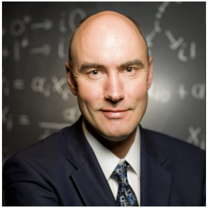
Evolutionary Graph Theory

How population structure affects evolutionary dynamics

David Brewster

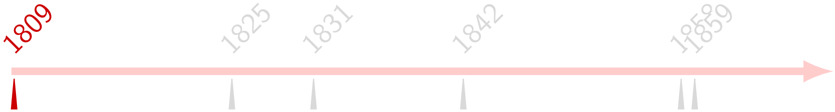
Harvard University



Martin Nowak

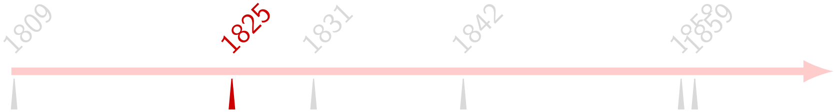
Josef “Pepa” Tkadlec

Timeline



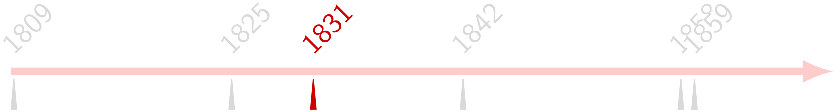
- 1809: Lamarck publishes *Philosophie zoologique*; Darwin born

Timeline



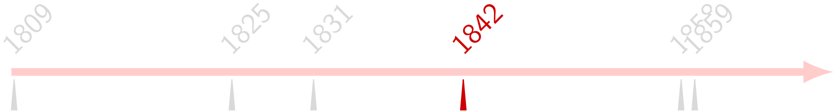
- 1825-31: Darwin student in Edinburgh and Cambridge

Timeline

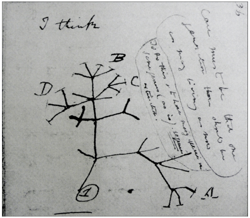


- 1831-36: *Voyage of the Beagle*

Timeline



- 1842: Pencil sketch



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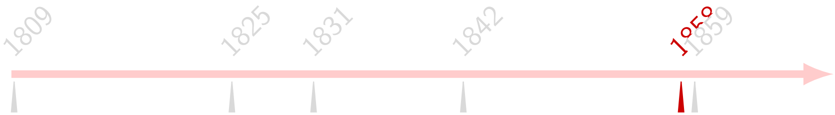
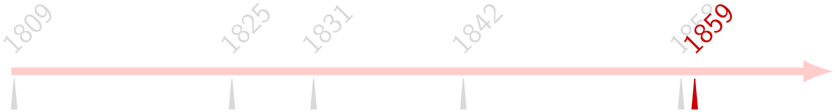


- 1858: Darwin and Wallace publish on natural selection

Timeline



- 1859: *On the origin of species*

Evolutionary graph theory

How does stuff propagate through networks?

