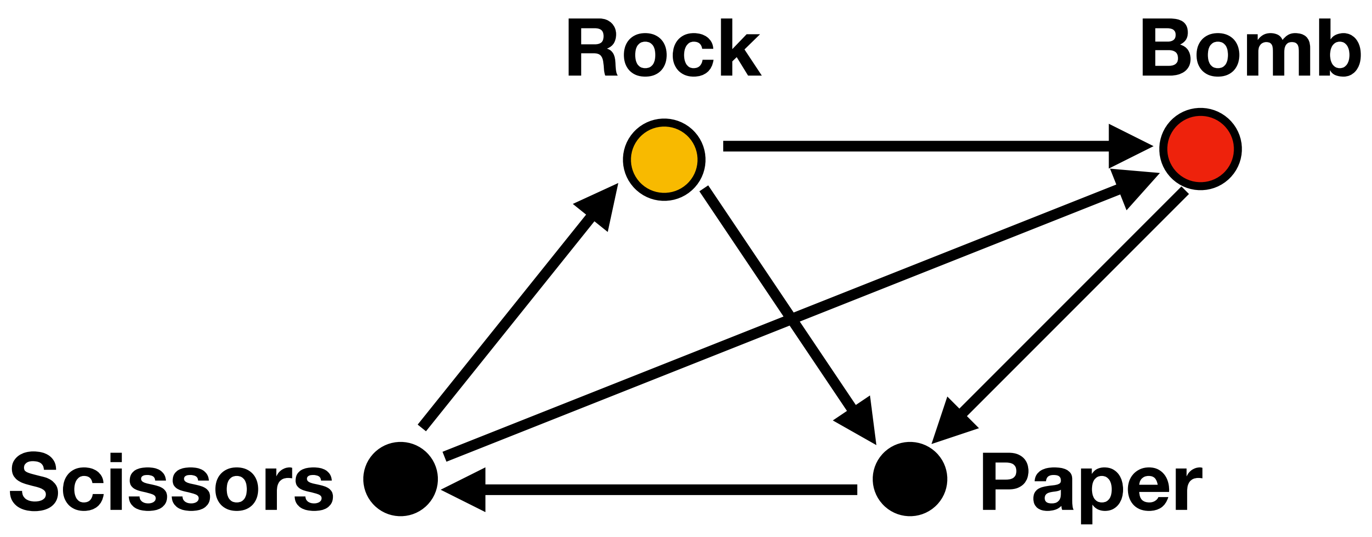
Simple models for neural computations:

competitive dynamics, domination, gluing dynamical motifs (dominoes), and inhibitory control



Carina Curto, Brown University

Janelia workshop: Grounding Cognition in Mechanistic Insight

April 30, 2025

Motivating ideas

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3. Network motifs can be composed as dynamic building blocks with predictable properties.

4. One network (by architecture/connectivity) is really many networks in the presence of neuromodulation or external control.

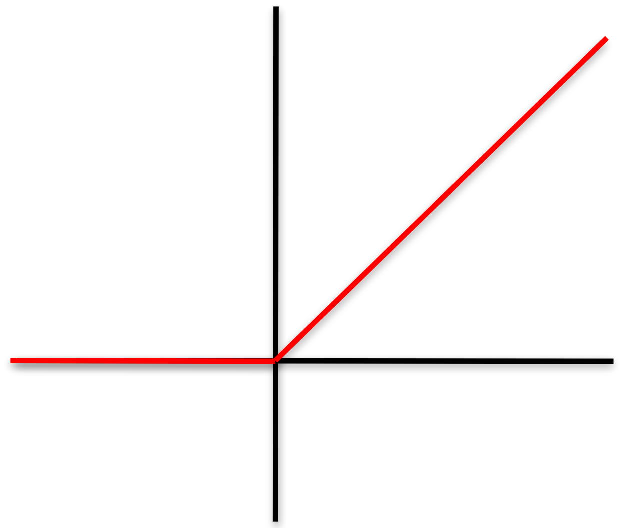
TLNs — nonlinear recurrent network models

Threshold-linear network dynamics:

$$\frac{dx_i}{dt} = -x_i + \left[\sum_{j=1}^{n} W_{ij}x_j + b_i\right]_+$$

W is an $n \times n$ matrix

$b \in \mathbb{R}^n$



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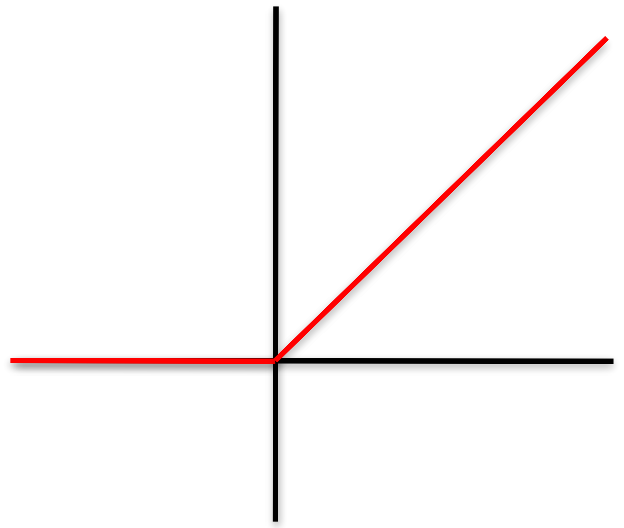

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Basic Question: Given (W,b), what are the network dynamics?

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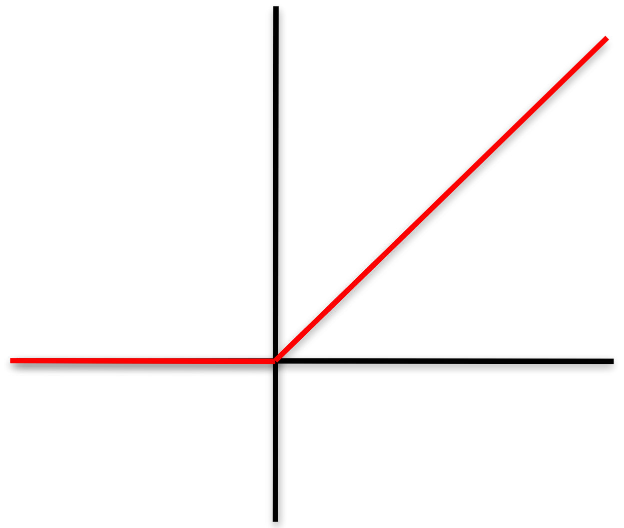


The TLN is defined by (W, b)

Linear network dynamics:

$$\frac{dx}{dt} = Ax + b$$

A is an $n \times n$ matrix

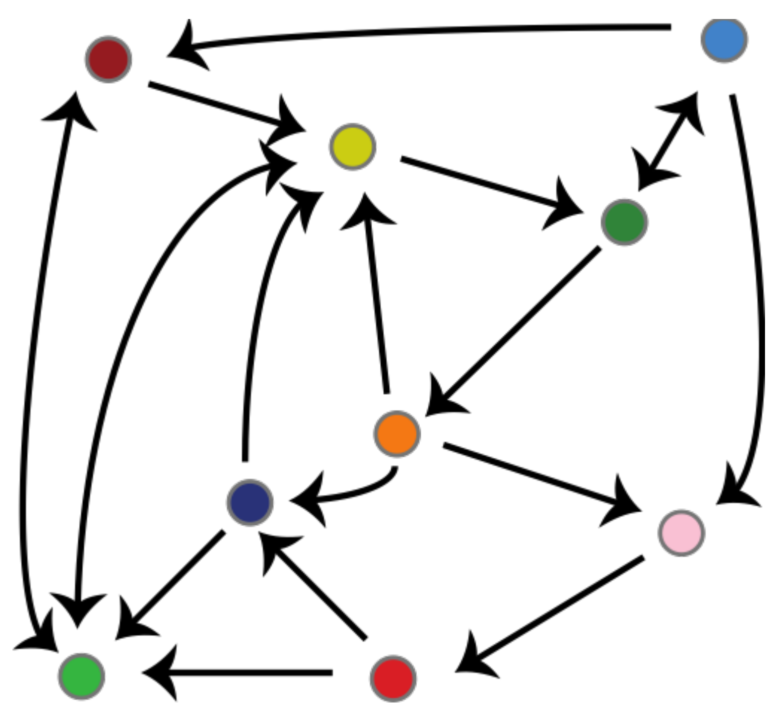
$b \in \mathbb{R}^n$

Long-term behavior is easy to infer from eigenvalues, eigenvectors — linear algebra tells us everything.

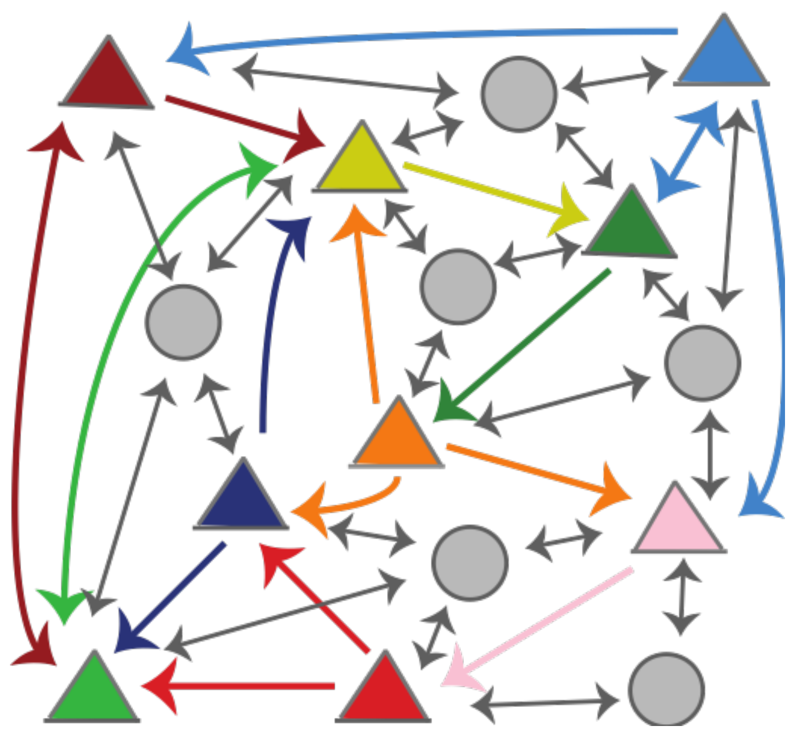
Basic Question: Given (W,b), what are the network dynamics?

The most special case: Combinatorial Threshold-Linear Networks (CTLNs)

graph G



Idea: network of excitatory and inhibitory cells



TLN dynamics:

$$\frac{dx_i}{dt} = -x_i + \left[\sum_{j=1}^{n} W_{ij}x_j + \theta\right]_+$$

Graph G determines the matrix W

$$W_{ij} = \begin{cases} 0 & \text{if } i = j \\ -1+\varepsilon & \text{if } i \leftarrow j \text{ in } G \\ -1-\delta & \text{if } i \not\leftarrow j \text{ in } G \end{cases}$$

parameter constraints:

$$\delta > 0 \quad \theta > 0 \quad 0 < \varepsilon < \frac{\delta}{\delta+1}$$

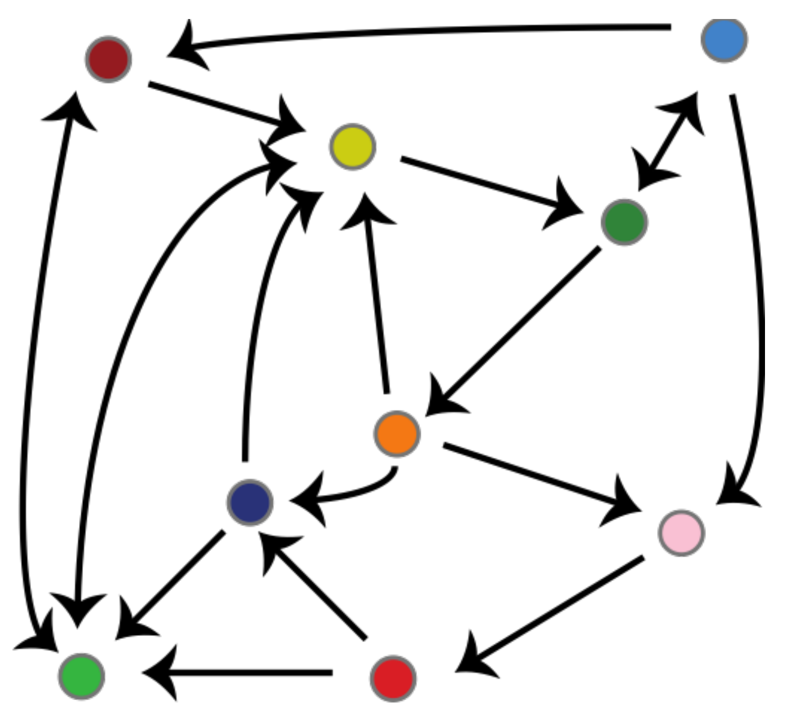
The graph encodes the pattern of weak and strong inhibition

Think: generalized WTA networks

For fixed parameters,
only the graph changes –
isolates the role of connectivity

Less special: generalized Combinatorial Threshold-Linear Networks (gCTLNs)

graph G



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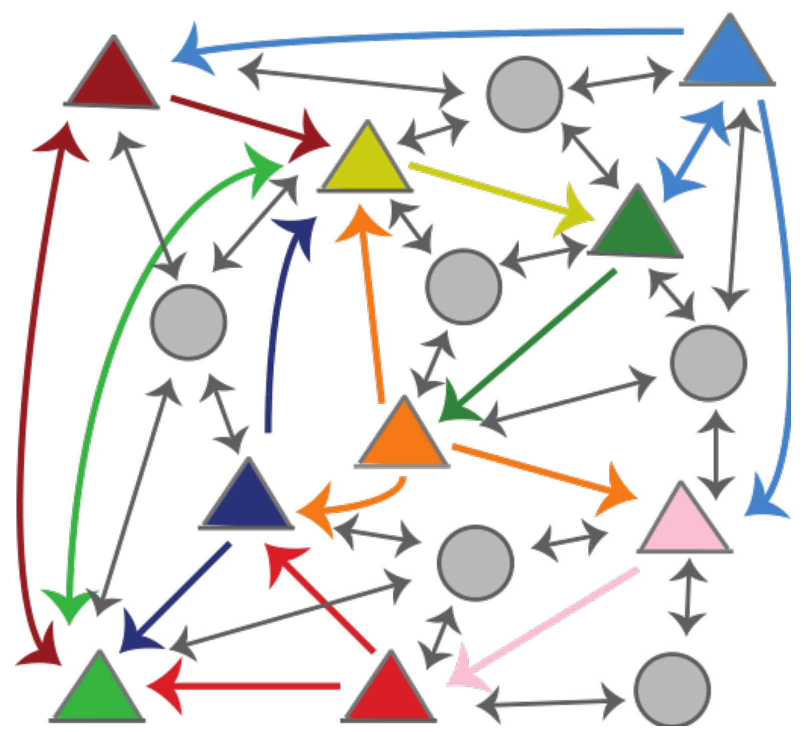

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The gCTLN is defined by a graph G and two vectors of parameters: ε, δ

$$W_{ij} = \begin{cases} -1+\varepsilon_j & \text{if } j \to i, \quad \text{weak inhibition} \\ -1-\delta_j & \text{if } j \not\to i, \quad \text{strong inhibition} \\ 0 & \text{if } i = j. \end{cases}$$

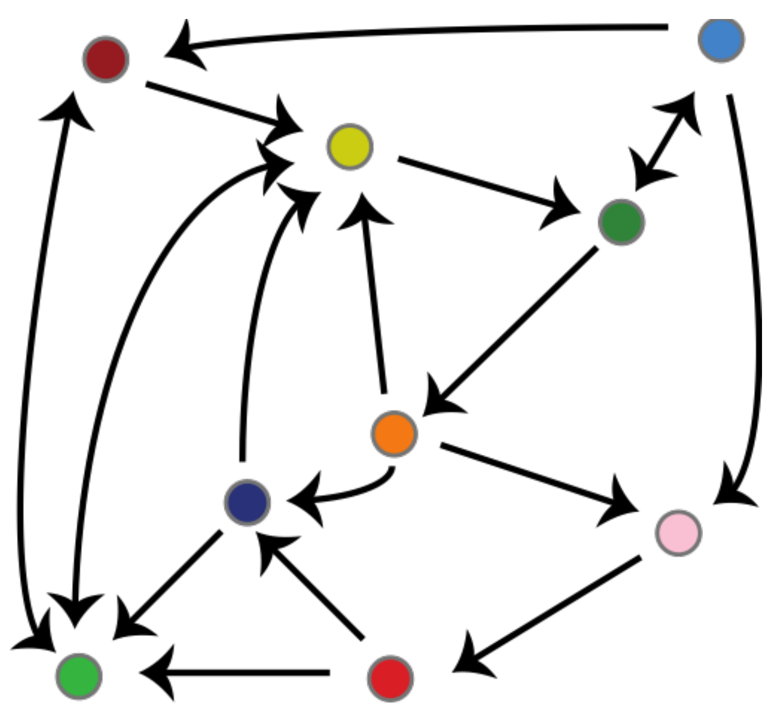
The graph encodes the pattern of weak and strong inhibition

$b_i = \theta > 0$ for all neurons

(default is uniform across neurons, constant in time)

Less special: generalized Combinatorial Threshold-Linear Networks (gCTLNs)

graph G



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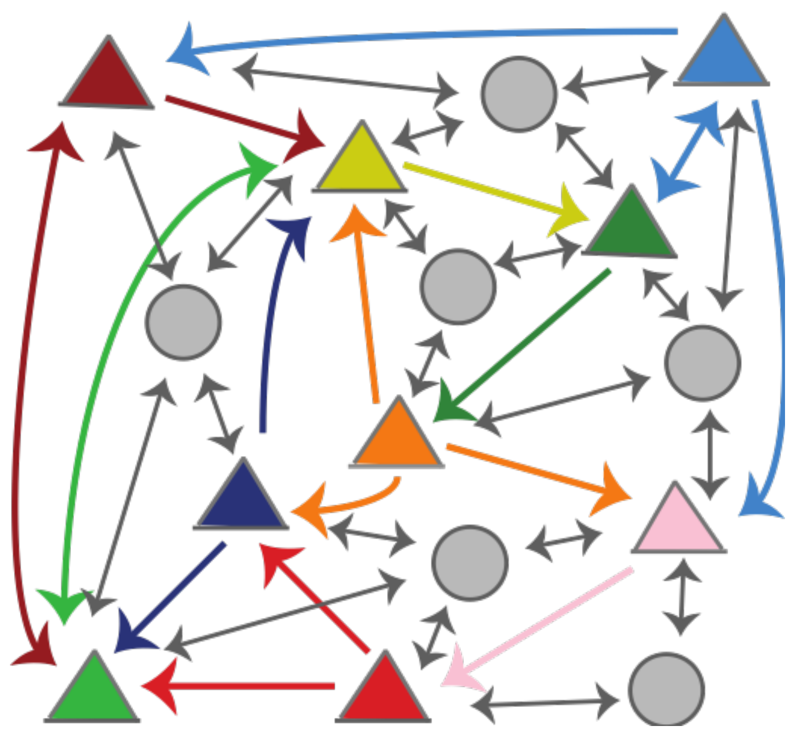

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weak inhibition (if $j \to i$)

strong inhibition (if $j \not\to i$)

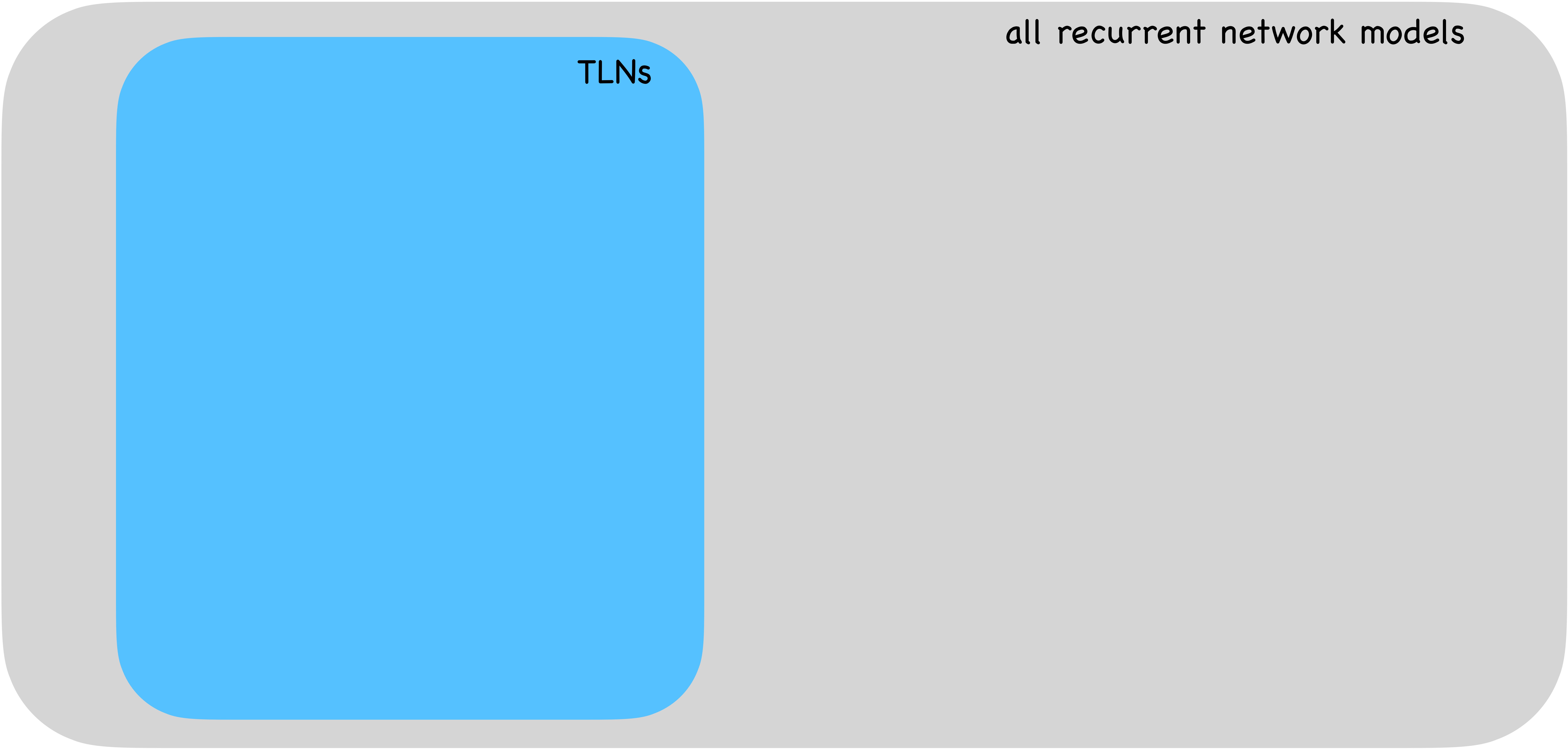
The graph encodes the pattern of weak and strong inhibition

$b_i = \theta > 0$ for all neurons

(default is uniform across neurons, constant in time)

Special case: if the parameters ε_j, δ_j are the same for all neurons, we have a CTLN.

TLNs, CTLNs, and gCTLNs



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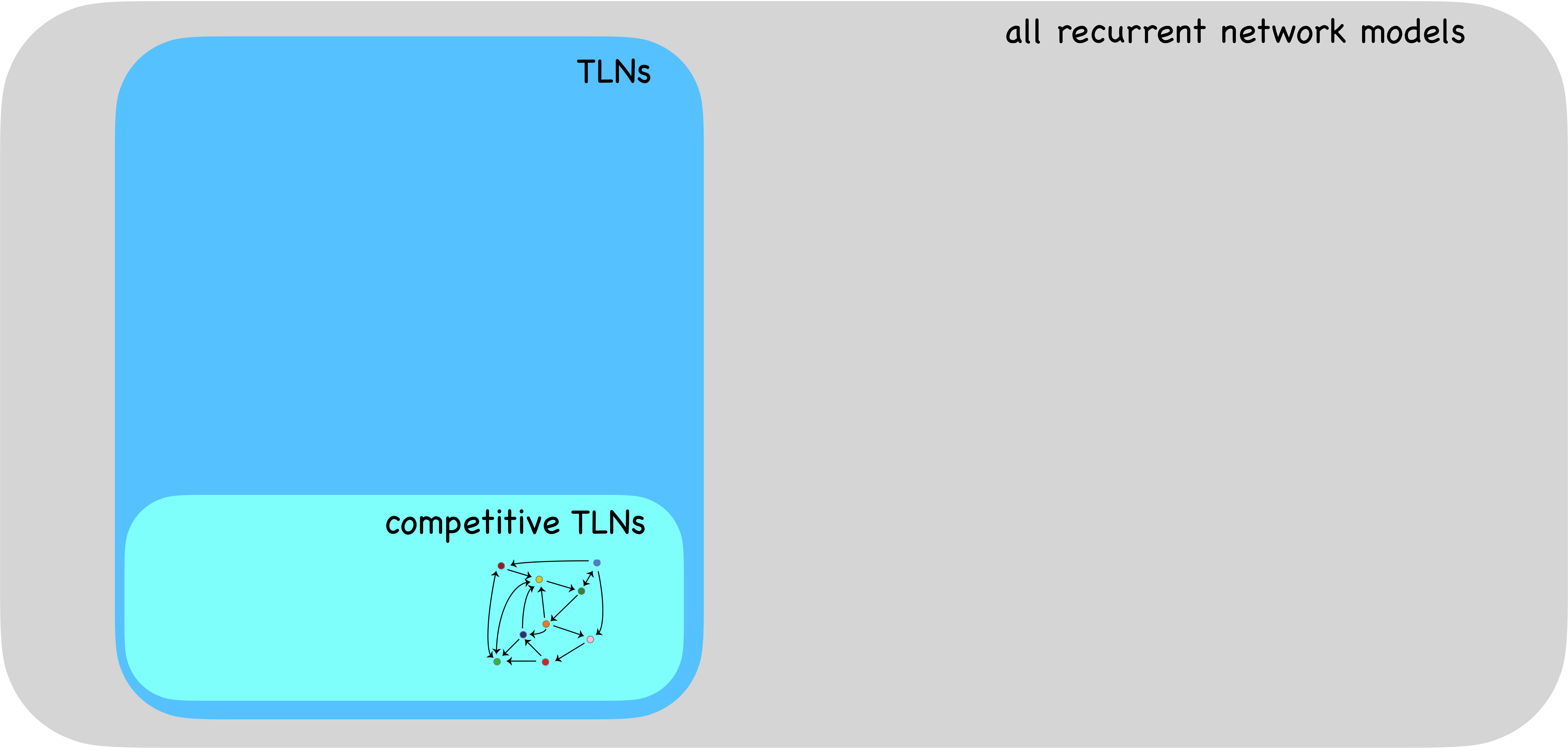

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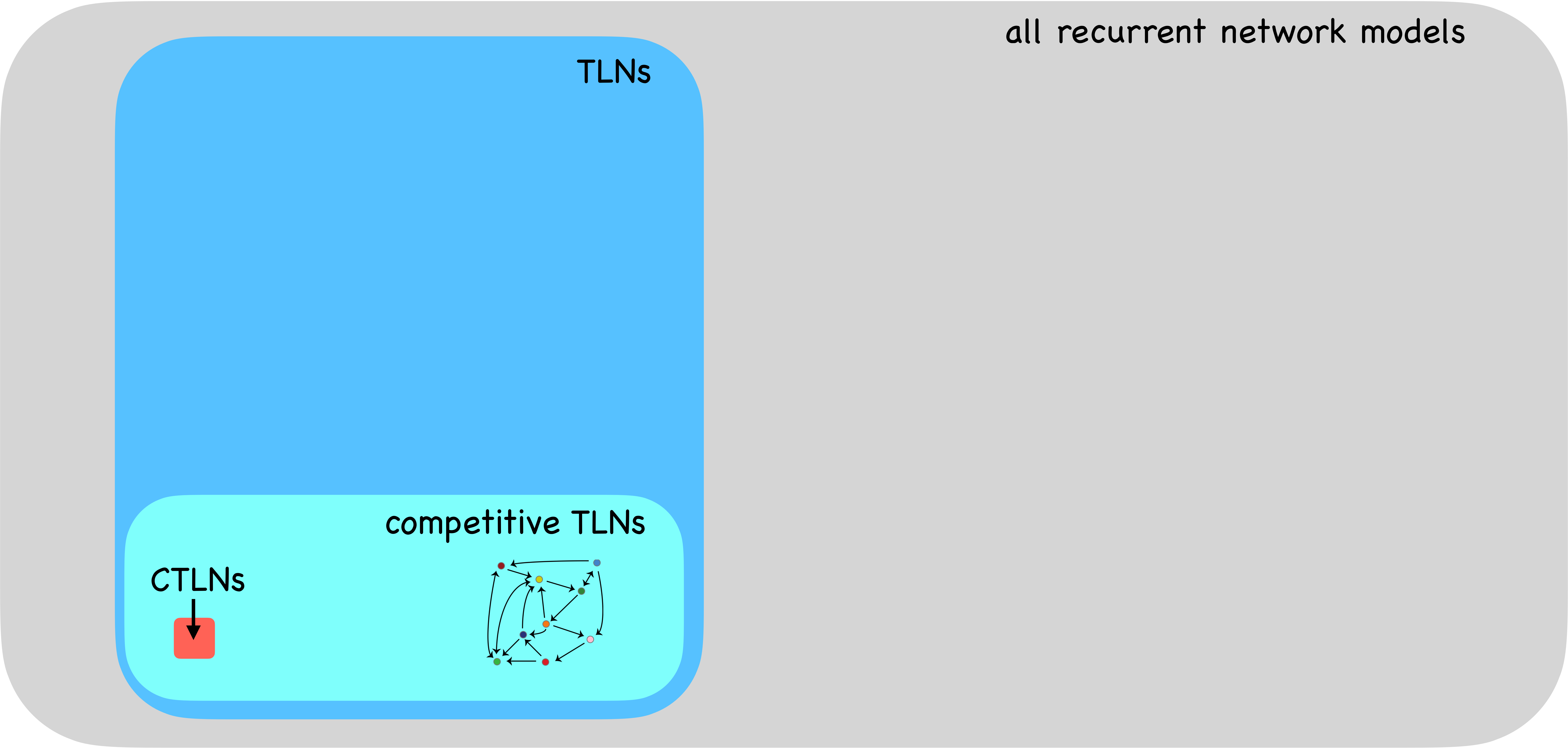

