Attractor landscapes in Boolean networks with firing memory

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Abstract

In this paper we study the dynamical behavior of Boolean networks with firing memory, namely Boolean networks whose vertices are updated synchronously depending on their proper Boolean local transition functions so that each vertex remains at its firing state a finite number of steps. We prove in particular that these networks have the same computational power than the classical ones, *i.e.* any Boolean network with firing memory composed of m vertices can be simulated by a Boolean network by adding vertices. We also prove general results on specific classes of networks. For instance, we show that the existence of at least one delay greater than 1 in disjunctive networks makes such networks have only fixed points as attractors. Moreover, for arbitrary networks composed of two vertices, we characterize the delay phase space, *i.e.* the delay values such that networks admits limit cycles or fixed points. Finally, we analyze two classical biological models by introducing delays: the model of the immune control of the λ-phage and that of the genetic control of the floral morphogenesis of the plant *Arabidopsis thaliana*.

Keywords: Discrete dynamical systems, Boolean networks, Biological network modeling

1 Introduction

In the context of gene regulation modeling, the choice of the methodology highly depends on the nature of the underlying real system and on the objective of the study, that can be oriented towards quantitative or qualitative analysis of the dynamical behaviors of the networks. From the qualitative point of view, Boolean networks (BNs) are one of the simplest model and for

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more than forty years, they have been used to analyze and understand several biological phenomena. Notably, several BN models of real biological systems have become popular: the immunity control network of bacteriophage λ [44], the floral morphogenesis network of *Arabidopsis thaliana* [30], the fission yeast cell-cycle network [9], the budding yeast cell-cycle network [26], the mammalian cell-cycle network [15], the *p53-mdm2* network [7], and the blood cancer large granular lymphocyte (T-LGL) leukemia network [51].

Introduced by Kauffman at the end of the 1960's [24] by generalizing the classical formal neural networks of McCulloch and Pitts [28], this model consists in a network where the vertices represent genes that can be expressed (or active, *i.e.* vertex value 1) or not (inactive, *i.e.* vertex value 0), and the edges represent regulatory relations between the genes. The dynamics of a network is then given by a set of Boolean functions, one for each vertex. Starting from any of the 2^n possible configurations (a configuration being a vector of $\mathbb{B}^n = \{0,1\}^n$), for a network composed of n vertices, the dynamics of the network eventually converges towards ordered sets of recurrent configurations that repeat endlessly and periodically which we classically call attractors. When an attractor is composed of one configuration, it is called a fixed point; when it is composed of at least two configurations, we call it a limit cycle. Attractors are particularly relevant in the context of biological modeling because they are used to represent differentiated cellular types or tissues (in the case of fixed points) and biological rhythms or oscillations (in the case of limit cycles).

One of the characteristics of BNs is that they are associated with an update mode that defines the way vertices update their states along time. The parallel mode in which all the vertices are updated at each time step is canonical (*i.e.* it is directly derived from the network definition) and belongs to the class of block-sequential update modes [10, 20, 40]. Block-sequential modes are deterministic and periodic and are defined by ordered partitions of the set of vertices. Another classical approach in the domain is to consider non-deterministic (and non-stochastic) update modes like the asynchronous one [36, 39, 45] (stochastic asynchronicity, however, has been well studied in the context of cellular automata [12, 13, 14, 35]). Numerous studies have focused on the influence of update modes on the dynamical behaviors. From the theoretical point of view, among the most impacting analyses are [4, 3, 19] in the context of deterministic modes and [34] in that of non-deterministic ones. In both of these, the very relevance comes from the fact that the authors succeeded in explaining the influence of update modes on the dynamics of BNs by relating it to their static structures. From the applied point of view, the dynamical behaviors of many biological networks

with different update schemes have been studied [11, 18, 31, 41, 42]. This manner of studying the dynamical behaviors of biological networks is desirable when searching for biologically meaningful updating modes. However, as a matter of fact, although it is deeply interesting and relevant from formal points of view like mathematical and computational ones, this manner that consists in studying biological networks by considering as much updating schemes as possible is rather tedious (due to the infinite number of updating schemes, an updating scheme being defined from a general point of view as a function associating any subset of nodes with each time step of $\mathbb{N}$, *i.e.* an infinite sequence of subsets of nodes) when the objective is fixed on the biological matter. Another approach that allows adding asynchronicity is based on the concept of delay. In the context of discrete modeling of biological regulation networks, among the first who have introduced delays is certainly Thomas [46, 47, 48] whose works have been followed by many other in different frameworks [1, 5, 16, 37, 38]. Here, we make choice using a distinct approach based on considering BNs with memory, as the model studied in [22, 23] that was initially developed by Graudenzi and Serra under the name of *gene protein Boolean networks* (GPBNs) [21]. As this name suggests, in this model, each vertex of the classical Boolean network is decoupled into both a gene vertex and a protein vertex, so that each pair of such vertices is associated with a decay time that acts as a memory standing for the number of steps during which the protein vertex remains active.

In the seminal papers [22, 23], the authors focus on the provision of the memory effect due the addition of decay times. In particular, thanks to numerical simulations, they highlight very interesting properties: the memory effect significantly affects the robustness of the computational model itself against state perturbations, with respect to the classical model of random BNs; the more the maximum decay time value, the less the network admits asymptotic degrees of freedoms, *i.e.* attractors; higher values of the maximum decay time results in longer limit cycles associated to attraction basins that are more ordered than in the case of (random) BNs.

From this, we are convinced that this model deserves to be deeply studied, from both theoretical and applied points of view. That is what we propose to do in this paper, by following a constructive approach. Indeed, we will see that the GPBN model proposed by Graudenzi et al. is not more powerful than that of classical BNs from a strictly computational standpoint. Doing so, we will develop another equivalent intermediate representation merging gene and protein vertices that simplify substantially the phase space. This representation will be called *Memory Boolean networks* (MBNs). We will also focus on specific classes of networks and pay particular attention to

two genes networks which, despite their small size, allow acquiring much knowledge about the model. In addition, under a biological context, network traditionally are small, for example: Quorum-sensing systems in the plant growth-promoting bacterium (5 nodes) [52], *lac* operon in *Escherichia coli* (10 nodes, which can be even further reduced to 3 nodes) [49], oxidative stress response (6 nodes) [25]. Furthermore, there are examples where no prior knowledge (key genes) is available, and therefore, key genes cannot be selected from the hundreds or thousands of genes beforehand. In these cases, small Boolean networks have been inferred, where the nodes are metagenes (a group of genes that have similar co-expression patterns) identified via clustering in an earlier stage of the analysis, for example, the network of *Arabidopsis thaliana* saline stress response (12 meta genes nodes, originally 569 genes that were differentially regulated due to salt exposure) [43]. Eventually, a pertinent constructive track initiated by Alon et al. [27, 33, 50] to achieve a better understanding of genetic networks consists in viewing them as compositions of small regulation motifs of 2 or 3 nodes (considered as "building blocks of complex networks") that deserve to be studied *per se* before tackling their compositions. As a consequence, theoretical analyses of small networks are of interest in the context of modeling.

This theoretical part will be followed by applications to two real biological systems: the immune control of the λ-phage and the genetic control of the floral morphogenesis of the plant *Arabidopsis thaliana*.

2   The models

2.1   Definitions and notations

2.1.1   Boolean networks (BNs)

A BN F of size n, *i.e.* composed of n genes, is a collection of n Boolean local transition functions such that $F = (f_i : \mathbb{B}^n \to \mathbb{B}, f_i(x) \mapsto x_i)_{i \in \{1,\ldots,n\}}$, where x denotes a *configuration* of F, and x_i denotes the state of gene i. In a function f_i, consider it being minimal, if there is a positive (resp. negative) literal, for instance x_j (resp. $\neg x_j$), this means that gene j tends to activate (resp. inhibit) gene i. In other terms, the state of i tends to mimic (resp. negate) that of j. From this can be easily derived a digraph $G = (V, E)$ where the vertex set is $V = \{1, \ldots, n\}$ and where $E = \{(j, s, i) \mid s = +$ (resp. $s = -$) if x_j (resp. $\neg x_j$) appears in the definition of $f_i\}$. Such a graph G is called the *interaction graph* of F. As in Kauffman's seminal work [24], let us consider for now on that BNs evolve in such a way that
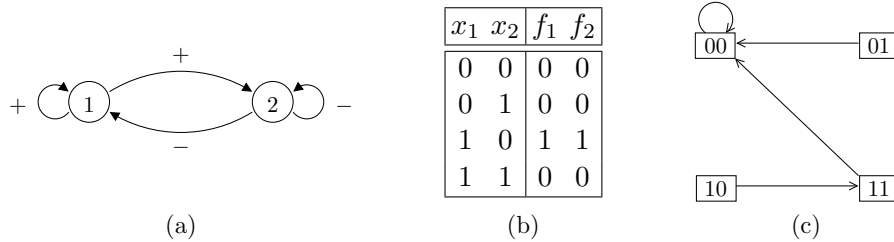
Figure 1: (a) Interaction graph, (b) truth tables of its local transition functions and (c) transition graph of the BN composed of two genes 1 and 2, defined by the local transition functions $f_1(x) = f_2(x) = x_1 \wedge \neg x_2$. The transition graph shows that this BN admits only one attractor, fixed point $(0, 0)$.

every gene updates its (expression) state at each time step, *i.e.* in parallel. In this specific framework, the (global) dynamics of a BN F is simply given by $\forall x \in \mathbb{B}^n$, $F(x) = (f_1(x), f_2(x), \ldots, f_n(x))$, and can be written (by emphasing time steps): $\forall i \in V, \forall t \in \mathbb{N}$, $x_i(t + 1) = f_i(x(t))$. Such a dynamics can be represented by its *transition graph* that is the digraph $\mathcal{G} = (\mathbb{B}^n, F)$ (see Figure 1). This graph represents more precisely the trajectories of all configurations towards attractors that are either fixed points or limit cycles as explained in the introduction.

2.1.2 Gene protein Boolean networks (GPBNs)

GPBNs were presented in [21]. A GPBN F can be viewed similarly to a BN by its interaction graph $G = (V, E)$, where each vertex of V is decoupled into a gene and its associated protein. So, each gene of the network is strictly linked to a unique and specific protein. The vertex set is defined as $V = \{G_1, \ldots, G_N, P_1, \ldots, P_N\}$ and the Boolean local transition functions are given by $(f_{G_i}, f_{P_i} : \mathbb{B}^N \to \mathbb{B})_{i \in \{1, \ldots, N\}}$. Let us consider configuration $x = (x_{G_1}, \ldots, x_{G_N}, x_{P_1}, \ldots, x_{P_N})$. If $x_{G_i} = 1$ (resp. 0) then it means that gene G_i is expressed or active (resp. unexpressed or inactive), and if $x_{P_i} = 1$ (resp. 0), it means that protein P_i is present (resp. absent) in the underlying cell. Every protein P_i, with $1 \leq i \leq N$, is associated with a *decay time* $dt_i \in \mathbb{N}$. This decay time dt_i defines the number of time steps during which P_i remains present in the cell after having been produced by the punctual expression of gene G_i. Moreover, in this model, a delay of one time step is considered between a gene punctual expression and a protein for it to be

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considered as present.

Formally, the global dynamics of a GPBN F is defined as $\forall x \in \mathbb{B}^n$, with $n = 2N$, $F(x) = (f_{G_1}(x), \ldots, f_{G_N}(x), f_{P_1}(x), \ldots, f_{P_N}(x))$, where $\forall i \in \{1, \ldots, N\}$ and for any time step $t \in \mathbb{N}$:

$$x_{G_i}(t+1) = f_{G_i}(x(t)) \quad \text{and} \quad x_{P_i}(t+1) = \begin{cases} 1 & \text{if } \Delta_i(t+1) \geq 1 \\ x_{G_i}(t) & \text{if } \Delta_i(t+1) = 0 \end{cases},$$

with:

$$\begin{cases} \Delta_i(0) &= \begin{cases} 0 & \text{if } x_{P_i}(0) = 0 \\ \alpha \in \{1, \ldots, dt_i\} & \text{if } x_{P_i}(0) = 1 \end{cases} \\ \Delta_i(t+1) &= \begin{cases} 0 & \text{if } x_{G_i}(t) = 0 \wedge \Delta_i(t) = 0 \\ \Delta_i(t) - 1 & \text{if } x_{G_i}(t) = 0 \wedge \Delta_i(t) > 0 \\ dt_i & \text{if } x_{G_i}(t) = 1 \end{cases} \end{cases}.$$

2.1.3 Memory Boolean networks (MBNs)

In this paper, we propose a new model, that of MBNs. A MBN is defined by a digraph $G = (V, E)$, with $V = \{1, \ldots, n\}$ and the Boolean local transition functions $(f_i : \mathbb{B}^n \to \mathbb{B})_{i \in \{1, \ldots, n\}}$. To this model is added a vector of delays $dt \in (\mathbb{N} \setminus \{0\})^n$ such that a firing vertex i will remain at state 1 during dt_i time steps. Given an initial condition $x(0) \in \{0, 1\}^n$ we consider the delays of each vertex so that $\Delta_i(0) = 0$ if $x_i(0) = 0$ and $\Delta_i(0) \in \{1, \ldots, dt_i\}$ if $x_i(0) = 1$. More formally, a MBN is defined as $\forall x \in \mathbb{B}^n$, $F(x) = (f_1(x), f_2(x), \ldots, f_n(x))$, where the update is:

$$x_i(t+1) = \begin{cases} 1 & \text{if } \Delta_i(t+1) \geq 1 \\ f_i(x(t)) & \text{if } \Delta_i(t+1) = 0 \end{cases},$$

and the delays are:

$$\Delta_i(t+1) = \begin{cases} 0 & \text{if } f_i(x(t)) = 0 \text{ and } \Delta_i(t) = 0 \\ \Delta_i(t) - 1 & \text{if } f_i(x(t)) = 0 \text{ and } \Delta_i(t) > 0 \\ dt_i & \text{if } f_i(x(t)) = 1 \end{cases}.$$

In the sequel, we will use an abuse of notation for not burdening the reading. Rather than decoupling the state $x_i \in \mathbb{B}$ of a vertex i from its associated delay $dt_i \in \mathbb{N}$, we will simply change the notation into $x_i \in \{0, \ldots, dt_i\}$ so that, for all $i \in V$, if $x_i = 1$ and $dt_i = 2$, we will usually write $x_i = 2$. Due to

this abuse of notation, if we consider for instance a MBN of size 3 such that $dt = (2, 1, 1)$, configuration x at time step t denoted by $x(t) = (2, 0, 1)$ stands for the Boolean configuration $(1, 0, 1)$ (with $dt = (1, 1, 1)$) in the model such as it has been formally defined above.

2.2 Equivalence(s) between BNs, GPBNs, MBNs

Definitions of BNs, GPBNs and MBNs above emphasize that these models match on many aspects. Here we will show that these models are equivalent in the following sense: given a GPBN F, it is always possible to build a MBN F' and a BN $\tilde{F}'$ such that F, F' and $\tilde{F}'$ admit equivalent asymptotic behaviors, in terms of type and number of attractors (of course, the attractors are not exactly composed of the same recurrent configurations because of the compression induced by the construction).

First, let us analyze the equivalence between GPBNs and MBNs that have similar characteristics (as delay memory). Now, if we eliminate the intermediate translation of the genetic state 1 to the protein state from the GPBN framework, both behaviors are the same. More precisely, if in the GPBN model we define $f_i : \mathbb{B}^N \to \{0, 1\}$ as

$$\forall i, \ x_i(t+1) = f_i(x(t)) = \begin{cases} 1 & \text{if } \Delta_i(t+1) \geq 1 \\ f_{G_i}(x(t)) & \text{if } \Delta_i(t+1) = 0 \end{cases},$$

and we take $x = (x_1, \ldots, x_N)$ where, $\forall i \in \{1, \ldots, N\}$, $x_i = x_{P_i}$ and

$$\Delta_i(0) = \begin{cases} 0 & \text{if } x_i(0) = 0 \\ \alpha \in \{1, \ldots, dt_i\} & \text{if } x_i(0) = 1 \end{cases}$$

$$\Delta_i(t+1) = \begin{cases} 0 & \text{if } f_{G_i}(x(t)) = 0 \text{ and } \Delta_i(t) = 0 \\ \Delta_i(t) - 1 & \text{if } f_{G_i}(x(t)) = 0 \text{ and } \Delta_i(t) > 0 \\ dt_i & \text{if } f_{G_i}(x(t)) = 1 \end{cases},$$

we get the MBN model.

