Accessible paths on the hypercube

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In collaboration with Julien Berestycki and Zhan Shi (LPMA UPMC)

Population with asexual reproduction

- A genome with L loci ($=$ location of genes)

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Genome of a wild individual

0	0	0	0	0	0	0	0	0	0	0	0

0	0	0	0	0	0	0	0	0	1	0	0

With one mutation

0	0	0	0	0	0	1	0	0	1	0	0

With two mutations

Population with asexual reproduction

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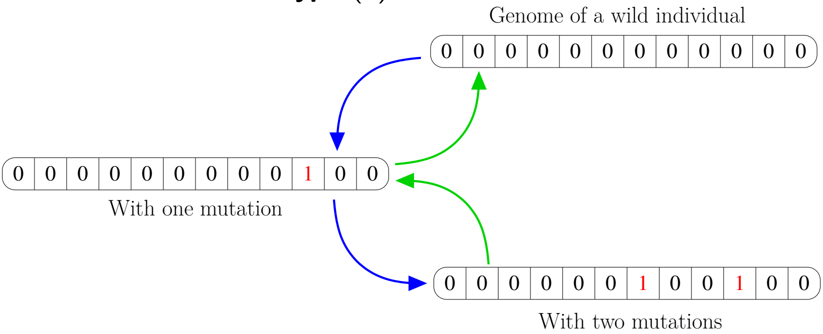
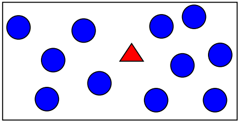


- During reproduction, when a mutation occurs, **only one gene is affected**.

$0 \longrightarrow 1$: forward mutation $\qquad$ $1 \longrightarrow 0$: backward mutation

Low mutation rate, population not too large

When a mutation occurs,



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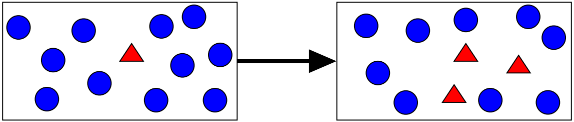

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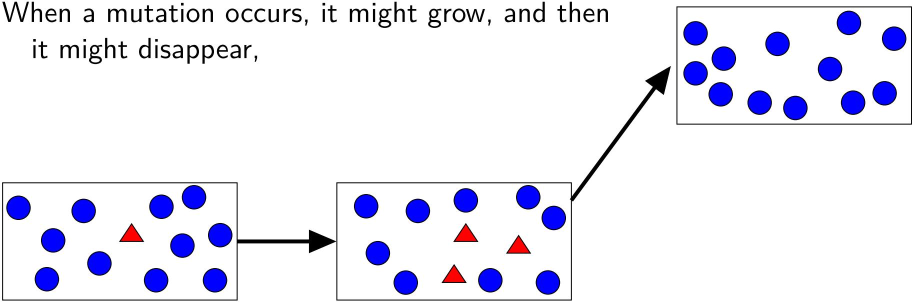

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When a mutation occurs, it might grow, and then

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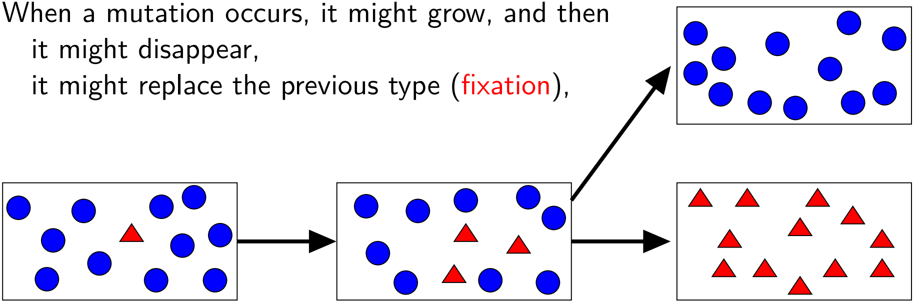
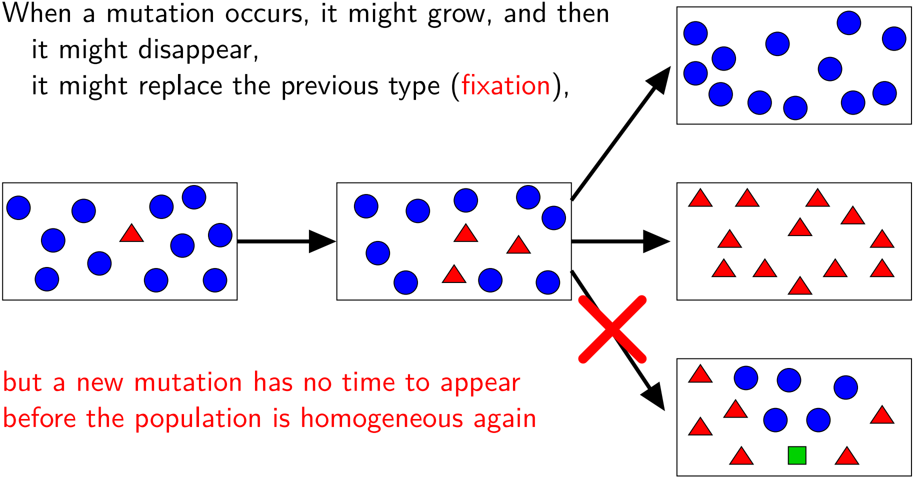
- it might replace the previous type (fixation),



