Negative cycles and fixed points in Boolean networks

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Joint work with
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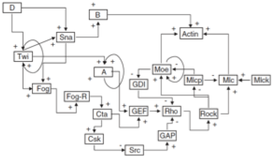
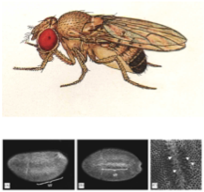
Motivation of Boolean networks in biology

A gene regulatory network consists of a set of genes, proteins, small molecules, and their mutual interactions. Elements:

- **Vertex** = A gene or a gene product.
- **States** = 1 (activated), 0 (inactivated).
- **Interaction Graph** = Interaction of genes and genes products each other.
- **Activation function** = Regulation function.
- **Updating** = parallel (in the most cases).
- **Fixed points** = Cellular phenotypes.





(Aracena J. et al. Journal of Theoretical Biology, 2006.)

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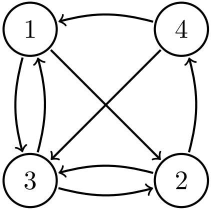
- f_v *depends on variable* x_u *if and only if* $(u, v) \in A$, *i.e.* $f_v(x) = f_v(x_u : (u, v) \in A)$.

Example of Boolean network

- $F\colon \{0,1\}^4 \to \{0,1\}^4$
- $f_1(x) := x_3 \wedge x_4$
- $f_2(x) := x_1 \wedge x_3$
- $f_3(x) := (x_1 \wedge x_2) \vee \overline{x}_4$
- $f_4(x) := \overline{x}_2$
- $F(x) = (f_1(x), f_2(x), f_3(x), f_4(x))$

G: Interaction graph



Dynamical behavior of Boolean networks

Given $N = (G, F)$ a Boolean network, the value of each variable x_v of N on time $t + 1$ is given by:

$$x_v(t + 1) = f_v(x(t)).$$

Thus, the **dynamical behavior** of N is given by:

$$\forall x(t) \in \{0, 1\}^n,\ x(t + 1) = F(x(t)).$$

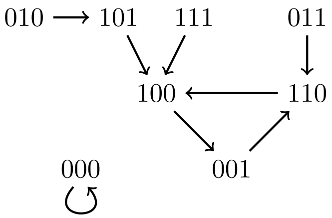
A vector $x \in \{0, 1\}^n$ is said to be a **fixed point** of N if $F(x) = x$.
The set of fixed points of (G, F) is denoted by $\mathrm{FP}(G, F)$.

Example. $n = 3$ and $F = (f_1, f_2, f_3)$ defined by

$$\begin{cases} f_1(x) & = x_2 \vee x_3 \\ f_2(x) & = \overline{x_1} \wedge x_3 \\ f_3(x) & = \overline{x_3} \wedge (x_1 \oplus x_2) \end{cases}$$

x	$F(x)$
000	000
001	110
010	101
011	110
100	001
101	100
110	100
111	100

Dynamics:



Many applications

- Neural networks [McCulloch & Pitts 1943]
- Gene networks [Kauffman 1969, Tomas 1973]
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Natural question: - *What can be said on the fixed points of a network according to its interaction graph ?*

Boolean networks with signed interaction digraphs

(regulatory Boolean networks)

Regulatory Boolean networks

Let (G, F) be a Boolean network, then:

- f_v is monotonically increasing on input u if $f_v(x_1, \ldots, x_u = 0, \ldots, x_n) \leq f_v(x_1, \ldots, x_u = 1, \ldots, x_n)$.

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Example. $f_v(x_1, x_2, x_3) = (\bar{x}_1 \vee \bar{x}_3) \wedge (x_1 \vee x_2)$ is non monotonically increasing nor monotonically decreasing on x_1 .

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Examples of RBNs: threshold Boolean networks, monotone networks, AND-OR-NOT networks, etc.

