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Limit cycles and update digraphs in Boolean networks

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Abstract

Deterministic Boolean networks (BNs) have been used as models of gene regulation and other biological networks. One key element in these models is the update schedule, which indicates the order in which states have to be updated. In Aracena et al. (2009) was defined equivalence classes of deterministic update schedules according to the labeled digraph associated to a BN (update digraph). It was proved that two schedules in the same class yield the same dynamical behavior of a given BN. In this paper we study the relationships between the update digraphs and the preservation of limit cycles of BNs which differ only in the update schedules. We exhibite necessary conditions in the connection digraph architecture in order to preserve limit cycles. Besides, we construct some update schedule classes whose elements yield a same limit cycle under certain conditions.

Key words: Boolean network, update schedule, robustness, update digraph, limit cycle

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1. Introduction

Boolean networks (BNs), originally introduced by Kauffman (1969, 1993), are the most simple model for genetic regulatory networks, as well as for other simple distributed dynamical systems. Despite their simplicity, they provide a realistic model in which different phenomena can be reproduced and studied, and indeed, many regulatory models published in the biological literature fit within their framework (Shmulevich et al., 2003; Thomas, 1973). Moreover, some of the theorems obtained are easily extended to networks with finite (not necessarily binary) states.

In the modeling of genetic regulatory networks, the attractors are associated to distinct types of cells defined by patterns of gene activity. In particular, the limit cycles are often associated with mitotic cycles in cells (Aracena et al., 2006; Huang, 1999).

A BN is said to be robust for a certain dynamical property if small changes in the network do not affect some characteristic observed. There are several kinds of perturbations in a BN: perturbations of the states of the nodes in a given global state of the network, changes in the local activation functions, or modifications of the type of update schedule. The last two ones correspond to changes in the definition of the network and therefore they can yield variations on the set of attractors.

This paper deals the robustness of attractors of BNs against changes in the iteration schedule, which may range from the parallel update, the most common (Kauffman, 1969; Thomas, 1991), to the sequential update, passing through all the combinations of block-sequential updates (which are sequential over the sets of a partition, but parallel inside of each set).

The robustness of BNs has been greatly studied, mainly from a statistical point of view, in random BNs (RBN), where the local activation functions are probabilistically chosen. However, there exist only a few analytical studies. Aldana and Cluzel (2003) show that RBNs with architecture scale-free, where a small set of nodes are highly connected and the rest poorly connected, are robust. Shmulevich et al. (2003) study the robustness of RBNs whose local functions belong to certain Post classes. More recently, comparative analysis between synchronous and asynchornous update in BNs has been made by Goles and Salinas (2008).

Some analytical works about perturbations of update schedules have been made in a particular class of discrete dynamical networks, called sequential dynamical systems, where the connection digraph is symmetric or equivalently an undirected graph and the update schedule is sequential. For this class of networks, the team of Barrett, Mortveit and Reidys studied the set of sequential update schedules preserving the whole dynamical behavior of the network Mortveit and Reidys (2001) and the set of attractors in a certain class of Cellular Automata (Hansson et al., 2005).

In Aracena et al. (2009) was defined equivalence classes of deterministic update schedules according to the labeled digraph associated to a given BN (update digraph). It was proved that two schedules in the same class yield the same dynamical behavior of a given BN. Besides, it was exhibited that the limit cycles of a BN are very little robust againts to changes in the update schedule. Here, we study the update schedules preserving a set of given limit cycles of a given BN. Because, the schedules in the same equivalence class preserve the whole dynamics of a BN, then we focus on the problem of determing the distinct equivalence classes whose elements preserve the limit cycles of a BN, but not necessarily the whole dynamics.

2. Definitions and Notation

A BN N = (F, s) is defined by a finite set of variable states $x \in \{0, 1\}^n$, a global activation function $F : \{0, 1\}^n \to \{0, 1\}^n$, where $F(x) = (f_1(x), \ldots, f_n(x))$ (f_i are called local activation functions), and an update schedule s.

An update schedule is defined by an update function that we denote $s : \{1, \ldots, n\} \to \{1, \ldots, n\}$, such that $s(\{1, \ldots, n\}) = \{1, \ldots, m\}$ for some $m \leq n$. A synchronous or parallel update is given by an update function s such that $\forall i \in \{1, \ldots, n\}, s(i) = 1$. A sequential update corresponds to a permutation function over $\{1, \ldots, n\}$. Others kinds of update functions can be considered as a block-sequential updates.

