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Analogues of the Smale and Hirsch theorems for cooperative Boolean and other discrete systems

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Dedicated to Avner Friedman, on the occasion of his 75th birthday

Discrete dynamical systems defined on the state space $\Pi = \{0, 1, \ldots, p-1\}^n$ have been used in multiple applications, most recently for the modelling of gene and protein networks. In this paper, we study to what extent well-known theorems by Smale and Hirsch, which form part of the theory of (continuous) monotone dynamical systems, generalize or fail to do so in the discrete case.

We show that arbitrary m-dimensional systems cannot necessarily be embedded into n-dimensional cooperative systems for $n = m+1$, as in the Smale theorem for the continuous case, but we show that this is possible for $n = m+2$ as long as p is sufficiently large.

We also prove that strict cooperativity, a natural weakening of the notion of strong cooperativity, implies non-trivial bounds on the lengths of periodic orbits in discrete systems and imposes a condition akin to Lyapunov stability on all attractors. Finally, we explore several natural candidates for definitions of irreducibility of a discrete system. While some of these notions imply the strict cooperativity of a given cooperative system and impose even tighter bounds on the lengths of periodic orbits than strict cooperativity alone, other plausible definitions allow the existence of exponentially long periodic orbits.

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1. Introduction

Let $(L, \leq)$ be a linearly ordered set, let $n \geq 1$ and $L_1, \ldots, L_n \subseteq L$ with the induced order, and consider the set $\Pi = \prod_{i=1}^{n} L_i$. A map $g : \Pi \to \Pi$ defines the discrete dynamical system

$$x(t+1) = g(x(t)), x(t) \in \Pi. \tag{1}$$

We call (1) an *n-dimensional, discrete system* and also identify it with the pair (Π, g). For most of this paper, L will be the set of real numbers with the natural order, and $L_i = \{0, \ldots, p-1\}$ for some fixed integer $p > 1$. In this case, we speak of an *n-dimensional, p-discrete system*. The case $p = 2$ corresponds to the so-called *Boolean networks* or *Boolean systems* which are used in various disciplines, notably in the study

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of gene regulatory systems [1,11,12,17,21,22,27,29]. If all L_i s are finite, then we may, without loss of generality, assume that $L_i = \{0, \ldots, p_i - 1\}$ for some $p_i > 1$, but the p_i's are not necessarily all equal. In this case, we speak of a *finite discrete system*.

Define a partial order on Π by $x \leq y$, if $x_i \leq y_i$ for $i = 1, \ldots, n$. We call this relation the *cooperative order*, and we will not make a notational distinction between it and the order relation on L. A discrete system (1) is said to be *cooperative* if $x(0) \leq y(0)$ implies $x(t) \leq y(t)$ for every $t \geq 0$, where $x(t)$and$y(t)$ are the solutions of the system with initial conditions $x(0)$ and $y(0)$, respectively. Clearly, this is equivalent to the property that $x \leq y$ implies $g(x) \leq g(y)$. Discrete cooperative systems have been proposed as a tool to study genetic networks by Sontag and others [27,28].

The cooperativity property has a well-studied counterpart in continuous dynamical systems

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = f_i(x), \quad i = 1, \ldots, n, \tag{2}$$

for C^1 vector fields $f : \mathbb{R}^n \to \mathbb{R}^n$. Namely, the system (2) is *cooperative* if $x(t)$ and $y(t)$ are two solutions such that $x_i(0) \leq y_i(0)$, $i = 1, \ldots, n$, then $x_i(t) \leq y_i(t)$ for every $t > 0$, $i = 1, \ldots, n$. Cooperative systems are canonical examples of the so-called monotone systems, which have been studied extensively by Hirsch, Smith, Matano, Poláčik and others, and more recently by Sontag et al. in the context of gene regulatory networks under exclusively positive feedback [3,7,9,19,24].

1.1 The Smale and Hirsch theorems

In the present paper, we consider two important results from the theory of (continuous) monotone dynamical systems, and we show to what extent these results either generalize or fail to do so in the context of cooperative discrete systems (1).

The first result was originally published by Smale [23] in the 1970s. It states in this context that any compactly supported, $(n - 1)$-dimensional, C^1 dynamical system defined on $H = \{x \in \mathbb{R}^n | x_1 + \cdots + x_n = 0\}$ can be embedded into some cooperative C^1 system (2). Equivalently, the dynamics of cooperative systems can be completely arbitrary on unordered hyperplanes such as H. See also [5], where the cooperative system (2) is shown to have bounded solutions and has only two equilibria outside of H.

One way to regard the Smale theorem in the discrete case would be to ask whether discrete cooperative systems can have arbitrary dynamics on unordered sets $H = \{x \in \Pi | x_1 + \cdots + x_n = \text{ const.}\}$. This is trivially true (see Lemma 1).

An alternative approach is to study whether one can embed an arbitrary m-dimensional p-discrete system (1) into a cooperative $(m + 1)$-dimensional p-discrete system. We show that the answer to this question is *no* (Theorem 8, item 3), but that the statement is true (for sufficiently large p) if '$m + 1$' is weakened to '$m + 2$' (Theorem 8, item 2).

The second result for continuous cooperative systems was proved by Hirsch [7]. A continuous cooperative system is *strongly cooperative* if for every two different initial conditions $x(0) \leq y(0)$, we have $x_i(t) < y_i(t)$ for all $i = 1, \ldots, n$ and $t > 0$. A closely related definition involves the digraph G associated with the system: in the cooperative case, G is defined as having nodes $1, \ldots, n$, and an arc from i to j is present if and only if $\partial f_j / \partial x_i(x) > 0$ on $\mathbb{R}^n$. A continuous cooperative system (2) is strongly cooperative if the digraph G is strongly connected [24]; we refer to the latter property as the *irreducibility* of the system (2). Hirsch's theorem states that almost every bounded solution of a strongly cooperative system (2) converges towards the set of equilibria. This result rules out stable periodic orbits and chaotic behaviour. It was also generalized for abstract-order relations in Banach spaces by Hirsch and extended to continuous-space, discrete-time maps by Tereščák, Poláčik and collaborators [6,8,19,20].

For finite discrete systems, we will consider analogue definitions related to strong cooperativity and of irreducibility of a cooperative system (1). We are particularly interested in whether these definitions rule out the existence of exponentially long periodic orbits, which in finite discrete systems can be considered analogues of chaotic attractors. In particular, we study the notion of strict cooperativity, a slight weakening of strong cooperativity that still remains meaningful in the context of discrete systems. We show that strict cooperativity does not rule out periodic orbits altogether, but that it puts a non-trivial, subexponential bound on their lengths and imposes a condition akin to Lyapunov stability on all attractors. Finally, we explore several natural candidates for definitions of irreducibility of a finite discrete system. We show that predicted properties of the system can dramatically change when subtle changes to our definitions are made. While one plausible definition of irreducibility still allows for exponentially long periodic orbits in cooperative systems (and hence does not imply strict cooperativity), a slightly different notion of irreducible cooperative systems implies strict cooperativity and imposes a bound of n (the dimension of the system) on the lengths of periodic orbits. This is a much tighter bound than the one implied by strict cooperativity alone.

