Attractors in coherent systems of differential equations

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ABSTRACT

Attractors of cooperative dynamical systems are particularly simple; for example, a nontrivial periodic orbit cannot be an attractor, and orbits are nowhere dense. This paper provides characterizations of attractors for the wider class of *coherent* systems, defined by the property that all directed feedback loops are positive. Several new results for cooperative systems are obtained in the process. Connections with biological models are discussed.

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1. Introduction

We consider differential equations

$$\frac{dx}{dt} = F(x), \quad x \in X, \ t \geqslant 0, \tag{1}$$

where $X \subset \mathbb{R}^n$ is a nonempty convex set in which its interior $\mathrm{Int}_{\mathbb{R}^n} X$ is dense. Our main results postulate further restrictions on X.

The maximally defined solutions $t \mapsto \Phi_t(a)$, $t \geqslant 0$, $a \in X$, generate the local semiflow $\Phi := \{\Phi_t\}_{t \in \mathbb{R}_+}$. We refer to F (or $(F, X, \mathbb{R}^n)$, or $(F, X, \mathbb{R}^n, \Phi)$) as a *system*. Dynamical notions are applied interchangeably to F and Φ.

Many biological situations are modeled by *cooperative* systems, meaning that

$$\frac{\partial F_j}{\partial x_i} \geqslant 0 \quad \text{for } j \neq i.$$

The biological interpretation of this is that an increase of species i tends to increase the population growth rate of every other species j. When this holds and X is convex, Φ is *monotone*, meaning it preserves the vector order. Monotonicity causes the crude dynamics to be comparatively simple; for example, there are no attracting cycles and every orbit is nowhere dense (Hadeler and Glas [13], Hirsch [16]).

Our goal is to show that some of the dynamical advantages of cooperative systems extend to systems having a significantly weaker property: F is *coherent* (another name is *positive feedback system*) if the following holds:

Whenever $i_0, \ldots, i_\nu$, $\nu \in \{1, \ldots, n\}$ are such that

$$i_\nu = i_0, \quad i_{k-1} \neq i_k, \quad \text{and} \quad \frac{\partial F_{i_{k-1}}}{\partial x_{i_k}} \not\equiv 0 \quad (1 \leqslant k \leqslant \nu) \tag{2}$$

then

$$\frac{\partial F_{i_{k-1}}}{\partial x_{i_k}} \text{ is everywhere } \geqslant 0 \text{ or everywhere } \leqslant 0$$

and the set

$$\left\{ k \in \{1, \ldots, n\} \colon \ (\exists p \in X) \ \frac{\partial F_{i_{k-1}}}{\partial x_{i_k}}(p) < 0 \right\}$$

has even cardinality.

Our chief combinatorial result, Theorem 10, shows that by permuting the variables x_i and changing the signs of some of them, any coherent system can be transformed into a dynamically equivalent system $(F, X, \mathbb{R}^n, \Phi)$ with the following properties:

- F is not merely coherent, it has the stronger property of being *quasicooperative*: for any $(i_0, \ldots, i_\nu)$ as in (2), $\frac{\partial F_{i_{k-1}}}{\partial x_{i_k}}$ is everywhere $\geqslant 0$;

- if F is not cooperative, there exists a cooperative system $(F^1, X^1, \mathbb{R}^{n_1}, \Phi^1)$, $1 \leqslant n_1 < n$, such that the natural projection

$$\Pi : \mathbb{R}^n \to \mathbb{R}^{n_1}, \quad (x_1, \ldots, x_n) \mapsto (x_1, \ldots, x_{n_1})$$

maps X onto X^1, and Π semiconjugates F to F^1 and Φ to Φ^1:

$$\Pi \circ F(x) = F^1 \circ \Pi(x), \qquad \Pi \circ \Phi_t(x) = \Phi_t^1 \circ \Pi(x) \quad \text{if } \Phi_t(x) \text{ is defined.}$$

Mild geometrical conditions on X will guarantee that for each equilibrium p of F^1, the restriction of F to $X_p := X \cap \Pi^{-1}(p)$ is equivalent to a quasicooperative system $(\hat{F}_p, \hat{X}_p, \mathbb{R}^{n-n_1})$. This is the basis for inductive proofs of our main results.

Examples. Let $f, g, h : \mathbb{R} \to \mathbb{R}$ be C^1 functions. The differential equations

$$\dot{x} = f(x),$$

$$\dot{y} = x + g(y) - 2z,$$

$$\dot{z} = x + h(z)$$

generate a quasicooperative system $(F, \mathbb{R}^3, \mathbb{R}^3)$ that cannot be transformed to a cooperative system by changing signs of variables. This type of system is called an "incoherent feedforward loop" in the systems biology literature [2]. (The terminology in that textbook is, unfortunately, contradictory with ours; in fact, "coherent" in [2] means the same as "monotone system" in dynamical systems language.)

More generally, a system of the general form

$$\dot{x} = f(x),$$

$$\dot{y} = g(x, y, z),$$

$$\dot{z} = h(x, y, z)$$

is coherent if either $\frac{\partial g}{\partial z} \leqslant 0$ and $\frac{\partial h}{\partial y} \leqslant 0$, or $\frac{\partial g}{\partial z} \geqslant 0$ and $\frac{\partial h}{\partial y} \geqslant 0$. Replacing y by $-y$ makes the system quasipositive, but if either $\frac{\partial g}{\partial x}$ or $\frac{\partial h}{\partial x}$ changes sign, or if there is some point $p = (x, y, z)$ such that

$$\frac{\partial g}{\partial z}(p) \frac{\partial g}{\partial x}(p) \frac{\partial h}{\partial x}(p) < 0,$$

the system cannot be made cooperative by changing signs of variables.

1.1. Attractors

We call a set $A \subset X$ *positively invariant* for Φ if $\Phi_t(a)$ is defined and belongs to A for all $t \geqslant 0$, $a \in A$. If in addition A is nonempty and $\Phi_t(A) = A$ for all $t \geqslant 0$ then A is *invariant*.

A set $A \subset X$ *attracts* a point y if the orbit closure $\overline{\gamma(y)}$ is compact and $\omega(y) \subset A$. The set of such points y is the *basin* of A. A is *attracting* if it is invariant and compact, and its basin is a neighborhood of A. If in addition A has arbitrarily small positively invariant neighborhoods, A is an *attractor*.[1] An attractor is *global* if its basin is all of X. An equilibrium is *globally asymptotically stable* if it is the global attractor.

Three types of attractors A have received special attention:

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[1] There are many definitions of "attractor" in current use, not mutually consistent. The one adopted here is equivalent to that of Conley [8], and (for compact invariant sets) those of Hale [14] and Sell and You [38]. It is analogous to the definitions for discrete-time systems in Smale [39] and Akin [1].

Point attractors: A is single point, necessarily an equilibrium.

Periodic attractors: A is a cycle, i.e., a periodic orbit that is not an equilibrium.

Strange attractors, often called "chaotic". This somewhat vague term usually signifies that A is neither an equilibrium nor a cycle, and the dynamics in A exhibits "sensitive dependence on initial conditions", and sometimes that A is *topologically transitive*, i.e., some orbit is dense in A. For some authors chaos also require that periodic orbits be dense in A.

This paper is motivated by the question: What kind of nonequilibrium attractors A can exist in coherent systems? Theorem 1 shows that A cannot be topologically transitive; Theorems 2 and 3 give further dynamical information. Theorem 9 is the key combinatorial result. Results 11 to 18 contain new dynamical results for general monotone systems.

1.2. Ordered spaces

By an *ordered space* we mean a topological space Z together with an order relation $\mathcal{R} \subset Z \times Z$ that is topologically closed. If $x, y \in Z$ we write:

$$x \succcurlyeq y \quad \text{and} \quad y \preccurlyeq x \quad \text{if } (x, y) \in \mathcal{R}, \qquad x \succ y \quad \text{and} \quad y \prec x \quad \text{if } x \succcurlyeq y,\ x \neq y. \tag{3}$$

The *vector order* in any subset of $\mathbb{R}^n$ is defined by

$$u \succcurlyeq v \quad \Longleftrightarrow \quad u - v \in \mathbb{R}^n_+$$

where $\mathbb{R}^n_+$ denotes the positive orthant $[0, \infty)^n \subset \mathbb{R}^n$.

A subset of an ordered space is *unordered* if none of its points are related by $\succ$.