Maximizing the spread of influence through a social network
D Kempe, J Kleinberg, É Tardos - … of the ninth ACM SIGKDD international …, 2003 - dl.acm.org
Models for the processes by which ideas and influence propagate through a social network have been studied in a number of domains, including the diffusion of medical and technological innovations, the sudden and widespread adoption of various strategies in game-theoretic settings, and the effects of" word of mouth" in the promotion of new products. Recently, motivated by the design of viral marketing strategies, Domingos and Richardson posed a fundamental algorithmic problem for such social network processes: if we can try to …
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E Lieberman, C Hauert, MA Nowak - Nature, 2005 - nature.com
… Here we introduce **evolutionary graph** theory, which suggests a promising new lead in the effort to provide a general account of how population structure affects **evolutionary dynamics**. …
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[HTML] Complex networks: Structure and dynamics
S Boccaletti, V Latora, Y Moreno, M Chavez… - Physics reports, 2006 - Elsevier
Coupled biological and chemical systems, neural networks, social interacting species, the Internet and the World Wide Web, are only a few examples of systems composed by a large …
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[HTML] **Evolutionary games** on **graphs**
G Szabó, G Fath - Physics reports, 2007 - Elsevier
Game theory is one of the key paradigms behind many scientific disciplines from biology to behavioral sciences to economics. In its **evolutionary** form and especially when the …
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Statistical physics of **social dynamics**
C Castellano, S Fortunato, V Loreto - Reviews of modern **physics**, 2009 - APS
… best to mention relevant **social** science literature and highlight connections to it, the main focus of this work remains a description of the **statistical physics** approach to **social dynamics**. …
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[HTML] **Statistical physics** of human cooperation
M Perc, JJ Jordan, DG Rand, Z Wang, S Boccaletti… - **Physics** Reports, 2017 - Elsevier
… the relevance of **physics** in all of this. Methods of **statistical physics** have recently been … **Statistical physics** of **social dynamics** [13], of evolutionary games in structured populations […
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- coronavirus among humans
- influence (opinion, gossip, fake news) on social media
- genetic mutation in a population of individual organisms

Evolutionary graph theory

Evolutionary biology 101:

- Evolution acts on populations
- Individuals: bacteria in a Petri dish, cells in a tissue, birds in an archipelago, ...
- Individuals reproduce (sexually/asexually) and die
- type = genetic information, alters the fitness

Two main forces:

1. mutation: generates variety
2. selection: reduces variety

When mutations are rare: What is the fate of a single new mutant?

Model: Moran process on a graph

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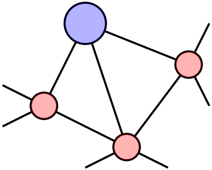

	fitness
mutant	r
resident	1

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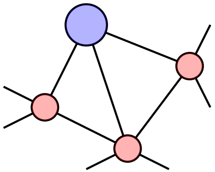

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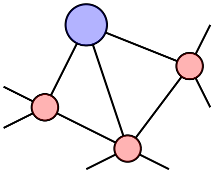

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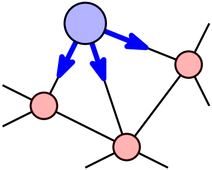

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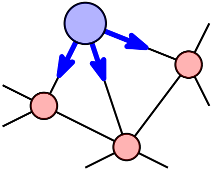

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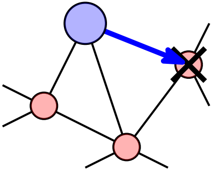

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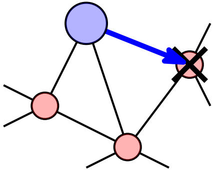

	fitness
● mutant	r
● resident	1

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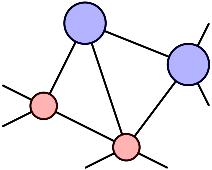

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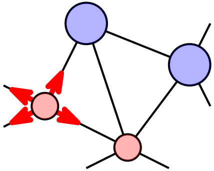

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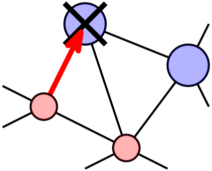

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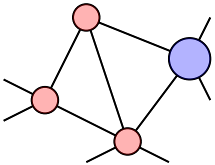

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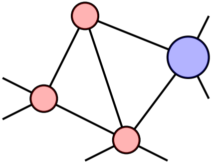

	fitness
mutant	r
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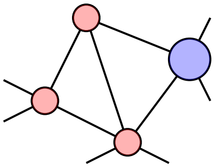
Some features of the Moran process



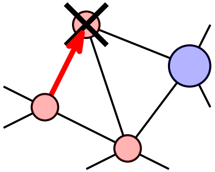
	fitness
mutant	r
resident	1

1. It is stochastic (random).
2. In some steps, nothing happens.
3. Nodes can toggle back and forth (more opinions than gossip).
4. Eventually, all nodes become the same type (no mutation).
5. Variants exist (e.g. death-Birth updating).

