MONOTONE DYNAMICAL SYSTEMS: REFLECTIONS ON NEW ADVANCES & APPLICATIONS

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Abstract. The article contains the author’s reflections on recent developments in a very select portion of the now vast subject of monotone dynamical systems. Continuous time systems generated by cooperative systems of ordinary differential equations, delay differential equations, parabolic partial differential equations, and control systems are the main focus and results are included which the author feels have had a major impact in the applications. These include the theory of competition between two species or two teams and the theory of monotone control systems.

1. Introduction. The theory of monotone dynamical systems grew out of the ground-breaking work of M.W. Hirsch [31, 32, 34, 35, 36, 37] and H. Matano [61, 63, 64] in the 1980s, largely focusing on ordinary differential equations and systems of parabolic partial differential equations. Since then, the theory has been extended to discrete-time dynamical systems [30, 78, 86, 81, 41, 69], to non-autonomous dynamical systems [14, 73, 96, 50, 69], to stochastic systems [16, 13], and to systems and control [2, 8, 90, 1]. The review article [77] and monograph [79] review much of the earlier theoretical developments; more recent reviews are [39, 38].

The aim of this paper is to provide some personal reflections on more recent developments in theory as well as new applications. It is most definitely not a review since that would require an enormous bibliography. Therefore, I must begin by apologizing to the many recent contributors to the literature on monotone systems whose work is not cited here. Of course, the research reported here will necessarily be biased toward areas with which I am most familiar and, to keep the length reasonable, I will focus on continuous time, autonomous, monotone dynamical systems.

Almost three decades since its development, the theory and applications continue to expand. A search on MathSciNet for journal articles since 2000 reveals 75 papers containing “monotone dynamical system”, 106 containing “monotone system”, and 225 containing “cooperative system”. Application areas cited: consensus in multi-agent networks, ecological systems [58, 26, 9, 19, 10, 25, 54, 15, 47, 46], control theory [2, 8], in-vivo disease modeling, chemical reaction dynamics [56, 4], epidemiology [2010 Mathematics Subject Classification. 34C11, 34C15, 34C25, 34C35, 34K15, 34K20, 35B40, 35B50, 35K55, 37N25.

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Monotone systems generated by ordinary differential equations on $\mathbb{R}^n$ with the usual componentwise ordering are commonly referred to as cooperative systems. The vector field $f$ in

$$x' = f(x) \quad (1.1)$$

must satisfy the quasi-monotone condition: $x_j \to f_i(x)$ is nondecreasing for $j \neq i$. In that case, the flow is order preserving

$$x_0 \leq x_1 \Rightarrow x(t,x_0) \leq x(t,x_1), \quad t > 0,$$

where $x(t,x_0)$ denotes the solutions satisfying $x(0,x_0) = x_0$. If $x,y \in \mathbb{R}^n$, we write $x \leq y$ ($x \ll y$) if $x_i \leq y_i$ ($x_i < y_i$) holds for all $i$ and write $x < y$ if $x \leq y$ and $x \neq y$. If, in addition, $f$ is smooth and its Jacobian matrix $Df(x)$ is irreducible for most $x$, then the flow is strongly order preserving

$$x_0 < x_1 \Rightarrow x(t,x_0) \ll x(t,x_1), \quad t > 0.$$

See e.g. [39, 38]. Recall that a matrix is irreducible if its directed incidence graph is strongly connected. We say that system (1.1) is cooperative and irreducible if these conditions are met.

An example is the simple model of a single species inhabiting a fragmented habitat consisting of $n$ “patches”:

$$x'_i = r_i x_i (1 - x_i/K_i) + \sum_j d_{ji} x_j - \sum_j d_{ij} x_i, \quad 1 \leq i \leq n$$

where $d_{ij} \geq 0$ represents the rate of migration from patch $i$ to patch $j$. It was considered by Lu and Takeuchi [58]. The system is cooperative and irreducible if matrix $(d_{ij})$ is irreducible.

A model of malaria infection of humans and mosquitos, formulated in [29], in which both humans and mosquitos spend time in various habitats is given by

$$x'_i = \left( \sum_{j=1}^{n} \rho_i^{-1} p_{ij} \rho_j P_0 \alpha_j^{-1} r_j y_j \right) (1 - x_i) - r_i x_i$$

$$y'_i = \left( \sum_{j=1}^{n} q_{ij} \alpha_j \mu_j x_j \right) (1 - y_i) - \mu_i x_i, \quad 1 \leq i \leq n,$$

where $x_i$ ($y_i$) represents the proportion of human (mosquito) residents of patch $i$ that are infected, $p_{ij}$ ($q_{ij}$) is the fraction of time a human (mosquito) resident of patch $i$ spends in patch $j$. The system is cooperative and irreducible on $[0,1]^2n$ if both $PQ$ and $QP$ are irreducible matrices [17, 71].

Additive neural networks are often described by the system

$$x'_i = -A_i x_i + \sum_{j=1}^{n} \tanh(x_j) W_{ij} + I_i$$

where $W_{ij}$ is the weight of connection $j$ to $i$. Here, $x_i$ denotes the activity level of the $i$-th neuron. If matrix $W_{ij} \geq 0, i \neq j$ and matrix $W$ is irreducible, then the system is cooperative and irreducible. See [94, 92, 18] for more work on cooperative neural networks.
Competition between two teams or two species can be modeled by the system

\[
x_1' = f_1(x_1, x_2), \quad (x_1, x_2) \in \mathbb{R}^k \times \mathbb{R}^{n-k},
\]

\[
x_2' = f_2(x_1, x_2).
\]

Here, \(x_1\) denotes the density of team one while \(x_2\) denotes that of team two. Competition between teams is captured by the following hypotheses:

(a) diagonal blocks \(\frac{\partial f_i}{\partial x_i}(x)\) have nonnegative off-diagonal entries.

(b) off-diagonal blocks \(\frac{\partial f_i}{\partial x_j}(x) \leq 0\) have non-positive entries.

Note that \(0 \leq k \leq n\) and that if \(k = 0, n\), the system satisfies the quasi-monotone condition considered above.

The competition (south-east) order relation on \(\mathbb{R}^n = \mathbb{R}^k \times \mathbb{R}^{n-k}\) is described as follows:

\[x = (x_1, x_2) \leq_C (\bar{x}_1, \bar{x}_2) = \bar{x} \iff x_1 \leq \bar{x}_1 \land x_2 \geq \bar{x}_2.\]

If \(x_i\) denotes densities of team \(i\), then team one is advantaged over team two in state \((\bar{x}_1, \bar{x}_2)\) versus state \((x_1, x_2)\) since it has greater density and team two has less.

The system (1.2) preserves the competitive ordering:

\[x(0) \leq_C \bar{x}(0) \Rightarrow x(t) \leq_C \bar{x}(t), \quad t \geq 0,\]

and, if \(D(f_1, f_2)\) is irreducible, the stronger condition

\[x(0) <_C \bar{x}(0) \Rightarrow x(t) \ll_C \bar{x}(t), \quad t \geq 0,\]

where \(<_C\) and \(\ll_C\) are defined analogous to \(<, \ll\). We include such systems among the cooperative and irreducible systems since a simple coordinate change in (1.2) leads to a system (1.1) satisfying the quasi-monotone condition [77].