Every subspace $X \subset Z$ inherits an order relation from Z. If $M \subset Z$ then $x \succ M$ means $x \succ y$ for all $y \in M$, and similarly for the other relations in (3). For $x, y \in X$ we write

$$x \vartriangleright_X y \quad \text{if } x \succ \text{ a neighborhood of } y,$$

$$x \vartriangleleft_X y \quad \text{if } x \prec \text{ a neighborhood of } y.$$

Note the notational anomaly that $x \vartriangleright_X y$ and $y \vartriangleleft_X x$ are not equivalent statements for general ordered spaces. For example, if $X = \mathbb{R}^2_+$ with the vector order, we have $(0, 0) \vartriangleleft_X (0, 1)$ but not $(0, 1) \vartriangleright_X (0, 0)$. On the other hand, if $X \subset \mathbb{R}^n$ is open and has the vector order then $x \vartriangleright_X y \Leftrightarrow y \vartriangleleft_X x$ because they both mean $x_i > y_i,\ i = 1, \ldots, n$.

Let X be a subset of an ordered space Z. We call $q \in X$ *strongly accessible in X from above* (respectively, *from below*) if every neighborhood of q in X contains a point $x \vartriangleright_X q$ (respectively, $x \vartriangleleft_X q$).[2]

Some of our inductive proofs need the domain of the dynamics to have simple geometry. A convenient class of such sets are defined as follows. By a *coordinate halfspace* in $\mathbb{R}^n$ we mean a set of the form

$$H^n(l, \alpha, c) := \left\{ x \in \mathbb{R}^n \colon \alpha x_l \geqslant c \right\}, \quad l \in \{1, \ldots, n\},\ \alpha \in \{\pm 1\},\ c \in \mathbb{R}.$$

A *positive coordinate cone* in $\mathbb{R}^n$ is a set of the form

$$\bigcap_{j=1}^{\nu} H^n(l_j, 1, c_j), \quad 1 \leqslant l_1 < \cdots < l_\nu \leqslant n.$$

A coordinate halfspace is a positive coordinate cone, as is $\mathbb{R}^n_+$.

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[2] Slightly stronger properties with the same names are used in Hirsch and Smith [18].

1.3. Statement of the main results

We call a set *A finitely transitive* if it is the union of the omega limit sets of finitely many members of *A*. Every cycle is finitely transitive, and more generally, every orbit closure is. For example, an irrational flow on a torus has the whole torus as a finitely transitive set.

Theorem 1. *Let $(F, X, \mathbb{R}^n)$ be a system satisfying one of the following two conditions*:

(i) *F is coherent and X is open in $\mathbb{R}^n$ or a coordinate halfspace*;
(ii) *F is quasicooperative and X is open in $\mathbb{R}^n$ or a positive coordinate cone.*

Then every connected, compact, finitely transitive attracting set is an equilibrium. In particular, there does not exist an attracting cycle.

A stronger conclusion for monotone semiflows is proved in Theorem 18.

Theorem 2. *If $(F, X, \mathbb{R}^n)$, $n \geqslant 2$, is a coherent system, every orbit is nowhere dense.*

Conjecture. *In a coherent system with $n \geqslant 2$, every orbit closure has measure zero.*

Even for cooperative systems this is known only for $n = 2$.
A subset of a $\mathbb{R}^n$ is a *rectangle* if it has the form $I_1 \times \cdots \times I_n$ where each $I_n \subset \mathbb{R}$ is a (nonempty) interval (open, closed or half-open).

Theorem 3. *Let $(F, X, \mathbb{R}^n)$ be a coherent system with X open in a rectangle, and assume there is a global attractor. Then there exists an equilibrium q. If X is open in $\mathbb{R}^n$ and q is the unique equilibrium, then q is globally asymptotically stable.*

Proposition 16 extends a basic result previously known only for strongly order-preserving local semiflows. The development of the concept "attractor" is discussed in Appendix A.
As an illustration of an application of the above theorems, we have the following example.

Example. Let $\mathsf{K} \subset \mathbb{R}^n$ be a closed orthant and denote the corresponding open orthant by $\mathsf{K}^o := \operatorname{Int} \mathsf{K}$. Let $F : \mathsf{K}^o \to \mathbb{R}^n$ be a C^1 vector field whose components have the form

$$F_i(x) = g_i(x) \left(\sum_{j=1}^n M_{ij} x_j + B_i \right) \quad (i = 1, \ldots, n). \tag{4}$$

The functions $g_i : \mathsf{K}^o \to \mathbb{R}$ are nonzero everywhere, and M_{ij} and B_i denote real constants.

A special case is the restriction of a Lotka–Volterra system to the open positive orthant $\operatorname{Int}(\mathbb{R}^n_+)$, for which $g_i(x) = x_i$. Hofbauer and So [19] have found a Lotka–Volterra system in $\mathbb{R}^3_+$ whose restriction to the open orthant has a global attractor containing two attracting periodic orbits; see also Lu and Luo [25], Xiao and Li [49]. The following result says that such systems cannot be coherent:

Proposition 4. *Assume the system $(F, \mathsf{K}^o, \mathbb{R}^n)$ defined by Eq. (4) is coherent and has a global attractor $A \subset \mathsf{K}^o$. Then A is an equilibrium.*

Proof. By Theorem 3 there exists an equilibrium q and it suffices to prove that q is unique. Every equilibrium p lies in K^o, hence all its coordinates are nonzero. As $g_i(p) \neq 0$ we therefore have

$$p \in \mathcal{E} \quad \Longleftrightarrow \quad \sum_j M_{ij} p_j + B_i = 0 \quad (i = 1, \ldots, n).$$

Assuming p and q are distinct equilibria, we will reach a contradiction. Let $L \subset \mathbb{R}^n$ denote the line through p and q. Then

$$L \cap \mathsf{K}^o \subset \mathcal{E}.$$

As $\mathcal{E}$ is closed in A, it is a compact set in K^o, hence

$$\overline{L \cap \mathsf{K}^o} \subset \mathsf{K}^o.$$

But this not possible, because $\overline{L \cap \mathsf{K}^o}$ meets $\mathsf{K} \backslash \mathsf{K}^o$. $\quad\square$

1.4. Motivations

To every system $(F, X, \mathbb{R}^n)$ there is associated a directed labeled interaction graph $\Gamma(F)$ (defined below) with the property that F is coherent if and only if every directed loop is positive. A more restrictive condition, for graphs that are not necessarily strongly connected, is the requirement that *all* loops, directed and undirected, are positive. In that case changing the signs of certain variables makes the system cooperative. We obtain analogous transformations for coherent systems.

In the classic and often quoted 1981 paper [46], R. Thomas conjectured that coherent systems do not have any periodic attractors: "the presence of at least one negative loop in the logical structure appears as a necessary (but not sufficient) condition for a permanent periodic behavior". It is frequently claimed that Thomas' conjecture was settled by Snoussi [40] and Gouze [12] (see e.g. Pigolotti et al. [31]). However, these references dealt only with the more restricted monotone case. Theorem 1 implies that, indeed, coherent systems do not admit periodic attractors ("persistent periodic behaviors"), thus settling the conjecture in the positive.

A different motivation for this result comes from current research in molecular systems biology. As discussed in Sontag [41], many biological networks, while not monotone, may still lack negative cycles. A concrete example is that of the yeast *Saccharomyces cerevisiae* gene regulatory network published in [28] (the graph may be downloaded from [52]). This network has 690 nodes and 1082 edges, of which 221 are negative and 861 are positive.[3] Current knowledge does not provide a precise mathematical model of this yeast gene regulatory network. However, if one assumes that each node represents a scalar variable such as the concentration of a protein, or even that each node represents a vector of variables whose components are intermediates (mRNA concentrations, occupancy of transcription factor binding sites, and so forth), the corresponding system will be coherent. This guarantees, in view of the results presented here, that there are no topologically transitive attractors. This by itself does not preclude exotic attractors, but it means that any that exist must be much more complex than the traditional "chaotic" attractors, such as horseshoes, as these are finitely transitive but are not equilibria. It is known that the system is not monotone with respect to any orthant order. This assertion can be made quantitative, in the following sense: From the algorithm described in [10], it was estimated in [41] that one must remove, or change the sign of, approximately 43 of the edges of the interaction graph in order to obtain a monotone system. (Later computational work, in [20], showed that the precise minimal number of required deletions or sign changes is 42.)

