Structure-to-Function Theory for Boolean Networks

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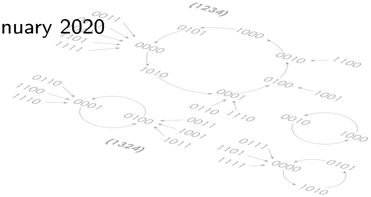
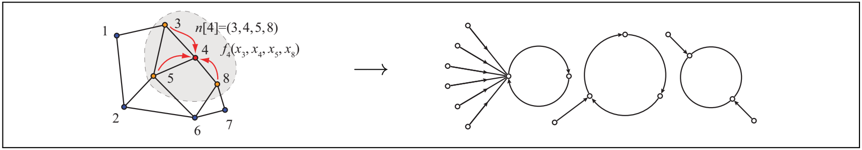


What is Structure-to-Function Theory for BNs?

- The structure of a Boolean network includes:
  - the vertex functions $(f_i)_{i=1}^n$
  - the update mechanism (e.g., parallel, sequential)
  - the variable dependency graph G (defined by the vertex functions)

- Structure-to-function theory for BNs relates the properties of the above components to properties of the associated phase spaces:



- Most of the theory and results shown in this presentation hold for generalizations of BNs (referred to as for example graph dynamical systems/automata networks/polynomial dynamical systems/finite dynamical systems/sequential dynamical systems).

Terminology and Notation: Sequential Graph Dynamical Systems (I)

- **Structure:**
  - A (vertex) function sequence $(f_i)_{i=1}^n$ with $f_i \colon K^n \longrightarrow K$ with K a finite set (for example $K = \{0, 1\}$.)
  - A corresponding function sequence $(F_i)_{i=1}^n \colon K^n \longrightarrow K^n$ defined by

$$F_i\big(x = (x_1, x_2, \ldots, x_n)\big) = (x_1, \ldots, x_{i-1}, f_i(x), x_{i+1}, \ldots, x_n) \ .$$

  - A permutation $\pi = \big(\pi_1, \ldots, \pi_n\big) \in S_n$.

Definition

The *sequential graph dynamical system map* $F_\pi \colon K^n \longrightarrow K^n$ given by $f = (f_i)_i$ and π is

$$F_\pi = F_{\pi_n} \circ F_{\pi_{n-1}} \circ \cdots \circ F_{\pi_2} \circ F_{\pi_1} \ .$$

Terminology and Notation: Sequential Graph Dynamical Systems II

Definition

The **variable dependency graph** G of $(f_i)_i$ is the simple graph with vertex set $V(G) = \{1, 2, \ldots, n\}$ and edge set $E(G)$ all undirected edges $\{i, j\}$ for which f_i depends non-trivially on x_j or f_j depends non-trivially on x_i. The symmetric group on $V(G)$ is denoted by S_G (the set of all permutation update sequences).

Definition

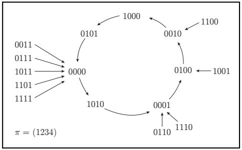
The **phase space** of $F\colon K^n \longrightarrow K^n$ is the directed graph Γ with vertex set K^n and edge set $\{(x, F(x)) \mid x \in K^n\}$.

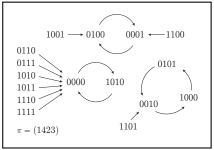
Example I: a Structure-to-Function Result for ABNs

- Boolean vertex functions $f = (f_i)_{i=1}^4$ defined by (indices modulo 4):

$$f_k(x_1, x_2, x_3, x_4) = \mathrm{nor}_3(x_{k-1}, x_k, x_{k+1}) = (1 + x_{k-1})(1 + x_k)(1 + x_{k+1}) \mod 2$$

- Dependency graph G is a square.
- Example phase spaces $\Gamma(F_\pi)$ with $\pi \in S_G$:





Theorem

For any $\pi \in S_G$ and ABN map F_π where each vertex function is a nor*-function,* $\mathrm{Per}(F_\pi)$ *is in a 1-1 correspondence with the set of independent sets of G.*

(For $I \in \mathcal{I}$ define $x_I = (x_v)_v$ by $x_v = 1$ if and only if $v \in I$.)

