What is a Boolean Network?

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A model

A Boolean network (BN) is a discrete mathematical model of a network of interacting entities.

The entities are the vertices of a directed graph, that represents the influences amongst entities.

Each entity i has:

- a Boolean state $x_i \in \{0,1\}$;
- an update function $f_i(x_j, x_k, \dots)$ which depends on the other states of its in-neighbourhood.

Some pictures of BNs

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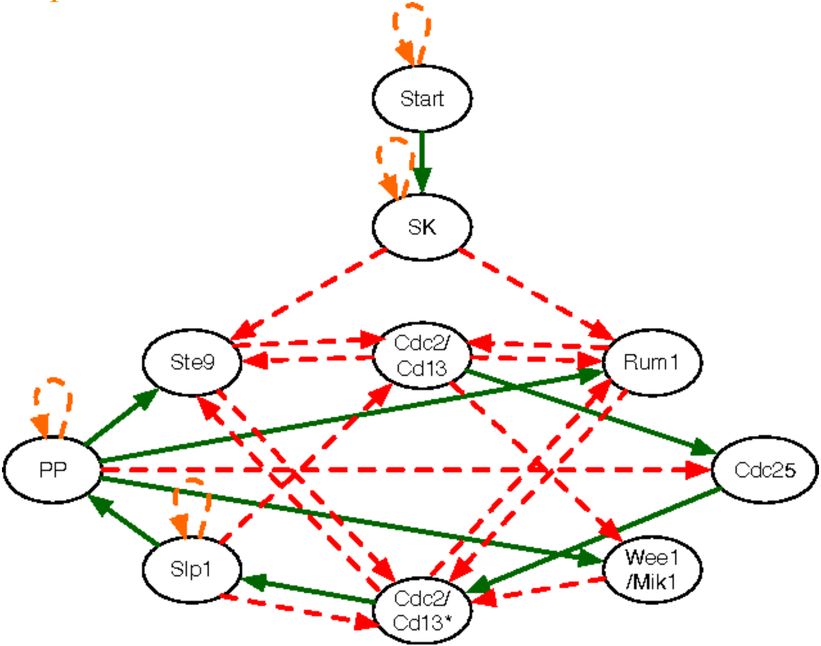
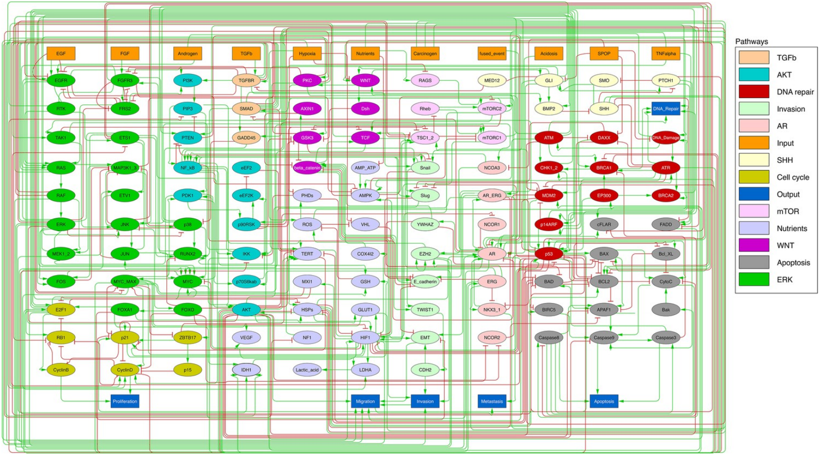


Some pictures of BNs



What do we do with those things?

Three main kinds of study (amongst others):

Synthesis Given some behaviour of the BN (e.g. trajectories) and some of the underlying graph, can we reconstruct the BN?

Control Given a BN, can we manipulate it to obtain a certain behaviour (e.g. reach a particular stable state)?

Analysis Given partial information about the BN (e.g. the graph, the nature of local functions), what can we say about it?

A transformation of $\mathbb{B}^n$

A (Boolean) configuration is $x = (x_1, \ldots, x_n) \in \mathbb{B}^n$.

A Boolean network (BN) of dimension n is a mapping $f : \mathbb{B}^n \to \mathbb{B}^n$.
It can be decomposed as

$$f = (f_1, \ldots, f_n), \quad \text{where } f_i : \mathbb{B}^n \to \mathbb{B} \ \forall i$$

We denote the set of BNs of dimension n as $\mathrm{F}(n)$.
Example of a BN in F(3):

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

$$f_1(x) = x_1x_2 \vee x_1x_3 \vee x_2x_3$$
$$f_2(x) = x_1$$
$$f_3(x) = \neg(x_1x_2 \vee x_1x_3 \vee x_2x_3).$$

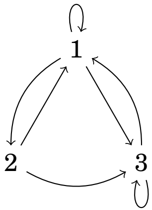
Interaction graph

The local function f_j depends essentially on x_i if there exist two configurations a, b s.t.