Low mutation rate, population not too large

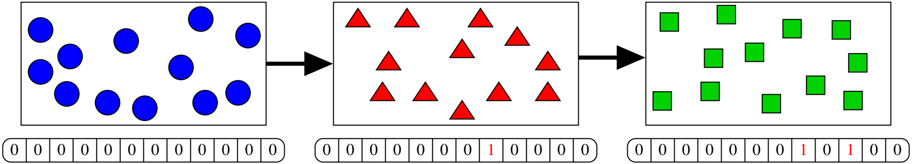
When a mutation occurs, it might grow, and then
it might disappear,
it might replace the previous type (fixation),

but a new mutation has no time to appear
before the population is homogeneous again



Evolutionary paths and Hypercube

Big simplification:



Gillespie 1983, Kauffman Levin 1987

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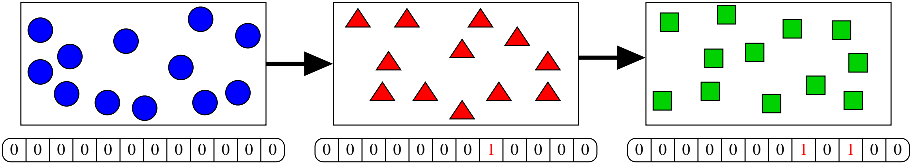
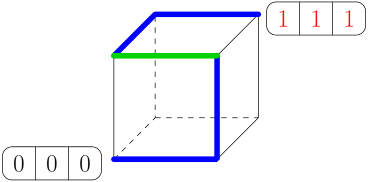


Evolutionary path = walk on the hypercube



(0 ⟶ 1: forward mutation   1 ⟶ 0: backward mutation)

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Fitness and selection

Evolutionary path = walk on the hypercube

- To each of the 2^L genomes one associates a fitness value
- Assume strong selection

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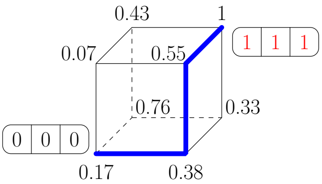
Evolutionary path = walk on the hypercube

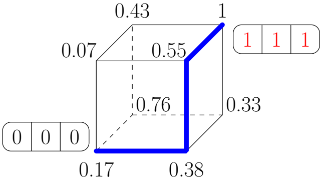
- To each of the 2^L genomes one associates a fitness value
- Assume strong selection
- A transition (= a mutation fixates) may occur only if the fitness value increases



Open or accessible evolutionary path =
walk on the hypercube such that fitness values increase along the walk

Choosing the fitness values

- Flat landscape: fitness value proportional to number of mutations. All forward paths are accessible.
- Rough landscape: no clear relationship between fitness value and number of mutations. Lots of local extrema, valleys and dead ends.



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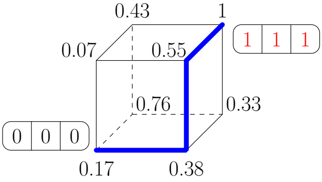

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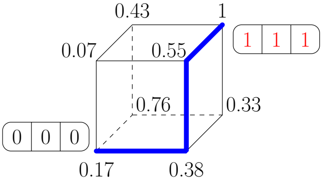

Roughest landscape of all

the House of Cards model

Fitness values are independent random numbers

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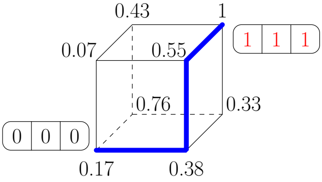

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The question: can the population reach the fittest possible state?

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- asexual population
- low mutation rate
- high selection
- House of Cards fitnesses

Is there an accessible path to the fittest site ? How many are there ?

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Results

- When one allows only forward mutations
- When one allows both forward and backward mutations

Only forward mutations

- No backward mutation, only $0 \to 1$ and never $1 \to 0$, path length is L.
- Starting from $(0, 0, 0, \ldots, 0)$, assume fittest site is $(1, 1, 1, \ldots, 1)$

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$$\boxed{\mathbb{E}^x(\text{nb of open paths}) = L(1-x)^{L-1}} \quad \begin{cases} \propto L & \text{If } x \lesssim \frac{1}{L} \\ \propto 1 & \text{If } x \approx \frac{\ln L}{L} \\ \ll 1 & \text{If } x \gg \frac{\ln L}{L} \end{cases}$$

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$$\mathbb{P}(\text{nb of open paths} \neq 0) \leq \frac{\ln L + \text{Cste}}{L}$$

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Assume fittest site is $(1, 1, 1, \ldots, 1)$.

Theorem (Hegarty-Martinsson 2012)

As $L \to \infty$,

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If $a(L) \to \infty$ $\quad$ (but, typically, $a(L) \ll \ln L$),

$$\mathbb{P}^{\frac{\ln L - a(L)}{L}}(\text{nb of open paths} \neq 0) \to 1 \qquad \left(\begin{array}{c}\text{If starting position has a fitness below} \\ (\ln L)/L, \text{ there are some open paths.}\end{array}\right)$$

$$\mathbb{P}^{\frac{\ln L + a(L)}{L}}(\text{nb of open paths} \neq 0) \to 0 \qquad \left(\begin{array}{c}\text{If starting position has a fitness above} \\ (\ln L)/L, \text{ there are no open paths.}\end{array}\right)$$

Only forward mutations — summary

Assume fittest site is $(1, 1, 1, \ldots, 1)$.