Example II: a Structure-to-Function Result for BNs

Definition (Threshold vertex function)

Let $K = \{0,1\}$, let $A = (a_{ij})_{i,j=1}^{n}$ be a real symmetric matrix, let $\theta = (\theta_1, \dots, \theta_n) \in \mathbb{R}^n$, and let $\mathbf{F} = (f_1, \dots, f_n)\colon K^n \longrightarrow K^n$ be the function defined coordinate-wise by

$$f_i(x_1, \dots, x_n) = \begin{cases} 0, & \text{if } \sum_{j=1}^{n} a_{ij} x_j < \theta_i \\ 1, & \text{otherwise .} \end{cases}$$

Theorem (Goles & Olivos [1])

If $\mathbf{F}$ is a BN map over a graph G where each vertex function is a generalized threshold function as above, then all $x \in \{0,1\}^n$, are forward asymptotic to a fixed point or a 2-cycle.

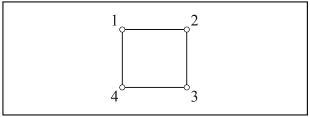
Main Presentation Outline

- **Setup:** will consider a fixed list of vertex function $(f_v)_v$ (and therefore a fixed graph G), and will vary the update sequence $\pi \in S_G$.
- **Goals:**
  - Demonstrate how one may compare maps F_π and $F_{\pi'}$ using various types of comparisons using properties of G
  - Give algorithms for deriving complete sets of update sequence representatives for exploring the diversity of dynamics under the various comparisons (i.e., equivalence notions)
- **Comparisons:**
  - **Functional equivalence** – identify of maps
  - **Dynamical equivalence** – topological conjugacy of maps
  - **Cycle equivalence** – topological conjugacy of maps restricted to their periodic points
- **Associated structures and combinatorics:**
  - The set of acyclic orientations of G, denoted by $\boxed{\mathrm{Acyc}(G)}$
  - Toric equivalence $\sim_\kappa$ on $\mathrm{Acyc}(G)$ and its set of equivalence classes $\boxed{\mathrm{Acyc}(G)/\sim_\kappa}$
  - The automorphism group of G, denoted by $\boxed{\mathrm{Aut}(G)}$ (if time permits)

Acyclic Orientations and Functional Equivalence I — $\mathrm{Acyc}(G)$

- **Question:** for $\pi, \pi' \in S_G$, when is $\mathbf{F}_\pi = \mathbf{F}_{\pi'}$?
- **Key insight**: $F_4 \circ F_1 \circ F_3 \circ F_2 = F_4 \circ F_3 \circ F_1 \circ F_2$

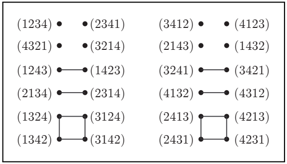
$G = \mathrm{Circle}_4$



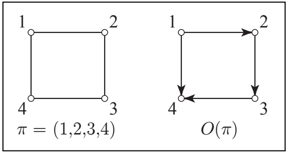
Definition ($\sim_\alpha$ on S_G)

Two permutations $\pi, \pi' \in S_G$ are α-related if they differ by exactly one transposition of two consecutive elements π_i and π_{i+1} where $\{\pi_i, \pi_{i+1}\} \notin E(G)$.
The equivalence relation $\sim_\alpha$ on S_G is the transitive and reflexive closure of the α-relation.

$U(\mathrm{Circle}_4)$



- The map $f'_G \colon S_G \longrightarrow \mathrm{Acyc}(G)$ is defined by mapping $\pi \in S_G$ to the acyclic orientation $O(\pi)$ where each edge is oriented according to π (as a linear order.)



Acyclic Orientations and Functional Equivalence II — $\mathrm{Acyc}(G)$

- Let $f = (f_i)_i$. We set $\alpha_f(G) = |\{F_\pi \mid \pi \in S_G\}|$.

