A dynamical characterisation of finite dynamical systems with acyclic interaction graphs

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Abstract

Finite dynamical systems, and in particular boolean networks, are a versatile model used to represent networks of interacting entities, such as gene regulatory networks, neural networks, and more. Each entity has a finite-valued state, which evolves over time according to a deterministic rule. One major problem in the analysis of these systems is to understand the impact of the structure of network (i.e. which entities influence each other) on the dynamics of the system (e.g., will it converge toward a fixed point?). As such, previous work has shown that some structural properties imply some strong dynamical properties. In this paper, we go further and we show that a fundamental structural property of an FDS is actually equivalent to a dynamical property. Namely, we show that an FDS has an acyclic interaction graph if and only if it is recursive-order-nilpotent, which basically means that the system and all its subsystems can be made to converge by a common sequence of updates.

1 Introduction

Let \([q] = \{0, 1, \ldots, q - 1\}\) be a finite integer interval, and let \(n\) be a positive integer. A finite dynamical system is any mapping \(f : [q]^n \rightarrow [q]^n\). If \(q = 2\), such a system is called boolean network. Finite dynamical systems, and boolean networks in particular, have many applications: they have been used to model gene networks [12, 17, 11], neural networks [13, 10, 5, 6], social interactions [15, 9] and more (see [18, 8]).

The interaction graph is a fundamental structural property of an FDS, for it indicates the overall architecture of the system, namely it indicates which local update functions depend on which local variables. In many contexts, as in molecular biology, the interaction graph is known—or at least well approximated—, while the actual function \(f\) is not. A major problem is then: what can be said about a finite dynamical system according to its interaction graph only? As such, a lot of work (see examples below) has shown that certain properties of the interaction graph influenced the dynamics of the system. However, up to author’s knowledge, there is no known equivalence between a structural property and a dynamical property of an FDS.

FDSs with acyclic interaction graphs are a very important subclass of FDSs, due to their simple structure (one can sort the interaction graph in topological order), which yields specific dynamics. Notably, they have a unique fixed point, which can be reached from any initial state by applying the mapping at most \(n\) times. FDSs with acyclic interaction graphs are also the building blocks for strong results on general FDSs, such as the the feedback bound on the number of fixed points [1, 16], bounds on the stability and instability of FDSs [3, 4], or refinements based on signed interaction graphs without positive or negative cycles (see [14] for a survey).

In this paper, we give a characterisation of FDSs with acyclic interaction graphs based on a dynamical property, the so-called recursive-order-nilpotence. The latter means that there is an order of local updates which makes all the states converge toward a unique fixed point (order-nilpotent) and that this order can also be used for all the subsystems of the FDS, i.e. even when some local states are fixed.

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2 Order nilpotent finite dynamical systems

Let \([q] = \{0, 1, \ldots, q - 1\}\) for some \(q \geq 2\) and \(n\) be a positive integer. A Finite Dynamical System (FDS) is a mapping \(f: [q]^n \rightarrow [q]^n\), and we denote the set of such FDSs as \(F(n, q)\). We decompose \(f\) as \(f = (f_1, \ldots, f_n)\) where \(f_i: [q]^n \rightarrow [q]\), and similarly we decompose \(\pi \in [q]^n\) as \(x = (x_1, \ldots, x_n)\).

The interaction graph of \(f\) is the digraph \(G(f) = (V, E)\), where \(V := \{1, \ldots, n\}\) and \((i, j) \in E(G(f))\) if and only if \(f_j\) depends on \(x_i\), i.e.

\[ \exists a, b \in [q]^n : a_i \neq b_i, a_k = b_k \forall k \neq i, f_j(a) \neq f_j(b). \]

Note that \(f_i\) can depend on \(x_i\), in which case there is a loop \((i, i)\) in \(G(f)\), which we view as a cycle of length one. We denote the set of FDSs \(f: [q]^n \rightarrow [q]^n\) with interaction graph \(D\) as \(F(D, q)\). We say that an FDS is acyclic if its interaction graph is acyclic. For more on digraphs, the reader is referred to [2].

For any \(i \in V\), we denote the update of the \(i\)-th component according to \(f\) by \(f^{(i)}\), where

\[ f^{(i)}(x) := (x_1, \ldots, x_{i-1}, f_i(x), x_{i+1}, \ldots, x_n), \]

ore more concisely, \(f^{(i)}(x) = (x \setminus f_i(x)).\) A sequential schedule is any finite word \(\sigma = (\sigma_1, \ldots, \sigma_T)\) over the alphabet \([n]\). We then denote the FDS obtained by applying the updates given by \(\sigma\) as \(f^\sigma\), where

\[ f^\sigma = f^{(\sigma_T)} \circ \cdots \circ f^{(\sigma_2)} \circ f^{(\sigma_1)}. \]

See, for example, [9, 5, 7] for works on the dynamics of different systems under sequential schedules.

