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STRONG MONOTONICITY FOR ANALYTIC ORDINARY DIFFERENTIAL EQUATIONS

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Abstract. We present a necessary and sufficient criterion for the flow of an analytic ordinary differential equation to be strongly monotone; equivalently, strongly order-preserving. The criterion is given in terms of the reducibility set of the derivative of the right-hand side. Some applications to systems relevant in biology and ecology, including nonlinear compartmental systems, are discussed.

1. Introduction

The qualitative theory of cooperative ordinary differential equations was initiated by Hirsch [4], [5], who proved a number of strong results on limit sets, in particular on convergence to stationary points. Hirsch, Smith and others extended the theory to monotone semiflows on ordered metric spaces; see the monograph by Smith [14] and the article by Hirsch and Smith in [7] for an account and overview of the theory. The strong order-preserving (SOP) property for monotone semiflows is of particular importance in this context: As stated in Smith [14, Ch. 1, Thm. 4.3], quasiconvergence is generic for SOP monotone semiflows that satisfy certain compactness properties for forward trajectories. The SOP property is closely related to (eventual) strong monotonicity.

Limit sets of monotone dynamical systems may still be very complicated, even in the SOP scenario; see the recent paper by Enciso [3] which extends a classical result by Smale [13]. Moreover, the question of relaxing or replacing conditions for quasiconvergence or convergence is of continuing interest. Thus the investigation of limit sets for monotone dynamical systems continues to be a very active area of research. Some recent contributions are due to Jiang and Wang [10] on Kolmogorov systems (in particular in dimension three), to Hirsch and Smith [8] on the existence of asymptotically stable equilibria, and to Sontag and Wang [15] who showed that the limit set dichotomy is not always satisfied. Hirsch and Smith, in their survey [7], improved and extended a number of results.

The present note is concerned with a technical issue: How can strong monotonicity for cooperative ordinary differential equations $\dot{x} = f(x)$ be established? The basic result is due to Hirsch [5]; see also Smith's monograph [14, Ch. 4, Thm. 1.1]:

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If the derivative $Df(x)$ is irreducible at every point then the local flow is strongly monotone and therefore SOP. It has been noted (see e.g. [14, Ch. 4, Remark 1.1]) that the condition can be relaxed. For the related problem of a non-autonomous cooperative linear system $\dot{x} = A(t)x$, Andersen and Sandqvist [1] proved that the following condition for strong monotonicity is necessary and sufficient: The matrix $A(t)$ is irreducible for all t in an everywhere dense set. Hirsch and Smith gave several strong monotonicity criteria for non-autonomous and autonomous systems; see [7, Lemma 3.7, Theorem 3.8, Corollary 3.11 and Theorem 3.13].

We will prove a necessary and sufficient strong monotonicity criterion for the autonomous analytic case, building on Smith [14], and Hirsch and Smith [7]: Informally speaking, the system is not strongly monotone if and only if its reducibility set (to be defined below) contains an invariant subset with certain geometric properties. Analyticity is required because the identity theorem will be used at some points. Moreover, analyticity allows a quite strong statement of the criterion, which therefore is useful in actual computations. We demonstrate this by a number of examples with relevance to biology and ecology.

2. Reducibility sets and strong monotonicity

Let us first introduce some notation and terminology. Given a positive integer n, let $N := \{1, \dots, n\}$. If S is a nonempty and proper subset of N, we say that a matrix $C = (c_{ij}) \in \mathbb{R}^{(n,n)}$ is *S-reducible* if $c_{ij} = 0$ for all $i \in S$ and $j \in N \setminus S$. Hence the subspace

$$W_S := \{x \in \mathbb{R}^n : x_i = 0 \text{ for all } i \in S\},$$

is mapped to itself by an S-reducible matrix. Note that C is reducible in the usual sense if it is S-reducible for some $\emptyset \subset S \subset N$. A reducible matrix C may be S_1-reducible and S_2-reducible with different subsets S_1 and S_2 of N. In this case, one easily verifies that C is also $S_1 \cap S_2$-reducible if $S_1 \cap S_2 \neq \emptyset$. Now let $D \subseteq \mathbb{R}^p$ be open and nonempty, and

$$D \to \mathbb{R}^{(n,n)}, \quad t \mapsto A(t)$$

an analytic map. The *S-reducibility set* of A is defined as

$$R_S = R_S(D) := \{t \in D : A(t) \text{ is } S\text{-reducible}\},$$

and the *reducibility set* $R = R(D)$ of A is defined as the union of all R_S. One may extend this notion to $R_S(V)$ and $R(V)$ for subsets $V \subseteq D$.