Quantities of interest:

1. Fixation probability $\text{fp}^r(G)$: Average probability that, starting from a single node, mutants spread to all sites.
2. Fixation time $\text{T}^r(G)$: Average time until one type wins.
   - Measured in steps or better in generations.

Some features of the Moran process



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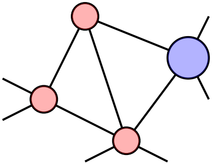

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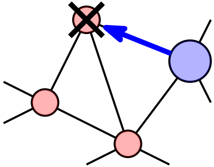

	fitness
mutant	r
resident	1

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2. In some steps, nothing happens.
3. Nodes can toggle back and forth (more opinions than gossip).
4. Eventually, all nodes become the same type (no mutation).
5. Variants exist (e.g. death-Birth updating).

Quantities of interest:

1. Fixation probability $\mathrm{fp}^r(G)$: Average probability that, starting from a single node, mutants spread to all sites.
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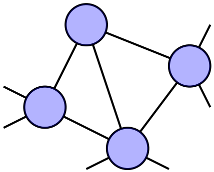

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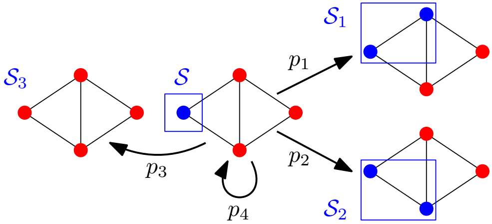
Computing $\text{fp}^r(G)$

Claim. $\text{fp}^r(G)$ can be computed by solving a system of 2^n linear equations.

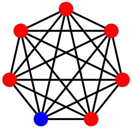


Proof. Suppose G has n nodes. There are 2^n configurations of nodes occupied by mutants. For each configuration $\mathcal{S}$, let $\text{fp}^r(G, \mathcal{S})$ be the fixation probability if mutants initially occupy $\mathcal{S}$. Then

$$\text{fp}^r(G, \mathcal{S}) = \sum_{\mathcal{S}'} p_{\mathcal{S}\to\mathcal{S}'} \cdot \text{fp}^r(G, \mathcal{S}')$$

and $\text{fp}^r(G, \emptyset) = 0$, $\text{fp}^r(G, [n]) = 1$.

Special case: $r = 1$



Claim. $\mathrm{fp}^r(K_n) =$

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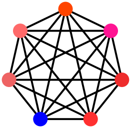

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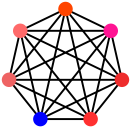

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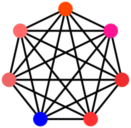

Claim. $\text{fp}^r(K_n) = 1/n$.

On any G, when $r = 1$ then fixation probability is additive, that is,

$$\text{fp}^r(G, \mathcal{S}) = \sum_{v \in \mathcal{S}} \text{fp}^r(G, \{v\}).$$

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→ Also, $\text{fp}^r(G) = 1/n$ for any graph G_n on n nodes.

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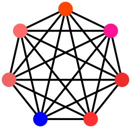

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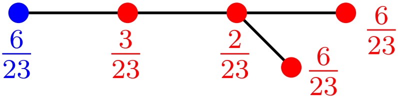
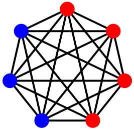
Claim. When G is undirected then $\mathrm{fp}^r(G, \{v\}) \propto 1/\deg(v)$.



Special case: Complete graph K_n and $r > 1$



$$F = kr + (n-k)$$

$$\left.\begin{aligned} p_k^+ &= \frac{kr}{F} \cdot \frac{n-k}{n-1} \\ p_k^- &= \frac{n-k}{F} \cdot \frac{k}{n-1} \end{aligned}\right\} \quad \frac{p_k^+}{p_k^-} = r$$

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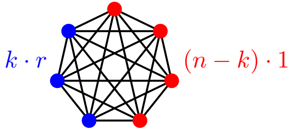

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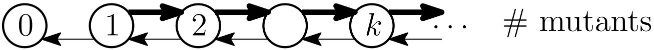
It turns out that we are always r-times more likely to gain than to lose a mutant. Thus the process can be mapped to a 1-dimensional random walk, with a constant forward bias r.