1.2 Outline of the sections

In Section 2, we give a general condition under which an arbitrary m-dimensional, p-discrete system can be embedded into a cooperative n-dimensional, q-discrete system (Proposition 4). We rely on several standard results from the literature, especially a generalization of the classical Sperner theorem. In Section 3, we provide bounds on the maximum size $d_{n,p}$ of an unordered subset of Π, and we use these bounds to study the special cases $n = m + 1$ and $n = m + 2$ in the p-discrete case (Theorem 8). In Section 4, we prove a general result on extensions of cooperative partial functions on Π to cooperative systems on Π and discuss how our results are related to a certain generalization of Smale's theorem. We give a short discussion in Section 5 about applying Theorem 8 to the case of *almost cooperative* discrete systems [27], by showing a simple example of an almost cooperative Boolean system of dimension m that cannot be embedded into a cooperative Boolean system of dimension $m + 1$. In Section 6, we study strict cooperativity, a slight weakening of strong cooperativity (1) and show that for finite discrete systems it imposes substantial restrictions on the possible dynamics. In particular, we show that strictly cooperative p-discrete systems cannot have exponentially long periodic orbits. In Section 7, we explore several natural definitions of irreducibility for finite discrete systems and prove bounds on the lengths of periodic orbits in cooperative systems that are irreducible in the sense of these definitions.

2. Unordered sets and cooperative embeddings of *p*-discrete systems

Let $\Sigma := \prod_{i=1}^{m} L_i$ and $\Pi = \prod_{i=1}^{n} L_i^*$ and consider an arbitrary map $f : \Sigma \to \Sigma$. A *cooperative embedding* of (Σ, f) into a cooperative system (Π, g) as in (1) is an injective function $\phi : \Sigma \to \Pi$ such that $g(\phi(x)) = \phi(f(x))$ for every $x \in \Sigma$. A subset $A \subseteq \Pi$ is said to be *unordered* if no two different elements $a, b \in A$ satisfy $a \leq b$. If $\Pi = \prod_{i=1}^{n} \{0, \ldots, p_i - 1\}$, then we define $S(x) = x_1 + \cdots + x_n$ for $x = (x_1, \ldots, x_n) \in \Pi$. These definitions will be used throughout this paper.

A basic property of unordered sets is the following 'trivial embedding' result, which is well known at least for the Boolean case [27].

Lemma 1. *Assume that each set L_i is finite. Let $A \subseteq \Pi$ be unordered, and let $\gamma : A \to A$ be an arbitrary function. Then there exists a cooperative system* (1) *such that $g|_A = \gamma$.*

Proof. Let $\hat{A}$ be any unordered subset of Π which contains A, and which is maximal with respect to this property. Define $g(a) := \gamma(a)$ for $a \in A$, and $g(a) = a$ for $a \in \hat{A} - A$. For all other $x \in \Pi$, there must exist $a \in \hat{A}$ such that either $a \leq x$ or $x \leq a$, by the maximality of $\hat{A}$. If $x \leq a$ let $g(x) := [0, \ldots, 0]$, and if $a \leq x$ let $g(x) := [p_1 - 1, \ldots, p_n - 1]$. □

For the remainder of this section and the next one, let $\Pi = \{0, \ldots, p-1\}^n$ for some fixed integer $p > 1$. Given an arbitrary positive integer m, we will compute the least dimension n such that any m-dimensional p-discrete system (Σ, f) can be embedded into an n-dimensional cooperative system (Π, g). Define the set

$$D := \{x \in \Pi | S(x) = \lfloor n(p-1)/2 \rfloor\}, \quad d_{n,p} := |D|. \tag{3}$$

This set D is clearly unordered, because if $x \leq y$ and $x \neq y$, then necessarily $S(x) < S(y)$, and both x, y cannot be in D. Notice that

$$d_{n,2} = \binom{n}{\lfloor n/2 \rfloor}.$$

We quote a generalization of Sperner's Theorem [2,4], which states that D is a set of maximum size in Π with this property.

Lemma 2. *Consider the set $\Pi = \{0, 1, \ldots, p-1\}^n$, under the cooperative order $\leq$. Then $|A| \leq d_{n,p}$, for any unordered set* A.

The following lemma will be important below, see Proposition 5.2 in [9] for a proof.

Lemma 3. *Consider a cooperative map g defined on a space Π. Then any periodic orbit is unordered.*

Proposition 4. *Let n, m, p and q be positive integers with $p, q > 1$. Then the following are equivalent:*

(i) *Any m-dimensional q-discrete system can be embedded into a cooperative n-dimensional p-discrete system.*
(ii) $q^m \leq d_{n,p}$.

Proof. Suppose first that $q^m \leq d_{n,p}$ and consider any discrete system (Σ, f). We use an arbitrary injective function $\phi : \Sigma \to \Pi$ such that $A := \mathrm{Im}(\phi) \subseteq D$. Let $\gamma(y) := \phi(f(x))$ whenever $y \in A$, where $x = \phi^{-1}(y)$. Thus by construction, $\gamma(\phi(x)) = \gamma(y) = \phi(f(x))$ holds for $x \in \Sigma$. Apply Lemma 1 to define g and obtain a full cooperative embedding.

Now assume (i) in the statement. To prove that (ii) must hold, simply consider a map f on Σ which generates a single orbit with period q^m. By (i), there exists an embedding into Π, and the image of Σ is unordered in Π by Lemma 3. The inequality follows from Lemma 2. □

Another form of cooperative embedding was given by Smith [25] for a large class of non-cooperative but possibly continuous maps. In that case $n = 2m$ holds. By Proposition 4, a much sharper bound holds for the discrete case. See also the references [13–15,18,26].

3. Bounds on cooperative embeddings

Let $p > 1$ and $n > 0$ be arbitrary and $\Pi = \{0, \ldots, p-1\}^n$, $D, d_{n,p}$ be as in the previous section. We begin this section with several lemmas.

LEMMA 5. $d_{n,p} \geq (p^{n-1}/n)$.

Proof. Let $S_j := \{x \in \Pi | S(x) = j\}$, for $j = 0, \ldots, n(p-1)$. Each of these sets is unordered, and therefore $|S_j| \leq d_{n,p}$ by Lemma 2. Therefore,

$$p^n = \sum_{j=0}^{n(p-1)} |S_j| \leq (n(p-1)+1)d_{n,p} \leq npd_{n,p}.$$

□

LEMMA 6. *Let c be such that* $0 < c < p$. *Then* $d_{n,p} \geq c^n$, *for all sufficiently large n.*

Proof. By Lemma 5, it is sufficient to show that $p^{n-1}/n \geq c^n$. But this is equivalent to $\ln p \geq \ln c + (\ln n + \ln p)/n$. This inequality holds for large n since $\ln p > \ln c$. □

We now prove an upper bound for $d_{n,p}$.

LEMMA 7. *Let* $p, n > 1$. *Then* $d_{n+1,p} < p^n$.

Proof. We prove the equivalent statement that $d_{n,p} < p^{n-1}$ for $p > 1$, $n > 2$. Let x be a randomly chosen element of $\{0, \ldots, p-1\}^n$ with the uniform distribution. For x to be in D, we must have $\lfloor n(p-1)/2 \rfloor - p + 1 \leq x_1 + \cdots + x_{n-1} \leq \lfloor n(p-1)/2 \rfloor$ and $x_n = \lfloor n(p-1)/2 \rfloor - x_1 - \cdots - x_{n-1}$. Let A be the event that $\lfloor n(p-1)/2 \rfloor - p + 1 \leq x_1 + \cdots + x_{n-1} \leq \lfloor n(p-1)/2 \rfloor$. Our assumption on n implies that $P(A) < 1$. Moreover, note that $P(x_n = \lfloor n(p-1)/2 \rfloor - x_1 - \cdots - x_{n-1} | A) = 1/p$. Thus $d_{n,p}/p^n = P(x \in D) < (1/p)$ and the lemma follows. □

The above estimates have important consequences for embeddings of m-dimensional finite discrete systems into n-dimensional cooperative finite discrete systems. In particular, unlike for continuous systems, for large m, an m-dimensional p-discrete system can not always be embedded into an $(m+1)$-dimensional p-discrete cooperative system.