As usual, we denote by P the closed positive orthant in $\mathbb{R}^n$, and write $z \le w$ if $w - z \in P$, $z < w$ if $w - z \in P$ and $w \neq z$, and $z \ll w$ if $w - z \in \operatorname{int} P$.

The following results are essentially taken from Smith [14, Chapter 4, Theorem 1.1], and its proof; they can also be deduced from Andersen and Sandqvist [1]. We include a proof here for the reader's convenience, and because some aspects will be important later on. Note that the analyticity requirement leads to sharper results.

Lemma 2.1. *Let $D \subseteq \mathbb{R}$ be a nonempty open interval with $0 \in D$, and let*

$$D \to \mathbb{R}^{(n,n)}, \quad t \mapsto A(t) = (a_{ij}(t))$$

be analytic such that for all distinct i, j and all $t \ge 0$ one has $a_{ij}(t) \ge 0$. Let $X(t) = (x_{ij}(t))$ satisfy the linear matrix equation

$$\dot{X}(t) = A(t) \cdot X(t),$$

with $X(0) = E$, the unit matrix. Then the following hold:

(a) *Given $i, j \in N$, one has $x_{ij}(t) \geq 0$ for all $t \geq 0$. Furthermore, either $x_{ij} = 0$ or $x_{ij}(t) > 0$ for all $t > 0$ in D. In case $i = j$ the second alternative holds.*
(b) *Let i, j be such that $x_{ij} = 0$, and let*

$$\widetilde{S} = \widetilde{S}(j) := \{k \in N : x_{kj} = 0\}.$$

Then $a_{k\ell} = 0$ for all $k \in \widetilde{S}$ and $\ell \in N \setminus \widetilde{S}$, hence $A(t)$ is $\widetilde{S}$-reducible for all $t \in D$.

Proof. One has

$$\dot{x}_{ij}(t) = \sum_{\ell=1}^{n} a_{i\ell}(t)x_{\ell j}(t) \tag{2.1}$$

for all $t \in D$ and all $1 \leq i, j \leq n$, and the x_{ij} are analytic functions of t. If there is some $t_0 \geq 0$ such that $x_{ij}(t_0) = 0$, and all $x_{\ell j}(t_0) \geq 0$, then the equality in (2.1) shows $\dot{x}_{ij}(t_0) \geq 0$. This is sufficient, by standard arguments on positive invariance, to ensure $x_{ij}(t) \geq 0$ for all $t \in D$, $t \geq 0$. (See [14, Ch. 3, Remark 1.3], and [7, Prop. 2.3.]) Now let $t_1 \in D$ with $t_1 \geq 0$ such that $x_{ij}(t_1) > 0$. Then (2.1) shows

$$\dot{x}_{ij}(t) \geq a_{ii}(t)x_{ij}(t)$$

and therefore

$$x_{ij}(t) > 0 \text{ for all } t \geq t_1$$

by properties of scalar differential inequalities. Thus, if $t_2 > 0$ and $x_{ij}(t_2) = 0$ then $x_{ij} = 0$ due to the identity theorem.

As for part (b), we first note that $\widetilde{S}$ is nonempty by definition, and $\widetilde{S} \neq N$ due to $x_{ii} \neq 0$. Let $k \in \widetilde{S}$, thus $x_{kj} = 0$. Then (2.1) shows

$$0 = \dot{x}_{kj}(t) = \sum_{\ell=1}^{n} a_{k\ell}(t)x_{\ell j}(t) = \sum_{\ell \in N \setminus \widetilde{S}} a_{k\ell}(t)x_{\ell j}(t).$$

For all $t > 0$ and $\ell \in N \setminus \widetilde{S}$ we have $x_{\ell j}(t) > 0$ by part (a), thus $a_{k\ell}(t) = 0$. □

Remark. From Andersen and Sandqvist [1] one sees that, in this scenario, the matrix $X(t)$ will also be $\widetilde{S}$-reducible. Essentially their argument uses the unique solution property of the differential equation.