$\mathbb{E}(\text{nb of open paths}) = 1$	(a lie: typical nb of open paths $\neq 1$)
$\mathbb{E}^x(\text{nb of open paths}) = L(1-x)^{L-1}$	(truth: correct order of magnitude)
$\mathbb{P}(\text{nb of open paths} \neq 0) \sim \dfrac{\ln L}{L}$	(value of x for which $\mathbb{E}^x(\ldots) \approx 1$)

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Theorem (Berestycki-Brunet-Shi 2013)

If $x = \frac{X}{L}$, as $L \to \infty$,

$$\frac{\text{nb of open paths}}{L} \xrightarrow{\text{in law}} e^{-X} \times \mathcal{E} \times \mathcal{E}'$$

where $\mathcal{E}$ and $\mathcal{E}'$ are two independent exponential numbers.

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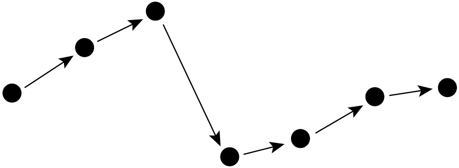

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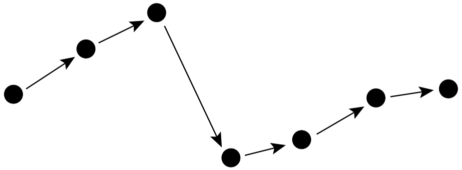

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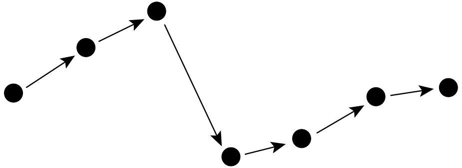

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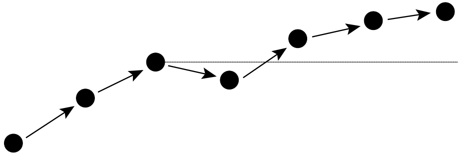

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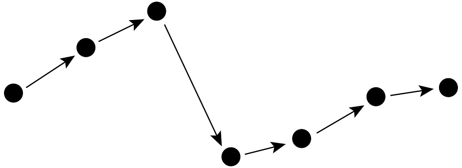

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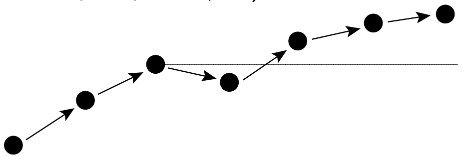

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Helps a bit: Proba(nb of open paths $\neq 0$) $\sim (p+1)\frac{\ln L}{L}$
($p =$ number of "tunnels" allowed)

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For large L, when the location of the fittest site is at $(1, 1, 1, \dots, 1)$

- There are no open paths is starting fitness is larger than $0.11863\dots$.
- There are open paths otherwise. (Not our result...)

For large L, when the location of the fittest site is random

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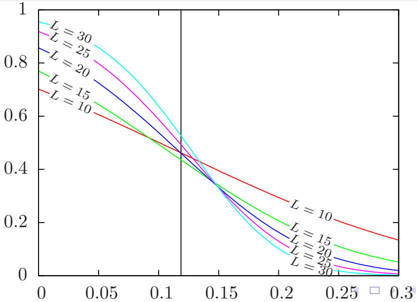

Paths with forward and backward mutations

We allow paths to do $0 \to 1$ or $1 \to 0$. Assume fittest site is $(1, 1, 1, \ldots, 1)$.

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2 backsteps	length $L + 4$
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		nb of self-avoiding paths
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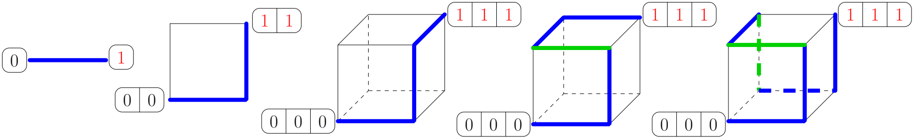

$a_1 = 1, \quad a_2 = 2, \quad a_3 = 18$

Paths with forward and backward mutations

We allow paths to do $0 \to 1$ or $1 \to 0$. Assume fittest site is $(1,1,1,\dots,1)$.

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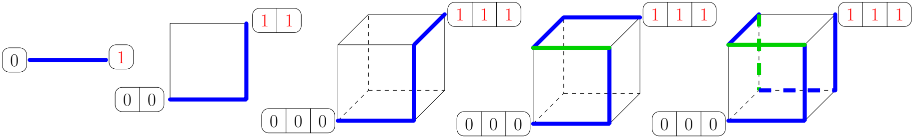

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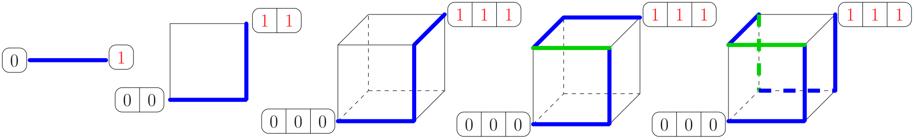

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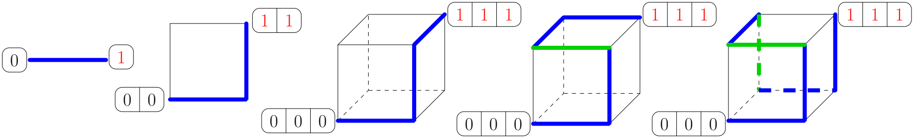

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How many are open ?

