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A Unified Approach to Persistence

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1. Repellers in dynamical systems

Let f^t be a flow on a compact metric space X and M be a closed invariant subset of X.

Theorem 1. *If M is isolated then one of the following three alternatives hold.*

(a) *M is an attractor.*

(b) *M is a repeller.*

(c) *M is a 'saddle': there exist $x, y \notin M$ such that $\omega(x) \subset M$ and $\alpha(y) \subset M$.*

Remark. 'Attractor' stands here for the 'stable attractor' of [1, ch.V], or as used by Conley [5]. In case (b), when M is a repeller, there is a dual attractor which attracts all orbits in $X \setminus M$ (see [5, ch.II.5]).

Actually, we need only the following special case.

Theorem 2. *M is a repeller if and only if*

(1) *M is isolated, and*

(2) *$W^s(M) \subset M$, so that no orbit from $X \setminus M$ converges to M.*

Remark. For completeness we sketch the (simple) proof. Choose a compact isolating neighborhood U of M. $\omega(x)$ of any $x \notin M$ must meet $X \setminus U$ if neither (1) nor (2) is violated. Then $X \setminus U$ is a weakly attracting region for $X \setminus M$. Its forward invariant closure $\gamma^+(X \setminus U)$ is then still compact and contains an attractor for $X \setminus M$ whose dual repeller is M. [Consult the 'weak attractor theorem' of [1, ch. V, 1.25] or, in a more modern and concise language, Conley [5, II.5.1.D] (with reversed time) or Hutson's [15] Lemma 2.1 for details]. The general result, Theorem 1, follows immediately from Theorem 2 and its time reversal.

COROLLARY 1. *Let $P : X \to \mathbb{R}$ be a continuous function on X satisfying the following conditions.*

(a) *$P(x) = 0$ for $x \in M$ and $P(x) > 0$ for $x \in X \setminus M$.*

(b) *For every x in a neighbourhood U of M there exists a time $t > 0$ such that $P(xt) > P(x)$. Then M is a repeller.*

Proof: Suppose, for some $x \in U \setminus M$, $\gamma^+(x) \subset U$. Then there is a $y \in \overline{\gamma^+(x)}$ such that $P(y) \geq P(z)$ for all $z \in \gamma^+(x)$ and in particular $P(y) \geq P(yt)$ for $t \geq 0$. This contradicts (b). Hence U is an isolating neighbourhood of M and for no $x \in U \setminus M$, $\omega(x) \subset U$. Hence, by Theorem 2, M is a repeller. □

As shown by Fonda [6] this condition readily implies those given earlier by Gard and Hallam [9] in terms of 'persistence functions' and Hofbauer [11] and Hutson [15] in terms of 'average Ljapunov functions' which are more accessible to concrete applications, since they involve only conditions for $x \in M$:

COROLLARY 2. *If P is differentiable along orbits then condition (b) can be replaced by*

(b') *There is a continuous function $\psi : X \to \mathbb{R}$, such that $\dot{P}(x) \geq P(x)\psi(x)$ for all $x \in X$, and for each $x \in M$ there is a time $T > 0$ such that*

$$\int_0^T \psi(x(t))\, dt > 0. \tag{1}$$

It is also sufficient that (1) holds for all $x \in \omega(M)$.

Up to now no information on the flow on M was assumed or required. However, sometimes it is useful to exploit the structure of the flow on M. The main idea is, if an orbit $x \in X \setminus M$ converges to M then its ω-limit cannot be any closed invariant subset of M, but has the crucial property of being *chain transitive* (see [2]). To explain this we need some notation.