2. Fibre systems

We will need to consider certain more general dynamical situations, where the domain of the local semiflow lies in an affine subspace of $\mathbb{R}^n$. Consider a system $(F, X, \mathbb{R}^n, \Phi)$. Suppose $n_1 \in \{1, \dots, n-1\}$ is such that the first n_1 coordinates of $F(x)$ depend only on the first n_1 coordinates of x. This means there is a system $(F^1, X^1, \mathbb{R}^{n_1}, \Phi^1)$ with the following properties:

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[3] In the original data set, there is one edge labeled as "neutral"; this edge was arbitrarily labeled as positive in [41], but the conclusions do not change substantially if it is labeled as negative instead, or deleted.

- the natural projection $\Pi : \mathbb{R}^n \to \mathbb{R}^{n_1}$ on the first n_1 coordinates satisfies

$$\Pi(X) = X^1, \qquad \Pi \circ F(x) = F^1 \circ \Pi(x) \quad (x \in X); \tag{5}$$

- Π semiconjugates the local semiflow Φ of F to the local semiflow Φ^1 in X^1 generated by F^1:

$$\Pi \circ \Phi_t(x) = \Phi^1_t \circ \Pi(x) \quad \text{if } \Phi_t(x) \text{ is defined.} \tag{6}$$

We summarize this by saying that $\Pi : F \twoheadrightarrow F^1$ is a *cascade*.

Now assume $p \in \mathcal{E}(F^1)$ and set

$$E_p := \Pi^{-1}(p),$$

which is an $(n - n_1)$-dimensional affine subspace of $\mathbb{R}^n$ and a coset of the kernel of Π. The set

$$X_p := X \cap E_p$$

is *positively invariant* under Φ, that is, $\Phi_t(x) \in X_p$ provided $x \in X_p$ and $\Phi_t(x)$ is defined. Thus Φ restricts to a local semiflow Φ^p in X_p.

The map

$$T_p : \mathbb{R}^{n-n_1} \to E_p, \quad y \mapsto (p_1, \ldots, p_{n_1}, y_1, \ldots, y_{n-n_1})$$

is an affine isomorphism. Set

$$\hat{X}_p := T_p^{-1}(X_p) \subset \mathbb{R}^{n-n_1}$$

and define $\hat{\Phi}^p$ as the local semiflow in $\hat{X}_p$ that conjugates to Φ^p by T_p, characterized by

$$\hat{\Phi}^p_t(x) = (T_p)^{-1} \circ \Phi_t \circ T_p(x) \quad \text{if } x \in \hat{X}_p \text{ and } \Phi_t\big(T_p(x)\big) \text{ is defined.} \tag{7}$$

The vector field $\hat{F}_p : \hat{X}_p \to \mathbb{R}^{n-n_1}$ corresponding to $\hat{\Phi}^p$ is transformed by T_p to $F|X_p$:

$$(T_p)'(y)\big(\hat{F}_p(y)\big) = F(p, y) \quad (y \in \hat{X}_p).$$

The trajectories of $\hat{\Phi}^p$ are the maximally defined solutions to

$$\frac{dx}{dt} = \hat{F}_p\big(\hat{\Phi}^p_t x\big) \quad (x \in \hat{X}_p, \ t \geqslant 0).$$

Evidently the following conditions are equivalent:

- $(\hat{F}_p, \hat{X}_p, \mathbb{R}^{n-n_1}, \hat{\Phi}^p)$ is a system;
- $\hat{X}_p$ is the closure of its relative interior in $\mathbb{R}^{n-n_1}$;
- X_p is the closure of its relative interior in E_p.

When these conditions hold for a particular $p \in \mathcal{E}(F^1)$ we call $(\hat{F}_p, X_p, \mathbb{R}^{n-n_1})$ the *fibre system* over p. When they hold for all $p \in \mathcal{E}(F^1)$ we say F *has fibre systems over* $\mathcal{E}(F^1)$.

For inductions on dimension we need conditions ensuring that fibre systems exist and their domains have nice geometry. The following result is far from exhaustive in this regard, but it suffices for present purposes.

Consider the following conditions on pairs (X, n):

$P_1(X, n)$: X is open in $\mathbb{R}^n$;
$P_2(X, n)$: X is open in a coordinate halfspace in $\mathbb{R}^n$;
$P_3(X, n)$: X is open in a positive coordinate cone in $\mathbb{R}^n$;
$P_4(X, n)$: X is open in a rectangle in $\mathbb{R}^n$.

Proposition 5. *Assume* $P_j(X, n)$ *for some* $j \in \{1, \ldots, 4\}$ *and let* $\Pi : (F, \mathbb{R}^n, X) \twoheadrightarrow (F^1, X_1, \mathbb{R}^{n_1})$ *be a cascade.*

(a) *Either* $P_j(\Pi(X), n_1)$ *holds or else* $\Pi(X) = \mathbb{R}^{n_1}$.

Assume $p \in \mathcal{E}(F_1)$.

(b) *If* $j \in \{1, 4\}$, *then* $P_j(\hat{X}_p, n - n_1)$ *is satisfied. If* $j \in \{2, 3\}$, *then* $P_k(\hat{X}_p, n - n_1)$ *is satisfied for some* $k \in \{1, 2, 3\}$. *Therefore* F *has a fibre system* $(\hat{F}_p, \hat{X}_p, \mathbb{R}^{n-n_1})$ *over* p.
(c) *If* $j \in \{1, 2, 3\}$, *every point of* $\hat{X}_p$ *is strongly accessible in* $\mathbb{R}^{n-n_1}$ *from above and below.*

Proof. Left to the reader. $\quad\square$

Structure of proofs. The proofs of Theorems 1–3 have a common pattern which we now discuss. The theorem is proved first for a cooperative system, which includes the case $n = 1$. The proof proceeds by induction on n. If the coherent system in question is not cooperative, by Theorem 10 below it is transformed, through permuting and changing signs of variables, to a dynamically equivalent system $(F, X, \mathbb{R}^n)$ having the following properties:

- F is quasicooperative;
- there is a cooperative system $(F^1, X^1, \mathbb{R}^{n_1})$ with $n_1 < n$ and a cascade $\Pi : F \twoheadrightarrow F^1$ having fibre systems over $\mathcal{E}(F^1)$;
- each fibre system is quasicooperative.

The inductive hypothesis implies the conclusion of the theorem holds for F^1 and each fibre system, and this is used to complete the induction.

2.1. Local semiflows

A *local semiflow* Φ in a metrizable space Z is a collection $\Phi = \{\Phi_t\}_{t \in \mathbb{R}_+}$ of continuous maps $\Phi_t : D_t \to R_t$ between nonempty subsets of Z, with D_t open. The notation $\Phi_t x$ indicates $x \in D_t$, absent contraindications. Φ is required to have the following properties:

- The set $\Omega := \{(t, x) \in \mathbb{R}_+ \times Z : x \in D_t\}$ is an open neighborhood of $\{0\} \times Z$ in $\mathbb{R}_+ \times Z$, and the map $\Omega \to Z$, $(t, x) \mapsto \Phi_t x$ is continuous.
- $x \in (\Phi_s)^{-1} D_t \Rightarrow \Phi_s \circ \Phi_t(x) = \Phi_{s+t}(x)$.
- Φ_0 is the identity map of Z.

We also say that (Φ, Z) is a local semiflow. When Φ is obtained by solving Eq. (1) each map Φ_t is a homeomorphism, but this is not assumed for general local semiflows.

The *orbit* and *omega limit set* of x are respectively

$$\gamma(x) := \{\Phi_t x : x \in D_t\}, \qquad \omega(x) := \bigcap_{t \in D_t} \overline{\gamma(\Phi_t x)},$$

p is an *equilibrium* if $\Phi_t p = p$ for all t. The set of equilibria is denoted by $\mathcal{E}(\Phi)$, and by $\mathcal{E}(F)$ when Φ is generated by the vector field F.

3. Graphs

By a *directed graph* $\Gamma := (V_\Gamma, E_\Gamma)$ we mean a nonempty finite set $V := V_\Gamma$ (the set of vertices) together with a binary relation $E := E_\Gamma \subset V \times V$ (the set of *directed edges*, usually referred to simply as "edges"). We always assume E is totally nonreflexive i.e., $(i, i) \notin E$.