Paths with forward and backward mutations

Fittest site is $(1, 1, 1, \dots, 1)$

$$\boxed{\mathbb{E}(\text{nb of open paths}) = \sum_p a_{L,p} \frac{1}{(L+2p)!}}$$

But...

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Theorem (Berestycki-Brunet-Shi 2013)

$$\Big[\mathbb{E}^x(\text{nb of open paths})\Big]^{1/L} \xrightarrow[L\to\infty]{} \sinh(1-x).$$

Corollary: if $x > \underbrace{1 - \sinh^{-1}(1)}_{0.11863...}$, $\quad \mathbb{P}^x(\text{nb of open paths} \neq 0) \to 0.$

Generalization

Fittest site is $(1, 1, 1, \dots, 1)$: $\left[\mathbb{E}^x(\text{nb of open paths})\right]^{\frac{1}{L}} \to \sinh(1 - x)$

$$\text{No open path if } x > x^*(1) = \underbrace{1 - \sinh^{-1}(1)}_{0.11863...}$$

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Theorem (Martinsson 2015 and Li 2015)

Expectations are telling the truth. $\mathbb{P}^x(\text{nb of open paths} \neq 0) \to 1$ if $x < x^*$ with x^* given above. Furthermore, $\mathbb{P}(\text{nb of open paths} \neq 0) \to x^*$

Outline of proof

Forward and backward mutations, fittest is $(1, 1, 1, \ldots, 1)$.

$$\left[\mathbb{E}^x(\text{nb of open paths})\right]^{\frac{1}{L}} = \left[\sum_p a_{L,p} \frac{(1-x)^{L+2p-1}}{(L+2p-1)!}\right]^{\frac{1}{L}} \to \sinh(1-x)$$

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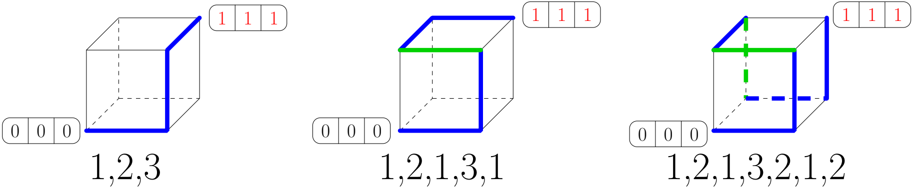
- Code paths as sequence of numbers



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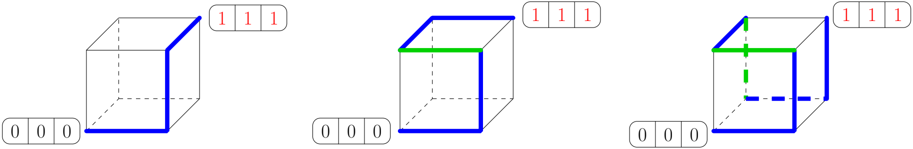

1,2,3   1,2,1,3,1   1,2,1,3,2,1,2

- A path in $a_{L,p}$ has a sequence of length $L + 2p$

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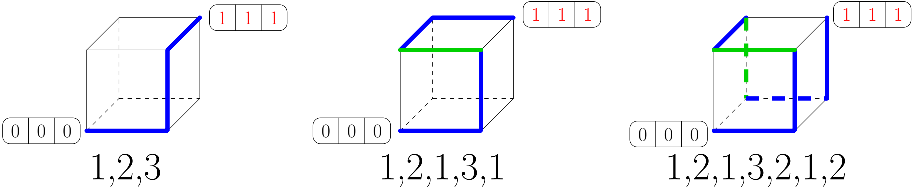

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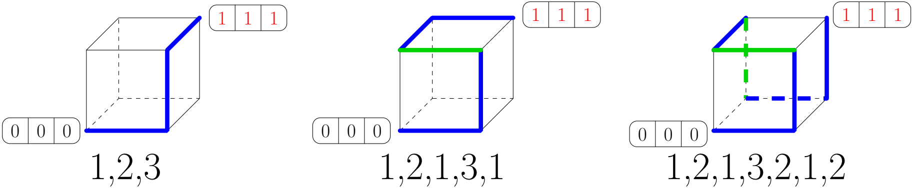

- A path in $a_{L,p}$ has a sequence of length $L + 2p$
- A path reaches $(1, 1, 1, \dots, 1)$ if each number between 1 and L appears oddly many times in the sequence
- A path is self-avoiding if in any non-empty substring, at least one number appears oddly many times

Outline of proof

Strategy: $m_{L,p} \le a_{L,p} \le M_{L,p}$

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- $M_{L,p}$ counts all the paths of length $L + 2p$ to $(1, 1, 1, \ldots, 1)$, even self-intersecting ones

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Example

$m_{3,0}$:	123 132 213 231 312 321
$a_{3,0}$:	123 132 213 231 312 321
$M_{3,0}$:	123 132 213 231 312 321

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$m_{3,1}$:					31323	32313			
$a_{3,1}$:	12131	13121	21232	23212	31323	32313			
$M_{3,1}$:	12131	13121	21232	23212	31323	32313	11123	12113	. . .