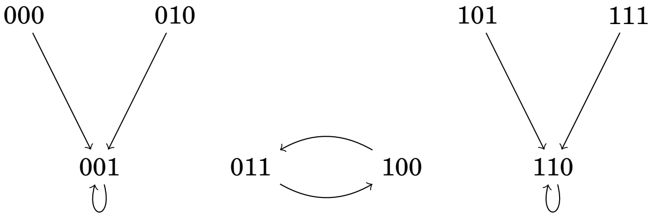
$$a_{-i} = b_{-i}, \quad f_j(a) \neq f_j(b).$$

The interaction graph of f is the graph $G(f) = (V = [n], E)$, where $(i,j) \in E$ iff f_j depends essentially on x_i.

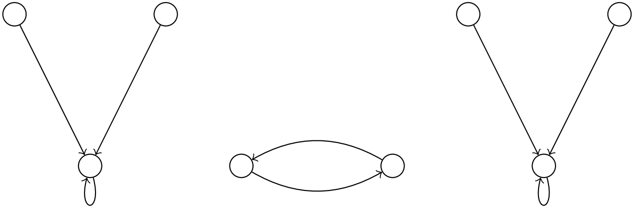
$$\begin{aligned} f_1(x) &= x_1x_2 \vee x_1x_3 \vee x_2x_3 \\ f_2(x) &= x_1 \\ f_3(x) &= \neg(x_1x_2 \vee x_1x_3 \vee x_2x_3). \end{aligned}$$



(Synchronous) dynamics



If we remove the labels, we get a dynamics.



Dynamical properties

Dynamical properties include: the number of fixed points, periodic points, bijectivitiy, period, pre-period, etc.

Some classical examples:

Robert's theorem (Robert 80) If the interaction graph is acyclic, then the BN converges to a unique fixed point.

Feedback bound (Riis 07, Aracena 08) The number of fixed points is at most $2^{\tau(G(f))}$, where $\tau(G)$ is the transversal number of G.

Bijectivity (Gadouleau 18) If f is bijective, then $G(f)$ can be covered by vertex-disjoint cycles.

New trend of work (Bridoux, Perrot, Picard Marchetto, Richard 23), (Aracena, Bridoux, Gadouleau, Guillon, Perrot, Richard, Theyssier 24+) etc.: Given a dynamics, what are the interaction graphs of the BNs with that dynamics?

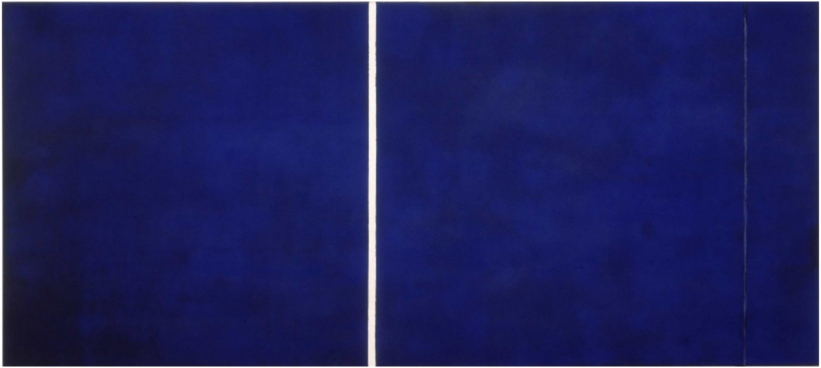
A transformation of the hypercube

There is a natural metric on $\mathbb{B}^n$, namely the Hamming metric:

$$d(x,y) = |\{i \in [n] : x_i \neq y_i\}|.$$

The hypercube is the graph where two vertices are at distance 1.