Now consider an ordinary differential equation

$$\dot{x} = f(x) \text{ on } U \subseteq \mathbb{R}^n, \tag{2.2}$$

with U nonempty, open, connected and P-convex, and f analytic. We denote the solution with initial value y at $t = 0$ by $\Phi(t, y)$, and call Φ the local flow of (2.2). Recall that $D_2\Phi(t, y)$ satisfies the variational equation

$$\frac{\partial}{\partial t} D_2\Phi(t, y) = Df\big(\Phi(t, y)\big)D_2\Phi(t, y)$$

with initial value E. In this paper we will always assume that (2.2) is cooperative on U, thus for $i, j \in N$ with $i \neq j$ and for all $x \in U$ the inequalities

$$\frac{\partial f_i}{\partial x_j}(x) \geq 0$$

hold. We note that for every $y \in U$, Lemma 2.1 is applicable to the matrix $X(t) = D_2\Phi(t, y)$ with $A(t) = Df\big(\Phi(t, y)\big)$.

Due to cooperativity, the local flow of (2.2) is monotone. The local flow of the cooperative system (2.2) is said to be strongly order-preserving (SOP) if for all

$z, w \in U$ with $z < w$ there are neighborhoods V_z of z and V_w of w and some $t_0 > 0$ such that $\Phi(t_0, V_z) \leq \Phi(t_0, V_w)$. The following characterization is essentially known from [14] or [7]. We include a proof of one implication for the reader's convenience.

Lemma 2.2. *For the cooperative analytic system* (2.2) *the following are equivalent:*
(i) Φ *is strongly monotone, thus for all* $z, w \in U$ *with* $z < w$ *one has* $\Phi(t, z) \ll \Phi(t, w)$ *for all* $t > 0$.
(ii) Φ *is eventually strongly monotone, thus for all* $z, w \in U$ *with* $z < w$ *there is some* $t_0 > 0$ *such that* $\Phi(t_0, z) \ll \Phi(t_0, w)$.
(iii) Φ *is SOP.*

Proof. "(ii) $\Rightarrow$ (i)": If Φ is not strongly monotone then there exist $z < w$ and $t_0 > 0$ such that

$$(\Phi(t_0, w) - \Phi(t_0, z))_i = 0 \quad \text{for some } i.$$

Then monotonicity shows $(\Phi(t, w) - \Phi(t, z))_i = 0$ for $0 \leq t \leq t_0$, thus for all $t > 0$ by the identity theorem, and Φ is not eventually strongly monotone.
"(ii) $\Leftrightarrow$ (iii)": See [14, Ch. 1, Lemma 1.1] and [7, Prop. 1.2]. □

The starting point for any discussion of ordering properties is the following identity:

$$\Phi(t, w) - \Phi(t, z) = \int_0^1 D_2\Phi(t, z + s(w - z)) \cdot (w - z)\, \mathrm{d}s \tag{2.3}$$

One can use this to give a quite precise description of analytic monotone local flows that are not strongly monotone.

Theorem 2.3. *Let the cooperative analytic system* (2.2) *be given on the P-convex, open and connected set U, and denote by Φ its local flow. Then the following are equivalent:*
(a) Φ *is not strongly monotone.*
(b) *There exist* $z, w \in U$ *with* $z < w$ *and a subset* $\emptyset \neq S \subset N$ *such that:*
  (i) $w - z \in W_S$, *thus* $w_i - z_i = 0$ *for all* $i \in S$;
  (ii) $Df\,(\Phi(t, z + s(w - z)))$ *is S-reducible for* $0 \leq s \leq 1$ *and all t in the (respective) maximal existence interval.*

Proof. One direction of the proof is immediate: If $Df(\Phi\,(t, z + s(w - z))$ is S-reducible for all $t > 0$ and $0 \leq s \leq 1$ then the same holds for $D_2\Phi\,(t, z + s(w - z))$, as noted in the Remark following Lemma 2.1. Now a straightforward application of (2.3) shows the assertion.