Example 1. Consider the GPBN defined by means of the local transition functions $f_{G_1} = f_{G_2} = x_{P_1} \wedge \neg x_{P_2}$ and delay vector $dt = (2, 1)$. The interaction graph of this network in Figure 2.a. Denoting each state $x_{P_i} = k$ when $x_{P_i} = 1$ with variable memory k, *i.e.* if delays $dt = (dt_1, dt_2) = (2, 1)$ then $(x_{P_1}, x_{P_2}) \in \{0, 1, 2\} \times \{0, 1\}$, then we transform the model into this equivalent form in which delays are integrated to the protein states:

$$x_{P_1}(t+1) = \begin{cases} \Delta_1(t+1) & \text{if } \Delta_1(t+1) \geq 1 \\ x_{G_1}(t) & \text{if } \Delta_1(t+1) = 0 \end{cases} \quad \text{and} \quad x_{P_2}(t+1) = x_{G_2}(t).$$

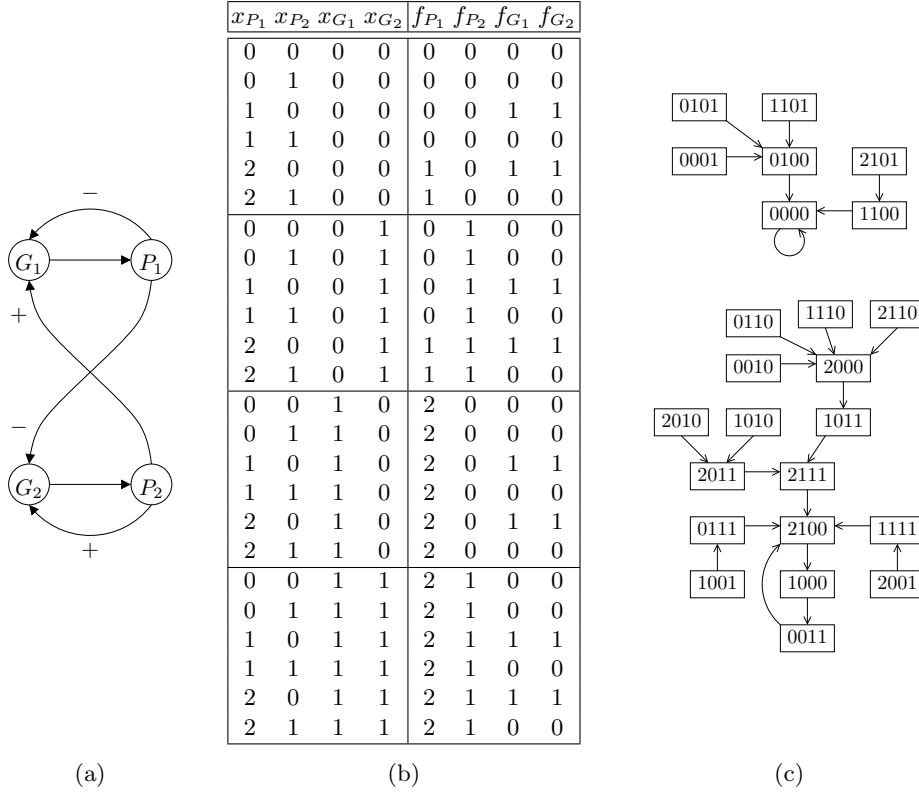| x_{P_1}	x_{P_2}	x_{G_1}	x_{G_2}	f_{P_1}	f_{P_2}	f_{G_1}	f_{G_2}
0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0
1	0	0	0	0	0	1	1
1	1	0	0	0	0	0	0
2	0	0	0	1	0	1	1
2	1	0	0	1	0	0	0
0	0	0	1	0	1	0	0
0	1	0	1	0	1	0	0
1	0	0	1	0	1	1	1
1	1	0	1	0	1	0	0
2	0	0	1	1	1	1	1
2	1	0	1	1	1	0	0
0	0	1	0	2	0	0	0
0	1	1	0	2	0	0	0
1	0	1	0	2	0	1	1
1	1	1	0	2	0	0	0
2	0	1	0	2	0	1	1
2	1	1	0	2	0	0	0
0	0	1	1	2	1	0	0
0	1	1	1	2	1	0	0
1	0	1	1	2	1	1	1
1	1	1	1	2	1	0	0
2	0	1	1	2	1	1	1
2	1	1	1	2	1	0	0

(a)   (b)   (c)

Figure 2: (a) Interaction graph, (b) transition tables of its local transition functions and (c) transition graph of the GPBN of Example 1, with $dt = (2, 1)$.

Figures 2.b and c picture the dynamical behavior of the GPBN, emphasizing the existence of two attractors, the fixed point $(0, 0, 0, 0)$ and a limit cycle of size 3. Now, by eliminating the intermediate translation from gene state 1 to the protein state, this GPBN can be easily transformed into a MBN whose vertex set is $V = \{P_1, P_2\}$, local transition functions are:

$$x_{P_i}(t+1) = f_i(x(t)) = \begin{cases} 1 & \text{if } \Delta_i(t+1) \geq 1 \\ x_{P_1}(t) \wedge \neg x_{P_2}(t) & \text{if } \Delta_i(t+1) = 0 \end{cases},$$

and delay vector is $dt = (2, 1)$, as pictured in Figure 3.

Now, let us see to what extent the MBN model is equivalent to the BN model. To do so, let us consider a MBN F defined over an interaction graph
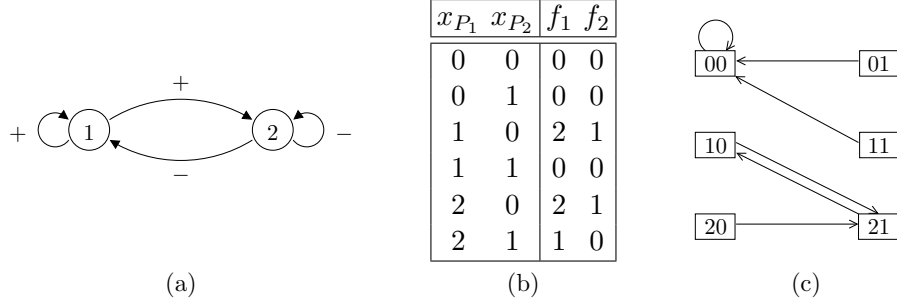
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Figure 3: (a) Interaction graph, (b) transition tables of its local transition functions f_1 and f_2 and (c) transition graph of the MBN related to the GPBN given in Example 1.

$G = (V = \{1, \ldots, n\}, E)$ with n Boolean functions $(f_1, \ldots, f_n)$ and delay vector dt. The idea is to find a BN $\tilde{F}$ without delays that simulates the asymptotic dynamics of F. To do so, to every vertex $v \in V$ we associate a set of vertices $\{[v, 1], \ldots, [v, dt_v]\}$, consider the neighborhood of vertex v, $\mathcal{N}_v = \{j \in V \mid (j, v) \in E\} = \{j_1, \ldots, j_r\}$. So in the new network (constructed by replacing each vertex v by a set of dt_v vertices) we consider the following Boolean functions:

$$\forall v \in V, \quad \begin{aligned} \tilde{f}_{[v,dt_v]}(x_{[1,1]}, \ldots, x_{[n,dt_n]}) &= f_v(x_{[j_1,1]}, \ldots, x_{[j_r,1]}) \\ \tilde{f}_{[v,dt_v-1]}(x_{[1,1]}, \ldots, x_{[n,dt_n]}) &= f_v(x_{[j_1,1]}, \ldots, x_{[j_r,1]}) \vee x_{[v,dt_v]} \\ &\vdots \\ \tilde{f}_{[v,1]}(x_{[1,1]}, \ldots, x_{[n,dt_n]}) &= f_v(x_{[j_1,1]}, \ldots, x_{[j_r,1]}) \vee x_{[v,2]} \end{aligned},$$

where the evolution of $\tilde{F}$ is such that $\tilde{x}_{[v,dt_v]}(t+1) = f_v(x_{[j_1,1]}(t), \ldots, x_{[j_r,1]}(t))$ and $\tilde{x}_{[v,a]}(t+1) = f_v(x_{[j_1,1]}(t), \ldots, x_{[j_r,1]}(t)) \vee x_{[v,a+1]}(t)$, $1 \leq a < dt_v$. This construction emphasizes an injective encoding ϕ of MBNs into BNs such that for any configuration x of F, if $x \mapsto F(x)$ then $\tilde{x} = \phi(x) \mapsto \tilde{F}(\phi(x)) = \tilde{F}(\tilde{x})$, where $\tilde{x}$ is a configuration of $\tilde{F}$. Thus, if there exists a fixed point (resp. a limit cycle) among the attractors of F, $\tilde{F}$ admits also a fixed point (resp. a limit cycle) that is the encoding of the latter according to the given construction.

Example 2. Let us consider the MBN of Example 1, in which we rename each protein vertex P_i by its index i such that $V = \{1, 2\}$. From the construction given above, we obtain its related BN as pictured at the right of
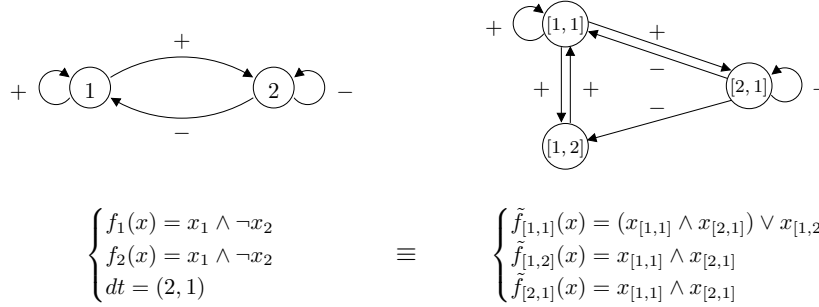
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$$\begin{cases} f_1(x) = x_1 \wedge \neg x_2 \\ f_2(x) = x_1 \wedge \neg x_2 \\ dt = (2,1) \end{cases} \qquad \equiv \qquad \begin{cases} \tilde{f}_{[1,1]}(x) = (x_{[1,1]} \wedge x_{[2,1]}) \vee x_{[1,2]} \\ \tilde{f}_{[1,2]}(x) = x_{[1,1]} \wedge x_{[2,1]} \\ \tilde{f}_{[2,1]}(x) = x_{[1,1]} \wedge x_{[2,1]} \end{cases}$$

Figure 4: (left) Interaction graph and local transition functions defining the MBN of Example 1 and (right) its associated and equivalent BN.

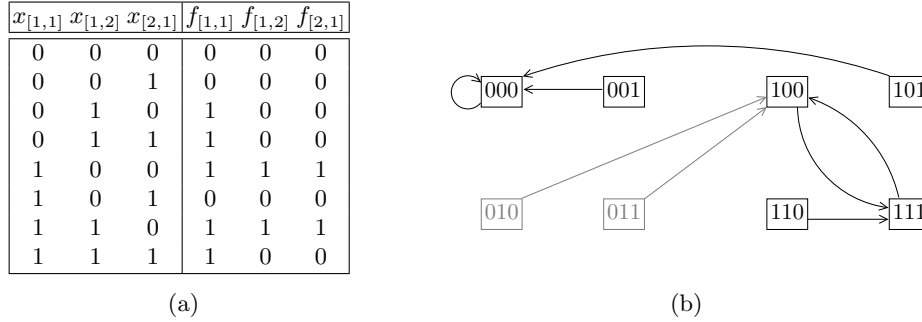| $x_{[1,1]}$	$x_{[1,2]}$	$x_{[2,1]}$	$f_{[1,1]}$	$f_{[1,2]}$	$f_{[2,1]}$
0	0	0	0	0	0
0	0	1	0	0	0
0	1	0	1	0	0
0	1	1	1	0	0
1	0	0	1	1	1
1	0	1	0	0	0
1	1	0	1	1	1
1	1	1	1	0	0

(a)

(b)

Figure 5: (a) Truth tables of the local transition functions $f_{[1,1]}$, $f_{[2,1]}$, $f_{[1,2]}$ and (b) transition graph of the BN constructed in Figure 4 that is equivalent to the MBN of Example 1.

Figure 4 whose local transition function truth tables and transition graph are illustrated in Figure 5.

Notice that by construction of our simulation, $x_{[1,1]}(t) = 0$ implies that $x_{[1,2]}(t) = 0$. More precisely, $x_{[1,1]}(t) = 0 \iff x_{[1,1]}(t) = f_1(x_{[1,1]}(t-1), x_{[2,1]}(t-1)) \vee x_{[1,2]}(t-1) = 0$ that implies that $x_{[1,2]}(t-1) = 0$ and $f_1(x_{[1,1]}(t-1), x_{[2,1]}(t-1)) = 0$. As a consequence, since $x_{[1,2]}(t) = f_1(x_{[1,1]}(t-1), x_{[2,1]}(t-1)) = x_{[1,1]}(t) = 0$, the configurations $x = (x_{[1,1]}, x_{[1,2]}, x_{[2,1]}) = (0, 1, a)$, with $a \in \{0, 1\}$, are artefacts of the construction and are not real parts of the dynamical behavior.

2.3 Some particular classes of MBNs

In this section, we present general results that hold for specific classes of MBNs. For our purpose, let us first focus on the class of positive disjunctive MBNs, *i.e.* MBNs in which every vertex is associated with a local transition function composed only of the Boolean operator OR with no negated variables. Before presenting any result, let us give two definitions [6]. First, the *index of imprimitivity* $\eta(G)$ of a strongly connected digraph G is the greatest common divisor of the lengths of all cycles of G. Second, the adjacency matrix M of a strongly connected digraph G is *primitive* if and only if M is an irreducible square matrix for which there exists a positive integer m such that $\forall k \geq m$, M^k is a strictly positive matrix. These definitions are related by the fact that, given a strongly connected digraph, its index of imprimitivity equals 1 if and only if its adjacency matrix is primitive. Proposition 1 below emphasizes that such networks cannot admit limit cycles.

Proposition 1. *Let F be a strongly connected positive disjunctive MBN and let $G = (V, E)$ be its interaction graph. If F is such that at least one vertex v admits a delay greater than 1 ($dt_v \geq 2$), then F does not have any limit cycle and can only converge towards two fixed points: $(0, \ldots, 0)$ and $(dt_1, \ldots, dt_n)$.*

Proof. Let us consider F such that it is composed of a vertex $v_0 \in V$ of delay $dt_{v_0} \geq 2$. Following the construction proposed above, we can obtain a BN $\tilde{F}$ of interaction graph $\tilde{G} = (\tilde{V}, \tilde{E})$ that simulates F. G being strongly connected by hypothesis, v_0 belongs to a cycle C in G. Let us admit that C is of length q and such that:

$$C = \quad v_0 \longleftarrow v_1 \longleftarrow \cdots \longleftarrow v_{q-1} \; .$$

From this, we derive that, in $\tilde{G}$, there are at least the two following cycles $\tilde{C}$ and $\tilde{C}'$ (the latter being the direct consequence of $dt_{v_0} \geq 2$):

$$\tilde{C} = \quad [v_0, 1] \longleftarrow [v_1, 1] \longleftarrow \cdots \longleftarrow [v_{q-1}, 1]$$

and:

$$\tilde{C}' = \quad [v_0, 1] \longleftarrow [v_0, 2] \longleftarrow [v_1, 1] \longleftarrow \cdots \longleftarrow [v_{q-1}, 1],$$

of respective lengths $|\tilde{C}|$ and $|\tilde{C}'|$ such that $|\tilde{C}'| = |\tilde{C}| + 1$, which implies that $\gcd(|\tilde{C}|, |\tilde{C}'|) = 1$. Thus, $\eta(\tilde{G}) = 1$ and $\tilde{F}$ is primitive. In this context, this means that for every configuration $x \neq (0, \ldots, 0)$, there exists $t \in \mathbb{N}$ such that $x(t) = x \cdot \tilde{M}^t = (1, \ldots, 1)$, where $\tilde{M}$ is the adjacency matrix of $\tilde{G}$ [17]. As a result, $\tilde{F}$ does not admit any limit cycle but two fixed

points $(0, \ldots, 0)$ and $(1, \ldots, 1)$. From this, and because of the disjunctive nature of the underlying MBN, the only attractors of F are $(0, \ldots, 0)$ and $(dt_1, \ldots, dt_n)$. $\qquad\square$

Example 3. In order to illustrate Proposition 1, let us consider the positive disjunctive BN defined as $(f_1(x) = x_2, f_2(x) = x_1 \vee x_3, f_3(x) = x_2)$. This BN admits three attractors: the fixed points $(0, \ldots, 0)$ and $(1, \ldots, 1)$ and the limit cycle $010 \leftrightarrows 101$. Consider now the related MBN with the same local transition functions in which $dt = (2, 1, 1)$. For this network, the only attractors are $(0, \ldots, 0)$ and $(2, 1, 1)$.

Because positive disjunctive BNs may admit fixed points and limit cycles (cf. Example 3), Proposition 1 highlights that *the introduction of "memory" may freeze the dynamics (i.e. limit cycles may disappear)*. Now, the question is to know if this freezing property is invariant under the addition of delays. Proposition 2 below shows that it is true for digraphs with no cycles except possibly positive loops. Notice that this result is an extension of that of Robert [40] about acyclic BNs.

Proposition 2. *Let F be a BN whose interaction graph $G = (V, E)$ such that $|V| = n$ does not induce cycles except possibly positive loops. Every MBN built on F admits only fixed points.*

Proof. With or without positive loops, G can be represented by layers of different depths as a classical directed acyclic graph. Now, let us focus on the first layer $\mathcal{L}_1 = \{i \mid f_i(x) \text{ is constant } \vee f_i(x) = x_i\}$, *i.e.* the layer that contains only vertices that are either source vertices or mimic vertices. By definition of the local transition functions, all the vertices of this layer will remain fixed after at most $\max_{i \in \mathcal{L}_1}(dt_i)$ time steps. Once fixed, an induction on the layers depths suffices to show that the stability of the whole MBN is reached and, considering that there are k layers in the graph, that it is reached in at most $\sum_{j=1}^{k} \max_{i \in \mathcal{L}_j} dt_i$ time steps. $\qquad\square$

The BN class of the previous proposition is not the only one for which the freezing property remains invariant. As Proposition 3 states, it is also the case for decreasing (resp. increasing) BNs that are such that $\forall x \in \mathbb{B}^n, F(x) \leq x$ (resp. $F(x) \geq x$), where $F(x) \leq x$ (resp. $F(x) \geq x$) if and only if $\forall i \in \{1, \ldots, n\}, f_i(x) \leq x_i$ (resp. $f_i(x) \geq x_i$).

Proposition 3. *Let F be a decreasing (resp. increasing) BN. Any MBN associated to F necessarily converges towards fixed points only.*

Proof. Let us consider the case of a decreasing BN F where $\forall x \in \mathbb{B}^n, F(x) \leq x$. Such a global transition function implies locally that if $x_i = 0$, it remains at that state because no transitions from state 0 to state 1 are possible. As a consequence, whatever the delay vector dt we decide to associate to F to create a MBN, the network cannot admit limit cycles. The case of an increasing BN is analogous. □

However, despite the two classes previously presented, *there obviously exist MBNs for which the introduction of "memory" does not lead to freeze their dynamics.* For instance, Figure 1 depicts a BN of size 2 that admits only one fixed point, configuration $(0, \ldots, 0)$. Figure 3 pictures the related MBN with $dt = (2, 1)$ in which a limit cycle of length 2 appears. Another more general example follows. Let us consider the BN $F : \mathbb{B}^n \to \mathbb{B}^n$ defined as:

$$F(x) = \begin{cases} (0, \ldots, 0, \overset{a}{0}, \overset{b}{1}, 0, \ldots, 0) & \text{if } x = (0, \ldots, 0, \overset{a}{1}, \overset{b}{0}, 0, \ldots, 0) \\ (0, \ldots, 0, \overset{a}{1}, \overset{b}{0}, 0, \ldots, 0) & \text{if } x = (0, \ldots, 0, \overset{a}{1}, \overset{b}{1}, 0, \ldots, 0) \\ (0, \ldots, 0) & \text{otherwise} \end{cases}.$$

Clearly, this BN converges towards the fixed point $(0, \ldots, 0)$. However, adding delay can make a limit cycle appear. For instance, consider the associated MBN such that $dt = ((1, \ldots, 1) \overset{a}{2} (1, \ldots, 1))$, *i.e.* $\forall i \neq a, dt_i = 1$ and $dt_a = 2$. It is easy to see that this MBN admits a limit cycle of length 2 that is: $(0, \ldots, 0, \overset{a}{1}, \overset{b}{1}, 0, \ldots, 0) \leftrightarrows (0, \ldots, 0, \overset{a}{2}, \overset{b}{0}, 0, \ldots, 0)$.