An example is the repressilator, a 2-gene regulatory circuit, that can lead to bi-stable behavior. Each gene product acts to repress transcription of the other gene:

\[
x_i' = \beta_i (y_i - x_i)
\]

\[
y_i' = \alpha_i f_i(x_j) - y_i, \quad j \neq i
\]

where \(\alpha_i, \beta_i > 0\) and \(f_i > 0\) satisfies \(f'_i < 0\). \(x_i\) denotes the intra-cellular concentration of the protein product (transcription factor) of gene \(i\), \(y_i\) is the mRNA concentration of gene \(i\). The system generates a cooperative and irreducible system on \(\mathbb{R}_+^2 \times \mathbb{R}_+^2\), preserving the competitive ordering. See [24, 65].

Competition between Neanderthals and modern humans has been modeled by Gilpin et al [25]. Here, \(N_1\) represents Neanderthal densities and \(z_1\) represents a measure of the cultural level of Neanderthals; \(N_2, z_2\) denotes corresponding values.
for modern humans, 
\[ N_i' = r_i N_i \left( 1 - \frac{N_i + b_{ij} N_j}{M_i(z_i)} \right) \]
\[ z_i' = -\gamma_i z_i + \delta_i N_i, \quad i \neq j. \]

The carrying capacities \( M_i \) are assumed to be increasing with cultural level, dramatically so beyond a certain threshold value of cultural level. This leads to bi-stability in the single-species dynamics: a stable small population at low cultural level and a stable high population level at high cultural level. The competition coefficients are also assumed to depend monotonically on cultural levels
\[ b_{ij} = b_0 (1 + \epsilon (z_j - z_i)), \quad M'_i(z) > 0, \quad \epsilon > 0, \]
so that a higher cultural level species exerts a greater competitive effect on a lower cultural level rival: \( b_{ij} > b_{ji} \iff z_j > z_i \). Since humans are assumed to differ little from Neanderthals, it is natural to start by looking at the symmetric case where the parameters are independent of species. A large number of symmetric and asymmetric coexistence equilibria exist for the system but the focus of attention is on whether a relatively small group of modern humans can invade and drive to extinction a larger population of Neanderthals. The authors find that competitive exclusion is favored over coexistence as \( \epsilon, b_0 \) increase [25]. In this election year, it is tempting to apply these ideas to the two major political parties in the U.S., with slight changes in meaning of parameters.

A natural question is how to know if a given system of differential equations may be expressed in suitable coordinates as a cooperative system. Very little attention has been paid to this problem. Often a fortuitous nonlinear change of coordinates reveals a system with the required properties. See for example the variable changes in the model of population genetics in [28] to make it a cooperative planar system with competitive ordering. We can answer a less ambitious question, namely, given a system of differential equations, can it be expressed in the form (1.2) after suitable permutation of coordinates. The following conditions on the Jacobian matrix 
\[ Df(x) = (\frac{\partial f_i}{\partial x_j}(x))_{i,j} \]
characterize when the system, defined on a convex domain, can be put in the canonical form (1.2) by a permutation of variables:

(i) Sign Stability: no sign change of \( \frac{\partial f_i}{\partial x_j}(x) \), \( i \neq j \).
(ii) Sign Symmetry: \( \frac{\partial f_i}{\partial x_j}(x) \frac{\partial f_j}{\partial x_i}(y) \geq 0, \quad i \neq j, \forall x, y \).
(iii) Consistency: every loop in the (undirected) signed influence graph for the Jacobian \( Df(x) \) has an even number of negative edges.

The signed influence graph for the \( n \)-dimensional system, assuming that it is sign stable and sign symmetric, has vertices 1, 2, \ldots, \( n \). A positive edge joins vertex \( i \) to \( j \neq i \) if \( \frac{\partial f_i}{\partial x_j}(x) + \frac{\partial f_j}{\partial x_i}(x) \) is positive for some \( x \); a negative edge joins them if it is negative for some \( x \). See e.g. [83] for a proof and more details. It may be remarked that the requirement of sign stability is far more prevalent in systems that arise in the biological or chemical sciences where state variables are often intrinsically nonnegative than in the physical sciences where they are not.

An influential and inspiring introduction to systems biology and how monotone systems theory, as well as control theory ideas, may play a significant role in mathematical modeling in the field is contained in the article by E. Sontag [90]. An example from that paper is a model of a Mitogen-Activated Protein Kinase (MAPK) signaling cascade. These are common signaling modules in eukaryotic
cells, involved in such diverse cellular processes as proliferation, differentiation, development, movement, and apoptosis. The variables appearing in the model below represent the intra-cellular concentrations of various signaling molecules:

\[
\begin{align*}
    x' &= -\frac{v_2 x}{k_2 + x} + v_0 u + v_1 \\
    y_1' &= \frac{v_6 (y_{tot} - y_1 - y_3)}{k_6 + (y_{tot} - y_1 - y_3)} - \frac{v_3 y_1}{k_3 + y_1} \\
    y_3' &= \frac{v_4 x (y_{tot} - y_1 - y_3)}{k_4 + (y_{tot} - y_1 - y_3)} - \frac{v_5 y_3}{k_5 + y_3} \\
    z_1' &= \frac{v_{10} (z_{tot} - z_1 - z_3)}{k_4 + (z_{tot} - z_1 - z_3)} - \frac{v_7 y_3 z_1}{k_7 + z_1} \\
    z_3' &= \frac{v_8 y_3 (z_{tot} - z_1 - z_3)}{k_4 + (z_{tot} - z_1 - z_3)} - \frac{v_9 z_3}{k_9 + z_3}
\end{align*}
\]

Input \( u \) represents some upstream signaling molecule. The associated (directed) signed influence graph is depicted here. There are two loops each with a pair of negative edges in the graph and as a consequence the system is cooperative but not irreducible. We will have more to say about monotone control systems below.

Delay differential equations may also generate order-preserving dynamics. Consider again the repressilator but now we include delay in transcription of the gene and in its translation to protein product.

\[
\begin{align*}
    x_i'(t) &= \beta_i[y_i(t - \mu_i) - x_i(t)] \\
    y_i'(t) &= \alpha_i f_i(x_{i-1}(t - \tau_{i-1})) - y_i(t), \quad i = 1, 2
\end{align*}
\]

The natural state space is

\[
X = C([-\tau_1, 0], \mathbb{R}_+) \times C([-\mu_1, 0], \mathbb{R}_+) \times C([-\tau_2, 0], \mathbb{R}_+) \times C([-\mu_2, 0], \mathbb{R}_+),
\]

where \( \mathbb{R}_+ = [0, \infty) \). Using the natural point-wise ordering in function spaces \( f \leq g \) when \( f(\theta) \leq g(\theta), \forall \theta \), the competitive ordering on \( X \) is defined by \( (x_1, y_1, x_2, y_2) \leq (\hat{x}_1, \hat{y}_1, \hat{x}_2, \hat{y}_2) \) whenever \( x_1 \leq \hat{x}_1, y_1 \leq \hat{y}_1 \) and \( x_2 \geq \hat{x}_2, y_2 \geq \hat{y}_2 \). It is preserved by the dynamics of the delayed repressilator. These models have also been extended to include stochastic parameter dependence in [16, 60].