The iteration of a BN with an update function s is given by:

$$x_i^{r+1} = f_i(x_1^{l_1}, \dots, x_j^{l_j}, \dots, x_n^{l_n}),$$
(1)

where $l_j = r$ if $s(i) \leq s(j)$ and $l_j = r + 1$ if s(i) > s(j). The exponent represents the time step.

This is equivalent to applying a function $F^s : \{0,1\}^n \to \{0,1\}^n$ in a parallel way, with $F^s(x) = (f_1^s(x), \ldots, f_n^s(x))$ and

$$f_i^s(x) = f_i(g_{i,1}^s(x), \dots, g_{i,n}^s(x)),$$

where the function $g_{i,j}^s$ is defined by $g_{i,j}^s(x) = x_j$ if $s(i) \le s(j)$ and $g_{i,j}^s(x) = f_j^s(x)$ if s(i) > s(j). Thus, the function F^s corresponds to the dynamical behavior of the network N = (F, s).

We say that two BNs $N_1 = (F_1, s_1)$ and $N_2 = (F_2, s_2)$ have the same dynamical behavior if $F_1^{s_1} = F_2^{s_2}$.

Since $\{0, 1\}^n$ is a finite set, we have two limit behaviors for the iteration of a Boolean network N = (F, s):

- Fixed Point. We define a fixed point as $x \in \{0, 1\}^n$ such that $F^s(x) = x$.
- Limit Cycle. We define a cycle of length p > 1 as the sequence $[x^k]_{k=0}^p = [x^0, \ldots, x^{p-1}, x^0]$ such that $x^j \in \{0, 1\}^n$, x^j are pairwise distinct and $F^s(x^j) = x^{j+1}$, for all $j = 0, \ldots, p-1$ and $x^p \equiv x^0$. The set of limit cycles of N is denoted by CL(N).

We say that a node is *frozen* for a limit cycle if its state is constant on it (Greil et al., 2007; Kauffman, 1990).

The digraph associated to a BN N = (F, s), called connection digraph, is the directed graph $G^F = (V, A)$, where $V = \{1, \ldots, n\}$ is the set of vertices or nodes and $A \subseteq V \times V$ is the arc set such that $(i, j) \in A$ if and only if f_j depends on x_i , i.e. if there exists $x \in \{0, 1\}^n$ such that

$$f_j(x_1,\ldots,x_{i-1},0,x_{i+1},\ldots,x_n) \neq f_j(x_1,\ldots,x_{i-1},1,x_{i+1},\ldots,x_n).$$

The node set of G^F is referred to as $V(G^F)$, its arc set as $A(G^F)$. An arc $(i, i) \in A(G^F)$ is called a *loop* of G^F .

A function $f : \{0,1\}^n \to \{0,1\}$ is monotonic on input i if for every $x \in \{0,1\}^n$

$$f(x_1,\ldots,x_{i-1},0,x_{i+1},\ldots,x_n) \le f(x_1,\ldots,x_{i-1},1,x_{i+1},\ldots,x_n).$$

A loop (i, i) is monotonic if f_i is monotonic on input *i*.

Given G = (V, A) a digraph of n nodes and $s : \{1, \ldots, n\} \to \{1, \ldots, n\}$ an update function, we denote $G_s = (G, \text{lab}_s)$ the labeled digraph, named update digraph, where the function $\text{lab}_s : A \to \{\bigotimes, \bigotimes\}$ is defined as:

$$lab_{s}(i,j) = \begin{cases} \textcircled{o} & \text{if } s(i) \ge s(j) \\ \textcircled{o} & \text{if } s(i) < s(j) \end{cases}$$

The update digraph associated to a BN N = (F, s) is defined by $G_s^F = (G^F, \text{lab}_s)$. Thus, we define the following equivalence relation between update schedules s and s':

$$s \sim_{G^F} s' \iff G_s^F = G_{s'}^F$$

We denote $[s]_{G^F}$ the equivalente class of s induced by \sim_{G^F} .

Example 1. See an example of update digraph G_s in Figure 1. Note that the label on a loop will always be \ge .