3 MBN with two genes

In this section, we analyze the dynamical behavior of every network composed of two vertices that admit fixed points. The idea is to highlight some of the main theoretical features of such interaction networks, which constitutes a first step for further formal studies of more general MBNs.

3.1 Networks admitting one fixed point

Here, we focus on networks that admit a unique fixed point. Because the other cases can be studied similarly (and do not reveal other dynamical peculiarities), we pay only attention to networks that converge towards the fixed point $(0, 0)$. First of all, it is trivial to list all the 27 BNs that admit

x	[1,00]	[2,00]	[3,00]	[4,00]	[5,00]	[6,00]	[7,00]	[8,00]	[9,00]
00	00	00	00	00	00	00	00	00	00
01	00	00	00	00	00	00	00	00	00
10	00	00	00	01	01	01	11	11	11
11	00	01	10	00	01	10	00	01	10

x	[10,00]	[11,00]	[12,00]	[13,00]	[14,00]	[15,00]	[16,00]	[17,00]	[18,00]
00	00	00	00	00	00	00	00	00	00
01	10	10	10	10	10	10	10	10	10
10	00	00	00	01	01	01	11	11	11
11	00	01	10	00	01	10	00	01	10

x	[19,00]	[20,00]	[21,00]	[22,00]	[23,00]	[24,00]	[25,00]	[26,00]	[27,00]
00	00	00	00	00	00	00	00	00	00
01	11	11	11	11	11	11	11	11	11
10	00	00	00	01	01	01	11	11	11
11	00	01	10	00	01	10	00	01	10

Table 1: Exhaustive list of the 27 BNs that admits configuration $(0,0)$ as their unique fixed point.

$(0,0)$ as their unique fixed point. For the sake of clarity, let us introduce the following notation that allows to specify the 27 distinct networks at stake here.

Notation 1. $[k,x]$, *with* $k \in \{1,\ldots,27\}$ *and* $x \in \mathbb{B}^2$, *denotes the network of size* 2 *whose local transition functions are represented by* k *and defined by their truth tables in Table 1 and that admits* x *as its unique fixed point (represented as a binary word).*

Let us also denote by $\mathrm{F}[x]$ the set composed of all BNs that admit x as their unique fixed point, $\mathrm{FP}[x] \subseteq \mathrm{F}[x]$ the set of BNs for which x is the unique attractor, and $\mathrm{LC}[x] \subseteq \mathrm{F}[x]$ the set of BNs that admit at least a limit cycle. From now on, let us analyze the dynamical behavior of networks belonging to $\mathrm{F}[x]$. Notice that in general, besides the fixed point x, a BN may (or may not) admit limit cycles. The peculiar question that we address now deals with the asymptotic behavior invariance when we add delays to a BN and thus change it into a MBN. Actually, what follows aims at determining the delay vectors $dt = (dt_1, dt_2)$ for which a given network $f \in F[x]$ admits a particular attractor (say the fixed point x, or a limit cycle which appears only when delays are added). First of all, it is easy to see from Table 1 that

$$\mathrm{FP}[00] = \{[1,00],[2,00],[3,00],[4,00],[5,00],[6,00],[7,00],[8,00],$$
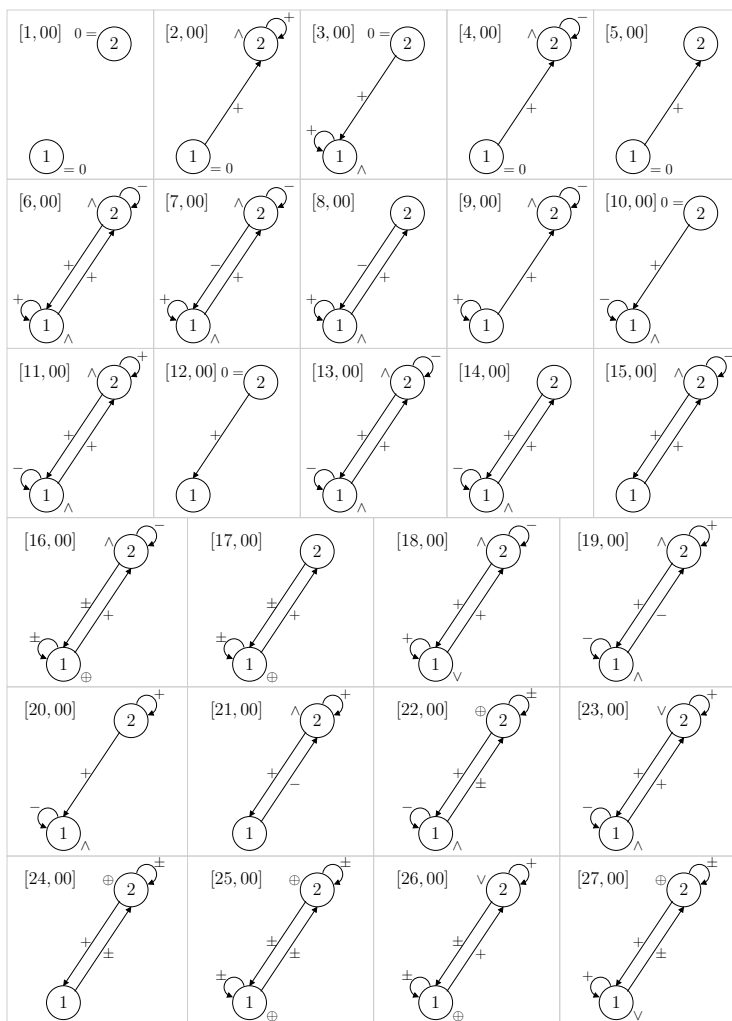$$[10,00],[11,00],[12,00],[16,00],[19,00],[21,00],[22,00],[25,00]\},$$

Figure 6: Interaction graphs of all the networks that admit $(0,0)$ as a fixed point, whose local transition functions are given in Table 1. In some of these graphs, abusing notations for not burdening the reading, an arc (x, y) that is labeled by $\pm$ stands for the actual existence of two arcs from x to y, one labeled by $+$, the other by $-$. Such an arc highlights notably that the local transition function of y is not locally monotonic, and more precisely a XOR (denoted by the operator $\oplus$) in this case.

and that

$$\mathrm{LC}[00] = \{[9, 00], [13, 00], [14, 00], [15, 00], [17, 00], [18, 00],$$
$$[20, 00], [23, 00], [24, 00], [26, 00], [27, 00]\}.$$

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Notation 2. *In what follows, we will make particular use of the following notations:*

- *Delay vector $dt = (dt_1, dt_2)$ will be denoted by $dt = (\alpha, \beta)$.*

- *Initial configuration (Δ_1, Δ_2) will be denoted by (ρ, γ), with $0 \leq \rho \leq \alpha$ and $0 \leq \gamma \leq \beta$.*

- *We will write $(x_1(0), x_2(0)) \xrightarrow{n} (x_1(n), x_2(n))$ to refer to $(x_1(0), x_2(0)) \to (x_1(1), x_2(1)) \to \cdots \to (x_1(n), x_2(n))$. Furthermore, we will use $x \xrightarrow{*} x'$ to indicate that x' belongs to the configurations that are successors of x.*

Let us now study separately both classes FP[00] and LC[00].

3.1.1   Analysis of FP[00]

Let us divide FP[00] into two sub-classes $\mathrm{FP}_{\mathrm{s}}^{[00]}$ and $\mathrm{FP}_{\mathrm{c}}^{[00]}$ such that $\mathrm{FP}_{\mathrm{s}}^{[00]} = \{[1, 00], \ldots, [5, 00], [8, 00], [10, 00], [12, 00], [21, 00]\}$ and $\mathrm{FP}_{\mathrm{c}}^{[00]} = \mathrm{FP}[00] \backslash \mathrm{FP}_{\mathrm{s}}^{[00]}$. Propositions 4 and 5 below respectively show that MBNs related to BNs of $\mathrm{FP}_{\mathrm{s}}^{[00]}$ cannot admit limit cycles whereas MBNs related to BNs of $\mathrm{FP}_{\mathrm{c}}^{[00]}$ can.

Proposition 4. *For any delay vector dt, all the MBNs built on a BN belonging to $\mathrm{FP}_{\mathrm{s}}^{[00]}$ have a unique attractor, the fixed point $(0, 0)$.*

Proof. Let us first consider BN $[1, 00]$. Because its local transition functions are both constant and equal to 0, it is trivial that any MBN built on it can only converge towards fixed point $(0, 0)$, in at most $\max(\alpha, \beta)$ time steps.

Now, let us consider any MBN built on the BNs that belongs to the subset of $\mathrm{FP}_{\mathrm{s}}^{[00]}$ defined as $\{[2, 00], [3, 00], [5, 00], [12, 00]\}$ such that $dt = (\alpha, \beta)$. As pictured in Figure 6, their interaction graphs do not induce cycles of length greater than or equal to 2 and the only loops they contain are positive. So, from Proposition 2, we derive that $(0, 0)$ is the unique attractor of MBNs built on them and that it is reached in at most $\alpha + \beta$ time steps.

About MBNs built on BN $[4, 00]$ with any initial configuration (ρ, γ), because of function $f_1(x)$ that is constant and equal to 0, x_1 is necessarily fixed to 0 after $\rho \leq \alpha$ time steps. Once $x_1 = 0$, by definition of $f_2(x)$, x_2 will decrease to reach 0 after at most β time steps. A similar reasoning can be used on the basis of BN $[10, 00]$ because they are symmetric networks. Moreover, they both converge towards $(0, 0)$ in at most $\alpha + \beta$ time steps.

Now, concerning MBNs built on BN $[8, 00]$, let us consider two cases. The first case is when $x_1 = 0$. By definition of $f_1(x)$, once x_1 at 0 it remains fixed to 0 and according to the definition of f_2, the value of x_2 necessarily decreases to 0. Thus, $(0, x_2)$ converges towards $(0, 0)$ in at most β time steps. Consider now the case where $0 < x_1 \leq \alpha$. We have: if $x_2 \geq 1$ then $(x_1, x_2) \rightarrow (x_1 - 1, \beta) \xrightarrow{x_1 - 1} (0, \beta) \xrightarrow{\beta} (0, 0)$, and the network converges in $x_1 + \beta$ time steps; if $x_2 = 0$ then $(x_1, 0) \rightarrow (\alpha, \beta) \rightarrow (\alpha - 1, \beta) \xrightarrow{\alpha - 1} (0, \beta) \xrightarrow{\beta} (0, 0)$ and the network converges in $\alpha + \beta + 1$ time steps. Thus, such MBNs (resp. MBNs built on BN $[21, 00]$ by symmetry) converge towards their unique attractor, fixed point $(0, 0)$, in at most $\alpha + \beta + 1$ time steps.

Hence, all the MBNs of $\mathrm{FP}_{\mathrm{s}}^{[00]}$ admit $(0, 0)$ as their unique attractor. $\qquad\square$

Proposition 5. *For any BN of* $\mathrm{FP}_{\mathrm{c}}^{[00]}$*, there exist delay vectors dts such that their related MBNs admit limit cycles.*

Proof. In this proof, for BNs belonging to $\mathrm{FP}_{\mathrm{c}}^{[00]}$, we exhibit delay vectors with which the associated MBN evolves towards a limit cycle.
Let us now consider a MBN built on BN $[6, 00]$. First, suppose that $\alpha = 1$. Then, for all β, either $\rho = 0$ and x_1 will stay fixed to 0, which leads inevitably x_2 to decrease to 0 and remain fixed in γ time steps, or $\rho = 1$: in this case: if $\gamma = 0$, then after one time step, $x_1 = 0$ and we get back to the previous case; otherwise, $\gamma \geq 1$ and the dynamics is $(1, \gamma) \xrightarrow{\gamma} (1, 0) \rightarrow (0, \gamma)$, and we get back to previous item in $\gamma + 1$ time steps. As a consequence, in order for MBNs associated with BN $[6, 00]$ to admit limit cycles, α needs to be greater than 1 (except if β is also equal to 1 of course). Now let us consider $dt = (\alpha \geq 2, \beta)$ and initial configuration $(\rho = \alpha, \gamma = \beta)$. Its dynamics is $(\alpha, \beta) \rightarrow (\alpha, \beta - 1) \xrightarrow{\beta - 1} (\alpha, 0) \rightarrow (\alpha - 1, \beta) \rightarrow (\alpha, \beta - 1)$. So, there exist recurrent configurations and thus a limit cycle. Notice that this limit cycle is of length β. Furthermore, for the same reasons as those given for the case where $\alpha = 1$, initial configurations such that $\rho = 0$ or $(\rho = 1, \gamma = 0)$ converges towards fixed point $(0, 0)$ in at most $\beta + 1$ time steps. All the other configurations, *i.e.* those such that $(\rho \geq 2, \gamma \geq 0)$ and $(\rho = 1, \gamma = 0)$ evolves to (α, β) and thus towards the limit cycle. By symmetry, a similar reasoning can be used for BN $[11, 00]$.
About MBNs built on BN $[7, 00]$, for all (α, β), notice that by definition of f_1 and because of the positive loop, when $x_1 = 0$, it remains fixed to 0. Moreover, when $x_1 = 0$, it leads x_2 to decrease until it reaches 0 also. Let us now detail the dynamics of this network depending on the initial configurations, considering $1 \leq \rho \leq \alpha$ and $1 \leq \gamma \leq \beta$:

- if $\rho \leq \gamma$ then $(\rho, \gamma) \xrightarrow{\rho} (0, \gamma - \rho) \xrightarrow{\gamma - \rho} (0, 0)$ that is reached in γ time steps.

- if $\rho > \gamma$ then $(\rho, \gamma) \xrightarrow{\gamma} (\rho - \gamma, 0) \to (\alpha, \beta)$. From configuration (α, β), we have: if $\alpha = \beta$ then $(\alpha, \alpha) \to (\alpha - 1, \alpha - 1) \xrightarrow{\alpha - 1} (0, 0)$ that is reached in $\gamma + \alpha + 1$ time steps; if $\alpha < \beta$ then $(\alpha, \beta) \xrightarrow{\alpha} (0, \beta - \alpha) \xrightarrow{\beta - \alpha} (0, 0)$ that is reached in $\gamma + \beta + 1$ time steps; if $\alpha > \beta$ then $(\alpha, \beta) \xrightarrow{\beta} (\alpha - \beta, 0) \to (\alpha, \beta)$, which emphasizes a limit cycle of length β.

Thus, any MBN built on BN $[7, 00]$ such that $\alpha > \beta$ admits a limit cycle of length β. The unique other possible attractor is fixed point $(0, 0)$ that is reached in at most $2 \max(\alpha, \beta) + 1$ time steps. By symmetry, a similar reasoning can be used for BN $[19, 00]$.

Now, let us focus on BN $[16, 00]$. First of all, by definition of its local transition functions, it is easy to check that for all (α, β), if $\rho = \gamma$ then the configuration converges towards fixed point $(0, 0)$. Indeed, we have $(\rho, \rho) \to (\rho - 1, \rho - 1) \xrightarrow{\rho - 1} (0, 0)$, that is reached in ρ time steps, *i.e.* in at most $\min(\alpha, \beta)$ time steps. Now, let us deal with all possible α and β. First, consider that $\alpha = \beta$. Then, according to the initial configuration, if $\rho < \gamma$, the dynamics of (ρ, γ) is $(\rho, \gamma) \xrightarrow{\rho} (0, \gamma - \rho) \to (\alpha, \gamma - \rho - 1) \xrightarrow{\gamma - \rho - 1 < \alpha} (\alpha - \gamma + \rho + 1, 0) \to (\alpha, \alpha) \xrightarrow{\alpha} (0, 0)$ that is reached in $\alpha + \gamma + 1$ time steps; otherwise, if $\rho > \gamma$, it is $(\rho, \gamma) \xrightarrow{\gamma} (\rho - \gamma, 0) \to (\alpha, \alpha) \xrightarrow{\alpha} (0, 0)$ that is reached in $\alpha + \gamma + 1$ time steps. Thus, if $\alpha = \beta$, any configuration converges towards fixed point $(0, 0)$ in at most $2\alpha + 1 = 2\beta + 1$ time steps.

Now, consider that $\alpha > \beta$. In this case, if $\rho < \gamma$, the dynamics of (ρ, γ) is $(\rho, \gamma) \xrightarrow{\rho} (0, \gamma - \rho) \to (\alpha, \gamma - \rho - 1) \xrightarrow{\gamma - \rho - 1 < \alpha} (\alpha - \gamma + \rho + 1, 0) \to (\alpha, \beta) \xrightarrow{\beta} (\alpha - \beta, 0) \to (\alpha, \beta)$; otherwise, if $\rho > \gamma$, the dynamics of (ρ, γ) is $(\rho, \gamma) \xrightarrow{\gamma} (\rho - \gamma, 0) \to (\alpha, \beta) \xrightarrow{\beta} (\alpha - \beta, 0) \to (\alpha, \beta)$. Thus, when $\alpha > \beta$, for all initial configurations (ρ, γ), with $\rho \neq \gamma$, the network evolves towards a limit cycle of length β.