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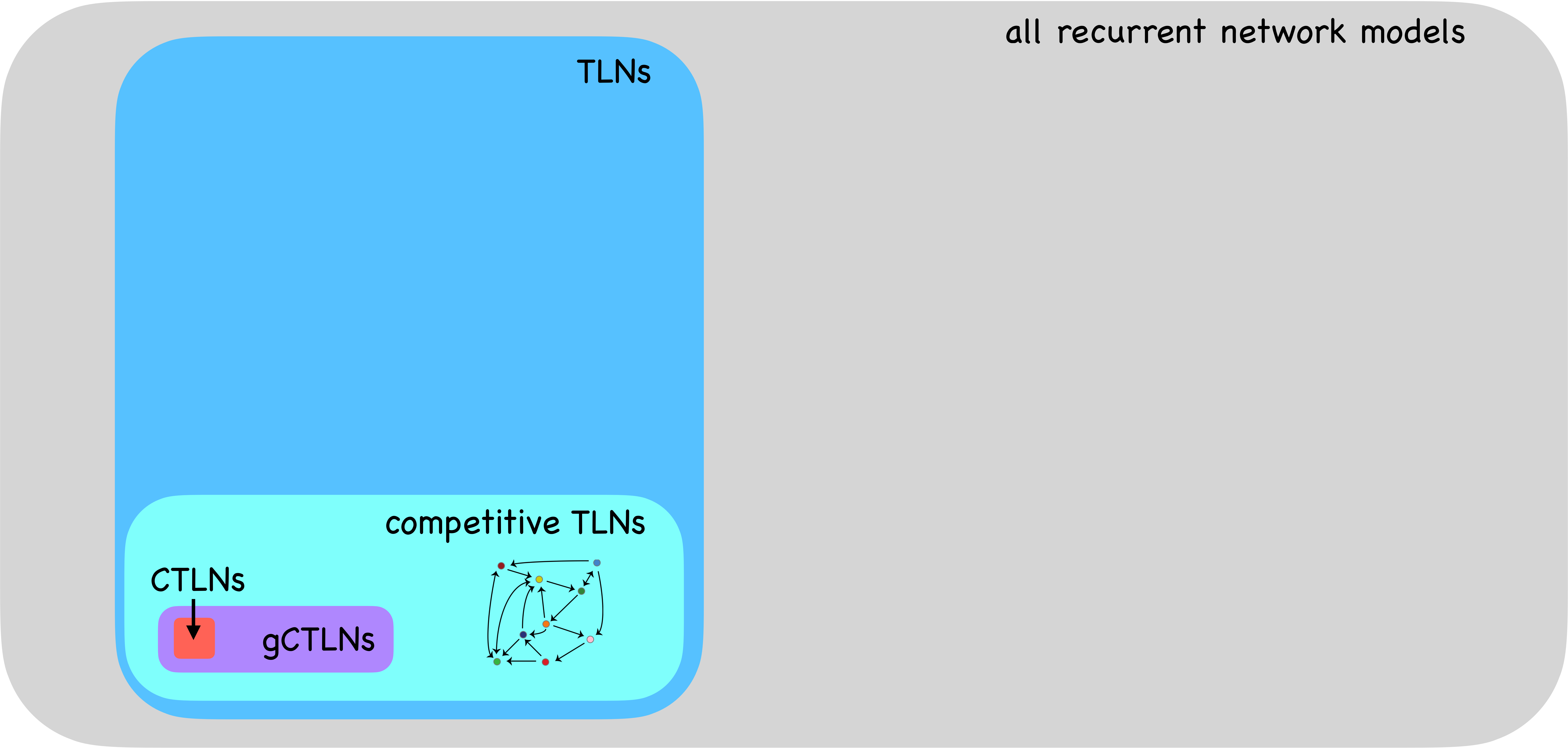

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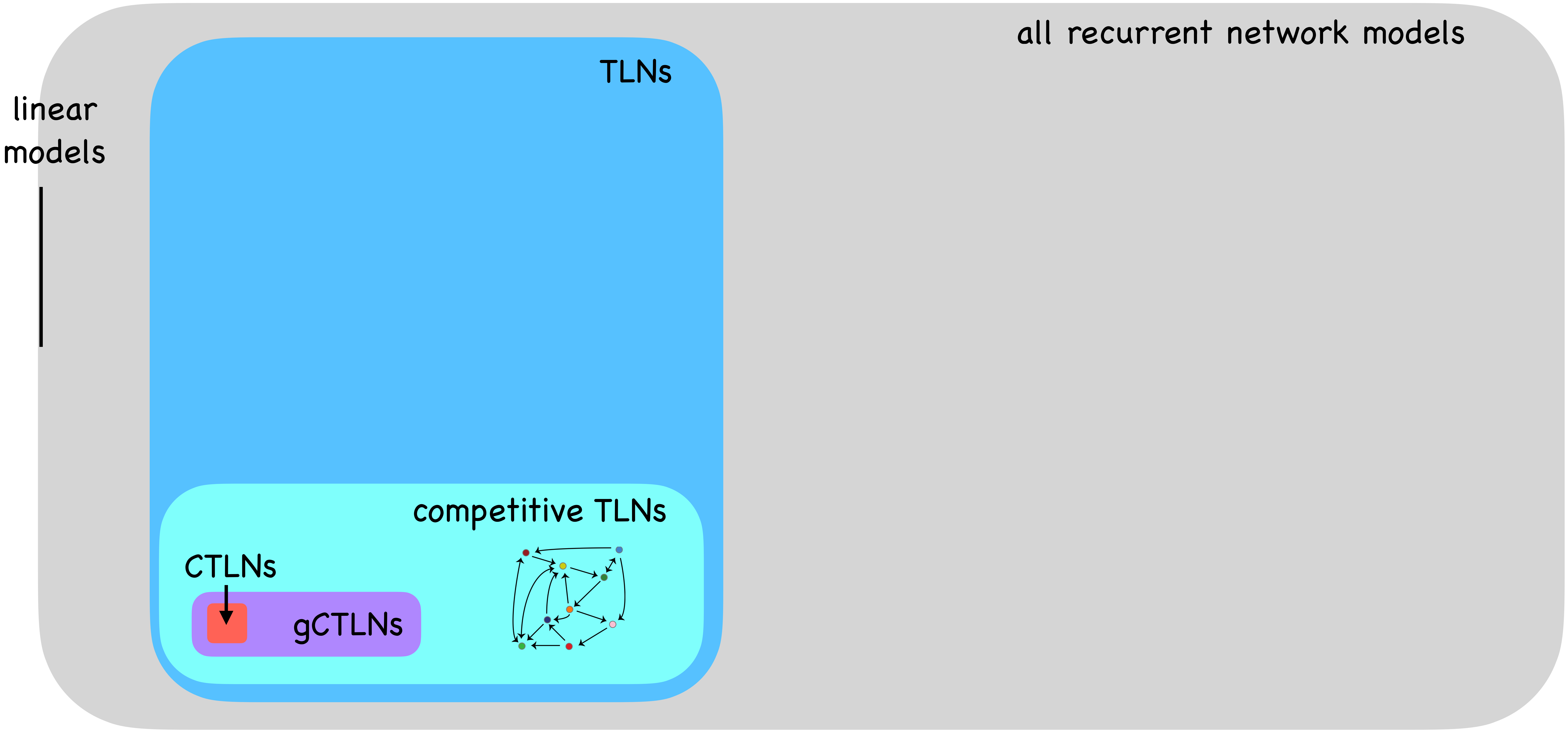
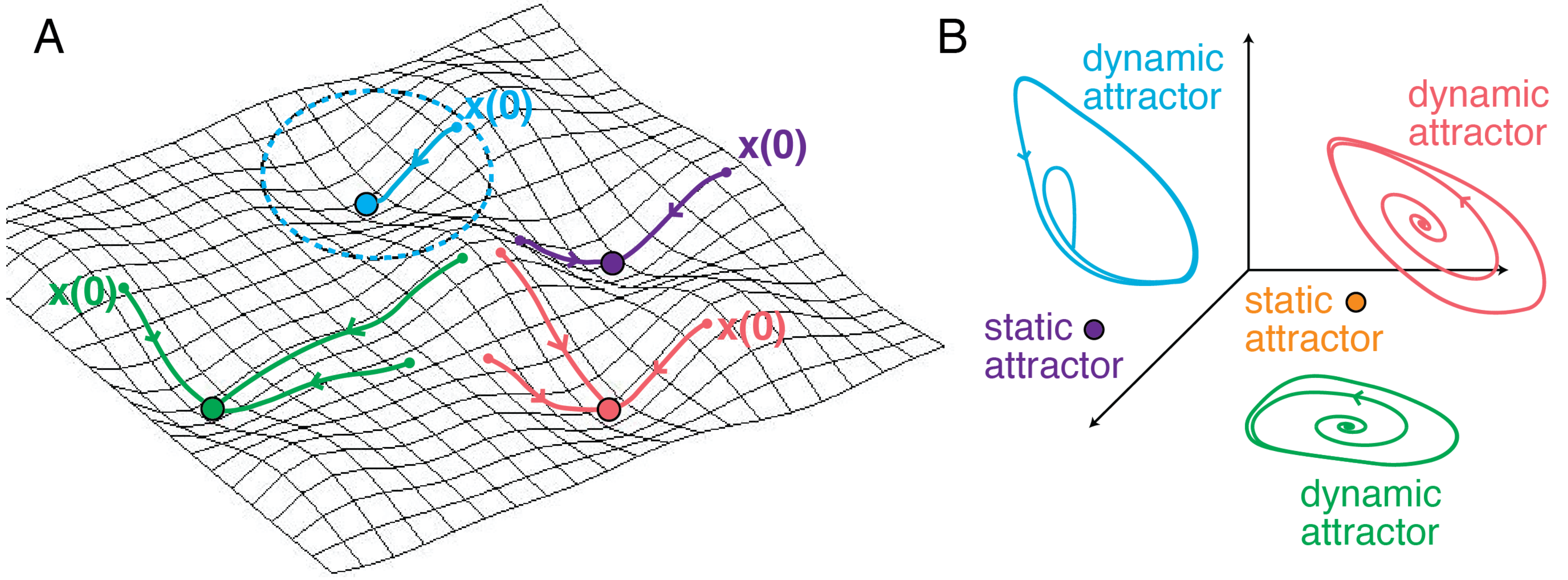


TLNs, CTLNs, and gCTLNs

1. Display rich nonlinear dynamics: multistability, limit cycles, chaos…

static attractors (fixed pts)

dynamic attractors
(correspond to certain unstable fixed pts)



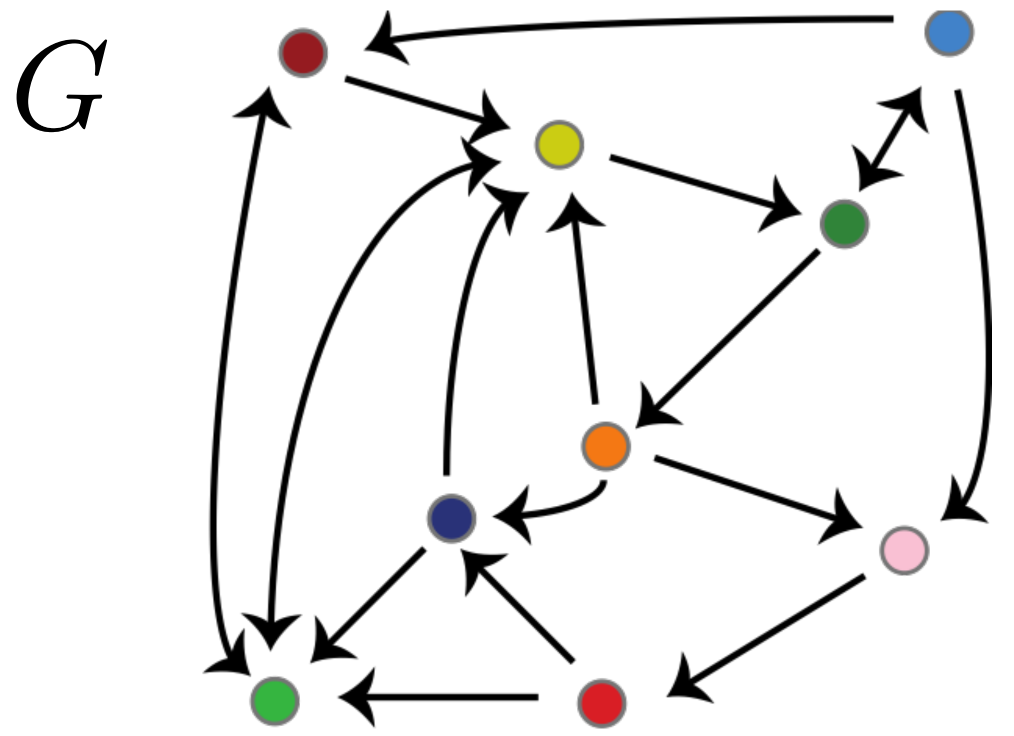
Curto & Morrison, 2023 (review paper)

TLNs, CTLNs, and gCTLNs

1. Display rich nonlinear dynamics: multistability, limit cycles, chaos…

2. Mathematically tractable: we can prove theorems directly connecting graph structure to dynamics.

graph structure



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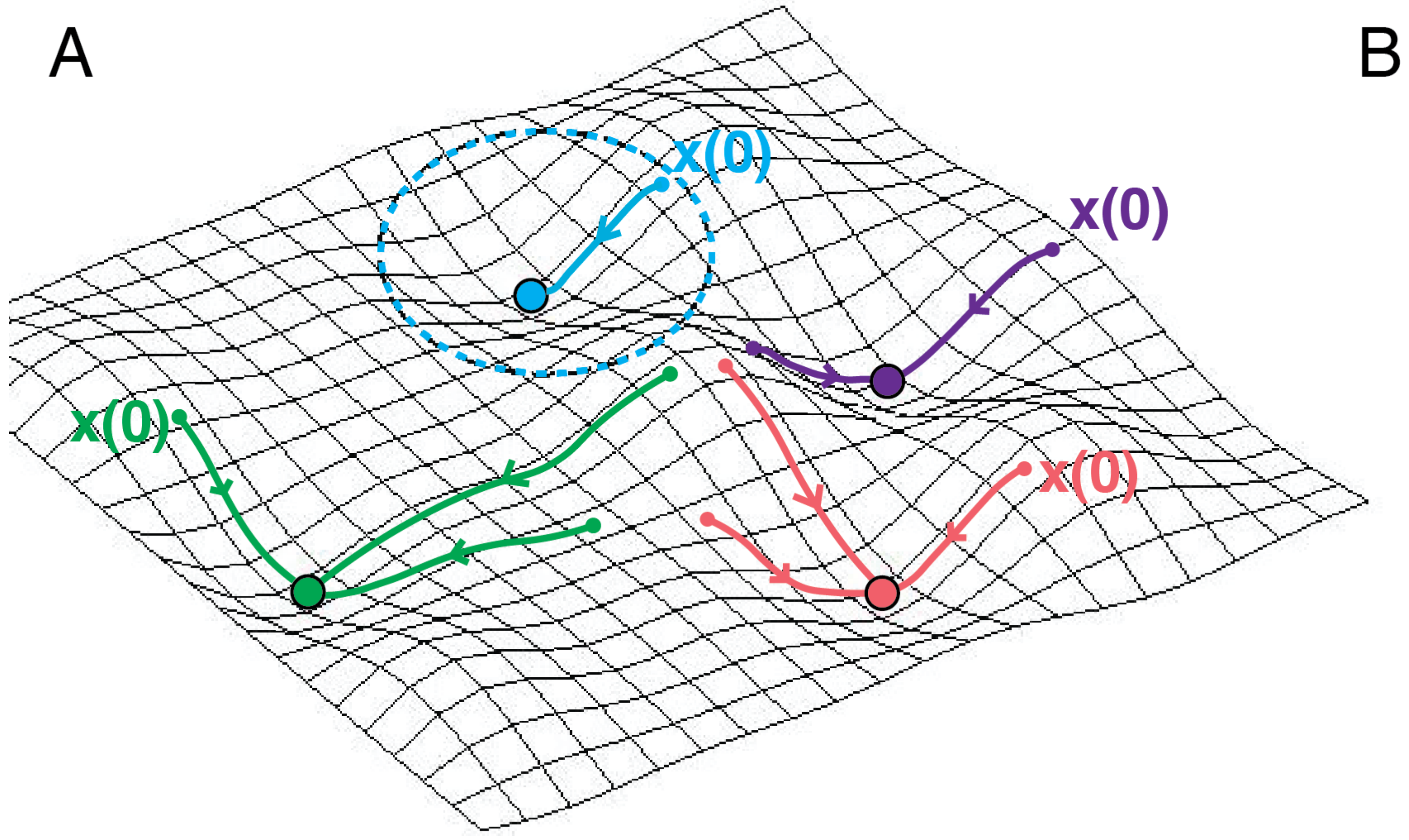

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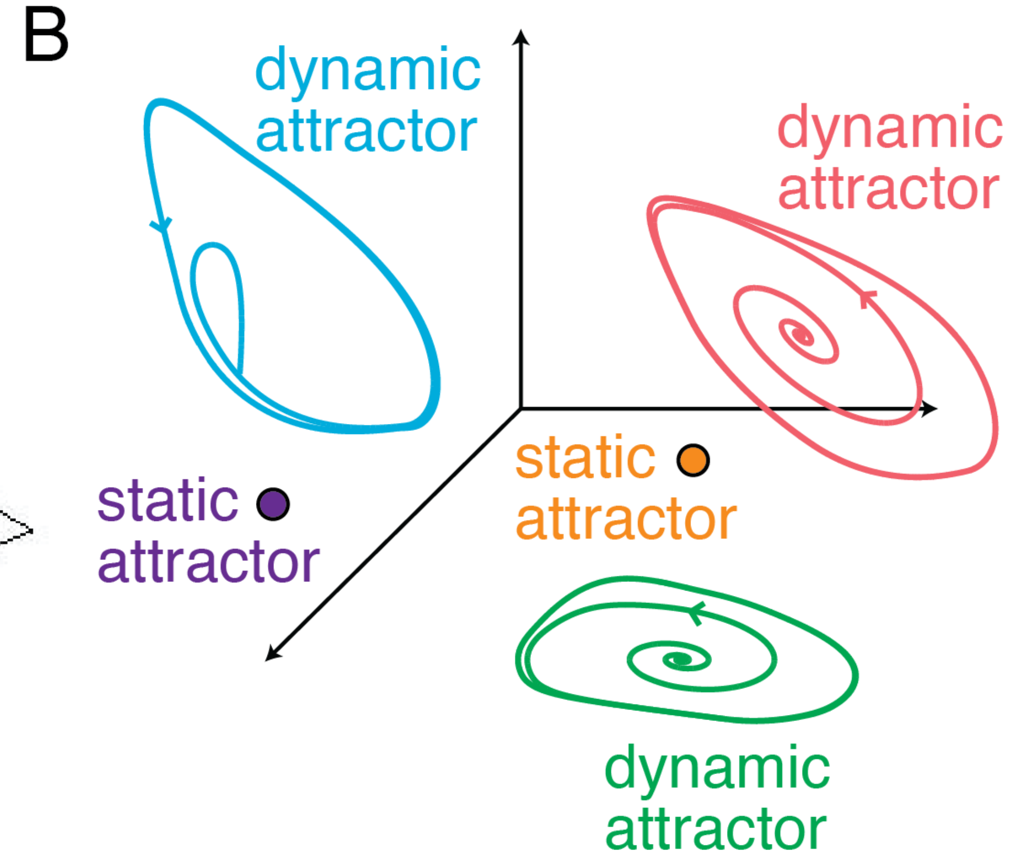


Curto & Morrison, 2023 (review paper)

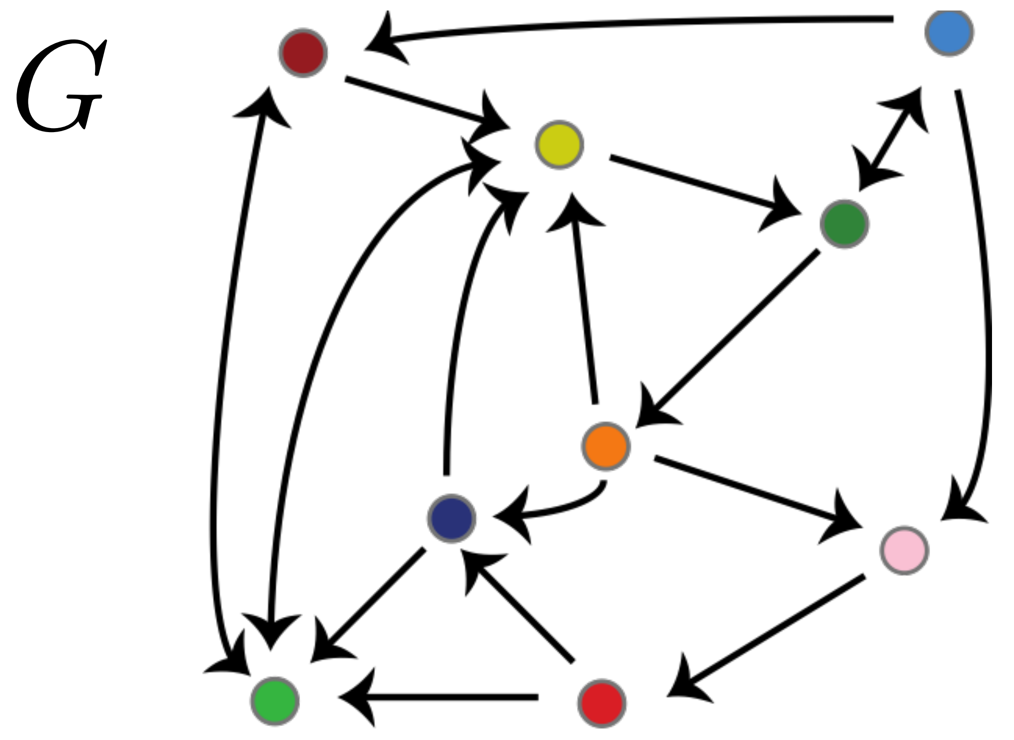
TLNs, CTLNs, and gCTLNs

1. Display rich nonlinear dynamics: multistability, limit cycles, chaos…

2. Mathematically tractable: we can prove theorems directly connecting graph structure to dynamics.

3. Both stable and unstable fixed points play a critical role in shaping the dynamics (the vector field).

graph structure



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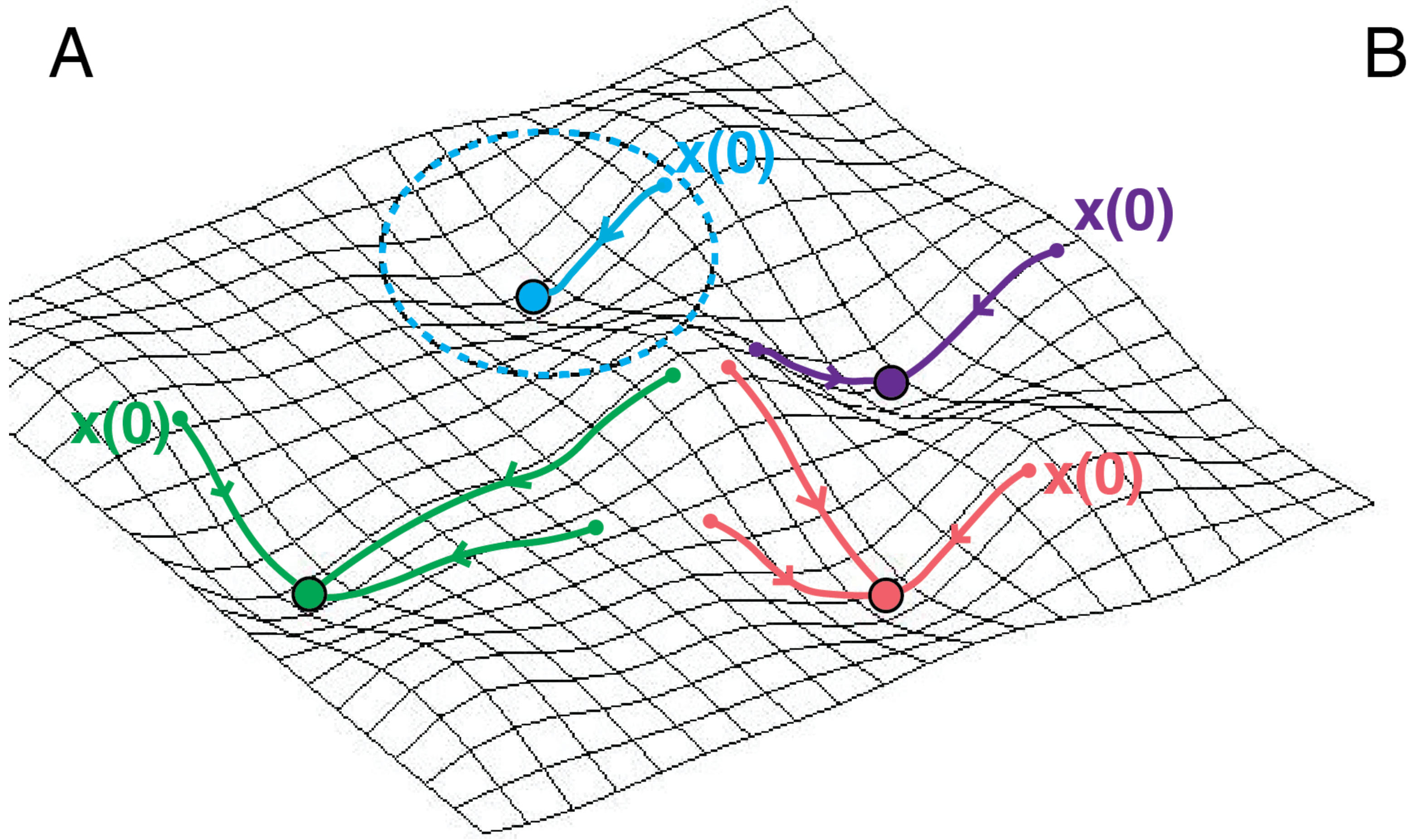

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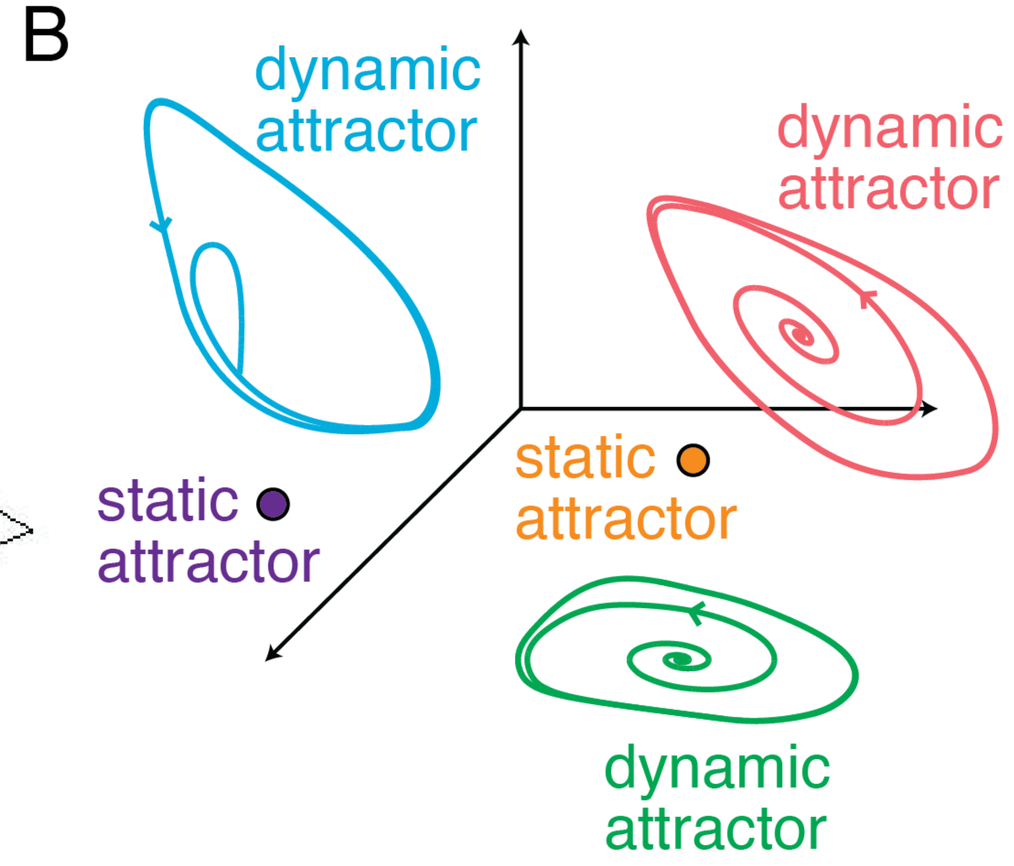


$$\mathrm{FP}(G) = \mathrm{FP}(G, \varepsilon, \delta) = \{ \text{ fixed points (stable and unstable) } \}$$

Curto & Morrison, 2023 (review paper)

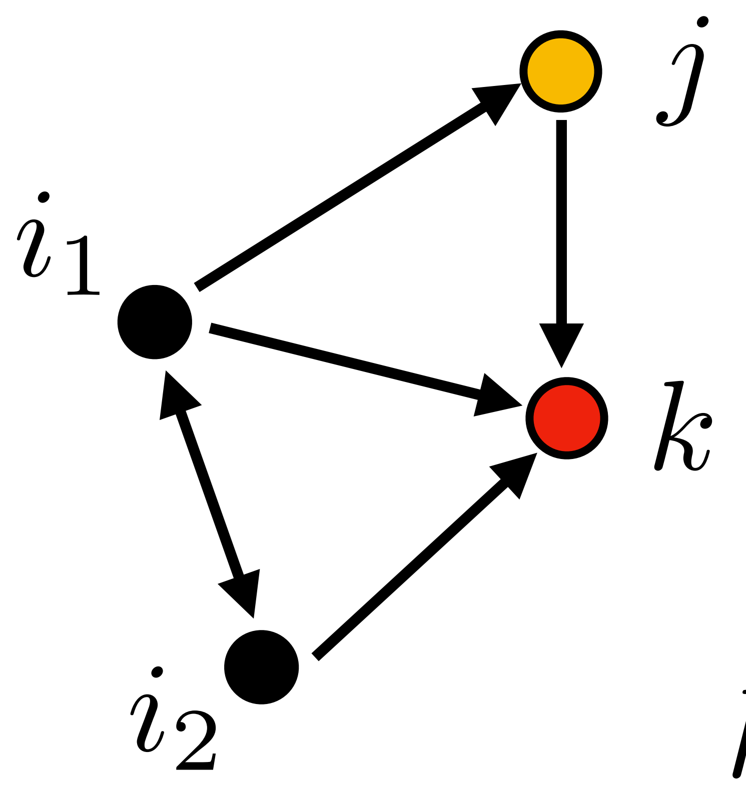
Domination

Definition 1.1. Let $j, k \in [n]$ be vertices of G. We say that k *graphically dominates* j in G if the following two conditions hold:

(i) For each vertex $i \in [n] \setminus \{j, k\}$, if $i \to j$ then $i \to k$.

(ii) $j \to k$ and $k \not\to j$.

If there exists a k that graphically dominates j, we say that j is a *dominated node* (or *dominated vertex*) of G. If G has no dominated nodes, we say that it is *domination free*.