An *isomorphism* between a pair of directed graphs is a bijection f between their vertex sets such that $f \times f$ restricts to a bijection f_* between their edge sets.

Our chief tool for analyzing the crude dynamics of systems $(F, X, \mathbb{R}^n)$ is the *interaction graph* $\Gamma := \Gamma(F)$. This is the labeled directed graph with vertex set is $V = V(\Gamma) := \{1, \ldots, n\}$, whose set of (directed) edges is

$$E = E(\Gamma) := \left\{ (j, i) \in V \times V : \; j \neq i \text{ and } \frac{\partial F_i}{\partial x_j} \text{ is not identically 0 in } X \right\}.$$

Edge (j, i) is assigned the label $h(j, i) \in \{+1, -1, \theta\}$ according to the rule:

$$h(j, i) = \begin{cases} 1 & \text{if } \frac{\partial F_i}{\partial x^j}(x) \geqslant 0 \text{ for all } x \in X, \\ -1 & \text{if } \frac{\partial F_i}{\partial x^j}(x) \leqslant 0 \text{ for all } x \in X, \\ \theta & \text{otherwise.} \end{cases} \tag{8}$$

A *path* of length $k \in \mathbb{N}_+$ is a sequence $(u_0, \ldots, u_k)$ of vertices such that (u_{j-1}, u_j) is an edge for $j = 1, \ldots, k$. The *concatenation* of an ordered pair (λ, μ) of paths,

$$\lambda = (u_0, \ldots, u_k), \qquad \mu = (u_k, \ldots, u_{k+l}),$$

is the path

$$\lambda \cdot \mu := (u_0, \ldots, u_k, u_{k+1}, \ldots, u_{k+l})$$

obtained by transversing first λ and then μ.

A *loop* of length $\mu \in \mathbb{N}_+$ is a sequence of $\mu \geqslant 2$ edges having the form

$$(i_0, i_1), (i_1, i_2), \ldots, (i_{\mu-1}, i_\mu), \quad i_\mu = i_0.$$

As our graphs are totally nonreflexive, there are no self-loops: $i_j \neq i_{j-1}, \; j = 1, \ldots, \mu$.

A path is *positive* (respectively, *negative*) if each of its edges is labeled 1 or -1 and the product of these labels is $+1$ (respectively, -1). All other paths are *ambiguous*.

We define three types of graphs in increasing order of generality:

Γ is *positive* if every edge is positive;
Γ is *quasipositive* if every loop has only positive edges;
Γ has the *positive loop property* if every loop is positive.

Paraphrasing some of the earlier definitions, we define corresponding types of systems F:

F is *cooperative* if $\Gamma(F)$ is positive;
F is *quasicooperative* if $\Gamma(F)$ is quasipositive;
F is *coherent* if $\Gamma(F)$ has the positive loop property.

Evidently *cooperative* $\Rightarrow$ *quasicooperative* $\Rightarrow$ *coherent*.

The term "graph" is shorthand for "finite directed graph having edges labeled in $\{1, -1, \theta\}$". Graphs are denoted by Greek capitals Γ, Λ, perhaps with indices. The sets of vertices and edges of Γ are denoted by $V(\Gamma)$ and $E(\Gamma)$, respectively, and the labeling function is denoted by

$$h_\Gamma : E(\Gamma) \to \{1, -1, \theta\}.$$

We extend h_Γ to the function (also denoted by h) mapping the set of paths into $\{1, -1, \theta\}$, as follows. If $\lambda = (u_0, \ldots, u_k)$ is a path of length $k > 1$ then

$$h(\lambda) = \begin{cases} \theta & \text{if some edge of } \lambda \text{ is ambiguous,} \\ h(u_1, u_0) \times \cdots \times h(u_k, u_{k-1}) & \text{otherwise.} \end{cases}$$

Two graphs Γ, Λ are *isomorphic* if there is an isomorphism $f : V(\Gamma) \to V(\Lambda)$ between the underlying directed graphs such that $h_\Lambda \circ f_* = h_\Gamma$.

Λ is a *subgraph* of Γ provided

$$V(\Lambda) \subset V(\Gamma), \qquad E(\Lambda) \subset E(\Gamma), \qquad h_\Lambda = h_\Gamma | E(\Lambda).$$

We abuse notation and denote this by $\Lambda \subset \Gamma$, saying that Λ contained in Γ.

If Λ, Λ' are subgraphs their *graph union* is the subgraph with vertex set $V(\Lambda) \cup V(\Lambda')$ and edge set $E(\Lambda) \cup E(\Lambda')$.

A graph Γ is *connected* if for each pair of distinct vertices j, k there is a sequence of vertices $j = i_0, \ldots, i_m = k$ such that (i_{l-1}, i_l) or (i_l, i_{l-1}) is an edge of Λ $(l = 1, \ldots, m)$. A *component* of Γ is a maximal connected subgraph. Γ is *strongly connected* if for any ordered pair (a, b) of distinct vertices there is a path in Λ from a to b. When every component is strongly connected, Γ is *weakly reversible* (Feinberg [11]).

These definitions imply:

- A graph with no edges is weakly reversible, but a graph with only one edge is not.
- The graph union of weakly reversible graphs is weakly reversible.
- If Γ is quasipositive, every weakly reversible subgraph is positive.

A subgraph $\Lambda \subset \Gamma$ is called:

- *full* provided it contains all edges in Γ joining vertices of Λ,
- *initial* if no edge of Γ is directed from a vertex outside Λ to a vertex of Λ,
- *terminal* if no directed edge of Γ joins a vertex of Λ to a vertex not in Λ,
- *fundamental* if it is initial and strongly connected, and no other subgraph containing Λ has these properties.

Lemma 6. *The following hold for every graph*:

(a) *fundamental subgraphs are full*;
(b) *if fundamental subgraphs share a vertex, they coincide*;
(c) *every strongly connected initial subgraph is contained in a unique fundamental subgraph*;
(d) *every vertex belongs to a fundamental subgraph.*

Proof. (a) and (b) follow directly from definitions. (c) is proved by showing that the graph union of a maximal nested family of strongly connected initial subgraphs is fundamental. As a graph with a single vertex is strongly connected and initial, (d) is a consequence of (c). $\quad\square$

3.1. Graphs and systems

Let $(F, X, \mathbb{R}^n)$ denote a system.

Proposition 7. *Assume $\Pi : F \twoheadrightarrow F^1$ is a cascade, $p \in \mathcal{E}$, and F_p is a fibre system. Then*:

(a) $\Gamma(F^1)$ *is a full subgraph of $\Gamma(F)$,*
(b) $\Gamma(F_p)$ *is isomorphic to a subgraph (not necessarily full) of $\Gamma(F)$,*
(c) *when F is cooperative (respectively: quasicooperative, coherent), so are F^1 and F_p.*

Proof. By the cascade assumption:

$$\frac{\partial F_i}{\partial x_j} = 0 \quad \text{if } i \leqslant n_1 < j \ (i, j \in \{1, \ldots, n\}) \tag{9}$$

and the Jacobian matrices of F have lower triangular block decompositions of the form

$$F'(x) = \begin{bmatrix} M_{11}(x) & O \\ M_{21}(x) & M_{22}(x) \end{bmatrix} \tag{10}$$

where $M_{11}(x) = (F^1)'(\Pi x) \in \mathbb{R}^{n_1 \times n_1}$, and O stands for a matrix of zeroes.
  (a) and (b), which imply (c), are proved by inspecting the block decomposition (10) of the matrix of functions $F'(x)$. $\quad\square$

Proposition 8. *Let $\Gamma^1 \subset \Gamma(F)$ be an initial full subgraph such that $V(\Gamma_1) = \{1, \ldots, n_1\}$. Then*:

(i) *There is a cascade $\Pi : (F, X, \mathbb{R}^n) \twoheadrightarrow (F^1, X^1, \mathbb{R}^{n_1})$ such that $\Gamma(F^1) = \Gamma^1$.*
(ii) *Suppose F is quasicooperative. Then F^1 and all fibre systems are quasicooperative, and if Γ_1 is weakly reversible then F^1 is cooperative.*

Proof. Initiality and fullness of Γ^1 means that (9) holds. Therefore (5) defines a cascade satisfying (i). The first assertion in (ii) follows from Proposition 7(c). The second assertion holds because Γ_1 is quasipositive, and if it is weakly reversible then every edge is in a loop and is therefore positive. $\quad\square$

3.2. Spin assignments

A *spin assignment* for a graph Γ is any function $\sigma : V(\Gamma) \to \{\pm 1\}$. It is *consistent* if $h(u, v) = \sigma(u)\sigma(v)$ for every edge (u, v) belonging to a loop.[4]

Theorem 9. *Γ has the positive loop property if and only if it has a consistent spin assignment.*

Proof. Assume Γ has the positive loop property. Let Γ' be obtained from Γ by keeping the same vertices but deleting the edges not contained in loops. Evidently Γ' is weakly reversible and has the positive loop property. Moreover, if σ is a consistent spin assignment on Γ' it is also a consistent spin assignment on Γ. Therefore it suffices to consider the case that Γ is strongly connected.