Now, in the case where $\alpha < \beta$, we have:

- if $\rho > \gamma$, the dynamics is $(\rho, \gamma) \xrightarrow{\gamma} (\rho - \gamma, 0) \to (\alpha, \beta)$. Here, suppose that $\alpha < \beta < 2\alpha + 1$. Then we have $(\alpha, \beta) \xrightarrow{\alpha} (0, \beta - \alpha) \to (\alpha, \beta - \alpha - 1) \xrightarrow{\beta - \alpha - 1} (\alpha - (\beta - \alpha - 1), 0) \to (\alpha, \beta)$. Now, if $\beta = 2\alpha + 1$, the trajectory of (α, β) is $(\alpha, \beta) \xrightarrow{\alpha} (0, \beta - \alpha) \to (\alpha, \beta - \alpha - 1) \xrightarrow{\alpha} (0, \beta - 2\alpha - 1) = (0, 0)$, that is reached in at most $2\beta + 1$ time steps. More generally, if there exists $k \in \mathbb{N}$ such that $\beta = k \cdot (\alpha + 1) - 1$ then, the trajectory

of (α, β) is $(\alpha, \beta) \xrightarrow{k \cdot (\alpha+1)-1} (0, \beta - k \cdot (\alpha + 1) - 1) = (0, 0)$, that is reached from any (ρ, γ) in at most $2\beta + 1$ time steps. Now, suppose that $\forall k \in \mathbb{N}, \beta \neq k \cdot (\alpha+1) - 1$ and ℓ the greatest natural number such that $\beta > \ell \cdot (\alpha+1) - 1$ (*i.e.* $\ell \cdot (\alpha+1) - 1 < \beta < (\ell+1)(\alpha+1-1)$), then the trajectory of (α, β) is $(\alpha, \beta) \xrightarrow{\ell \cdot (\alpha+1)-1} (0, \beta - (\ell \cdot (\alpha + 1) - 1) \neq 0) \to (\alpha, \beta - \ell \cdot (\alpha+1)) \xrightarrow{\beta - \ell \cdot (\alpha+1)} (\alpha - (\beta - \ell \cdot (\alpha+1)) \neq 0, 0) \to (\alpha, \beta)$.

- if $\rho < \gamma$, if we suppose that $\gamma = \rho + \alpha + 1$, the dynamics is $(\rho, \gamma) \xrightarrow{\rho} (0, \gamma - \rho) \to (\alpha, \gamma - \rho - 1) \xrightarrow{\gamma - \rho - 1} (\alpha - \gamma + \rho + 1 = 0, 0)$, that is reached in at most β time steps. More generally, by supposing that given $k > 1 \in \mathbb{N}, \gamma = \rho + k \cdot (\alpha+1)$, we have $(\rho, \gamma) \xrightarrow{\rho} (0, \gamma - \rho) \to (0, \gamma - \rho - 1) \xrightarrow{\alpha} (0, \gamma - \rho - 1 - \alpha) \xrightarrow{(k-1)(\alpha+1)} (0, \gamma - \rho - k \cdot (\alpha+1)) = (0, 0)$, that is reached in at most β time steps. Now, suppose that $\forall k \in \mathbb{N}, \gamma \neq \rho + k \cdot (\alpha+1)$ and that ℓ is the greatest natural number such that $\gamma > \rho + \ell \cdot (\alpha+1)$, *i.e.* $\rho + \ell \cdot (\alpha + 1) < \gamma < \rho + (\ell + 1) \cdot (\alpha + 1)$, the trajectory of (ρ, γ) is $(\rho, \gamma) \xrightarrow{\rho + \ell \cdot (\alpha+1)} (0, \gamma - \rho - \ell \cdot (\alpha + 1)) \to (\alpha, \gamma - \rho - \ell \cdot (\alpha + 1) - 1) \xrightarrow{\gamma - \rho - \ell \cdot (\alpha+1)-1} (\alpha - (\gamma - \rho - \ell \cdot (\alpha + 1) - 1) \neq 0, 0) \to (\alpha, \beta)$, for which it suffices to apply the case discussed in the previous sub-item.

As a consequence, when $\alpha < \beta$, initial configurations can evolve either towards the fixed point $(0, 0)$ in at most $2\beta + 1$ time steps or towards a limit cycle of length β only if $\beta \neq k \cdot (\alpha + 1) - 1, \forall k \in \mathbb{N}$. By symmetry, a similar reasoning can be used for BN $[22, 00]$.

Concerning MBNs built on BN $[25, 00]$, first of all, because this network is a symmetric XOR network, it is easy to check that if $\rho = \gamma$, whatever α and γ are, the trajectory of the initial configuration is $(\rho, \rho) \to (\rho - 1, \rho - 1) \xrightarrow{\rho-1} (0, 0)$, and converges thus towards fixed point $(0, 0)$ in ρ time steps, *i.e.* in at most $\min(\alpha, \beta)$ time steps. From now on, let us focus on initial configurations such that $\rho \neq \gamma$. Suppose that $\alpha > \beta$. The underlying dynamics is $(\rho, \gamma) \xrightarrow{\min(\rho, \gamma)+1} (\alpha, \beta) \xrightarrow{\beta} (\alpha - \beta, 0) \to (\alpha, \beta)$, which highlights a limit cycle of length β. Symmetrically, in the case where $\alpha < \beta$, (ρ, γ) evolves towards the cycle $(\alpha, \beta) \xrightarrow{\alpha} (0, \beta - \alpha) \to (\alpha, \beta)$. Lastly, if $\alpha = \beta$, the trajectory of (ρ, γ) is $(\rho, \gamma) \xrightarrow{\min(\rho, \gamma)+1} (\alpha, \alpha) \xrightarrow{\alpha} (0, 0)$, and there is convergence towards the unique fixed point in at most $2\alpha + 1$ time steps. $\square$

Proposition 5 emphasizes that *adding delays to BNs to make them become MBNs can lead to the creation of limit cycles in the set of network attractors.* Now, let us focus on the class LC[00].

3.1.2 Analysis of LC[00]

By definition, the BNs that belong to LC[00] have the feature of having, besides the fixed point $(0,0)$, a limit cycle. This limit cycle is of length 2 for $[\{9, 13, 14, 15, 18, 20, 23, 26, 27\}, 00]$ and of length 3 for $[\{17, 24\}, 00]$. Often, in BN models of real genetic regulatory networks, the biological meaning comes from the fixed point. Indeed, except in networks modeling biological rhythms sustained oscillations in which limit cycles are of course meaningful, the latter correspond to spurious asymptotic behaviors. Thus, in a modeling framework, finding a way of removing limit cycles can be particularly relevant. Classically, it is done by using an asynchronous updating mode. As Example 3 highlighted it, adding delays can serve in this context. More generally, we will see that changing BNs into MBNs may allow to obtain this desirable property of avoiding spurious attractors. More precisely, for all the BNs that belong to LC[00], we analyze the delay parameter space for knowing the regions in which the limit cycle disappears. This analysis is presented by the following propositions.

Proposition 6. *Every MBN built on BN $[9, 00]$ (resp. on $[20, 00]$) admits a limit cycle that is reached by all configurations such that $\rho \geq 1$ (resp. $\gamma \geq 1$).*

Proof. Consider a MBN built on BN $[9, 00]$. Whatever α and β are, by definition of f_1, x_1 is maintained by the positive loop. As a consequence: if $\rho = 0$, the network converges towards the fixed point $(0, 0)$ in γ time steps, *i.e.* in at most β time steps; if $\rho \geq 1$, by definition of f_2, the initial configuration $(\rho, \gamma = \beta)$ has the following dynamics: $(\rho, \beta) \to (\rho, \beta - 1) \xrightarrow{\beta - 1} (\rho, 0) \to (\rho, \beta)$. Thus, any configuration $(\rho \geq 1, \gamma)$ belongs to a limit cycle of length β. By symmetry, a similar reasoning can be used for BN $[20, 00]$. $\quad\square$

Proposition 7. *Consider a MBN M based on BN $[13, 00]$. We have:*

1. *If M is such that $\gcd(\alpha + 1, \beta + 1) = 1$, all its configurations converge towards fixed point $(0, 0)$.*

2. *If M is such that $\gcd(\alpha + 1, \beta + 1) > 1$, any configuration (ρ, γ) such that $\rho + \ell_0(\alpha + 1) = \gamma + k_0(\beta + 1)$, with $0 \leq k_0 \leq k$ and $0 \leq \ell_0 \leq \ell$ with $\ell(\alpha + 1) = k(\beta + 1) = \mathrm{lcm}(\alpha + 1, \beta + 1)$, converges towards fixed point $(0, 0)$. Otherwise, it evolves towards a limit cycle of length $\mathrm{lcm}(\alpha + 1, \beta + 1)$.*

Proof. In this proof, we deal with the two distinct items of the statement separately.

1. Let us first consider a MBN such that $\gcd(\alpha + 1, \beta + 1) = 1$ and such that $\alpha < \beta$. Let (ρ_t, γ_t) be the configuration obtained after $t \in \mathbb{N}$ time steps from any possible initial configuration (ρ, γ). In this case, inevitably, there exists t, with $0 \leq t < (\alpha + 1) \cdot \beta + 1$, such that $\rho_t = \gamma_t$. Indeed, suppose on the contrary that $\forall t \in \mathbb{N}$ such that $0 \leq t < (\alpha + 1) \cdot \beta + 1$, $\rho_t \neq \gamma_t$. Then, we know that there exist $(\alpha + 1) \cdot \beta$ different ordered pairs of integers (*i.e.* configurations) such that $\rho_t \neq \gamma_t$. Thus, necessarily, there exist $i \neq j \in \{0, \ldots, (\alpha + 1) \cdot \beta\}$ such that $(\rho_i, \gamma_i) = (\rho_j, \gamma_j)$, which implies the existence of a limit cycle of length $|i - j|$. More precisely, given $0 \leq h \leq \beta$, $k < \alpha + 1$ and $\ell < \beta + 1$, we have:

$$(\rho_i, \gamma_i) \xrightarrow{|i-j|} (\rho_i, \gamma_i) \implies (\alpha, \beta - h) \xrightarrow{|i-j| = \ell(\alpha+1) = k(\beta+1)} (\alpha, \beta - h),$$

which implies that $\alpha + 1$ and $\beta + 1$ are not coprime, which is a contradiction. Therefore, there exists a time step t at which $\rho_t = \gamma_t$. Now, given the local transition functions, it is easy to remark that all the configurations whose two terms are equal converge towards fixed point $(0,0)$.

By symmetry of the rule, the same reasoning applies for the case where $\alpha > \beta$. Moreover, by the hypothesis highlighting that $\gcd(\alpha + 1, \beta + 1) = 1$, the case where $\alpha = \beta$ does not exist.

2. Now, let us consider a MBN such that $\gcd(\alpha + 1, \beta + 1) = \lambda > 1$. Consider an initial configuration (ρ, γ) and distinguish two cases:

   - (ρ, γ) satisfies

$$\rho + \ell_0(\alpha + 1) = \gamma + k_0(\beta + 1) \tag{1}$$

   for some k_0, ℓ_0 such that $0 \leq k_0 \leq k$, $0 \leq \ell_0 \leq \ell$, with $\ell(\alpha + 1) = k(\beta + 1) = \mathrm{lcm}(\alpha + 1, \beta + 1)$. First of all, as evoked above in the previous item, given the nature of the MBN, it is trivial to remark that for all $dt = (\alpha, \beta)$, an initial configuration such that $\rho = \gamma$ (this initial condition satisfies Equation 1 above with $k_0 = \ell_0 = 0$) admits the trajectory $(\rho, \rho) \to (\rho - 1, \rho - 1) \xrightarrow{(\rho-1)} (0, 0)$, and converges towards fixed point $(0,0)$ in ρ time steps, *i.e.* in at most $\min(\alpha, \beta)$ time steps. Now, let us admit that $\alpha < \beta$ and that $\rho > \gamma$. If the lower values of k_0 and ℓ_0 satisfying Equation 1 are both equal to 1 then the configuration admits the following trajectory: $(\rho, \gamma) \xrightarrow{\gamma} (\rho - \gamma, 0) \to (\rho - \gamma - 1, \beta) \xrightarrow{\rho-\gamma-1} (0, \beta -$

$(\rho - \gamma - 1)) \rightarrow (\alpha, \beta - (\rho - \gamma) = \alpha)$. Moreover, if the lower values of k_0 and ℓ_0 satisfying Equation 1 are such that $k_0 > 1$ and $\ell_0 \geq 1$ then the configuration admits the following trajectory: $(\rho, \gamma) \xrightarrow{\rho+1+(\ell_0-1)(\alpha+1)=\gamma+1+k_0(\beta+1)-(\alpha+1)} (\alpha, \alpha)$. Hence, in both cases, (ρ, γ) converges towards fixed point $(0, 0)$.

With the same reasoning, it can be shown that the result holds also for initial configurations such that $\rho < \gamma$. Furthermore, by symmetry of the rule, the same reasoning applies for the case where $\alpha > \beta$. Moreover, if $\alpha = \beta$, the only way for Equation 1 to hold is when $\rho = \gamma$ and this case has already been dealt with.

- (ρ, γ) satisfies $\rho + \ell_0(\alpha + 1) \neq \gamma + k_0(\beta + 1)$ for some k_0, ℓ_0 such that $0 \leq k_0 \leq k$, $0 \leq \ell_0 \leq \ell$, with $\ell(\alpha + 1) = k(\beta + 1) = \mathrm{lcm}(\alpha + 1, \beta + 1)$. First, let us consider the case where $\alpha = \beta$. In this case, the only way for the negation of Equation 1 to hold is when $\rho \neq \gamma$. So, let us consider a configuration where $\rho > \gamma$. Its trajectory is $(\rho, \gamma) \xrightarrow{\gamma} (\rho - \gamma, 0) \rightarrow (\rho - \gamma - 1, \alpha) \xrightarrow{\rho-\gamma-1} (0, \alpha - (\rho - \gamma - 1)) \rightarrow (\alpha, \alpha - (\rho - \gamma)) \xrightarrow{\alpha-(\rho-\gamma)} (\rho - \gamma, 0)$, which highlights a limit cycle of length $\alpha + 1$. With the same reasoning, we can show that a configuration such that $\rho < \beta$ evolves also towards a limit cycle of length $\alpha + 1$. Now, let us consider the case where $\alpha < \beta$. By the hypothesis stating that $\rho + \ell_0(\alpha + 1) \neq \gamma + k_0(\beta + 1)$, the trajectory of a configuration such that $\rho > \gamma$ is $(\rho, \gamma) \xrightarrow{\gamma} (\rho - \gamma, 0) \rightarrow (\rho - \gamma - 1, \beta) \xrightarrow{\rho-\gamma-1} (0, \beta - (\rho - \gamma - 1)) \rightarrow (\alpha, \beta - (\rho - \gamma)) \xrightarrow{\ell(\alpha+1)=k(\beta+1)} (\alpha, \beta - (\rho - \gamma))$, which corresponds to a limit cycle of length $\mathrm{lcm}(\alpha + 1, \beta + 1)$. In other terms, if $\alpha + 1$ and $\beta + 1$ are not coprime and if $\rho + \ell_0(\alpha + 1) \neq \gamma + k_0(\beta + 1)$ then the network admits a limit cycle.

  With the same reasoning, it can be shown that the result holds also for initial configurations such that $\rho < \gamma$. Furthermore, by symmetry of the rule, the same reasoning applies for the case where $\alpha > \beta$.

$\square$

Proposition 8. *Let $S = \{[9, 00], [13, 00], [20, 00]\}$. Every MBN built on a BN belonging to $\mathrm{LC}[00] \setminus S$ admits a limit cycle that is reached by all configurations except $(0, 0)$.*

Proof. Let us consider a MBN built on $[14, 00]$ and an initial configuration

such that $\rho \geq 1$ and $\gamma \geq 2$. By definition of f_2, x_2 is set and stays at β while x_1 is positive. Notice also that x_1 decreases until reaching 0 by definition of f_1. Thus, we have the following trajectory: $(\rho, \gamma) \rightarrow (\rho - 1, \beta) \xrightarrow{\rho - 1} (0, \beta) \rightarrow (\alpha, \beta - 1) \rightarrow (\alpha - 1, \beta) \xrightarrow{\alpha - 1} (0, \beta)$, which highlights the evolution towards a limit cycle of length $\alpha + 1$. Now, let us focus on an initial configuration defined as $(\rho \geq 1, \gamma = 0)$. Its trajectory is $(\rho, 0) \rightarrow (\rho - 1, \beta) \xrightarrow{\rho - 1} (0, \beta) \rightarrow (\alpha, \beta - 1) \rightarrow (\alpha - 1, \beta) \xrightarrow{\alpha - 1} (0, \beta)$. As a consequence, for any MBN built on BN $[14, 00]$ (resp. on BN $[15, 00]$ by symmetry), all configurations except fixed point $(0, 0)$ evolves towards a limit cycle of length $\alpha + 1$ (resp. $\beta + 1$). Notice that a similar reasoning applies for MBNs based on BNs $[17, 00]$, $[23, 00]$, $[26, 00]$, and for their respective symmetric BNs $[24, 00]$, $[18, 00]$ and $[27, 00]$. $\qquad\square$

Thanks to Propositions 4 to 8 above, we obtain the following theorem that recapitulates all the results that characterize the dynamical behaviors of all MBNs that can be constructed from BNs of size 2 having the unique fixed point $(0, 0)$.

Theorem 1. *Table 2 gives the dynamical behavior of any MBN built on the basis of a BN belonging to* $\mathrm{FP}(0, 0)$*, with delays* $dt = (\alpha, \beta)$*, initial condition* $0 \leq \rho \leq \alpha$*,* $0 \leq \gamma \leq \beta$ *and* $k, \ell \in \mathbb{N}$*.*

Now the dynamical properties of MBNs of size 2 with a unique fixed point have been characterized, let us pay attention to MBNs of the same size with two fixed points.

3.2 Networks admitting two fixed points

In this section, we focus on the MBNs that can be built on the basis of BNs of size 2 that admit two fixed points. First of all, let us notice that there exist 6 distinct classes of such networks, each of which being composed of 9 networks. As what has been presented above, let us introduce the following notations.