Proposition

Let $f = (f_i)_i$ be a function sequence with dependency graph G.

(i) *We have $\pi \sim_\alpha \pi'$ implies $F_\pi = F_{\pi'}$.*

(ii) *The map f'_G extends to a well-defined bijection $f_G \colon S_G/{\sim_\alpha} \longrightarrow \mathrm{Acyc}(X)$ by $[\pi] \overset{f_G}{\mapsto} O(\pi)$.*

(iii) *We have $\alpha_{\mathrm{nor}}(G) = \alpha(G)$.*

- Implications and results:
  - $\mathrm{Nor}_\pi = \mathrm{Nor}_{\pi'}$ if and only if $\pi \sim_\alpha \pi'$.
  - Have a computationally efficient, graph-based, sufficient condition to guarantee equality of maps F_π and $F_{\pi'}$: if $O(\pi) = O(\pi')$ then $F_\pi = F_{\pi'}$
  - Can enumerate $\alpha(G)$ through the deletion/contraction recursion relation:

$$\alpha(X) = \alpha(X/e) + \alpha(X \setminus e)$$

  Note that $\alpha(G) = T_G(2,0)$. Here T_G is the Tutte polynomial of G. (Remark: the point $(2,0)$ is in the computationaly intractable domain (D. Welsh).)

Acyclic Orientations and Functional Equivalence III — $\mathrm{Acyc}(G)$

- Summary:
  - Have linked $\mathrm{Acyc}(G)$ to functional equivalence of ABN maps F_π
  - Have an efficient, sufficent condition to determine if $F_\pi = F_{\pi'}$ using $O(\pi)$ and $O(\pi')$
  - The condition is valid for any fixed list of vertex funtions $(f_v)_v$ for any state set K (even infinite)
  - Have an upper bound for the number of distinct maps F_π that can be constructed by varying π: $\alpha(G) = |\mathrm{Acyc}(G)|$
  - These results are also valid for directed graphs G

Cycle Equivalence

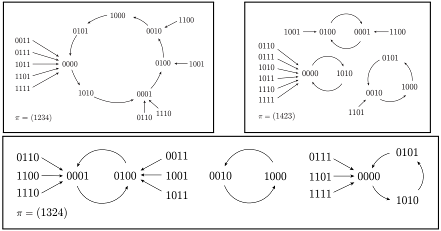
Definition (**Cycle Equivalence**)

Two maps ϕ and ψ over finite state spaces are *cycle equivalent* if there is a bijection h such that

$$\psi \circ h = h \circ \phi$$

holds when restricted to the periodic points of ϕ. (Or: multi-sets of cycle sizes are equal.)

- **Example:** Nor_π for selected permutation update sequences over $G = \mathrm{Circle}_4$:



- Note: there are 2 distinct cycle structures in the phase spaces above: $\{7(1)\}$ and $\{2(2), 3(1)\}$

Theorem (Macauley & Mortveit, Nonlinearity 2009)

Let $f = (f_i)_i$ be a sequence of vertex functions and assume that the state space satisfies $|K| < \infty$. For any permutation $\pi \in S_G$, the maps F_π and $F_{\mathrm{shift}(\pi)}$ are cycle equivalent.

Proof idea: $F_1 \circ (F_n \circ \cdots \circ F_2 \circ F_1) = (F_1 \circ F_n \circ \cdots \circ F_2) \circ F_1$.