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$M_{3,1}$:	12131 13121 21232 23212 31323 32313 11123 12113 ...

$m_{3,2}$:	
$a_{3,2}$:	1213212 1312313 2123121 2321323 3132131 3231232
$M_{3,2}$:	1213212 1312313 2123121 2321323 3132131 3231232 1211333 ...

$(M_{3,1} = 60,\ M_{3,2} = 4920\ldots)$

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The paths in $m_{L,p}$ (resp. $M_{L,p}$) have the property that if all occurrence of L is removed, what remains is in $m_{L-1,p'}$ (resp. $M_{L-1,p'}$).

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$$G_L(X) := \sum_p M_{L,p} \frac{X^{L+2p}}{(L+2p)!}$$

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Martinsson's result

$$\mathbb{E}^x(\text{nb of open paths}) \leq -\partial_x[\sinh^L(1-x)] \xrightarrow[L\to\infty]{} \quad \text{if } x \leq 1 - \sinh^{-1}(1)$$

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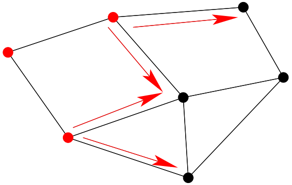
First passage percolation



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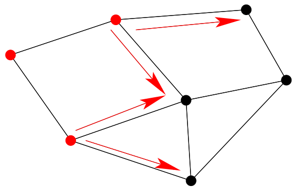

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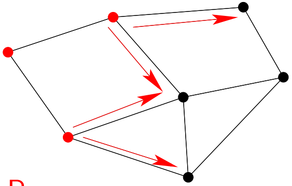

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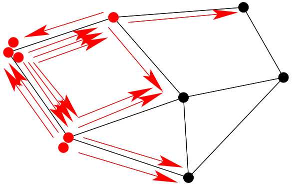

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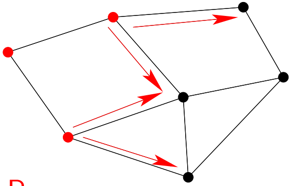

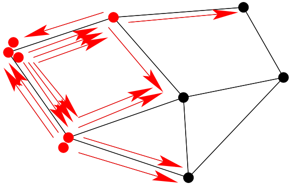

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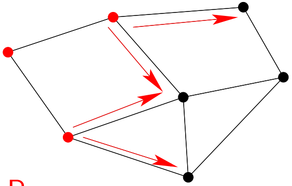

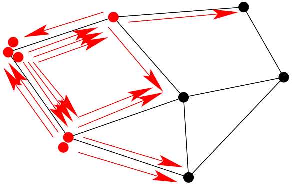

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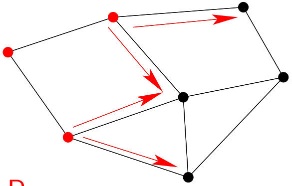

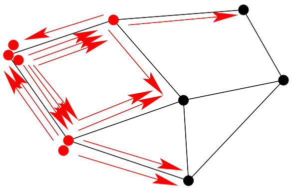

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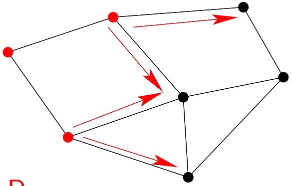

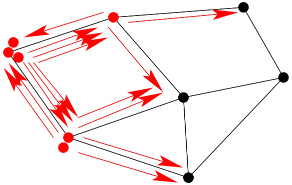

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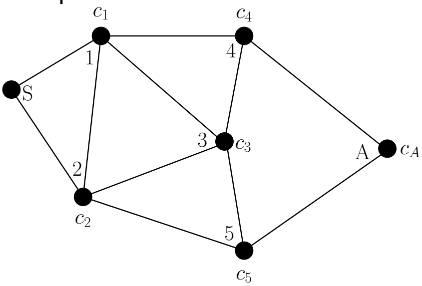
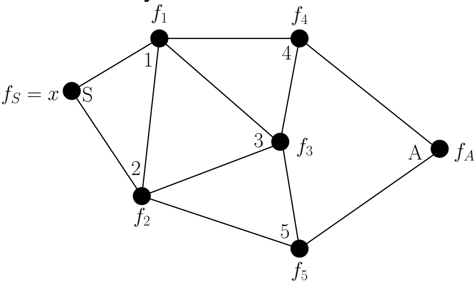
Martinsson's result for any graph

Site percolation



Accessibility



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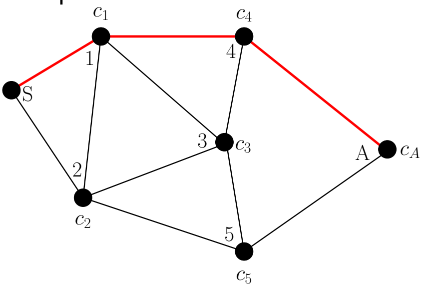