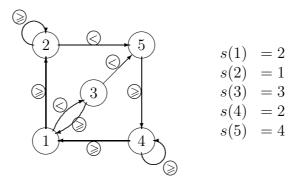


Figure 1: Example of update digraph G_s .

Given $G^F = (V, A)$, the connection digraph of a BN N = (F, s), we denote

$$V^{-}(j) = \{i \in \{1, \dots, n\}/(i, j) \in A\}$$

and

$$V^+(i) = \{ j \in \{1, \dots, n\} / (i, j) \in A \}$$

Thus, we can write $f_j(x) = f_j(x_i : i \in V^-(j))$. Besides, we denote $d^-(i) = |V^-(i)|$ and $\Delta^-(G) = \max\{d^-(i) : i \in V\}$ the input degree of a vertice $i \in V$ and the maximum in-degree of G, respectively.

Finally, let G = (V, A) be a digraph and $i_1, i_m \in V$, we say $P = i_1, \ldots, i_m$ is a path from i_1 to i_m in G if $\forall k = 1, \ldots, m-1$, $(i_k, i_{k+1}) \in A$. Thus, for every $i \in V$ we define:

 $J^{-}(i) = \{t \in V : \exists P \text{ a path from } t \text{ to } i \text{ in } G\}.$

3. Update digraphs and preservation of limit cycles

The following result was proved in Aracena et al. (2009).

Theorem 1. Let $N_1 = (F, s_1)$ and $N_2 = (F, s_2)$ be two BNs that differ only in the update schedule. If $G_{s_1}^F = G_{s_2}^F$, then N_1 and N_2 have the same dynamical behavior.

Hence, for a given BN N = (F, s) and for every BN N' = (F, s') with $s' \in [s]_{G^F}$, CL(N) = CL(N'). Therefore, we focus on the equivalence classes of update schedules preserving a set of given limit cycles instead of each update schedule.

It seems natural to define a new equivalence relation between update schedules, relaxing the condition of equal induced update digraphs, such that elements in the same class preserve a set of given limit cycles and not necessary the whole dynamics of the network. However, this relation is not possible as shown in the following theorem.

Theorem 2. Let G be a digraph of n nodes and let s_1, s_2 be two different update functions such that $G_{s_1} \neq G_{s_2}$. There exists a function $F : \{0, 1\}^n \rightarrow \{0, 1\}^n$, with $G^F = G$, such that $N_1 = (F, s_1)$ and $N_2 = (F, s_2)$ verify $CL(N_1) \neq CL(N_2)$.

PROOF. We will define F such that $C = [\vec{0}, \vec{1}, \vec{0}]$ is a limit cycle of N_1 but not of N_2 , where $\vec{0} = (0, 0, \dots, 0), \ \vec{1} = (1, 1, \dots, 1) \in \{0, 1\}^n$.

For each $i \in V(G)$, we define

$$f_i(x) = \bigwedge_{\operatorname{lab}_{s_1}(k,i) = \textcircled{>}} \neg x_k \land \bigwedge_{\operatorname{lab}_{s_1}(k,i) = \textcircled{<}} x_k$$

In particular, if $s_1(i_1) = 1$, then

$$f_{i_1}(x) = \bigwedge_{k \in V^-(i_1)} \neg x_k$$

Hence, by induction on the nodes in increasing order according the value of s_1 , we obtain that $\forall i \in V(G), f_i(\vec{0}) = 1 \land f_i(\vec{1}) = 0$. Thus, $F^{s_1}(\vec{0}) = \vec{1} \land F^{s_1}(\vec{1}) = \vec{0}$. Therefore, $C = [\vec{0}, \vec{1}, \vec{0}]$ is a limit cycle of N_1 . On the other hand, let $j \in V(G)$ such that $\exists k \in V^{-}(j)$, $\operatorname{lab}_{s_1}(k, j) \neq \operatorname{lab}_{s_2}(k, j)$. If $\operatorname{lab}_{s_1}(k, j) = \bigotimes$, then $\operatorname{lab}_{s_2}(k, j) = \bigotimes$ and

$$f_j^{s_2}(\vec{0}) = \bigwedge_{l \in V^-(i_1)} a_l \wedge \neg f_k^{s_2}(\vec{0}), \quad a_l \in \{0, 1\}.$$

Hence, if $f_k^{s_2}(\vec{0}) = 1$, then $f_j^{s_2}(\vec{0}) = 0$. Therefore, *C* is not a limit cycle of N_2 . The same conclusion is drawn in the case $lab_{s_1}(k, j) = \bigcirc$.