THEOREM 8. *The following statements hold:*

(1) *For every* $p > 1$, *and for every* $m > 0$, *there exists* $n > m$ *such that every* m*-dimensional* p*-discrete system can be embedded into an* n*-dimensional cooperative* p*-discrete system.*
(2) *For every* $m > 0$, *there exists* p_0 *such that for every* $p > p_0$ *every* m*-dimensional* p*-discrete system can be embedded into a cooperative* p*-discrete system of dimension* $m+2$.
(3) *For every* $m, p > 1$ *there exists an* m*-dimensional* p*-discrete system that cannot be embedded into a cooperative* p*-discrete system of dimension* $m+1$.

Proof. The first two statements are immediate consequences of Lemma 5 and Proposition 4. For the first one, let n be large enough so that $p^m \leq p^{n-1}/n$. Then $p^m \leq d_{n,p}$ and the conclusion follows. For the second statement, let simply $p \geq m+2$. Then

$$p^m \leq \frac{p^{m+1}}{m+2} = \frac{p^{(m+2)-1}}{m+2} \leq d_{m+2,p}.$$

For the third statement, let $m, p > 1$. Let f be defined on Π so as to generate a single orbit of length p^m. Then the image of Π under any embedding ϕ into $\Sigma = \{0, \ldots, p-1\}^{m+1}$ would also generate a periodic orbit of this length. Assuming that the system defined on Σ is cooperative, the set Im (ϕ) must be unordered by Lemma 3, and therefore $p^m \leq d_{m+1,p}$ by Lemma 2. But by Lemma 7, $d_{m+1,p} < p^m$, a contradiction. □

Note that we are restricting our attention to the case where $p = q$, i.e. both systems have the same level of discretization. This is relevant, for instance, in the special case of Boolean networks. But if we allow $q \neq p$, then the analogue of point 3 of Theorem 8 may fail. To see this, note that for $q > p$ and sufficiently large m we will have $p^m \leq (q^m/(m+1))$. Thus, Lemma 5 implies that in this case $m+1$-dimensional q-discrete systems contain sufficiently large unordered sets to embed every m-dimensional p-discrete system.

One important consequence of this discussion is that cooperative systems may have exponentially long cycles, which can be considered a form of chaotic behaviour in discrete systems.

COROLLARY 9. *Let $p > 1$ and let c be an arbitrary real number with $1 < c < p$. Then for sufficiently large n, there exist n-dimensional cooperative p-discrete systems with periodic orbits of length $> c^n$.*

Proof. Apply Lemma 1, by letting $A := D$ and defining $\gamma : A \to A$ so that it generates a single period of length $d_{n,p}$. The result follows from Lemma 6. □

While Lemmas 5–7 are sufficient for deriving our conclusions about embeddings into cooperative systems, let us remark that one can prove the sharper estimate

$$\lim_{n\to\infty} d_{n,p} \left(\frac{p^n}{\sqrt{2\pi n \sigma^2}} \right)^{-1} = 1,$$

for arbitrary $p > 1$ and $\sigma^2 = (1/12)(p-1)(p+1)$ (see Proposition 10 of [10]).

4. Smale extensions

Assume $\prod = \prod_{i=1}^n L_i$ and each L_i has a smallest and a largest element. Let $A \subseteq L$ and $\gamma : A \to L$. We say that γ is *cooperative* if for all $x, y \in A$ the implication $x \leq y \to \gamma(x) \leq \gamma(y)$ holds. Clearly, if A is unordered, then γ is cooperative, and since L has a largest and a smallest element, a construction such as that used in the proof of Lemma 1 implies that γ can be extended to a cooperative function on Π. However, the construction used in this proof is too crude to allow for such extensions if A contains comparable elements. Here, we use a different construction to show that any cooperative partial function on Π can be extended to a cooperative function on Π.

LEMMA 10. *Let* $\prod = \prod_{i=1}^{n} L_i$, *where* $(L_i, <)$ *is complete in the sense that every subset of* L_i *has a supremum and an infimum in* L_i. *Let* $A \subseteq \Pi$ *and* $\gamma : A \to \Pi$ *be cooperative. Then there exists a cooperative* $g : \Pi \to \Pi$ *such that* $\gamma = g \upharpoonright A$.

Proof. Let Π, A, γ be in the assumption. First note that we may without loss of generality assume that for all $z \in \Pi$ there exists $x \in A$ such that $x \leq z$ or $z \leq x$. If not, then extend A to a set A^* with this property and such that $A^* \backslash A$ is unordered and each $x \in A^* \backslash A$ is incomparable with each $z \in A$. Extend γ to $\gamma^* : A^* \to \Pi$ in an arbitrary way, and note that γ^* must still be cooperative.

Given $z \in \Pi$, define $U(z) := \{x \in A : x \geq z\}$ and $\Pi_U := \{z \in \Pi : U(z) \neq \emptyset\}$. Note that $A \subseteq \Pi_U$. Let $\Pi_L := \Pi \backslash \Pi_U$, and for all $z \in \Pi_L$ define $L(z) := \{x \in \Pi_U : x \leq z\}$. Note that our assumption on A implies that $L(z) \neq \emptyset$ for all $z \in \Pi_L$. Let $\gamma(U(z)) := \{\gamma(x) : x \in U(z)\}$.

Now define $g(z) := \inf \gamma(U(z))$ for $z \in \Pi_U$ and let $g(L(z)) := \{g(x) : x \in L(z)\}$ for $z \in L(z)$. Finally, define $g(z) := \sup g(L(z))$ for $z \in \Pi_L$. □

CLAIM 11. *The map g defined above is cooperative and satisfies* $g \upharpoonright A = \gamma$.

Proof. By completeness of $\leq$ on each L_i, infima and suprema under the cooperative order of non-empty subsets of Π exist and are elements of Π. Thus g is well defined.

Suppose that $z \in A \subseteq \Pi_U$. Then $\gamma(z) \leq \gamma(x)$ for every $x \in U(z)$ by cooperativity of γ, hence $\gamma(z) = \inf \gamma(U(z)) = g(z)$. Thus $g \upharpoonright A = \gamma$.

To see that g is cooperative, let $y, z \in \Pi$ be such that $y \leq z$. If $y, z \in \Pi_U$, then $U(z) \subseteq U(y)$, and hence $g(y) = \inf \gamma(U(y)) \leq \inf \gamma(U(z)) = g(z)$. If $y, z \in \Pi_L$, then $L(y) \subseteq L(z)$, and hence then $g(y) = \sup g(L(y)) \leq \sup g(L(z)) = g(z)$. The only other possibility consistent with $y \leq z$ is $z \in \Pi_L$ and $y \in \Pi_U$. In this case, $y \in L(z)$ and hence $g(y) \leq \sup g(L(z)) = g(z)$. □

We will refer to the function g constructed in the proof of Lemma 10 as the *Smale extension of* γ, since this is the same type of extension as he considered in [23] – even though the actual form of the function is somewhat different in the discrete case.

Now suppose Π is either $\{0, \ldots, p-1\}^n$ or $[0,1]^n$ with the natural cooperative order, and let A be a hyperplane of the form $A = \{x \in \Pi : S(x) = r\}$. If A is non-empty (which will happen for suitable values of r), then A is a maximal incomparable subset of Π.

Note that if A is a hyperplane as above, then the definition of the Smale extension g of γ can be written as

$$g(z) = \begin{cases} \inf \gamma(U(z)), & \text{for } z \in \Pi_U, \\ \sup \gamma(L(z)), & \text{for } z \in \Pi_L. \end{cases} \tag{4}$$

For $x \in \Pi$, let $\|x\| = \max\{|x_1|, \ldots, |x_n|\}$ be the ∞-norm in $\mathbb{R}^n$.