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Set $P_k = \mathrm{Per}(F_{\mathrm{shift}_k(\pi)})$. The diagram

$$\begin{array}{ccc} P_{k-1} & \xrightarrow{F_{\mathrm{shift}_{k-1}(\pi)}} & P_{k-1} \\ {\scriptstyle F_{\pi(k)}}\downarrow & & \downarrow{\scriptstyle F_{\pi(k)}} \\ P_k & \xrightarrow[F_{\mathrm{shift}_k(\pi)}]{} & P_k \end{array}$$

commutes for all $1 \leq k \leq n$, and $F_{\pi(k)}(P_{k-1}) \subset P_k$.
The restriction map $F_{\pi(k)} \colon P_{k-1} \longrightarrow F_{\pi(k)}(P_{k-1})$ is an injection, so $|P_{k-1}| \leq |P_k|$ and

$$|\mathrm{Per}(F_\pi)| \leq |\mathrm{Per}(F_{\mathrm{shift}_1(\pi)})| \leq \cdots \leq |\mathrm{Per}(F_{\mathrm{shift}_{n-1}(\pi)})| \leq |\mathrm{Per}(F_\pi)| \,.$$

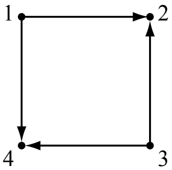
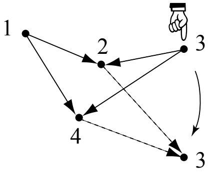
All inequalities are equalities, and since the graph and state space are finite, all the restriction maps $F_{\pi(k)}$ are bijections.

Cycle Equivalence - III

- **Observation 1:** if two permutations $\pi, \pi' \in S_G$ differ by (*i*) a sequence of consecutive, non-adjacent transpositions and (*ii*) cyclic shifts, then F_π and $F_{\pi'}$ are cycle equivalent. If π, π' are related in this manner, then we say they are *torically equivalent*.

- **Observation 2:** toric equivalence of permutations is succinctly captured through sequences of *source-to-sink conversions* of acyclic orientations.

- **Example:**

$O(\pi = (1, 3, 2, 4)) =$   $= O(\pi' = (3, 2, 4, 1))$

Definition (Toric equivalence $\sim_\kappa$ on $\mathrm{Acyc}(G)$)

For acyclic orientations $O, O' \in \mathrm{Acyc}(G)$ we say that O is κ-related to O' if O can be converted to O' by converting exactly one source vertex $v \in G$ of O to a sink.
The *toric equivalence* relation $\sim_\kappa$ on $\mathrm{Acyc}(G)$ is the transitive- and reflexive closure of the κ-relation.

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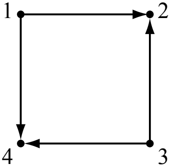

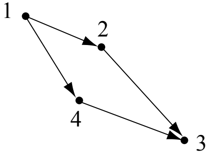

$= O(\pi' = (3, 2, 4, 1))$

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Combinatorics and Dynamics Related to Toric Equivalence

- We set $\kappa(G) = |\mathrm{Acyc}(G)/\sim_\kappa|$, the number of toric equivalence classes.

- By the previous theorem, $\kappa(G)$ is an upper bound for the number of distinct cycle structure that one can generate by maps of the form F_π for a fixed sequence $(f_v)_v$.

Theorem (Macauley & Mortveit, Proc. AMS.)

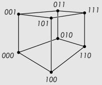
$$\kappa(G) = \begin{cases} \kappa(G_1)\kappa(G_2), & e \text{ is a bridge linking } G_1 \text{ and } G_2\,, \\ \kappa(G/e) + \kappa(G \setminus e), & e \text{ is a cycle-edge}\,. \end{cases}$$

Corollary (Macauley & Mortveit)

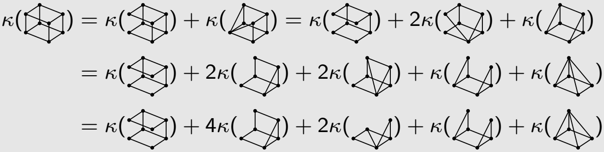
Let $f = (f_i)_i$ be a sequence of vertex functions whose dependency graph G is a tree. Then all maps F_π have the same periodic orbit structure.

- Because: for a tree G we have $\kappa(G) = 1$.