Parabolic partial differential equations generate infinite dimensional dynamical systems that may also be order preserving. Of course, the choice of state space is more of an issue than for ordinary differential equations. Below, we give some
examples where we could employ the function spaces $C(\bar{\Omega}) \times C(\bar{\Omega})$ to model two-species competition and the obvious extension of the competitive ordering to function spaces: $(U, V) \leq C (U, V)$ if $U \leq \bar{U}$ and $V \geq \bar{V}$. An extremely influential paper is that of Dockery, Hutson, Mischaikow and Pernarowski [19], who considered the $n$-species generalization of the following two species competition model

\begin{align*}
U_t &= d_1 \Delta U + U(m(x) - U - V) \\
V_t &= d_2 \Delta V + V(m(x) - U - V), \ x \in \Omega, \ t > 0 \\
\partial_n U &= \partial_n V = 0, \ x \in \partial \Omega, \ t > 0 \\
U(x, 0) &= U_0(x), \ V(x, 0) = V_0(x), \ x \in \Omega.
\end{align*}

Here $\Omega$ is a bounded smooth domain in $\mathbb{R}^N$ with $\nu$ denoting the outward unit normal vector on the boundary $\partial \Omega$, and $\partial_n = \nu \cdot \nabla$ is the outer normal derivative. Habitat suitability, assumed to be non-constant and identical for the two species, is modeled by $m(x)$. For the case of two species, the authors show that if $0 < d_2 < d_1$, then $U_1$ goes extinct. In an inhomogeneous environment, random dispersal does not pay off because the organism cannot remain near favorable areas. This work has stimulated a large and growing body of research focusing on which movement strategies are most advantageous in head to head competition. The theory of two-species competition has played a key role in this research.

For example, Cantrell, Cosner and Lou [10, 11] added advection up an environmental gradient to the repertoire of species $U$ to get:

\begin{align*}
U_t &= \nabla \cdot (d_1 \nabla U - \alpha U \nabla m) + U(m(x) - U - V) \\
V_t &= d_2 \Delta V + V(m(x) - U - V), \ x \in \Omega, \ t > 0 \\
\partial_n V &= d_1 \partial_n U - \alpha U \partial_n m = 0, \ x \in \partial \Omega, \ t > 0 \\
U(x, 0) &= U_0(x), \ V(x, 0) = V_0(x), \ x \in \Omega,
\end{align*}

where $\alpha > 0$ measures the extent of advection towards favorable habitat and $m$ is non-constant. The results are subtle and depend on the geometry of the domain $\Omega$. If it is convex then $U$ can have a competitive advantage over $V$ even if $0 < d_2 < d_1$ is not too large. When $d_1 = d_2$, $\Omega$ is convex, and $\alpha$ is small, then $U$ is the winner but this does not hold for some non-convex domains. Finally, it is shown in [11] that if $d_1, d_2 > 0$ and for generic, smooth, non-constant $m$ with positive average, the system has at least one stable coexistence steady state for all sufficiently large $\alpha$. Work on these sorts of problems have proceeded at such a rapid pace that it is difficult to keep up. See Lam and Ni [5] and the very nice review in [12].

The mathematical theory of competition between two entities plays an important role in evolutionary theory since it captures, in a simple way, the scenario where an initially rare mutant phenotype must compete with the resident phenotype. Will it ultimately be weeded out by competition or will it succeed in establishing itself, possibly even displacing the resident or reaching some coexistence with the resident? In the dispersal studies mentioned above, the mutant is a new different movement strategy.

The organization of the paper is as follows. In section two, we briefly describe the signature result of monotone dynamical systems theory, namely that the generic solution converges to the equilibrium set. Then, motivated by the extensive recent literature on competition between two species/agents/teams, we review the general theory in section three. A final section offers a brief synopsis of some recent developments in monotone systems theory, particularly monotone control systems.
2. Monotone dynamics: Some key results. We begin with some definitions. The natural state space for the theory is that of an ordered metric space X with metric d and partial order relation ≤, which the reader will recall must be reflexive, transitive and antisymmetric. We write \( x < y \) if \( x \leq y \) and \( x \neq y \). Given two subsets \( A \) and \( B \) of \( X \), we write \( A \leq B \) (\( A < B \)) when \( x \leq y \) \((x < y)\) holds for each choice of \( x \in A \) and \( y \in B \). It is assumed that the order relation and the topology on \( X \) are compatible: \( x \leq y \) whenever \( x_n \to x \) and \( y_n \to y \) as \( n \to \infty \) and \( x_n \leq y_n \) for all \( n \). For \( A \subset X \) we write \( \overline{A} \) for the closure of \( A \) and \( \text{Int} A \) for the interior of \( A \). A subset of an ordered space is unordered if it does not contain points \( x, y \) such that \( x < y \). We write \( x \ll y \) if there exist open sets \( U \) containing \( x \) and \( V \) containing \( y \) such that \( U \leq V \).

In most applications, \( X \) is a subset of an ordered Banach space \( Y \) and the partial order relation is generated by a non-empty closed cone \( \lambda Y^+ \subset Y^+ \) for \( \lambda \geq 0 \) and \( Y^+ \cap (-Y^+) = \{0\} \). We write \( x \leq y \) whenever \( y-x \in Y^+ \). For example, if \( Y = \mathbb{R}^n \), we may take \( Y^+ = \{ y \in \mathbb{R}^n : y_i \geq 0 \} \) or \( \mathbb{R}^n_+ \times (-\mathbb{R}^n_+)^k \). The latter yields the competitive ordering \( \leq_C \).

In the case that \( Y = C(\overline{\Omega}) \times C(\overline{\Omega}) \) as for [1, 5], the cone \( Y^+ = C(\overline{\Omega}, \mathbb{R}_+) \times -C(\overline{\Omega}, \mathbb{R}_+) \) generates the competition ordering.

A semiflow on \( X \) is a continuous map \( \Phi : \mathbb{R}^+ \times X \to X \), \((t, x) \mapsto \Phi_t(x)\) such that:
\[
\Phi_0(x) = x, \quad (\Phi_t \circ \Phi_s)(x) = \Phi_{t+s}(x) \quad (t, s \geq 0, \ x \in X)
\]
The orbit of \( x \) is the set \( O(x) = \{ \Phi_t(x) : t \geq 0 \} \). An equilibrium is a point \( x \) for which \( O(x) = \{ x \} \). The set of equilibria is denoted by
\[
E = \{ x \in X : O(x) = \{ x \} \}.
\]
The omega limit set \( \omega(x) \) of \( x \in X \), defined in the usual way, is closed and positively invariant. A point \( x \in X \) is quasiconvergent if \( \omega(x) \subset E \). The set of such points is denoted by
\[
Q = \{ x \in X : \omega(x) \subset E \}.
\]
If \( \omega(x) \) is single point, necessarily an equilibrium, then \( x \) is convergent. The set of convergent points is denoted by \( C \).

Let \( \Phi \) denote a semiflow in an ordered space \( X \). We call \( \Phi \) monotone provided
\[
\Phi_t(x) \leq \Phi_t(y) \text{ whenever } x \leq y \text{ and } t \geq 0.
\]
\( \Phi \) is strongly monotone if \( x < y \) implies that \( \Phi_t(x) \ll \Phi_t(y) \) for all \( t > 0 \) and eventually strongly monotone if it is monotone and \( x < y \) implies that \( \Phi_t(x) \ll \Phi_t(y) \) for all large \( t > 0 \). \( \Phi \) is strongly order-preserving, SOP for short, if it is monotone and whenever \( x < y \) there exist open subsets \( U, V \) of \( X \) with \( x \in U \) and \( y \in V \) and \( t_0 \geq 0 \) such that
\[
\Phi_{t_0}(U) \leq \Phi_{t_0}(V).
\]
Monotonicity of \( \Phi \) then implies that \( \Phi_t(U) \leq \Phi_t(V) \) for all \( t \geq t_0 \). Strong monotonicity implies eventual strong monotonicity which implies SOP. See e.g. [25, 27].