Claim: If λ^1, λ^2 are paths from a to b then $h(\lambda^1) = h(\lambda^2) \in \{\pm 1\}$. To see this, choose a path μ from b to a. Since every loop is positive by hypothesis, for $j = 1, 2$ we have

$$1 = h(\lambda^j \cdot \mu) = h(\lambda^j)h(\mu).$$

Therefore $h(\lambda^1) = h(\mu) = h(\lambda^2)$.

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[4] This terminology is not the same as in Sontag [41], which further required every edge to be consistent.

Now fix a vertex p of Γ and for each vertex v choose a path λ_v from p to v. Define $\sigma(p) = 1$ and $\sigma(v) = h(\lambda_v)$, which by the claim is independent of the choice of λ_v. For any edge $e = (u, v)$ we can fix λ_u and define $\lambda_v := \lambda_u \cdot e$. Then we have

$$\sigma(u) = h(\lambda_u), \qquad \sigma(v) = h(\lambda_u \cdot e) = h(\lambda_u)h(e),$$

which implies $h(e) = \sigma(u)\sigma(v)$. The converse implication is left to the reader. $\quad\square$

Remark. The foregoing proof can be expressed homologically. Let $\hat{\Lambda}$ denote the 1-dimensional cell complex corresponding to a prime subgraph $\Lambda \subset \Gamma$, having the vertices of Λ as 0-cells and the edges of Λ as 1-cells. In the cellular chain groups of $\hat{\Lambda}$ with coefficients in $\mathbb{Z}_2$ (identified with the multiplicative group $\{\pm 1\}$), a labeling h is a 1-cochain, spin assignments are 0-cocycles, and a spin assignment σ is consistent for h if its coboundary is $\delta\sigma = h$. As the evaluation of cochains on chains induces a dual pairing $H^1(\hat{\Lambda}; \mathbb{Z}_2) \times H_1(\hat{\Lambda}; \mathbb{Z}_2) \to \mathbb{Z}_2$, the positive loop property makes the cohomology class of h trivial. Thus $h = \delta\sigma$, proving that σ is consistent.

A change of variables $x \mapsto y$ is called *elementary* if there is a permutation $i \mapsto i'$ of $\{1, \ldots, n\}$ and an n-tuple $\rho \in \{\pm 1\}^n$ such that $y_i = \rho_i x_{i'}$.

Theorem 10. *Assume $(F, X, \mathbb{R}^n)$ is a coherent system with X open in $\mathbb{R}^n$ or in a positive coordinate cone. Suppose F is not cooperative. Then there is an elementary change of variables that transforms $(F, X, \mathbb{R}^n)$ to a system $(G, Y, \mathbb{R}^n)$ admitting a cascade $\Pi : (G, Y, \mathbb{R}^n) \twoheadrightarrow (F^1, X^1, \mathbb{R}^{n_1})$, $1 \leqslant n \leqslant n - 1$, with the following properties*:

(a) $(G, Y, \mathbb{F}^n)$ *is quasicooperative and* $(F^1, X^1, \mathbb{R}^{n_1})$ *is cooperative*;
(b) $\Pi : G \twoheadrightarrow F^1$ *has fibre systems over the equilibria of F^1. Each of these fibre systems is quasicooperative, and its domain open in $\mathbb{R}^{n-n_1}$ or in a positive coordinate cone in $\mathbb{R}^{n-n_1}$.*

Proof. By Theorem 9 we choose a consistent spin assignment σ. The elementary change of variables $L : \mathbb{R}^n \to \mathbb{R}^n$,

$$y = Lx, \qquad y_i := \sigma(i)x_i,$$

transforms $(F, X, \mathbb{R}^n)$ into a system

$$\big(G, L(X), \mathbb{R}^n\big),$$

such that $\Gamma(G)$ and $\Gamma(F)$ have the same directed edges, but the labeling on some edges may change sign. For every directed edge (j, i) of $\Gamma(G)$:

$$h_{\Gamma(G)}(j, i) = \text{sign}\left(\frac{\partial G_i}{\partial y_j}\right) = \sigma_j \sigma_i \, \text{sign}\left(\frac{\partial F_i}{\partial x_j}\right)\sigma_j \sigma_i h_{\Gamma(F)}(j, i).$$

If (j, i) belongs to a loop then $h_{\Gamma(F)}(j, i) = \sigma_j \sigma_i$ by the consistency condition. Therefore

$$\text{sign}\left(\frac{\partial G_i}{\partial y_j}\right)(\sigma_j \sigma_i)^2 = (\pm 1)^2 = 1,$$

showing that G is quasicooperative. After reindexing variables we assume by Lemma 6(d) that there is a fundamental subgraph $\Gamma^1 \subset \Gamma(F)$ with vertex set $\{1, \ldots, n_1\}$, $1 \leqslant n_1 \leqslant n$. Now apply Propositions 5 and 8. $\quad\square$

4. Monotone dynamics

Throughout this section we assume:

- $\Phi := \{\Phi_t\}_{t \geqslant 0}$ is a local semiflow in an ordered metric space X;
- Φ is *monotone*: $x \succcurlyeq y \Rightarrow \Phi_t x \succcurlyeq \Phi_t y$.

To simplify notation we may write $x(t) := \Phi_t x$ whenever $\Phi_t x$ is defined. It is well known for the data in Eq. (1) that if F is cooperative and X is convex, the local semiflow Φ defined by integral curves of X is monotone. This is a corollary of the Müller–Kamke theorem [21,29] on differential inequalities (Hirsch [16]).

Proposition 11. *The following are true for all $x \in X$:*

(a) *No points of $\omega(x)$ are related by $\rhd_X$ or $\lhd_X$;*
(b) *$\omega(x)$ is a singleton in the following cases:*
  (i) *$\overline{\gamma(x)}$ is compact and there exist $t_* \geqslant 0$, $\varepsilon > 0$ such that*

$$t_* < t < t_* + \varepsilon \quad \Longrightarrow \quad \Phi_t x \prec x \quad or \quad \Phi_t x \succ x;$$

  (ii) *$\overline{\gamma(x)}$ is compact and there exists $t > 0$ such that*

$$x \lhd_X \Phi_t x \quad or \quad x \rhd_X \Phi_t x.$$

Proof. (a) and (b)(i) are sharpenings of Hirsch and Smith [18, Theorems 1.8, 1.4], respectively. Assertion (b)(ii) follows from (b)(i). □

Proposition 12. *Assume $A \subset X$ is attracting.*

(a) *If each point of A is strongly accessible in X from either above or below, then A contains an equilibrium.*
(b) *If each point of A is strongly accessible in X from both above and below and $A \cap \mathcal{E} = p$ then $A = p$.*

Proof. The conclusions of (a) and (b) were obtained in Hirsch [17, Theorems III.3.1 and III.3.3] under the hypothesis that X is open in a strongly ordered Banach space. □

Proposition 13. *Assume $B \subset \omega(x)$. Let $q \in B$ be a minimal (respectively, maximal) point of B, and assume q has a neighborhood $N \subset X$ such that some point $y \prec N$ (respectively, $y \succ N$) is attracted to B. Then $q = \inf \omega(x)$ (respectively, $q = \sup \omega(x)$), and $q = \omega(y)$.*

Remark 14. When X is a subset of $\mathbb{R}^n$ with the induced order and topology, then Proposition 13 has the stronger conclusion $q = \omega(x)$. This is a consequence of Proposition 16 below.

Proof of Proposition 13. To fix ideas we assume q is a minimal point of B and $y \prec N$. Notation is simplified by setting $w(t) := \Phi_t w$ when $w \in X$, $t \geqslant 0$, and $\Phi_t w$ is defined.