Example (Enumerations)



Let $G = Q_2^3$, the binary 3-cube for which $|S_G| = 8! = 40320$.



$$= 27 + 64 + 16 + 12 + 14 = \boxed{133}$$

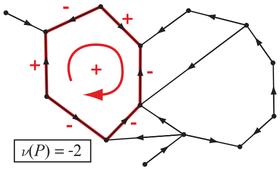
- Can show in a similar way that $\alpha(Q_2^3) = |\mathrm{Acyc}(Q_2^3)| = 1862$.
- Moreover, we have $\delta(G) = 67$ and $\bar{\alpha}(G) = 54$ and $\bar{\kappa}(Q_2^3) = 8$, but that is for another talk.
- All bounds, as they pertain to dynamics, are attained for using vertex functions $(\mathrm{nor}_i)_i$.

Determining if $\pi \sim_\kappa \pi'$ — Coleman's ν-function

- Let $P = (v_1, v_2, \ldots, v_k)$ be a (possibly closed) simple path in G. The map

$$\nu_P \colon \mathrm{Acyc}(G) \longrightarrow \mathbb{Z}$$

is defined by $\nu_P(O) = n_P^+(O) - n_P^-(O)$ where n_P^+ (resp. n_P^-) is the number of edges of the form $\{v_i, v_{i+1}\}$ in G oriented as (v_i, v_{i+1}) $\big($resp. $(v_{i+1}, v_i)\big)$ in O.



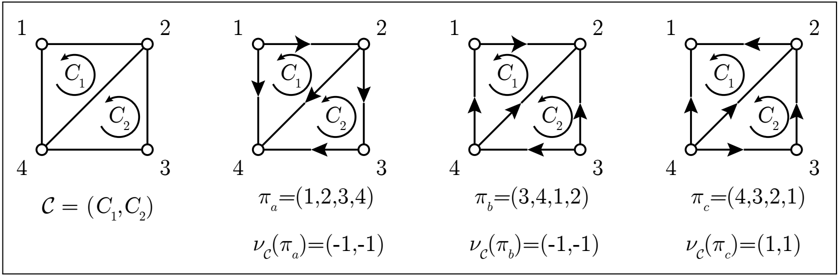
Lemma

Let C be a simple, closed path in the simple graph G. The map ν_C induces a map $\nu_C^* \colon \mathrm{Acyc}(G)/\!\sim_\kappa \longrightarrow \mathbb{Z}$.

Determining if $\pi \sim_\kappa \pi'$, thus implying that F_π and $F_{\pi'}$ are cycle equivalent.

Proposition (Macauley & Mortveit, EJC.)

Let $\mathcal{C} = (C_1, \ldots, C_m)$ be a cycle basis of G. Extended to $\mathcal{C}$, the function $\nu^*_{\mathcal{C}}$ is complete invariant for κ-equivalence



- **Implications:**
  - The map $\nu^*_{\mathcal{C}}$ provides a computationally efficient method to assess if $\pi \sim_\kappa \pi'$, and in turn:
  - We have a computationally efficient, graph/sequence-based, sufficient condition to test if F_π and $F_{\pi'}$ are cycle equivalent.

Constructing a complete phase space atlas for cycle structures

Proposition (Macauley & Mortveit, Proc. AMS)

Let $\mathrm{Acyc}_v(G)$ be the subset of $\mathrm{Acyc}(G)$ consisting of all elements where the vertex v is the unique source. For any fixed vertex v of a connected graph G, there is a bijection

$$\phi_v\colon \mathrm{Acyc}_v(G) \longrightarrow \mathrm{Acyc}(G)/\!\sim_\kappa \;.$$

▶ **Cycle Structure Atlas Recipe.** [Mortveit and Pederson, Math. Bull. 2019 [2]] Constructing all possible cycle structures for maps F_π under fixed vertex functions $(f_v)_v$.

- Pick a vertex v of maximal degree, and construct $\mathrm{Acyc}_v(G)$.
- For each $O \in \mathrm{Acyc}_v(G)$ pick a permutation representative π (using for example $f_G^{-1}(\mathrm{Acyc}_v(G))$).
- Determine the cycle structure of F_π.