Next, we will show that the existence of several classes preserving a set of given limit cycles strongly depends on the in-degree of the connection digraph G^{F} . Previously, some technical results.

Lemma 3. Let N = (F, s) be a BN such that $\Delta^{-}(G^{F}) = 1$ with G^{F} connected and let $C = [x^{k}]_{k=0}^{p}$ be a limit cycle. Then

$$\forall i \in V(G^F), \ \exists k \in \{0, 1, \dots, p-1\} : x_i^k \neq x_i^{k+1}$$

PROOF. By contradiction, let us suppose that:

$$\exists i \in V(G^F), \, \forall k \in \{0, 1, \dots, p-1\}, \, x_i^k = x_i^{k+1}$$

Then, since $V^{-}(i) = \{j\}, x_i^{k+1} = f_i^s(x_j^k), \forall k$. Therefore,

$$f_i^s(x_j^k) = x_i^{k+1} = x_i^k = f_i^s(x_j^{k-1}), \ \forall k.$$

However,

$$f_i^s(x_j^k) = \begin{cases} f_i(x_j^k) &, \text{ if } \operatorname{lab}_s(j,i) = \textcircled{o}\\ f_i(x_j^{k+1}) &, \text{ if } \operatorname{lab}_s(j,i) = \textcircled{o}\end{cases}$$

and,

$$f_i^s(x_j^{k-1}) = \begin{cases} f_i(x_j^{k-1}) &, \text{ if } \operatorname{lab}_s(j,i) = \textcircled{o} \\ f_i(x_j^k) &, \text{ if } \operatorname{lab}_s(j,i) = \textcircled{o} \end{cases}$$

In any case,

$$f_i(x_j^k) = f_i(x_j^{k+1}), \ \forall k.$$

Since f_i only depends on variable j, then

$$x_j^k = x_j^{k+1}, \ \forall \ k.$$

On the other hand, let $l \in V^+(i)$, then $V^-(l) = \{i\}$, and thus $x_l^{k+1} = f_l^s(x_i^k), \forall k$. Therefore, since *i* is a frozen node for *C*, then $x_l^{k+1} = x_l^k$, $\forall k, \forall l \in V^+(i)$.

Hence, by induction and connectivity of G^F , it holds that $x_t^k = x_t^{k+1}, \forall t \in V(G^F)$, which is a contradiction.

The following result was proved in Aracena et al. (2009).

Lemma 4. Let N = (F, s) and N' = (F, s') be two BNs with different update schedules, $j \in V(G^F)$ a node without a loop or with a monotonic loop, such that $lab_s(i, j) = \bigotimes, \forall i \in V^-(j)$ and $lab_{s'}(i, j) = \bigotimes, \forall i \in V^-(j) \setminus \{j\}$. If C is a limit cycle for N and N' then j is a frozen node in C.

Thus, we have the following relationship between the update digraph structure and the preservation of limit cycles in BNs.

Theorem 5. Let $N_i = (F, s_i), i = 1, 2$ two BNs such that $\Delta^-(G^F) = 1$, G^F is connected and $[s_1]_{G^F} \neq [s_2]_{G^F}$. Then, $CL(N_1) \cap CL(N_2) = \emptyset$.

PROOF. Let $C = [x^k]_{k=0}^p$, p > 1 be a limit cycle for both N_1 and N_2 .

Since $G_{s_1}^F \neq G_{s_2}^F$ and $\Delta^-(G^F) = 1$, we have that, $\exists j \in V(G^F)$, $\exists ! i \in V^-(j) : \operatorname{lab}_{s_1}(i,j) \neq \operatorname{lab}_{s_2}(i,j)$.

By Lemma 4, j is a frozen node in C, which is contradictory with Lemma 3.