LEMMA 12. *Suppose* Π *is either* $\{0, \ldots, p-1\}^n$ *or* $[0,1]^n$ *with the natural cooperative order, and* $A = \{x \in \Pi : S(x) = r\}$ *is a non-empty hyperplane. Let* $\gamma, \gamma_1 : A \to \Pi$ *be cooperative and* $\varepsilon, \delta > 0$ *be such that*

$$\forall x, y \in A \; \|x - y\| < (2n+1)\delta \Rightarrow \|\gamma(x) - \gamma_1(y)\| < \frac{\varepsilon}{3}. \tag{5}$$

Let g *and* g_1 *be the Smale extensions of* γ *and* γ_1. *Then*

$$\forall x, y \in \Pi \; \|x - y\| < \delta \Rightarrow \|g(x) - g_1(y)\| < \varepsilon. \tag{6}$$

Proof. Let A,γ,ε and δ be as in the assumption. First note that

$$\forall x, y \in \Pi_U \quad \forall a \in U(x) \exists b \in U(y) \|a - b\| \leq (n-1)\|x - y\|. \tag{7}$$

To see this, let $x, y \in \Pi_U$ and $a \in A$ with $x \leq a$. Let $b \in U(y)$ be such that $\sum|b_i - a_i|$ is minimal. Such b exists by compactness of A. Note that we must have $b_i \leq \max\{a_i, y_i\}$ for all $i \in \{1, \ldots, n\}$: If not, since $S(a) = S(b)$, there would be some j with $y_j \leq b_j < a_j$. Letting $\beta = \min\{b_i - \max\{a_i, y_i\}, a_j - b_j\}$ and $b_i^* = b_i - \beta, b_j^* = b_j + \beta$ and $b_k^* = b_k$ for all $k \neq i,j$, we would have $y \leq b^* \in A$ and $\sum|b_i^* - a_i| < \sum|b_i - a_i|$, contradicting the choice of b. Thus, $|b_i - a_i| \leq \|x - y\|$ for all i with $b_i > a_i \geq x_i$. Now consider i with $y_i \leq b_i < a_i$. In this situation, we must have $a_i - b_i \leq \sum \max\{0, b_j - a_j\} \leq (n-1)\|x - y\|$. The inequality $\|a - b\| \leq (n-1)\|x - y\|$ follows.

Furthermore, note that

$$\forall x \in \Pi_U, \quad \forall y \in \Pi_L, \quad \forall a \in U(x) \quad \forall b \in L(y) \|a - b\| \leq (2n+1)\|x - y\|. \tag{8}$$

To see this, let $x \in \Pi_U, y \in \Pi_L, a \in U(x)$ and $b \in L(y)$. Fix $i \in \{1, \ldots, n\}$. Then, $a_i - x_i \leq S(a) - S(x) = r - S(x) \leq S(y) - S(x) \leq n\|y - x\|$. Similarly, $y_i - b_i \leq S(y) - S(b) = S(y) - r \leq S(y) - S(x)$. Now, it follows from the triangle inequality that $|a_i - b_i| \leq 2(S(y) - S(x)) + |y_i - x_i| \leq (2n+1)\|y - x\|$.

Now, let x and y be such that $\|x - y\| < \delta$.

First assume that $x, y \in \Pi_U$. Fix $i \in n$, and let $a \in U(x)$ be such that $|(g(x))_i - (\gamma(a))_i| < \varepsilon/3$. Such a exists by (4). Choose $b \in U(y)$ as in (7). It follows from (5) that $\|\gamma(a) - \gamma_1(b)\| < \varepsilon/3$. In particular, $|(\gamma(a))_i - \gamma_1(b)_i| < \varepsilon/3$. Since $y \leq b$, definition (4) implies that $(g_1(y)_i) \leq (\gamma_1(b))_i$ and the inequality $(g_1(y))_i < (g(x))_i + 2\varepsilon/3$ follows. By symmetry of the assumption, we will also have $(g(x))_i < (g_1(y))_i + 2\varepsilon/3$ in this case.

By the alternative definition (4) of the Smale embedding, the argument in the case when $x, y \in \Pi_L$ is dual.

Now, assume $x \in \Pi_U$ and $y \in \Pi_L$. Fix $i \in n$, and let $a \in U(a)$ and $b \in L(b)$ be such that $|(g(x))_i - (\gamma(a))_i| < \varepsilon/3$ and $|(g_1(y))_i - (\gamma_1(b))_i| < \varepsilon/3$. By (8), $\|a - b\| \leq (2n+1)\|y - x\| < (2n+1)\delta$, and (5) implies that $|(\gamma(a))_i - \gamma_1(b)_i| < \varepsilon$. Now (6) follows from the triangle inequality.

The argument in the case when $x \in \Pi_L$ and $y \in \Pi_U$ is symmetric. □

By letting $\gamma = \gamma_1$ in Lemma 12, we immediately get the following result. Since traditionally discrete dynamical systems are defined by a continuous map, the following lemma shows in particular that the Smale extension is a well-defined (continuous) map if γ is continuous.

Corollary 13. *Suppose $\Pi = [0,1]^n$ with the natural cooperative order, and $A = \{x \in \Pi : S(x) = r\}$ for some $0 \leq r \leq 1$. Let $\gamma : A \to \Pi$ be cooperative and $g : \Pi \to \Pi$ be the Smale extension of γ.*

(i) *If γ is continuous, so is* g.
(ii) *If γ is Lipschitz-continuous with Lipschitz constant ℓ, then* g *is Lipschitz continuous with Lipschitz constant $\leq (6n+3)\ell$.*

Now consider any discrete-time dynamical system $([0,1]^n, f)$, let $A = \{x \in [0,1]^{n+1} : S(x) = (n+1)/2\}$ and $\phi : [0,1]^n \to A$ be a Lipschitz-continuous homeomorphism. Let $\gamma : A \to A$ be such that $\gamma(\phi(x)) = \phi(f(x))$ for all $x \in [0,1]^n$. If f is (Lipschitz)-continuous, then so is γ, and Corollary 13 implies that ϕ is a (Lipschitz)-continuous embedding of $([0,1]^n, f)$ into a discrete-time dynamical system $([0,1]^{n+1}, g)$ for which g is (Lipschitz)-continuous. This is analogous to Smale's embedding theorem for C^1-systems [23] and is our motivation for calling the function g of Lemma 10 the *Smale extension* of γ.

If $([0,1]^n, f)$ and $(\{0, \ldots, p-1\}^n, f_1)$ are two discrete-time systems and $\varepsilon > 0$, then we will say that f_1 is an ε-approximation of f if $\|(1/p-1)f_1(\lfloor(p-1)x\rfloor) - f(x)\| < \varepsilon$ for all $x \in [0,1]^n$.

Let A be as in the previous paragraph, let $D = \{y \in \{0, \ldots, p-1\}^{n+1} : S(y) = \lfloor(n+1)(p-1)/2\rfloor\}$ and define $D^* := \{a \in A : (p-1)a \in D\}$. It is clear that if f is continuous and $\delta > 0$ is given, $\beta > 0$ is sufficiently small relative to δ, p is odd and sufficiently large, and if ϕ, γ are as in the previous paragraph, then there exist:

- a β-approximation $(\{0, \ldots, p-1\}^n, f_1)$ of $([0,1]^n, f)$,
- and a function $\gamma_1 : A \rightarrow D^*$ such that $\|\gamma(y) - \gamma_1(y)\| < \delta$ for all $y \in A$,
- a function $\phi_1 : \{0, \ldots, p-1\}^n \rightarrow D^*$ such that $\|\phi(x/(p-1)) - \phi_1(x)\| < \delta$ and $\gamma_1(\phi_1(x)) = \phi_1(f(x))$ for all $x \in \{0, \ldots, p-1\}^n$.