▶ Have Python code for the above computations (see [2]):

`git@github.com:HenningMortveit/gds-framework-python.git`,

Example: gene-regulatory network for *Arabidopsis thaliana*

- Computational scaling of previous algorithm: how large networks can be handled?
- In practice, many application networks (e.g., biological) contain "parameter vertices" or are asymoptotically fixed.
- **Illustration:** Model from Demongeot et al. [3]; considers 12 genes and their associated regulatory network for the plant *Arabidopsis thaliana*
- Model class: generalized, binary, threshold GDS (same as earlier, but using their notation here)
- $W = [W_{ij}] \in \mathbb{R}^{n\times n}$ *matrix of weights*
- $\theta = [\theta_i] \in \mathbb{R}^n$ vector of *thresholds*
- GDS $F\colon K^n \longrightarrow K^n$ defined by (H the Heaviside step function):

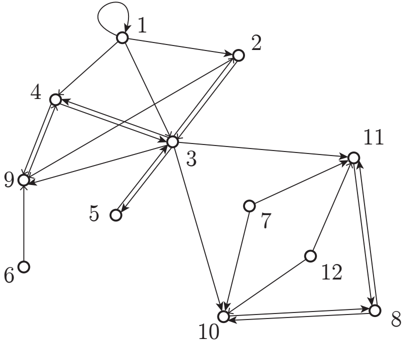
$$\big(F(x)\big)_i = H\big((\sum_j w_{ij}x_j) - \theta_i\big) \tag{1}$$

- Goal: investigate the dynamical diversity of attractors for the asynchronous update scheme using permuations.

Example: gene-regulatory network for *Arabidopsis thaliana*

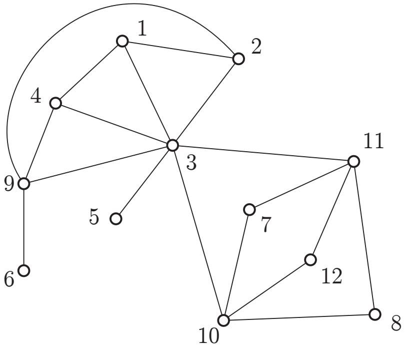
- Translation table from gene name (abbrvs.) to integers:

Abbrv.	ID	Abbrv.	ID	Abbrv.	ID	Abbrv.	ID
EMF1	1	TFL1	2	LFY	3	AP1	4
CAL	5	LUG	6	UFO	7	BFU	8
AG	9	AP3	10	PI	11	SUP	12



Example: gene-regulatory network for *Arabidopsis thaliana*

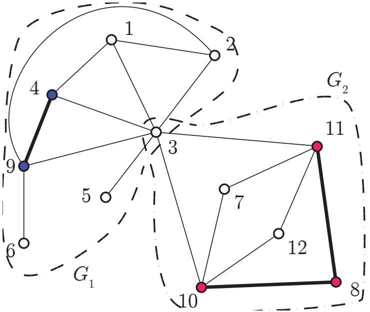
- Associated combinatorial graph (theory is identical):



- $\kappa(G) = \kappa(G_1)(G_2) = (2^4 - 2) \times (2^4 - 1) = 210$
- Thus: at most 210 distinct attractor structures (compare to $12! = 479,001,600$
- This holds for any choice of vertex functions.
- However, for the specific choice here we can do more.

Example: gene-regulatory network for *Arabidopsis thaliana*

▶ By the particular form of the GDS map H (i.e. the matrix W) many states will be fixed on attractors. For each choice of initial value for $x_1 = x_1(0)$ we obtain the following simplified graph (induced by colored vertices):