Notation 3. $[k, x, y]$*, with* $k \in \{1, \ldots, 9\}$ *and* $x, y \in \mathbb{B}^2$*, denotes the network of size* 2 *whose local transition functions are represented by* k *and defined by their truth tables in Tables 3, 4, 5 and 6 and that admits* x *and* y *as its fixed points (represented as binary words).*

Let us also denote by $\mathrm{F}[x, y]$ the set composed of all BNs that admit x and y as their unique fixed points, $\mathrm{FP}[x, y] \subseteq \mathrm{F}[x, y]$ the set of BNs for which

Rules	Attractors	Delays $dt = (\alpha, \beta)$	Initial conditions (ρ, γ)
$[1,00], [2,00],$ $[3,00], [4,00],$ $[5,00], [8,00],$ $[10,00], [12,00],$ $[21,00]$	FP	$\forall(\alpha,\beta)$	$\forall(\rho,\gamma)$
	LC	$\emptyset$	$\emptyset$
$[6,00]$	FP	$\alpha = 1$ $\forall(\alpha,\beta)$	$\forall(\rho,\gamma)$ $(\rho = 1 \wedge \gamma = 0) \vee (\rho = 0 \wedge \gamma \geq 0)$
	LC	$(\alpha,\beta) \geq (2,1)$	$(\rho \geq 2 \wedge \gamma \geq 0) \vee (\rho = 1 \wedge \gamma = 1)$
$[11,00]$	FP	$\beta = 1$ $\forall(\alpha,\beta)$	$\forall(\rho,\gamma)$ $(\rho = 0 \wedge \gamma = 1) \vee (\rho \geq 0 \wedge \gamma = 0)$
	LC	$(\alpha,\beta) \geq (1,2)$	$(\rho \geq 0 \wedge \gamma \geq 2) \vee (\rho = 1 \wedge \gamma = 1)$
$[7,00]$	FP	$\alpha \leq \beta$ $\alpha > \beta$	$\forall(\rho,\gamma)$ $\rho \leq \gamma$
	LC	$\alpha > \beta$	$\rho > \gamma$
$[19,00]$	FP	$\alpha \geq \beta$ $\alpha < \beta$	$\forall(\rho,\gamma)$ $\rho \geq \gamma$
	LC	$\alpha < \beta$	$\rho < \gamma$
$[9,00]$	FP	$\forall(\alpha,\beta)$	$\rho = 0$
	LC	$\forall(\alpha,\beta)$	$\rho \geq 1$
$[20,00]$	FP	$\forall(\alpha,\beta)$	$\gamma = 0$
	LC	$\forall(\alpha,\beta)$	$\gamma \geq 1$
$[13,00]$	FP	$\gcd(\alpha+1, \beta+1) = 1$ $\gcd(\alpha+1, \beta+1) > 1$	$\forall(\rho,\gamma)$ $\rho + \ell_0(\alpha+1) = \gamma + k_0(\beta+1)$ with $0 \leq k_0 \leq k, 0 \leq \ell_0 \leq \ell,$ $\ell(\alpha+1) = k(\beta+1) = \operatorname{lcm}(\alpha+1, \beta+1)$
	LC	$\gcd(\alpha+1, \beta+1) > 1$	$\rho + \ell_0(\alpha+1) \neq \gamma + k_0(\beta+1)$ with $0 \leq k_0 \leq k, 0 \leq \ell_0 \leq \ell,$ $\ell(\alpha+1) = k(\beta+1) = \operatorname{lcm}(\alpha+1, \beta+1)$
$[14,00], [15,00],$ $[17,00], [18,00],$ $[23,00], [24,00],$ $[26,00], [27,00]$	FP	$\forall(\alpha,\beta)$	$(\rho,\gamma) = (0,0)$
	LC	$\forall(\alpha,\beta)$	$(\rho,\gamma) \neq (0,0)$
$[16,00]$	FP	$\alpha < \beta$ $\alpha = \beta$ $\alpha > \beta$	$(\rho = \gamma) \vee (\rho + k(\alpha+1) = \gamma) \vee$ $(\beta + 1 = k(\alpha+1))$ $\forall(\rho,\gamma)$ $\rho = \gamma$
	LC	$\alpha < \beta$ $\alpha < \beta$ $\alpha > \beta$	$(\rho < \gamma) \wedge (\gamma \neq \rho + k \cdot (\alpha+1)) \wedge$ $(\beta + 1 \neq k(\alpha+1))$ $(\rho > \gamma) \wedge (\beta + 1 \neq k(\alpha+1))$ $\rho \neq \gamma$
$[22,(0,0)]$	FP	$\alpha < \beta$ $\alpha = \beta$ $\alpha > \beta$ 24	$\rho = \gamma$ $\forall(\rho,\gamma)$ $(\rho = \gamma) \vee (\gamma + k(\beta+1) = \rho) \vee$ $(\alpha + 1 = k(\beta+1))$
	LC	$\alpha < \beta$ $\alpha > \beta$ $\alpha > \beta$	$\rho \neq \gamma$ $(\rho > \gamma) \wedge (\rho \neq \gamma + k \cdot (\beta+1)) \wedge$ $(\alpha + 1 \neq k(\beta+1))$ $(\rho < \gamma) \wedge (\alpha + 1 \neq k(\beta+1))$
$[25,00]$	FP	$\alpha = \beta$ $\alpha \neq \beta$	$\forall(\rho,\gamma)$ $\rho = \gamma$
	LC	$\alpha \neq \beta$	$\rho \neq \gamma$

x	[1, 00, 01]	[2, 00, 01]	[3, 00, 01]	[4, 00, 01]	[5, 00, 01]	[6, 00, 01]	[7, 00, 01]	[8, 00, 01]	[9, 00, 01]
00	00	00	00	00	00	00	00	00	00
01	01	01	01	01	01	01	01	01	01
10	00	00	00	01	01	01	11	11	11
11	00	01	10	00	01	10	00	01	10

x	[1, 00, 10]	[2, 00, 10]	[3, 00, 10]	[4, 00, 10]	[5, 00, 10]	[6, 00, 10]	[7, 00, 10]	[8, 00, 10]	[9, 00, 10]
00	00	00	00	00	00	00	00	00	00
01	00	00	00	10	10	10	11	11	11
10	10	10	10	10	10	10	10	10	10
11	00	01	10	00	01	10	00	01	10

Table 3: Truth tables of all the 9 BNs that admit (up) fixed points $(0, 0)$ and $(0, 1)$ and (down) fixed points $(0, 0)$ and $(1, 0)$.

x and y are the unique attractors, $\mathrm{LC}[x, y] \subseteq \mathrm{F}[x, y]$ the set of BNs that admits at least a limit cycle.

3.2.1 MBNs based on $\mathrm{F}[00, 01]$ and $\mathrm{F}[00, 10]$

Concerning the classes of BNs $\mathrm{F}[00, 01]$ and $\mathrm{F}[00, 10]$, notice first that they are symmetric. Thus, all the results obtained for $\mathrm{F}[00, 01]$ have their symmetric that hold for $\mathrm{F}[00, 10]$. So, let us focus only on $\mathrm{F}[00, 01]$.

Remark 1. *For every network of* $\mathrm{F}[00, 01]$*, since* $(0, 0)$ *and* $(0, 1)$ *are fixed points, whatever* α *and* β *are, configuration* $(0, 0)$ *cannot change, admits the following trajectory* $(0, 0) \circlearrowleft$ *and is a fixed point, and the trajectory of any initial configuration such that* $\rho = 0$ *and* $\gamma \geq 1$ *is* $(0, \gamma) \rightarrow (0, \beta) \circlearrowleft$ *that leads to fixed point* $(0, \beta)$*.*

Therefore we analyze the dynamical behavior of all the initial configurations of the form (ρ, γ) where $\rho \neq 0$. From Table 3 (up), a basic enumeration gives that $\mathrm{FP}[00, 01] = \mathrm{F}[00, 01] \backslash \{[9, 00, 01]\}$, and $\mathrm{LC}[00, 01] = \{[9, 00, 01]\}$. Now, let us partition $\mathrm{FP}[00, 01]$ into the following two sub-classes: $\mathrm{FP}_{\mathrm{s}}^{[00, 01]} = \{[1, 00, 01], \ldots, [5, 00, 01], [8, 00, 01]\}$, and $\mathrm{FP}_{\mathrm{c}}^{[00, 01]} = \mathrm{FP}[00, 01] \setminus \mathrm{FP}_{\mathrm{s}}^{[00, 01]} = \{[6, 00, 01], [7, 00, 01]\}$. Proposition 9 below shows that MBNs based on BNs of $\mathrm{FP}_{\mathrm{s}}[00, 01]$ admits only two fixed points, $(0, 0)$ and $(0, \beta)$.

Proposition 9. *For any delay vector dt, every MBN built on a BN that belongs to* $\mathrm{FP}_{\mathrm{s}}^{[00, 01]}$ *admits only two attractors, fixed points* $(0, 0)$ *and* $(0, \beta)$*.*

Proof. Let us first consider MBNs built on BNs $[1, 00, 01]$, $[2, 00, 01]$ or $[3, 00, 01]$. Table 3 (up) shows that they are decreasing networks. As a consequence, by Proposition 3, they admit only fixed points that are $(0, 0)$

and $(0, \beta)$ by definition of the local transition functions. All the MBNs built on $[1, 00, 01]$, $[2, 00, 01]$ (resp. on $[3, 00, 01]$) converge in at most α (resp. $\alpha + \beta$) time steps.

Moreover, Table 3 (up) highlights also that the interaction graph of BN $[5, 00, 01]$ does not induce cycles except a positive loop on vertex 2. Thus, by Proposition 2, any MBN built on $[5, 00, 01]$ admits only fixed points that are $(0, 0)$ and $(0, \beta)$. More precisely, for any delay vector $dt = (\alpha, \beta)$ and $\rho \geq 1$, we have the following trajectory: $(\rho, \gamma) \xrightarrow{\rho} (0, \beta) \circlearrowleft$ that is reached in at most α time steps.

Consider a MBN built on BN $[4, 00, 01]$. Let (ρ, γ) be any initial configuration. If $\rho = \gamma$, its trajectory is $(\rho, \rho) \xrightarrow{\rho} (0, 0) \circlearrowleft$ and the network converges in at most $\min(\alpha, \beta)$ time steps. If $\rho < \gamma$, its trajectory is $(\rho, \gamma) \xrightarrow{\rho} (0, \gamma - \rho) \to (0, \beta) \circlearrowleft$ and the network converges in $\alpha + 1$ at most. Now, if $\rho > \gamma$, the trajectory begins by $(\rho, \gamma) \xrightarrow{\gamma} (\rho - \gamma, 0) \to (\rho - \gamma - 1, \beta)$, and the trajectory of $(\rho - \gamma - 1, \beta)$ is either $(\rho - \gamma - 1, \beta) \xrightarrow{\rho - \gamma - 1} (0, \beta) \circlearrowleft$ if $\rho - \gamma \neq k(\beta + 1)$, or $(\rho - \gamma - 1, \beta) \xrightarrow{\rho - \gamma - 1} (0, 0) \circlearrowleft$ otherwise. Thus the network converges towards these two fixed points in at most α time steps.

Consider finally a MBN built on BN $[8, 00, 01]$. For any delay vector $dt = (\alpha, \beta)$, we have: if $\rho \geq 1$ and $\gamma \geq 1$ then $(\rho, \gamma) \to (\rho - 1, \beta) \xrightarrow{\rho - 1} (0, \beta) \circlearrowleft$ that is reached in ρ time steps, and if $\rho \geq 1$ and $\gamma = 0$ then $(\rho, 0) \to (\alpha, \beta) \xrightarrow{\alpha} (0, \beta) \circlearrowleft$ that is reached in $\alpha + 1$ time steps. Thus, the network admits only the two fixed points $(0, 0)$ and $(0, \beta)$ and its convergence time is at most $\alpha + 1$ time steps. $\square$

Proposition 10 shows that there exist specific conditions under which MBNs built on BNs belonging to $\mathrm{FP_c}[00, 01]$ evolve towards a limit cycle.

Proposition 10. *For all the BNs of $\mathrm{FP_c}[00, 01]$, there exist delay vectors dts such that any associated MBN admits a limit cycle.*

Proof. Consider BN $[6, 00, 01]$. Let us consider two cases for α and begin with $\alpha > 1$. The different possible evolutions are: if $\rho \geq 1, \gamma \geq 1$ then $(\rho, \gamma) \xrightarrow{\gamma} (\alpha, 0) \to (\alpha - 1, \beta) \to (\alpha, \beta - 1) \xrightarrow{\beta - 1} (\alpha, 0)$, which emphasizes a limit cycle of length $\beta + 1$; if $\rho > 1, \gamma = 0$ then $(\rho, 0) \to (\rho - 1, \beta) \to (\alpha, \beta - 1) \xrightarrow{\beta - 1} (\alpha, 0)$ that belongs to a limit cycle of length $\beta + 1$; if $\rho = 1, \gamma = 0$ then $(1, 0) \to (0, \beta) \circlearrowleft$. Now, consider that $\alpha = 1$. The different possible evolutions are: if $\rho = 1, \gamma = 0$ then $(1, 0) \to (0, \beta) \circlearrowleft$; if $\rho = 1, \gamma \geq 1$ then $(1, \gamma) \xrightarrow{\gamma} (1, 0) \to (0, \beta) \circlearrowleft$ and reaches its fixed point in $\gamma + 1$ time steps.

x	[1, 00, 11]	[2, 00, 11]	[3, 00, 11]	[4, 00, 11]	[5, 00, 11]	[6, 00, 11]	[7, 00, 11]	[8, 00, 11]	[9, 00, 11]
00	00	00	00	00	00	00	00	00	00
01	00	00	00	10	10	10	11	11	11
10	00	01	11	00	01	11	00	01	11
11	11	11	11	11	11	11	11	11	11

Table 4: Truth tables of all the 9 BNs that admit fixed points $(0, 0)$ and $(1, 1)$.

Thus, the MBNs built on BN $[6, 00, 01]$ converge to their fixed points in at most $\beta + 1$ time steps and can admit a limit cycle of length $\beta + 1$.

Now, consider BN $[7, 00, 01]$. Let us consider three cases depending on the initial configuration (ρ, γ). First, if $\rho > \gamma$, we have: if $\alpha > \beta$ then $(\rho, \gamma) \xrightarrow{\gamma} (\rho - \gamma, 0) \to (\alpha, \beta) \xrightarrow{\beta} (\alpha - \beta, 0) \to (\alpha, \beta)$, which emphasizes a limit cycle of length $\beta + 1$; if $\alpha < \beta$ then $(\rho, \gamma) \xrightarrow{\gamma} (\rho - \gamma, 0) \to (\alpha, \beta) \xrightarrow{\alpha} (0, \beta - \alpha) \to (0, \beta) \circlearrowleft$, and reaches its fixed point in $\alpha + \gamma + 2$ time steps; if $\alpha = \beta$ then $(\rho, \gamma) \xrightarrow{\gamma} (\rho - \gamma, 0) \to (\alpha, \alpha) \xrightarrow{\alpha} (0, 0) \circlearrowleft$, and reaches its fixed point in $\alpha + \gamma + 1$ time steps. Now, whatever dt is: if $\rho < \gamma$ then $(\rho, \gamma) \xrightarrow{\rho} (0, \gamma - \rho) \to (0, \beta) \circlearrowleft$, and reaches its fixed point in $\rho + 1$ time steps; if $\rho = \gamma$ then $(\rho, \rho) \xrightarrow{\rho} (0, 0) \circlearrowleft$, and reaches its fixed point in ρ time steps. Thus, the MBNs built on BN $[7, 00, 01]$ converge to their fixed points in at most $\alpha + \beta + 2$ time steps and can admit a limit cycle of length $\beta + 1$. □

Proposition 11 shows the same principle for $[0, 00, 01] \in \mathrm{LC}[00, 01]$.

Proposition 11. *Considering* $[9, 00, 01]$ *the unique element of* $\mathrm{FP_c}[00, 01]$, *for all delay vectors dt, there exist initial conditions such that any associated MBN admits a limit cycle.*

Proof. Consider any dt and an initial configuration such that $\rho \geq 1$. We have: if $\gamma = 0$ then $(\rho, 0) \to (\alpha, \beta) \xrightarrow{\beta} (\alpha, 0) \to (\alpha, \beta)$, which emphasizes a limit cycle of length $\beta + 1$; if $\gamma \geq 1$ then $(\rho, \gamma) \xrightarrow{\gamma} (\alpha, \beta)$ that belongs to a limit cycle of length $\beta + 1$. Thus, the MBNs built on BN $[9, 00, 01]$ converge to their fixed points in at most 1 time step and can admit a limit cycle of length $\beta + 1$. □

3.2.2 MBNs based on F[00, 11]

The class of BNs F[00, 11] does not admit a symmetric class and what follows gives a characterization of the dynamics of MBNs built on it.

Remark 2. *For every network of* F[00, 11]*, since* (0, 0) *and* (1, 1) *are fixed points, whatever* α *and* β *are, configuration* (0, 0) *cannot change, admits the following trajectory* (0, 0) $\circlearrowleft$ *and is a fixed point, and any initial configuration such that* $\rho \geq 1$ *and* $\gamma \geq 1$ *admits the following trajectory* $(\rho, \gamma) \rightarrow (\alpha, \beta)$ $\circlearrowleft$ *that leads to fixed point* (α, β).

Therefore we analyze the dynamical behavior of all the initial configurations of the form $(0, \gamma)$ where $\gamma \neq 0$ and $(\rho, 0)$ where $\rho \neq 0$. From Table 4, a basic enumeration gives that FP[00, 11] = F[00, 11] \ {[5, 00, 11]}, and LC[00, 11] = {[5, 00, 11]}. Proposition 12 below shows that all the MBNs built on BNs of FP[00, 11] converge towards fixed points (0, 0) and (α, β) that are the only attractors.

Proposition 12. *For any delay vector dt, every MBN built on a BN that belongs to* FP[00, 11] *admits only two attractors, fixed points* (0, 0) *and* (α, β).

Proof. First, from Table 4, it derives that network [1, 00, 11] (resp. [9, 00, 11]) is decreasing (resp. increasing). So, from Proposition 3, any MBN based on it (resp. on [9, 00, 11]) converges towards its two fixed points (0, 0) and (α, β). It does so in at most max(α, β) time steps (resp. 1 time step).

Furthermore, the interaction graph of network [3, 00, 11] (resp. [7, 00, 11] by symmetry) is acyclic. So, from Proposition 2, any MBN based on it (resp. on [7, 00, 11]) converges towards the two fixed points and it does so in at most β (resp. α) time steps.

Moreover, it is easy to see also that network [6, 00, 11] (resp. [8, 00, 11] by symmetry) is a positive disjunctive BN. So, from Proposition 1, any MBN based on it (resp. based on [8, 00, 11]) converges towards the two fixed points. It does so in at most $\beta + 1$ (resp. $\alpha + 1$ and 1) time steps.

Let us now focus on the MBNs built on BN [2, 00, 11], given any delay vector *dt*. We have: if $\rho = 0$ and $\gamma \geq 1$ then $(0, \gamma) \xrightarrow{\gamma} (0, 0)$ $\circlearrowleft$ that is a fixed point reached in γ time steps; if $\rho = 1$ and $\gamma = 0$ then $(1, 0) \rightarrow (0, \beta) \xrightarrow{\beta} (0, 0)$ $\circlearrowleft$ that is a fixed point reached in $\beta + 1$ time steps; if $\rho > 1$ and $\gamma = 0$ then $(\rho, 0) \rightarrow (\rho - 1, \beta) \rightarrow (\alpha, \beta)$ $\circlearrowleft$ that is a fixed point reached in 2 time steps. So, every MBN based on BN [2, 00, 11] (resp. on BN [4, 00, 11] by symmetry) admits only two attractors, fixed points (0, 0) and (α, β), and its convergence time is at most $\beta + 1$ (resp. $\alpha + 1$) time steps. $\qquad\square$

Now, Proposition 13 shows that there exist specific conditions under which MBNs built on BN [5, 00, 11] of LC[00, 11] evolve towards a limit cycle.