Below we assume \( \Phi \) is a monotone semiflow in an ordered metric space \( X \), such that every orbit has compact closure. The fundamental building blocks of the theory of monotone systems are contained in the following result. Proofs can be found in the works of Hirsch [31, 39], in the monograph [79], or in the survey [39].

**Theorem 2.1** (Key Building Blocks). Let \( \Phi \) be SOP on \( X \). Then
(a) Convergence Criterion: If \( O(x) \) contains two ordered points then \( x \in C \).
(b) Non-ordering of Limit Sets: No points of \( \omega(z) \) are related by \(< \).
(c) Limit Set Dichotomy: If \( x < y \) then either \( \omega(x) < \omega(y) \), or \( \omega(x) = \omega(y) \subset E \).

The limit set dichotomy is the key tool to prove (i) of the following result.

**Theorem 2.2.** [Generic Quasi-Convergence] Let \( \Phi \) be an SOP semiflow. Then

(i) If \( J \subset X \) is a totally ordered compact arc, then \( J \setminus Q \) is countable.
(ii) If \( X \) is a convex subset of an ordered Banach space, then \( Q \) is residual in \( X \).
(iii) If every point of \( X \) can be approximated either from above or from below and if \( \Phi \) satisfies compactness condition \( (C) \), then \( \text{Int} \ Q \) is dense in \( X \) and \( X = Q \) if \( E \) is a singleton.
(iv) If \( X \subset C(A, \mathbb{R}^n) \) where \( A \) is a compact Hausdorff space and the order relation is the restriction to \( X \) of the usual pointwise ordering where \( \mathbb{R}^n \) is ordered by an orthant cone, then \( \text{Int} \ Q \) is dense in \( X \).
(v) If \( X \subset \mathcal{B} \), a separable Banach space, then \( \text{Int} \ Q \) is prevalent in \( X \).

Technical definitions of terminology in Theorem 2.2 are given here. A totally ordered compact arc is the image of a nontrivial interval \( I \subset \mathbb{R} \) by a continuous map \( f : I \to X \) satisfying \( f(s) < f(t) \) when \( s, t \in I \) satisfy \( s < t \). Recall that a subset of \( X \) is residual if it contains the intersection of countably many dense open subsets of \( X \). In a complete metric space, every residual subset is dense in \( X \). We say that \( x \in X \) can be approximated from below (above) in \( X \) if there exists a sequence \( \{x_n\} \subset X \) satisfying \( x_n < x_{n+1} \) \( x \) \( x_n+1 < x \) \( x_{n+1} < x_n \) for \( n \geq 1 \) and \( x_n \to x \). The compactness condition \( (C) \) requires that if a sequence \( \{x_n\} \) approximates \( x_0 \) from below or from above, then \( \bigcup_n \omega(x_n) \) is compact. It is satisfied if, for example, each compact subset \( K \subset X \) has a bounded orbit \( O(K) = \bigcup_{x \in K} O(x) \) and if \( \Phi_t \) is conditionally completely continuous for some \( t > 0 \). An orthant cone in \( \mathbb{R}^n \) is one of the \( 2^n \) orthants \( \{x : (-1)^{m_i}x_i \geq 0, 1 \leq i \leq n\} \) where \( m_i \in \{1, 2\} \). A set \( W \subseteq \mathcal{B} \) is shy if there exists a nontrivial compactly supported Borel measure \( \mu \) on \( \mathcal{B} \), such that \( \mu(W + x) = 0 \) for every \( x \in \mathcal{B} \). A set is said to be prevalent if its complement is shy. The notion of a shy set is a natural generalization to separable Banach spaces of the notion of Lebesgue measure zero for euclidean spaces since in finite dimensions \( W \) is shy if and only if \( W \) has Lebesgue measure zero. A shy set has empty interior; see [32] for further properties.

We may remark that Theorem 2.2 (i) is proved by careful consideration of the continuity properties of the map \( x \to \omega(x) \) on \( J \).

The assertions (ii)-(v) of Theorem 2.2 are actually special cases of more general results that would require even more technicalities to state. Assertions (i) and (ii) appear in [39] with appropriate attribution, (iii) is taken from [39], (iv) is a special case of the main result in [40], and (v) is taken from [21]. Similar results hold with \( C \) replacing \( Q \). See [39].

A reader who is new to monotone systems may naturally ask whether the above results, establishing that most initial data correspond to trajectories that converge to the set of equilibria, reflects our inability to establish that \( X = Q \). This is not the case. The famous construction of Smale [74] shows that one can start with an arbitrary vector field on the \( n - 1 \) dimensional simplex \( \sum_i x_i = 1 \) in the positive orthant \( \mathbb{R}^n_+ \) and extend it to a monotone system on the orthant in such a way that the invariant simplex is a repelling separatrix separating the basin of attraction of the origin and the basin of attraction of the point at infinity. As a result, arbitrarily complex dynamics can be embedded in a monotone system but it is manifestly unstable. In fact, this scenario where complicated dynamics may occur on the boundary of basins of attraction of equilibria turns out to be the generic case.
Theorem 2.3. Let $\Phi$ be strongly monotone on a subset $X$ of an ordered Banach space. Suppose that $\Phi_t$ is compact for $t > 0$, and that compact sets have bounded orbits. If $x$ can be approximated from below and from above in $X$ and if $\omega(x)$ is not contained in $E$, then there exist $p, q \in E$ such that $p \ll \omega(x) \ll q$ and

(i) $\omega(y) = p$ if $p < y < w$, some $w \in \omega(x)$.
(ii) $\omega(y) = q$ if $w < y < q$, some $w \in \omega(x)$.

Moreover, if the Banach space is separable, then $\omega(x) \subset H$, where $H$ is an unordered, positively invariant, co-dimension one, Lipschitz manifold.

Proof. By hypothesis, there is a sequence $x_n$ satisfying $x_n < x_{n+1} < x$ for all $n$ and converging to $x$ and a sequence converging to $x$ from above as well but we will not need it, appealing instead to symmetry. The existence of $p, q \in E$ with $p \ll \omega(x) \ll q$ such that $p = \sup \{ e \in E : e < \omega(x) \}$ and $q = \inf \{ e \in E : \omega(x) < e \}$ is immediate from the sequential limit set trichotomy \cite{35}, case (b), and, by passing to a subsequence, $\omega(x_n) = p$ for all $n$. Note that if $u \in E$ and $u < w$ for some $w \in \omega(x)$, then it follows that $u < \omega(x)$ and hence $u \leq p$. A similar conclusion with inequalities reversed holds if $w < u$ for some $w \in \omega(x)$.