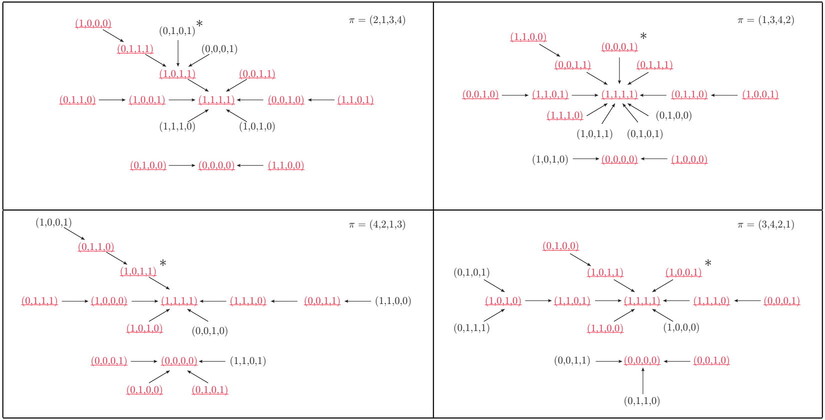
▶ The highlighted subgraph is a tree, so its κ-value is 1. Taking into account the two possible initial values for x_1 we therefore conclude that **there are at most** 2 **attractor structures for this network under sequential update schemes.**

▶ **Quiz:** What do the cycle structures look like?

Beyond Cycle Structure: Toric Equivalence and Transient Structure I

- The map $F_{\pi_1} : \Gamma_{F_\pi} \longrightarrow \Gamma_{F_{\sigma_1(\pi)}}$ is a graph morphism mapping each edge $(x, F_\pi(x)) \in \Gamma_{F_\pi}$ to the edge $(F_{\pi_1}(x), F_{\pi_1}(F_\pi(x))) \in \Gamma_{F_{\sigma_1(\pi_1)}}$.

- **Example:** the graph is Circle_4 with vertex set $\{1, 2, 3, 4\}$ plus the additional diagonal edge $\{1, 3\}$; Each vertex function is a bi-threshold functions with $k^{\uparrow} = 1$ and $k^{\downarrow} = 3$.



Beyond Cycle Structure: Toric Equivalence and Transient Structure II

Theorem (Under review.)

Assume that $x = x^{(0)} \in \mathrm{GoE}(F_\pi)$ *with maximal transient path* $P_0 = P_{F_\pi}(x^{(0)})$ *satisfies* (i) $F_\pi(x) \notin \mathrm{Per}(F_\pi)$ *and* (ii) $F_\pi^{-1}\big(F_\pi(x)\big) \subset \mathrm{GoE}(F_\pi)$*. Then* (a) *the states* $x^{(k)} \in K^n$ *defined by*

$$x^{(k)} = F_{\pi_k} \circ \cdots \circ F_{\pi_1}(x) \text{ in } \Gamma(F_{\sigma_k(\pi)}), \quad \text{with} \quad 0 \leq k \leq n-1\ ,$$

are all transient states of their respective phase spaces. Moreover, (b) *any sequence of maximal transient paths* $(P_k)_k$ *with* P_k *containing* $x^{(k)}$ *satisfies the inequality*

$$|\ell(P_k) - \ell(P_0)| \leq 1\ ,$$

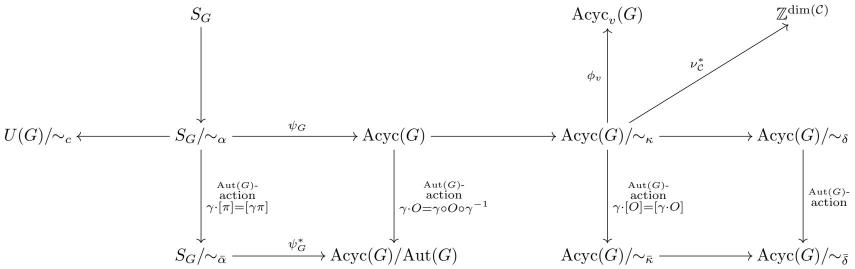
and (c)

$$\big|\{k \mid \ell(P_k) \neq \ell(P_{k+1})\}\big| \leq 2\ .$$

Corollary

For each toric equivalence class $[O(\pi)]_\kappa$ *there exists* k *such that the maximal transient length* $\ell_{\max}(F_\pi)$ *satisfies* $k-1 \leq \ell_{\max}(F_\pi) \leq k$*.*

Summary: Equivalences of Maps F_π and Overview of Structures



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