Signed interaction graph

Let $(G = (V, A), F)$ be a regulatory Boolean network, then

- we can define a sign function $\sigma : A \to \{+1, -1\}$ by

$$\sigma(i,j) = \begin{cases} +1 & \text{if } f_j \text{ is monotonically increasing on input } i \\ -1 & \text{otherwise.} \end{cases}$$

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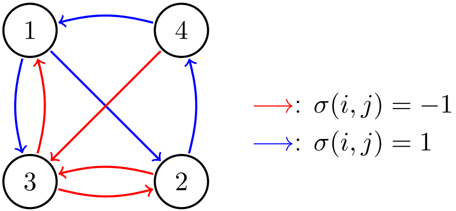
- The sign of a cycle c of (G, σ), denoted by $\sigma(c)$, is equal to the product of the signs of the arcs of c.
- A cycle c of G is said to be positive if $\sigma(c) = +1$ and negative if $\sigma(c) = -1$.

Example of positive and negative cycles



$\sigma(c_1 : 1,3,1) = -1$ (c_1 is a negative cycle) and $\sigma(c_2 : 4,3,2,4) = 1$ (c_2 is a positive cycle).

The roles of positive and negative cycles in gene regulatory networks

Thomas' conjectures (Thomas 1981)

The presence of a positive (resp. negative) circuit is a necessary condition for the presence of multiple stable states (resp. a cyclic attractor).

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These conjectures have been proved for differential systems (Plathe et al. 1995; Snoussi 1998; Gouzé 1998; Cinquin and Demongeot 2002; Soulé 2003, 2006) and discrete systems (Aracena et al. 2004; Remy and Ruet 2006; Richard and Comet 2007; Aracena 2008; Remy et al. 2008; Richard 2010).

Positive and negative cycles and fixed points in Boolean networks

Problem: Given a signed digraph (G, σ) with $|V(G)| = n$, to determine

$$\phi(G, \sigma) = \max\{card(\mathrm{FP}(G, F)) \mid F : \{0,1\}^n \to \{0,1\}^n \text{ a function}\}.$$

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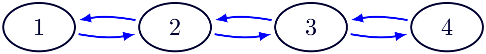

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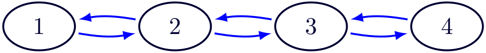

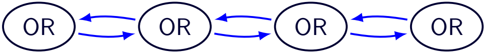

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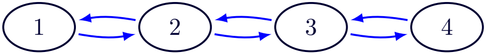

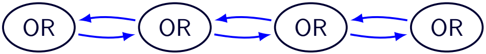

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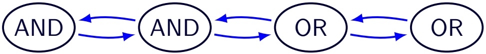

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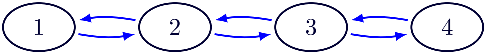

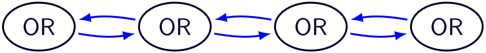

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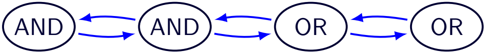

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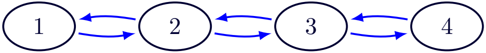
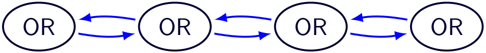
$(P_4, \sigma \equiv +1)$: 



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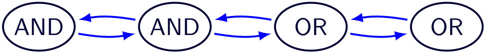

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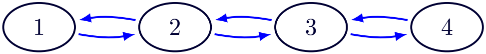

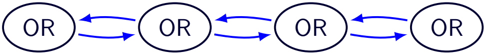

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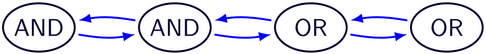

$\Longrightarrow$ 3 fixed points

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¿$\phi(P_n, \sigma \equiv +1)$?

Positive feedback vertex set

Positive transversal number

$\tau^+(G,\sigma) :=$ minimum size of a set of vertices meeting every **positive** cycle

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Positive transversal number

$\boldsymbol{\tau}^+(\boldsymbol{G}, \boldsymbol{\sigma}) :=$ minimum size of a set of vertices meeting every **positive** cycle

Remark 1. $\tau^+ \leq \tau$

Remark 2. τ^+ is invariant under subdivisions of arcs preserving signs

Example of positive feedback vertex set

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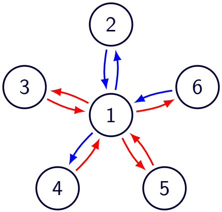