For the reverse direction, assume that Φ is not strongly monotone. Then there exist $z, w \in U$ such that $w > z$ and $\Phi(t, w) - \Phi(t, z) \notin \operatorname{int} P$ for all positive t in some neighborhood of 0. Let $T > 0$ such that $\Phi(t, z + s(w - z))$ exists for $0 \leq s \leq 1$ and $0 \leq t < T$, and abbreviate

$$B(t, s) = (b_{ij}(t, s)) := D_2\Phi\,(t, z + s(w - z))\,, \quad 0 \leq s \leq 1,\ 0 \leq t < T.$$

Recall from (2.3) that

$$\Phi(t, w) - \Phi(t, z) = \int_0^1 B(t, s) \cdot (w - z)\, \mathrm{d}s.$$

By Lemma 2.1 all entries of $B(t, s)$ are nonnegative and the diagonal entries are > 0. Hence $\Phi(t, w) - \Phi(t, z) \notin \operatorname{int} P$ for some $t > 0$ implies that $w - z \notin \operatorname{int} P$. Therefore

$$S^* := \{i \in N : w_i - z_i = 0\}$$

is nonempty, and, by the same observation on diagonal entries of B,

$$(B(t,s)\cdot(w-z))_j = 0 \text{ for } t>0 \text{ only if } j\in S^*$$

whence

$$S := \{j\in N : (B(t,s)\cdot(w-z))_j = 0 \text{ for } t>0\}$$

is a subset of S^*, and $S\neq\emptyset$ due to the hypothesis. Now $b_{jk}(t,s)=0$ for all $j\in S$, $k\in N\setminus S^*$, $0\le s\le 1$ and $t>0$, in view of

$$0=\sum_\ell b_{j\ell}(w_\ell - z_\ell) = \sum_{k\in N\setminus S^*} b_{jk}(w_k-z_k).$$

For $k\in N\setminus S^*$ define $\widetilde{S}(k) := \{j\in N : b_{jk}=0\}$. Lemma 2.1 and the proven part of the assertion show $\widetilde{S}(k)$-reducibility. From

$$S=\cap_{k\in N\setminus S^*}\widetilde{S}(k)$$

we obtain S-reducibility. □

Note that in the scenario of Theorem 2.3 certain matrix entries of

$$Df\left(\Phi(t,z+s(w-z))\right)$$

vanish for all $(s,t)\in(0,1)\times(0,T)$, and hence (by the identity theorem) for all t where the solution is defined. Thus all $\Phi(t,z+s(w-z))$ lie in the S-reducibility set $R_S(U)$ for $x\mapsto Df(x)$. This means that $R_S(U)$ contains an invariant subset for (2.2), which in turn contains z and w. We have shown:

Corollary 2.4. *Let the cooperative analytic system* (2.2) *be given. Assume that for every nonempty proper subset S of N the S-reducibility set does not contain an invariant subset Y such that*

$$\{z+s(w-z) : 0\le s\le 1\}\subseteq Y$$

for some $z<w$ with $w-z\in W_S$. Then the local forward flow is SOP. In particular, if the reducibility set of Df does not contain an invariant subset of (2.2) *then the local forward flow is SOP.*

Remark. One may sharpen the condition on Y by requiring connectedness. This is obvious from invariance.

The following technical observation will be of some use in practical applications.

Corollary 2.5. *Given the scenario of Theorem 2.3(b), abbreviate*

$$y(t,s) := \Phi\left(t,z+s(w-z)\right).$$

Then

$$\frac{\partial}{\partial t}\frac{\partial}{\partial s}y(t,s) = Df\left(y(t,s)\right)\frac{\partial}{\partial s}y(t,s), \tag{2.4}$$

In particular, $y(t,s)\ge 0$ for all s and all $t\ge 0$.