An order schedule for \(V = \{1, \ldots, n\}\) is a sequential schedule \(\pi = (\pi_1, \ldots, \pi_n)\) such that all the \(\pi_i\) elements are distinct. We denote the order schedule for \(V \setminus S\) obtained by removing \(S\) from \(\pi\) as \(\pi \setminus S\). For example, let \(n = 5, \pi = (1, 3, 4, 5, 2)\) and \(S = \{2, 3\}\), then \(\pi \setminus S = (1, 4, 5)\). We say that \(f\) is order-nilpotent if there is an order schedule \(\pi\) of \(V\) such that \(f^\pi\) is constant.

We first obtain the following results on the interaction graphs of order-nilpotent networks. Let us recall some basic facts about digraphs. A strong component of a digraph is an equivalence class, where two vertices \(u\) and \(v\) are equivalent if there is a (directed) path from \(u\) to \(v\). A strong component is trivial if it consists of a single vertex without a loop on it. An initial component is a strong component \(C\) such that if \(c \in C\), then its in-neighbourhood is contained in \(C\). A source is a vertex with empty in-neighbourhood. Clearly, all initial components of a digraph \(D\) are trivial if and only if for every vertex, there is a path from a source to that vertex (or that vertex is itself a source).

**Theorem 1.** The following hold for any digraph \(D\) and any \(q \geq 2\).

1. There exists an order-nilpotent FDS in \(F(D, q)\) if and only if all initial components of \(D\) are trivial.

2. All the FDSs in \(F(D, q)\) are order-nilpotent if and only if \(D\) is acyclic.

**Proof.** 1. Suppose that \(f\) is order-nilpotent but \(G(f)\) has a non-trivial initial component \(C\). Let \(f^\pi\) be constant, and let \(c\) be the first vertex of \(C\) appearing in \(\pi\), say \(c = \pi_a\). Since the in-neighbourhood of \(c\) is contained in \(C\), we have \(f_c(x) = f_c(x_C)\). Let \(y_C\) and \(z_C\) such that \(f_c(y_C) \neq f_c(z_C)\), then for any \(t \in [q]^{\setminus C}\),

\[ f_c^{(\pi_1, \ldots, \pi_a-1, \pi_a)}(t, y_C) = f_c(f_c^{(\pi_1, \ldots, \pi_a-1)}(t), y_C) = f_c(y_C) \]

\[ \neq f_c(z_C) = f_c(f_c^{(\pi_1, \ldots, \pi_a-1)}(t), z_C) = f_c^{(\pi_1, \ldots, \pi_a-1, \pi_a)}(t, z_C), \]

and hence \(f^\pi(t, y_C) \neq f^\pi(t, z_C)\), which is the desired contradiction.
Conversely, if all initial components of \( D \) are trivial, let \( S \) be the set of sources of \( D \) and let

\[
\begin{align*}
  f_s(x) &:= 0, & \forall s \in S, \\
  f_v(x) &:= \min\{x_u : (u, v) \in E(D)\} & \forall v \in V \setminus S.
\end{align*}
\]

For all \( 0 \leq d \leq n - 1 \), let \( S_d \) be the set of vertices at distance \( d \) from \( S \); let \( S_0 := S \) and

\[
S_d := \{v \in V : \exists i \in S_{d-1} (i, v) \in E(D)\} \setminus S_{d-1}
\]

for \( d \geq 1 \). We let \( m \) be the maximum value of \( d \) such that \( S_d \) is non-empty. Enumerate these sets as \( S_d = \{s^1_d, \ldots, s^m_d\} \), then it is easy to verify that

\[
f(s^1_d, s^2_d, \ldots, s^m_d) = (0, \ldots, 0).
\]

2. Clearly, if \( D \) is acyclic, then all the FDSs in \( F[D, q] \) are order-nilpotent. Conversely, let \( D \) have a cycle. If \( D \) has no sources, then by the result above, no FDS in \( F[D, q] \) is order-nilpotent. Otherwise, let \( S \) be the set of sources of \( D \) and let

\[
\begin{align*}
  f_s(x) &:= 1, & \forall s \in S, \\
  f_v(x) &:= \min\{x_u : (u, v) \in E(D)\} & \forall v \in V \setminus S.
\end{align*}
\]