Some point on the orbit of x lies in N and its omega limit set contains B. After replacing x by such a point we assume $x \in N$. Therefore $y \prec x$ and

$$y(t) \preccurlyeq x(t) \quad (t \geqslant 0). \tag{11}$$

There is a positive sequence $t_n \to \infty$ such that $x(t_n) \in N$ and

$$x(t_n) \to q. \tag{12}$$

Because $\omega(y) \subset B$, after passing to a subsequence we have

$$y(t_n) \to b \in B. \tag{13}$$

It follows from (11)–(13) and closedness of the order relation that $b \preccurlyeq q$. Minimality of q implies $b = q$, hence $y(t_n) \to q$.

Choose n_0 so that $y(t_{n_0}) \in N$. If $I \subset \mathbb{R}_+$ is a sufficiently small open interval about t_{n_0} then $s \in I \Rightarrow y(s) \in N$, hence $y(s) \succcurlyeq y$. Proposition 11(b)(i) now shows $y(t)$ converges, necessarily to q, whence $\omega(y) = q$. It follows from (11) that $q \leqslant \omega(x)$, hence $q = \inf \omega(x)$. $\square$

In the rest of this section we assume:

Hypothesis 15. $X \subset \mathbb{R}^n$ with the vector ordering.

Proposition 16. *If* $\inf \omega(x) = p$ *or* $\sup \omega(x) = p$ *then* $\omega(x) = p$.

For strongly order-preserving local semiflows a stronger conclusion holds: Every omega limit set is unordered (Hirsch and Smith [18, Corollary 1.9]).

Proof of Proposition 16. For each subset $\Sigma \subset \{1, \dots, n\}$ the corresponding *face* of $\mathbb{R}_+^n$ is

$$\mathsf{J} := \mathsf{J}(\Sigma) = \left\{z \in \mathbb{R}_+^n \colon z_i > 0 \ \Rightarrow \ i \in \Sigma\right\}.$$

When $\Sigma \neq \emptyset$ the corresponding *open face* is

$$\mathsf{J}^o := \mathsf{J}^o(\Sigma) = \left\{z \in \mathbb{R}_+^n \colon z_i > 0 \ \Leftrightarrow \ i \in \Sigma\right\}.$$

Fix $x, p \in X$ such that $\inf \omega(x) = p$ or $\sup \omega(x) = p$; we have to prove $\omega(x) = p$. To fix ideas we assume $p = 0 = \inf \omega(x)$.

Claim: $\Phi_t(x)$ is defined for all $t \geqslant 0$. It is well known that this is the case if the orbit closure of x is compact. If it is not compact, the orbit intersects the boundary of some open ball centered at 0 in an infinite set. Consequently $\omega(x)$ contains a point $\neq p$, which implies the claim.

For any $I \subset [0, \infty)$ set $\Phi(I, x) := \{\Phi_t x \colon t \in I\}$. By the Baire category theorem there is a dense open subset $S \subset [0, \infty)$ such that for each component I of S there is a unique open face $\mathsf{J}_I^o \supset \Phi(I, x)$.

There is a sequence $\{I_k\}_{k \in \mathbb{N}}$ of components of S and points $t_k \in I_k$ such that as $k \to \infty$ we have

$$t_k \to \infty, \quad x(t_k) \succ 0, \quad x(t_k) \to 0.$$

Passing to a subsequence we assume there is an open face K^o such that $\mathsf{J}_{I_k}^o = \mathsf{K}^o$ for all k, and K^o has the largest possible dimension. Then there exists $t_* \geqslant 0$ such that

$$t \geqslant t_* \quad \Longrightarrow \quad x(t) \in \mathsf{K}^o.$$

For if $x(t_0) \in \mathsf{K}^o$ and $\varepsilon > 0$ is such that $x(t) \notin \mathsf{K}^o$ for $t \in (t_0, t_0 + \varepsilon]$, then $x(t')$ for some $t' \in (t_0, t_0 + \varepsilon]$ belongs to an open face of larger dimension, and this can only happen finitely many times.

Let $N \subset \mathbb{R}_+^n$ be a neighborhood of 0 such that $N \prec x(t_*)$. Since $0 \in \omega(x)$, there is an interval $I > t_*$ such that $\Phi(I, x) \subset N \cap \mathsf{K}_0$. Then

$$\Phi(I, x) \prec x(t_*),$$

which by Proposition 11(b)(i) implies the trajectory of $x(t_*)$ converges, necessarily to 0. Therefore $\omega(x) = \omega(x(t_*)) = 0$. $\square$

Corollary 17. *Assume $0 \in X \subset \mathbb{R}^n_+$. If $0 \in \omega(x)$, then $0 = \omega(x)$.*

Proof. Follows from Proposition 16 because $0 = \inf \omega(x)$. $\quad \square$

Remark. We digress to interpret this result biologically. Let $x_i \geqslant 0$ stand for the "size" of species i (population, biomass, density, ...) and call $S(x) := \sum_{i=1}^{n} x_i$ the "total size". Assume that from each initial state $x(0) \in \mathbb{R}^n_+$ the species develop along a curve $x(t) = (x_1(t), \ldots, x_n(t)) \in \mathbb{R}^n_+$, $t \geqslant 0$, governed by a cooperative system (suggesting symbiosis or commensalism) in $\mathbb{R}^n_+$. Then:

- *Let $x(t)$ be a trajectory. If the total population does not die out, the total size is bounded above 0. That is, either $\lim_{t \to \infty} x(t) = 0$, or else $\inf_{t \geqslant 0} S(t) > 0$.*

This follows from the contrapositive of the corollary.

The next result will be used to start the inductive proof of Theorem 1. It applies only to cooperative systems, but the assumptions on X and A are weaker than in Theorem 1. Recall that every nonempty compact set in an ordered space contains a maximum point and a minimum point (Ward [50]).

Theorem 18. *Assume $X \subset \mathbb{R}^n$ has the vector ordering and Φ is a monotone local semiflow in X. Let $A \subset X$ be compact connected set that is attracting and finitely transitive for Φ. Then A reduces to an equilibrium in the following cases:*

(a) *$n = 1$;*
(b) *some maximal point of A is strongly accessible in X from above;*
(c) *some minimal point of A is strongly accessible in X from below;*
(d) *X is open in $\mathbb{R}^n$ or in a positive coordinate cone.*

Proof. Case (a) is trivial because every omega limit set is an equilibrium. Cases (b) and (c) can be shown to be formally isomorphic by reversing the order relation. Property (d) implies (b). Therefore it suffices to give the proof under assumption (b).

Henceforth q denotes a maximal point of A, assumed to be strongly accessible in X from above. We will prove:

(i) there exists $y \rhd q$ with $\omega(y) \subset A$,
(ii) if $\omega(v) \subset A$ and $q \in \omega(v)$ then $\omega(v) = q \in \mathcal{E}$.

Assertion (i) holds because A attracts all nearby points. To prove (ii), assume $q \in \omega(v) \subset A$. As q is maximal in A, it is *a fortiori* maximal in $\omega(v)$, whence $q = \sup \omega(v)$ by Proposition 13. Therefore (ii) follows from (i) and Proposition 11(b)(ii).

Now assume *per contra* that $A \neq q$. Since the set A is connected, there is a sequence $\{a_k\}$ in A converging to q with the property that $a_k \neq q$ and $\omega(a_k) \subset A$. By finite transitivity of A there is a finite set $V \subset A$ such that each a_k is an omega limit point of some member of V. By finiteness of V and compactness of A we find a subsequence $\{b_k\}$ of $\{a_k\}$ and a point $v \in V$ such that $b_k \in \omega(v)$ and hence $\omega(b_k) \subset \omega(v)$, for all k. Therefore $q \in \omega(v)$, whence $q = \omega(v)$ by (ii). This can only happen if $b_k = q$ for all k, contradicting the assumption that $a_k \neq q$. $\quad \square$

5. Proofs of the main theorems

We will use the following fact, whose proof is straightforward, concerning an arbitrary cascade $\Pi : F \twoheadrightarrow F^1$:

- *If $A \subset X$ is invariant, or finitely transitive for F, then $\Pi(A)$ has the same property for F^1. Likewise, if A is a (global) attractor for F then $\Pi(A)$ is a (global) attractor for F^1.*

Proof of Theorem 1. When F is cooperative, Φ is monotone because X is convex, and the conclusion follows from Theorem 18.