Now, let $\varepsilon > 0$ be given. By Lemma 12, if we choose the above objects for δ sufficiently small relative to ε and if g is the Smale extension of γ, while g_1 is the Smale extension of γ_1, then $\|g(y) - g_1(y)\| < \varepsilon$ for all $y \in [0,1]^{n+1}$. Let $g_1^*(x) := (p-1)g_1(x/(p-1))$ for all $x \in \{0, \ldots, p-1\}^{n+1}$. From the definition of the Smale extension it follows that g_1^* maps $x \in \{0, \ldots, p-1\}^{n+1}$ into itself, and the inequality $\|g(y) - g_1(y)\| < \varepsilon$ implies that g_1^* is an ε-approximation of g. Moreover, we will have $g_1^*(\phi_1(x)) = \phi_1(f_1(x))$ for all $x \in \{1, \ldots, p-1\}^n$. However, we cannot necessarily assume that ϕ_1 is a cooperative embedding of $(\{0, \ldots, p-1\}^n, f_1)$ into $(\{0, \ldots, p-1\}^{n+1}, g_1^*)$, since the results of Section 3 indicate that the function ϕ_1 may not be injective.

5. Almost cooperative systems

Cooperative systems are so named because increasing the value of one variable tends to increase the values of other variables in the system. For instance, in the continuous case, a condition equivalent to the cooperativity of the system (2) is $\partial f_i/\partial x_j(x) \geq 0$ for $i \neq j$ [24]. It has been conjectured that a system might have interesting properties if it is 'almost cooperative', i.e. if the latter condition is satisfied with the exception of a single pair $i \neq j$ (see the concept of *consistency deficit* in [27]).

We can define a discrete counterpart of this notion as follows. Let $\Pi = \prod_{i=1}^n \{0, \ldots, p_i - 1\}^n$, $x \in \Pi$ and $i \in \{1, \ldots, n\}$. Define $x^{i+} \in \Pi$ by letting $(x^{i+})_i = \min\{x_i + 1, p_i - 1\}$ and $(x^{i+})_j = x_j$ for $j \neq i$. Similarly, define $x^{i-} \in \Pi$ by letting $(x^{i-})_i = \max\{x_i - 1, 0\}$ and $(x^{i-})_j = x_j$ for $j \neq i$. It is easy to see that cooperativity of a system (Π, g) is equivalent to the condition that

$$\forall x \in \Pi \quad (g(x^{i-}))_j \leq (g(x))_j \leq (g(x^{i+}))_j, \tag{9}$$

for all $i, j \in \{1, \ldots, n\}$. Let us call (Π, g) *almost cooperative* if condition (9) holds with the exception of exactly one pair $< i^*, j^* >$ with $i^* \neq j^*$ for which an order-reversal takes place:

$$\forall x \in \Pi \quad (g(x^{i^*-}))_{j^*} \geq (g(x))_{j^*} \geq (g(x^{i^*+}))_{j^*}. \tag{10}$$

One might expect that almost cooperative p-discrete systems are similar to cooperative systems. In particular, one might expect that m-dimensional almost cooperative Boolean systems can always be embedded into cooperative Boolean systems of dimension $m+1$. However, this is not the case.

Consider the following simple example with $p=n=2$. In this case $|\Pi|=4$ and

$$d_{3,2}=\binom{3}{2}=3.$$

Define $g(x_1,x_2):=(1-x_2,x_1)$, so that $g(0,0)=(1,0)$, $g(1,0)=(1,1)$, $g(1,1)=(0,1)$ and $g(0,1)=(0,0)$. The system (Π,g) consists of a single orbit of length 4. By Proposition 4, this system cannot be embedded into any cooperative Boolean system of dimension 3. Moreover, note that x_1 promotes the increase of the variable x_2, while x_2 inhibits the variable x_1. Thus condition (9) holds with the exception of the pair $<i,j>=<2,1>$ and hence the system is almost cooperative.

6. Strict cooperativity for finite discrete systems

Throughout the remaining two sections, we will assume that the state space Π of our dynamical system is finite. Without loss of generality, this means that $\Pi=\prod_{i=1}^{n}\{0,\ldots,p_i-1\}$, where the p_i's are integers such that $p_1\geq\cdots\geq p_i\geq\cdots\geq p_n>1$. Of course, p-discrete systems are exactly those among the above systems for which $p_i=p>1$ for all i.

Our first task is to come up with a suitable counterpart of strong cooperativity for such systems. Let us write $x<y$ if $x\leq y$ in the cooperative order but $x\neq y$, and let us write $x\ll y$ if $x_i<y_i$ for all $i=1,\ldots,n$. Recall that a continuous system is strongly cooperative if for every two initial conditions $x(0)<y(0)$ we have $x(t)\ll y(t)$ for all $t>0$. One adaptation of this definition to finite discrete systems would be the following:

$$\forall x(0)<y(0)\exists t_0>0\forall t\geq t_0 \quad x(t)\ll y(t). \tag{11}$$

This property is commonly known as eventual strong cooperativity [24]. Unfortunately, no finite discrete system of dimension $n>1$ satisfies (11). To see this, note that if $n>1$, then there exist $x^0(0)<x^1(0)<\cdots<x^{p_1}(0)$. On the other hand, $x(t)\ll y(t)$ implies $n+S(x(t))\leq S(y(t))$. Now (11) would imply $S(x^{p_1}(t))\geq np_1$ for sufficiently large t. But this is a contradiction, since $S(x)\leq(p_1-1)n$ for all $x\in\Pi$.

So let us study a weaker version of strong cooperativity that is still meaningful in the context of finite cooperative systems. Consider the following properties:

$$\forall x(0)<y(0) \quad S(y(0)-x(0))\leq S(y(1)-x(1)), \tag{12}$$

$$\forall x(0)<y(0) \quad x(1)<y(1), \tag{13}$$

$$\forall x(0) \quad S(x(1))=S(x(0)). \tag{14}$$

LEMMA 14. *For any finite cooperative discrete system, conditions* (12)–(14) *are equivalent.*

Proof. Clearly, condition (12) implies conditions (13) and (14) implies condition (12) for cooperative systems.

Now assume an n-dimensional finite system (Π,g) satisfies condition (13). Let $x(0)\in\Pi$. Let $N:=\sum_{i=1}^{n}(p_i-1)$, and consider initial states $x^0(0)<x^1(0)<\cdots<x^N(0)$

such that $x(0) = x^{i_0}(0)$, where $i_0 = S(x)$. Note that we must have $S(x^i(0)) = i$ for $0 \leq i \leq N$. By (13), $x^0(1) < x^1(1) < \cdots < x^N(1)$. It follows that $S(x^i(1)) = S(x^i(0)) = i$ for all i, and in particular $S(x(0)) = S(x(1)) = i_0$. Property (14) follows. □

We will say that a finite cooperative system (Π, g) is *strictly cooperative* if it satisfies conditions (12)–(14). This definition is consistent with that for Equation (13) given in Section 5.2 of [9]. Note that this is a strong assumption to make, for instance, (14) implies that every hyperplane induced by S is invariant for such a system. But this condition is satisfied for various important systems, e.g. for those determined by a permutation as described below.

For example, let $\pi : \{1, \ldots, n\} \rightarrow \{1, \ldots, n\}$ be a permutation, and define g_π by $(g_\pi(x))_{\pi(i)} = x_i$ for all $x \in \Pi$ and $i \in \{1, \ldots, n\}$. Note that if $\Pi = \{0, \ldots, p-1\}^n$, then g_π maps Π into Π for all permutations π of $\{1, \ldots, n\}$, but for other sets Π, this will be the case only for some but not for all permutations. If g_π does map Π into Π, then (Π, g_π) is a strictly cooperative system.

The *order* of a permutation π is the smallest integer $r > 0$ such that π^r is the identity. Let $R(n)$ be the maximum order of a permutation π of $\{1, \ldots, n\}$. It can be shown that $R(n) = \mathrm{e}^{\sqrt{n \ln n}(1+o(1))}$ as $n \rightarrow \infty$ [16]. In particular, note that $R(n)$ grows *subexponentially in n*, that is, for every $b > 1$ and sufficiently large n, we will have $R(n) < b^n$.