$k > j$

"k dominates j"

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Curto, Geneson, Morrison, 2019

domination is a property of G

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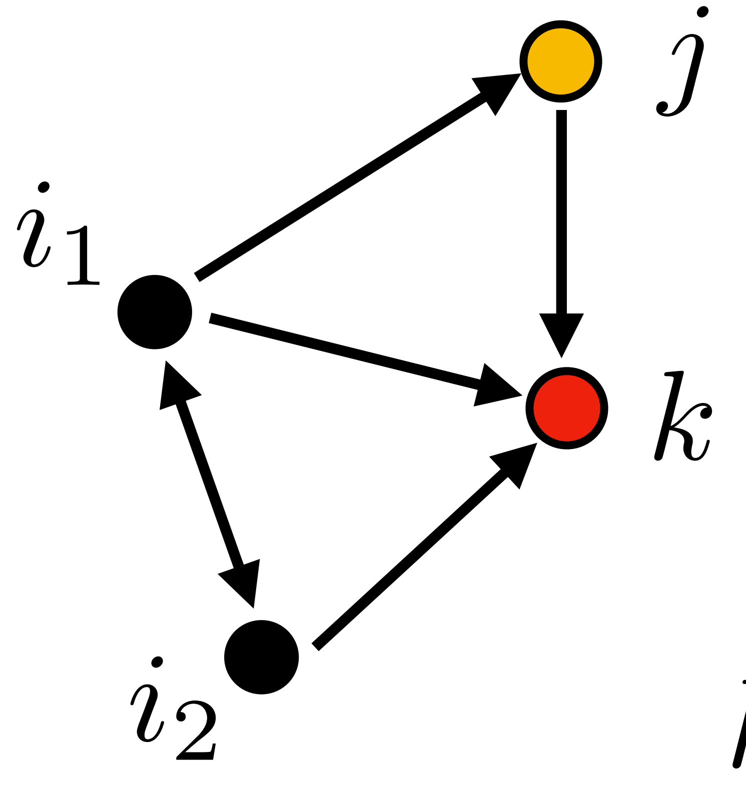

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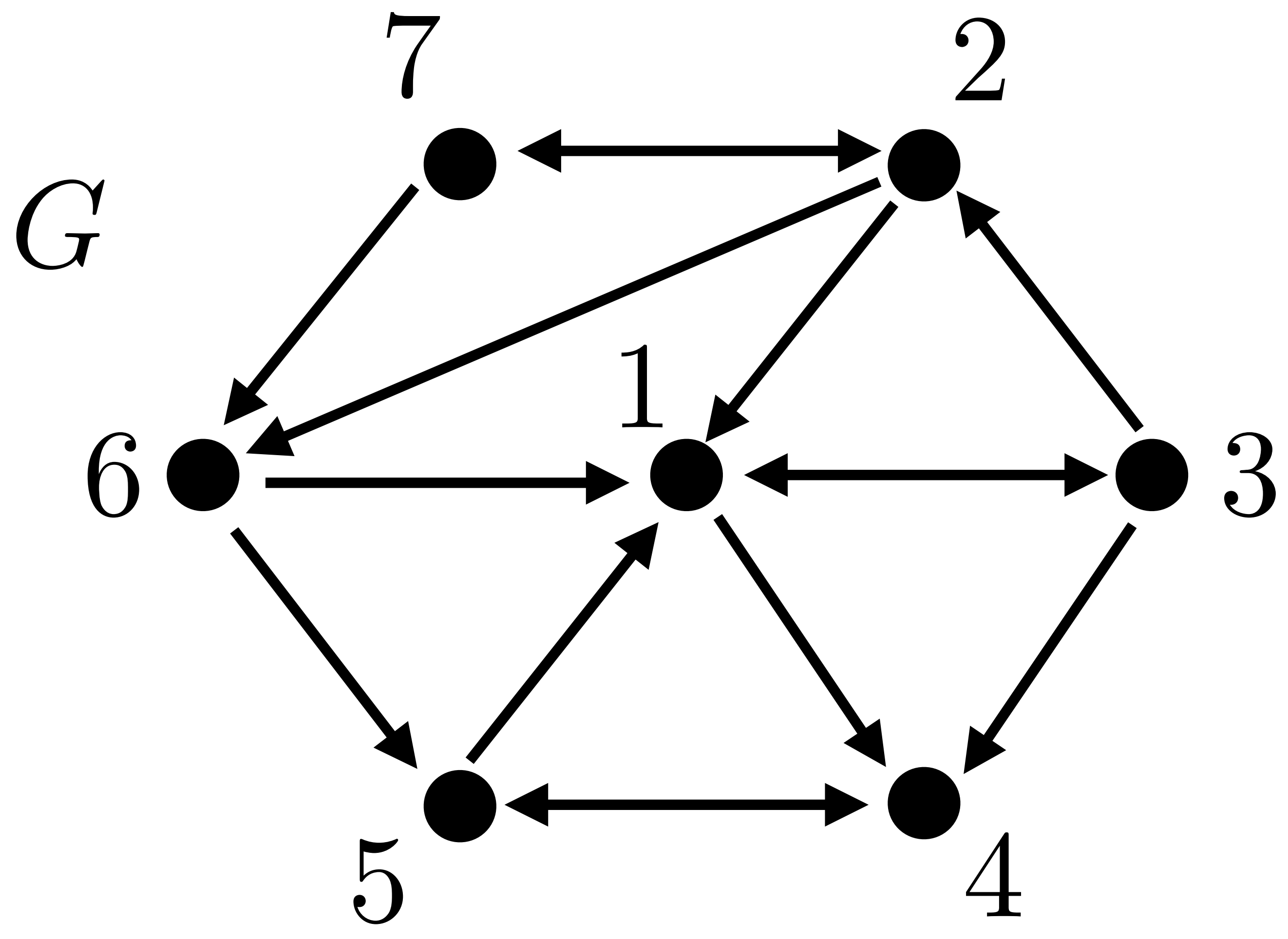

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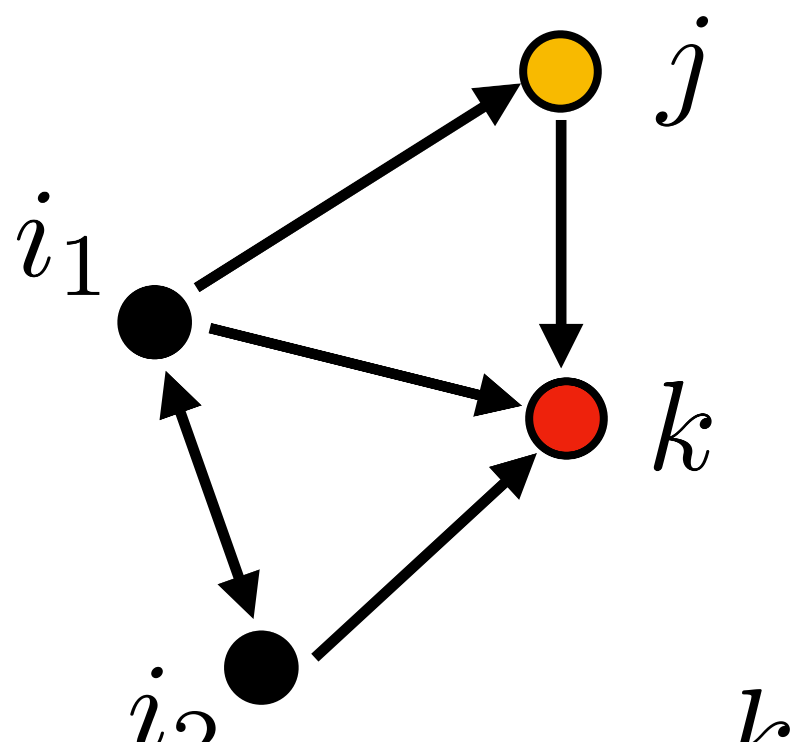

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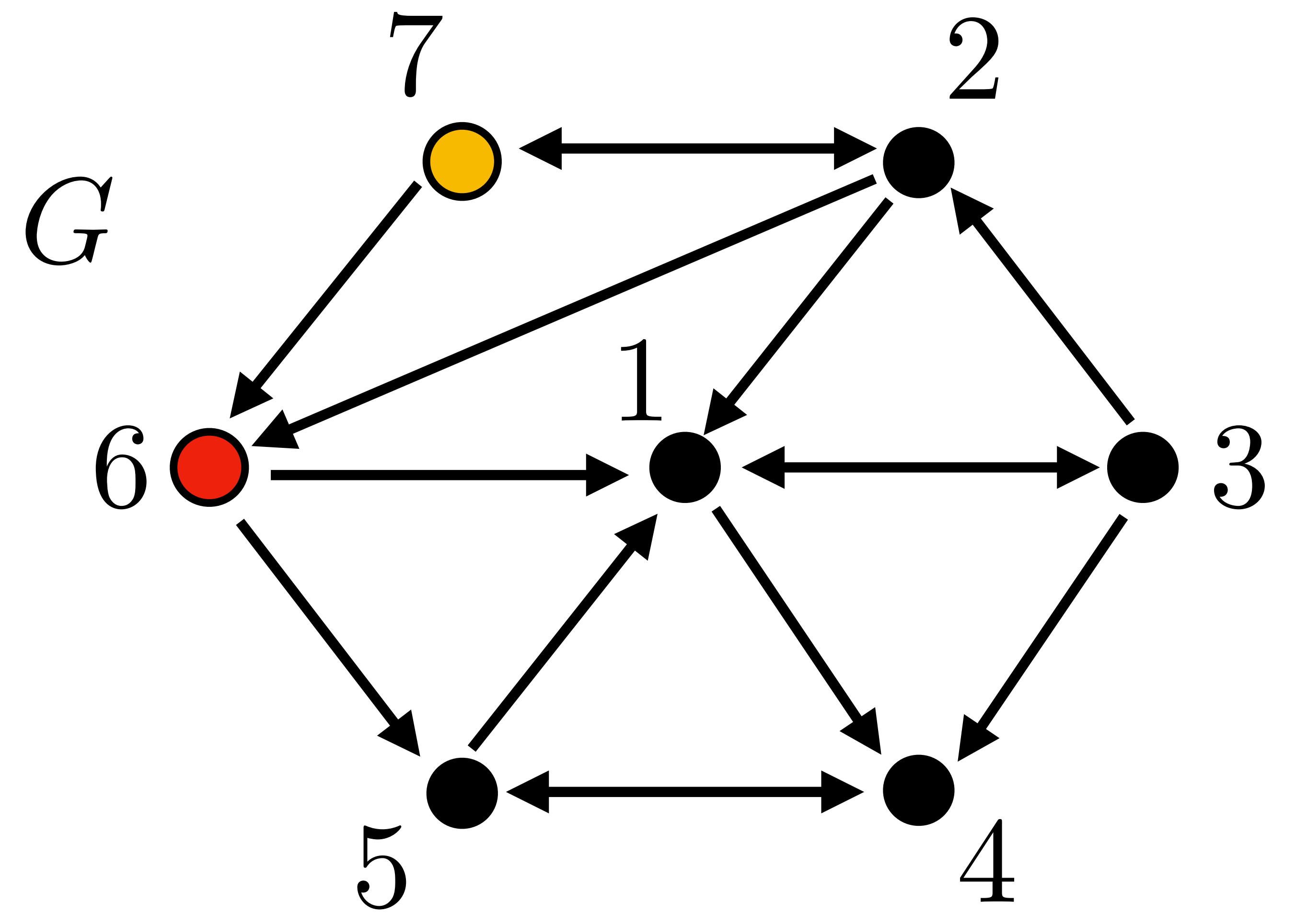

$6 > 7$

domination is a property of G

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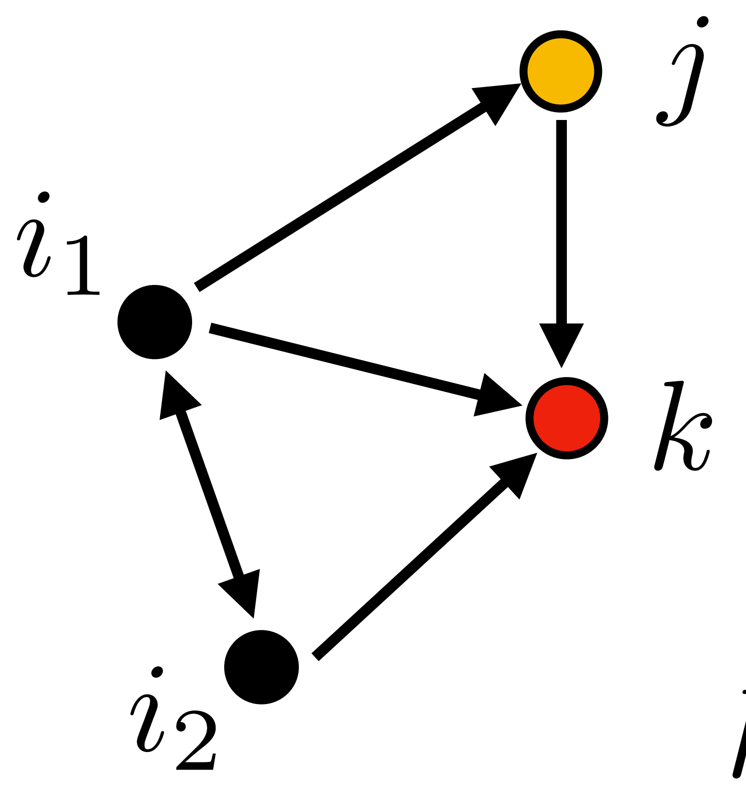

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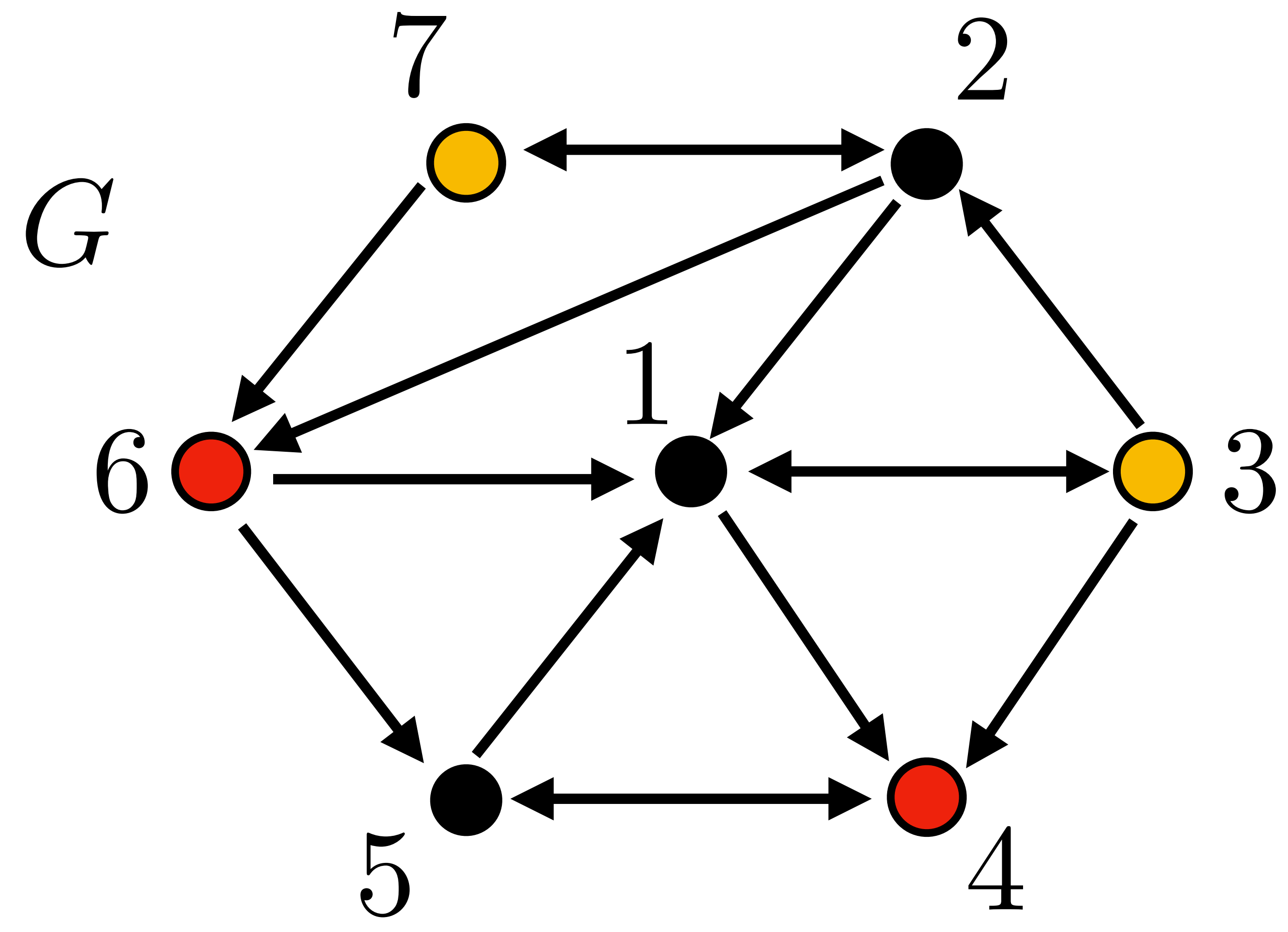


$6 > 7$

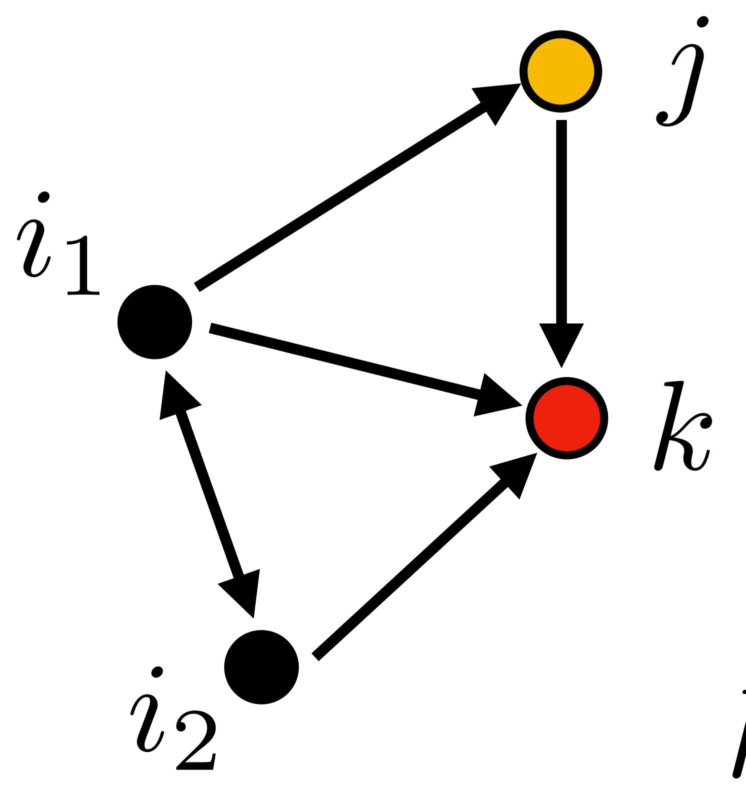
$4 > 3$

domination is a property of G

Domination

Old Theorem (2019)
If k dominates j in G, then j, k cannot both be active at any fixed point of a CTLN built from G.

$$\{j, k\} \not\subseteq \sigma \text{ for any } \sigma \in \mathrm{FP}(G)$$



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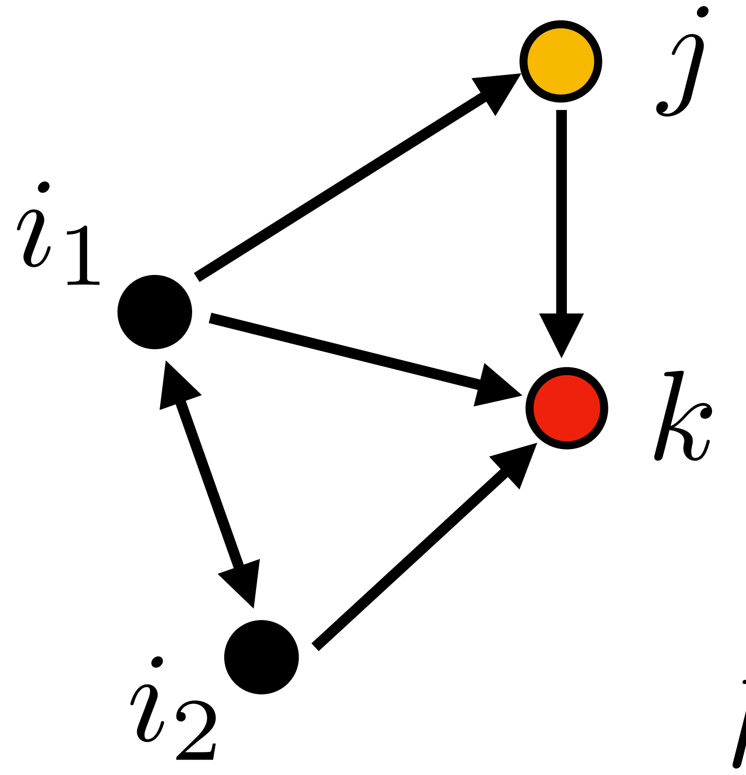

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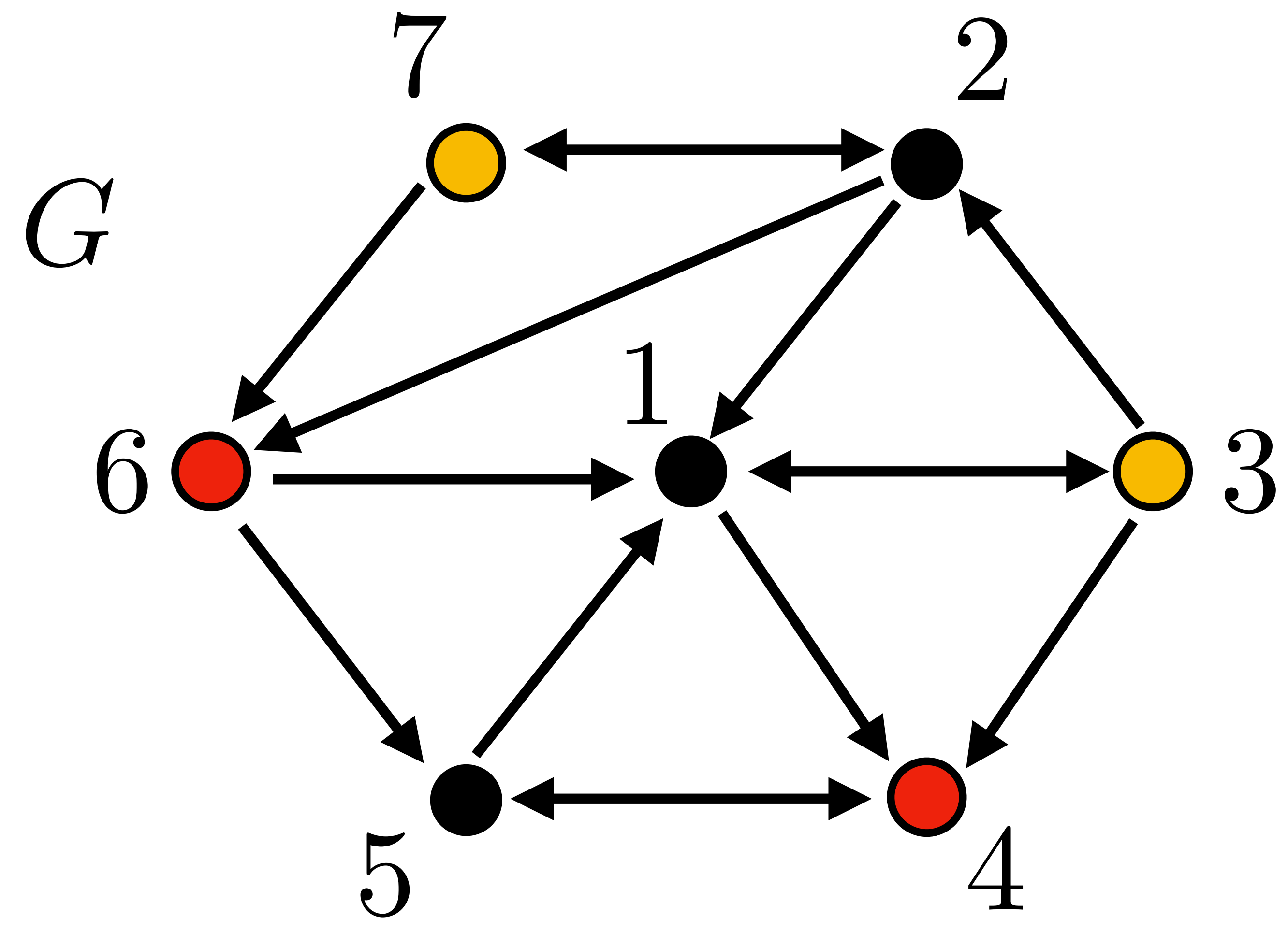


$6 > 7$

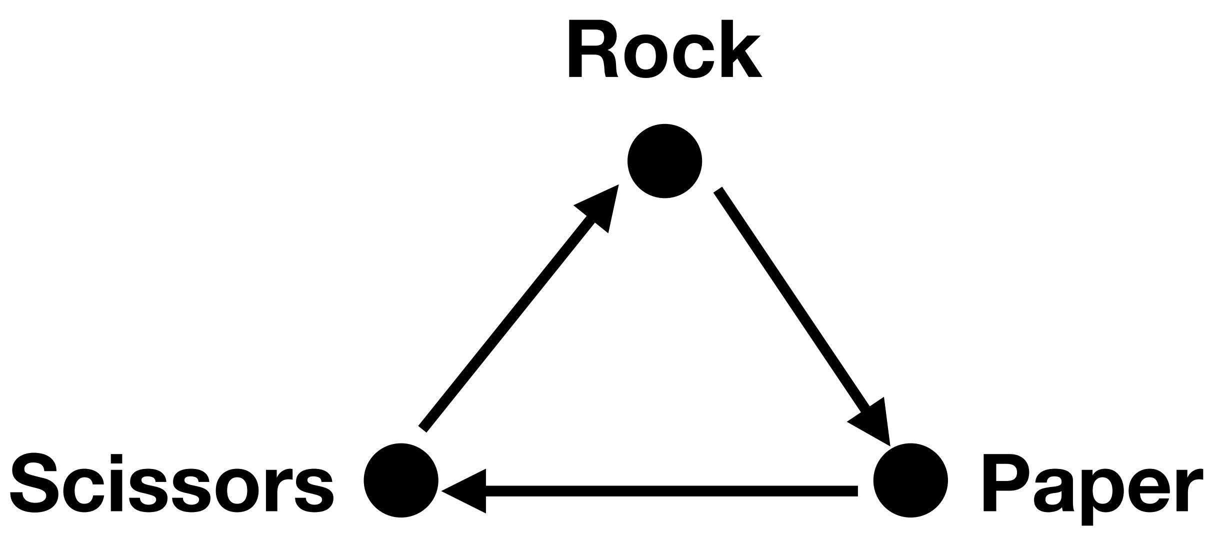
$4 > 3$

Old Theorem says: for any CTLN built from G, FP(G) cannot have any fixed points with both {6,7} or both {3,4}.

But it's not like we can remove 3 and 7; they may still affect or participate in other fixed points (for all we know).

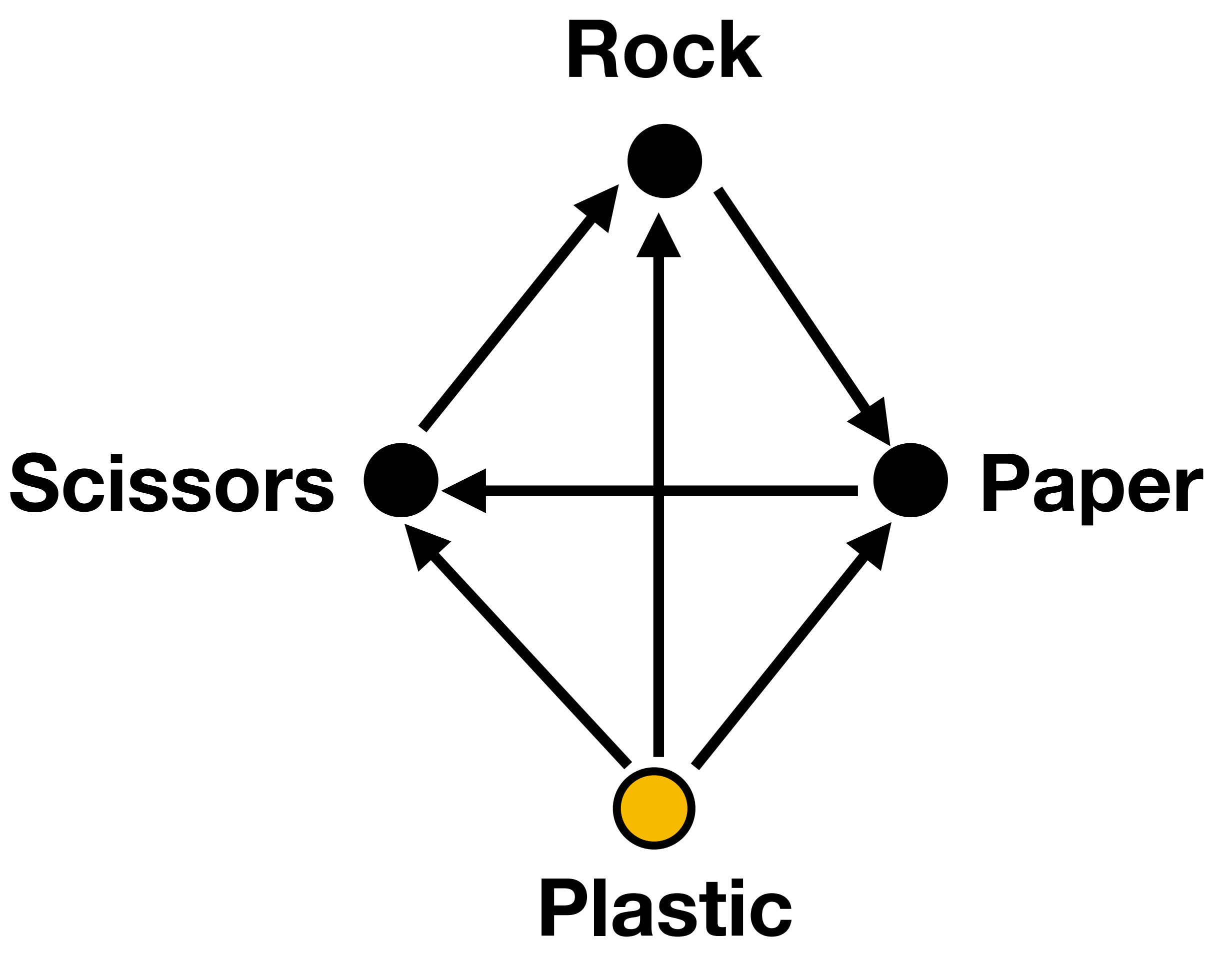
Curto, Geneson, Morrison, 2019

Rock-Paper-Scissors: a true story



March 2024

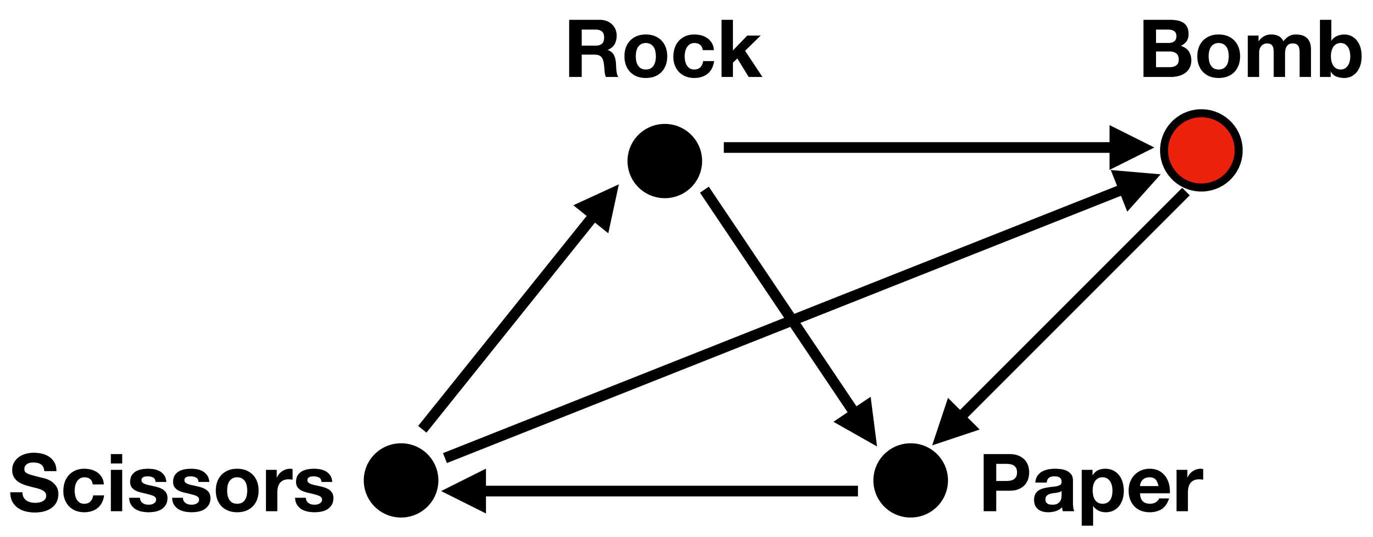
Rock-Paper-Scissors: a true story



Plastic loses to everyone, so nobody would ever pick it as a strategy.