We proceed by induction on n. The case $n = 1$ is trivial because every omega limit set is an equilibrium. Assume inductively: $n > 1$ and the conclusion holds for smaller values of n. We can assume F is not cooperative. By Theorem 10, after performing an elementary change of variables we can assume there is a cooperative system $(F^1, X^1, \mathbb{R}^{n_1})$ with $1 \leqslant n_1 < n$ and a cascade $\Pi : F \twoheadrightarrow F^1$ having fibre systems over equilibria of F^1, and such that for every $p \in \mathcal{E}(F^1)$ the fibre system $(\hat{F}_p, \hat{X}_p, \mathbb{R}^{n-n_1}, \hat{\Phi}^p)$ is quasicooperative. The geometrical conditions on the pair $(X, \mathbb{R}^n)$ postulated by Theorem 1 are inherited by $(\Pi(X), \mathbb{R}^n)$ and $(\hat{X}_p, \mathbb{R}^{n-n_1})$, according to Proposition 5.

Let $A \subset X$ be a compact, connected, finitely transitive attracting set. The set $\Pi(A) \subset X^1$ has these same properties for F^1, hence $\Pi(A) = p \in \mathcal{E}(F^1)$ by the inductive assumption. Thus A lies in the invariant set $X_p = X \cap \Pi^{-1}(p)$, and A is attracting and finitely transitive for $\Phi|X_p$. This local semiflow is conjugate to $\hat{\Phi}^p$, which is quasicooperative. Therefore the inductive hypothesis applied to $\hat{\Phi}^p$ shows that A is an equilibrium. This completes the induction. $\square$

Proof of Theorem 2. Consider first the case that F is cooperative, so that Φ is monotone by convexity of X. Assume *per contra* that the orbit closure of some $x \in X$ contains a nonempty relatively open subset U of X. As X is the closure of its interior in $\mathbb{R}^n$, we can take U open in $\mathbb{R}^n$. Therefore $\omega(x)$ contains points a, b such that $a \lhd_X b$. But this contradicts Proposition 11(a).

Now assume F is not cooperative.

By Theorem 10, after performing an elementary change of variables we assume there is a cooperative system F^1 and a cascade $\Pi : F \twoheadrightarrow F^1$. Suppose U is open in X and γ is an orbit of F. Then $\Pi(U)$ is open in X^1 and $\Pi(\gamma)$ is an orbit of F^1. As F^1 is cooperative, $\Pi(\gamma) \cap \Pi(U)$ is not dense in $\Pi(U)$, whence $\gamma \cap U$ is not dense in U. $\square$

Proof of Theorem 3. If F is cooperative, as when $n = 1$, the conclusion follows from Proposition 12. We proceed by induction on n, assuming that $n > 1$ and the theorem holds for smaller values.

We can assume F is not cooperative. By Theorem 10 and Proposition 5 we assume, after an elementary change of variables, that there is a cascade $\Pi : F \twoheadrightarrow F^1$ onto a cooperative system $(F^1, X^1, \mathbb{R}^{n_1})$, $n_1 < n$, with fibre systems over equilibria of F^1, such that $\hat{F}^1$ is cooperative and each fibre system is quasicooperative.

As in the proof of Theorem 1, the inductive hypothesis applies to F^1. Therefore there exists $p \in \mathcal{E}(F^1)$. Applying the inductive hypothesis to $\hat{F}_p$, we obtain $q \in \mathcal{E}(F_p) \subset \mathcal{E}(F)$. This proves the first assertion of Theorem 3. Now assume X is open in $\mathbb{R}^n$ and $\mathcal{E}(F) = q$. Then $E(F^1) = p$ and $\mathcal{E}(F_p) = q$, hence the induction hypothesis implies (i) p is the global attractor for F^1, and (ii) q is the global attractor for Φ^p. From (ii) we infer $A \subset X_p$, and now (i) implies $A = q$. This completes the induction. $\square$

Acknowledgments

Appendix A. Notes on the development of the concept "attractor"

In spite of the fact that everyone who is interested in dynamics has a more or less vague intuition of what an attractor of a map $f : M \to M$ should be, there is no generally accepted mathematical definition for this concept even if M is a smooth manifold and f is also smooth.

H. Bothe [5]

The first mathematical use of the word "attractor" may be in Coddington and Levinson's 1955 book [7], where it refers to an asymptotically stable equilibrium. The term was subsequently extended to

include attracting cycles. Today there are many definitions, usually meaning an invariant set (of some kind) that is approached uniformly (in some sense) by the forward orbits of all (or most) points in some neighborhood of the set.

Attractors do not occur explicitly in the work of Poincaré or Birkhoff. These authors were primarily interested in Hamiltonian systems, which have no attractors because they preserve volume.

An early proof of existence of a unique attracting periodic orbit for a general class of systems is in the 1942 paper of N. Levinson and O. Smith [23].[5]

Early computer simulations revealed what appear to be attractors. As far back as 1952, Turing [47] published pictures of numerical simulations of a nonlinear dynamical model of cell development, exhibiting striking pattern formation. Simulations by Stein and Ulam [42,43] and Lorenz [24] gave persuasive pictorial evidence of complicated structure in attractors, but attracted little attention when they were published. Hamming's review [15] of [43] was unenthusiastic:

> Many photographs of cathode ray tube displays are given, a fondness for citing large numbers of iterations and machine time used is revealed, and a crude classification of the limited results is offered, but there appears to be no firm new results of general mathematical interest...
>
> One can only wonder what will happen to mathematics if we allow the undigested outputs of computers to fill our literature. The present paper shows only slight traces of any digestion of the computer output.

Much of the early theoretical work on attractors on global analysis was concerned with characterizing them in terms of Liapunov functions and topological dynamics (e.g., Ura [48], Auslander et al. [3], Mendelson [26], Bhatia [4]). Little was known of their internal dynamics beyond the existence of fixed points in global attractors for flows in Euclidean space (Bhatia and Szegö [6]).

In the 1960s a number of articles on attractors and related forms of stability were inspired by Sell [37]. In his seminal 1967 work on global analysis, Smale gave detailed constructions and analyses of hyperbolic attractors and other invariant sets, which would later be called "chaotic" and "fractal", and proved them structurally stable. He called attention to the vast mixture of periodic, almost periodic, homoclinic and other phenomena found in structurally stable attractors, even in rather simply given systems.

"Strange attractors" were proposed in 1971 as a model of turbulence by Ruelle and Takens [33,35, 36] and Newhouse et al. [30]. The physical significance of this route to chaos is still debated.

In his controversial 1972 book on morphogenesis [44,45] the late René Thom issued a bold manifesto proclaiming a fundamental scientific role for attractors:

> 1. Every object, or every physical form, can be represented by an *attractor C* of a dynamical system in a space *M* of *internal variables*.
> 2. Such an object possesses no stability, and for this reason cannot be perceived, unless the corresponding attractor is *structurally stable*.
> 3. Every creation or destruction of forms, every morphogenesis, can be described by the disappearance of the attractors representing the initial forms and their replacement through capture by the attractors representing the final forms. This process, called *catastrophe*, can be described in a space of *external variables*. ...

In recent years much work has been devoted to analysis of attractors in specific classes of chaotic systems, such as those named after Duffing, Lorenz, Hénon and Chua, and to attractors having particular topological properties, such as R. Williams' expanding attractors (Williams [51], Plykin and Zhirov [32]). A novel measure-theoretic type of attractor due to Milnor [27] has stimulated several papers.

Many authors have investigated attractors in infinite-dimensional systems, especially for partial differential equations, a prime desideratum being finite-dimensional global attractors. The large liter-

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[5] Thanks to George Sell for this reference.

ature includes books by Constantin et al. [9], Hale [14], Ladyzhenskaya [22], Ruelle [34], Sell and You [38], and others.

Attractors, being objects defined by topological limiting processes, resist classification and even description. A general theory appears quite distant.

References

[1] E. Akin, The General Topology of Dynamical Systems, Amer. Math. Soc., Providence, RI, 1993.

[2] U. Alon, An Introduction to Systems Biology: Design Principles of Biological Circuits, Chapman & Hall, 2006.

[3] J. Auslander, N.P. Bhatia, P. Seibert, Attractors in dynamical systems, Bol. Soc. Mat. Mexicana (2) 9 (1964) 55–66.