Proof. Use (2.2) for $y(t,s)$ and differentiate with respect to s to obtain the identity (2.4). Moreover, $y(0,s)=z+s(w-z)$ implies

$$\frac{\partial}{\partial s}y(0,s) = w-z\ge 0,$$

and the assertion follows from cooperativity. □

Condition (i) of Theorem 2.3(b) is familiar; its importance has been recognized in Hirsch and Smith [7, Lemma 3.7, Theorem 3.8, Corollary 3.11 and Theorem 3.13]. Invariance - in the analytic case - appears to be a new aspect. As will be seen below, this property is quite useful in practical applications.

Obviously one can extend the arguments above to cooperative systems with (sufficiently) continuously differentiable right-hand side, but it seems more appropriate to do so on a case-by-case basis, rather than try to write down a rather unwieldy list of conditions. One problem is that Lemma 2.1 is not generally true in the non-analytic setting; an other problem is that - even if Lemma 2.1 holds for some equation - the invariance condition from Corollary 2.4 needs to be replaced by a weaker condition of local positive invariance.

Hirsch and Smith [7, Sections 3.1 and 3.2] present an extension of many results to systems cooperative with respect to an arbitrary order cone (with nonempty interior); see Volkmann [16], and also [17]. It is natural to ask about possible extensions of the results presented above; hence we will briefly address this question. The notion of S-reducibility can be generalized to the notion of reducibility with respect to a nontrivial face of the cone. The main problem is that no good counterpart to Lemma 2.1 (which rests on specific properties of the positive orthant P) seems to exist. Moreover, there is no obvious generalization of Andersen and Sandqvist [1] to more general cones. (Andersen and Sandqvist essentially consider linear systems with matrix in block triangular form; this is only possible for orthants as order cones.) Of course, some of the arguments leading to Theorem 2.3 and the two corollaries can be carried over, mutatis mutandis, as demonstrated by Hirsch and Smith in [7], and this extends to the invariance argument. As there seem to be no applications readily available, we will not carry this further.

3. Examples and applications

Example 1: A biochemical control circuit. The system

$$\begin{aligned} \dot{x}_1 &= g(x_n) - \alpha_1 x_1 \\ \dot{x}_i &= x_{i-1} - \alpha_i x_i \quad 2 \le i \le n \end{aligned} \tag{3.1}$$

on (some neighborhood of) the positive orthant in $\mathbb{R}^n$ models a biochemical control circuit; see Murray [11, Section 6.2] and Smith [14, Ch. 4, Section 2]. The function g sends $\mathbb{R}_+$ to $\mathbb{R}_+$ and is bounded. In the case of positive feedback (which we will consider here), g is strictly increasing. For analytic g, this is equivalent to the property that $g' \ge 0$ and g' not identically zero. The derivative of the right-hand side is given by

$$C(x) = (c_{ij}(x)) = \begin{pmatrix} * & 0 & \cdots & \cdots & 0 & g'(x_n) \\ 1 & * & \ddots & & & 0 \\ 0 & \ddots & \ddots & & & \vdots \\ \vdots & & & & \ddots & \vdots \\ \vdots & & \ddots & \ddots & * & 0 \\ 0 & \cdots & \cdots & 0 & 1 & * \end{pmatrix}$$

If $g' > 0$ then, as noted in Smith [14], this matrix is irreducible for all x, and thus the forward flow of (3.1) is strongly monotone. Let us now replace the condition

$g' > 0$ by the more natural requirement that g is strictly increasing, albeit at the expense of requiring analyticity.

If C is S-reducible for some set S then $i \in S$ and $i > 1$ imply $i - 1 \in S$ because of $c_{i,i-1} \neq 0$. This only leaves the possibilities

$$S = \{1, \dots, k\}, \quad \text{some } k < n,$$

and

$$x \in R_S \Leftrightarrow g'(x_n) = 0.$$

We will verify strong monotonicity for the flow. Assume that for $S = \{1, \dots, k\}$ there exist a connected invariant set $Y \subseteq R_S$, and $\{z + s(w - z)\} \subseteq Y$ with $w > z$ and $w - z \in W_S$. Since the roots of g' are isolated, all elements of Y have the same n^{th} component, say c, and the solution $y = y(t, s)$ (see Corollary 2.5) satisfies $y_n = c$. This implies $z_n = w_n$.