Time (or cost) $= c_1 + c_4 + c_A$

$T_A =$minimal time to reach A

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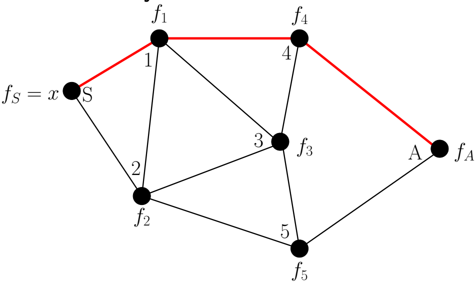

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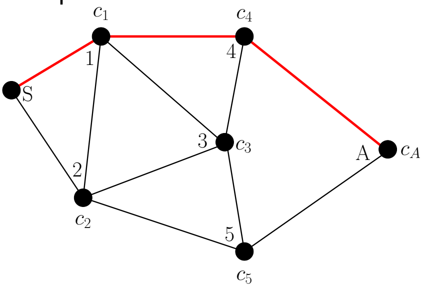

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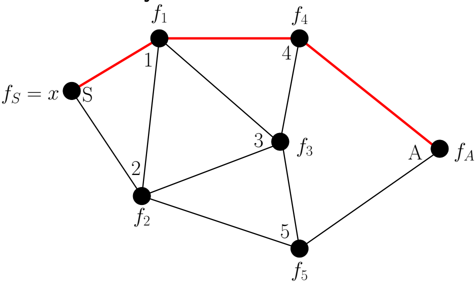

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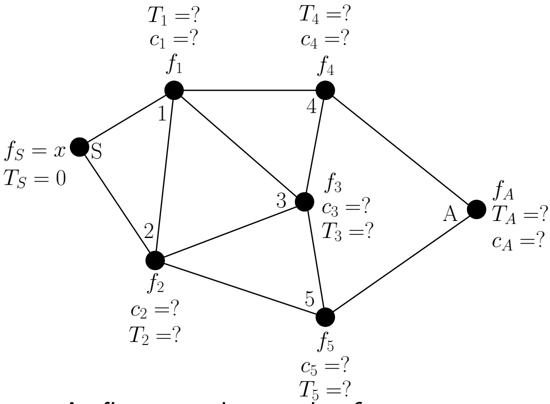
(Martinsson 2015)

$$\mathbb{P}(T_A < 1 - x) \quad = \quad \mathbb{P}^x(A \text{ is accessible})$$

But no relation betwen the number of paths with a time smaller than $1 - x$ and the number of accessible paths!

Outline of Martinsson's proof



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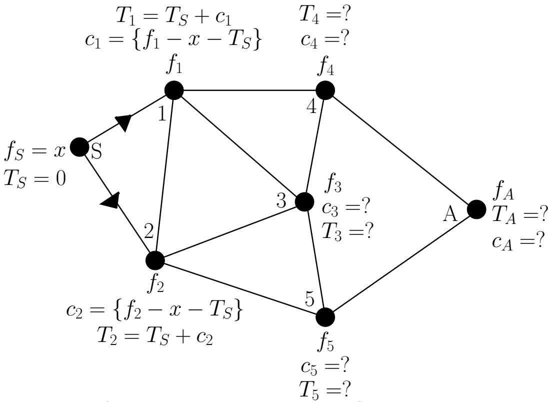

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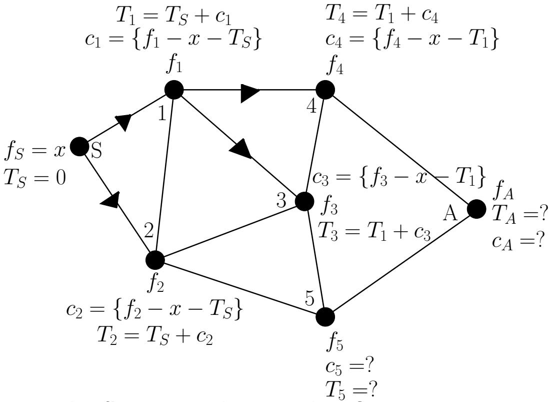

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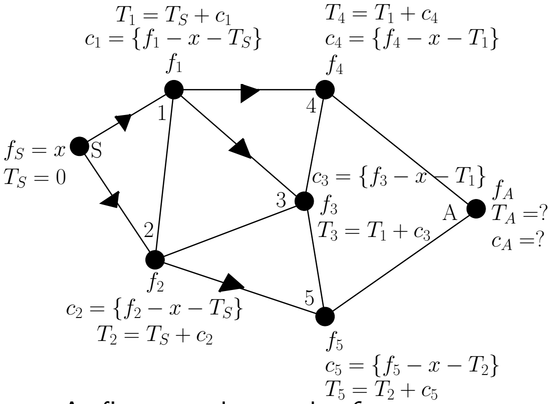