If $p < y < w$ for some $w \in \omega(x)$, then by invariance of the limit set, $p \ll \Phi_t(y) \ll w$, $t > 0$ and therefore $p \leq \omega(y) \leq w$. Consider the case that $\omega(y) \subset E$. Let $a \in \omega(y)$ and suppose that $a < w$. By the paragraph above, we conclude that $a \leq p$. But as $p \leq \omega(y)$, the non-ordering of limit sets implies that $\omega(y) = a$ and hence $\omega(y) = p$. Therefore, in the case that $\omega(y) \subset E$, either $\omega(y) = w \in E$ or $\omega(y) = p$.

We show that the first alternative cannot hold. For if $\omega(y) = w \in E \cap \omega(x)$, then since $\Phi_t(y) \ll w$ it follows that $\Phi_t(y) \ll \Phi_s(x)$ for some large $s$ and, by continuity, $\Phi_t(y) \ll \Phi_s(x_n)$ for large $n$. The latter leads to $w = \omega(y) \leq \omega(x_n) = p$, a contradiction. We have shown that if $\omega(y) \subset E$, then $\omega(y) = p$. But if $p < y < w$, we may as well assume that $\omega(y) \subset E$ because we can always find a quasiconvergent point $z$ on the open line segment joining $y$ to $w$ by Theorem 2.2 (i) and since $\omega(z) = p$ by the argument above, it follows by comparison that $\omega(y) = p$. This proves (i).

Symmetric arguments apply to show (ii). The remaining conclusions follow from Proposition 1.2 of \cite{91}.

A result similar to Theorem 2.3 was proved for ODEs by Hirsch as Theorem 3.1 in \cite{35} and for the general case of a separable Banach space by P. Takač as Theorem 0.1 in \cite{91}.

As an application of Theorem 2.2 (v), consider a reaction-diffusion system for $u = (u_1, \ldots, u_m)$ given by:

$$
\frac{\partial u_i}{\partial t} = d_i \Delta u_i + f(u), \quad 1 \leq i \leq m, \quad x \in \Omega, \quad t > 0,
$$

$$
\frac{\partial \nu u_i}{\partial t} = 0, \quad x \in \partial \Omega, \quad t > 0,
$$

$$
u(0,x) = u_0(x), \quad x \in \Omega,
$$

where $d_i > 0$ and $\nu$ denotes the outward pointing unit normal vector field.

Theorem 2.4 (Enciso, Hirsch, Smith \cite{21}). Assume that the $C^2$ system

$$
\dot{u} = f(u), \quad u \in \mathbb{R}^m,
$$

is cooperative and irreducible and that initial value problems have bounded solutions for $t \geq 0$. If $\Omega \subset \mathbb{R}^n$ is a convex domain with smooth boundary, then the set of initial conditions $u_0 \in C(\Omega, \mathbb{R}^m)$ corresponding to solutions of (2.1) that converge towards a uniform, i.e., constant, equilibrium is prevalent in $C(\Omega, \mathbb{R}^m)$. 

Convexity of the domain plays a key role here since Kishimoto and Weinberger [51] showed that a non-constant equilibrium is linearly unstable under the hypotheses of the theorem, a result that is false for nonconvex domains [62]. See [62, 9, 34, 60, 39, 42, 64, 79, 66, 67, 68] for more applications of monotone systems theory to parabolic partial differential equations.

3. Competition between two agents/teams: An equation-free theory. Peter Hess and Alan Lazer [30] were the first to observe that the dynamics of two-species competition has common features regardless of the details of the mathematical model, or its dimension. Hsu, Waltman and Ellermeyer considered continuous time competitive systems using monotone dynamical systems theory [43] and later Hsu, Smith, and Waltman [44] extended these results. See [80] for a review. Further progress was made by Smith and Thieme [86], particularly in the bi-stable case and when the semiflow is smooth. Liang and Jiang [57] and later Jiang et al [49] extended the theory, in the latter making use of the powerful idea of order decomposition introduced by Takač in [91].

Here we survey some of the salient results based largely on [44, 86]. One can summarize them by recalling the four well-known dynamical scenarios exhibited by the simple planar Lotka-Volterra model of competing species: competitive exclusion, coexistence, and bi-stability. As uniqueness of a coexistence equilibrium, should one exist, is not generally valid, the results are slightly more complicated.

For $i = 1, 2$, let $X_i$ be ordered Banach spaces with positive cones $X_i^+$. Denote by $\text{Int} X_i^+$ the interior of $X_i^+$, $X_i^+$ is the state space for competitor $i$. For simplicity, we assume that $X_i^+$ has nonempty interior for $i = 1, 2$. See [80] for the more general case. The same symbol for the partial orders generated by the cones $X_i^+$ are used.

If $x, y_i \in X_i$ satisfies $x < y_i$, then the order interval $[x_i, y_i]$ is defined by $[x_i, y_i] = \{ u \in X_i : x_i \leq u \leq y_i \}$. If $x_i \ll y_i$, then $[[x_i, y_i]] = \{ u \in X_i : x_i \ll u \ll y_i \}$ is called an open order interval. We use the same notation for the norm in both $X_1$ and $X_2$, namely $\| \bullet \|$. Let $X = X_1 \times X_2$ and given $x = (x_1, x_2) \in X$, we define $\| x \| = \| x_1 \| + \| x_2 \|$. Then $X^+ = X_1^+ \times X_2^+$ is a cone in $X$ with $\text{Int} X^+ = \text{Int} X_1^+ \times \text{Int} X_2^+$. It represents the state space for two species competition. Cone $X^+$ generates the usual componentwise orderings $\leq, \ll, \ll$. In particular, if $x = (x_1, x_2)$ and $\bar{x} = (\bar{x}_1, \bar{x}_2)$, then $x \leq \bar{x}$ if and only if $x_i \leq \bar{x}_i$, for $i = 1, 2$. For our purposes, the more important cone is “south-east” cone $C = X_1^+ \times (-X_2^+)$, the interior of which is given by $\text{Int} C = \text{Int} X_1^+ \times (-\text{Int} X_2^+)$. It generates the competition partial order relations $\leq_C, \ll_C, \ll_C$. In this case, $x \leq_C \bar{x} \iff x_1 \leq \bar{x}_1$ and $\bar{x}_2 \leq x_2$.

A similar statement holds with $\ll_C$ replacing $\leq_C$ and $\ll$ replacing $\leq$.

Assume that $\Phi : [0, \infty) \times X^+ \to X^+$ is a continuous semiflow.

We introduce the following assumptions.

(H1) $\Phi$ is strictly order preserving on $X^+$ with respect to $\ll_C$. For each $t > 0$, $\Phi_t$ is order compact: $\Phi_t([0, x_1] \times [0, x_2])$ has compact closure in $X$ for each $x = (x_1, x_2) \in X^+$.

(H2) $E_0 = (0, 0)$ is a repelling equilibrium: there exists a neighborhood $U$ of $E_0$ such that for each $x \in U$, there is $t_0 > 0$ such that $\Phi_t(x) \notin U$.

(H3) $\Phi_t(X_1^+ \times \{0\}) \subset X_1^+ \times \{0\}$ for all $t \geq 0$. There exists $\hat{x}_1 > 0$ such that $E_1 = (\hat{x}_1, 0) \in E$ and $\Phi_t(x) \to E_1$ for all $x \in X_1^+ \times \{0\}$. Symmetric conditions hold for $\Phi$ on $\{0\} \times X_2^+$ with globally attracting equilibrium point $E_2 = (0, \hat{x}_2)$. 