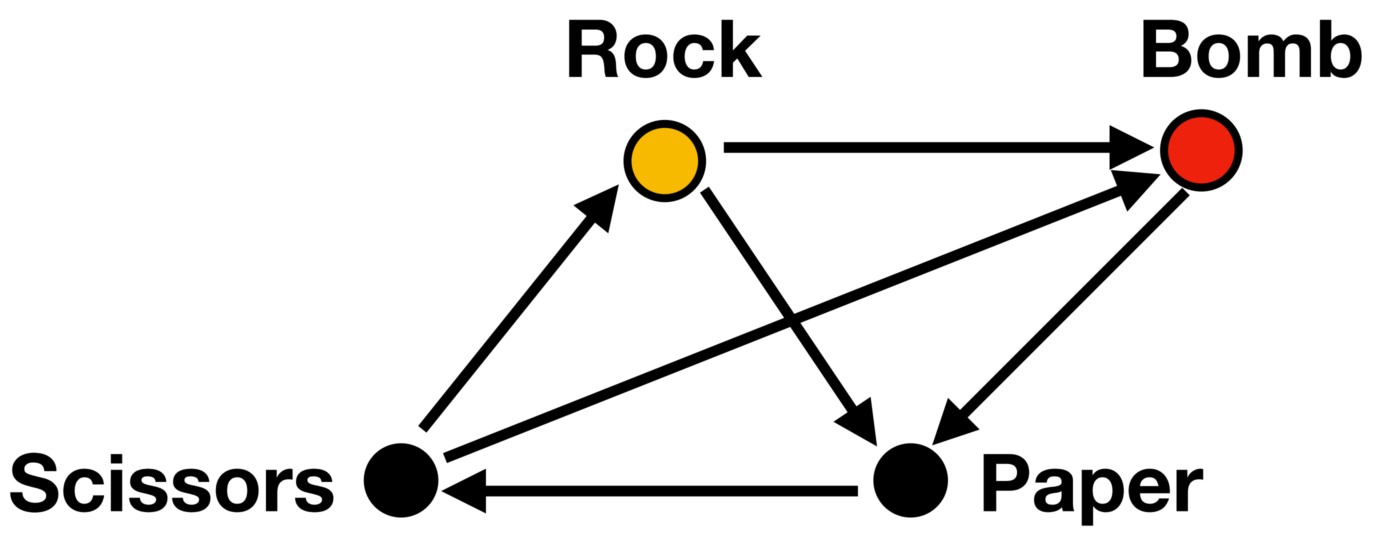
It drops out.

Rock-Paper-Scissors: a true story



Bomb beats Scissors and loses to Paper, just like Rock.
But Bomb also beats Rock.

Rock-Paper-Scissors: a true story

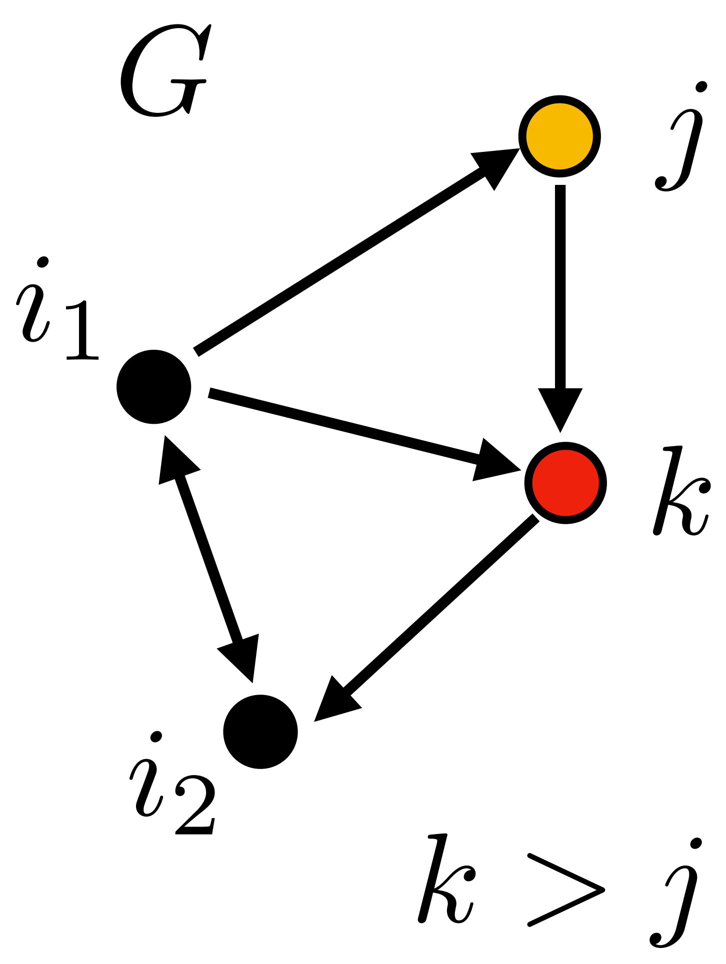


Bomb beats Scissors and loses to Paper, just like Rock.
But Bomb also beats Rock.

So now nobody would ever pick Rock as a strategy.
Rock drops out!

Domination - New Theorems

Theorem 1 (2024)
If j is a dominated node in G, then it drops out!
I.e., in any gCTLN, we have: $\text{FP}(G) = \text{FP}(G|_{[n]\setminus j})$



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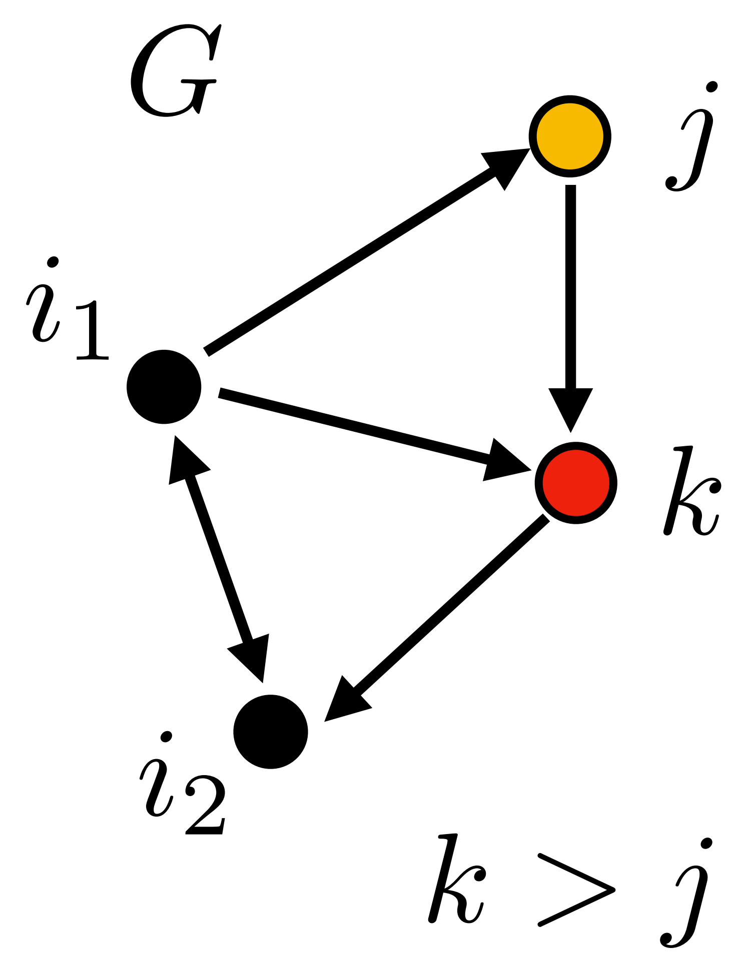

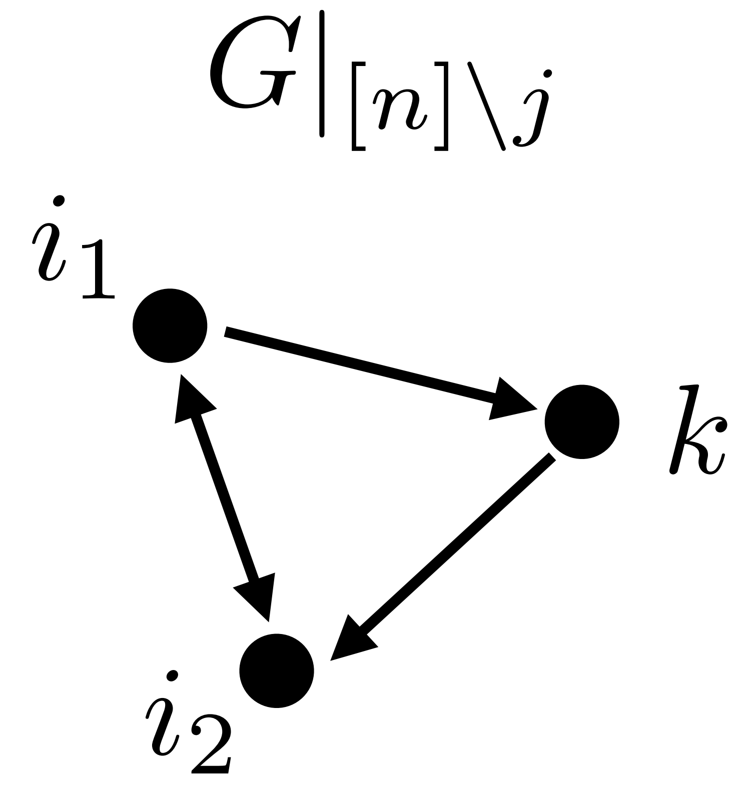

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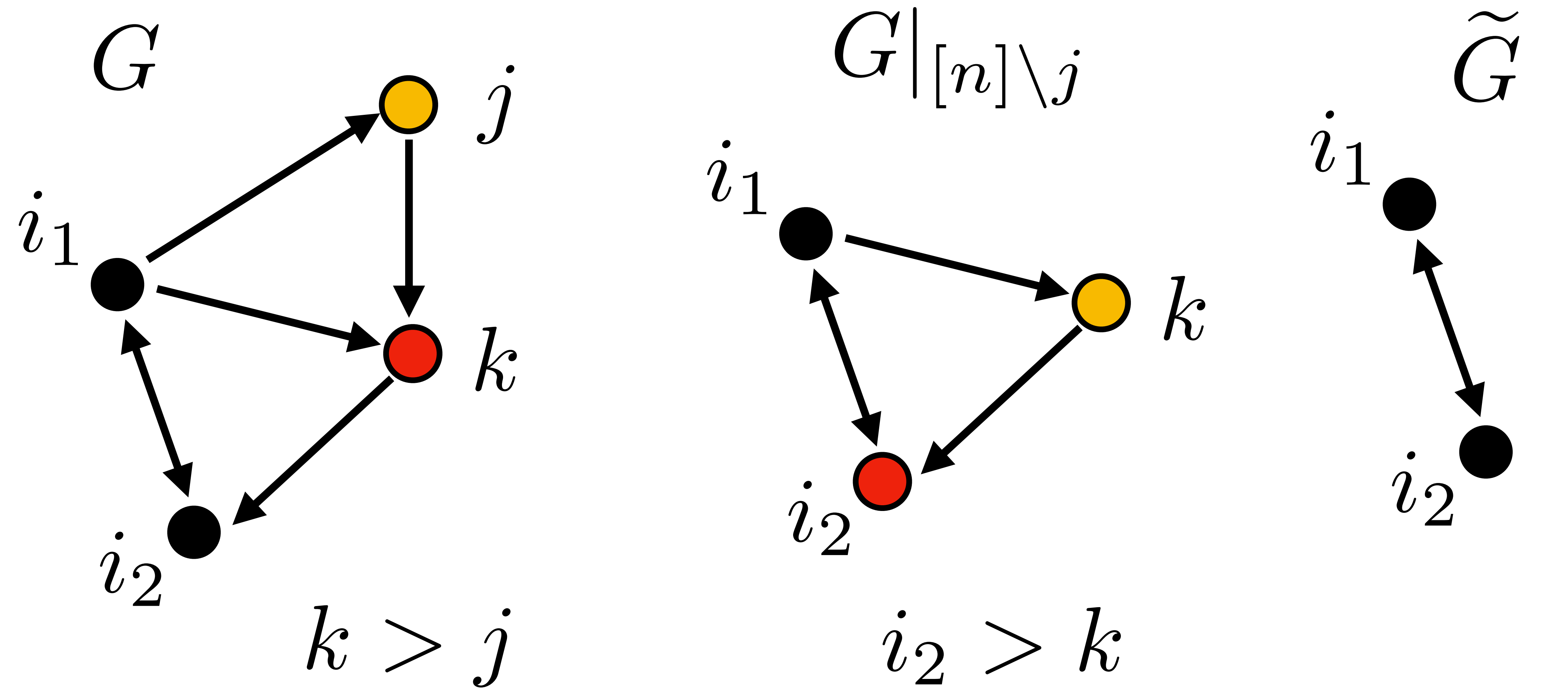

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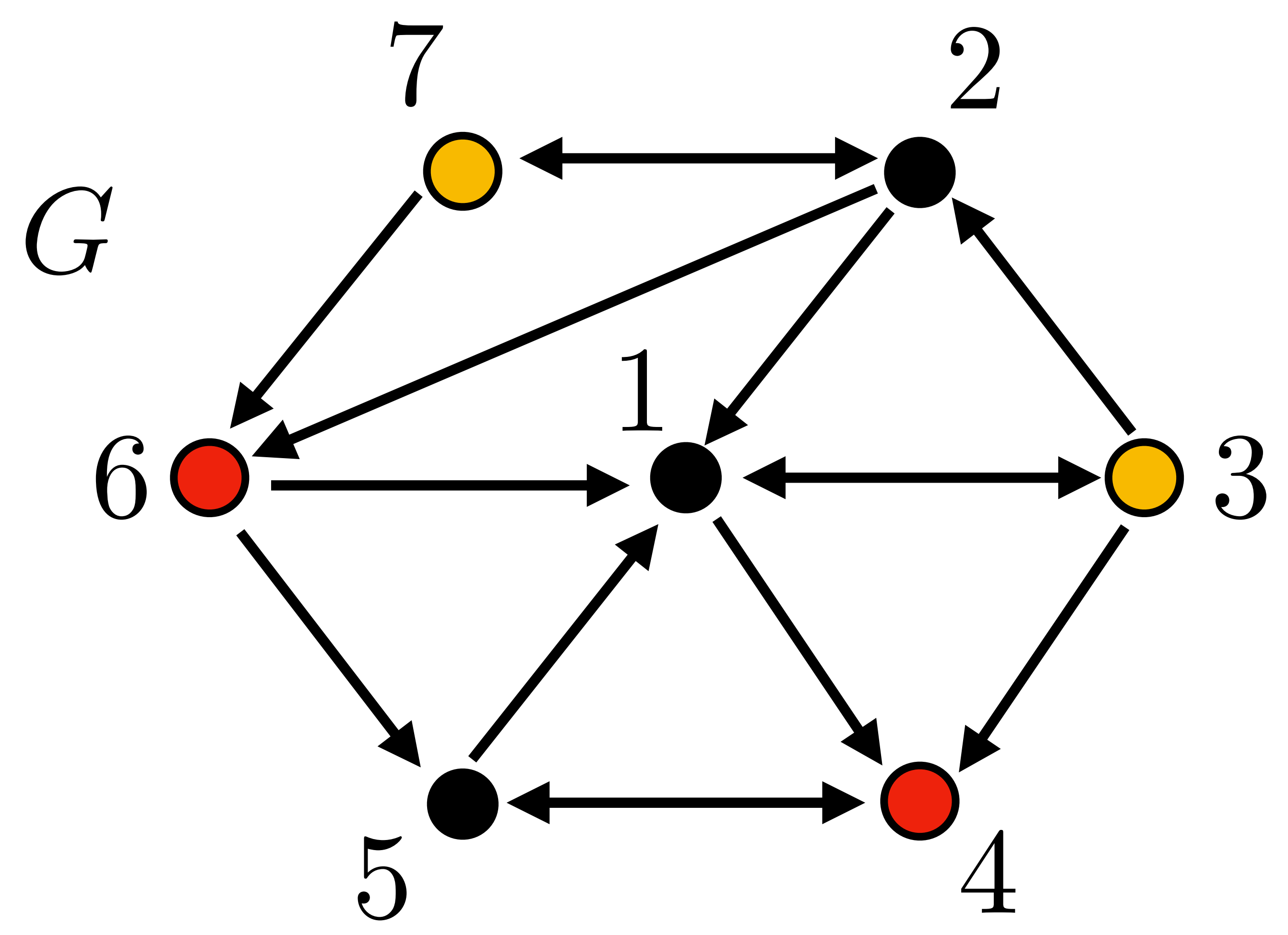

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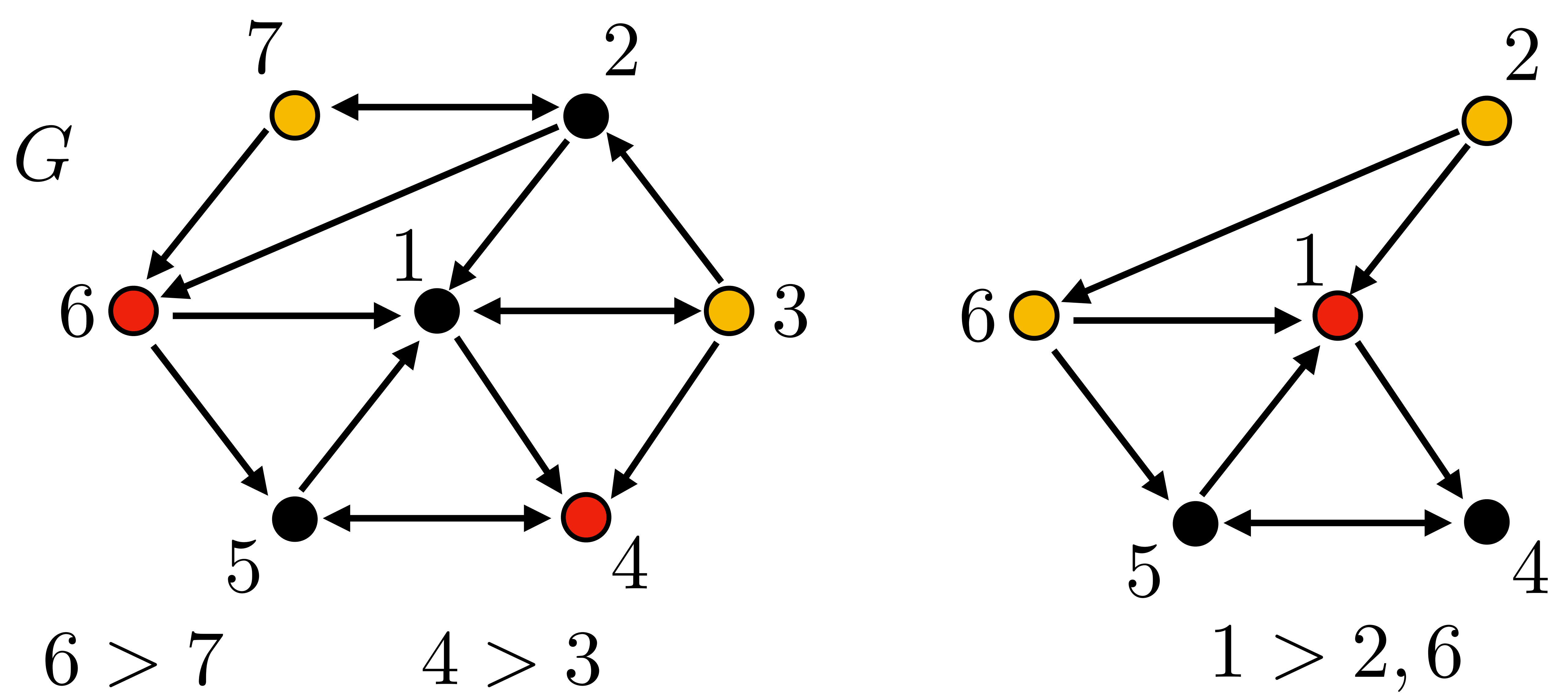

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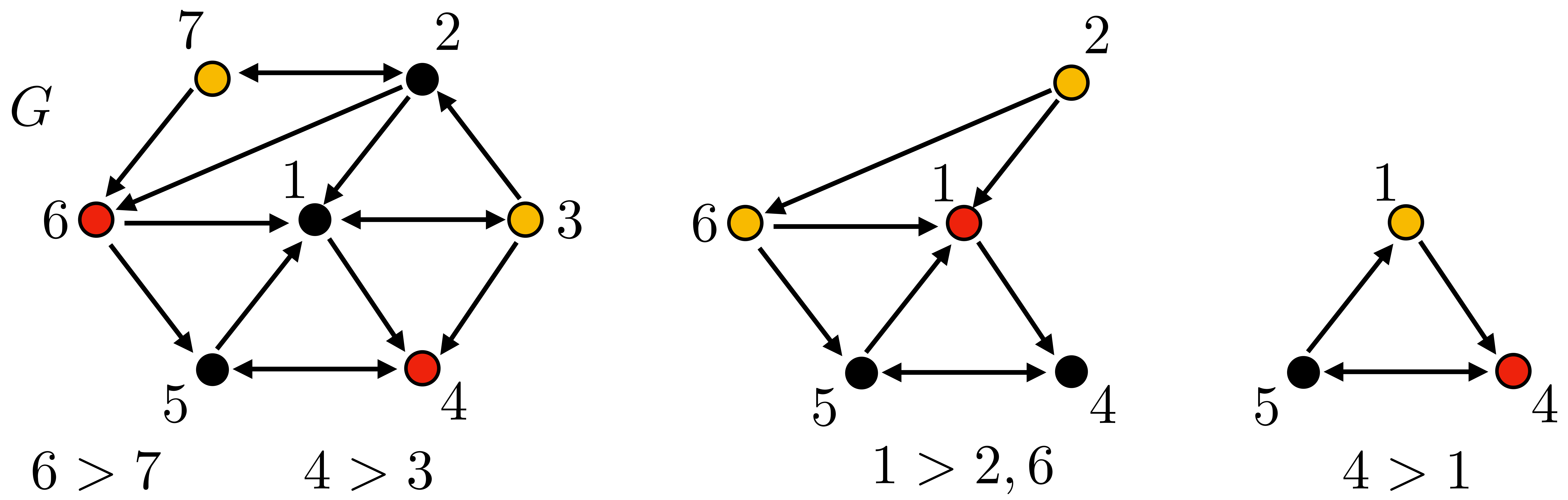

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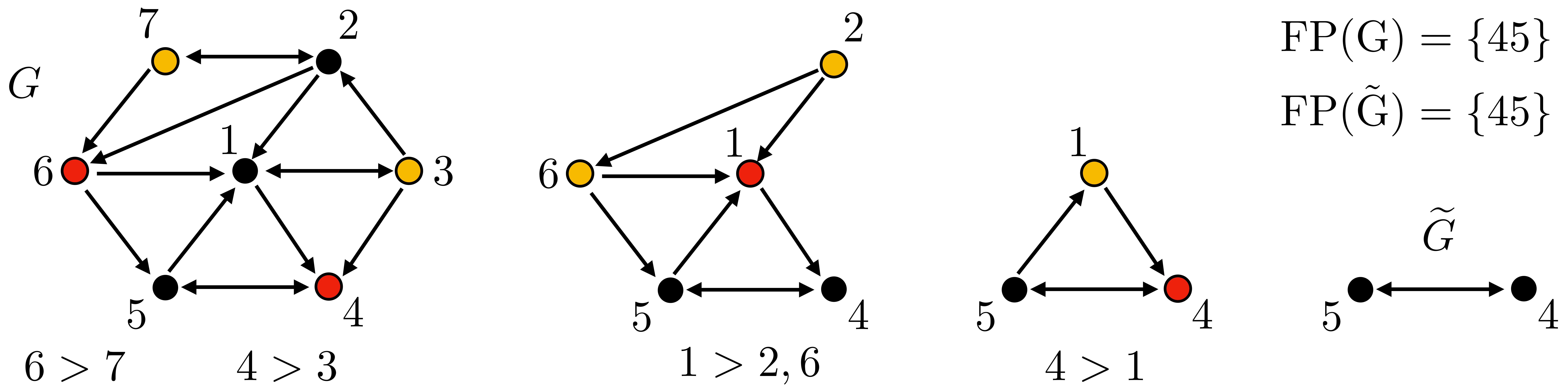
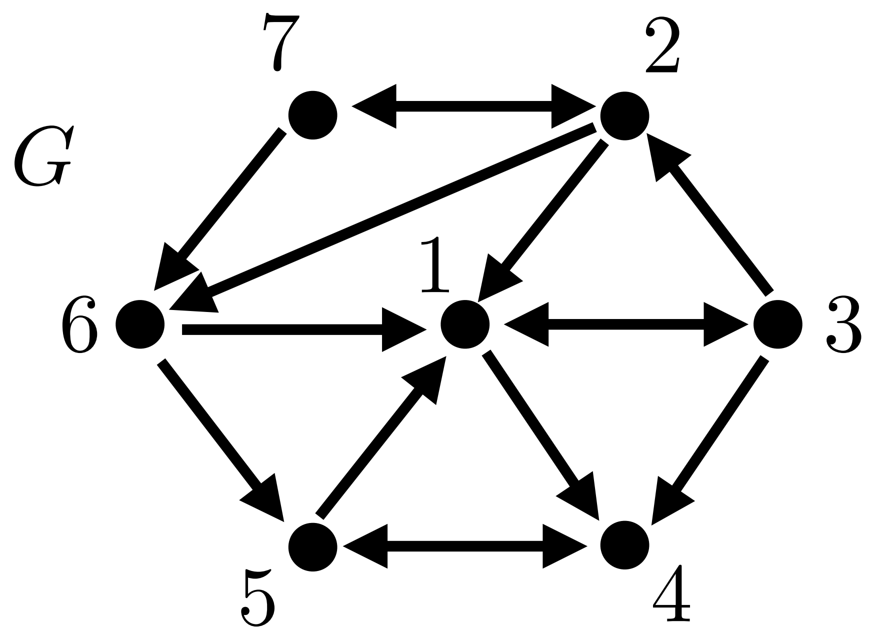
Theorem 2 (2024)
By iteratively removing dominated nodes, the final reduced graph G-tilde is unique. Moreover, $\mathrm{FP}(G) = \mathrm{FP}(\widetilde{G})$

Example

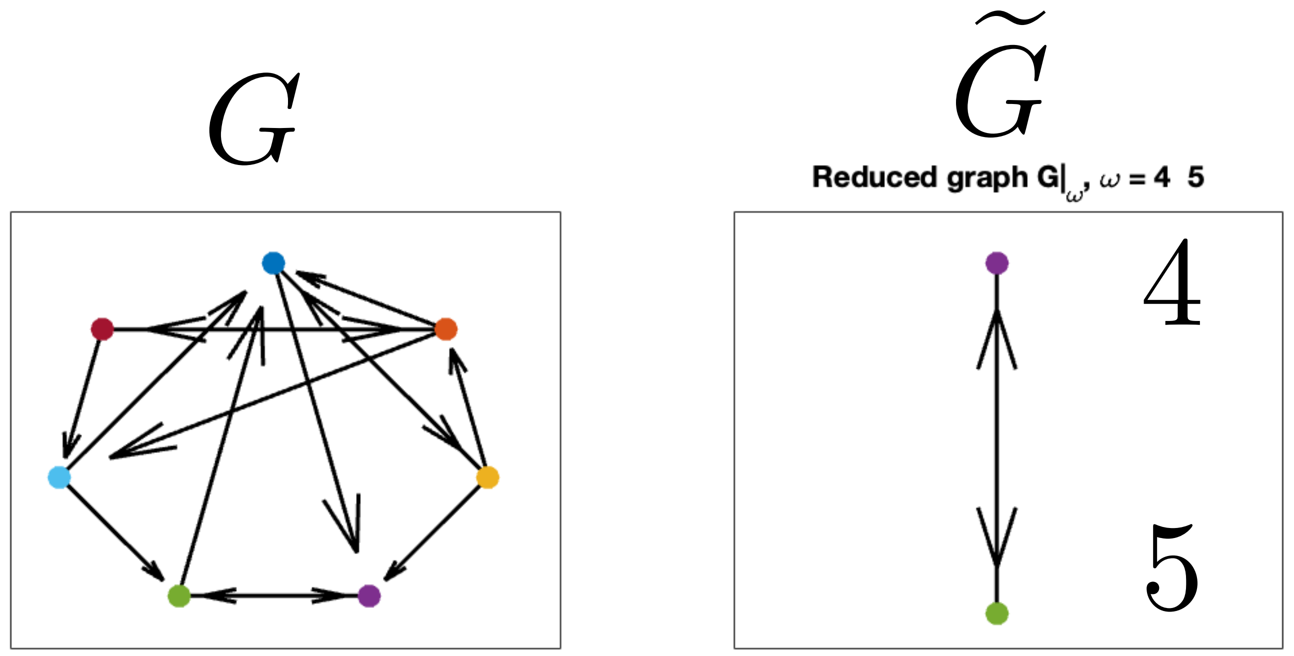


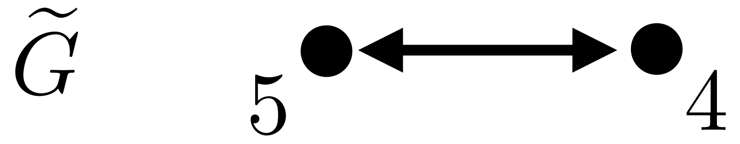
Computational Experiments

Example



$\mathrm{FP}(G) = \{45\}$





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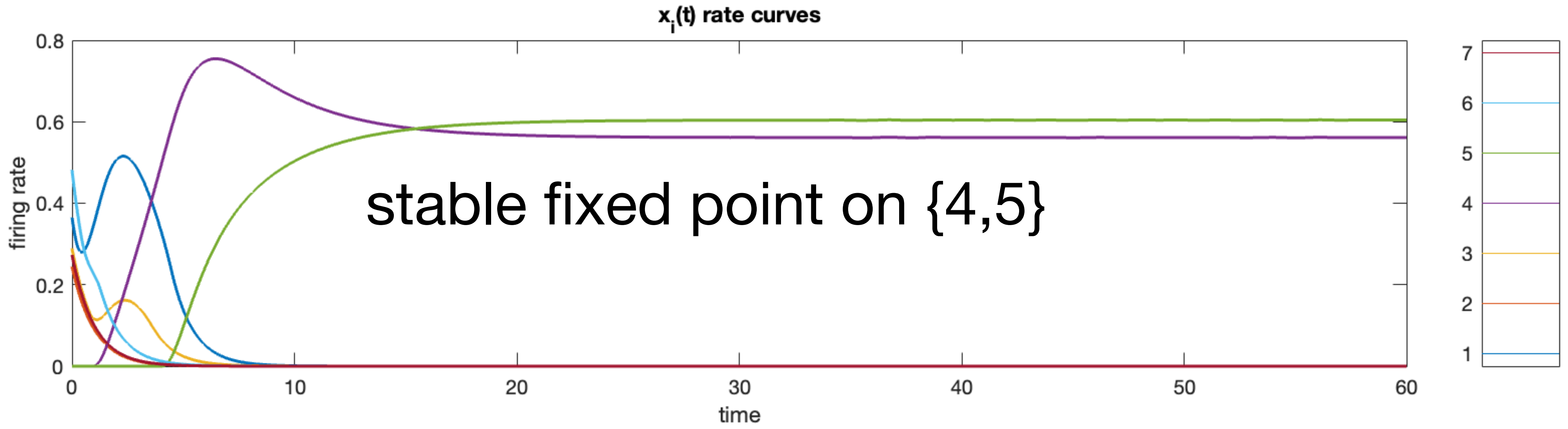