An (ε, T)-*pseudoorbit* or (ε, T)-*chain* for f^t is the union $\bigcup_{i=1}^n x_i[0, \tau_i]$ of pieces of orbits of length $\tau_i \geq T$ and the jumps obeying $d(x_i\tau_i, x_{i+1}) < \varepsilon$. If the flow f^t is given by a C^1 vector field $\dot{x} = g(x)$ then one could use ε-*approximate solutions* $\{y(t) : 0 \leq t \leq T'\}$ satisfying $|\dot{y}(t) - g(y(t))| < \varepsilon$ instead. We say *x is chained to y* if for all (small) $\varepsilon > 0$ and all (large) $T > 0$ there is an (ε, T)-chain with $x_0 = x$ and $x_{n+1} = y$. If x is chained to x, then it is said to be a *chain recurrent* point, and we write $x \in \mathcal{R}$. Now $x \notin \mathcal{R}$ iff there exists an open set U such that $f^t\bar{U} \subset U \quad \forall t > 0$ and $x \in U \setminus f^tU$ for some $t > 0$, or equivalently, iff there exists an attractor A, such that $x \in W^s(A) \setminus A$. Thus $\mathcal{R} = \bigcap A \cup A^*$, the intersection over all attractor-repeller pairs (A, A^*). The connected components Λ_i of $\mathcal{R}$, sometimes called the ***basic sets*** of the flow, are the maximal ***chain transitive*** subsets of X: for all $x, y \in \Lambda_i$, x is chained to y, with chains lying completely in Λ_i.

This is the essence of the ***structure theorem*** of Conley [5] for general dynamical systems. In the following theorem we assume that the structure of the flow f^t on M is given.

Theorem 3. *Let Λ_i be the basic sets of M. Then M is a repeller iff each basic set Λ_i of M satisfies the following two conditions.*

(1) *Λ_i is M-isolated in X, in the sense that some neighbourhood U of Λ_i in X contains a full orbit $\gamma(x)$ only if $x \in M$.*

(2) *$W^s(\Lambda_i) \subset M$.*

In some sense this result is best possible since a priori each basic set in M is a candidate for an ω-limit set of an orbit $x \in X \setminus M$.

Proof. That (1) and (2) are necessary conditions, is clear. For the converse we have to show that (1) and (2) of Theorem 2 are fulfilled. As already pointed out, (2) is a consequence of the chain transitivity of ω-limit sets. It remains to show that M is isolated. Suppose not. Then there exists a sequence of compact invariant sets $\Gamma_k \not\subset M$ which can be chosen to be chain transitive such that $\Gamma_k \subset \{x : d(x, M) \leq \frac{1}{k}\}$. A subsequence of (Γ_k) will converge in the Hausdorff metric to a compact set $\Gamma \subset M$ which is again invariant and chain transitive. (See the appendix in [18] for details.) Thus Γ must be contained in a single basic set Λ_i. But then any neighborhood of Λ_i contains some Γ_k for large k. Hence Λ_i is not M-isolated. □

Basic sets need not be isolated in M (not even generically) and there may even be uncountably many of them. Hence it is often difficult to determine the complete decomposition into basic sets. Usually it is more convenient to find a finite covering $\{M_1, M_2, ..., M_n\}$ such that each basic set lies in one M_i. Such a *Morse decomposition* into closed invariant sets $\{M_1, \ldots, M_n\}$ is characterized by the property that for each $x \in M$, either $x \in M_i$ for some i, or $\omega(x) \subset M_i$ and $\alpha(x) \subset M_j$ for some $i < j$.

COROLLARY 3. *Let $\{M_1, \ldots, M_n\}$ be a Morse decomposition for M such that each Morse set M_i is also isolated in X. Then M is a repeller if and only if no M_i attracts orbits from $X \setminus M$, i.e. for each M_i, $W^s(M_i) \subset M$.*

Remark. This is essentially the Butler-Freedman-Waltman persistence theorem (see Theorem 3.1 of [4]). Their acyclic covering of the ω-limit sets of M is indeed a Morse decomposition, as shown e.g. in [7]. The proof of this uses the so-called Butler-McGehee lemma, which by itself is a simple consequence of the

Ura-Kimura theorem. We conclude with a simple combination of Corollary 1 and Theorem 3.