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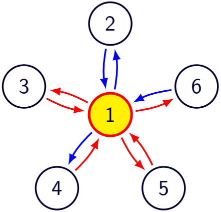

$$\tau^+ = 1$$
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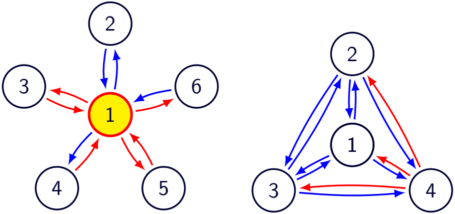

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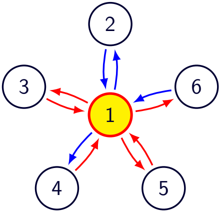

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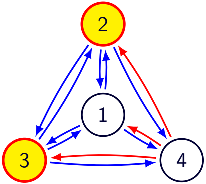

$\tau^{+} = 2$

$\tau = 3$

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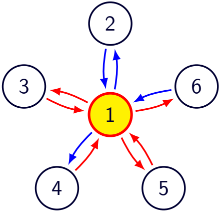

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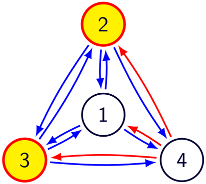

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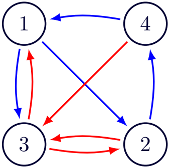

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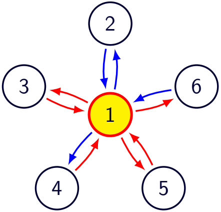

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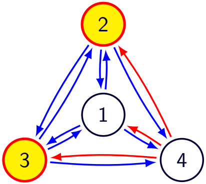

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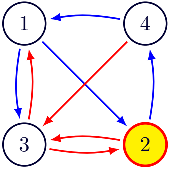

$\tau^+ = 1$
$\tau = 2$

Positive feedback vertex set

Theorem (Aracena, Goles, Demongeot, 2004; Aracena, 2008)

$\phi(G,\sigma) \leq 2^{\tau^+(G,\sigma)}$ *fixed points*

Positive feedback vertex set

Theorem (Aracena, Goles, Demongeot, 2004; Aracena, 2008)

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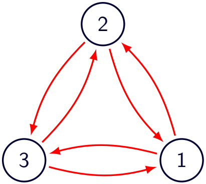
Remark 3. (G, σ) has no cycles $\Rightarrow$ $\phi(G, \sigma) = 1$ (F. Robert, 1986).

Example.



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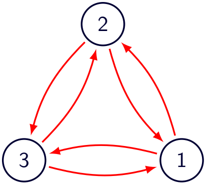

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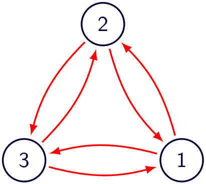

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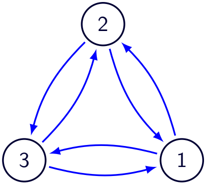

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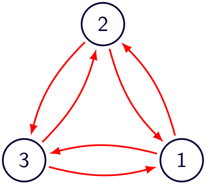

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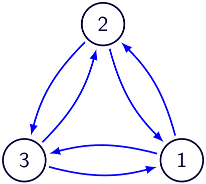

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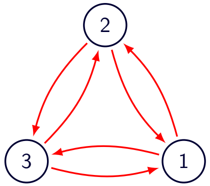

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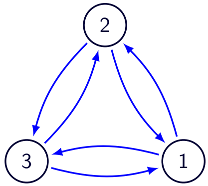

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Question: Which is the role of the negative cycles regarding the number of fixed points in a RBN?

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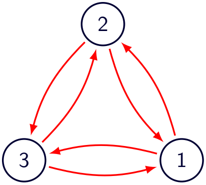

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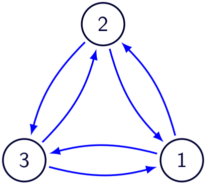

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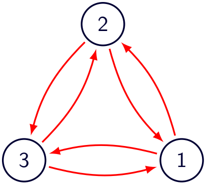

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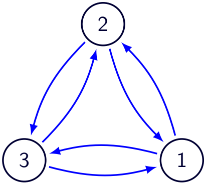

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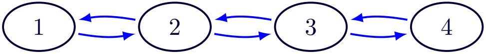