Corollary 6. Let $N_i = (F, s_i), i = 1, 2$ two BNs such that $\Delta^-(G^F) = 1$ and G^F is connected. Then,

$$CL(N_1) = CL(N_2) \quad \lor \quad CL(N_1) \cap CL(N_2) = \emptyset.$$

PROOF. By Theorem proved in Aracena et al. (2009), if $G_{s_1}^F = G_{s_2}^F$, then $F^{s_1} = F^{s_2}$. This implies $CL(N_1) = CL(N_2)$. Otherwise, by Theorem 5 $CL(N_1) \cap CL(N_2) = \emptyset$.

The Corollary 6 tell us that for a BN N = (F, s), with G^F connected and $\Delta^-(G^F) = 1$, and whose limit cycle set is not empty, the unique equivalence class of update schedules yielding this set is $[s]_{G^F}$. This is not true if some condition on G^F does not hold (see Example 2). Indeed, it is just sufficient that there exists only a node $i \in V(G^F)$ with $|V^-(i)| \ge 2$ for having different limit cycle set in BNs which differ only in the update schedule.

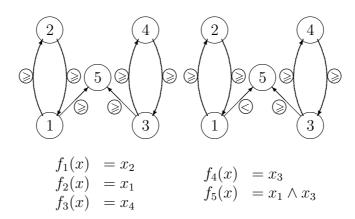


Figure 2: Example of BNs: $N_1 = (F, s_1)$ and $N_2 = (F, s_2)$, where $s_1(i) = 1$, $\forall i = 1, ..., 5$ and $s_2(1) = s_2(2) = 1$; $s_2(3) = s_2(4) = 3$; $s_2(5) = 2$. Here, G^F is connected, $\Delta^-(G^F) = 2$ and $G^F_{s_1} \neq G^F_{s_2}$.

Example 2. Let N_1 and N_2 be BNs defined as in Figure 2. Each network has six limit cycles, but only three of them are common in both networks. More precisely, $CL(N_1) \cap CL(N_2) = \{C_1, C_2, C_3\}$, where $C_1 = [x^1, x^2, x^1]$, $C_2 = [x^3, x^4, x^3]$ and $C_3 = [x^5, x^6, x^5]$ with:

$$x^{1} = \begin{pmatrix} 1\\0\\0\\0\\0 \end{pmatrix}, x^{2} = \begin{pmatrix} 0\\1\\0\\0\\0 \end{pmatrix}, x^{3} = \begin{pmatrix} 0\\0\\1\\0\\0 \end{pmatrix}, x^{4} = \begin{pmatrix} 0\\0\\0\\1\\0 \end{pmatrix}, x^{5} = \begin{pmatrix} 1\\0\\0\\1\\0 \end{pmatrix}, x^{6} = \begin{pmatrix} 0\\1\\1\\0\\0 \end{pmatrix}.$$

For BNs N = (F, s), where $\Delta^{-}(G^{F}) \geq 2$ and $CL(N) \neq \emptyset$, it is not possible to guarantee the existence of another equivalence class $[s']_{G^{F}}$ different from $[s]_{G^{F}}$ such that CL(F, s') = CL(N), only knowing the update digraph G_{s}^{F} as established in Theorem 2. It is necessary have some additional knowledge about the local activation functions of the network.

4. Construction of classes preserving limit cycles

In Aracena et al. (2009) was shown that the limit cycles of a BN are very sensible to small changes in the update schedules. In this section we are interested in determining distinct equivalence classes of update schedules which preserve limit cycles of a given BN. The results in this section deal with the case of only a limit cycle. However, these are easily extensive to the case of more than one.

The results exhibited in Theorem 5 about BNs N = (F, s) with $\Delta^{-}(G^{F}) =$ 1 can be applied to networks which do not have this structural characteristic in order to yield necessary conditions for having a same limit cycle in BNs which differ only in the update schedule. The next Corollary is a direct consequence of Theorem 5 and shows this kind of application.

Previously, given a digraph G = (V, A) we will say that G' is a source digraph of G if $V(G') \subseteq V(G)$, $A(G') \subseteq A(G)$ and $\forall v \in V(G')$, $(u, v) \in A(G') \Rightarrow u \in V(G')$.

Corollary 7. Let $N_i = (F, s_i), i = 1, 2$ be two BNs and C a limit cycle of both networks. If G' is a source subdigraph of G^F such that verifies the properties stated in Theorem 5, then every node $j \in V(G')$ is frozen in C.