COROLLARY 4. *Suppose that for each basic set Λ (or each Morse set M_i of a Morse decomposition of M) there is a function P which is defined in a neighbourhood U of Λ (resp. M_i) and satisfies the conditions of Corollary 1 or 2 in this neighbourhood U. Then M is a repeller.*

In applications to ecological problems one usually encounters the nonnegative orthant $\mathbb{R}^n_+$ as state space, and a dissipative flow thereon. Considering the one-point compactification $X = \mathbb{R}^n_+ \cup \{\infty\}$, the system is *permament* or *uniformly persistent* iff the closed invariant subset $M = \mathrm{bd}\mathbb{R}^n_+ \cup \{\infty\}$ is a repeller. Another way would be to take X_1 as the set of all bounded orbits in $\mathbb{R}^n_+$, that is the dual attractor of the repeller $\{\infty\}$, and M_1 the dual attractor to $\{\infty\}$ in $\mathrm{bd}\mathbb{R}^n_+$.

Corollary 4 above provides a natural combination of the two dual approaches to persistence problems, opened by Freedman and Waltman [8] and Schuster and Sigmund [19], respectively. It seems the most effective for concrete applications: Determine first the basic sets of M, or find at least a suitably fine Morse decomposition. Then use Ljapunov type arguments to show that no orbit $x \in X \setminus M$ converges to or even stays near one of these basic sets. For a typical application see section 3.

Theoretically, the problem of persistence is thus reduced to the study of the local behaviour around basic sets. In ecological applications such basic sets - additionally to the 'classical' ones (fixed points, periodic orbits, suspensions of subshifts, etc.) - frequently occur as 'heteroclinic cycles' (a preliminary definition might be C^1-robust chain transitive set which is not contained in the interior of a single face of $\mathrm{bd}\mathbb{R}^n_+$). In simple cases the stability and bifurcation of such heteroclinic cycles in arbitrary dimensions has been discussed in [12], but further analysis is necessary.

2. Time averages and permanence of Lotka-Volterra equations

In this section we consider the familiar Lotka-Volterra equations

$$\dot{x}_i = x_i\Big(r_i + \sum_{j=1}^{n} a_{ij}x_j\Big) \qquad i = 1,\dots,n \tag{2}$$

and assume throughout that they are dissipative, i.e. their orbits are uniformly bounded for $t \to +\infty$: there is a constant K such that

$$\limsup_{t\to+\infty} x_i(t) \le K \qquad \text{for all } x \in \mathbb{R}^n_+.$$

Explicit criteria for this are given in [14, ch. 21.2].

There are two sufficient conditions for permanence for such Lotka-Volterra systems, see Jansen [16] and Hofbauer and Sigmund [13,14].

Theorem 4. *If the system of linear inequalities*

$$\sum_{i=1}^{n} p_i\big(r_i + (Ax)_i\big) > 0, \tag{3}$$

where x runs through all boundary fixed points of (2), admits a positive solution $p_i > 0$ then (2) is permanent.

Theorem 5. *If the convex hull C of all boundary fixed points is disjoint from the set $D = \{x \in \mathbb{R}^n_+ : r + Ax \leq 0\}$ then (2) is permanent.*

The proof of Theorem 4 consists in checking that $P(x) = \prod x_i^{p_i}$ is an average Ljapunov function and satisfies (b') of Corollary 2. Theorem 5 can be reduced to Theorem 4. It is the aim of this section to give a new, independent proof of this 'geometric condition' for permanence, without recourse to average Ljapunov functions.

The key is to study the asymptotic behaviour of time averages for Lotka-Volterra equations for which we introduce the following notation:

$$\begin{aligned} m_T(x) &= \frac{1}{T}\int_0^T x(t)\,dt \\ \mu(x) &= \{y : y = \lim_{T_n \to +\infty} m_{T_n}(x)\} \\ \mu(A) &= \bigcup_{x \in A} \mu(x) \end{aligned} \tag{4}$$

A classical result (going back to Volterra) states that for a 'persistent' orbit $x(t)$, $\mu(x)$ consists only of interior fixed points (in general a unique one). This follows from the identity

$$\frac{\log x_i(T) - \log x_i(0)}{T} = r_i + \big(Am_T(x)\big)_i. \tag{5}$$

If $\liminf_{t\to+\infty} x_i(T) > 0$, the left hand side goes to 0. Hence any $z \in \mu(x)$ is a fixed point of (2).