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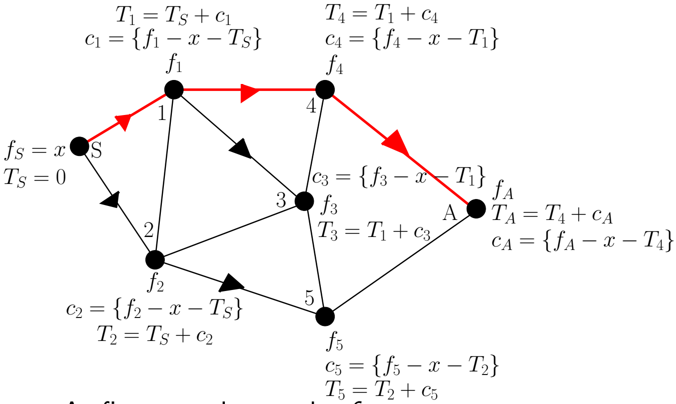

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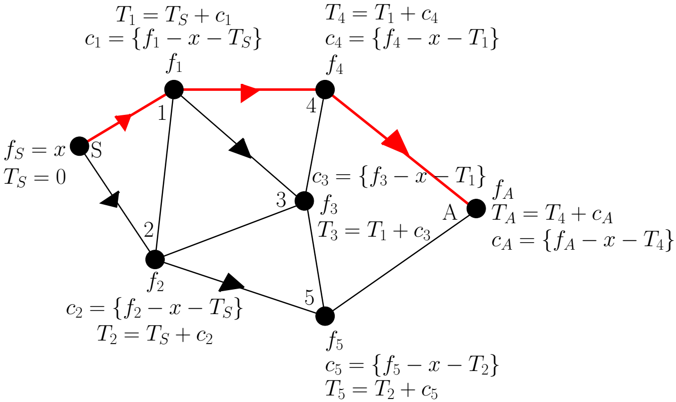

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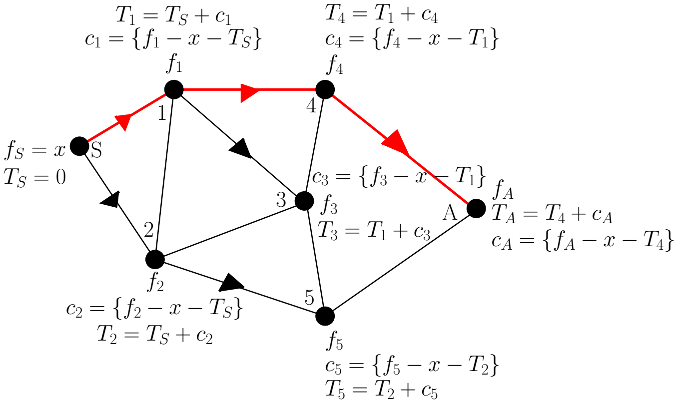

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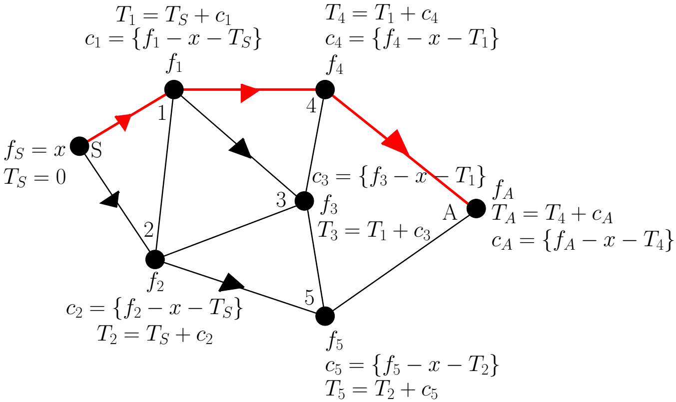

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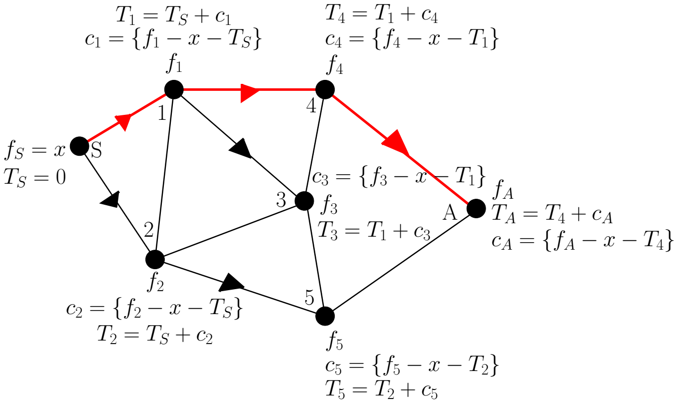

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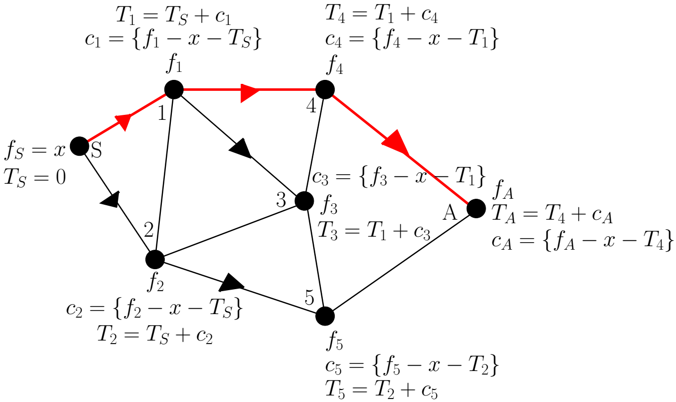