We prove that \( f \) is not order-nilpotent. Let \( \pi \) be any order schedule for \( V \) and \( \pi_{i_1}, \ldots, \pi_{i_k} \) be a cycle in \( D \), with \( i_1 < \cdots < i_k \). Then

\[
f_{\pi_{i_1}}(1, \ldots, 1) = 1 \neq 0 = f_{\pi_{i_1}}(0, \ldots, 0),
\]

and hence \( f^\pi(1, \ldots, 1) \neq f^\pi(0, \ldots, 0) \). \( \Box \)

### 3 Recursive-order-nilpotent finite dynamical systems

A **subsystem** of \( f \) is obtained by fixing the value of certain coordinates. More formally, let \( S = \{s_1, \ldots, s_k\} \) be a non-empty proper subset of \( V \) and \( a \in [q]^S \), then we denote by \( f_{[S,a]} \) the FDS in \( F(V \setminus S, q) \) such that

\[
f_{[S,a]}(x V \setminus S) := f(x V \setminus S, a).
\]

Any such \( f_{[S,a]} \) is called a proper subsystem of \( f \). By convention, \( f \) is its own subsystem (for \( S \) being the empty set). If \( S = \{v\} \) is a singleton, we denote \( f_{[v,a]} \) and we call this a direct subsystem of \( f \).

Since any subsystem of an acyclic FDS is itself acyclic, we may want to consider “hereditary” order-nilpotent FDSs. However, as shown below, there always exists a non-acyclic FDS such that all its subsystems are order-nilpotent.

**Proposition 1.** For any \( q \geq 2 \) and \( n \geq 3 \), there exists \( f \) in \( F(n, q) \) such that \( f \) is order-nilpotent, all its proper subsystems are acyclic, and \( \forall f \) is not acyclic.

**Proof.** Consider the FDS \( f : [q]^n \to [q]^n \) with

\[
\begin{align*}
  f_1(x) &:= 0, \\
  f_{\{2, \ldots, n\}}(x) &:= \begin{cases} (x_n, 0, \ldots, 0) & \text{if } x_1 = 0, \\
                                                                  (0, x_2, \ldots, x_{n-1}) & \text{if } x_1 \neq 0.
\end{cases}
\end{align*}
\]

Then \( f \) is order-nilpotent since \( f^{(1,3,\ldots,n,2)}(x) = (0, \ldots, 0) \) for all \( x \). Moreover, it is easily checked that all its direct subnetworks are acyclic (and hence all its proper subnetworks are acyclic), but \( f \) itself is not acyclic. \( \Box \)

We then have to introduce a slightly stronger dynamical property. We say that \( f \) is **recursive-order-nilpotent** if there is an order schedule \( \pi \) of \( V \) such that \( f_{[S,a]}^{\pi \setminus S} \) is constant for all subsystems \( f_{[S,a]} \) of \( f \).
Theorem 2. An FDS is recursive-order-nilpotent if and only if it is acyclic.

Proof. If \( f \) is acyclic, then it is easily checked that \( f \) is recursive-order-nilpotent (take \( \pi \) to be any topological order of its interaction graph).

Let us prove the converse by induction on \( n \). It is clear for \( n = 1 \); let us settle the case \( n = 2 \). Suppose \( f \) is recursive-order-nilpotent, then \( f^{(\pi_1, \pi_2)} \) is constant, which implies that \( f_{\pi_1} \) is a constant function, and for any \( a \in [q] \), \( f^{(\pi_1, a)}_{\pi_2} \) is also a constant function, hence \( f_{\pi_2} \) does not depend on \( x_{\pi_2} \). Therefore, the interaction graph of \( f \) only has at most the arc \((\pi_1, \pi_2)\) and is hence acyclic.

Henceforth assume \( n \geq 3 \) and that it holds for up to \( n - 1 \). Let \( f \) be recursive-order-nilpotent, then all its proper subnetworks are recursive-order-nilpotent as well, and hence acyclic. Let \((i, j)\) be an arc of \( G(f) \) (\( i \) and \( j \) are not necessarily distinct), then \((i, j)\) is an arc in the interaction graph of the subsystem \( f_{[V \setminus \{i,j\} : a]} \) for some \( a \). If \( i = \pi_c \) and \( j = \pi_d \), then necessarily \( c < d \) (in order to make \( f_{[V \setminus \{i,j\} : a]}^{(\pi: [V \setminus \{i,j\}])} \) constant); thus \( \pi \) is a topological order of \( G(f) \), which must be acyclic. \( \square \)

References