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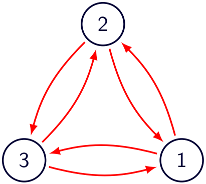

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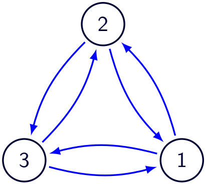

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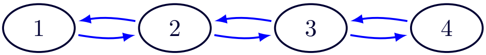

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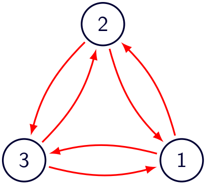

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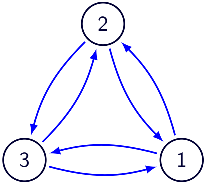

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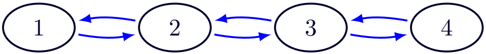

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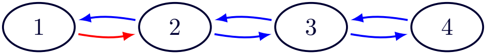

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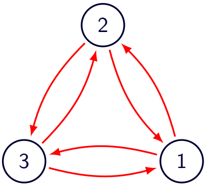

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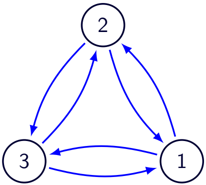

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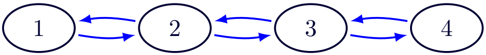

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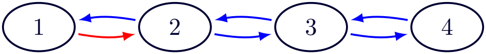

$$\phi(P_4, \sigma) = 2!$$

Monotone Boolean networks
(Boolean networks without negative cycles)

(J. Aracena, A. Richard, L. Salinas. Number of fixed points and disjoint cycles in monotone Boolean networks, SIAM Journal of Discrete Mathematics, 2016. Accepted.)

Boolean networks without negative cycles

Definition

Given a signe digraph (G, σ) and I a subset of vertices of G, the **I-switch** *of (G, σ) is the signed digraph (G, σ^I) where σ^I is defined by*

$$\forall uv \in A(G), \quad \sigma^I(uv) = \begin{cases} \sigma(uv) & \text{if } u, v \in I \text{ or } u, v \notin I, \\ -\sigma(uv) & \text{otherwise.} \end{cases}$$

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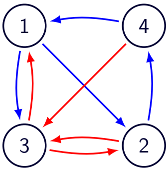

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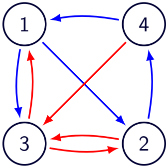

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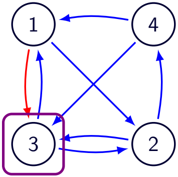

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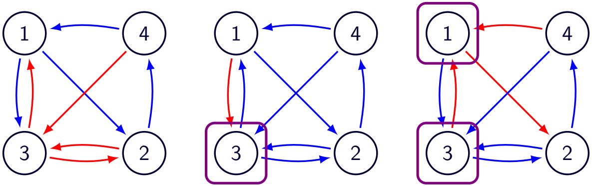

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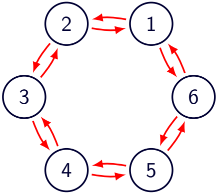

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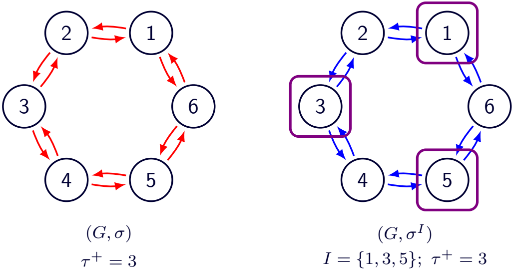

Monotone networks

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A Boolean network (G, F) *is said to be* **monotone** *if*

$$\forall x, y \in \{0,1\}^n,\ x \leq y \ \Rightarrow\ F(x) \leq F(y),$$

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Packing number

$\boldsymbol{\nu(G)}$:= maximum number of vertex-disjoint cycles of G.