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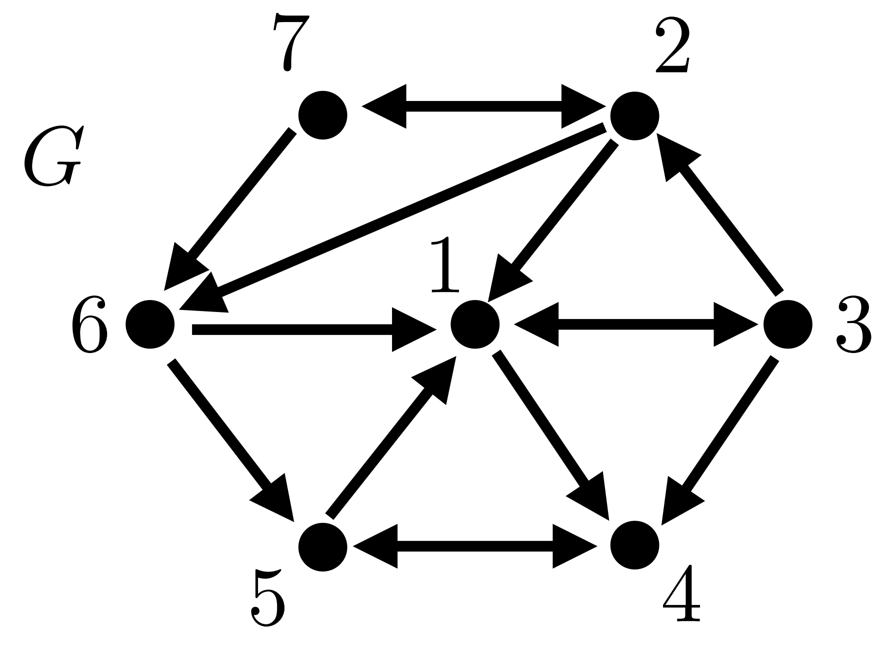

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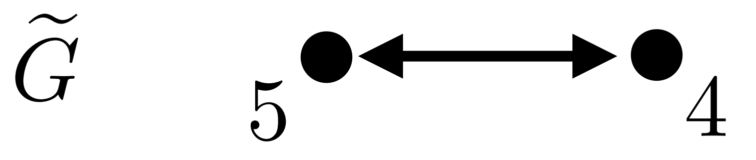

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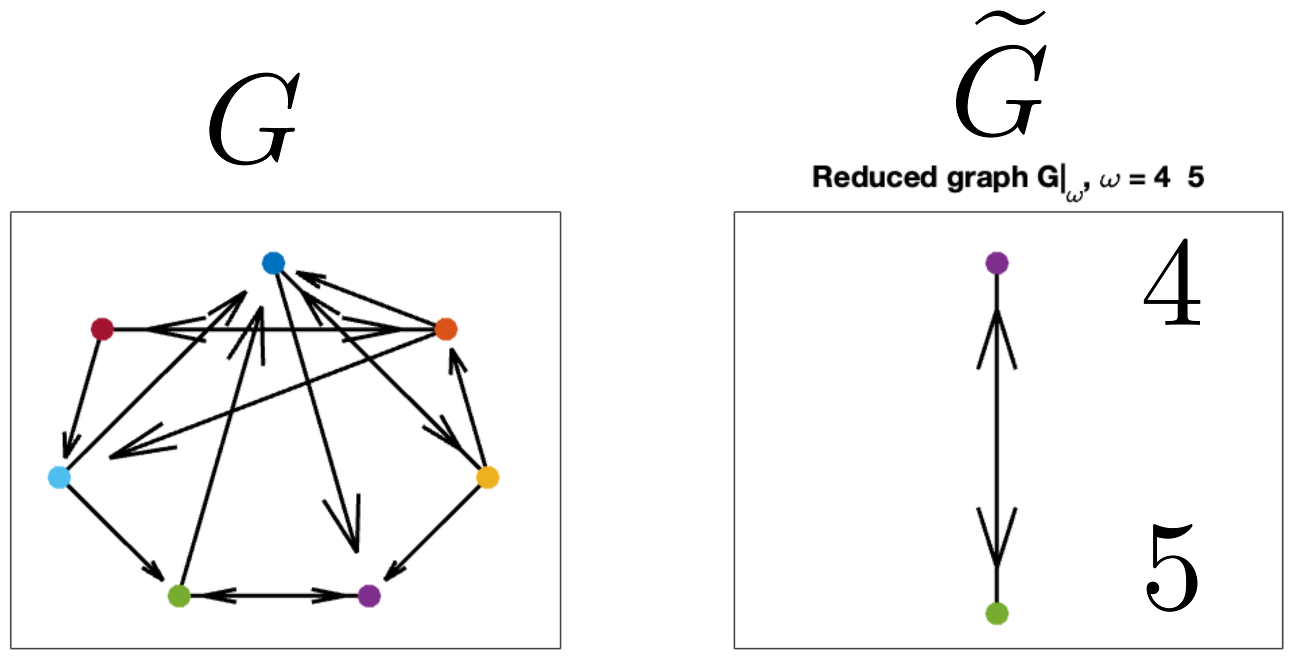
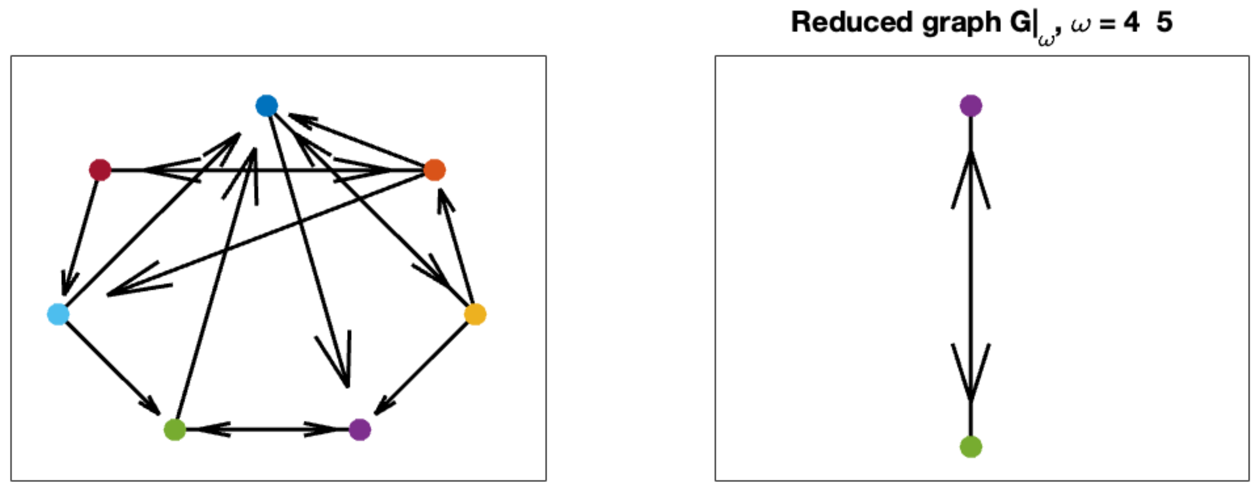
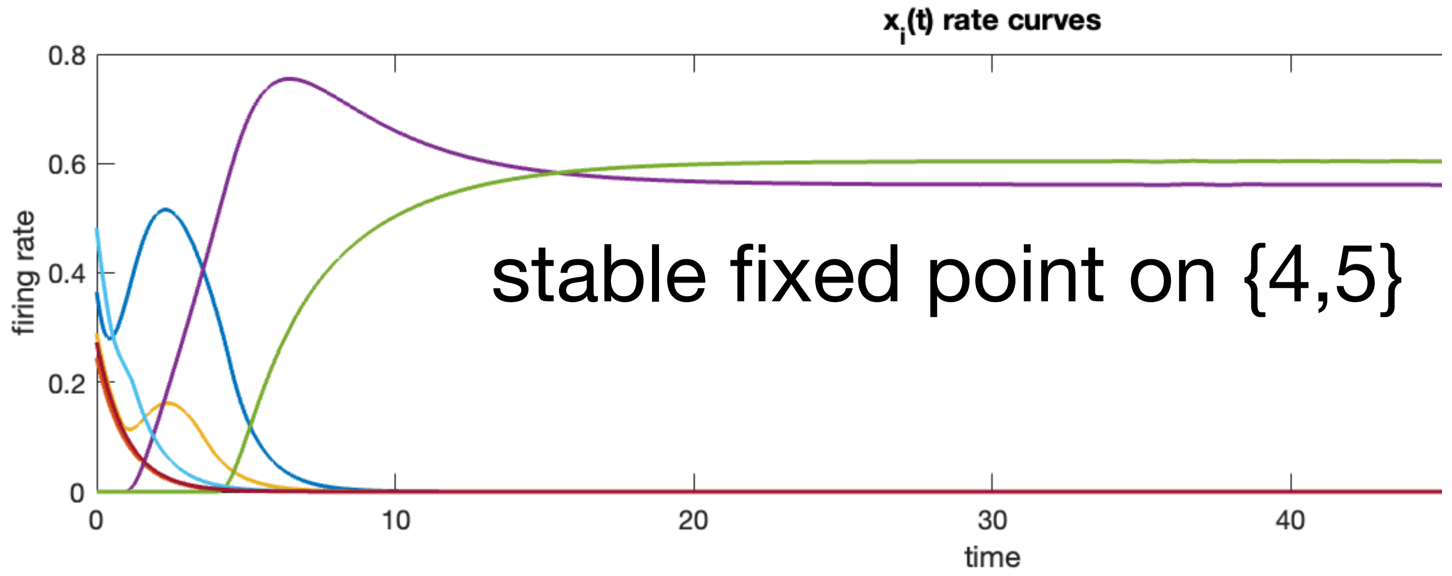
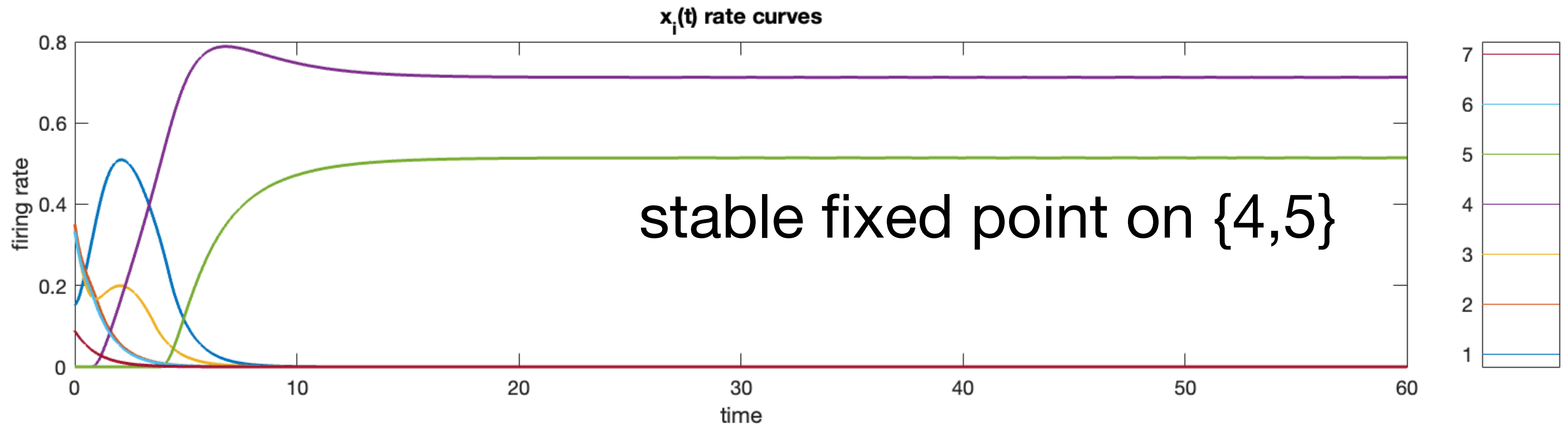


same graph, different gCTLN parameters

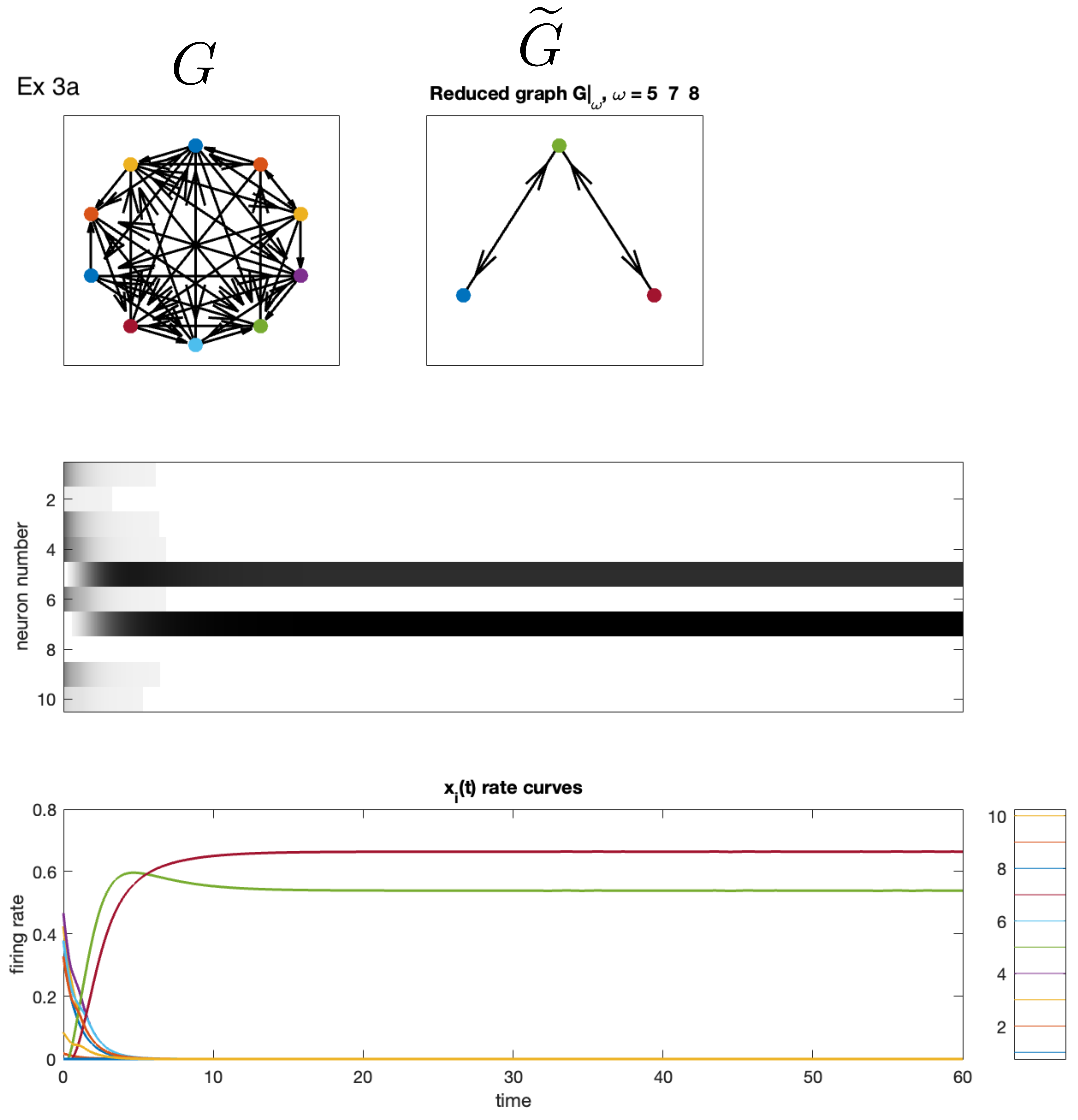


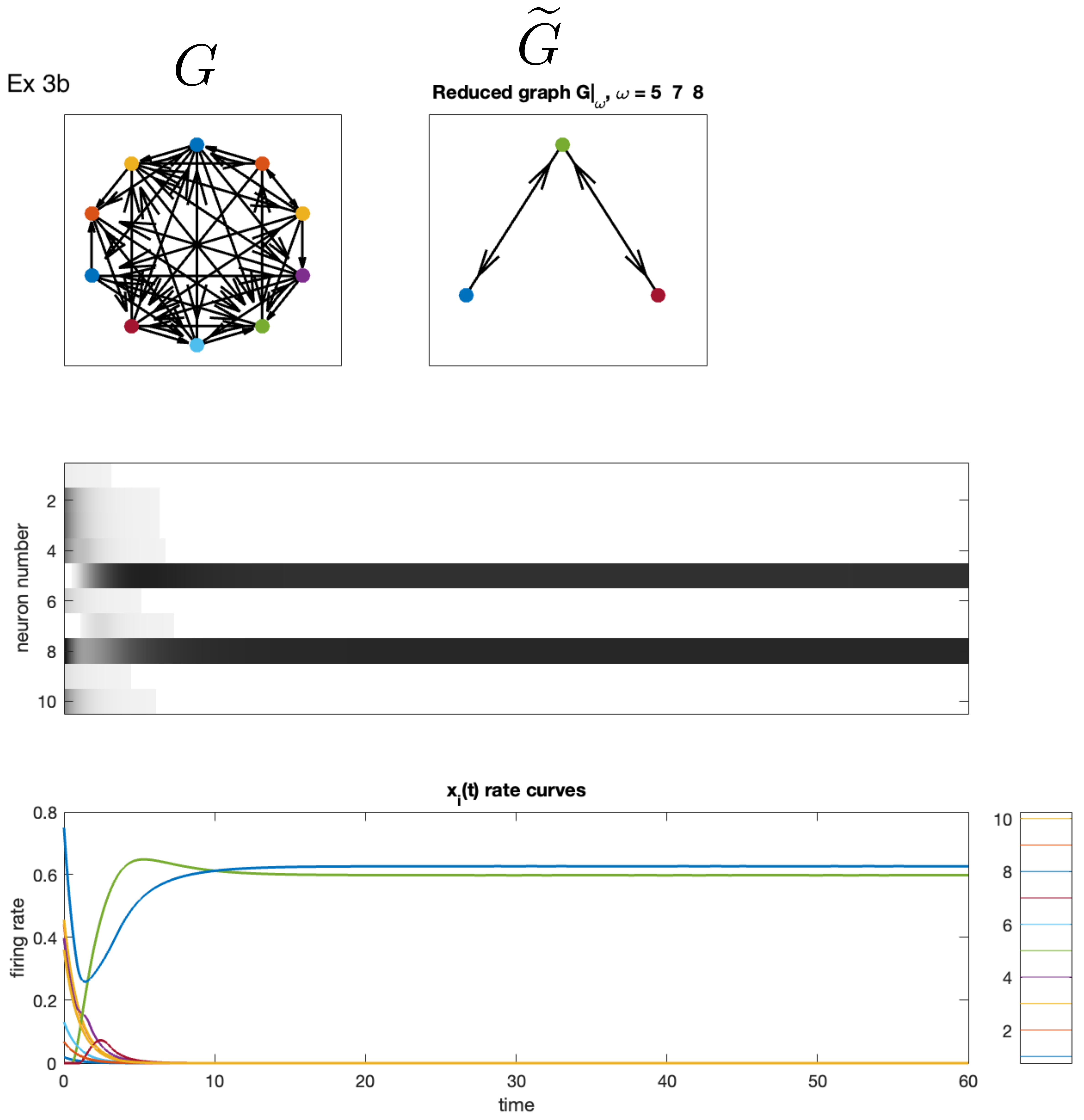




Conjecture: network activity flows from any initial condition on the graph to the reduced network $\widetilde{G}$

E-R random graphs with p=0.5





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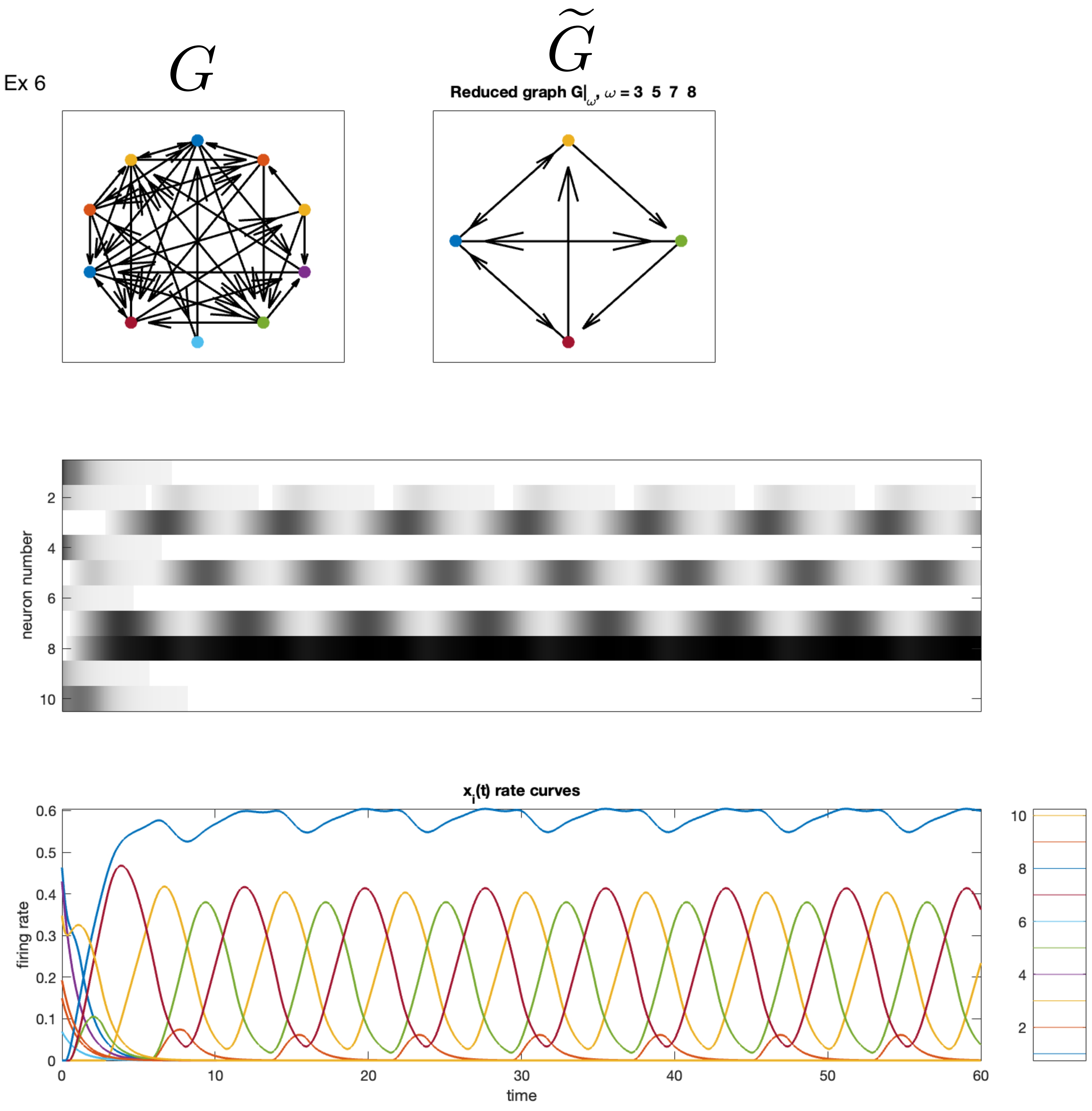
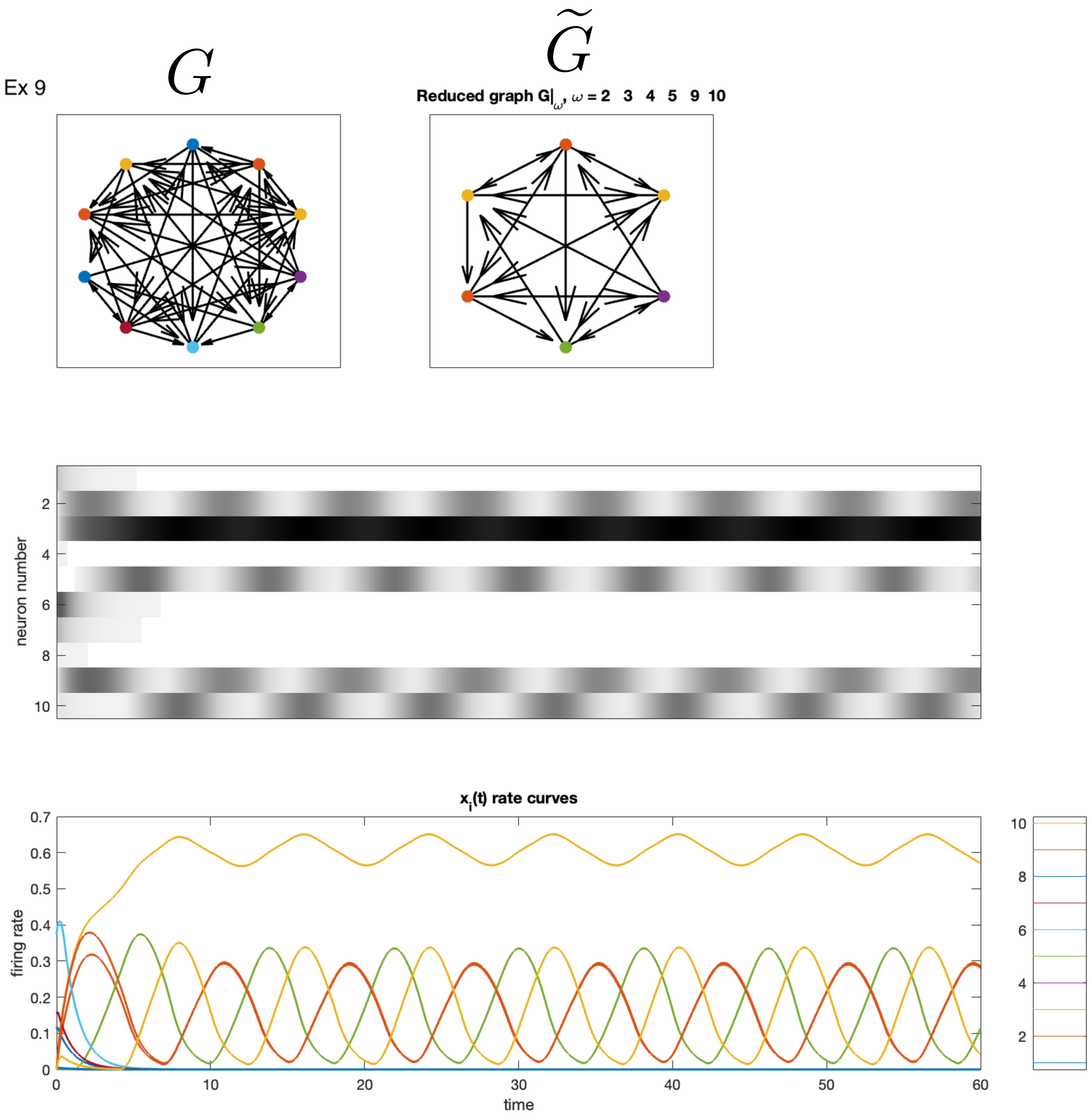
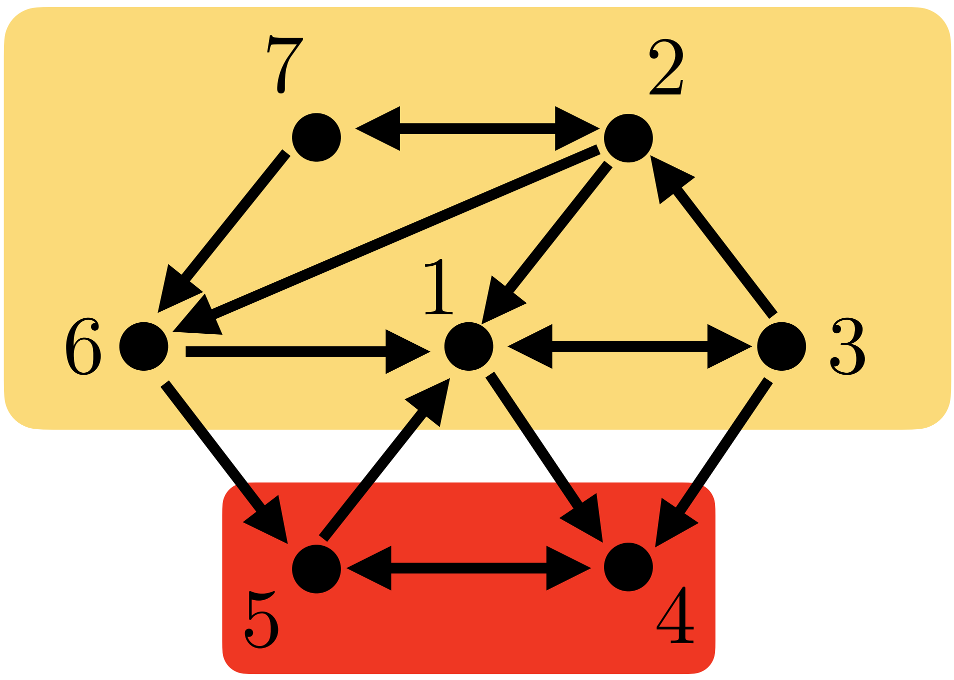




Dominoes!