(H4) If \( x = (x_1, x_2) \in X^+ \) satisfies \( x_i > 0, i = 1, 2 \), then \( \Phi_1(x) \in \text{Int}X^+ \) for \( t > 0 \). If \( x, y \in X^+ \) satisfy \( x \leq_C y \) and either \( x \) or \( y \) belongs to \( \text{Int}X^+ \), then \( \Phi_1(x) \leq_C \Phi_1(y) \) for \( t > 0 \).

The order interval
\[
I = [0, \hat{x}_1] \times [0, \hat{x}_2]
\]
plays a distinguished role in the theory.

The following result from [44] implies that either competitive exclusion holds or a coexistence equilibrium exists.

**Theorem 3.1.** Let (H1)-(H4) hold. Then the omega limit set of every orbit, in particular \( E \), is contained in \( I \) and exactly one of the following holds:

(a) There exists a coexistence equilibrium belonging to \( I \cap \text{Int}X^+ \).
(b) \( \Phi_1(x) \to E_1 \) for all \( x = (x_1, x_2) \in I \) with \( x_1 > 0, i = 1, 2 \).
(c) \( \Phi_1(x) \to E_2 \) for all \( x = (x_1, x_2) \in I \) with \( x_1 > 0, i = 1, 2 \).

Finally, if (b) or (c) hold, \( x = (x_1, x_2) \) with \( x_1 > 0, i = 1, 2 \) and \( x \notin I \), then either \( \Phi_1(x) \to E_1 \) or \( \Phi_1(x) \to E_2 \).

Sufficient conditions for the existence of a coexistence equilibrium are given next.

**Corollary 3.1.** Let (H1)-(H4) hold. Then \( \Phi \) has a coexistence equilibrium in \( I \cap \text{Int}X^+ \) if any of the following holds.

(i) Both \( E_1 \) and \( E_2 \) are stable relative to \( I \) with respect to the order topology.
(ii) Both \( E_1 \) and \( E_2 \) are unstable relative to \( I \) with respect to the order topology.
(iii) There is a point \( x \in X^+ \) and a point \( z \in \omega(x) \) such that \( z \in \text{Int}X^+ \).

The order topology on \( X \) is generated by the open order intervals \( [(x_1, y_1)] \times [(x_2, y_2)] \) where \( x_i < y_i \). It is a norm topology with norm \( ||x||_v = \inf \{ \lambda \geq 0 : -\lambda v \leq x \leq \lambda v \} \) for \( v \in \text{Int}X^+ \). Every order open set is open in the topology of \( X \).

For \( i = 1, 2 \), let
\[
B_i = \{ x \in X^+ : \omega(x) = \{ E_i \} \}.
\]

Persistence and Bi-stability are especially important in applications. The following result focuses on these two cases. See [44] [86]

**Theorem 3.2.** Let (H1)-(H4) hold.

**Persistence:** Assume that both \( E_1 \) and \( E_2 \) are isolated and unstable relative to \( I \) with respect to the order topology. Then there exist equilibria \( E^* \) and \( E^{**} \) in \( I \cap \text{Int}X^+ \), possibly identical, such that
\[
E_2 \leq_C E^{**} \leq_C E^* \leq_C E_1
\]
and for all \( x = (x_1, x_2) \in I \) with \( x_i \neq 0, i = 1, 2 \), we have \( E^{**} \leq_C \omega(x) \leq_C E^* \).

Assume, in addition, that for \( j = 1, 2 \), there are \( t_j > 0 \) such that \( \Phi_{t_j} \) can be extended to a neighborhood of \( E_j \) in \( X \) on which it is \( C^1 \) with the spectral radius of \( D_x \Phi_{t_j}(E_j) \) being greater than one and its essential spectral radius less than one. Then for \( x = (x_1, x_2) \in X^+ \) with \( x_i \neq 0, i = 1, 2 \), we have \( E^{**} \leq_C \omega(x) \leq_C E^* \).

**Bi-stability:** Assume that there is a unique equilibrium \( E^* \in I \cap \text{Int}X^+ \) and it is a saddle point: \( \Phi_{t_0} \) is \( C^1 \) on a neighborhood of \( E^* \) and the spectral radius of \( D_x \Phi_{t_0}(E^*) \) is strictly greater than one for some \( t_0 > 0 \), and its essential spectral radius is strictly less than one.

Then:

(a) \( \{ x \in X^+ : x \leq_C E^{**} \} \subset B_2 \) and \( \{ x \in X^+ : E^* \leq_C x \} \subset B_1 \).
(b) $S \equiv X^+ \setminus (B_1 \cup B_2)$ is an un-ordered, positively invariant set consisting of $E_0, E^*, \{x \in X^+: \omega(x) = E^*\}$, and a set of non-quasi-convergent points.

(c) $B_1 \cup B_2$ is open and dense in $X^+$; it is also prevalent ($S$ is shy).

See Theorem 2.1 in [49] for a similar result in the bi-stable case. There, it is shown that $S$ is a Lipschitz manifold of co-dimension one in the order norm if $\Phi$ is strongly monotone. This paper contains other useful results on basins of attraction and their boundaries.

K.-Y. Lam and D. Munther [55] have recently given detailed stability conditions for the boundary equilibria for a $C^1$ competitive system generated by a system of ODEs

$$\frac{du_i}{dt} = A_i u_i + f_i(u), \; i = 1, 2,$$

where $A_i$ are sectorial operators on $X_i$ and the $f_i$ are differentiable functions on $X$. These are based on principle eigenvalues of certain eigenvalue problems associated with the equilibria $E_i, \; i = 1, 2$. They also provide sufficient conditions for $E_i$ to attract all points of Int$X^+$ if it attracts Int$E$, even in the non-hyperbolic case.

The results of this section apply to the systems (1.4), (1.5), and (1.6). For example, one can show that no coexistence equilibrium can exist for (1.5) by using the fact that the principle eigenvalue of the elliptic eigenvalue problem $d\Delta u + q(x)u = \lambda u$ is strictly decreasing in $d$ if $q$ is non-constant. See [19]. Similar considerations then can be used to show that $E_1$ is linearly unstable while $E_2$ is stable.

4. Selected recent theoretical advances. It is well known that a strongly order-preserving semiflow cannot have a non-trivial periodic orbit that is attracting [28, 34, 39]. Recently, Angeli et al [6] extended this result to systems of ordinary differential equations which are not necessarily cooperative property but are “coherent” in the following sense: if there is a loop in the directed influence graph of the system, then the edges of the loop can be given an unambiguous sign and the number of negative edges is even. They also show global convergence to equilibrium for such systems having a unique equilibrium and, more generally, that every orbit is nowhere dense in $\mathbb{R}^n, \; n \geq 2$.

We have considered only very special partial order relations that might be preserved by a dynamical system. For ordinary differential equations, a quite general theory for order-preserving systems has been developed where the order relation is generated by a general cone $K \subset \mathbb{R}^n$. See [93, 39, 38] and the references therein. As an example from [93], the matrix Ricatti equation $x' = xa(t)x + b(t)x + c(t)$, with symmetric $m \times m$ matrices $a, b, c$, generates a monotone non-autonomous dynamical system on the space of symmetric matrices with respect to the cone of positive definite matrices.