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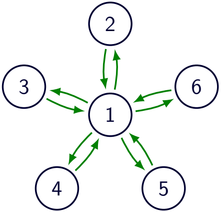

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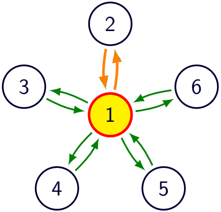

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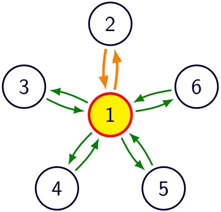

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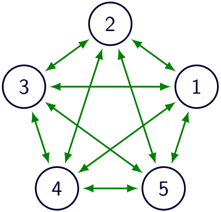

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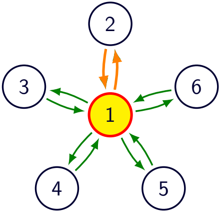

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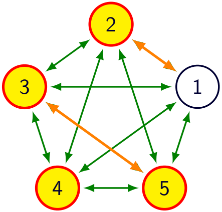

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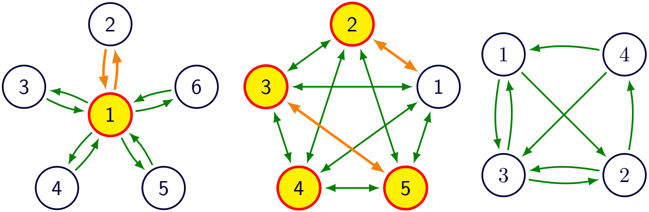

$\tau = \nu = 1$

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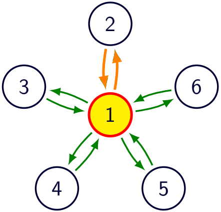

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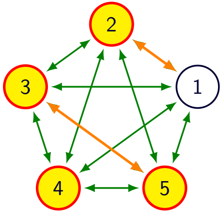

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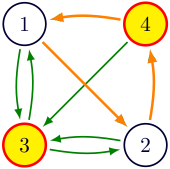

$\nu = 1, \tau = 2$

Theorem (Knaster-Tarski, 1928)

If f is monotone then $\mathrm{FP}(f)$ is a non-empty lattice

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Theorem (Aracena-Salinas-Richard, 2016)

If (G, F) is a monotone Boolean network, then $\mathrm{FP}(G, F)$ is isomorphic to a subset $L \subseteq \{0, 1\}^{\tau}$ s.t.

1. *L is a non-empty lattice*
2. *L has no chains of size $\nu + 2$*

Proof of Theorem part 2

If $\mathrm{FP}(G, F)$ has a chain of size k then $\nu \geq k - 1$

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Proof of Theorem part 2

If $\mathrm{FP}(G, F)$ has a chain of size k then $\nu \geq k-1$

$$\begin{array}{ll}
x^5 = & \mathbf{1}\ \mathbf{1}\ \mathbf{1}\ \mathbf{1}\ \ \mathbf{1}\ \mathbf{1}\ \mathbf{1}\ \mathbf{1}\ \mathbf{1}\ \ \mathbf{1}\ \mathbf{1}\ \mathbf{1}\ \mathbf{1}\ \ \boxed{\mathbf{1}\ \mathbf{1}\ \mathbf{1}\ \mathbf{1}\ \mathbf{1}} \\
x^4 = & \mathbf{1}\ \mathbf{1}\ \mathbf{1}\ \mathbf{1}\ \ \mathbf{1}\ \mathbf{1}\ \mathbf{1}\ \mathbf{1}\ \mathbf{1}\ \ \boxed{\mathbf{1}\ \mathbf{1}\ \mathbf{1}\ \mathbf{1}}\ \ \boxed{0\ 0\ 0\ 0\ 0} \\
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x^2 = & \boxed{\mathbf{1}\ \mathbf{1}\ \mathbf{1}\ \mathbf{1}}\ \ \boxed{0\ 0\ 0\ 0\ 0}\ \ 0\ 0\ 0\ 0\ \ 0\ 0\ 0\ 0\ 0 \\
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Thus $\mathrm{FP}(G,F)$ has no chains of length $\nu+2$ and so L

Theorem (Erdős, 1945)

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Corollary

$\phi(G, \sigma \equiv +1) = 2^{\tau(G)} \Longrightarrow \nu(G) = \tau(G)$

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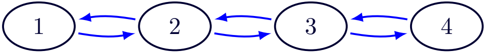

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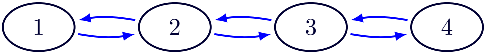