Proposition 13. *The only MBN built on BN* $[5,00,11]$ *that admits a limit cycle is set with* $\alpha = \beta = 1$, *i.e.* *BN* $[5,00,11]$ *itself.* *Any other MBN built* $[5,00,11]$ *admits only two attractors, fixed points* $(0,0)$ *and* (α,β).

Proof. When $\alpha = \beta = 1$, the dynamics of this MBN is trivially the same as that of BN $[5,00,11]$. The network admit three attractors, fixed points $(0,0)$ and $(1,1)$ and limit cycle $(0,1) \leftrightarrows (1,0)$. Now, let us consider MBNs such that $\alpha > 1$ or $\beta > 1$. We have: if $\alpha > 1$ and $\rho \geq 2$ then $(\rho,0) \to (\rho-1,\beta) \to (\alpha,\beta) \circlearrowright$; if $\rho = 1$ and $\beta > 1$ then $(1,0) \to (0,\beta) \to (\alpha,\beta-1) \to (\alpha,\beta) \circlearrowright$; if $\beta > 1$ and $\gamma \geq 2$ then $(0,\gamma) \to (\alpha,\gamma-1) \to (\alpha,\beta) \circlearrowright$; if $\gamma = 1$ and $\alpha > 1$ then $(0,1) \to (\alpha,0) \to (\alpha-1,\beta) \to (\alpha,\beta) \circlearrowright$. Hence, only the MBN that is BN $[5,00,11]$ itself can admit a limit cycle of length 2. All the others converge towards $(0,0)$ and (α,β) in at most 3 time steps. $\qquad\square$

3.2.3 MBNs based on $\mathrm{F}[01,10]$

As $\mathrm{F}[00,11]$, the class of BNs $\mathrm{F}[01,10]$ does not admit a symmetric class and what follows gives a characterization of the dynamics of MBNs built on it.

Remark 3. *For every network of* $\mathrm{F}[01,10]$, *since* $(0,1)$ *and* $(1,0)$ *are fixed points, whatever* α *and* β *are, we have: if* $\rho \geq 1$ *and* $\gamma = 0$ *then* $(\rho,0) \to (\alpha,0) \circlearrowright$ *that is a fixed point, and conversely, if* $\rho = 0$ *and* $\gamma \geq 1$ *then* $(0,\gamma) \to (0,\beta) \circlearrowright$ *that is a fixed point.*

Therefore we analyze the dynamical behavior of all the initial configurations of the form $(0,0)$ and (ρ,γ) where $\rho,\gamma \neq 0$. From Table 5, a basic enumeration gives that $\mathrm{FP}[01,10] = \mathrm{F}[01,10] \setminus \{[7,01,10]\}$, and $\mathrm{LC}[01,10] = \{[7,01,10]\}$. Proposition 14 below shows that all the MBNs built on BNs of $\mathrm{FP}[01,10]$ converge towards fixed points $(0,\beta)$ and $(\alpha,0)$ that are the only attractors.

Proposition 14. *For any delay vector dt, every MBN built on a BN that belongs to* $\mathrm{FP}[01,10]$ *admits only two attractors, fixed points* $(0,\beta)$ *and* $(\alpha,0)$.

x	$[1,01,10]$	$[2,01,10]$	$[3,01,10]$	$[4,01,10]$	$[5,01,10]$	$[6,01,10]$	$[7,01,10]$	$[8,01,10]$	$[9,01,10]$
00	01	01	01	10	10	10	11	11	11
01	01	01	01	01	01	01	01	01	01
10	10	10	10	10	10	10	10	10	10
11	00	01	10	00	01	10	00	01	10

Table 5: Truth tables of all the 9 BNs that admit fixed points $(0,1)$ and $(1,0)$.

Proof. First of all, let us focus on BN $[3, 01, 10]$. Its interaction graph does not induce cycles except one positive loop. So, by Proposition 2, any MBN built on it only admit fixed points. More precisely, whatever α and β are, configuration $(0, 0)$ converges towards $(0, \beta)$ in 1 time step. Any other configuration such that $\rho, \gamma \geq 1$ admits the following trajectory: $(\rho, \gamma) \rightarrow (\alpha, \gamma - 1) \xrightarrow{\gamma - 1} (\alpha, 0) \circlearrowleft$ that is reached in γ time steps. Thus, any MBN built on BN $[3, 01, 10]$ (resp. on BN $[5, 01, 10]$ by symmetry) converges towards two attractors, fixed points $(0, \beta)$ and $(\alpha, 0)$, and does so in at most β (resp. α) time steps.

Now, consider BN $[1, 01, 10]$. If $\rho > \gamma$ then the trajectory is $(\rho, \gamma) \xrightarrow{\gamma} (\rho - \gamma, 0) \rightarrow (\alpha, 0) \circlearrowleft$ that is reached in $\gamma + 1$ time steps. Conversely, if $\rho \leq \gamma$ then the trajectory is $(\rho, \gamma) \xrightarrow{\rho} (0, \gamma - \rho) \rightarrow (0, \beta)$ that is reached in $\rho + 1$ time steps. Thus, any MBN built on BN $[1, 01, 10]$ (resp. on BN $[4, 01, 10]$ by symmetry) converges towards two attractors, fixed points $(0, \beta)$ and $(\alpha, 0)$, and does so in at most $\max(\alpha, \beta) + 1$ time steps.

Concerning BN $[2, 01, 10]$, for all delay vector dt, $(0, 0)$ converges towards $(0, \beta)$ in one time step. Any other initial configuration (ρ, γ) such that $\rho, \gamma \geq 1$ admits the following trajectory: $(\rho, \gamma) \rightarrow (\rho - 1, \beta) \xrightarrow{\rho - 1} (0, \beta) \circlearrowleft$ that is reached in at most ρ time steps. Thus, any MBN built on BN $[2, 01, 10]$ (resp. on BN $[6, 01, 10]$ by symmetry) converges towards two attractors, fixed points $(0, \beta)$ and $(\alpha, 0)$, and does so in at most α (resp. β) time steps.

Lastly, concerning BN $[8, 01, 10]$, for all delay vector dt, $(0, 0)$ admits the following trajectory: $(0, 0) \rightarrow (\alpha, \beta) \xrightarrow{\alpha} (0, \beta) \circlearrowleft$ that is reached in $\alpha + 1$ time steps. Any other initial configuration (ρ, γ) such that $\rho, \gamma \geq 1$ admits the following trajectory: $(\rho, \gamma) \rightarrow (\rho - 1, \beta) \xrightarrow{\rho - 1} (0, \beta) \circlearrowleft$ that is reached in ρ time steps. Thus, any MBN built on BN $[8, 01, 10]$ (resp. on BN $[9, 01, 10]$ by symmetry) converges towards two attractors, fixed points $(0, \beta)$ and $(\alpha, 0)$, and does so in at most $\alpha + 1$ (resp. $\beta + 1$) time steps. $\square$

Now, Proposition 15 shows that there exist specific conditions under which MBNs built on BN $[7, 01, 10]$ of LC$[01, 10]$ evolve towards a limit cycle.

Proposition 15. *Every MBN built on BN $[7, 01, 10]$ with $\alpha = \beta$ admits a limit cycle. Any other admits only $(0, \beta)$ and $(\alpha, 0)$ as its unique attractors.*

Proof. Consider first that $\alpha = \beta$ and that $\rho = \gamma$. Then we have: $(\rho, \rho) \xrightarrow{\rho} (0, 0) \rightarrow (\alpha, \alpha) \xrightarrow{\alpha} (0, 0)$, which emphasizes a limit cycle of length α. Now, consider that $\alpha \neq \beta$ and that $\rho = \gamma$. We have the following trajectory: if $\alpha > \beta$ then $(\rho, \rho) \xrightarrow{\rho} (0, 0) \rightarrow (\alpha, \beta) \xrightarrow{\beta} (\alpha - \beta, 0) \rightarrow (\alpha, 0) \circlearrowleft$ that is

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x	$[1,01,11]$	$[2,01,11]$	$[3,01,11]$	$[4,01,11]$	$[5,01,11]$	$[6,01,11]$	$[7,01,11]$	$[8,01,11]$	$[9,01,11]$
00	01	01	01	10	10	10	11	11	11
01	01	01	01	01	01	01	01	01	01
10	00	01	11	00	01	11	00	01	11
11	11	11	11	11	11	11	11	11	11

x	$[1,10,11]$	$[2,10,11]$	$[3,10,11]$	$[4,10,11]$	$[5,10,11]$	$[6,10,11]$	$[7,10,11]$	$[8,10,11]$	$[9,10,11]$
00	01	01	01	10	10	10	11	11	11
01	00	10	11	00	10	11	00	10	11
10	10	10	10	10	10	10	10	10	10
11	11	11	11	11	11	11	11	11	11

Table 6: Truth tables of all the 9 BNs that admit (up) fixed points $(0,1)$ and $(1,1)$ and (down) fixed points $(1,0)$ and $(1,1)$.

reached in $\rho + \beta + 2$ time steps; if $\alpha < \beta$ then $(\rho,\rho) \xrightarrow{\rho} (0,0) \to (\alpha,\beta) \xrightarrow{\alpha} (0, \beta - \alpha) \to (0, \beta) \circlearrowleft$ that is reached in $\rho + \alpha + 2$ time steps. The last case to consider is when $\rho \neq \gamma$ whatever α and β, for which we have: if $\rho > \gamma$ then $(\rho, \gamma) \xrightarrow{\gamma} (\rho - \gamma, 0) \to (\alpha, 0) \circlearrowleft$ that is reached in $\gamma + 1$ time steps; if $\rho < \gamma$ then $(\rho, \gamma) \xrightarrow{\rho} (0, \gamma - \rho) \to (0, \beta) \circlearrowleft$ that is reached in $\rho + 1$ time steps. Hence, when built on BN $[7, 01, 10]$, only MBNs such that $\alpha = \beta$ admit a limit cycle of length α that can only be reached by configurations such that $\rho = \gamma$. All the others converge only towards $(0,0)$ and (α, β) in at most $\alpha + \max(\alpha, \beta) + 2$ time steps. □

3.2.4 MBNs based on $F[01, 11]$ and $F[10, 11]$

Concerning the classes of BNs $F[01, 11]$ and $F[10, 11]$, notice first that they are symmetric. Thus, the results obtained for $F[01, 11]$ have their symmetric that hold for $F[10, 11]$. So, let us focus only on $F[01, 11]$.

Remark 4. *For every network of* $F[01, 11]$*, since* $(0,1)$ *and* $(1,1)$ *are fixed points, whatever* α *and* β *are, configurations* $(0, \gamma)$*, with* $\gamma \geq 1$*, converge towards* $(0, \beta)$ *in one time step, and any initial configuration such that* $\rho \geq 1$ *and* $\gamma \geq 1$ *converges towards* (α, β) *in one time step.*

Therefore we analyze the dynamical behavior of all the initial configurations of the form $(\rho, 0)$, where $\rho \geq 0$. From Table 6 (up), a basic enumeration gives that $FP[00, 01] = F[00, 01] \setminus \{[4, 00, 01]\}$, and $LC[00, 01] = \{[4, 00, 01]\}$. Proposition 16 below shows that all the MBNs built on BNs of $FP[01, 11]$ converge towards fixed points $(0, \beta)$ and (α, β) that are the only attractors.

Proposition 16. *For any delay vector dt, every MBN built on a BN that belongs to* $FP[01, 11]$ *admits only two attractors, fixed points* $(0, \beta)$ *and* (α, β).

Proof. First of all, consider BNs $[3, 01, 11]$, $[6, 01, 11]$ and $[9, 01, 11]$ that are increasing according to their definition. So, by Proposition 3, all of the MBNs built on them admit only fixed points.

Concerning MBNs built on $[3, 01, 11]$, whatever α and β are, configuration $(0, 0)$ converges towards $(0, \beta)$ in 1 time step. Any other configuration such that $(\rho, 0)$, with $\rho \geq 1$, admits the following trajectory: $(\rho, 0) \to (\alpha, \beta) \circlearrowleft$ that is reached in 1 time step. Thus, any MBN built on BN $[3, 01, 11]$ admits only two attractors, fixed points $(0, \beta)$ and (α, β), and converge to them in at most 2 time steps.

Concerning MBNs built on $[6, 01, 11]$, whatever α and β are, configuration $(0, 0)$ becomes $(\alpha, 0)$ in one time step. Moreover, any configuration $(\rho, 0)$, with $1 \leq \rho \leq \alpha$, converges towards (α, β) in one time step. Thus, any MBN built on BN $[6, 01, 11]$ admits only two attractors, fixed points $(0, \beta)$ and (α, β), and converge to them in at most 2 time steps.

Concerning MBNs built on $[9, 01, 11]$, whatever α and β are, any configuration such that $(\rho, 0)$, with $\rho \geq 0$ converges towards (α, β) in 1 time step. So, such networks admit only two attractors, fixed points $(0, \beta)$ and (α, β), and converge to them in at most 1 time step.

Now, let us focus on BN $[2, 01, 11]$. Its interaction graph does not induce cycles except one positive loop. So, by Proposition 2, any MBN built on such a BN only admits fixed points. More precisely, whatever α and β are, configurations $(0, 0)$ and $(1, 0)$ converge towards $(0, \beta)$ in 1 time step. Any other configuration such that $(\rho, 0)$, with $\rho \geq 2$, admits the following trajectory: $(\rho, 0) \to (\rho - 1, \beta) \to (\alpha, \beta) \circlearrowleft$ that is reached in 2 time steps. Thus, any MBN built on BN $[2, 01, 11]$ admits only two attractors, fixed points $(0, \beta)$ and (α, β), and converge to them in at most 2 time steps.

Let us focus on BN $[1, 01, 11]$. Whatever α and β are, any configuration $(\rho, 0)$, with $\rho \geq 0$, admits the following trajectory: $(\rho, 0) \xrightarrow{\rho} (0, 0) \to (0, \beta) \circlearrowleft$ that is reached in $\rho + 1$ time steps. Thus, any MBN built on BN $[1, 01, 11]$ admits only two attractors, fixed points $(0, \beta)$ and (α, β), and converge to them in at most $\alpha + 1$ time steps.

Consider BN $[5, 01, 11]$. Whatever α and β are, configuration $(1, 0)$ converges towards $(0, \beta)$ in 1 time step. Configuration $(0, 0)$ follows the trajectory $(0, 0) \to (\alpha, 0) \to (\alpha - 1, \beta) \to (\alpha, \beta) \circlearrowleft$ that is reached in 3 time steps. Any other configuration such that $(\rho, 0)$, with $\rho \geq 2$, admits the following trajectory: $(\rho, 0) \to (\rho - 1, \beta) \to (\alpha, \beta) \circlearrowleft$ thay is reached in 2 time steps. Thus, any MBN built on BN $[5, 01, 11]$ admits only two attractors, fixed points $(0, \beta)$ and (α, β), and converge to them in at most 3 time steps.

Consider BN $[7, 01, 11]$. Whatever α and β are, any configuration $(\rho, 0)$,

with $\rho \geq 0$, admits the following trajectory: $(\rho, 0) \xrightarrow{\rho} (0,0) \to (\alpha, \beta) \circlearrowleft$ that is reached in $\rho + 1$ time steps. Thus, any MBN built on BN $[7, 01, 11]$ admits only two attractors, fixed points $(0, \beta)$ and (α, β), and converge to them in at most $\alpha + 1$ time steps.

Let us finally focus on BN $[8, 01, 11]$. Whatever α and β are, configuration $(0,0)$ (resp. $(1,0)$) converges towards (α, β) (resp. $(0, \beta)$) in 1 time step. Any other configuration such that $(\rho, 0)$, with $\rho \geq 2$, admits the following trajectory: $(\rho, 0) \to (\rho - 1, \beta) \to (\alpha, \beta) \circlearrowleft$ that is reached in 2 time steps. Thus, any MBN built on BN $[8, 01, 11]$ admits only two attractors, fixed points $(0, \beta)$ and (α, β), and converge to them in at most 2 time steps. $\square$

Now, Proposition 17 shows that there exist specific conditions under which MBNs built on BN $[4, 01, 11]$ of LC$[01, 11]$ evolve towards a limit cycle.

Proposition 17. *Every MBN built on BN $[4, 01, 10]$ admits a limit cycle that is reached by any configuration $(\rho, 0)$, with $0 \leq \rho \leq \alpha$.*

Proof. First, let us consider any configuration $(\rho, 0)$, with $\rho \geq 0$. Such a configuration follows the trajectory $(\rho, 0) \xrightarrow{\rho} (0,0) \to (\alpha, 0) \to (\alpha - 1, 0) \xrightarrow{\alpha - 1} (0,0)$, which emphasizes a limit cycle of length α composed of all the configurations $(\rho, 0)$. Thus, any MBN built on BN $[4, 01, 10]$ admits three attractors, the two fixed points $(0, \beta)$ and (α, β) that are reached in 1 time step, and a limit cycle of length α. $\square$

3.3 Networks admitting three fixed points

In this section, we focus on the MBNs that can be built on the basis of BNs of size 2 that admit three fixed points. First of all, let us notice that there exist 4 distinct classes of such networks, each of which being composed of 3 networks. As what has been presented above, let us introduce the following notations.

Notation 4. $[k, x, y, z]$, *with $k \in \{1, \ldots, 3\}$ and $x, y, z \in \mathbb{B}^2$, denotes the network of size 2 whose local transition functions are represented by k and defined by their truth tables in Tables 7 and 8, and that admits x, y and z as its fixed points (represented as binary words).*

Let us also denote by F$[x, y, z]$ the set composed of all BNs that admit x, y and z as their unique fixed points.

MBNs based on F[00, 01, 10] **and** F[01, 10, 11]

Concerning the classes of BNs F[00, 01, 10] and F[01, 10, 11], notice first that they are symmetric. Thus, all the results obtained for F[00, 01, 10] have their symmetric that hold for F[01, 10, 11]. So, let us focus only on F[00, 01, 10].