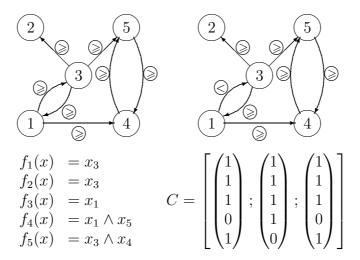


Figure 3: Example of BNs: $N_1 = (F, s_1)$ and $N_2 = (F, s_2)$, where $s_1(i) = 1$, $\forall i = 1..., 5$ and $s_2(1) = s_2(2) = s_2(4) = s_2(5) = 1$; $s_2(3) = 2$. $CL(N_1) \cap CL(N_2) = \{C\}$.

Example 3. Let N_1 and N_2 be BNs defined in Figure 3. The subdigraph $G' = (V' = \{1, 2, 3\}, E' = \{(1, 3), (3, 2), (2, 1)\})$ of G^F satisfies the condition established in Corollary 7 where $CL(N_1) \cap CL(N_2) = \{C\}$.

It is easy to see that in the case of a set $\{C_1, C_2, \ldots, C_k\}$ of limit cycles, the result in Corollay 7 is also valid changing " $j \in V(G')$ is frozen in C" by " $j \in V(G')$ is frozen in each C_i , $i = 1, \ldots, k$ ".

The following result is a sufficient condition for the existence of more then a equivalence class of update schedules preserving a limit cycle of a given BN.

Theorem 8. Let N = (F, s) be a BN, $C = [x^k]_{k=0}^p$, p > 1 a limit cycle of N and Z the set of frozen nodes in C. If $\exists i \in Z, V^-(i) \subseteq Z$, then there exists an update function \hat{s} with $G_{\hat{s}}^F \neq G_s^F$ and such that C is a limit cycle of $\hat{N} = (F, \hat{s}).$

PROOF. Let $i \in Z$ such that $V^{-}(i) \subseteq Z$. We must consider two cases:

Case 1: $\forall j \in V^{-}(i)$: $lab_s(j,i) = \bigotimes$. Defining \hat{s} by:

$$\hat{s}(i) = \min_{j \in V^{-}(i)} s(j)$$
 and $\hat{s}(l) = s(l), \forall l \neq i.$

We have that:

$$\operatorname{lab}_{\hat{s}}(j,i) = \bigotimes, \ \forall \ j \in V^{-}(i)$$

Thus,

$$f_i^{\hat{s}} \left(x_j^0 : j \in V^-(i) \right) = f_i \left(x_j^0 : j \in V^-(i) \right) = f_i \left(x_j^1 : j \in V^-(i) \right) = f_i^s \left(x^0 \right) = x_i^1.$$

Besides, since $\hat{s}(l) = s(l), \ \forall l \neq i \text{ and } x_i^0 = x_i^1$ (*i* is frozen node in *C*),

$$f_l^{\hat{s}}(x_j^0: j \in V^-(l)) = f_l^s(x_j^0: j \in V^-(l)) = x_l^1, \, \forall l \neq i.$$

Therefore, $F^{\hat{s}}(x^0) = F^s(x^0) = x^1$.

By applying induction on k we can prove that

$$F^{\hat{s}}(x^k) = F^s(x^k) = x^{k+1}, \ \forall k = 0, \dots, p-1.$$

Hence, C is a limit cycle of \hat{N} .

Case 2: $\exists j \in V^{-}(i), \text{ lab}_{s}(j,i) = \bigotimes$. Let $V_B^-(i) = \{j \in V^-(i), \operatorname{lab}_s(j, i) = \bigotimes\} \neq \emptyset$. Defining \hat{s} by:

$$\hat{s}(i) = \max_{j \in V_B^-(i)} s(j) + 1 \quad \text{and} \quad \hat{s}(l) = s(l), \ \forall \ l \neq i.$$

We have that:

$$\operatorname{lab}_{\hat{s}}(j,i) = \bigotimes, \forall j \in V^{-}(i)$$

Then,

$$\begin{aligned} f_i^{\hat{s}} \left(x_j^0 \colon j \in V^-(i) \right) &= f_i \left(x_j^1 \colon j \in V^-(i) \right) \\ &= f_i \left(x_j^0 \colon j \in V_B^-(i) \colon x_j^1 \colon j \in V^-(i) \setminus V_B^-(i) \right) \\ &= f_i^s \left(x^0 \right) = x_i^1. \end{aligned}$$

In the same way, we can prove by induction on k that

$$F^{\hat{s}}(x^k) = F^s(x^k) = x^{k+1}, \ \forall k = 0, \dots, p-1.$$

Therefore, C is also a limit cycle of \hat{N} .