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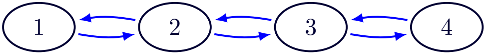

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Special packing and ν^*

Definition

A **special packing** *of size k is a collection $C_1, \ldots, C_k$ of disjoints cycles such that for every* principal path P *from C_p to C_q, $p \neq q$, there exists a* principal path P' *from C_q to the last vertex of P*

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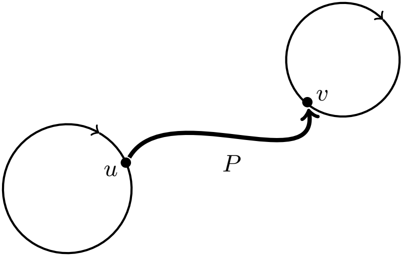

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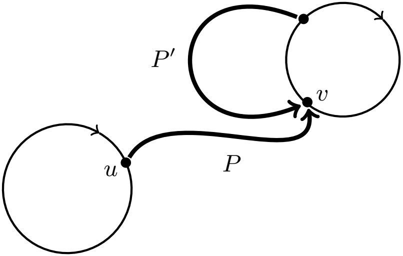

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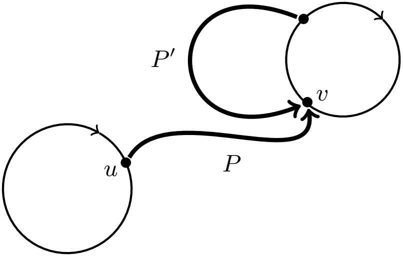

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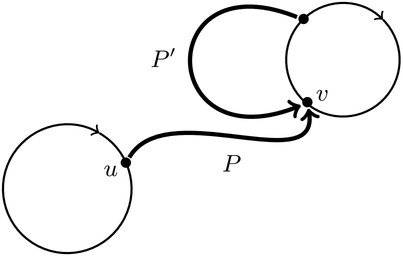

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Remark. $\nu^* \leq \nu \leq \tau$

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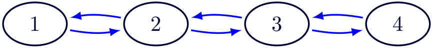

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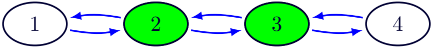

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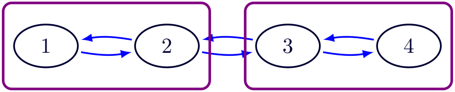

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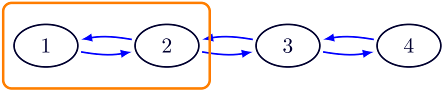

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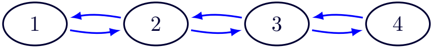

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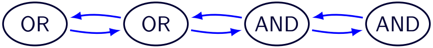

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Only three fixed points

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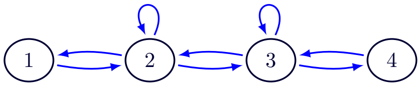

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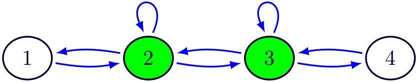

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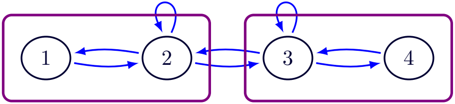

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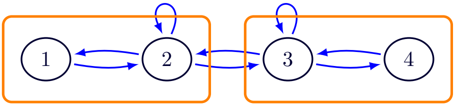

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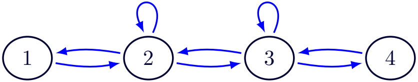

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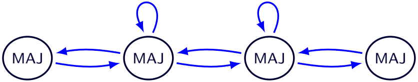

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Four fixed points

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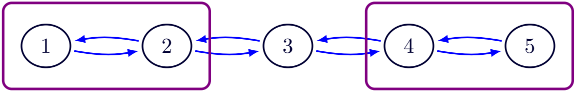

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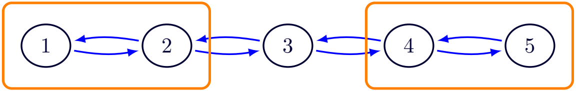

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Question: It is possible to prove directly that $\phi(G) \leq 2^{h(\nu)}$ without using Theorem of Reed et al., 1996?