Claim. $\mathrm{fp}^r(K_n) = \frac{1-1/r}{1-1/r^n} \to_{n\to\infty} \boxed{1-1/r}$.

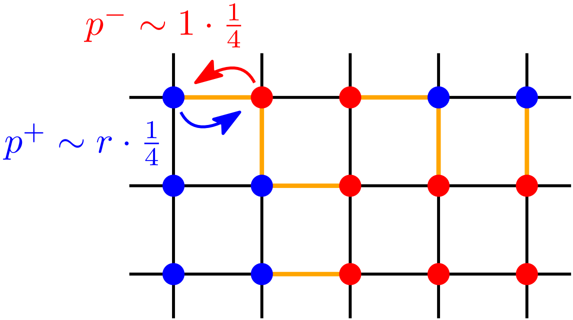
(Intuition. Let $x = 1 - \mathrm{fp}^r(K_n)$. Then $x = \frac{1}{r+1} \cdot 1 + \frac{r}{r+1} \cdot x^2$.)

Special case: Regular graphs R_n

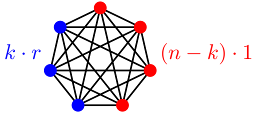
Claim (Isothermal theorem, '05). For any regular graph we have

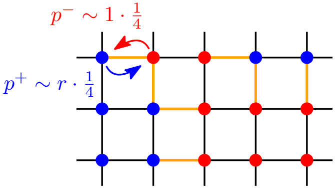
$$\mathrm{fp}^r(R_n) = \mathrm{fp}^r(K_n).$$

Proof. The same mapping works! We say that an edge is active if its endpoints are of different types. Each active edge is r-times more likely to be used in gaining rather than losing a mutant.

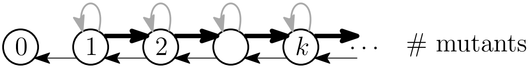


But #steps on regular graphs differ





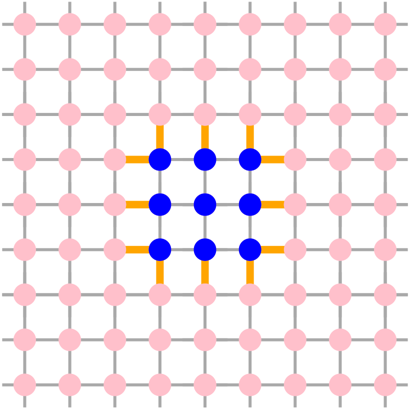
Intuition. If a of E edges are active, then, on average, roughly one in every E/a steps is active.



K_n: #edges $\sim n^2$, #active edges $\sim k(n-k)$
$\to$ #steps for $K_n \sim c \cdot n + \sum_k \frac{n^2}{k(n-k)} \sim \Theta(n \log n)$

Sq_n: #edges $\sim 4n$, #active edges $\in (\sqrt{k}, 4k)$
$\to$ #steps for Sq_n is $\mathcal{O}(n\sqrt{n})$ and $\Omega(n \log n)$.

#steps on large square grids



Intuition. Most of the time, the boundary should have size $\sqrt{k}$, so

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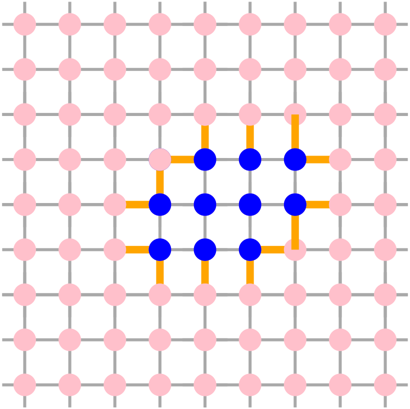