Remark 5. *For every network of* F[00, 01, 10]*, since* $(0,0)$*,* $(0,1)$ *and* $(1,0)$ *are fixed points, whatever* α *and* β *are, we have: if* $\rho = \gamma = 0$ *then there is trivially convergence towards fixed point* $(0,0)$*; if* $\rho = 0$ *and* $\gamma \geq 1$ *then* $(0, \gamma) \rightarrow (0, \beta)$ ↺ *that is a fixed point; if* $\rho \geq 1$ *and* $\gamma = 0$ *then* $(\rho, 0) \rightarrow (\alpha, 0)$ ↺ *that is a fixed point.*

Therefore, we analyze the dynamical behavior of all the initial configurations of the form (ρ, γ), where $\rho \geq 1$ and $\gamma \geq 1$. Proposition 18 below shows that all the MBNs built on BNs of F[00, 01, 10] converge towards fixed points $(0,0)$, $(0, \beta)$ and $(\alpha, 0)$ that are the only attractors.

x	[1, 00, 01, 10]	[2, 00, 01, 10]	[3, 00, 01, 10]	x	[1, 01, 10, 11]	[2, 01, 10, 11]	[3, 01, 10, 11]
00	00	00	00	00	01	10	11
01	01	01	01	01	01	01	01
10	10	10	10	10	10	10	10
11	00	01	10	11	11	11	11

(a)	(b)

Table 7: (a) Truth tables of all the 3 BNs that admit fixed points $(0,0)$, $(0,1)$ and $(1,0)$; (b) Truth tables of all the 3 BNs that admit fixed points $(0,1)$, $(1,0)$ and $(1,1)$.

Proposition 18. *For any delay vector dt, every MBN built on a BN that belongs to* F[00, 01, 10] *admits only three attractors, fixed points* $(0,0)$*,* $(0, \beta)$ *and* $(\alpha, 0)$*.*

Proof. Consider first BN [1, 00, 01, 10]. Whatever α and β are, given $\rho \geq 1$ and $\gamma \geq 1$, we have: if $\rho < \gamma$ then $(\rho, \gamma) \xrightarrow{\rho} (0, \gamma - \rho) \rightarrow (0, \beta)$ ↺ that is reached in $\rho + 1$ time steps; if $\rho > \gamma$ then $(\rho, \gamma) \xrightarrow{\gamma} (\rho - \gamma, 0) \rightarrow (\alpha, 0)$ ↺ that is reached in $\gamma + 1$ time steps; if $\rho = \gamma$ then $(\rho, \rho) \xrightarrow{\rho} (0, 0)$ ↺ that is reached in ρ time steps. Thus, any MBN built on BN [1, 00, 01, 10] admits three attractors, fixed points $(0,0)$, $(0, \beta)$ and $(\alpha, 0)$ that are reached in at most $\max(\alpha, \beta) + 1$ time steps.

Concerning BN [2, 00, 01, 10], whatever α and β are, any initial configuration such that $\rho \geq 1$ and $\gamma \geq 1$ admits the following trajectory: $(\rho, \gamma) \rightarrow (\rho -$

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$1, \beta) \xrightarrow{\rho-1} (0, \beta) \circlearrowleft$ that is reached in ρ time steps. Thus, any MBN built on BN $[2, 00, 01, 10]$ (resp. on BN $[3, 00, 01, 10]$ by symmetry) admits three attractors, fixed points $(0, 0)$, $(0, \beta)$ and $(\alpha, 0)$, and converges to them in at most α (resp. β) time steps. $\square$

MBNs based on F$[00, 01, 11]$ **and** F$[00, 10, 11]$

Concerning the classes of BNs F$[00, 01, 11]$ and F$[00, 10, 11]$, notice first that they are symmetric. Thus, all the results obtained for F$[00, 01, 11]$ have their symmetric that hold for F$[00, 10, 11]$. So, let us focus only on F$[00, 01, 11]$.

Remark 6. *For every network of* F$[00, 01, 11]$, *since* $(0, 0)$, $(0, 1)$ *and* $(1, 1)$ *are fixed points, whatever* α *and* β *are, we have: if* $\rho = \gamma = 0$ *then there is trivially convergence towards fixed point* $(0, 0)$; *if* $\rho = 0$ *and* $\gamma \geq 1$ *then* $(0, \gamma) \to (0, \beta) \circlearrowleft$ *that is a fixed point; if* $\rho \geq 1$ *and* $\gamma \geq 1$ *then* $(\rho, \gamma) \to (\alpha, \beta) \circlearrowleft$ *that is a fixed point.*

Therefore, we analyze the dynamical behavior of all the initial configurations of the form (ρ, γ), where $\rho \geq 1$ and $\gamma = 0$. Proposition 19 below shows that all the MBNs built on BNs of F$[00, 01, 11]$ converge towards fixed points $(0, 0)$, $(0, \beta)$ and (α, β) that are the only attractors.

Proposition 19. *For any delay vector dt, every MBN built on a BN that belongs to* F$[00, 01, 11]$ *admits only three attractors, fixed points* $(0, 0)$, $(0, \beta)$ *and* (α, β).

Proof. Consider first BN $[1, 00, 01, 11]$. Whatever α and β are, given $\rho \geq 1$ and $\gamma = 0$, configuration $(\rho, 0)$ admits the following trajectory: $(\rho, 0) \to (\rho - 1, 0) \xrightarrow{\rho-1} (0, 0) \circlearrowleft$ that is reached in ρ time steps. Thus, any MBN built on BN $[1, 00, 01, 11]$ admits three attractors, fixed points $(0, 0)$, $(0, \beta)$ and (α, β) that are reached in at most α time steps.

Concerning BN $[2, 00, 01, 11]$, whatever α and β are, given $\rho \geq 1$ and $\gamma = 0$, we have: if $\rho = 1$ then $(1, 0) \to (0, \beta) \circlearrowleft$ that is reached in 1 time step; if $\rho > 1$ then $(\rho, 0) \to (\rho - 1, \beta) \to (\alpha, \beta) \circlearrowleft$ that is reached in 2 time steps. Thus, any MBN built on BN $[2, 00, 01, 11]$ admits three attractors, fixed points $(0, 0)$, $(0, \beta)$ and (α, β) that are reached in at most 2 time steps.

Concerning BN $[3, 00, 01, 11]$, whatever α and β are, given $\rho \geq 1$ and $\gamma = 0$, any configuration $(\rho, 0)$ converges towards (α, β) in 1 time step. $\square$

To conclude on this theoretical analysis, let us simply add that it is trivial to show that MBNs of size 2 that are built on the only BN with 4 fixed

x	$[1, 00, 01, 11]$	$[2, 00, 01, 11]$	$[3, 00, 01, 11]$
00	00	00	00
01	01	01	01
10	00	01	11
11	11	11	11

(a)

x	$[1, 00, 10, 11]$	$[2, 00, 10, 11]$	$[3, 00, 10, 11]$
00	00	00	00
01	00	10	11
10	10	10	10
11	11	11	11

(b)

Table 8: (a) Truth tables of all the 3 BNs that admit fixed points $(0,0)$, $(0,1)$ and $(1,1)$; (b) Truth tables of all the 3 BNs that admit fixed points $(0,0)$, $(1,0)$ and $(1,1)$.

points cannot admit limit cycle. Their attractors are fixed points $(0,0)$, $(\alpha,0)$, $(0,\beta)$ and (α,β). Furthermore, as it could have been predicted, the more BNs admit degree of freedom (*i.e.* the less they admit fixed points), the more MBNs built on them may have complex behaviors. Eventually, as it has been highlighted in [22, 23], this section has formally shown that, for networks of size 2, higher delays results in longer limit cycles. However, it has also been shown that it is not true in general that the more the maximum delay value, the less the network admits attractors. Indeed, we have seen that this property holds in some cases but that there exist also networks for which increasing delays can create limit cycles asymptotically.

4 Application to specific genetic regulation networks

4.1 Immunity control in bacteriophage λ

In [48], Thieffry and Thomas proposed a logical model based on the Thomas' method [45, 47, 46] in order to analyze and achieve a better understanding of the role that specific genes have in the decision between lysis and lysogenization in bacteriophage λ. Notably, they first introduced an interaction graph, composed of four genes cI, cII, cro and N, that they voluntarily simplified in a two-genes model in order to focus especially on the interactions existing between cI and cro. Without entering neither into the details of the Thomas' method nor into those of the model itself (they can be obtained in the original paper), let us just give in Figure 7 the main static and dynamical features of the latter, in which we can see that the chosen modeling is not in the Boolean setting but in a discrete one. Indeed, although gene cI is associated with a Boolean variable, gene cro is associated

with a variable taking values into $\{0, 1, 2\}$. In this modeling, the network converges towards two attractors, a stable configuration $(1, 0)$, whose corresponding expression pattern is cI expressed and cro inhibited that stands for the bacterium lysing, and a stable oscillation $(0, 1) \leftrightarrows (0, 2)$ that stand for the bacterium becoming lysogenic.

From this model, considering that when gene cro is at its maximum expression level, it inevitably tends to decrease to its medium expression level whatever that of cI, it is trivial to reduce this model into the Boolean setting by merging states 1 and 2 of cro, without loss of qualitative information from the biological standpoint because two attractors are conserved exactly, through the two stable configurations $(1, 0)$ and $(0, 1)$. Hence, from Figure 7.b, it is easy to obtain the truth table of the Boolean local transition functions of cI and cro and consequently the associated BN. Then, we can obviously build the related interaction and transitions graphs (see Figure 8). Now, considering this network set in the MBN context, we obtain Theorem 2 below.

Theorem 2. *Any MBN built on the BN of the immunity control of the bacteriophage λ admits fixed points $(dt_{\mathrm{cI}}, 0)$ and $(0, dt_{\mathrm{cro}})$. Only those such that $dt_{\mathrm{cI}} = dt_{\mathrm{cro}}$ can admit a limit cycle of length dt_{cI}.*

Proof. First, for all dt_{cI} and dt_{cro} and initial configurations such that $\rho \neq \gamma$, we have: if $\rho > \gamma$ then $(\rho, \gamma) \xrightarrow{\gamma} (\rho - \gamma, 0) \rightarrow (dt_{\mathrm{cI}}, 0) \circlearrowright$ that is reached in at most dt_{cro} time steps, and if $\rho < \gamma$ then $(\rho, \gamma) \xrightarrow{\rho} (0, \gamma - \rho) \rightarrow (0, dt_{\mathrm{cro}}) \circlearrowright$ that is reached in at most dt_{cI} time steps. Now, let us consider that $\rho = \gamma$

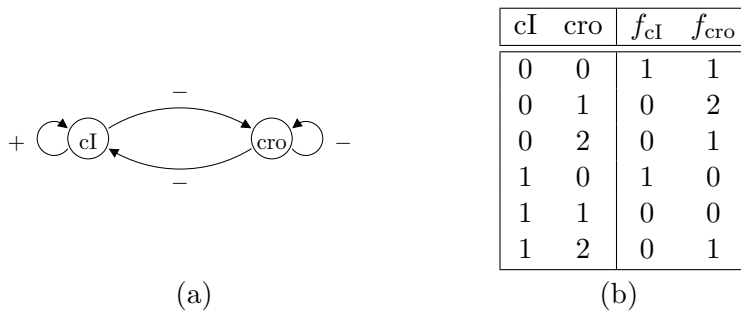| cI	cro	f_{cI}	f_{cro}
0	0	1	1
0	1	0	2
0	2	0	1
1	0	1	0
1	1	0	0
1	2	0	1

(a) (b)

Figure 7: (a) Interaction graph of the gene regulation network implying genes cI and cro in the immunity control of the bacteriophage λ introduced in [48]; (b) Table presenting the dynamical behavior of this network inferred from the phase diagram given by Thieffry and Thomas.

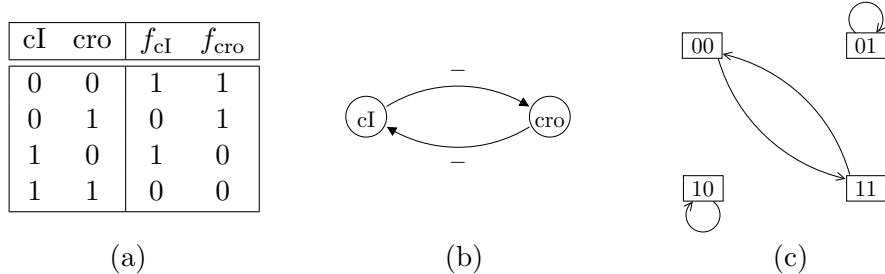| cI	cro	f_{cI}	f_{cro}
0	0	1	1
0	1	0	1
1	0	1	0
1	1	0	0

(a)　　　　　　　　　　(b)　　　　　　　　　　(c)

Figure 8: (a) Truth table of the Boolean local transition functions of cI and cro inferred from the Thomas' model of the immunity control of the bacteriophage λ; (b) Related interaction graph; (c) Related transition graph.

and compute its trajectory depending on dt_{cI} and dt_{cro}:

- if $dt_{\mathrm{cI}} = dt_{\mathrm{cro}}$ then $(\rho, \rho) \to (\rho - 1, \rho - 1) \xrightarrow{\rho-1} (0,0) \to (\rho, \rho)$, which emphasizes a limit cycle of length dt_{cI}.

- if $dt_{\mathrm{cI}} > dt_{\mathrm{cro}}$ then $(\rho, \rho) \xrightarrow{\rho} (0,0) \to (dt_{\mathrm{cI}}, dt_{\mathrm{cro}}) \xrightarrow{dt_{\mathrm{cro}}} (dt_{\mathrm{cI}} - dt_{\mathrm{cro}}, 0) \to (dt_{\mathrm{cI}}, 0) \circlearrowleft$ that is reached in at most $2dt_{\mathrm{cro}} + 2$ time steps.

- if $dt_{\mathrm{cI}} < dt_{\mathrm{cro}}$ then $(\rho, \rho) \xrightarrow{\rho} (0,0) \to (dt_{\mathrm{cI}}, dt_{\mathrm{cro}}) \xrightarrow{dt_{\mathrm{cro}}} (0, dt_{\mathrm{cro}} - dt_{\mathrm{cI}}) \to (0, dt_{\mathrm{cro}}) \circlearrowleft$ that is reached in at most $2dt_{\mathrm{cI}} + 2$ time steps.

$\square$

Remark 7. *As Theorem 2 states, in the case where $dt_{\mathrm{cI}} = dt_{\mathrm{cro}}$ and $\alpha = \beta$, the behavior of the network evolves towards a limit cycle. This limit cycle is a spurious asymptotic behavior induced by the perfect synchronicity created by both the parallel updating mode and the equality of all the control parameters dt_{cI}, dt_{cro}, α and β. These parameters could be useful to control synchronicity loss in genetic regulatory networks.*

4.2 Floral morphogenesis of *Arabidopsis thaliana*

In [30], Mendoza and Alvarez-Buylla introduced a network of the genetic control of the floral morphogenesis of the plant *Arabidopsis thaliana*. The mathematical model that they used to study the dynamical behavior of this network was that of threshold BNs. Threshold BNs are particular BNs in

$$\widetilde{W} = \begin{array}{c|cccccccccc} & \text{EMF1} & \text{TFL1} & \text{LFY} & \text{AP1} & \text{CAL} & \text{LUG} & \text{UFO} & \text{BFU} & \text{AG} & \text{AP3} \\ \hline \text{EMF1} & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{TFL1} & 1 & 0 & -2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{LFY} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{AP1} & -2 & 0 & 5 & 0 & 0 & 0 & 0 & 0 & -2 & 0 \\ \text{CAL} & 0 & 0 & 2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{LUG} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{UFO} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{BFU} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ \text{AG} & 0 & -2 & 1 & -2 & 0 & -1 & 0 & 0 & 0 & 0 \\ \text{AP3} & 0 & 0 & 3 & 0 & 0 & 0 & 2 & 1 & 0 & 0 \\ \text{PI} & 0 & 0 & 4 & 0 & 0 & 0 & 1 & 1 & 0 & 0 \\ \text{SUP} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{array} \qquad \widetilde{\Theta} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ -2 \\ 1 \\ 0 \\ 0 \\ 1 \\ -1 \\ 0 \\ 0 \\ 0 \end{pmatrix}$$
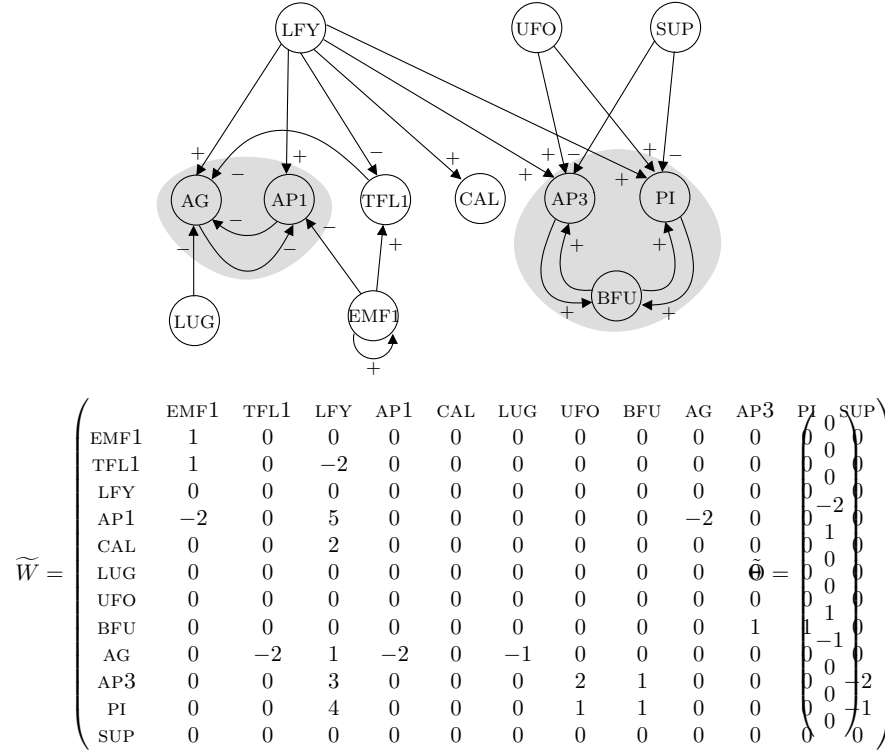
Figure 9: Symmetric version of the regulation network modeling the genetic control of *Arabisopsis thaliana* floral morphogenesis pointing out the dynamical role of the two strongly connected components $\mathcal{C}_1$ and $\mathcal{C}_2$.

which every local transition function $f_i(x)$ is a threshold Boolean function defined as:

$$f_i(x) = \mathbb{I}(\sum_{j \in V} w_{i,j} \cdot x_j - \theta_i),$$

where θ_i is the activation threshold of node i, $w_{i,j} \in \mathbb{R}$ is the interaction weight that node j has on node i, and $\mathbb{I} : \mathbb{R} \to \mathbb{B}$ is the Heaviside function defined as $\mathbb{I}(x) = 0$ if $x \leq 0$ and 1 otherwise. A very relevant result obtained by Mendoza and Alvarez-Buylla was that the dynamical behavior of this network, according to a specific block-sequential (or series-parallel) updating mode (see [40] for more details about this kind of updating mode), converges towards six fixed points among which four corresponds to the four floral cellular types: carpels, stamens, petals and sepals. The two other fixed points are respectively related to inflorescence and mutant cellular types.