[4] N. Bhatia, On asymptotic stability in dynamical systems, Math. Syst. Theory 1 (1967) 113–128.

[5] H. Bothe, Review of Milnor [27], Math. Reviews.

[6] N. Bhatia, G. Szegö, Weak attractors in R^n, Math. Syst. Theory 1 (1967) 129–133.

[7] E.A. Coddington, N. Levinson, Theory of Ordinary Differential Equations, McGraw–Hill, New York, 1955.

[8] C.C. Conley, Isolated Invariant Sets and the Morse Index, Published for the Conference Board of the Mathematical Sciences by the American Mathematical Society, CBMS Reg. Conf. Ser. Math., vol. 38, Amer. Math. Soc., Providence, RI, 1978.

[9] P. Constantin, C. Foias, B. Nicolaenko, R. Temam, Integral Manifolds and Inertial Manifolds for Dissipative Partial Differential Equations, Appl. Math. Sci., vol. 70, Springer-Verlag, New York, 1989.

[10] B. DasGupta, G.A. Enciso, E.D. Sontag, Y. Zhang, Algorithmic and complexity aspects of decompositions of biological networks into monotone subsystems, Biosystems 90 (2007) 161–178.

[11] M. Feinberg, Chemical reaction network structure and the stability of complex isothermal reactors, I. The deficiency zero and deficiency one theorems, Chem. Eng. Sci. 2 (1987) 2229–2268.

[12] J.L. Gouze, Positive and negative circuits in dynamical systems, J. Biol. Syst. 6 (1998) 11–15.

[13] K.P. Hadeler, D. Glas, Quasimonotone systems and convergence to equilibrium in a population genetic model, J. Math. Anal. Appl. 95 (1983) 297–303.

[14] J.K. Hale, Asymptotic Behavior of Dissipative Systems, Math. Surveys Monogr., vol. 25, Amer. Math. Soc., Providence, RI, 1988.

[15] R. Hamming, Review of Stein and Ulam [43], Math. Reviews #6666 29 (1965) 1248.

[16] M.W. Hirsch, Systems of differential equations which are competitive or cooperative. I: Limit sets, SIAM J. Math. Anal. 13 (1982) 167–179.

[17] M.W. Hirsch, The dynamical systems approach to differential equations, Bull. Amer. Math. Soc. 11 (1984) 1–64.

[18] M.W. Hirsch, H.L. Smith, Monotone dynamical systems, in: A. Cañada, P. Drábek, A. Fonda (Eds.), Handbook of Differential Equations: Ordinary Differential Equations, vol. 2, Elsevier North-Holland, Boston, 2005, pp. 239–258.

[19] J. Hofbauer, J. So, Multiple limit cycles for three dimensional competitive Lotka–Volterra equations, Appl. Math. Lett. 7 (1994) 65–70.

[20] F. Hüffner, N. Betzler, R. Niedermeier, Optimal edge deletions for signed graph balancing, in: Proceedings of the 6th Workshop on Experimental Algorithms (WEA07), June 6–8, 2007, Rome, Springer-Verlag, Heidelberg, 2007.

[21] E. Kamke, Zur Theorie der Systeme gewöhnlicher Differentialgleichungen II, Acta Math. 58 (1932) 57–85.

[22] O. Ladyzhenskaya, Attractors for Semigroups and Evolution Equations, Cambridge Univ. Press, Cambridge, UK, 1991.

[23] N. Levinson, O. Smith, A general equation for relaxation oscillations, Duke Math. J. 9 (1942) 382–403.

[24] E. Lorenz, Deterministic nonperiodic flows, J. Atmospheric Sci. 20 (1963) 130–141.

[25] Z. Lu, Y. Luo, Three limit cycles for a three-dimensional Lotka–Volterra competitive system with a heteroclinic cycle, Comput. Math. Appl. 46 (2003) 231–238.

[26] P. Mendelson, On unstable attractors, Bol. Soc. Mat. Mexicana (2) 5 (1960) 270–276.

[27] J. Milnor, On the concept of attractor, Comm. Math. Phys. 99 (1985) 177–195.

[28] R. Milo, S. Shen-Orr, S. Itzkovitz, N. Kashtan, D. Chklovskii, U. Alon, Network motifs: Simple building blocks of complex networks, Science 298 (2002) 824–827.

[29] M. Müller, Über das Fundamenthaltheorem in der Theorie der gewöhnlichen Differentialgleichungen, Math. Z. 26 (1926) 619–645.

[30] S. Newhouse, D. Ruelle, F. Takens, Occurrence of strange Axiom A attractors near quasiperiodic flows on T^m, $m \geqslant 3$, Comm. Math. Phys. 64 (1978–1979) 35–40.

[31] S. Pigolotti, S. Krishna, M.H. Jensen, Oscillation patterns in negative feedback loops, Proc. Natl. Acad. Sci. USA 104 (2007) 6533–6537.

[32] R.V. Plykin, A. Zhirov, Some problems of attractors of dynamical systems, Topology Appl. 54 (1993) 19–46.

[33] D. Ruelle, Strange attractors as a mathematical explanation of turbulence, in: Statistical Models and Turbulence (Proc. Sympos., Univ. California), La Jolla, CA, 1971, in: Lecture Notes in Phys., vol. 12, Springer-Verlag, Berlin, 1972.

[34] D. Ruelle, Turbulence, Strange Attractors, and Chaos, World Sci. Ser. Nonlinear Sci. Ser. A Monogr. Treatises, vol. 16, World Scientific, River Edge, NJ, 1995.

[35] D. Ruelle, F. Takens, On the nature of turbulence, Comm. Math. Phys. 20 (1971) 167–192.

[36] D. Ruelle, F. Takens, Note concerning our paper: "On the nature of turbulence", Comm. Math. Phys. 23 (1971) 343–344.

[37] G. Sell, Periodic solutions and asymptotic stability, J. Differential Equations 2 (1966) 143–157.

[38] G. Sell, Y. You, Dynamics of Evolutionary Equations, Appl. Math. Sci., vol. 143, Springer-Verlag, New York, 2002.

[39] S. Smale, Differentiable dynamical systems, Bull. Amer. Math. Soc. 73 (1967) 747–817.

[40] E.H. Snoussi, Necessary conditions for multistationarity and stable periodicity, J. Biol. Syst. 6 (1998) 3–9.

[41] E.D. Sontag, Monotone and near-monotone biochemical networks, Systems and Synthetic Biology 1 (2007) 59–87.

[42] P.R. Stein, S.M. Ulam, Quadratic transformations, part I, Los Alamos Report LA2305, Washington, Office of Technical Services, US Department of Commerce, 1959.

[43] P.R. Stein, S.M. Ulam, Non-Linear Transformation Studies on Electronic Computers, Dissertationes Math. (Rozprawy Mat.), vol. xxxix, Państwowe Wydawnictwo Naukowe, Warsaw, 1964.

[44] R. Thom, Stabilité structurelle et morphogénèse; essai d'une théorie generale des modéles, W.A. Benjamin, Reading, MA, 1972.

[45] R. Thom, Structural Stability and Morphogenesis: An Outline of a General Theory of Models, W.A. Benjamin, Reading, MA, 1975.

[46] R. Thomas, On the relation between the logical structure of systems and their ability to generate multiple steady states or sustained oscillations, in: Springer Ser. Synergetics, vol. 9, 1981, pp. 180–193.

[47] A.M. Turing, The chemical basis of morphogenesis, Philos. Trans. R. Soc. Lond. Ser. B 237 (1952) 37–72.

[48] T. Ura, Sur les courbes définies par les equations differentielles dans l'éspace à m dimensions, Ann. Sci. Ecole Norm. Sup. (3) 70 (1953) 287–360.

[49] D. Xiao, W. Li, Limit cycles for the competitive three dimensional Lotka–Volterra system, J. Differential Equations 164 (2000) 1–15.

[50] L. Ward, Partially ordered topological spaces, Proc. Amer. Math. Soc. 5 (1954) 144–161.

[51] R.F. Williams, Expanding attractors, in: Colloque de Topologie Différentielle, Mont-Aigoual, 1969, Université de Montpellier, Montpellier, pp. 79–89.

[52] http://www.weizmann.ac.il/mcb/UriAlon/Papers/networkMotifs/yeastData.mat.