The first four hypercubes



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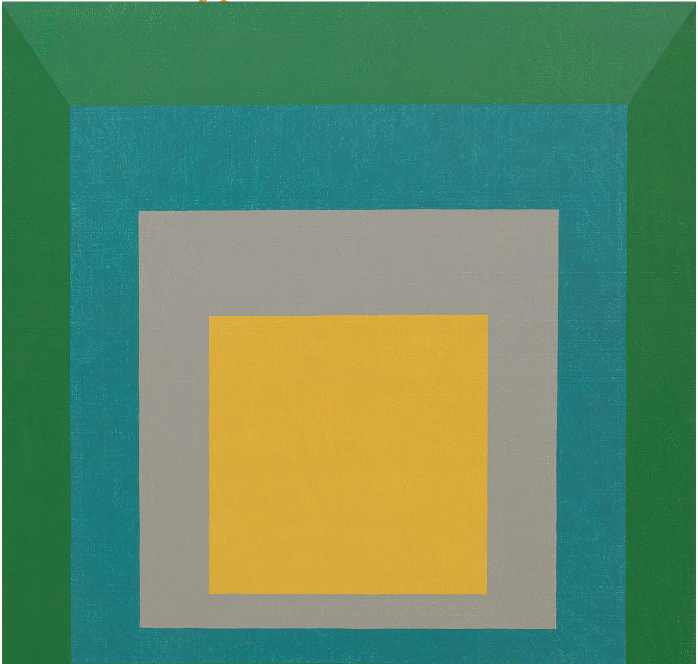

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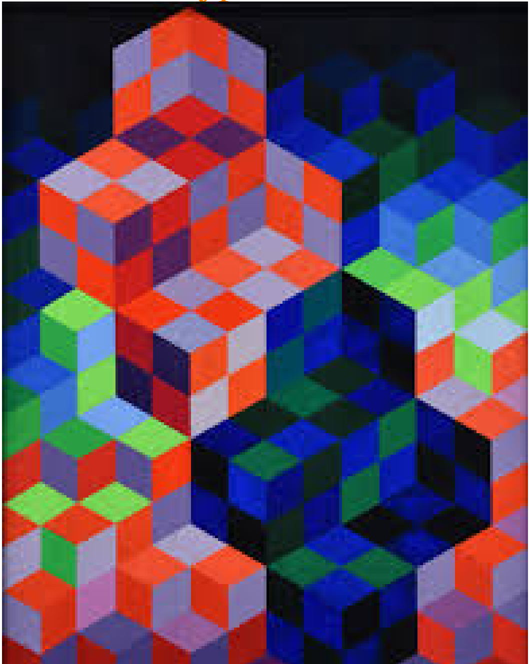

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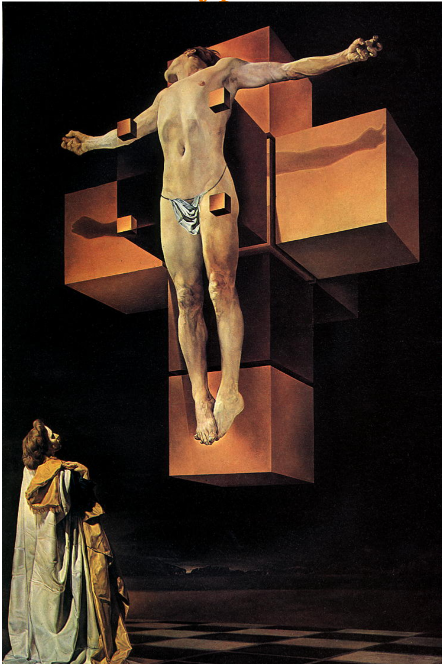


Stability of BNs and hat games

The stability of f is

$$s(f) = \min_{x \in \mathbb{B}^n} \{n - d(x, f(x))\}.$$

This can be explained via a hat game: every player guesses their hat colour; the team scores a point for every correct guess; the team then always scores at least $s(f)$ points.

(Gadouleau 18): Suppose $G(f)$ is irreflexive, then

1. $s(f) \leq n/2$,
2. $s(f) \leq \tau(G(f))$ (and in particular $s(f) = 0$ if $G(f)$ is acyclic),
3. if $s(f) = \tau(G(f))$, then there exists f' with $G(f') = G(f)$ and exactly $2^{\tau(G(f))}$ fixed points.

A transformation of the Boolean lattice

The is a natural order on $\mathbb{B}^n$, where

$$x \le y \iff x_i \le y_i \forall i.$$

Equivalently, $\mathbf{1}(x) \subseteq \mathbf{1}(y)$.

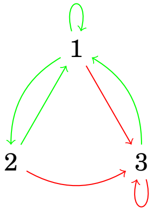
This order forms the lattice of subsets; every finite Boolean lattice is isomorphic to such a lattice of subsets.
(Gadouleau 23) generalises Robert's theorem and the feedback bound to arbitrary complete lattices.

A mapping that preserves the order is called monotone. By the Knaster-Tarski theorem, monotone mappings have a fixed point.

Signed interaction graph

Most interactions in biological systems are signed, i.e. monotonically increasing or decreasing. Hence the signed interaction graph:

$$f_1(x) = x_1x_2 \vee x_1x_3 \vee x_2x_3$$
$$f_2(x) = x_1$$
$$f_3(x) = \neg(x_1x_2 \vee x_1x_3 \vee x_2x_3).$$



Positive feedback bound (Aracena 08): f at most $2^{\tau^+(G^{signed}(f))}$ fixed points (in particular, one needs positive feedback for multistationarity)

A lot of work in that area, just ask Adrien!