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In [11], the authors emphasized that this network, when subjected to the parallel updating mode, has also seven limit cycles of size 2. Basing themselves on the results obtained by Goles in [17] about the convergence of symmetric threshold BNs, they showed that this original network was actually equivalent to another simpler one. The latter is simpler in the sense that its dynamical richness is entirely governed by two strongly connected components $\mathcal{C}_1$ and $\mathcal{C}_2$, of respective sizes 2 and 3 and such that $V_{\mathcal{C}_1} = \{\mathrm{AG}, \mathrm{AP1}\}$ and $V_{\mathcal{C}_2} = \{\mathrm{AP3}, \mathrm{BFU}, \mathrm{PI}\}$. This network, together with its related interaction matrix $\tilde{W}$ and threshold vector $\tilde{\Theta}$ is pictured in Figure 9. From the analysis of the dynamical behavior of this network given in [11], we derive Theorem 3 below.

Theorem 3. *Suppose that every node that does not belong to neither $\mathcal{C}_1$ nor $\mathcal{C}_2$ is at state 0. The following holds:*

i) *Any MBN associated with $\mathcal{C}_1$ admits the two fixed points $(dt_{\mathrm{AG}}, 0)$ and $(0, dt_{\mathrm{AP1}})$. Only those such that $dt_{\mathrm{AG}} = dt_{\mathrm{AP1}}$ can admit a limit cycle.*

ii) *For the $\mathcal{C}_2$ component, the behavior of any MBN built on it is the following:*

- *If $d_{\mathrm{BFU}} \geq 2$, then the set of attractors of the network is composed of two fixed points, $(0,0,0)$ and $(d_{\mathrm{AP3}}, d_{\mathrm{BFU}}, d_{\mathrm{PI}})$.*

- *If $(dt_{\mathrm{BFU}} = 1) \wedge (dt_{\mathrm{AP3}} \geq 2) \wedge (dt_{\mathrm{PI}} \geq 2)$ then the set of attractors of the network is composed of two fixed points, $(0,0,0)$ and $(dt_{\mathrm{AP3}}, dt_{\mathrm{BFU}}, d_{\mathrm{PI}})$.*

- *If $(d_{\mathrm{BFU}} = 1) \wedge ((d_{\mathrm{AP3}} = 1) \vee (d_{\mathrm{PI}} = 1))$) then the set of attractors of the network is composed of two fixed points, $(0,0,0)$ and $(dt_{\mathrm{AP3}}, dt_{\mathrm{BFU}}, d_{\mathrm{PI}})$, and of a limit cycle of length 2.*

Proof. Let us work on both sub-networks.

i) The proof is the same as that of Theorem 2.

ii) Let us denote by (ρ, δ, γ) the initial configuration. First, notice that whatever the delay vector, if the state of BFU is 0 and at least one of the other two is also 0 in the initial configuration then the latter converges towards the fixed point $(0,0,0)$. Indeed, $(0,0,\gamma) \to (0,0,\gamma - 1) \xrightarrow{\gamma - 1} (0,0,0) \circlearrowleft$ that is reached in γ time steps, *i.e.* in at most dt_{PI} time steps. Similarly, $(\rho, 0, 0) \to (\rho - 1, 0, 0) \xrightarrow{\rho - 1} (0,0,0) \circlearrowleft$ that is reached in γ time steps, *i.e.* in at most dt_{PI} time steps.

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Consider now that it is not the case so that the central site and one of its neighbors are not both at state 0 at the same time. Three cases are possible:

(a) $dt_{\text{BFU}} \geq 2$. Then, for $1 \leq \delta \leq dt_{\text{BFU}}$ and for any $\rho, \gamma \geq 0$ we have:

- if $\rho = 0$ or $\gamma = 0$ then $(\rho, \delta, \gamma) \rightarrow (dt_{\text{AP3}}, \delta - 1, dt_{\text{PI}})$. If $\delta - 1 = 0$ then
  - if $dt_{\text{AP3}} = dt_{\text{PI}} = 1$ then $(dt_{\text{AP3}}, 0, dt_{\text{PI}}) \rightarrow (0, dt_{\text{BFU}}, 0) \rightarrow (dt_{\text{AP3}}, dt_{\text{BFU}} - 1, dt_{\text{PI}}) \rightarrow (dt_{\text{AP3}}, dt_{\text{BFU}}, dt_{\text{PI}}) \circlearrowleft$.
  - if $dt_{\text{AP3}} = 1 \wedge dt_{\text{PI}} > 1$ then $(dt_{\text{AP3}}, 0, dt_{\text{PI}}) \rightarrow (0, dt_{\text{BFU}}, dt_{\text{PI}} - 1) \rightarrow (dt_{\text{AP3}}, dt_{\text{BFU}} - 1, dt_{\text{PI}}) \rightarrow (dt_{\text{AP3}}, dt_{\text{BFU}}, dt_{\text{PI}}) \circlearrowleft$.
  - if $dt_{\text{AP3}} > 1 \wedge dt_{\text{PI}} = 1$ then $(dt_{\text{AP3}}, 0, dt_{\text{PI}}) \rightarrow (dt_{\text{AP3}} - 1, dt_{\text{BFU}}, 0) \rightarrow (dt_{\text{AP3}}, dt_{\text{BFU}} - 1, dt_{\text{PI}}) \rightarrow (dt_{\text{AP3}}, dt_{\text{BFU}}, dt_{\text{PI}}) \circlearrowleft$.
  - if $dt_{\text{AP3}} > 1 \wedge dt_{\text{PI}} > 1$ then $(dt_{\text{AP3}}, 0, dt_{\text{PI}}) \rightarrow (dt_{\text{AP3}} - 1, dt_{\text{BFU}}, dt_{\text{PI}} - 1) \rightarrow (dt_{\text{AP3}}, dt_{\text{BFU}}, dt_{\text{PI}}) \circlearrowleft$.

  If $\delta - 1 \geq 1$ then $(dt_{\text{AP3}}, \delta - 1, dt_{\text{PI}}) \rightarrow (dt_{\text{AP3}}, dt_{\text{BFU}}, dt_{\text{PI}}) \circlearrowleft$.
- if $\rho \geq 1$ and $\gamma \geq 1$ then it is trivial that (ρ, δ, γ) converges directly towards $(dt_{\text{AP3}}, dt_{\text{BFU}}, dt_{\text{PI}})$.

Now, if $\rho \geq 1$, $\delta = 0$ and $\gamma \geq 1$ then

- if $\rho = \gamma = 1$ then $(1, 0, 1) \rightarrow (0, dt_{\text{BFU}}, 0) \rightarrow (dt_{\text{AP3}}, dt_{\text{BFU}} - 1, dt_{\text{PI}}) \rightarrow (dt_{\text{AP3}}, dt_{\text{BFU}}, dt_{\text{PI}}) \circlearrowleft$.
- if $\rho = 1 \wedge \gamma \geq 2$ then $(1, 0, \gamma) \rightarrow (0, dt_{\text{BFU}}, \gamma - 1) \rightarrow (dt_{\text{AP3}}, dt_{\text{BFU}} - 1, dt_{\text{PI}}) \rightarrow (dt_{\text{AP3}}, dt_{\text{BFU}}, dt_{\text{PI}}) \circlearrowleft$.
- if $\rho \geq 2 \wedge \gamma = 1$ then $(\rho, 0, 1) \rightarrow (\rho - 1, dt_{\text{BFU}}, 0) \rightarrow (dt_{\text{AP3}}, dt_{\text{BFU}} - 1, dt_{\text{PI}}) \rightarrow (dt_{\text{AP3}}, dt_{\text{BFU}}, dt_{\text{PI}}) \circlearrowleft$.
- if $\rho \geq 2 \wedge \gamma \geq 2$ then $(\rho, 0, \gamma) \rightarrow (\rho - 1, dt_{\text{BFU}}, \gamma - 1) \rightarrow (dt_{\text{AP3}}, dt_{\text{BFU}}, dt_{\text{PI}}) \circlearrowleft$.

Thus, when $dt_{\text{BFU}} \geq 2$, the network admits only two attractors, fixed point $(0, 0, 0)$ (resp. $(dt_{\text{AP3}}, dt_{\text{BFU}}, dt_{\text{PI}})$) towards which it converges in at most $\max(dt_{\text{AP3}}, dt_{\text{PI}})$ (resp. 4) time steps.

(b) $dt_{\text{BFU}} = 1$ and $(dt_{\text{AP3}} \geq 2)$ and $(dt_{\text{PI}} \geq 2)$. Given an initial configuration (ρ, δ, γ), we have:

- if $\delta = 0$ and $\rho \geq 1$ and $\gamma \geq 1$ then:
  - if $\rho = \gamma = 1$ then $(1, 0, 1) \rightarrow (0, 1, 0) \rightarrow (dt_{\text{AP3}}, 0, dt_{\text{PI}})$.
  - if $\rho = 1 \wedge \gamma \geq 2$ then $(1, 0, \gamma) \rightarrow (0, 1, \gamma - 1) \rightarrow (dt_{\text{AP3}}, 0, dt_{\text{PI}})$.

       – if $\rho \geq 2 \;\wedge\; \gamma = 1$ then $(\rho, 0, 1) \rightarrow (\rho - 1, 1, 0) \rightarrow (dt_{\mathrm{AP3}}, 0, dt_{\mathrm{PI}})$.

       – if $\rho, \gamma \geq 2$ then $(\rho, 0, \gamma) \rightarrow (\rho-1, 1, \gamma-1) \rightarrow (dt_{\mathrm{AP3}}, 0, dt_{\mathrm{PI}})$.

     Now, notice that $(dt_{\mathrm{AP3}}, 0, dt_{\mathrm{PI}}) \rightarrow (dt_{\mathrm{AP3}} - 1, 1, dt_{\mathrm{PI}} - 1) \rightarrow (dt_{\mathrm{AP3}}, dt_{\mathrm{BFU}}, dt_{\mathrm{PI}}) \circlearrowleft$.

  • if $\delta = 1$ and $\rho \geq 1$ and $\gamma \geq 1$ then it is trivial that there is a direct convergence towards $(dt_{\mathrm{AP3}}, dt_{\mathrm{BFU}}, dt_{\mathrm{PI}})$.

Thus, when $dt_{\mathrm{BFU}} = 1$ and $dt_{\mathrm{AP3}} \geq 2$ and $(dt_{\mathrm{PI}} \geq 2)$, the network necessarily converges towards either $(0,0,0)$ in at most $\max(dt_{\mathrm{AP3}}, dt_{\mathrm{PI}})$ time steps or $(dt_{\mathrm{AP3}}, dt_{\mathrm{BFU}}, dt_{\mathrm{PI}})$ in at most 4 time steps.

(c) $dt_{\mathrm{BFU}} = 1$ and $((dt_{\mathrm{AP3}} = 1) \vee (dt_{\mathrm{PI}} = 1))$. Let us first suppose that $dt_{\mathrm{AP3}} = 1$ and $dt_{\mathrm{AP3}} \geq 2$ and consider an initial configuration (ρ, δ, γ). We have:

  • if $\delta = 0$ and $\rho = 1$ and $\gamma \geq 1$ then $(1, 0, \gamma) \rightarrow (0, 1, \gamma - 1) \rightarrow (dt_{\mathrm{AP3}}, 0, dt_{\mathrm{PI}}) \leftrightarrows (0, 1, dt_{\mathrm{PI}} - 1)$, which highlights a limit cycle of length 2.

  • if $\delta = 1$ then:

       – $\forall \rho, \gamma$ such that $\rho = 0$ or $\gamma = 0$, $(\rho, 1, \gamma) \rightarrow (dt_{\mathrm{AP3}}, 0, dt_{\mathrm{PI}}) \leftrightarrows (0, 1, dt_{\mathrm{PI}} - 1)$, which highlights a limit cycle of length 2.

       – if $\rho = 1$ and $\gamma \geq 1$ then $(1, 1, \gamma) \rightarrow (dt_{\mathrm{AP3}}, dt_{\mathrm{BFU}}, dt_{\mathrm{PI}}) \circlearrowleft$.

The cases where $(dt_{\mathrm{AP3}} \geq 2 \;\wedge\; dt_{\mathrm{AP3}} = 1)$, and where $dt_{\mathrm{AP3}} = dt_{\mathrm{AP3}} = 1$ can be treated similarly.

$\square$

Theorem 3 shows that both components $\mathcal{C}_1$ and $\mathcal{C}_2$ that are the engines of the dynamical behavior of the network admit a limit cycle. However, here again, these two limit cycles are spurious in the sense that only very specific initial conditions allow to capture them. Furthermore, both of these components admit two fixed points: $(x_{\mathrm{AG}} = dt_{\mathrm{AG}}, x_{\mathrm{AP1}} = 0)$ and $(x_{\mathrm{AG}} = 0, x_{\mathrm{AP1}} = dt_{\mathrm{AP1}})$ for $\mathcal{C}_1$, and $(x_{\mathrm{AP3}} = 0, x_{\mathrm{BFU}} = 0, x_{\mathrm{PI}} = 0)$ and $(x_{\mathrm{AP3}} = dt_{\mathrm{AP3}}, x_{\mathrm{BFU}} = dt_{\mathrm{BFU}}, x_{\mathrm{PI}} = dt_{\mathrm{PI}})$. By combining them by making vectors $(x_{\mathrm{AG}}, x_{\mathrm{AP1}}, x_{\mathrm{AP3}}, x_{\mathrm{BFU}}, x_{\mathrm{PI}})$, we obtain four possible fixed points:

$$\mathrm{fp}_1 = (dt_{\mathrm{AG}}, 0, 0, 0, 0), \quad \mathrm{fp}_2 = (0, dt_{\mathrm{AP1}}, 0, 0, 0),$$

$$\mathrm{fp}_3 = (dt_{\mathrm{AG}}, 0, dt_{\mathrm{AP3}}, dt_{\mathrm{BFU}}, dt_{\mathrm{PI}}) \text{ and } \mathrm{fp}_4 = (0, dt_{\mathrm{AP1}}, dt_{\mathrm{AP3}}, dt_{\mathrm{BFU}}, dt_{\mathrm{PI}}),$$

that correspond exactly to the floral organs (sepals, petals, carpels and stamens) according to the ABC model [8, 32].

5 Conclusion and perspectives

This paper aimed at studying from the theoretical point of view the GPBN model of Graudenzi and Serra in [21, 22, 23]. This mathematical model was introduced as an extension of BNs allowing to consider nodes representing both genes (as Boolean variables) and proteins (as discrete decay times of their concentrations). By using an intermediary model, that we call MBNs, we first obtained a result emphasizing that GPBNs are computationally speaking equivalent to BNs. Indeed, given an arbitrary GPBN, it is possible to construct an dynamically equivalent BN composed of more nodes. This result led us to focus on theoretical properties of MBNs. For this model in general, we proved that: *(i)* positive disjunctive MBNs, as well as locally monotonic MBNs (*i.e.* MBNs whose global transition function is either decreasing or increasing for all x), necessarily converge towards fixed points; *(ii)* the only attractors that MBNs whose underlying interaction graphs do not induce any cycle except possible loops may have are fixed points. Then, before we presented applications to two well know examples of real genetic regulation networks, we analyzed exhaustively the possible dynamical behaviors of MBNs composed of two nodes. The underlying idea aimed at obtaining a subtle knowledge about the dynamical and computational properties of simple biological patterns. It led us to highlight the conditions under which this or that pattern admits only fixed points or limit cycles as limit behaviors. Moreover, it led us to show that adding memory to BNs is a pertinent way to freeze some cyclic behaviors, which is particularly interesting in the case of spurious complex attractors, but that it is also a way to create complex attractors in very specific networks having few attractors in their initial Boolean form. The features of such BNs would deserve to be studied more generally.

This work opens the following perspectives:

- *about other applications*: One of the first perspectives would be to use MBNs to model other networks known to model genetic controls in living systems. Among the networks that we think of are the embryonic segmentation of *Drosophila melanogaster* [2], B-cell differentiation [29] and the fission yeast cell cycle network [26].

- *about larger networks*: A natural opening of this work is to focus on the theoretical properties of the dynamics and the complexity of networks of larger sizes. A first axis would be to maintain our interest in biological patterns by paying attention to networks of size 3 and

4. Because of the intrinsic complexity (regarding the size of the phase space) of such a work, it would be judicious to focus on specific patterns that have been highlighted to be either statistically well represented in biological networks [33] or of specific importance such as regulons or feed-forward coherent and incoherent cycles. Moreover, of course, another axis should naturally be articulated around larger networks whose interaction graphs belong to specific classes, such as cycles and more generally graph family like cacti and caterpillars.

- *about synchronicity*: As evoked in Remark 7, MBNs get interesting features to understand the role of synchronicity and asynchonicity on the dynamics of regulatory networks. Indeed, when we work on BNs, the way to study and understand the influence of synchronicity is to play with the updating mode (parallel, block-sequential, sequential, randomly sequential, fair, asynchronous...). However, although there exist a lot of results in this domain, the comparison of their impact on networks is very tricky for mainly two reasons: the infinite number of possible updating modes in theory and their mathematical nature (*i.e.* deterministic vs non-deterministic, periodic vs non-periodic...). Here, with MBNs, while we keep the parallel updating mode, we can directly change synchronicity through initial configurations that play the role of synchronicity control parameters. From the biological point of view, this is of peculiar interest because in most cases, the synchronicity induced by the use of the parallel updating mode (that the most basic mathematically speaking) tends to produce cyclic attractors with no biological meaning. In this framework, future works will be oriented towards the characterizations of delays for distinct classes of MBNs ensuring to filter such spurious attractors by freezing the networks.

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