Theorem 15. *Suppose* $(\prod_{i=1}^n \{1, \ldots, p_i - 1\}^n, g$ *is an n-dimensional strictly cooperative finite discrete system, and let* $N = \sum_{i=1}^n (p_i - 1)$*. Then each periodic orbit in* (Π, g) *has length at most* $R(N)$.

Proof. Note that for any permutation π, the length of any periodic orbit of (Π, g_π) cannot exceed the order of π. However, not all strictly cooperative finite systems are of the form (Π, g_π) for some permutation π. For example, if $n = 2$ and $g(0,0) = (0,0)$, $g(0,1) = g(1,0) = (0,1)$ and $g(1,1) = (1,1)$, then g is a strictly cooperative Boolean system, but not of the form g_π for any permutation π.

Fortunately, Lemma 16 below suffices for the proof of our theorem in the Boolean case when $p_i = 2$ for all i and hence $N = n$. A state in a periodic orbit of a dynamical system, i.e. a state that is not transient, will be called *persistent*.

Lemma 16. *Let* (Π, g) *be a strictly cooperative n-dimensional Boolean system. Then there exists a permutation* π *of* $\{1, \ldots, n\}$ *such that* $g(x) = g_\pi(x)$ *for each persistent state x of* (Π, g).

Proof. We will prove the lemma by induction over n. Note that it is trivially true for $n = 1$. Now fix $n > 1$, assume the lemma is true for all $k < n$ and let (Π, g) be as in the assumption. We will identify elements x of Π with subsets of the set $\{1, \ldots, n\}$ and write $\#(x)$ instead of $S(x)$. Note that g maps one-element subsets of $\{1, \ldots, n\}$ to one-element subsets. More precisely, there exists a function $\sigma : \{1, \ldots, n\} \rightarrow \{1, \ldots, n\}$ such that $g(\{i\}) = \{\sigma(i)\}$ for all i. In general, σ does not need to be a bijection. However, if I is the set of all i such that $\{i\}$ is a persistent state of our system, then $I \neq \emptyset$ and $\sigma \restriction I$ is a permutation of I. Now strict cooperativity of g implies that $g(x) = g_{\sigma \restriction I}(x)$ for all $x \subseteq I$. Thus, if $I = \{1, \ldots, n\}$, we are done. If not, then define for $y \in \Pi$ such that $I \cap y = \emptyset$:

$$f(y) = g(y \cup I) \backslash I.$$

Since $g(I) = g_{\sigma \restriction I}(I) = I$, the function f is strictly cooperative on the set of all subsets of $J := \{1, \ldots, n\} \backslash I$. By the inductive assumption, there exists a permutation ϱ of J such that

$f(y) = g_\varrho(y)$ for all persistent states in the system defined by f. Note that $\pi := (\sigma \restriction I) \cup \varrho$ is a permutation of $\{1, \ldots, n\}$.

Now consider any $x = x(0) \in \Pi$. By strict cooperativity, we have

$$\#(x) = \#(g(x)) = \#(g(x) \cap I) + \#(g(x) \cap J).$$

On the other hand, $\#(x \cap I) = \#(g(x \cap I)) \leq \#(g(x) \cap I)$ because $g(x \cap I) \subseteq g(I) = I$. It follows that $\#(x(t) \cap J)$ is non-increasing along the trajectory of $x(0)$. In particular, for every persistent state x, we must have $g(x \cap I) = g(x) \cap I$ and hence $\#(x \cap J) = \#(g(x) \cap J)$.

It must also be the case that $g(x) \cap J \subseteq f(x \cap J)$. Since $\#(f(x \cap J)) = \#(x \cap J)$ by strict cooperativity of f, we must have $g(x) \cap J = f(x \cap J)$ for every persistent state x of (Π, g). It follows that if x is a persistent state of (Π, g), then $x \cap J$ is a persistent state of (Σ, f). Thus $g(x) = g_{\sigma \restriction I}(x \cap I) \cup g_\varrho(x \cap J) = g_\pi(x)$. □

Now consider the general case where $p_i \geq 2$ for all i. Unfortunately, we cannot hope to prove the exact analogue of Lemma 16. To see this, consider the system $(\{0, 1, 2\}^2, g)$, where $g(0, 0) = (0, 0)$, $g(0, 1) = (1, 0)$, $g(1, 0) = (0, 1)$, $g(1, 1) = g(2, 0) = g(0, 2) = (1, 1)$, $g(1, 2) = (1, 2)$, $g(2, 1) = (2, 1)$, $g(2, 2) = (2, 2)$. This system is clearly strictly cooperative. If π were a permutation as in Lemma 16, then we would need $\pi(0) = 1$ and $\pi(1) = 0$ because both (0,1) and (1,0) are persistent states. On the other hand, (2,1) and (1,2) are persistent steady states, so this would force π to be the identity.

Now let $\Pi = \prod_{i=1}^{n} \{1, \ldots, p_i - 1\}^n$ and (Π, g), N be as in the assumption of Theorem 15. Let $\Sigma := \{0, 1\}^N$. For each $i \in \{1, \ldots, n\}$, let J_i be the set of integers j such that $\sum_{k=1}^{i-1} (p_k - 1) < j \leq \sum_{k=1}^{i} (p_k - 1)$. For $1 \leq \ell \leq \#(J_i) = p_i - 1$, let $j(i, \ell)$ be the ℓ-th element of J_i. Define a map $\psi : \Pi \to \Sigma$ so that for $i \in \{1, \ldots, n\}$ and $\ell \in \{1, \ldots, p_i - 1\}$ we have $\psi(x)_{j(i,\ell)} = 1$ iff $x_i \geq \ell$. Clearly, ψ is an injection. For $y \in \Sigma$, define $z(y)$ by $z(y)_{j(i,\ell)} = 1$ iff $\ell \leq \#(\{\ell' : y_{j(i,\ell')} = 1\})$. Note that $z(y)$ is always in the range of ψ, and $z(y) = y$ whenever y is already in the range of ψ. Moreover, the function $y \mapsto z(y)$ is strictly cooperative. Now define $f : \Sigma \to \Sigma$ so that $f(y) = f(z(y))$ for all y and $f(\psi(x)) = \psi(g(x))$ for all $x \in \Pi$.

Then, ψ is an embedding of (Π, g) into (Σ, f). Moreover, if (Π, g) is strictly cooperative, then so is (Σ, f). Since the lemma is true for $p = 2$, each periodic orbit in (Σ, f) has length at most $R(N)$, and since ψ is an embedding, the same must be true for (Π, g). □

Open Problem 17. Suppose (Π, g) is an arbitrary n-dimensional strictly cooperative finite discrete system. Can the system have a periodic orbit of length greater than $R(n)$? What if we assume in addition that (Π, g) is p-discrete for some $p > 2$?

Our results can perhaps be considered analogues of the result in [19] for discrete-time continuous-space strictly cooperative systems. Our Theorem 15 gives a non-trivial, subexponential bound on the lengths of periodic orbits of strictly cooperative finite discrete systems. Moreover, strict cooperativity implies that ordered orbits in finite discrete systems are fairly robust, as shown in the next result.

Lemma 18. *Consider a strictly cooperative finite discrete system* (1)*, and let* $x(0)$ *and* $y(0)$ *be two arbitrary initial conditions* (*i.e. not necessarily ordered*)*. Then,* $S(|y(t) - x(t)|) \leq S(|y(0) - x(0)|)$ *for all* $t > 0$.