G



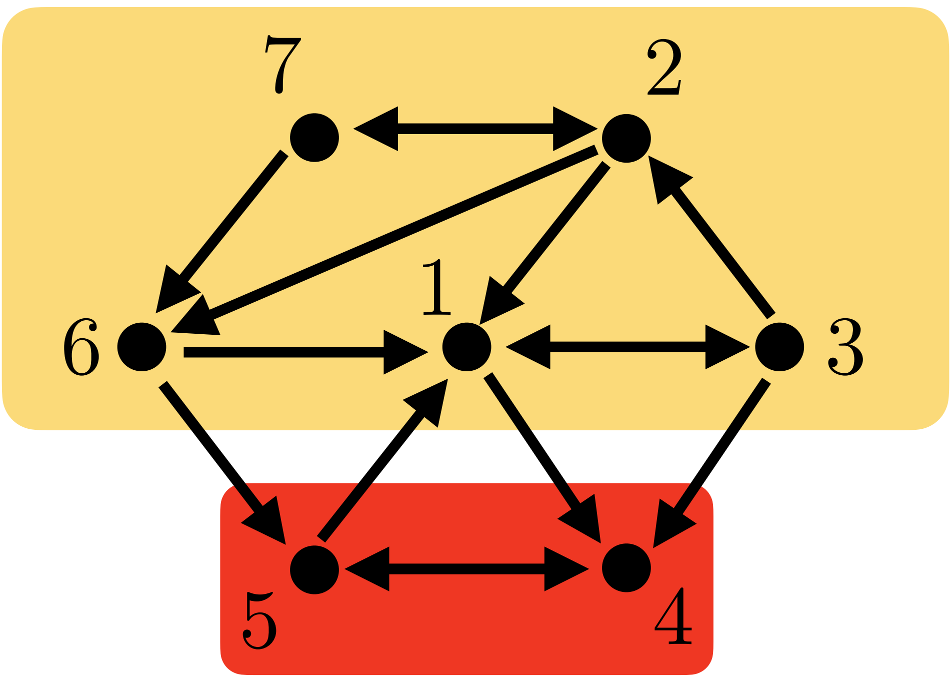
G_ω

$G_\tau = \widetilde{G}$

FP(G) = {45}

Dominoes!

G



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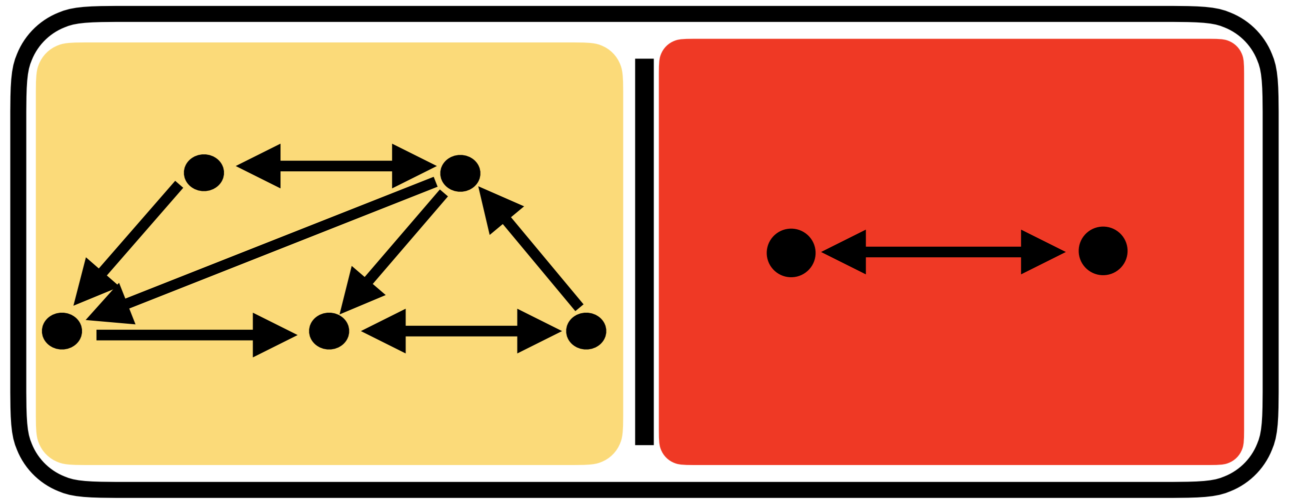
the "domino" of graph G



G_ω G_τ

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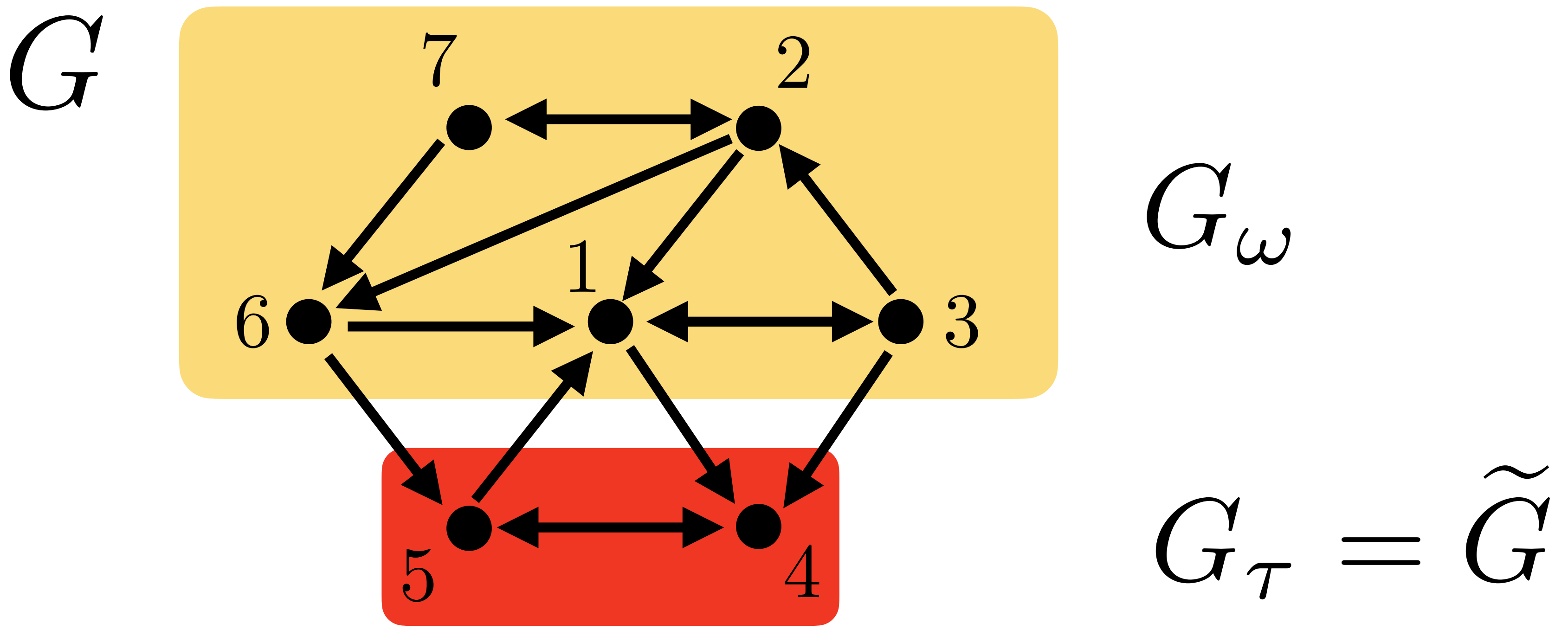

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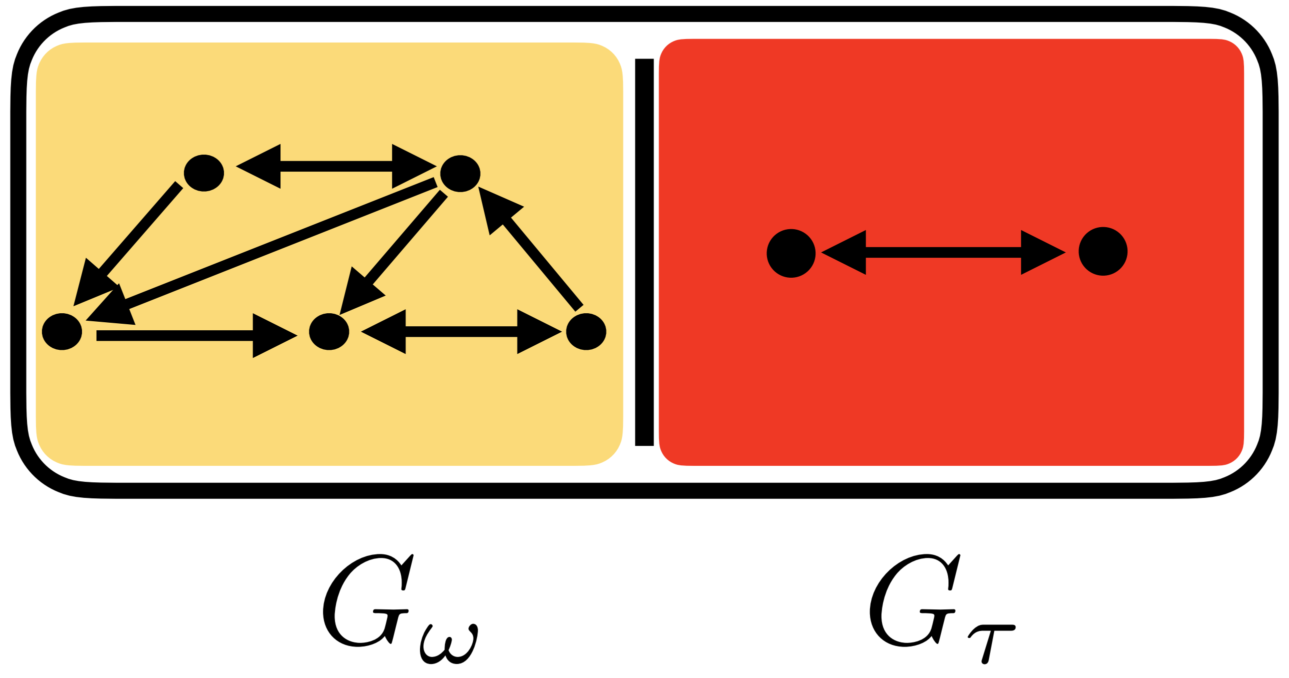
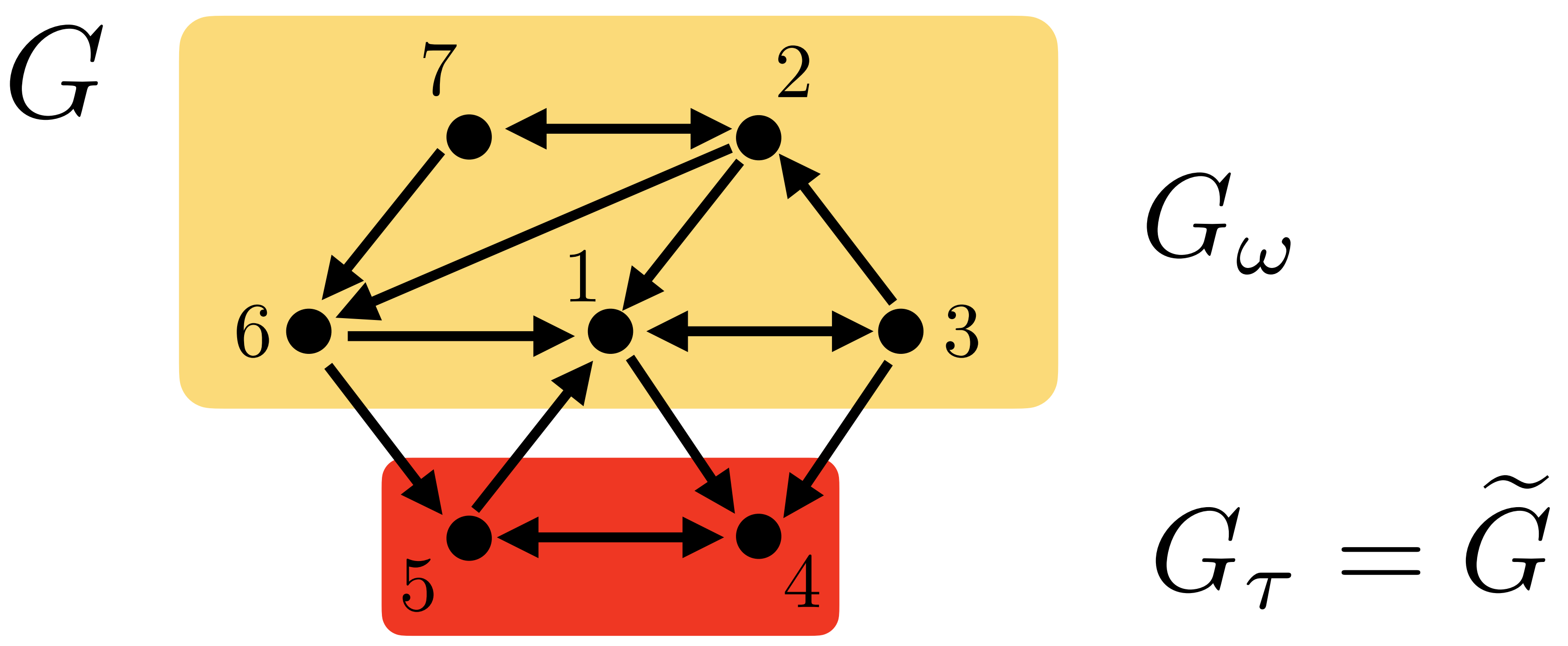


Fact (Thms 1 & 2): all the fixed points of G are supported in $G_\tau = \widetilde{G}$

Conjecture: network activity flows from $G_\omega \rightarrow G_\tau$

Dominoes!



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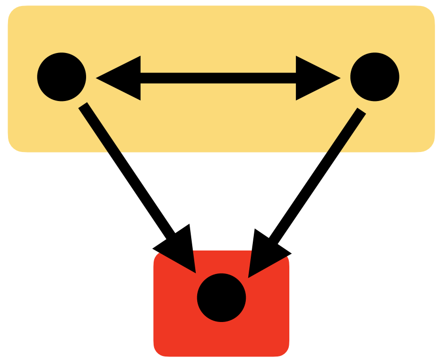

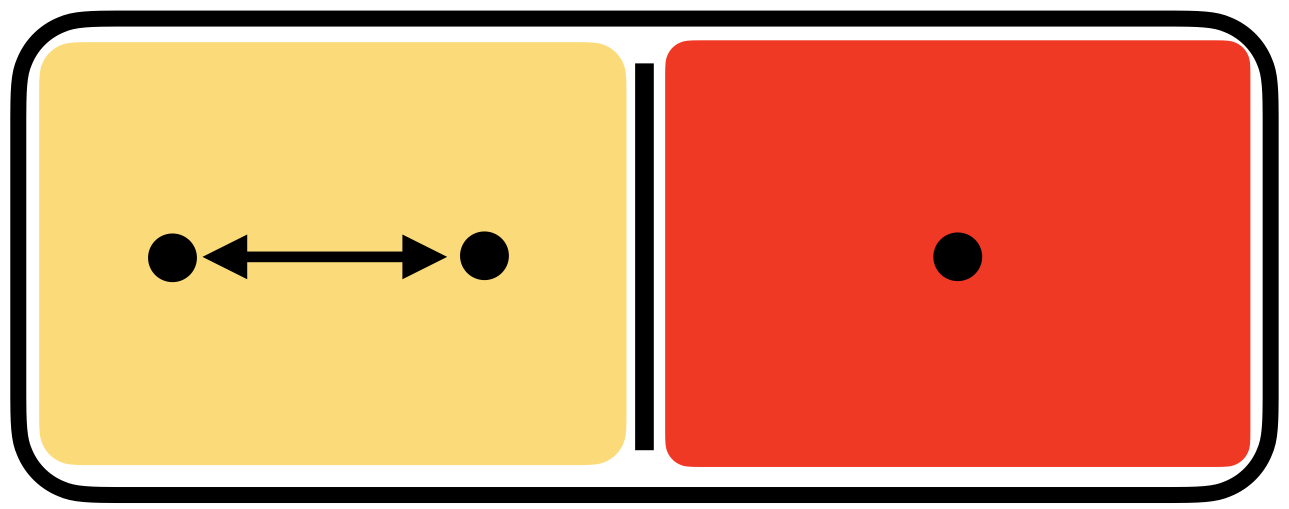

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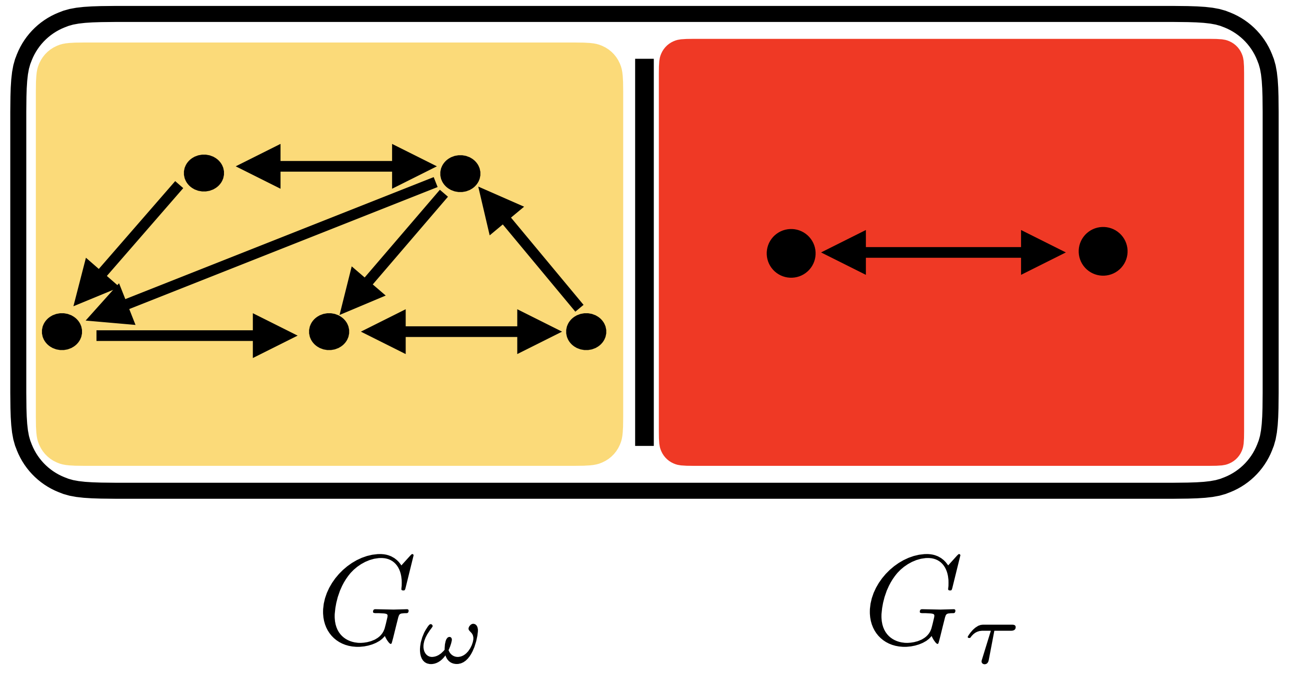

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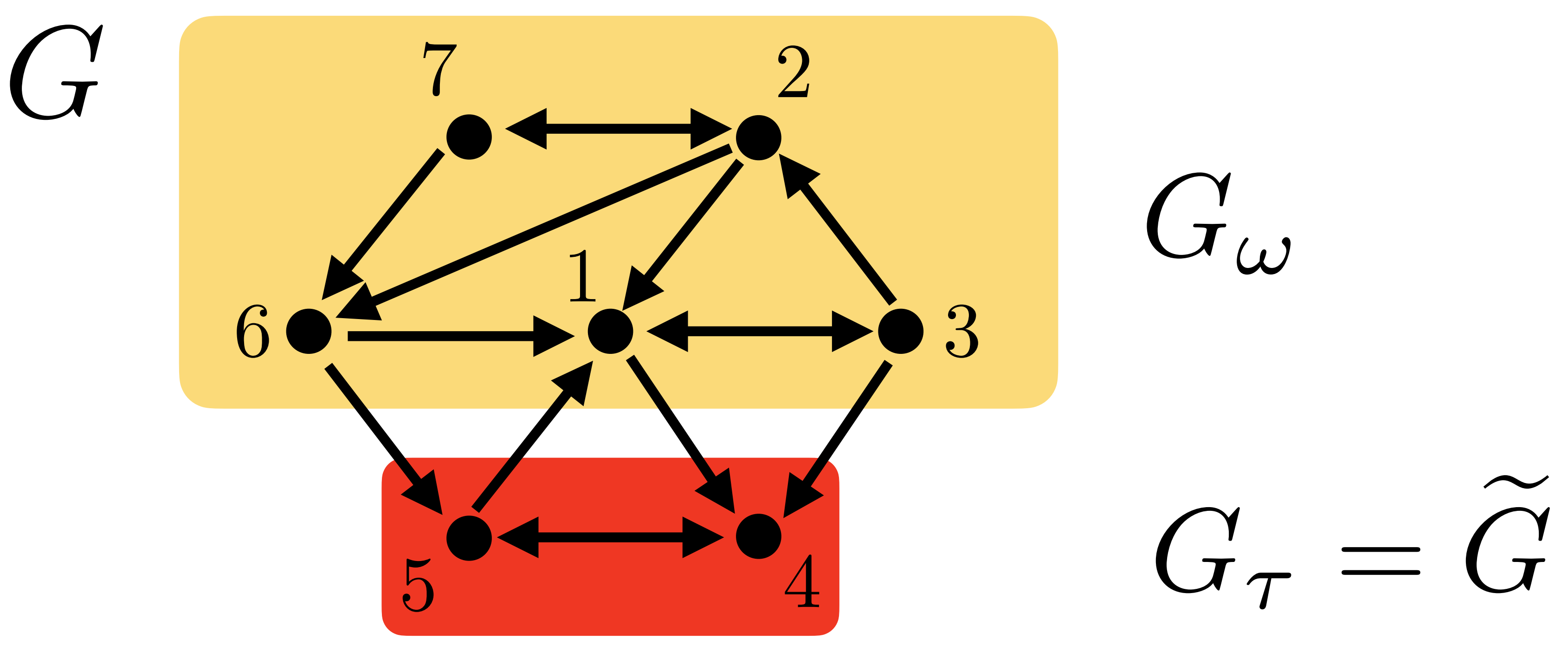

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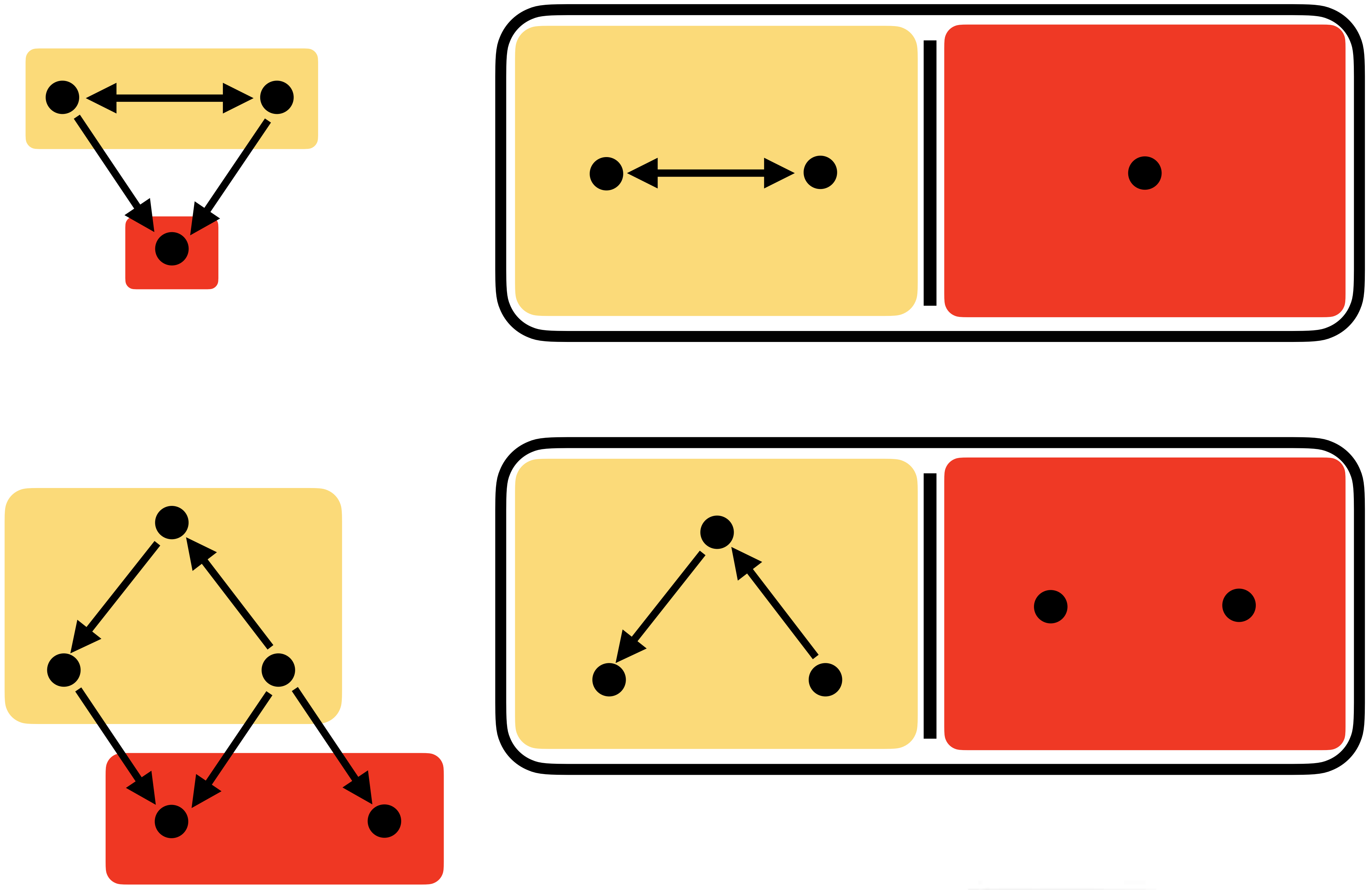

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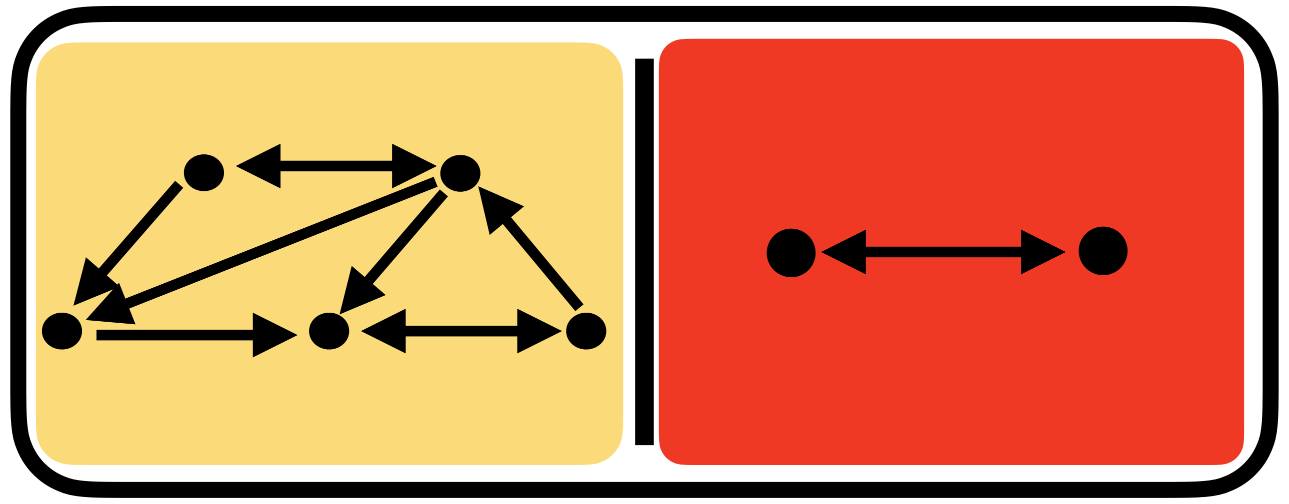

G_ω G_τ

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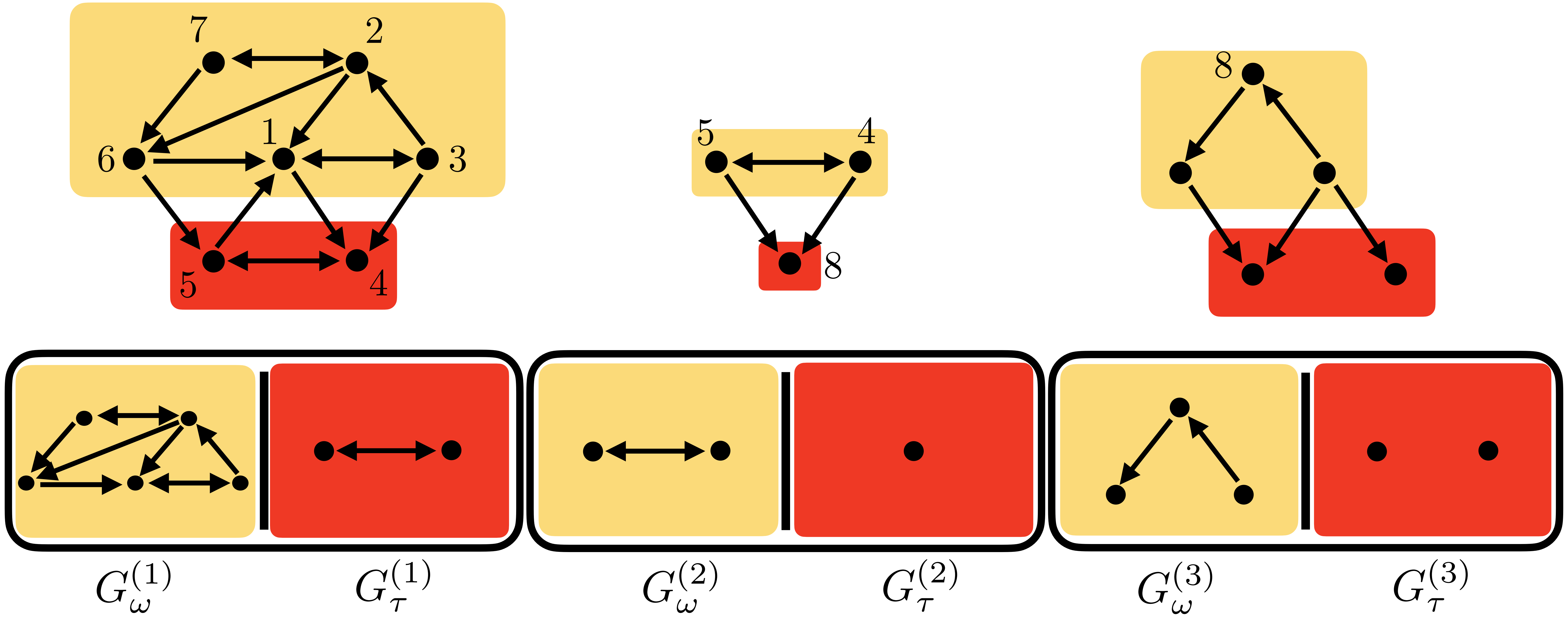
Dominoes! We can chain them together...