For arbitrary x this argument yields only

$$\mu(x) \subset D. \tag{6}$$

If one ignores the trivial case $\omega(x) = \{0\}$, then $0 \notin \omega(x)$ and hence $\mu(x) \subset \mathrm{bd}D$.

To get further information on $\mu(x)$ we first need a general fact on the limit sets $\mu(x)$ of time averages, valid for dynamical systems on a convex subset of a normed space.

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$$\mu(x) \subset conv\, \mu(\omega(x))$$

Proof. We show that for any given $\varepsilon > 0$, $\mu(x)$ is contained in the ε-neighbourhood of $\operatorname{conv} \mu(\omega(x))$. Obviously, for each z there is a time $T = T(\varepsilon, z)$ such that $d(m_T(z), \mu(z)) < \frac{\varepsilon}{2}$. Although T is in general not a bounded function of z (e.g. near an unstable fixed point), we still can conclude the existence of a constant $\tau = \tau(\varepsilon, K)$ such that

$$\forall z \in K \quad \exists\, T \in [1, \tau(\varepsilon, K)] : d\big(m_T(z), \mu(K)\big) < \frac{\varepsilon}{2}$$

for any compact set K which in our case will be $\omega(x)$ or $\overline{\gamma^+(x)}$. Now choose $\delta > 0$ such that

$$|y - z| < \delta \Longrightarrow |y(t) - z(t)| < \frac{\varepsilon}{2} \text{ for } 0 \le t \le \tau(\varepsilon) \text{ and } y, z \in \overline{\gamma^+(x)}$$

and hence

$$|m_T(y) - m_T(x)| < \frac{\varepsilon}{2} \text{ for } 0 \le T \le \tau(\varepsilon).$$

Now consider the orbit $x(t)$, and find a $t_0 > 0$ such that $d\big(x(t), \omega(x)\big) < \delta$ for all $t \ge t_0$. Then there exists a $z_0 \in \omega(x)$ such that $|x(t_0) - z_0| < \delta$ and hence a time $T_1 \in [1, \tau(\varepsilon)]$ with

$$|m_{T_1}(x(t_0)) - m_{T_1}(z_0)| < \frac{\varepsilon}{2} \text{ and } |m_{T_1}(z_0) - \mu(\omega(x))| < \frac{\varepsilon}{2}.$$

Thus we have a $T_1 \in [1, \tau(\varepsilon)]$ such that

$$d\big(m_{T_1}(x(t_0)), \mu(\omega(x))\big) < \varepsilon.$$

Repeating this argument, we find a point $z_1 \in \omega(x)$ near $x(t_0 + T_1)$, etc. Hence $m_T(x)$ can be represented as a convex linear combination of vectors $m_{t_0}(x), m_{T_1}(x(t_0)), m_{T_2}(x(t_0 + T_1)), \ldots$ each of which (up to the first and the last one, whose weight goes to 0 as $T \to \infty$) is ε-close to $\mu(\omega(x))$. So $m_T(x)$ itself is ε-close to $\operatorname{conv} \mu(\omega(x))$ for large T. □