From (2.4), we obtain

$$\frac{\partial}{\partial t} \frac{\partial}{\partial s} y(t, s)|_{t=0} = C\left(z + s(w - z)\right) \cdot (w - z).$$

Since $y_n(t, s)$ is constant, the left hand side has entry 0 at position n, as has $w - z$. The form of C then implies that $w - z$ has entry 0 at position $n - 1$. Proceed by obvious induction to arrive at $z = w$; a contradiction. Thus no such set Y exists, and we have strong monotonicity.

Example 2: A modified Michaelis-Menten system. The three-dimensional system

$$\begin{aligned} \dot{x}_1 &= -x_1 + (u + ax_1)x_2 + b(1 - x_1)h(x_3) \\ \dot{x}_2 &= c(x_1 - ax_1x_2 - vx_2) \\ \dot{x}_3 &= d(x_2 - x_3) \end{aligned} \tag{3.2}$$

on the positive orthant of $\mathbb{R}^3$ describes a biochemical reaction through a membrane; see Sanchez [12]. Here a, b, c, d, u, v are positive constants, and h is a decreasing function that sends $\mathbb{R}_+$ to itself. Following Sanchez [12], we focus interest on a certain positively invariant subset U which is contained in

$$\{x \in \mathbb{R}^3 : x_1 > 1, 0 < x_2 < a^{-1}, x_3 > 0\}.$$

On this set U the derivative of the right-hand side is given by

$$C(x) = \begin{pmatrix} * & u + ax_1 & b(1 - x_1)h'(x_3) \\ c(1 - ax_2) & * & 0 \\ 0 & d & * \end{pmatrix}$$

and the forward flow is therefore monotone. Sanchez [12] requires $h' < 0$ to conclude irreducibility of all $C(x)$ and thus strong monotonicity of the forward flow on U, on the way to proving convergence to the set of equilibria for any initial value in $\mathbb{R}^3_+$.

Again, we relax the condition on h' at the expense of requiring analyticity; thus we assume $h' \leq 0$ but not identically zero, and h strictly decreasing. The matrix $C(x)$ is reducible for $x \in U$ if and only if $h'(x_3) = 0$, and in this case the matrix is S-reducible only for $S = \{1, 2\}$. Assume that $Y \subseteq R_S(U)$ is invariant and connected. Then necessarily all elements of Y have the same third entry, say c, thus all $z, w \in Y$ satisfy $w_3 - z_3 = 0$. But then the condition $w - z \in W_S$ forces $z = w$, and Corollary 2.4 shows strong monotonicity.

Example 3: A cooperative Volterra-Lotka system with influx. Consider the n-dimensional system

$$\dot{x}_i = x_i\Big(\sum_j \beta_{ij}x_j + \gamma_i\Big) + \delta_i, \quad 1 \le i \le n, \tag{3.3}$$

with real constants $\delta_i \ge 0$, γ_i and β_{ij} on (some open neighborhood of) the positive orthant P, with $\beta_{ij} \ge 0$ whenever $i \ne j$. In the case that all $\delta_i = 0$ we have a Volterra-Lotka system for cooperating species. There is continued interest in Volterra-Lotka systems, both due to the (seeming) simplicity of their structure and to the challenges they pose to qualitative theory. We refer to the monograph [9] by Hofbauer and Sigmund for an introduction and an account of fundamental results. Note that Volterra-Lotka systems are special Kolmogorov systems.

Abbreviating the right-hand side of (3.3) by $f_i(x)$, $1 \le i \le n$, one sees that

$$\frac{\partial f_i}{\partial x_j} = \beta_{ij}x_i,$$

whenever $i \ne j$, hence the system is cooperative on the positive orthant. We now restrict attention to the special case of an irreducible matrix (β_{ij}). In this case we have

$$R_S(P) = W_S \cap P.$$

When all $\delta_i = 0$ then all R_S are invariant, as is well-known. Here one could say that the strong monotonicity criterion from Corollary 2.4 fails completely (and so does strong monotonicity). But on the other hand, consider the system when all $\delta_i > 0$ (influx of all species): Then no nonempty subset of the boundary of P is invariant, and therefore Corollary 2.4 shows that the forward flow is strongly monotone. This example illustrates the role of invariance in the criterion.