Observe that not necessarily \hat{s} is an update function, i.e. it verifies that $\hat{s}(\{1,\ldots,n\}) = \{1,\ldots,m\}, m \leq n$. In this case, we change \hat{s} by s', the update function that preserves the ordering in the nodes with respect to \hat{s} , i.e. $s'(i) < s'(j) \Leftrightarrow \hat{s}(i) < \hat{s}(j)$ and $s'(i) > s'(j) \Leftrightarrow \hat{s}(i) > \hat{s}(j)$. The rest of the proof is analogous.

Observe that the proof of Theorem 8 exhibits a different equivalence class of update schdule for each node $i \in Z$ such that $V^-(i) \subseteq Z$ (see Examples 4 and 5). This result is also valid for a limit cycle set, where in this case Z corresponds to the intersection of frozen node sets of each one. Furthermore, if we take $W = \{i \in Z : V^-(i) \subseteq Z\}$ (the nodes in Z who satisfies the condition of Theorem 8), we have the same result for every $U \subseteq W$ of independent nodes, applying simultaneously the update schedules of every node in U.

Example 4. Let $N_1 = (F, s_1)$ and C be the BN and the limit cycle defined in Figure 3. Each node $i \in \{1, 2, 3\}$ satisfies the conditions established in Theorem 8. Therefore, we can define three new update schedules s_2 , s_3 and s_4 such that C is also a limit cycle of the networks $N_i = (F, s_i)$, i = 2, 3, 4. The update schedule s_2 is described in Figure 3 and s_3 and s_4 , with the corresponding associated update digraphs, are shown in Figure 4. \blacklozenge

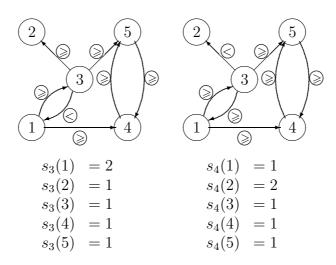


Figure 4: Update digraphs $G_{s_3}^F$ and $G_{s_4}^F$ corresponding to the BNs $N_3 = (F, s_3)$ and $N_4 = (F, s_4)$ mentioned in Example 3.

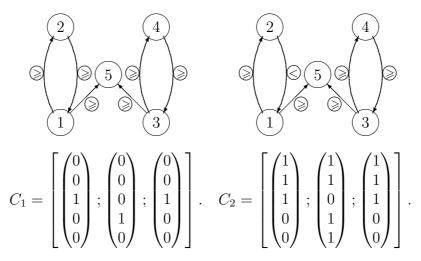


Figure 5: Example of BNs: $N_1 = (F, s_1)$ and $N_2 = (F, s_2)$, where $s_1(i) = 1, \forall i = 1, ..., 5$ and $s_2(1) = 2$; $s_2(2) = s_2(3) = s_2(4) = s_2(5) = 1$. Here, both networks share two limit cycles.

Example 5. Let N_1 and N_2 be BNs defined as in Figure 5 with the same function of Figure 2. Here we consider $Z = \{1, 2\}$, the set of frozen nodes common to C_1 and C_2 , limit cycles of N_1 . We see that the both nodes satisfies the condition of Theorem 8. The update schedule s_2 is given by setting i = 1.

Example 6. Let consider the BN and update schedules of Example 4. Since both nodes 1 and 2 are independent, we can apply both update schedules s_3 and s_4 at the same time to obtain a new one (different class), s_5 (shown at Figure 6), that also have C as a limit cycle. \blacklozenge

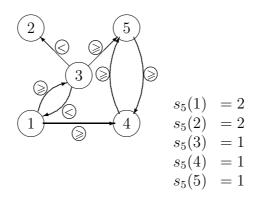


Figure 6: Update digraph and update schedule discussed in Example 6.

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