Proof. Suppose first that $S(|y(0) - x(0)|) = 1$. Then necessarily the two initial conditions are ordered; suppose without loss of generality $x(0) < y(0)$. By condition (14) and cooperativity,

$$S(|y(0) - x(0)|) = S(y(0) - x(0)) = S(y(0)) - S(x(0)) = S(y(1)) - S(x(1))$$
$$= S(|y(1) - x(1)|).$$

If $S(|y(0) - x(0)|) = k > 1$, then there exists a sequence of states $x = x^0, x^1, \ldots, x^k = y$, such that $S(|x^{j+1} - x^j|) = 1$ for every j. Then

$$S(|y(1) - x(1)|) \leq S(|x^k(1) - x^{k-1}(1)|) + \cdots + S(|x^1(1) - x^0(1)|)$$
$$= S(|x^k(0) - x^{k-1}(0)|) + \cdots + S(|x^1(0) - x^0(0)|) = k = S(|y(0) - x(0)|).$$

□

In other words, perturbations of initial conditions do not amplify along the trajectory, which implies an analogue of Lyapunov stability for all attractors.

7. Cooperative irreducible systems and long periodic orbits

In this section, we will explore several possible discrete counterparts of the notion of irreducible cooperative C^1-systems and will show how these conditions relate to strict cooperativity and what bounds they impose on the lengths of periodic orbits.

Recall that a digraph (directed graph) $G = (V, A)$ is *strongly connected* if every node w in V can be reached via a directed path from every node $v \in V$.

Now let us define discrete analogues of irreducible cooperative systems by associating directed graphs $G = (\{1, \ldots, n\}, A)$ with a cooperative system (Π, g). Recall that in the definition of irreducible cooperative C^1-systems, an arc $< i,j >$ was included in the arc set A iff $Df(x)_{ij} > 0$ on $\mathbb{R}^n$, where $Df(x)$ is the Jacobian of $f(x)$, and the system was called irreducible if the resulting directed graph G on $\mathbb{R}^n$ was strongly connected. Alternatively, a digraph G_x can be defined locally for every $x \in \mathbb{R}^n$ by letting $< i,j >$ be an arc in G_x if and only if $Df(x)_{ij} > 0$. A cooperative C^1-system in which G_x is strongly connected for every $x \in \mathbb{R}^n$ is still strictly cooperative; see, for instance, Corollary 3.11 in [9].

Recall the definitions of x^{i-} and x^{i+} from Section 5. For an n-dimensional finite discrete system (Π, g) and $x \in \Pi$, let us define a directed graph $G^*_x = (\{1, \ldots, n\}, A^*_x)$ by including an arc $< i,j > \in A^*_x$ iff $g(x)_j < g(x^{i+})_j$ or $g(x^{i-})_j < g(x)_j$. Moreover, let us define a directed graph $G_x = (\{1, \ldots, n\}, A_x)$ by including an arc $< i,j > \in A_x$ iff $< i,j > \in A^*_x$ and if $0 < x_i < p_i - 1$, then $g(x^{i-})_j < g(x)_j < g(x^{i+})_j$.

Let us call the system (Π, g) *strongly irreducible* if $(\{1, \ldots, n\}, \bigcap_{x \in \Pi} A_x)$ is strongly connected, *semistrongly irreducible* if $(\{1, \ldots, n\}, \bigcap_{x \in \Pi} A^*_x)$ is strongly connected, and *irreducible* if G_x is strongly connected for all $x \in \Pi$.

The three notions defined above are plausible discrete counterparts of the concept of irreducibility of ODE systems. We will see that for cooperative finite discrete systems, the notions of irreducibility and strong irreducibility coincide. Note that for Boolean systems, $A^*_x = A_x$ for all states x; hence the notions strong irreducibility and semistrong irreducibility coincide in the Boolean case. But, we will see that these two notions have dramatically different implications for the dynamics of non-Boolean finite discrete systems.

Let π be a permutation of $\{1, \ldots, n\}$. Recall the definition of the function g_π from the previous section. Note that a finite discrete system (Π, g_π) is strongly irreducible, iff (Π, g_π) is semistrongly irreducible and iff (Π, g_π) is irreducible iff the permutation π is cyclic.

Theorem 19. *Suppose* (Π, g) *is a cooperative irreducible finite discrete system. Then* (Π, g) *is strictly cooperative and strongly irreducible. Moreover, there exists a cyclic permutation* π *of* $\{1, \ldots, n\}$ *such that* $g = g_\pi$.

Proof. Let $x, y \in \Pi$ be such that $x < y$. Pick $i \in \{1, \ldots, n\}$ such that $x < x^{i+} \leq y$. Then there exists some j with $< i,j > \in A_x$; otherwise G_x could not be strongly connected. Thus $g(x)_j < g(x^{i+})_j \leq g(y)$ by cooperativity, and condition (13) follows. Thus, (Π, g) is strictly cooperative.

Now let us consider $A_{\vec{0}}$, where $\vec{0} = [0, \ldots, 0]$. Let us write $\{i\}$ for the $x \in \Pi$ with $x_i = 1 = S(x)$ and call such x a *singleton*. Note that $< i,j > \in A_{\vec{0}}$ iff $g(\{i\})_j > 0$. By strict cooperativity, $g(\{i\})$ is a singleton, and it follows that the outdegree of each i in $G_{\vec{0}}$ is at most one. Strong connectedness of $G_{\vec{0}}$ now implies that the indegrees and outdegrees in $G_{\vec{0}}$ of all nodes are exactly one. Let $\pi : \{1, \ldots, n\} \rightarrow \{1, \ldots, n\}$ be defined by $\pi(i) = j$ iff $< i,j > \in A_{\vec{0}}$. Then, π is a permutation. Moreover, if π could be decomposed into non-empty pairwise disjoint cycles, then $G_{\vec{0}}$ would not be strongly connected. Thus, π must be cyclic.

It remains to show that $g = g_\pi$. We will show this by induction over $S(x)$. If $S(x) = 0$, then $g(x) = x$ by strict cooperativity, hence $g(x) = g_\pi(x)$. By the way we defined π, we also have $g(x) = g_\pi(x)$ whenever $S(x) = 1$.

Now let us assume $g(x) = g_\pi(x)$ for all x with $S(x) = k$, and let y be such that $S(y) = k + 1$. Then, $y = x^{i+}$ for some i and x with $S(x) = k$. By the inductive assumption, $g(x) = g_\pi(x)$. If $x_i = 0$, then $(g_\pi(x))_{\pi(i)} = 0$ but we must have both $g(x) < g(y)$ and $g(\{i\}) = \{j\} \leq g(y)$, so $g_\pi(y) \leq g(y)$, and strict cooperativity implies $g(y) = g_\pi(y)$. If $x_i > 0$, then the definition of A_x implies that there must be j with $g(x^{i-})_j < g(x)_j < g(x^{i+})_j$. But by inductive assumption, the only j with $g(x^{i-})_j < g(x)_j$ is $\pi(i)$, so we must also have $g(x)_j < g(x^{i+})_j$. It again follows that $g_\pi(y) \leq g(y)$, and hence $g(y) = g_\pi(y)$ by strict cooperativity. □

Corollary 20. *Periodic orbits in cooperative irreducible n-dimensional finite discrete systems can have length at most n.*

Proof. The maximal order of a cyclic permutation on $\{1, \ldots, n\}$ is n. □

Corollary 20 gives a stronger bound than Theorem 15 does for strictly cooperative p-discrete systems.

For non-Boolean systems, the assumption of irreducibility in Theorem 19 or Corollary 20 cannot be replaced by the assumption of semistrong irreducibility.

Example 21. For every n there exists a cooperative semistrongly irreducible 4-discrete system (Π, g) of dimension n that contains a periodic orbit of length $d_{n,2}$.