Recently, Forni and Sepulchre [22] consider the case that the dynamical system is generated by a vector field $f$ on a Riemannian manifold $X$ whose tangent bundle $TX$ is endowed with a smooth cone field $x \to K(x) \subset T_x(X)$ where for each $x \in X$, $T_xX$ is the tangent space to $X$ at $x$ and $K(x)$ has the usual properties of a cone with non-empty interior. A curve $\gamma: I \subset \mathbb{R} \to X$ is coxal if $\gamma'(s) \in K(\gamma(s)), \; s \in I$. This notion leads to a local order relation $x_1 \preceq_K x_2$ if there is a conal curve $\gamma$ such that $x_1 = \gamma(s_1)$ and $s_1 \leq s_2$. Antisymmetry may fail so this relation is not a partial order. They call the system $x' = f(x)$ differentially positive if positive tangent vectors are mapped to positive tangent vectors in positive time by the linearized system. They define the system to be strictly differentially positive if there exists a smooth cone
field $R(x) \subset \text{Int}K(x)$ and $T > 0$ such that tangent vector $\delta x(t_0) \in K(x(t_0))$ is mapped to tangent vector $\delta x(t) \in R(x(t))$ for $t \geq t_0 + T$ by the linearized system. Using the Hilbert metric on the cones $K(x)$, strict differential positivity leads to the existence of a Perron-Frobenius vector field $w(x) \in \text{Int}K(x)$ on $X$ that attracts, in a pull-back sense, positive tangent vectors. The Perron-Frobenius vector field $w$ gives rise to a conal curve tangent to $w$. The authors prove that on an omega limit set, either (a) the vector field $f(x)$ is co-linear with $w(x)$ and $\omega(x)$ is either a periodic orbit or a set of fixed points and connecting arcs, or (b) the vector field $f$ is not co-linear with $w$ on $\omega(x) \setminus E$, and for $\eta \in \omega(x)$ either the linearized flow acting on $w(\eta)$ becomes unbounded or the trajectory through $\eta$ approaches $E$. As a simple example, the authors consider the the damped pendulum system on the cylinder $X = S^1 \times \mathbb{R}$

$$
\theta' = v,
$$

$$
v' = -\sin \theta - kv + u
$$

with applied torque $u \geq 0$. For $k > 2$ the eigenvalues of the linearization are real and the cone field

$$
K(\theta, v) = \{(\delta \theta, \delta v) : \delta \theta \geq 0, \delta \theta + \delta v \geq 0\}
$$

is strongly preserved by the linearization, making the system strictly differentially positive. Results of the authors confirm the existence of a periodic orbit for $u \geq 1$.

L. Sanchez makes an interesting geometrical observation regarding the use of order preservation induced by a cone $K$ in his recent paper [72]. He notes that the asymptotic behavior of solutions of cooperative and irreducible systems of ordinary differential equations “is conveniently projected either over straight lines contained in $K \cup -K$ or over hyper-planes outside $K \cup -K$. In the first case we get a one-dimensional, and hence trivial, dynamics. In the second case complicated behavior may appear, but the point is that it is highly unstable. Of course it is the further usage of the order structure what leads to the extremely precise description of the dynamics achieved in this theory. However it is conceivable that weaker structures which induce similar well-behaved projections would allow to establish dynamical properties for other classes of semiflows”. Following [23, 24], he defines a cone $C \subset \mathbb{R}^n$ of rank $k$ to be a closed set that is closed under scalar multiplication and contains a subspace of dimension $k$ but none of higher dimension. The closure of the complement of $C$ is also a cone, denoted by $C^c$, and called the complementary cone. For example, $T_k = \{x : x_i \neq 0, N(x) \leq k - 1\}$, where $N(x)$ denotes the number of sign changes in the sequence $x_1, x_2, \cdots, x_n$, is a cone of rank $k$ and $T_1 = \mathbb{R}^n_+ \cup -\mathbb{R}^n_+$. Another important example of a cone of rank $k$ is generated by a symmetric matrix $P$ with $k$ negative eigenvalues and $n - k$ positive ones via $C = \{x : Px \cdot x \leq 0\}$. Given a cone $C$ of rank $k$, one defines an “order” relation on $\mathbb{R}^n$ by $x \sim y$ if and only if $x - y \in C$ and a strong order relation $x \approx y$ if $x - y \in \text{Int}C \neq \emptyset$. The relation $\sim$ is not a partial order since it is neither antisymmetric nor transitive. Sanchez then asks what are the dynamical consequences of the preservation of this relation by the forward flow of system (1.1):

$$
x \sim y, \ x \neq y \Rightarrow \Phi_t(x) \approx \Phi_t(y), \ t > 0.
$$

Actually, he requires the above to hold in the slightly stronger sense that the linearized system preserves the strong ordering. Given that this holds with a cone of rank two, the complement of which is a cone of rank $n-2$, then a Poincaré-Bendixson
type result is proved in [72]: an omega limit set containing no equilibria of a solution \(x(t)\) such that \(x'(t_0) \in C\) for some \(t_0\) is a closed orbit. Roughly speaking, this result may be compared to the convergence criterion for strongly order preserving semiflows; in that case, when \(x'(t_0) \in K \cup -K\), then the solution converges monotonically to equilibrium. Remarkably, this Poincaré-Bendixson type result contains as special case many of the known extensions of the Poincaré-Bendixson theorem to dimensions higher than two in the literature.

D. Angeli and E. Sontag have extended monotone dynamical systems theory to the control theory setting in [2, 3]. This extension proves to be useful, even for the analysis of uncontrolled autonomous systems as we briefly describe here. In a control theory setting, one has inputs \(u(t) \in U, \ t \geq 0\), to the dynamical system with state \(x \in X\) and perhaps outputs \(y \in Y\):

\[
\begin{align*}
  x' &= f(x, u) \\
  y &= h(x)
\end{align*}
\]  

(4.1)

Inputs are required to be Lebesgue measureable and essentially bounded and one must be careful about the regularity assumptions on \(f\) but we ignore technicalities here.

If \(U, X, Y\) have partial order relations \(\leq_Z\), \(Z = U, X, Y\), then the system is said to be monotone if

\[
\begin{align*}
  u_1 \leq_U u_2, \ x_1 \leq_X x_2 \Rightarrow x(t, x_1, u_1) \leq_X x(t, x_2, u_2), \ t \geq 0
\end{align*}
\]

and \(h : X \to Y\) is a monotone mapping: \(x_1 \leq_X x_2 \Rightarrow h(x_1) \leq_Y h(x_2)\). The notation \(u_1 \leq_U u_2\) is understood in the point wise sense \(u_1(t) \leq_U u_2(t)\). The notation \(x(t, x_0, u)\) denotes the solution of \(x' = f(x, u(t))\), \(x(0) = x_0\).

Given a second monotone control system

\[
\begin{align*}
  z' &= g(z, y) \\
  w &= H(z)
\end{align*}
\]  

(4.2)

with input set the ordered space \((Y, \leq_Y)\) and output space \((W, \leq_W)\), then it follows, see [2], that the composite system, usually referred to as a cascade,

\[
\begin{align*}
  x' &= f(x, u), \ y = h(x), \\
  z' &= g(z, y) \\
  w &= H(z)
\end{align*}
\]  

(4.3)

is a monotone control system with state space \(X \times Z\) with the natural product space ordering: \((x_1, z_1) \leq (x_2, z_2) \Leftrightarrow x_1 \leq_X x_2 \land z_1 \leq_Z z_2\).