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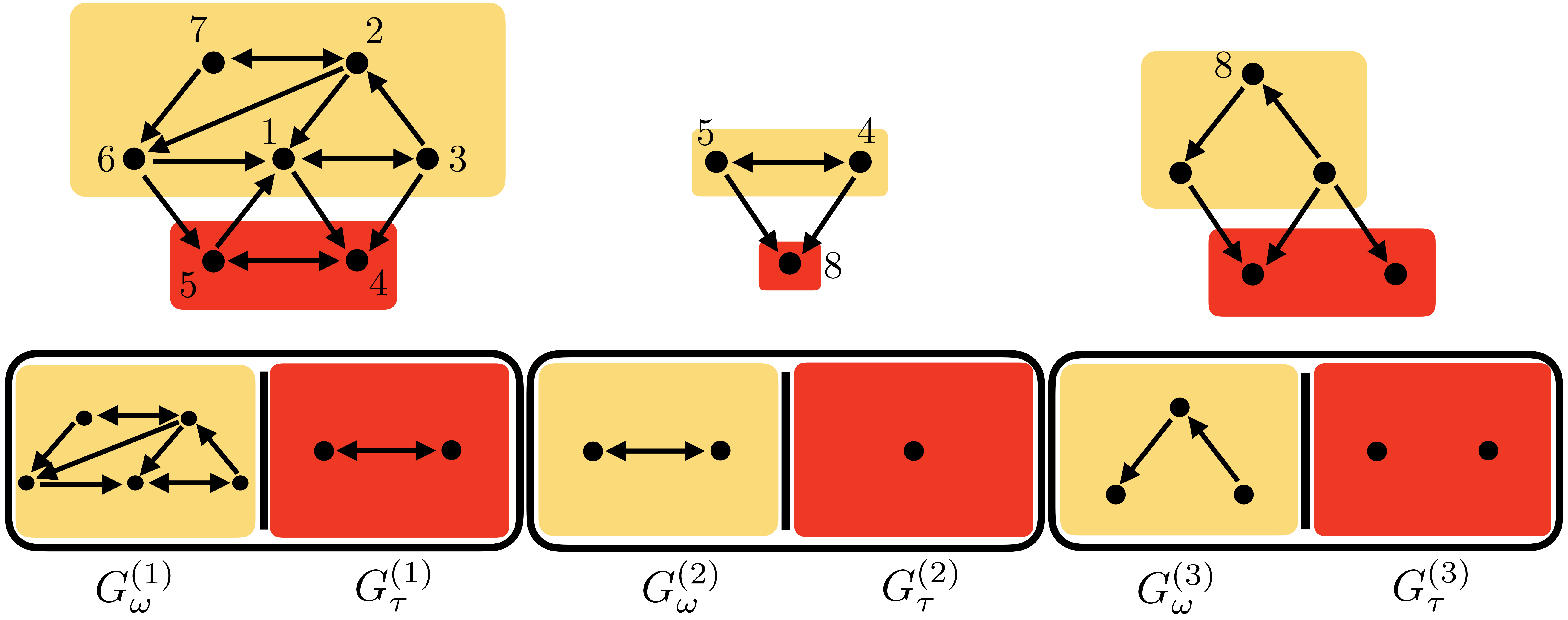

Theorem 3 (2024)

If we glue reducible graphs together along their dominoes, in a linear chain, so that G_τ of one is identified with a subgraph of G_ω of the next, then the glued graph reduces to the final $G_\tau^{(i)}$.

Curto 2024 (unpublished)

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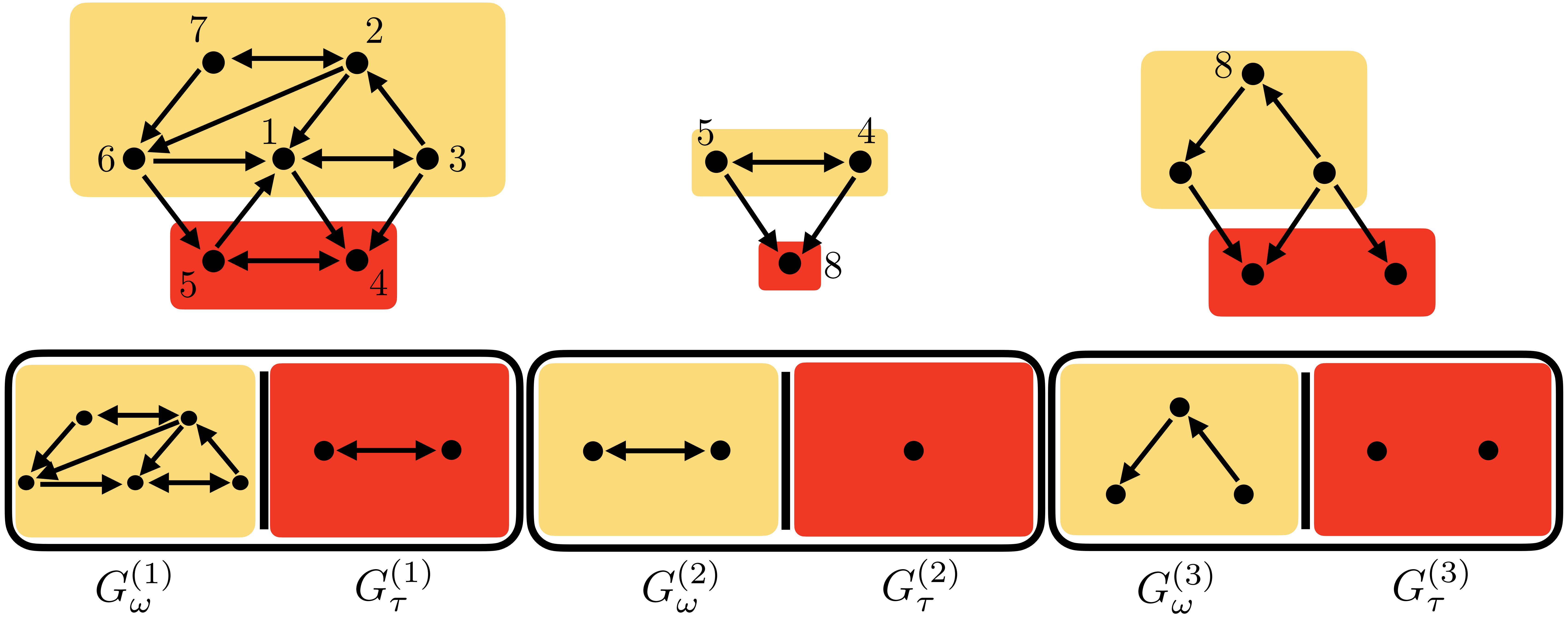
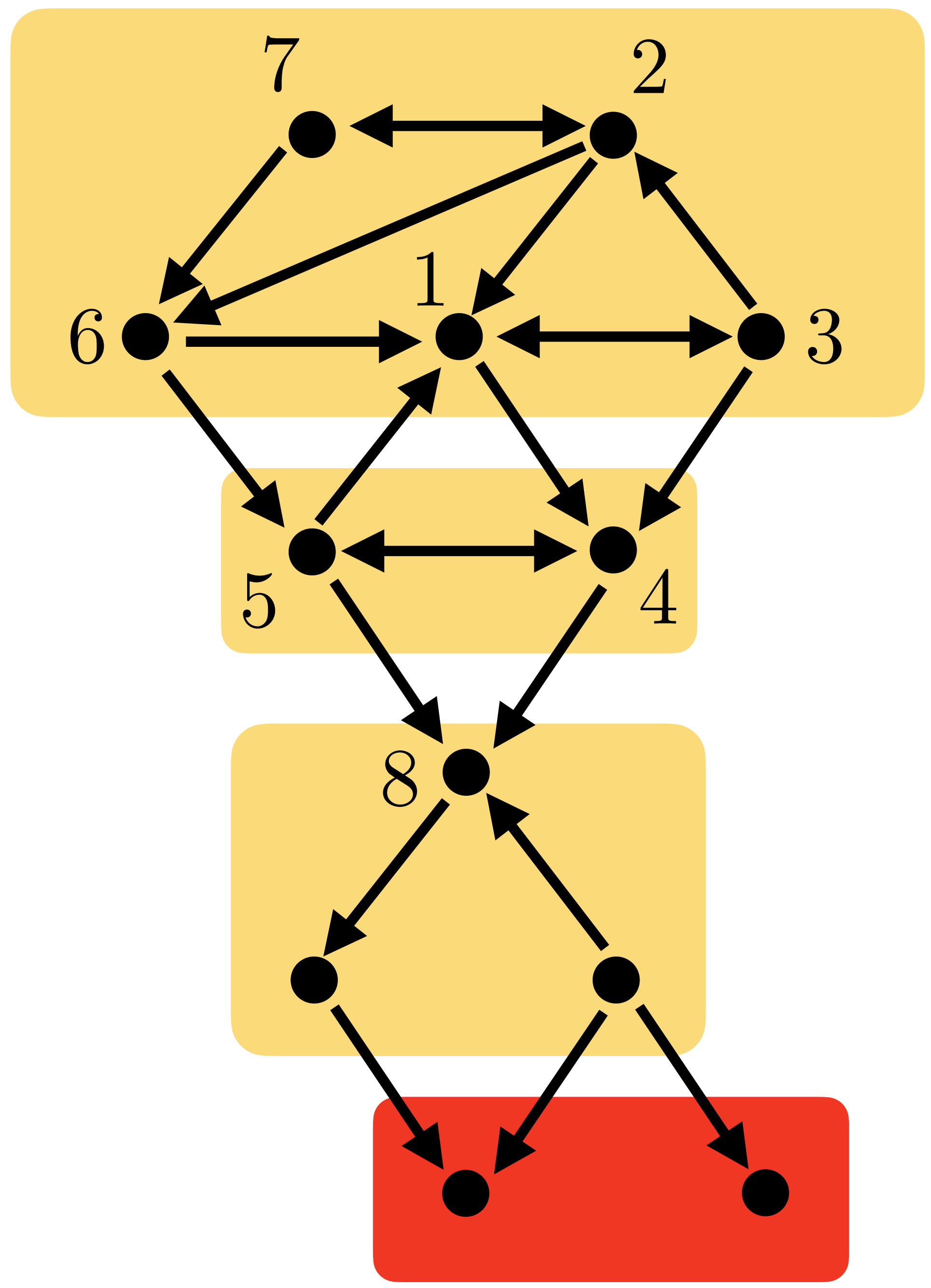


glued graph G



$$\widetilde{G} = G_\tau^{(3)}$$

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Domination - New Theorems - a word about the proofs

3. Proof of Theorem 1.5 Theorem 1

In order to prove Theorem 1.5, it will be useful to use the notation

$$y_i(x) = \sum_{j=1}^{n} W_{ij} x_j + b_i. \quad (3.1)$$

With this notation, the equations for a TLN (W, b) become:

$$\frac{dx_i}{dt} = -x_i + [y_i(x)]_+.$$

If x^* is a fixed point of (W, b), then $x_i^* = [y_i^*]_+$, where $y_i^* = y_i(x^*)$.

We can now prove the following technical lemma:

Lemma 3.2. *Let (W, b) be a TLN on n nodes and consider distinct $j, k \in [n]$. If $W_{ji} \leq W_{ki}$ for all $i \neq j, k$, and $b_j \leq b_k$, then for any fixed point x^* of (W, b) we have*

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Furthermore, if $W_{kj} > -1$ and $W_{jk} \leq -1$, then

$$y_j^* \leq 0. \quad (3.4)$$

Proof. Suppose x^* is a fixed point of (W, b) with support $\sigma \subseteq [n]$. Then, recalling that $W_{jj} = W_{kk} = 0$ and that $x_i^* = 0$ for all $i \notin \sigma$, from equation (3.1) we obtain:

$$y_j^* - W_{jk} x_k^* = \sum_{i \in \sigma \setminus \{j,k\}} W_{ji} x_i^* + b_j,$$
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The first statement now follows from recalling that $x_j^* = [y_j^*]_+$ and $x_k^* = [y_k^*]_+$, since we are at a fixed point.

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Lemma 3.5. *Suppose j is a dominated node in G. Then, for any associated gCTLN, $y_j^* \leq 0$ at every fixed point x^* (no matter the support).*

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need some more lemmas...

Lemma 3.6. *Let G be a graph with vertex set $[n]$. For any gCTLN on G,*

$$\sigma \in \mathrm{FP}(G) \Leftrightarrow \sigma \in \mathrm{FP}(G|_\omega) \text{ for all } \omega \text{ such that } \sigma \subseteq \omega \subseteq [n]$$

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Once again, if $y_j^* > 0$ we obtain a contradiction, so we can conclude that $y_j^* \leq 0$. □

Proof of Theorem 1

Proof of Theorem 1.5. Suppose j is a dominated node in G, and let (W, b) be an associated gCTLN. By Lemma 3.5, we know that $y_j^* \leq 0$ at every fixed point (W, b). It follows that $j \notin \sigma$ for all $\sigma \in \text{FP}(G)$. Hence,

$$\text{FP}(G) \subseteq \text{FP}(G|_{[n]\setminus j}).$$

It remains to show that $\text{FP}(G|_{[n]\setminus j}) \subseteq \text{FP}(G)$. By Lemma 3.6, this is equivalent to showing that for each $\sigma \in \text{FP}(G|_{[n]\setminus j})$, $\sigma \in \text{FP}(G|_{\sigma\cup j})$.

Suppose $\sigma \in \text{FP}(G|_{[n]\setminus j})$, with corresponding fixed point x^*. In this setting, we are not guaranteed that $y_j^* = y_j(x^*) \leq 0$, as x^* is not necessarily a fixed point of the full network. To see whether $\sigma \in \text{FP}(G|_{\sigma\cup j})$, if suffices to check the "off"-neuron condition for j: that is, we need to check if $y_j^* \leq 0$ when evaluating (3.1) at x^*.

Recall now that there exists a $k \in [n] \setminus j$ such that k graphically dominates j. It is also useful to evaluate y_k^* at x^*. Following the beginning of the proof of Lemma 3.2, we see that simply from the fact that $\text{supp}(x^*) = \sigma$, we obtain

$$y_j^* + W_{kj}x_j^* \leq y_k^* + W_{jk}x_k^*.$$

However, we cannot assume $x_j^* = [y_j^*]_+$, since we are not necessarily at a fixed point of the full network (W, b). We know only that $x_j^* = 0$ and $x_k^* = [y_k^*]_+$, as the fixed point conditions are satisfied in the subnetwork $(W_{[n]\setminus j}, b_{[n]\setminus j})$ that includes k. This yields,

$$y_j^* \leq y_k^*(1 + W_{jk}) \leq 0,$$

where the second inequality stems from the fact that $W_{jk} < -1$. So, as it turns out, we see that $y_j^* \leq 0$ not only for fixed points of (W, b), but also for fixed points from the subnetwork $(W_{[n]\setminus j}, b_{[n]\setminus j})$. We can thus conclude that $\text{FP}(G|_{[n]\setminus j}) \subseteq \text{FP}(G)$, completing the proof. □

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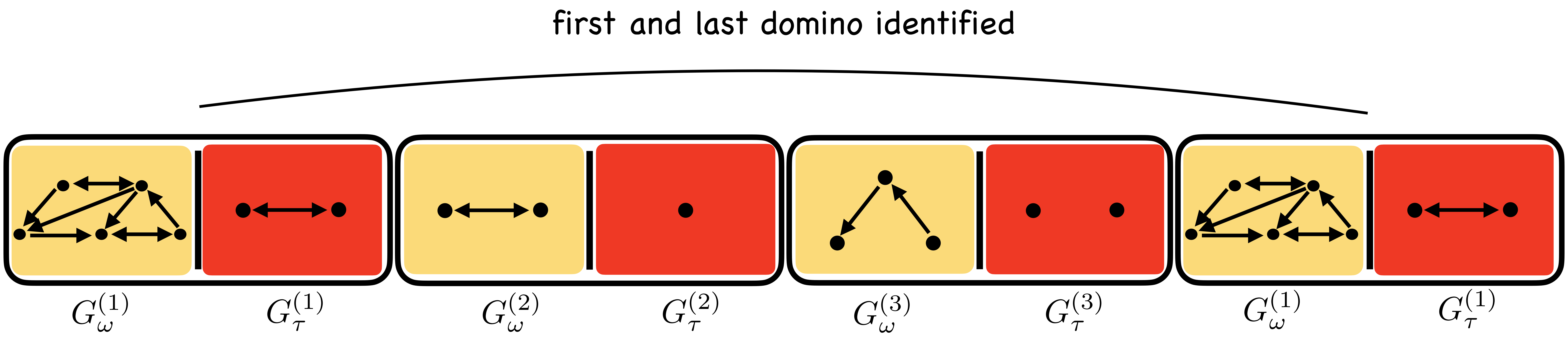
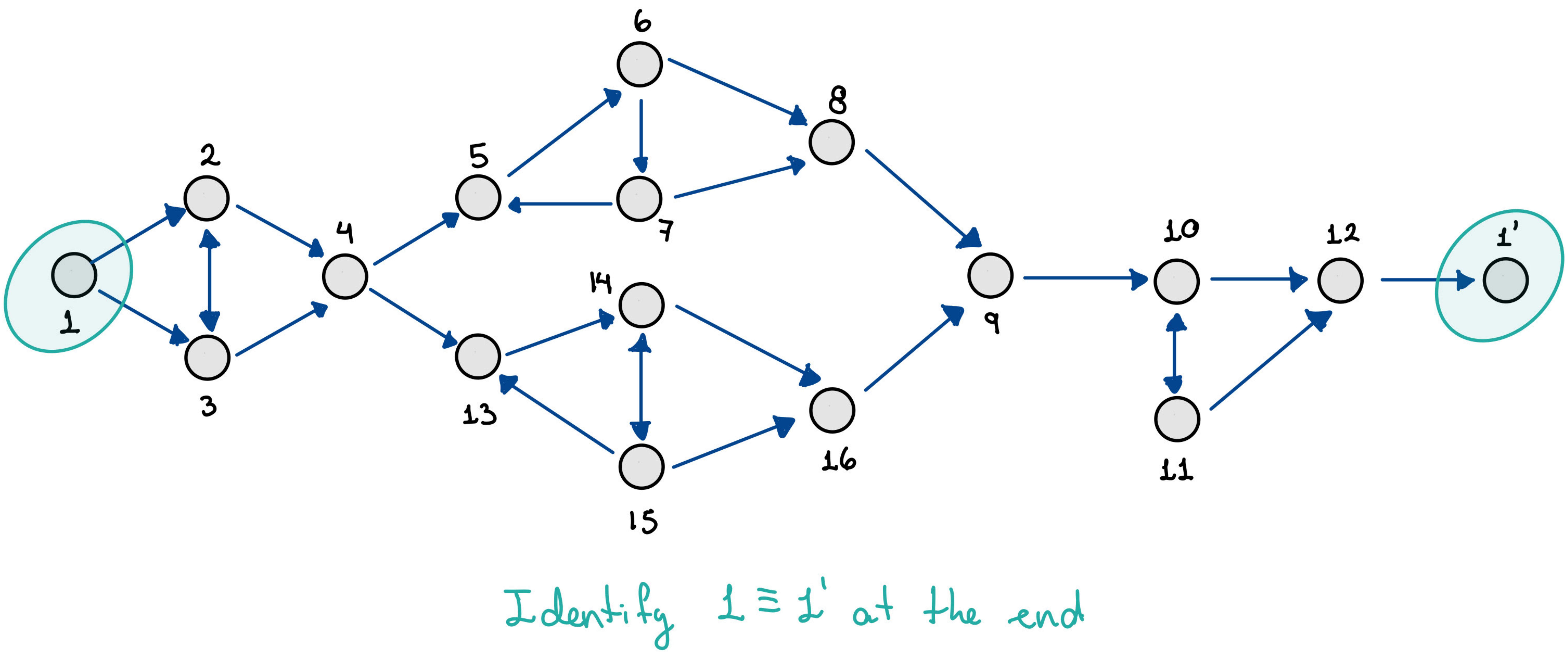
$$\Leftrightarrow \sigma \in \text{FP}(G|_\sigma) \text{ and } \sigma \in \text{FP}(G|_{\sigma\cup\ell}) \text{ for all } \ell \notin \sigma.$$

What about a cyclic chain?



Theorem 3 (2024)
If we glue reducible graphs together along their dominoes, in a linear chain,
so that G_τ of one is identified with a subgraph of G_ω of the next,
then the glued graph reduces to the final $G_\tau^{(i)}$.

Cyclic chain example

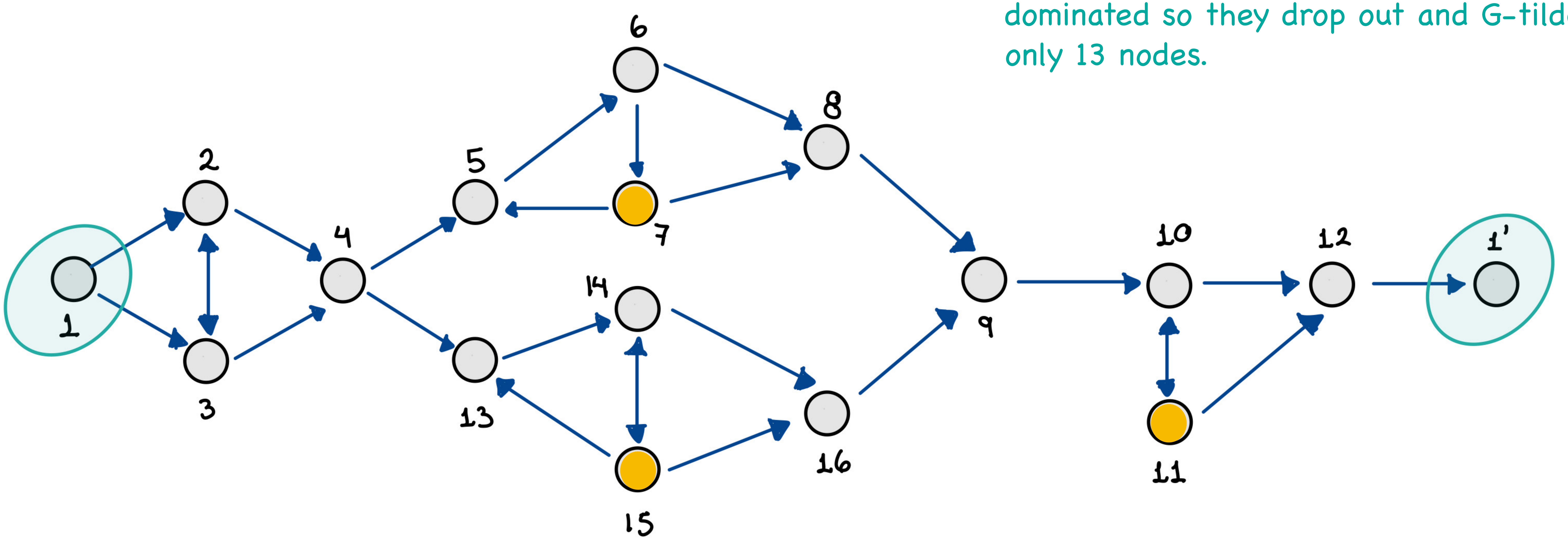


Domination reduction cannot be done, and the network activity will loop around.

Cyclic chain example

Domination reductions:

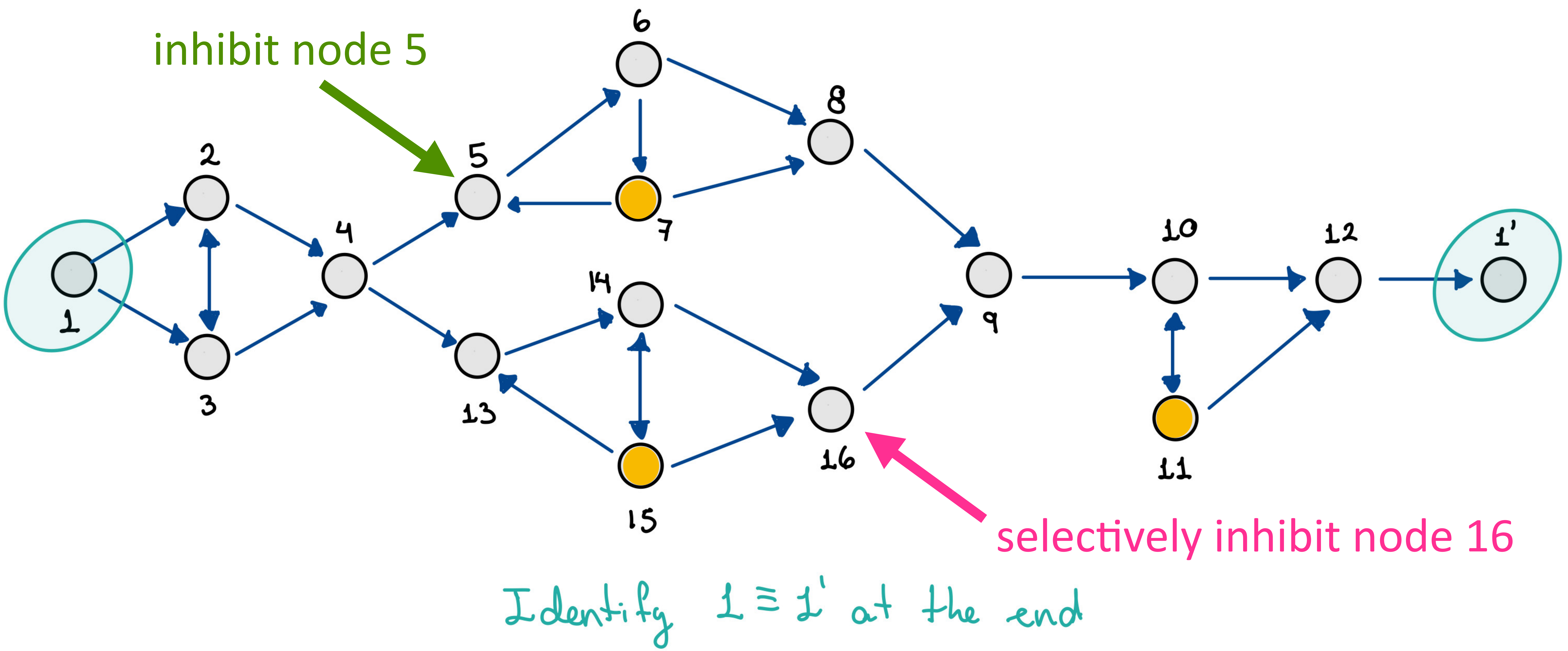
1) Without identifying 1′ and 1, G reduces to 1′
2) After identifying 1′ and 1, nodes 7, 11, 15 are dominated so they drop out and G-tilde has only 13 nodes.



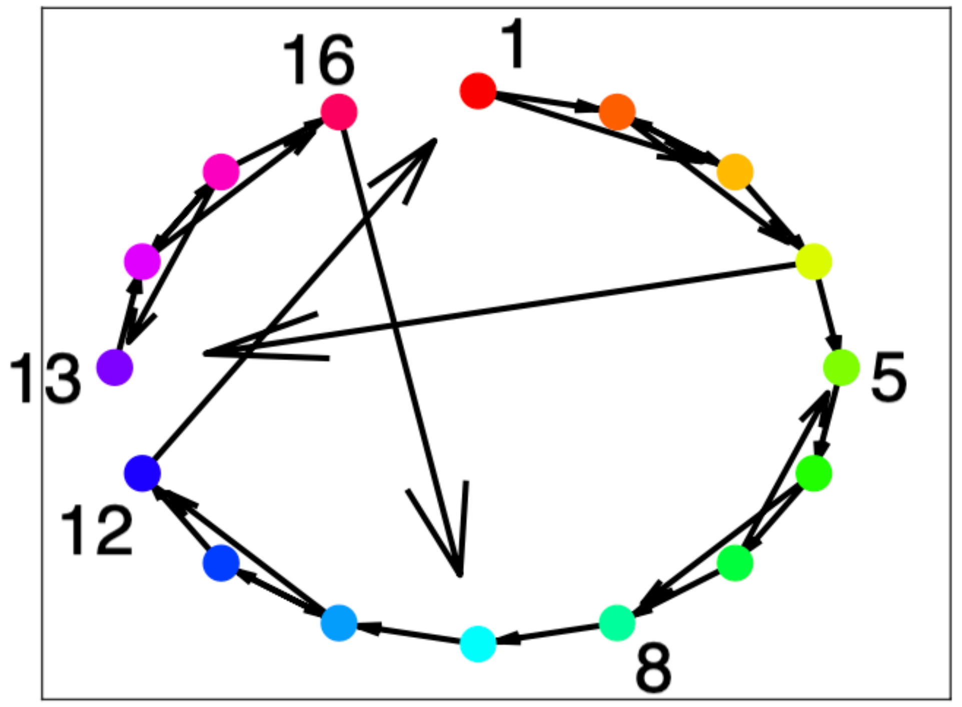
Identify 1 ≡ 1′ at the end

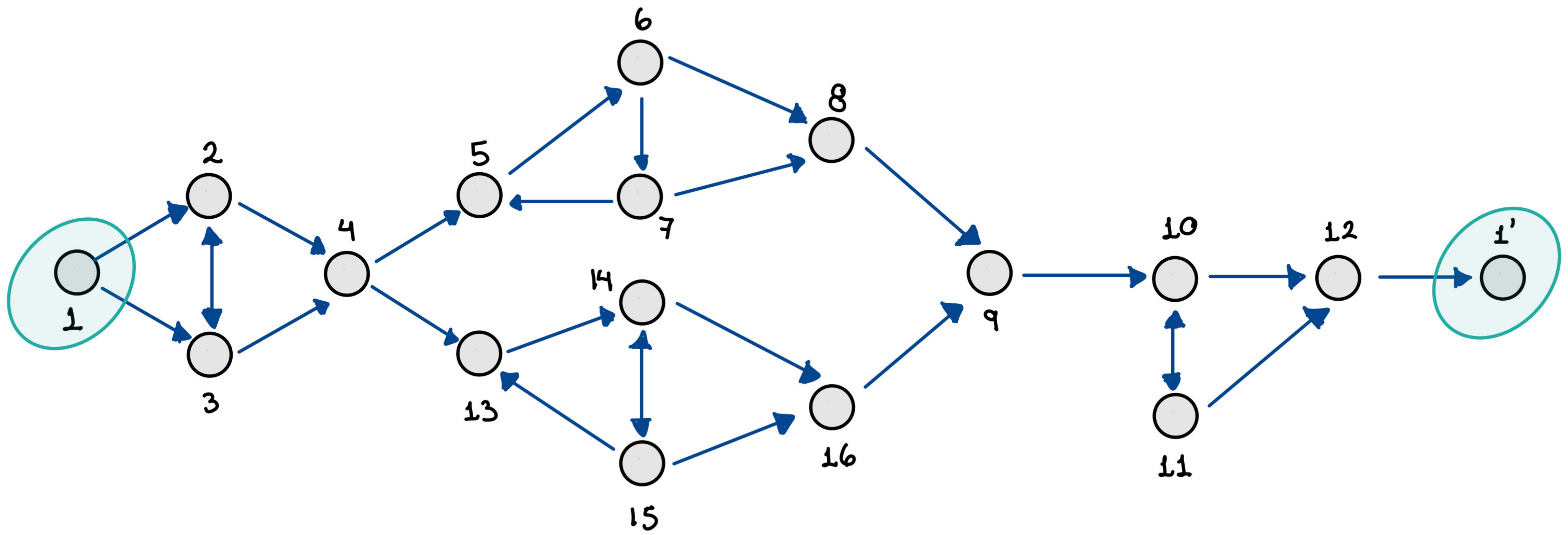
Domination reduction cannot be done, and the network activity will loop around.