Now let $\mathcal{F}_x$ denote the set of all open faces of $\mathbb{R}^n_+$ met by $\omega(x)$:

$$\mathcal{F}_x = \big\{I \subset \{1, \ldots, n\} : \exists z \in \omega(x), \operatorname{supp} z = I\big\},$$

and let $\mathcal{G}_x = \{F_I : I \in \mathcal{F}_x\}$ consist of all rest points $z = F_I$ with $r_i + (Az)_i = 0$ and $z_i \ge 0$ for $i \in I$ and $z_i = 0$ for $i \notin I$ in those faces, and let

$$C_x = \operatorname{conv} \mathcal{G}_x$$

be the convex hull of those fixed points. Then we have

Theorem 6. *For Lotka-Volterra equations: $\mu(x) \subset C_x$.*

Proof. By induction on the size of the support of x. Suppose w.l.o.g. that the statement is true for all $y \in \text{bd}\mathbb{R}^n_+$, and let $x \in \text{int}\mathbb{R}^n_+$. If $\omega(x) \subset \text{bd}\mathbb{R}^n_+$ then by induction hypothesis $\mu(y) \subset C_y \subset C_x$ for all $y \in \omega(x)$, since $\omega(y) \subset \omega(x)$. Hence $\text{conv}\,\mu(\omega(x)) \subset C_x$, and together with the lemma, $\mu(x) \subset C_x$.
If $\omega(x) \not\subset \text{bd}\mathbb{R}^n_+$ then we have to recall (5): if $\log x_i(T)/T > -\delta$ or $x_i(T) > e^{-\delta T}$ for all i then

$$|r + Am_T(x)| < \delta \qquad \text{for large } T. \tag{7}$$

For any given ε there is then a δ such that (7) implies that $m_T(x)$ is ε-close to an interior fixed point of (2). For a large time T consider now the last instance $T' \le T$ when $x_i(T') \ge e^{-\delta T'}$ holds for all i. For the remaining time $T' < t \le T$ at least one $x_i(t) < e^{-\delta t}$, so $x(t)$ is very close to $\text{bd}\mathbb{R}^n_+$. For this time interval we repeat the construction from the proof of the Lemma to find $m_{T-T'}(x(T'))$ ε-close to $\text{conv}\,\mu(\omega(x) \cap \text{bd}\mathbb{R}^n_+)$. Joining the two pieces puts $m_T(x)$ ε-close to C_x. □

As a consequence, $\mu(x) \subset C_x \cap D$. Now if $\omega(x) \subset \text{bd}\mathbb{R}^n_+$ then $C_x \subset C$, the convex hull of *all* boundary fixed points, and hence $\mu(x) \subset C \cap D$. This shows that *no interior orbit can converge to the boundary if $C \cap D = \emptyset$*, i.e. the second part (2) of Theorem 2. The isolatedness might be shown by a similar argument. We omit this here since we hope to replace it one day by a simple robustness argument.

Hence altogether the proof of Theorem 5 presented here won't be shorter than the original one. But the result on time averages might be of interest per se. A good example to illustrate it is the May-Leonard case where $\mu(x) = C_x \cap \text{bd}D$ equals the three sides of a triangle in $\text{int}\mathbb{R}^3_+$, see [14, ch. 9.5].

It has been shown in [14, ch. 22] that the conditions of Theorems 4 and 5 characterize robust permanence for $n = 3$. As shown in the next section, this is no longer true for $n \ge 4$. Like in section 1, the condition can be weakened, however. For a basic set Λ of $\text{bd}\mathbb{R}^n_+$, let $C_\Lambda = \bigcup_{x \in \Lambda} C_x$. Then the above proof yields

Theorem 7. *Suppose for each basic set Λ of the boundary $\text{bd}\mathbb{R}^n_+$, $C_\Lambda \cap D = \emptyset$, or equivalently that (3) holds for all fixed points $x \in C_\Lambda$. Then (2) is permanent.*

There is some evidence that Theorem 7 might even be a characterization of robust permanence for Lotka-Volterra equations.