AND-OR-NOT networks

- **J. Aracena, A. Richard, L. Salinas. Maximum number of fixed points in AND?OR?NOT networks. Journal of Computer and System Sciences 80 (2014), 1175-1190.**
- **J. Aracena, A. Richard, L. Salinas. Fixed points in conjunctive networks and maximal independent sets in graph contractions. Journal of Computer and System Sciences, 2015. Submitted.**

AND-NOT networks

- A BN $N = (G = (V, A), F)$ is an AND-NOT network if each local activation function is a conjunction of some variables o negated variables.
- That is, for all $i \in V$:

$$f_i(x) = \bigwedge_{j:(j,i) \in A} y_j, \quad y_j \in \{x_j, \bar{x}_j\}.$$

Example:

- $f_1(x) = \bar{x}_3 \wedge x_4$
- $f_2(x) = x_1 \wedge x_3$
- $f_3(x) = x_1 \wedge x_2 \wedge \bar{x}_4$
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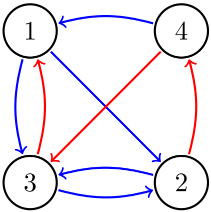

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- Every BN can be represented by an AND-NOT network with auxiliar variables.
- An AND-NOT network is completely defined by its signed interaction graph. Thus, we will denote by (G, σ) the AND-NOT network associated.

Maximum number of fixed points in AND-NOT networks

Theorem (Aracena-Demongeot-Goles, 2004)

The maximum number of points fixed in loop-less connected AND-NOT networks with n vertices and without negative cycles is $2^{(n-1)/2}$ for n odd and $2^{(n-2)/2}+1$ for n even.

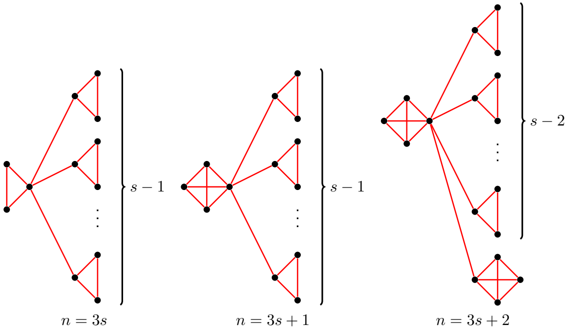
Maximum number of fixed points in AND-NOT networks

Theorem (Aracena,Richard, Salinas,2014)

The maximum number of points fixed in loop-less connected AND-NOT networks with n vertices is $\mu(n)$, where

$$\mu(n) = \begin{cases} 2 \cdot 3^{s-1} + 2^{s-1} & \textit{if } n = 3s \\ 3^s + 2^{s-1} & \textit{if } n = 3s+1 \\ 4 \cdot 3^{s-1} + 3 \cdot 2^{s-2} & \textit{if } n = 3s+2 \end{cases}$$

Fixed points in symmetric AND-NOT networks



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Theorem (Aracena-Richard-Salinas, 2015)

Let G be a loop-less symmetric digraph without a copy induced of C_4. Then, $(G, \sigma \equiv -1)$ has the maximum number of fixed points. Besides,
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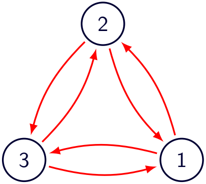

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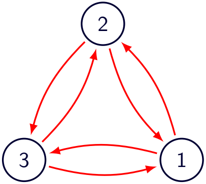

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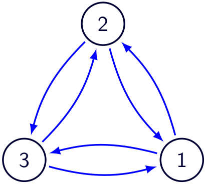

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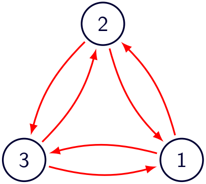

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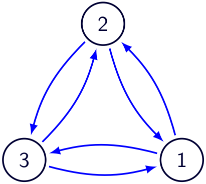

$\phi(K_3, \sigma_2) = 2;\ \tau^+ = 2$

Question: Given G a loop-less symmetric digraph, $\phi(G, \sigma) \leq (G, \sigma \equiv = -1)$?

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Bon Anniversaire Jacques!

Merci !