Proof. Fix n, let $(\{0, 1\}^n, f)$ be a cooperative Boolean system with a periodic orbit of length $d_{n,2}$ and π be a cyclic permutation of $\{1, \ldots, n\}$. Let $\Pi = \{0, 1, 2, 3\}^n$ and define a function $g : \Pi \rightarrow \Pi$ as follows. Let $S = \{x \in \Pi : \min x = 0 \leq \max x < 3\}$, $M = \{x \in$

$\Pi : 1 \leq \min x \leq \max x \leq 2\}$ and $L = \{x \in \Pi : \max x = 3\}$. For $x \in S$, let $g(x)_{\pi(i)} = 0$ whenever $x_i = 0$ and $g(x)_{\pi(i)} = 1$ whenever $x_i > 0$. For $x \in M$, let $g(x)_j = 1 + f(x - 1)$ and for $x \in L$ let $g(x)_{\pi(i)} = 2$ whenever $0 < x_i < 3$, $g(x)_{\pi(i)} = 0$ whenever $x_i = 0$ and $g(x)_{\pi(i)} = 3$ whenever $x_i = 3$.

Note that the restriction $g \upharpoonright M$ is isomorphic to f, hence the restriction of our system to M is cooperative and has a periodic orbit of length $d_{n,2}$. It also follows immediately from the definitions that the restriction of our system to S as well as its restriction to L cooperative. Moreover, consider $x \in S$, $y \in M$ and $z \in L$. Then $g(x) \leq g(y)$, and $x \leq z$ implies $g(x) \leq g(z)$. Similarly, $y \leq z$ implies $g(y) \leq g(z)$. Since no element of S can sit above an element of M or L, and no element of M can sit above an element of L, strict cooperativity of the whole system follows.

It remains to show that our system is semistrongly irreducible. It suffices to show that if $\pi(i) = j$, then $< i, j > \in A_x^*$ for all $x \in \Pi$. Fix x and i, j with $j = \pi(i)$. If $x_i = 3$, then $x \in L$ and $(g(x^{i-}))_j \leq 2 < 3 = (g(x))_j$. If $x_i = 2$, then $x^{i+} \in L$ and $(g(x))_j \leq 2 < 3 = (g(x^{i+}))_j$. Similarly, if $x_i = 1$, then $x^{i-} \in S \cup L$ and $(g(x^{i-}))_j = 0 < 1 \leq (g(x))_j$. Finally, if $x_i = 0$, then $x \in S \cup L$ and $(g(x))_j = 0 < 1 \leq (g(x^{i+}))_j$. □

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Note

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References

[1] R. Albert and H.G. Othmer, *The topology of the regulatory interactions predicts the expression*, J. Theoret. Biol. 223 (2003), pp. 1–18.
[2] I. Anderson, *Combinatorics of Finite Sets*, Dover Publications, Mineola, NY, 2002.
[3] D. Angeli and E.D. Sontag, *Multistability in monotone input/output systems*, Systems Control Lett. 51 (2004), pp. 185–202.
[4] G.F. Clements, *On uniqueness of maximal antichains of subsets of a multiset*, Period. Math. Hungar. 15 (1984), pp. 307–313.
[5] G.A. Enciso, *On a Smale theorem and nonhomogeneous equilibria in cooperative systems*, Proc. Amer. Math. Soc. 136(8) (2008), pp. 2901–2909.
[6] G.A. Enciso, M.W. Hirsch, and H.L. Smith, *Prevalent behavior of strongly order preserving semiflows*, J. Dynam. Differential Equations 20(1) (2008), pp. 115–132.
[7] M. Hirsch, *Systems of differential equations which are competitive or cooperative II: Convergence almost everywhere*, SIAM J. Math. Anal. 16(3) (1985), pp. 423–439.
[8] M.W. Hirsch, *Stability and convergence in strongly monotone dynamical systems*, Reine und Angew. Math. 383 (1988), pp. 1–53.
[9] M.W. Hirsch and H.L. Smith, *Monotone dynamical systems*, in *Handbook of Differential Equations, Ordinary Differential Equations*, A. Canada, P. Drabek, and A. Fonda, eds., Vol. 2, Elsevier, Amsterdam, 2004, pp. 239–357.
[10] W. Just and G. Enciso, *Analogues of the Smale and Hirsch theorems for cooperative Boolean and other discrete systems*, preprint (2007). Available at arXiv, math. 0711.0138v1.
[11] S.A. Kauffman, *Homeostasis and differentiation in random genetic control networks*, Nature 224 (1969), pp. 177–178.
[12] S.A. Kauffman, *Metabolic stability and epigenesis in randomly constructed genetic nets*, J. Theoret. Biol. 22(3) (1969), pp. 437–467.
[13] M.R.S. Kulenović and G. Ladas, *Dynamics of Second Order Rational Difference Equations*, Chapman & Hall/CRC, Boca Raton, FL, 2001.

[14] M.R.S. Kulenović, G. Ladas, and W.S. Sizer, *On the recursive sequence* $x_{n+1} = (\alpha x_n + \beta x_{n-1})/(\gamma x_n + c x_{n-1})$, Math. Sci. Res. Hot-Line 2(5) (1998), pp. 1–16.
[15] M.R.S. Kulenović and O. Merino, *A global attractivity result for maps with invariant boxes*, Discrete Contin. Dyn. Syst. Ser. B 6 (2006), pp. 97–110.
[16] E. Landau, *Handbuch der Lehre von der Verteilung der Primzahlen*, Chapter 13, Chelsea Publishing Company, New York, 1974, p. 225.
[17] K.-Y. Lau, S. Ganguli, and C. Tang, *Function constraints network architecture and dynamics: A case study on the yeast cell cycle Boolean network*, Phys. Rev. E 75(051907) (2007), pp. 1–9.
[18] R.L. Nussbaum, *Global stability, two conjectures and Maple*, Nonlinear Anal. TMA 66 (2007), pp. 1064–1090.
[19] P. Poláčik, *Parabolic equations: Asymptotic behavior and dynamics on invariant manifolds*, in *Handbook of Dynamical Systems*, Vol. 2, Chapter 16, Handbook of dynamical systems edition, Elsevier, Amsterdam, 2002, pp. 835–884.
[20] P. Poláčik and I. Tereščák, *Convergence to cycles as a typical asymptotic behavior in smooth strongly monotone discrete-time dynamical systems*, Arch. Ration. Mech. Anal. 116(4) (1992), pp. 339–360.
[21] A. Samal and S. Jain, *The regulatory network of* E. Coli *metabolism as a Boolean dynamical system exhibits both homeostasis and flexibility of response*, BMC Syst. Biol. 2(21) (2008).
[22] I. Shmulevich, E.R. Dougherty, and W. Zhang, *From Boolean to probabilistic Boolean networks as models of genetic regulatory networks*, Proc IEEE 90(11) (2002), pp. 1778–1792.
[23] S. Smale, *On the differential equations of species in competition*, J. Math. Biol. 3 (1976), pp. 5–7.
[24] H.L. Smith, *Monotone Dynamical Systems*, AMS, Providence, RI, 1995.
[25] H.L. Smith, *The discrete dynamics of monotonically decomposable maps*, J. Math. Biol. 53 (2006), pp. 747–758.
[26] H.L. Smith, *Global stability for mixed monotone systems*, J. Difference Equ. Appl. 14(10–11) (2008), pp. 1159–1164.
[27] E.D. Sontag, *Monotone and near-monotone biochemical networks*, J Syst. Synthetic Biol. 1 (2007), pp. 59–87.
[28] E.D. Sontag, A. Veliz-Cuba, R. Laubenbacher, and A.S. Jarrah, *The effect of negative feedback loops on the dynamics of Boolean networks*, Biophys. J. 95 (2008), pp. 518–526.
[29] I. Zaliapin, V. Keilis-Borok, and M. Ghil, *A Boolean delay equation model of colliding cascades. Part I: Multiple seismic regimes*, J. Stat. Phys. 111(3–4) (2004), pp. 815–837.