3. An example

Let us consider now the following two-prey two-predator system

$$\begin{aligned}
\dot{x}_1 &= x_1\left(1-\frac{2}{3}x_1-\frac{1}{3}x_2-by_1-y_2\right)\\
\dot{x}_2 &= x_2\left(1-\frac{1}{3}x_1-\frac{2}{3}x_2-y_1-by_2\right)\\
\dot{y}_1 &= y_1(-1+2x_1+x_2)\\
\dot{y}_2 &= y_2(-1+x_1+2x_2)
\end{aligned} \tag{8}$$

This example nicely illustrates the method for proving permanence described in section 1. Furthermore it shows that the conditions given in Theorems 4 and 5 do *not characterize* permanence of Lotka-Volterra equations if $n \geq 4$. I realized this example while reading between the lines of Kirlinger's thesis [17].

(8) has the following fixed points:

$$F_1 = \left(\frac{3}{2},0,0,0\right),\ F_{12} = (1,1,0,0),\ F_1^1 = \left(\frac{1}{2},0,\frac{2}{3b},0\right),\ F_1^2 = \left(1,0,0,\frac{1}{3}\right),$$

$$F_{12}^{12} = \left(\frac{1}{3},\frac{1}{3},\frac{2}{3(b+1)},\frac{2}{3(b+1)}\right)$$

and their symmetric images F_2, F_2^1, F_2^2. From the external eigenvalues

$$\frac{\dot{x}_2}{x_2}(F_1^1) = \frac{5b-4}{6b},\quad \frac{\dot{x}_1}{x_1}(F_2^1) = \frac{2-b}{3},\quad \frac{\dot{y}_1}{y_1}(F_{12}) = 2,$$

we see that, for $b > 2$, F_2^1 is the only saturated fixed point in the subsystem $\{y_2 = 0\}$ and hence globally stable there (see Fig 1a). Since

$$\frac{\dot{y}_1}{y_1}(F_2^2) = -\frac{1}{2} < 0,\quad \frac{\dot{y}_2}{y_2}(F_2^1) = 1 > 0,$$

F_2^2 attracts all orbits in $\{x_1 = 0\}$ (Fig 1b).

In particular this shows the existence of a heteroclinic cycle γ: $F_1^1 \to F_2^1 \to F_2^2 \to F_1^2 \to F_1^1$. Since all orbits on the boundary of $\mathbb{R}_+^4$ converge to fixed points we obtain the following graphic description of the boundary flow (Fig 2), or after identifying the irreducible component corresponding to γ (Fig 3). It shows the topological structure of the boundary flow, i.e. the basic sets O, F_1, F_2, F_{12}, and γ, and the connections between them.

Since γ is a "planar" heteroclinic cycle (at each fixed point there is just one positive and one negative external eigenvalue), its stability is easily determined