Inhibitory control



What if you selectively inhibit one of the neurons?

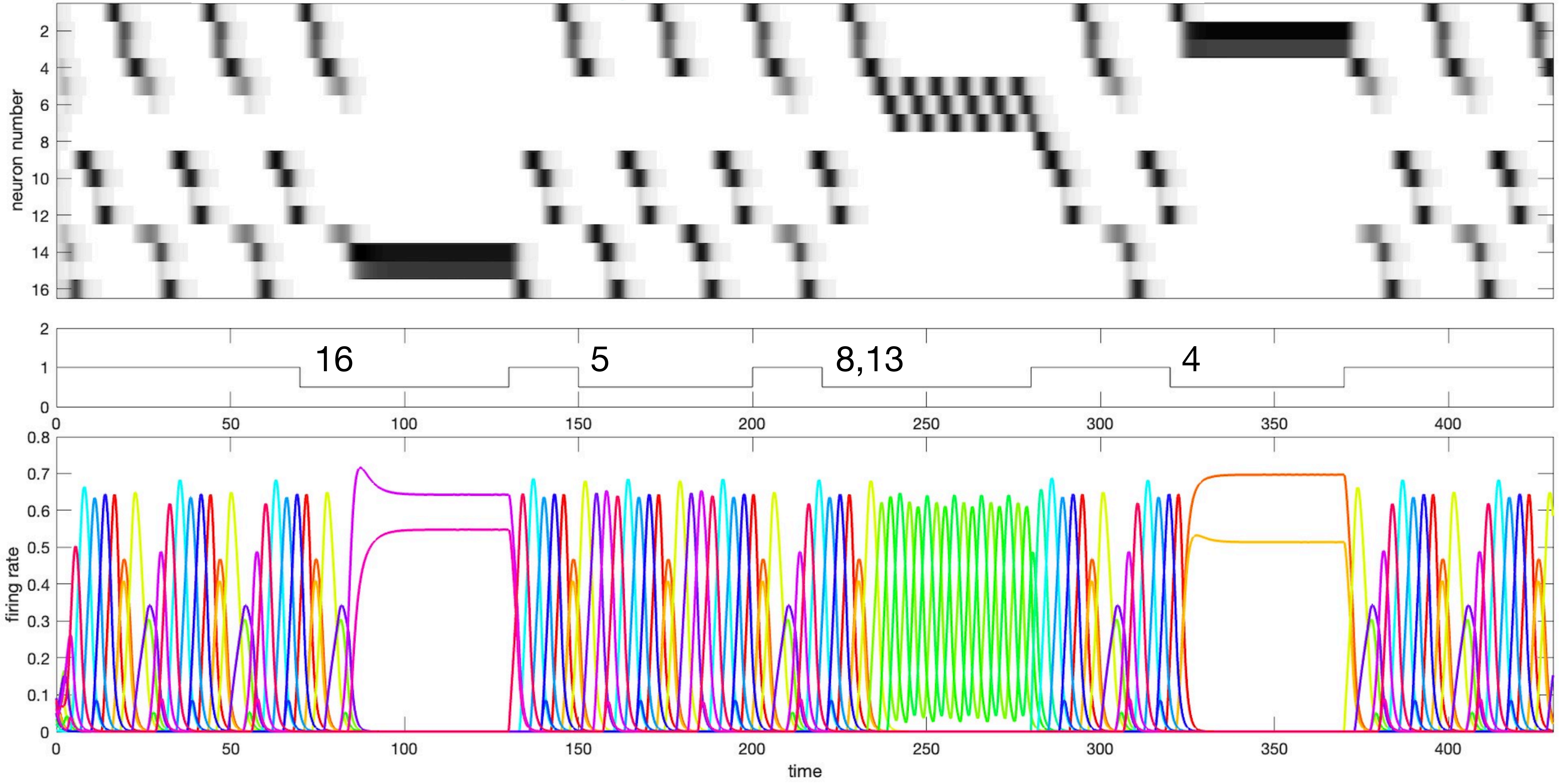


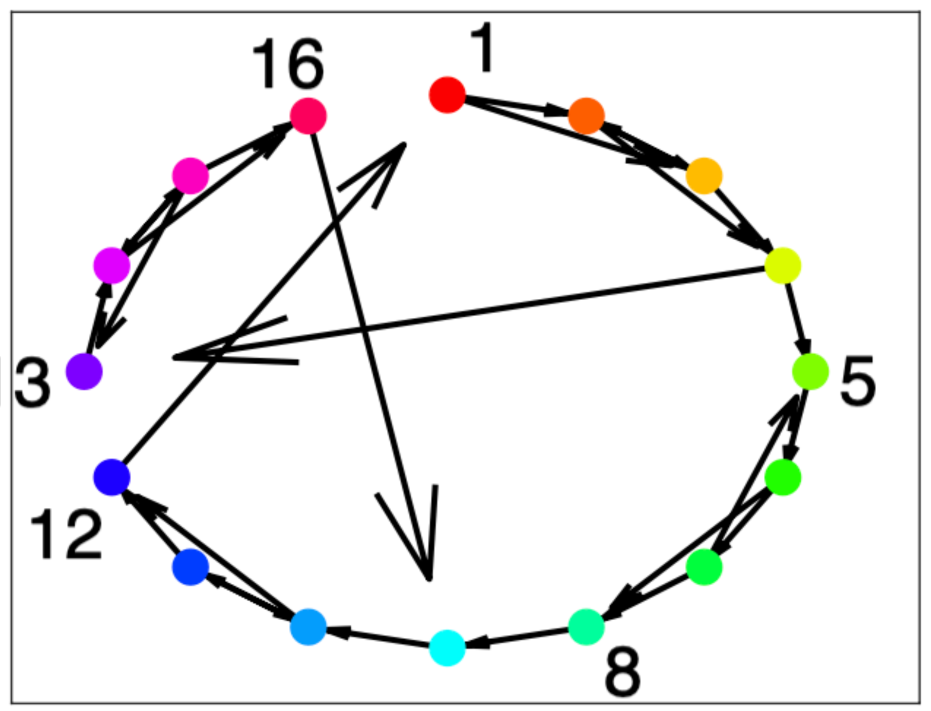


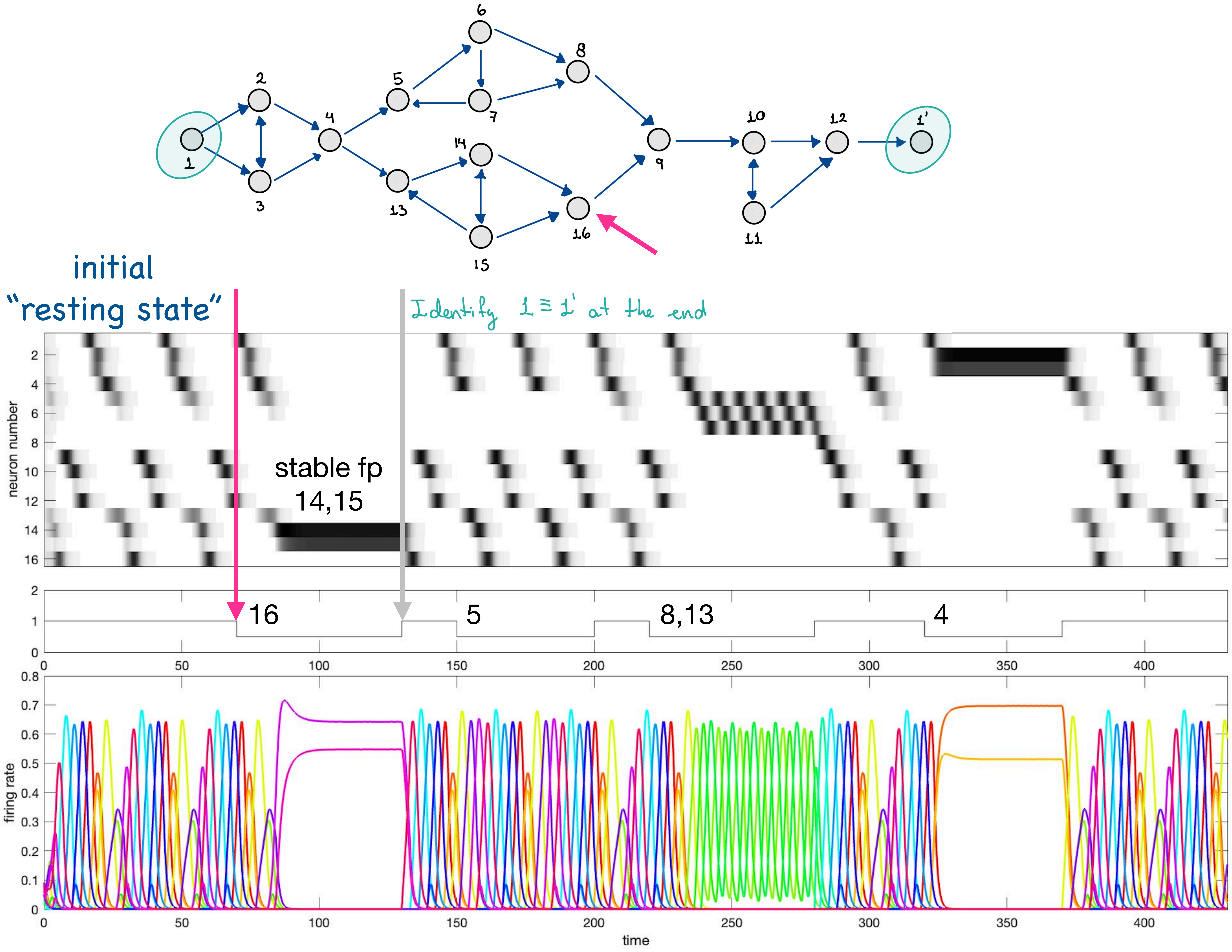
initial
"resting state"

Identify $1 \equiv 1'$ at the end

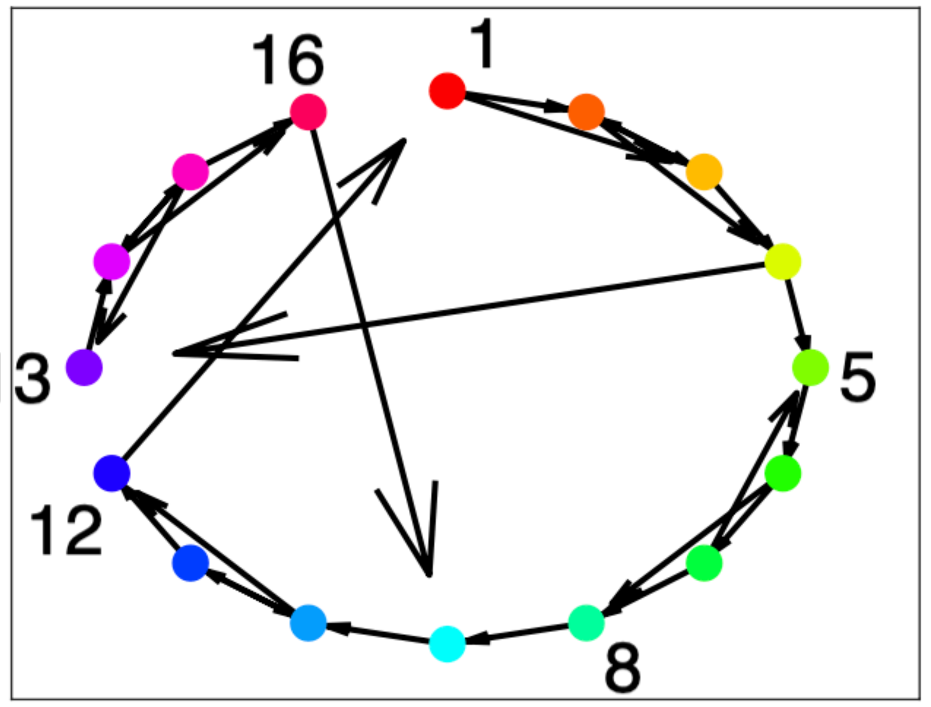
Control by inhibitory pulses:

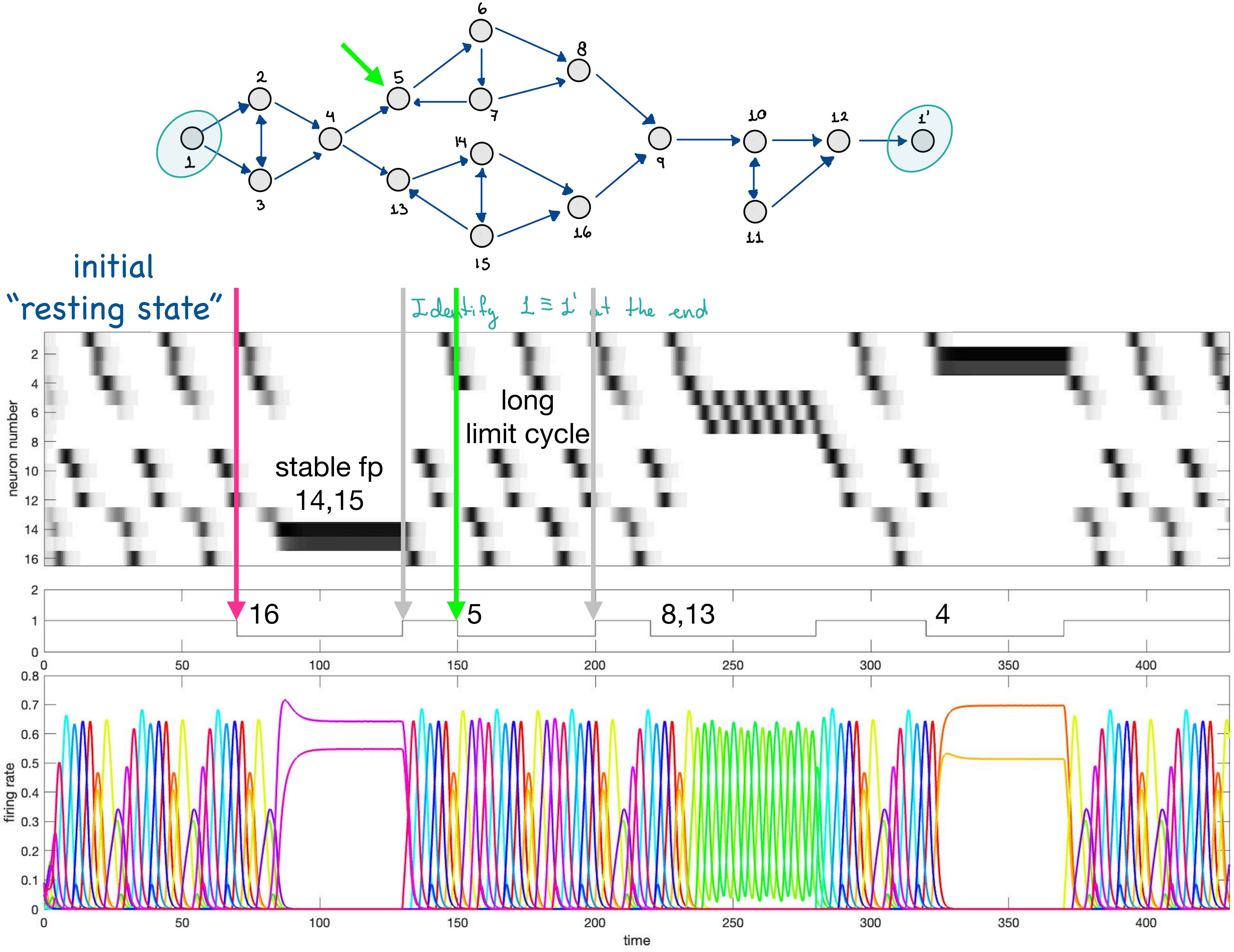




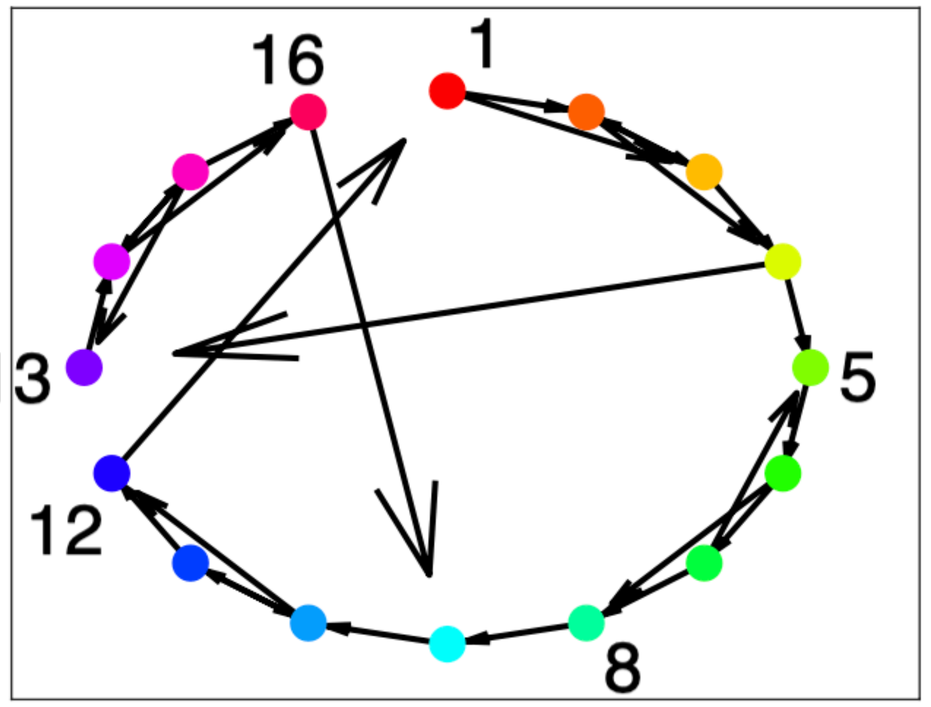


Control by inhibitory pulses:

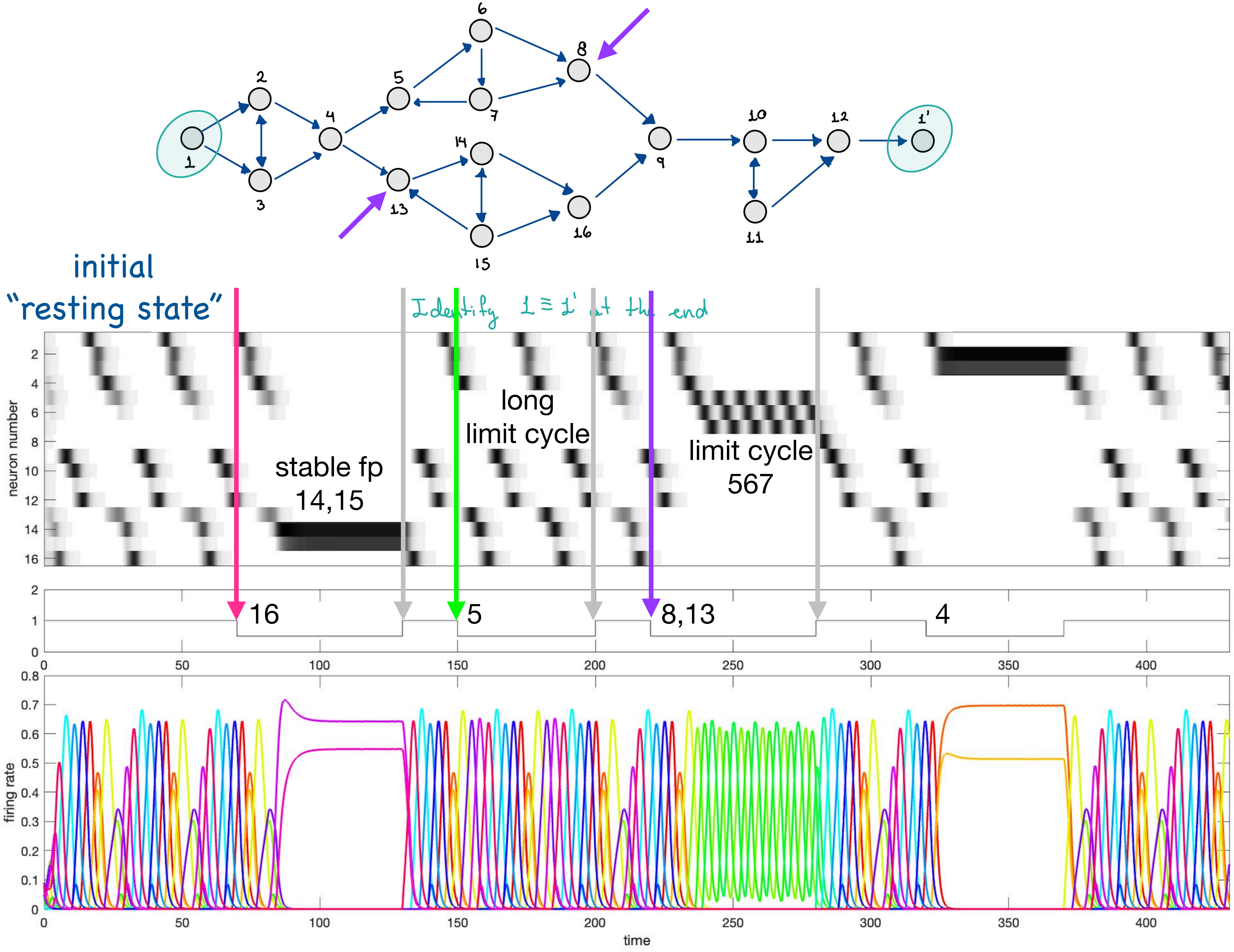


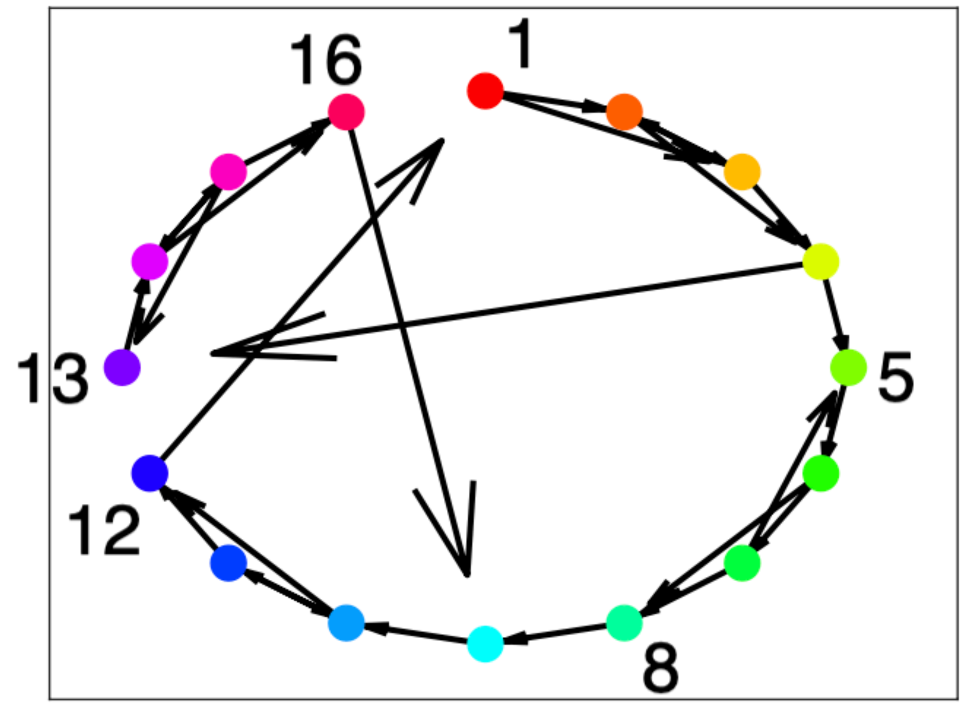


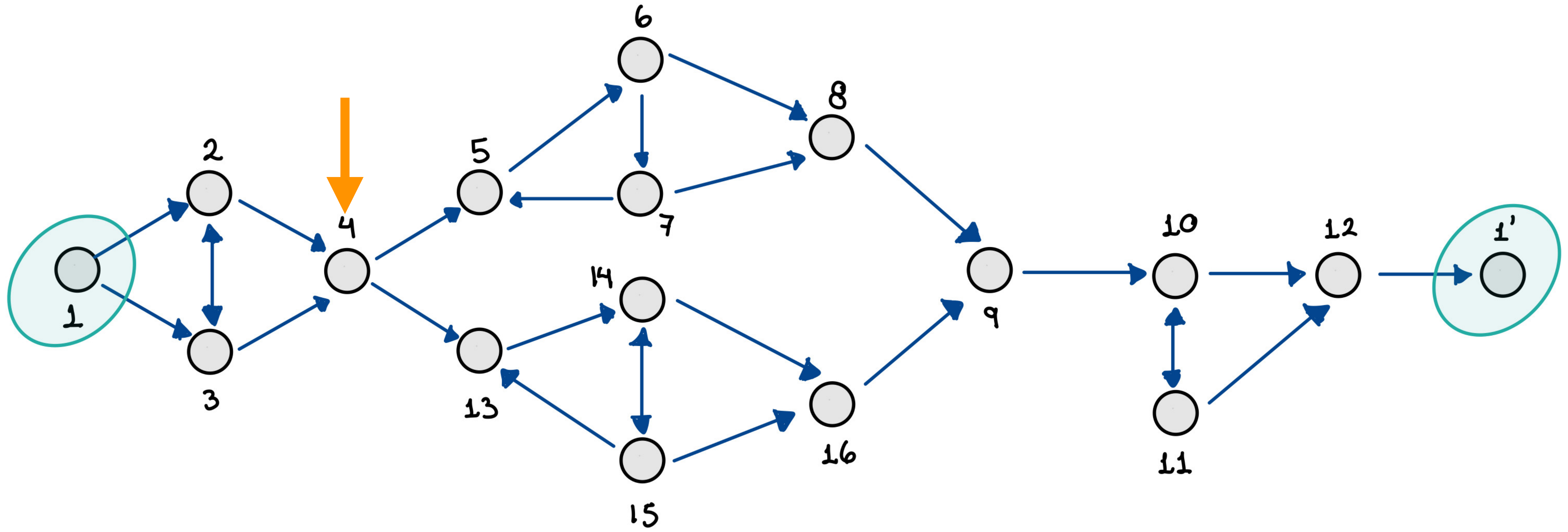
Control by inhibitory pulses:

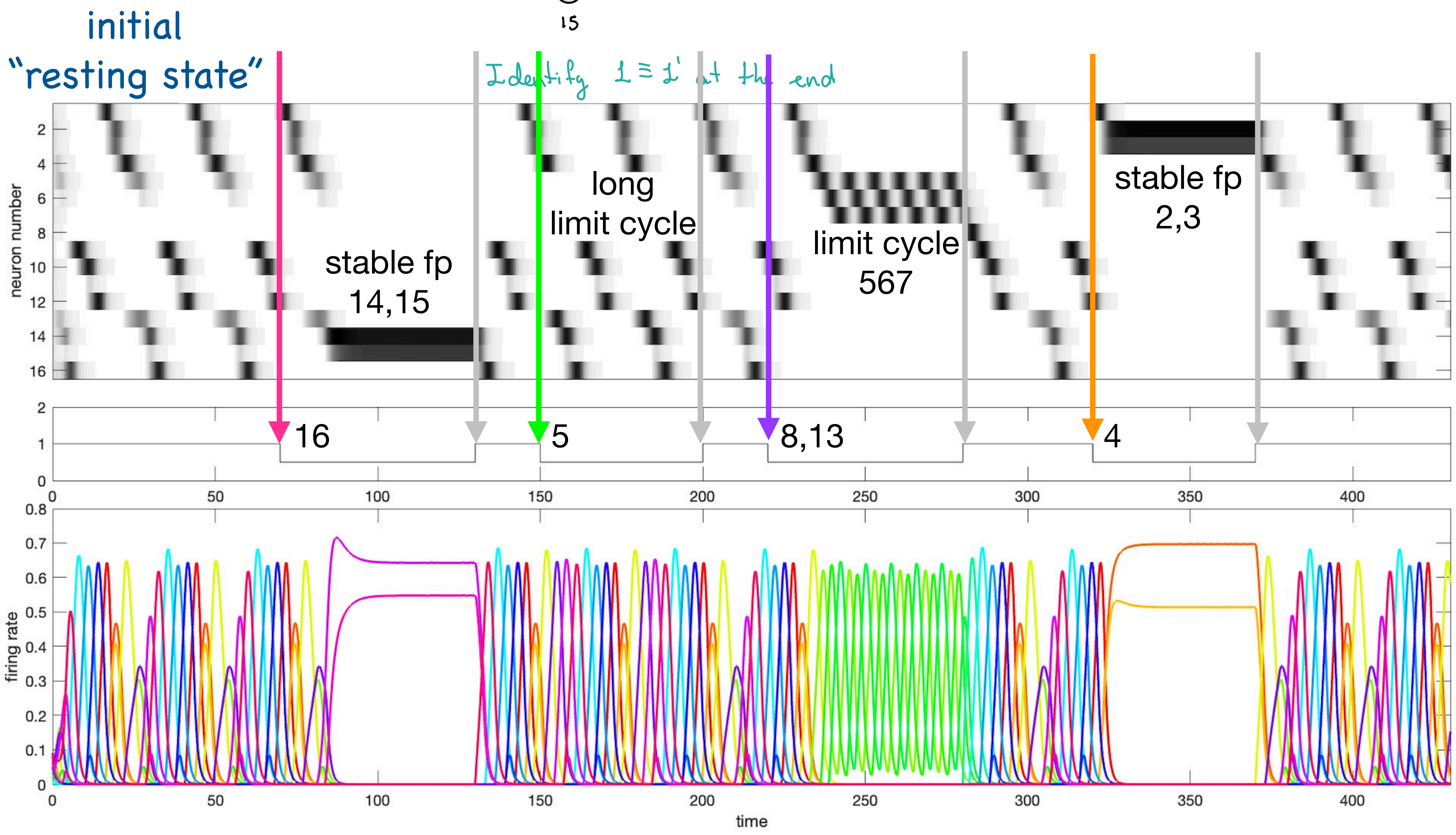


Control by inhibitory pulses:









Control by inhibitory pulses:

Thank you!

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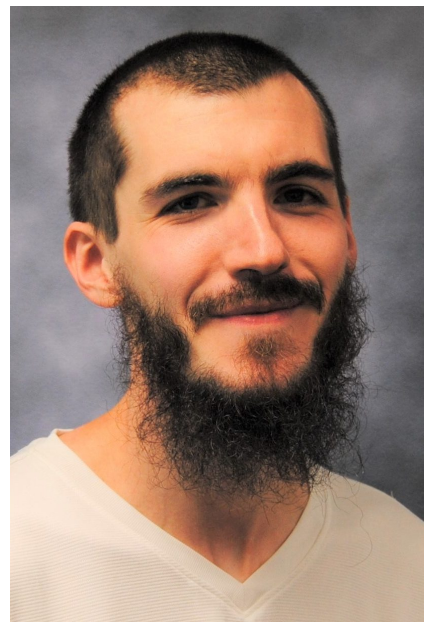

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