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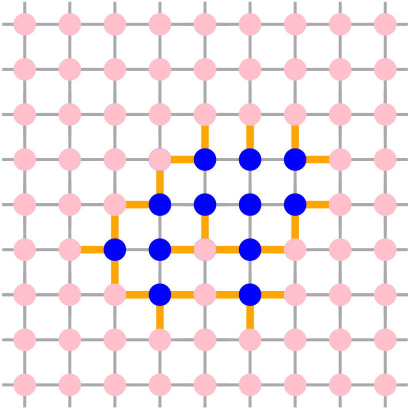

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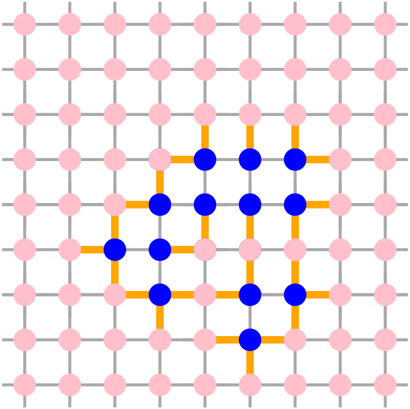

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Denote boundary of $S \subseteq V$ as ∂S.

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Theorem. [DGRS '16] #steps for d-regular graph G is at most

$$\frac{2 \cdot d \cdot n \cdot H_n}{i(G) \cdot \mathrm{fp}^r_{\min}(G)}$$

Bounding fixation time for any graph [DGMRSS '14]

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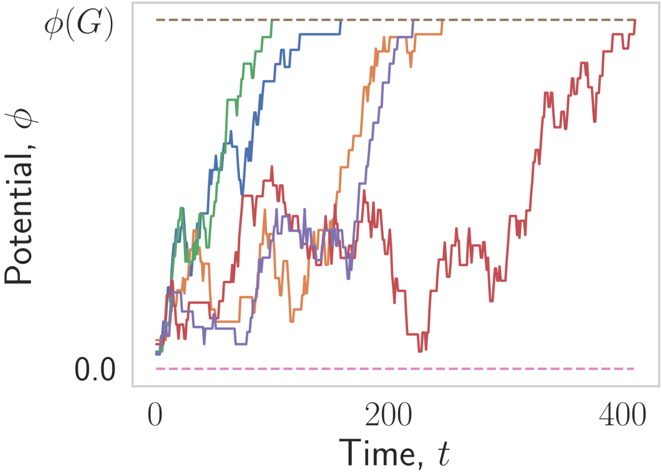

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... thus #steps is at most

$$\frac{\phi(G) - \mathbb{E}[\phi(X_0)]}{\mathrm{fp}^r_{\min}(G)} \cdot \frac{n^3}{1 - 1/r}$$

Directed graphs

Some directed graphs have exponentially long fixation time

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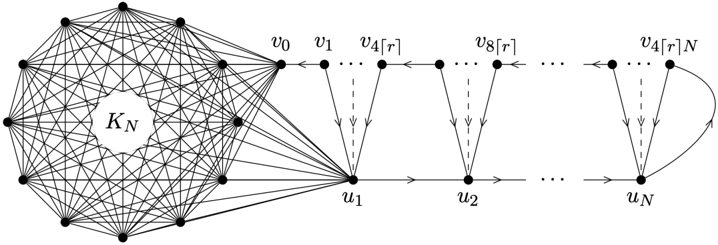

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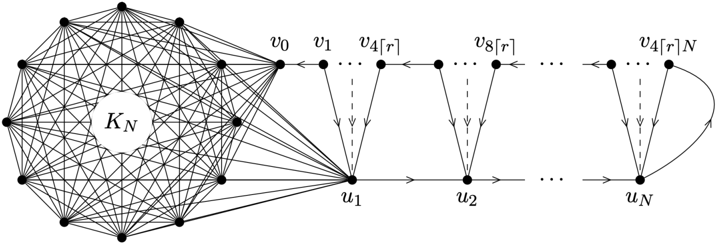