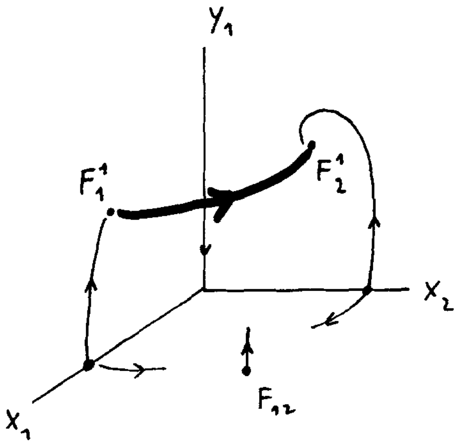

Figure 1a

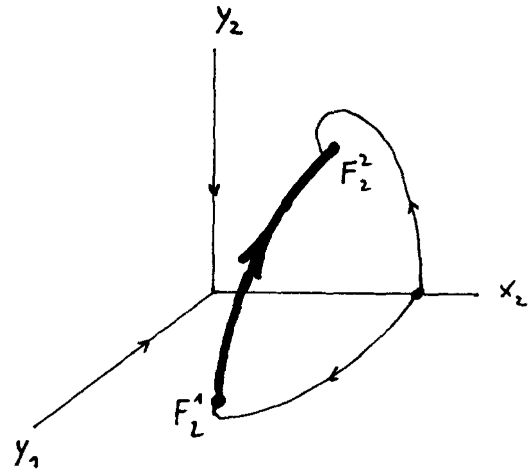

Figure 1b

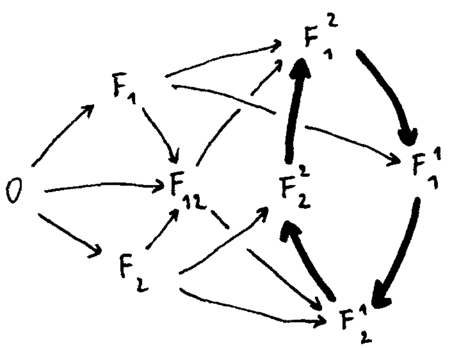

Figure 2

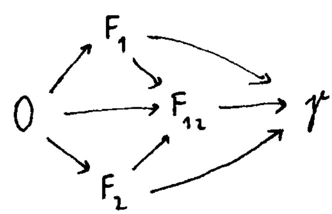

Figure 3

by the product of the ratios of the outgoing versus the incoming eigenvalues (see e.g. [11] or [14, ch. 22]). In view of the symmetry we only need to look at two fixed points, say F_1^1 and F_2^1):

$$\rho = \frac{5b-4}{6b} \cdot 2 \cdot \frac{3}{b-2} = \frac{5b-4}{b(b-2)}.$$

γ is attracting if $\rho < 1$, i.e. if $b > b_1 = \frac{7+\sqrt{33}}{2} \approx 6.4$, and repelling for $b < b_1$.

Hence the *system (8) is permanent for* $2 < b < b_1$, as a consequence of Theorem 3 since neither of the basic sets attracts interior orbits.

An alternative way to prove permanence of (8) would be to construct an average Ljapunov function P for the whole system and apply Corollary 2 (this way we need not know the complete structure of the basic sets, but use only the fact that all boundary orbits converge to fixed points):

$$P = (x_1 + x_2)^{p_0} x_1^{p_1} x_2^{p_2} y_1^{q_1} y_2^{q_2}$$

(this choice is motivated by Hutson [15]). Then

$$\frac{\dot{P}}{P} = p_0 \frac{\dot{x}_1 + \dot{x}_2}{x_1 + x_2} + p_1 \frac{\dot{x}_1}{x_1} + p_2 \frac{\dot{x}_2}{x_2} + q_1 \frac{\dot{y}_1}{y_1} + q_2 \frac{\dot{y}_2}{y_2}$$

Using the estimate

$$\frac{\dot{x}_1 + \dot{x}_2}{x_1 + x_2} \geq \min\left(\frac{\dot{x}_1}{x_1}, \frac{\dot{x}_2}{x_2}\right)$$

near the origin (the only point where $\dot{P}/P$ is not continuous), we need a solution of the following set of inequalities. (Those for F_1, F_2, and F_{12} are trivially satisfied.)

$$\begin{array}{ll} (O) & p_0 + p_1 + p_2 - q_1 - q_2 > 0 \\ (F_1^1) & \frac{5b-4}{6b} p_2 - \frac{1}{2} q_2 > 0 \\ (F_2^1) & -\frac{b-2}{3} p_1 + q_2 > 0 \\ (F_2^2) & \frac{5b-4}{6b} p_1 - \frac{1}{2} q_1 > 0 \\ (F_1^2) & -\frac{b-2}{3} p_2 + q_1 > 0 \end{array} \tag{9}$$

Because of the symmetry, we can set w.l.o.g. $p_1 = p_2 = p$ and $q_1 = q_2 = q$. Then (9) leads to

$$\frac{5b-4}{6b} > \frac{q}{p} > \frac{b-2}{3} \qquad \text{and} \qquad p_0 + 2p - 2q > 0.$$