It is productive to consider a special class of monotone control systems. Control system (4.1) possesses a static input-state characteristic \(k_x : U \to X\) if for each constant input \(u(t) \equiv u\), there exists a globally asymptotically stable equilibrium \(x = k_x(u)\). Then, one has the static input-output characteristic \(k_y = h \circ k_x\). By monotonicity of (4.1), it follows that \(k_x : U \to X\) is monotone and it is generically a smooth function by the implicit function theorem.

As an example, consider the dynamics of a single gene, modeled by the control system

\[
\begin{align*}
  x' &= \beta(y - x) \\
  y' &= u - y, \ z = \alpha f(x)
\end{align*}
\]  

(4.4)
where production of mRNA, $y$, is controlled perhaps externally and where the output $z$ is a function of the protein product $x$ of the gene, and $\alpha, \beta > 0$. It has static input-state characteristic $k(u) = (u,u)$ and input-output characteristic $k_z(u) = \alpha f(u)$. This is a monotone control system if input space $U$ is given the usual ordering on $\mathbb{R}$, state space $X = \mathbb{R}^2$ has the usual componentwise ordering, and if $f$ is monotone. Output space $Z$ has the usual order if $f$ is increasing and the opposite ordering if $f$ is decreasing.

Assume now that our monotone control system $\text{(4.1)}$ has scalar inputs and scalar outputs with the usual order relation $\leq$, $(U, \leq_U) = (Y, \leq_Y) = (\mathbb{R}, \leq)$, and that $\text{(4.1)}$ has static input-output characteristic $k_y : \mathbb{R} \to \mathbb{R}$. Then $k_y$ is nondecreasing and the closed-loop system

\[ x' = f(x, h(x)) \]

is a monotone dynamical system. There is a one-to-one correspondence between equilibria of the closed loop system and fixed points of the static input-output characteristic $k_y$, and, if the latter are non-degenerate, then under mild additional conditions, it is shown in [3] that almost all solutions of the closed loop system converge to an equilibrium corresponding to a stable fixed point of $k_y$. A very elementary application of this result to $\text{(4.4)}$ with $u = \alpha f(x)$ implies that all most all solutions converge to an equilibrium $(x, k_z(x))$ corresponding to a stable fixed point of the static input-output characteristic $k_z$ when $f$ is increasing. Of course, this result follows from a more elementary approach, but more interesting examples arise from cascades of single gene systems with compatible input-output orderings. Indeed, gene regulatory networks can often be viewed as closed looped cascades of the elementary single gene systems $\text{(4.4)}$.

It is shown in [2], that if $\text{(4.1)}$ is monotone and possesses an static input-state and input-output characteristics $k_x, k_y$ and system $\text{(4.2)}$ is monotone with input order $(Y, \leq_Y)$ compatible with output order for $\text{(4.1)}$ (so that the composite system $\text{(4.3)}$ is monotone) and has static input-state characteristic $k_z$, then the monotone control system $\text{(4.3)}$ has static input-state characteristic $\hat{k} : U \to X \times Z$ given by $\hat{k} = (k_x, k_z \circ k_y)$ provided order boundedness and boundedness agree in spaces $Y$ and $Z$.

One of the main results in [2] concerns a special class of dynamical systems that are not necessarily monotone. Now, assume the scalar input, scalar output case: i.e., that input and output spaces $U, Y$ and $W$ are subsets of $\mathbb{R}$, and consider the interconnected dynamical system:

\[ \begin{align*}
x' &= f(x,u), \quad y = h(x), \\
z' &= g(z,y), \quad u = H(z).
\end{align*} \tag{4.5} \]

Assume that:

1. $\text{(4.1)}$ is monotone where $U$ and $Y$ have the usual ordering on $\mathbb{R}$.
2. $\text{(4.2)}$ is monotone where $Y$ has the usual ordering on $\mathbb{R}$ but $W$ has the opposite ordering.
3. the respective static input-state characteristics $k_x$ and $k_z$ exist, implying that static input-output characteristics $k_y$ and $k_w$ exist, the former being increasing while the latter is decreasing.
4. every orbit of $\text{(4.5)}$ is bounded.
Then [4,5] has a globally asymptotically stable equilibrium provided that the scalar discrete-time dynamical system

\[ u_{k+1} = (k_w \circ k_y)(u_k) \]

has a unique globally attracting equilibrium. This result is sometimes referred to as the small gain theorem.

As an example, consider the genetic regulatory network consisting of two genes one of which activates the other which in turn represses its activator. Each gene can be considered as an open loop control system

\[ \begin{align*}
    x'_i &= \beta_i(y_i - x_i) \\
    y'_i &= u_i - y_i, \quad z_i = \alpha_i f_i(x_i)
\end{align*} \]

with input \( u_i \) providing the control of gene \( i \) regulation via its mRNA production and output \( z_i = \alpha_i f_i(x_i) \). As mentioned, we consider the case that \( f_1 \) is an increasing function and \( f_2 \) is a decreasing function of its argument. This means that gene one activates gene two but gene two represses gene one activity. Each system has static input-state characteristic \( k_i(u_i) = (u_i, u_i) \). The gene network results from the closed loop system where output \( z_1 = \alpha_1 f_1(x_1) \) from gene one is input \( u_2 \) to gene two, while output \( z_2 = \alpha_2 f_2(x_2) \) of gene two is fed into input \( u_1 \) to gene one. The small gain theorem implies that the network dynamics is globally convergent provided that the scalar discrete time dynamical system \( u_{k+1} = (\alpha_2 f_2 \circ \alpha_1 f_1)(u_k) \) has a globally convergent fixed point. See [25] for early results in this direction.

One goal of the control theory approach is aimed at illuminating the dynamics exhibited by uncontrolled dynamical systems by expressing the systems as interconnections of control systems with certain properties, such as monotonicity. Here, we mention the approach described by Enciso et al. [20]. Suppose that system \( x' = F(x) \) on \( \mathbb{R}^n \) can be expressed as the “closed-loop system” \( x' = f(x, h(x)) \) associated with the “open-loop” control system (4.1) where output \( y \in \mathbb{R}^n \) is the input \( u = y \). If the map \( x \to f(x, u) \) is a cooperative system, the map \( u \to f(x, u) \) is monotone non-decreasing with respect to the componentwise ordering on \( \mathbb{R}^n \), and \( x \to h(x) \) is componentwise non-increasing, then the symmetric system \( x' = f(x, h(y)), y' = f(y, h(x)) \) is monotone with respect to the competitive ordering \( \leq_C \) on \( \mathbb{R}^{2n} \) and the original system \( x' = F(x) = f(x, h(x)) \) is embedded in it along the invariant diagonal \( y = x \). Symmetry is reflected in the fact that \( (x(t), y(t)) \) is a solution if and only if \( (y(t), x(t)) \) is a solution. Strong restrictions on the asymptotic dynamics of the system \( x' = F(x) \) can be achieved, sometimes leading to the existence of a globally asymptotically stable equilibrium. These ideas have been extended to delay differential equations, to partial differential equations, and to discrete-time systems in [20].

The results described above provide a small taste of the kind of results that have been established in monotone control theory. See [1] [2] [3] [90] [60] and the references therein for more.

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