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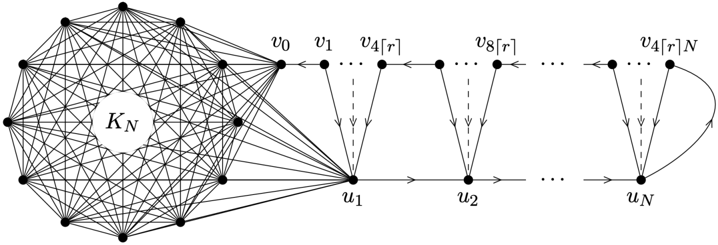

Theorem. [DGRS '16] *D*-regular digraphs fixate quickly.
Theorem. [BNT '23+] For *Eulerian* digraph with min degree δ and max degree Δ,

$$r \geq \Delta/\delta \implies \#\text{steps at most } \mathrm{poly}(n).$$

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Intuition. When $r = 1$, fixation probabilities satisfy

$$\mathrm{fp}^{r=1}(G, \{v\}) \sum_{u : u \to v \in E} \frac{1}{\deg^+(u)} = \frac{1}{\deg^+(v)} \sum_{w : v \to w \in E} \mathrm{fp}^{r=1}(G, \{w\})$$

for each $v \in V$.

Then a coupling and averaging argument gives a bound on #steps with $r \geq 1$ using only quantities involving $r = 1$.

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Consider similar model expect:

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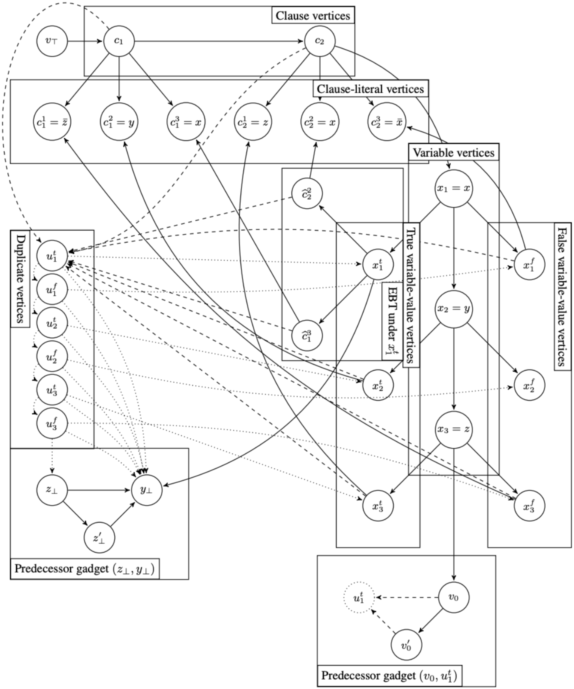
Theorem. [ICN '15]

- Deciding whether $\mathrm{fp}^r(G) > 0$ is NP-COMPLETE
- Approximating $\mathrm{fp}^r(G)$ is #P-COMPLETE



Clause vertices
Clause-literal vertices
Variable vertices
EBT under x_1^t
True variable-value vertices
False variable-value vertices
Duplicate vertices
Predecessor gadget $(z_\perp, y_\perp)$
Predecessor gadget (v_0, u_1^t)
$v_\top$
c_1
c_2
$c_1^1 = \bar{z}$
$c_1^2 = y$
$c_1^3 = x$
$c_2^1 = z$
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$c_2^3 = \bar{x}$
$\widehat{c}_2^2$
$\widehat{c}_1^3$
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$x_2 = y$
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x_1^t
x_2^t
x_3^t
x_1^f
x_2^f
x_3^f
u_1^t
u_1^f
u_2^t
u_2^f
u_3^t
u_3^f
$z_\perp$
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- Tighter bounds on complexity of computing fixation probabilities
- What does "time" mean if population size is not constant?

Questions?