The choice $p_0 = 0$, which corresponds to Theorem 4, is good only for $b < 5$. For $5 \leq b < b_1$ we need $p_0 \gg 0$ to satisfy the inequality for the origin. Geometrically (see Jansen [16] or the proof of Theorem 19.6.2 in [14]) this means that for $5 \leq b < b_1$, the interior fixed point F_{12}^{12} is contained in the convex hull of the five fixed points $O, F_1^1, F_1^2, F_2^1, F_2^2$ (but the cone D does not yet meet C_γ, the hyperplane through the four points F_i^j, and hence Theorem 7 applies). For $b = b_1$, F_{12}^{12} lies exactly on this hyperplane. For larger values of b, F_{12}^{12} lies in the hull of the F_i^j and F_{12}. So only for $b < 5$, F_{12}^{12} lies outside the convex hull of all boundary fixed points and Theorem 5 yields permanence.

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After presenting this lecture again at SISSA in Trieste in February 1988, F. Zanolin showed me a paper by B.M. Garay [10], who had the very same idea of applying the Ura-Kimura theorem and Conley's structure theorem to the question of persistence. I recommend his paper for more details.

References

1 N. P. Bhatia and G. P. Szegö: *Stability Theory of Dynamical Systems.* Grundlehren math. Wissensch. **161**. Berlin - Heidelberg - New York: Springer. 1970.

2 R. Bowen: ω-limit sets for Axiom A diffeomorphisms. J. Diff. Equ. **18**, 333-339 (1975).

3 G. Butler, H. I. Freedman and P. Waltman: Uniformly persistent systems. Proc. Amer. Math. Soc. **96**, 425-430 (1986).

4 G. Butler, P. Waltman: Persistence in dynamical systems. J. Diff. Equ. **63**, 255-263 (1986).

5 C. Conley: *Isolated invariant sets and the Morse index.* CBMS 38. Providence, R.I.: Amer. Math. Soc. 1978.

6 A. Fonda: Uniformly persistent semi-dynamical systems. Proc. Amer. Math. Soc. To appear.

7 H. I. Freedman and J. W.-H. So: Persistence in discrete semi-dynamical systems. Preprint (1987).

8 H. I. Freedman and P. Waltman: Mathematical analysis of some three-species food-chain models. Math. Biosci. **33**, 257-276 (1977).

9 T. C. Gard and T. G. Hallam: Persistence of food webs: I. Lotka-Volterra food chains. Bull. Math. Biol. **41**, 877-891 (1979).

10 B. M. Garay: Uniform persistence and chain recurrence. J. Math. Anal. Appl. To appear.

11 J. Hofbauer: A general cooperation theorem for hypercycles. Monatsh. Math. 91: 233-240 (1981).

12 J. Hofbauer: Heteroclinic cycles on the simplex. Proc. Int. Conf. Nonlinear Oscillations. Budapest 1987.

13 J. Hofbauer and K. Sigmund: Permanence for replicator equations. In: *Dynamical Systems.* Ed. A. B. Kurzhansky and K. Sigmund. Springer Lect. Notes Econ. Math. Systems **287**. 1987.

14 J. Hofbauer and K. Sigmund: *Dynamical Systems and the Theory of Evolution.* Cambridge Univ. Press 1988.

15 V. Hutson: A theorem on average Ljapunov functions. Monatsh. Math. **98**, 267-275 (1984).

16 W. Jansen: A permanence theorem for replicator and Lotka-Volterra systems. J. Math. Biol. **25**, 411-422 (1987).

17 G. Kirlinger: *Permanence of some four-species Lotka-Volterra systems.* Dissertation. Universität Wien. 1987.

18 C. Robinson: Stability theorems and hyperbolicity in dynamical systems. Rocky Mountain J. Math. **7**, 425-434 (1977).

19 P. Schuster, K. Sigmund and R. Wolff: Dynamical systems under constant organization. III. Cooperative and competitive behaviour of hypercycles. J. Diff. Equ. **32**, 357-368 (1979).

20 T. Ura and I. Kimura: Sur le courant exterieur a une region invariante. Theoreme de Bendixson. Comm. Math. Univ. Sanctii Pauli **8**, 23-39 (1960).