Example 4: A nonlinear compartmental system. Consider the n-dimensional system

$$\dot{x}_i = -\Big(\sum_{j\ne i} \rho_{ji}(x_i) + \gamma_i(x_i)\Big) + \sum_{j\ne i} \rho_{ij}(x_j) \tag{3.4}$$

on (some open neighborhood of) the positive orthant P. Thus we require the ρ_{ij} and γ_i to be defined and analytic on $(-\delta, \infty)$ for some $\delta > 0$. Moreover we require that for all distinct i and j the ρ_{ij} are nonnegative and increasing on $[0, \infty)$, with $\rho_{ij}(0) = 0$.

The differential equation thus describes a nonlinear compartmental system. Such systems are widely used in applications, e.g. in physiology and ecology; see the monographs by Anderson [2], and by Walter and Contreras [18]. Linear compartmental systems, which are very well-understood, satisfy $\rho_{ij}(x_j) = k_{ij} \cdot x_j$ with nonnegative constants k_{ij} for $i \ne j$. But nonlinear systems are common in applications, and in fact most linear compartmental systems should be seen as limiting cases of nonlinear ones. If one views the underlying model as a collection of reservoirs separated by membranes then it is quite natural to assume monotonicity of the transport rate from one reservoir to the other: Higher concentration of the substance in the reservoir leads to a higher outflow rate. This property translates to monotonicity of the ρ_{ij}.

Due to analyticity the ρ_{ij} are either strictly monotone or identically zero. Abbreviating the right-hand side of (3.4) by $f(x)$, we have

$$\frac{\partial f_i}{\partial x_j}(x) = \rho'_{ij}(x_j)$$

whenever $i \neq j$, and therefore the system is cooperative.

We will show: If the forward flow of (3.4) is not strongly monotone then there is a nonempty proper subset S^* of $N = \{1, \dots, n\}$ such that $R_{S^*}(P) = P$, thus $Df(x)$ is S^*-reducible for all $x \in P$. In other words: Unless there is no flow at all from some subsystem with labels in $N \setminus S^*$ to the complementary subsystem with labels in S^*, the forward flow will be strongly monotone. As usual, the technical problem in the proof is due to possible isolated zeros of the ρ'_{ij}.

Thus assume that there exists a connected invariant subset Y of P, contained in some $R_S(P)$, and containing all $z + s(w - z)$, where $z < w$ and $w - z \in W_S$. Let $y(t, s)$ be as in Corollary 2.5. Then we have

$$\rho'_{ij}\left(y_j(t, s)\right) = 0 \quad \text{for all } i \in S,\ j \in N \setminus S,$$

which implies either $y_j =$ const. or $\rho'_{ij} = 0$. If the second alternative always holds then the system is S-reducible. Otherwise there is some ℓ such that

$$y_\ell(t, s) = z_\ell = w_\ell = \text{const.},$$

thus $\frac{\partial}{\partial s} y_\ell(t, s) = 0$. By re-labelling, we may assume that there is an m such that

$$\begin{aligned} \frac{\partial}{\partial s} y_j(t, s) = 0 \quad &\text{for } 1 \leq j \leq m \\ \frac{\partial}{\partial s} y_j(t, s) \neq 0 \quad &\text{for } j > m. \end{aligned}$$

Note that $m < n$, otherwise $z = w$. Corollary 2.5 then implies

$$\frac{\partial}{\partial s} y_j(t, s) > 0 \quad \text{for } j > m,\ t > 0.$$

Now (2.4) shows directly that S^*-reducibility of $Df\left(y(t, s)\right)$, with $S^* := \{1, \dots, m\}$. Moreover, since y_j is not constant for any $j > m$, we find that $\rho'_{ij} = 0$ for all $i \in S^*$ and $j \notin S^*$. In other words, $Df(x)$ is S^*-reducible for all x.

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