A transformation of $\mathrm{GF}(2)^n$

The binary field is

$$\mathrm{GF}(2) = (\{0,1\}, + \mod 2, \times \mod 2).$$

As such, $\mathrm{GF}(2)^n$ is a vector space.

We can then focus on BNs that are linear (or affine), i.e $f(x) = xA$ or $f(x) = xA + u$ for $A \in \mathrm{GF}(2)^{n\times n}$, $u \in \mathrm{GF}(2)^n$.

Thanks to linear BNs, we can construct networks with many fixed points and sparse interaction graphs (Gadouleau, Riis 11). Affine BNs also produce nice solutions to hat games (Gadouleau 18).

Super-expansive BNs

(Bridoux, Gadouleau, Theyssier 21) A BN is expansive if it is bijective and for all $x \neq y$ and all $v \in V$, there exists $t > 0$ such that

$$f^t(x)_v \neq f^t(y)_v.$$

Equivalently, the initial configuration x can be recovered from any trace $(x_v, f(x)_v, f^2(x)_v, \dots)$.

Example: the cycle

$$f_v(x) = x_{v-1},$$

so that if $x_i \neq y_i$, we have $f^{v-i}(x)_v = x_i \neq y_i = f^{v-i}(y)_v$.

Super-expansive BNs

(Bridoux, Gadouleau, Theyssier 21) A BN is super-expansive if it is bijective and for all $x \neq y$ and all $z \neq 0$, there exists $t > 0$ such that

$$f^t(x) - f^t(y) = z.$$

In other words, the difference in the initial configuration not only propagates everywhere, but it actually takes all possible values!

How on Earth are we going to construct those?

A transformation of $\mathrm{GF}(2^n)$

But wait, $\mathrm{GF}(2^n)$ is itself a field!

Let $P(\xi)$ be a degree-n primitive polynomial over $\mathrm{GF}(2)$ and α be a root of $P(\xi)$, then

$$\mathrm{GF}(2^n) = \{x_0 1 + x_1\alpha + \cdots + x_{n-1}\alpha^{n-1} : x \in \mathrm{GF}(2)^n\} = \{0, 1, \alpha, \ldots, \alpha^{2^n-2}\}.$$

Example for $n = 3$: let $P(\xi) = \xi^3 + \xi + 1$, and α be a root of $P(\xi)$, so that $\alpha^3 = \alpha + 1$. Then

$$\mathrm{GF}(8) = \{0, 1, \alpha, \alpha^2, \alpha^3 = \alpha + 1, \alpha^4 = \alpha^2 + \alpha, \alpha^5 = \alpha^2 + \alpha + 1, \alpha^6 = \alpha^2 + 1\},$$

and $\alpha^7 = 1$.

Super-expansive

Theorem

Let α be a primitive element of $\mathrm{GF}(2^n)$ *and* $f(x) = \alpha x$*, then* f *is super-expansive.*

Proof: $x - y = \alpha^k$, $z = \alpha^i$ then

$$f^{i-k}(x) - f^{i-k}(y) = \alpha^{i-k}(x-y) = \alpha^i = z.$$

Example of super-expansive

We identify $\mathrm{GF}(2)^3$ and $\mathrm{GF}(2^3)$ as follows:

$$\begin{aligned}
000 &\sim 0\\
100 &\sim 1\\
010 &\sim \alpha\\
001 &\sim \alpha^2\\
110 &\sim \alpha+1=\alpha^3\\
011 &\sim \alpha^2+\alpha=\alpha^4\\
111 &\sim \alpha^2+\alpha+1=\alpha^5\\
101 &\sim \alpha^2+1=\alpha^6.
\end{aligned}$$

Then f is given as follows:

$$0 \mapsto 0, \quad 1 \mapsto \alpha \mapsto \alpha^2 \mapsto \alpha^3 \mapsto \alpha^4 \mapsto \alpha^5 \mapsto \alpha^6 \mapsto 1,$$

or from a Boolean network point of view:

$$000 \mapsto 000, \quad 100 \mapsto 010 \mapsto 001 \mapsto 110 \mapsto 011 \mapsto 111 \mapsto 101 \mapsto 100.$$

And so much more!

A BN is also:

1. a directed subgraph of the hypercube (the so-called asynchronous graph), so we can ask about the asynchronous dynamics, and we can do some sort of control (fixing words, reset words, etc.);
2. a computing machine, that can simulate other transformations asynchronously;
3. a vectorial (n, n)-Boolean function, in cryptography verbiage;
4. no doubt a lot more!