces a dense set \mathcal{F}_1 of systems with $\omega(\gamma) = q^+$, and another dense set \mathcal{F}_2 with $\omega(\gamma) = q^-$. By a detailed analysis of the Poincaré maps along Γ we have shown that for $f \in \mathcal{F}_1$, $\partial\mathbf{R}_+^n$ is repelling near Γ , whereas for $f \in \mathcal{F}_2$, Γ is attracting. This proves the Theorem.

4. AN ECOLOGICAL EXAMPLE

I conclude with an explicit system of ecological equations for which the construction in the previous section might apply, see again [9] for details. We consider a system consisting of five species: a prey (species 5), a predator (species 4), and three top predators (species 1, 2, and 3). One of the top predators (species 1) is an intraguild predator: it feeds on species 2 and 4. In order to generate a chaotic attractor, we assume that species 4 and species 1 have saturating functional responses with respect to their primary prey. For the sake of simplicity, we assume that all the other functional responses are linear and consider a model of the following form

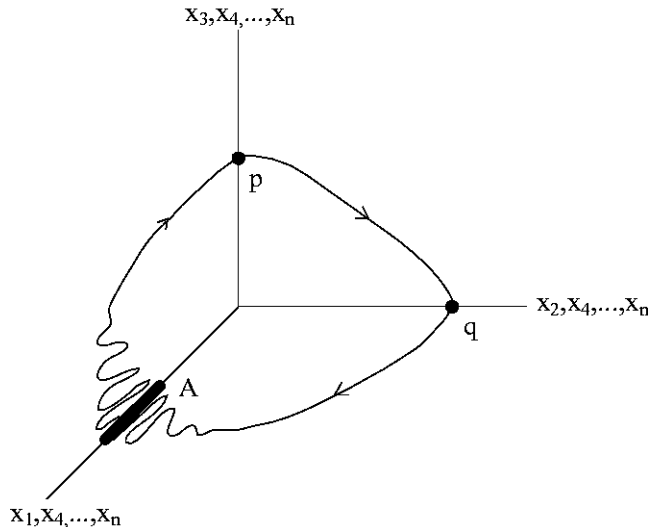
$$\begin{aligned}\dot{x}_1 &= x_1 \left(\frac{\theta_4 a_4 x_4}{1 + b_4 x_4} - d_1 + \theta_2 a_2 x_2 \right) \\ \dot{x}_2 &= x_2 (\theta_4 a_4 x_4 - d_2 - a_2 x_1) \\ \dot{x}_3 &= x_3 (\theta_4 a_4 x_4 - d_3) \\ \dot{x}_4 &= x_4 \left(\frac{\theta_5 a_5 x_5}{1 + b_5 x_5} - d_4 - \frac{a_4 x_1}{1 + b_4 x_4} - a_4 (x_2 + x_3) \right) \\ \dot{x}_5 &= x_5 \left(1 - x_5 - \frac{a_5 x_4}{1 + b_5 x_5} \right)\end{aligned}$$

The 145 food chain with saturating functional response can exhibit seemingly chaotic behaviour, see [6, 16]. The figure shows the ‘teacup attractor’ [6] with parameters $a_5 = 5.0$, $a_4 = 0.1$, $b_5 = 3.0$, $b_4 = 2.0$, $d_2 = 0.4$, $d_1 = 0.01$, and $\theta_4 = \theta_5 = 1$.



This attractor is unlikely to be hyperbolic, but Deng and Hines [1] using singular perturbation theory have proven for different parameter values that this food chain model can exhibit attractors containing a shift dynamics. For the other food chains, 345 and 245, we choose parameters such that they have a globally asymptotically stable equilibrium (p and q , respectively). This can be done, such that in absence of species 2, species 3 displaces species 1, driving the system from A to the equilibrium p in the 345 face. Furthermore, in

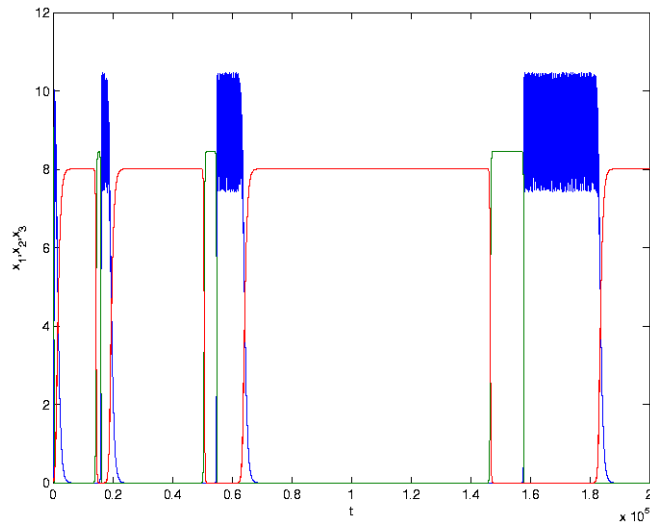
absence of the top predator (i.e., on the face $x_1 = 0$, but $x_2x_4x_5 > 0$), species 2 displaces species 3, moving the system from p to the equilibrium q in 245. Finally, on $x_3 = 0$, species 1 replaces 2, and leads from q back to the attractor A in 145, if we choose a_2 and θ_2 sufficiently large. This completes the heteroclinic cycle between the equilibria p, q and the attractor A as illustrated in the next figure.



The characteristic matrix of this heteroclinic cycle Γ is given by

	x_1	x_2	x_3	x_4	x_5
A	0	$-c_\mu$	e_μ	0	0
q	e_q	0	$-c_q$	0	0
p	$-c_p$	e_p	0	0	0

As above, if for all invariant probability measures μ on A , $e_p e_q e_\mu < (>) c_p c_q c_\mu$ then Γ is robustly attracting (robustly repelling). The final figure shows the time series for the parameter values $a_2 = 0.01$, $\theta_2 = 0.25$; the heteroclinic cycle Γ appears to be attracting, increasing periods of chaotic motion in A are interweaved with nearly constant behaviour near the equilibria p and q . Increasing the parameter θ_2 leads to coexistence of all five species and a repelling heteroclinic cycle ($\theta_2 = 2$). For intermediate values of θ_2 the heteroclinic cycle changes stability and we expect a range of parameters where the above phenomenon occurs in this explicit model of a five species system.



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