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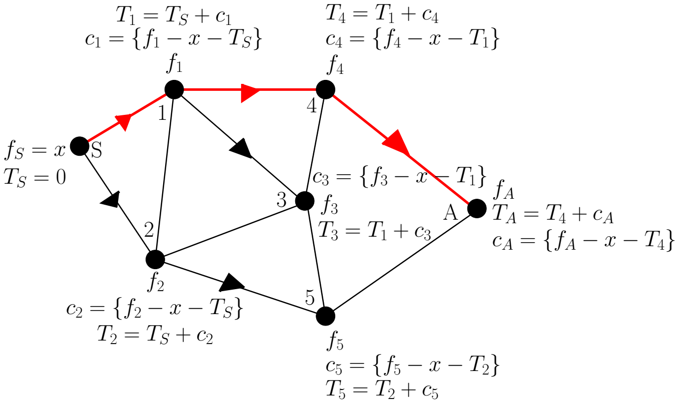

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When only forward steps are allowed

- Forward steps only are allowed
- Fittest site is $(1, 1, 1, \ldots, 1)$
- Starting site $(0, 0, 0, \ldots, 0)$ has fitness $x = X/L$
- $L \to \infty$

$$\boxed{\frac{1}{L}\left(\text{nb of open paths if starting fitness is } x = \frac{X}{L}\right) \to e^{-X} \times \mathcal{E} \times \mathcal{E}'}$$

with $\mathcal{E}$ and $\mathcal{E}'$ two independent exponential variables

One already knows that

- $\mathbb{E}^{\frac{X}{L}}(\text{nb of open paths}) = L(1-x)^{L-1} \sim Le^{-X}$

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- $\mathbb{E}^{\frac{X}{L}}(\text{nb of open paths}) = L(1-x)^{L-1} \sim Le^{-X}$
- There are indeed typically $\propto L$ open paths

Hypercube vs Tree

Hypercube is hard; try a tree!

1^{st} step: L choices; 2^{nd} step: $L-1$ choices; 3^{rd} step: $L-2$ choices; ...

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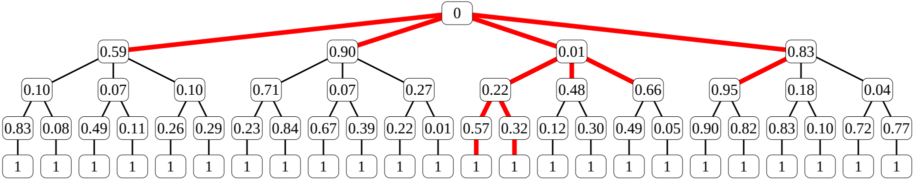

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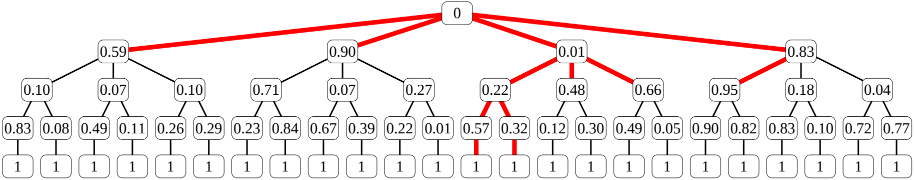

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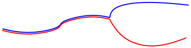

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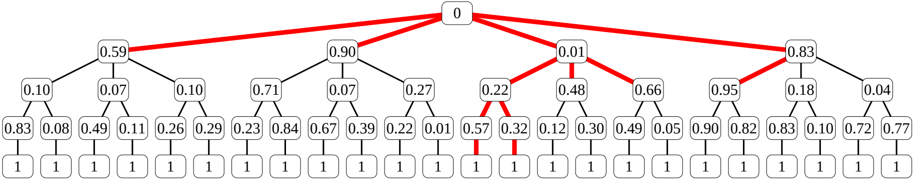

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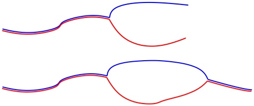
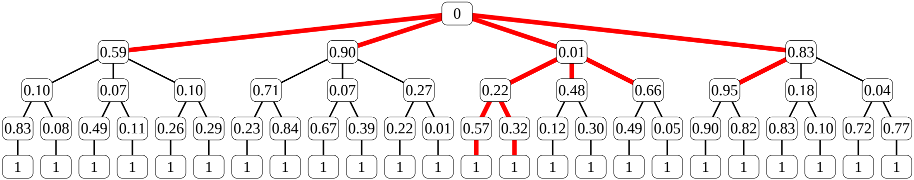


On the tree



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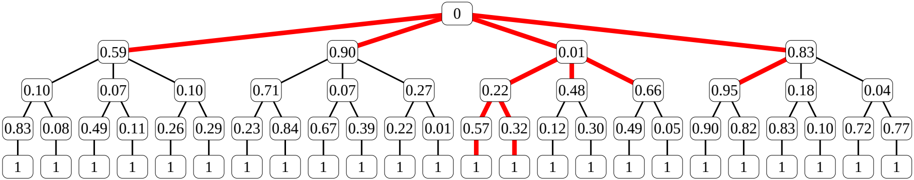

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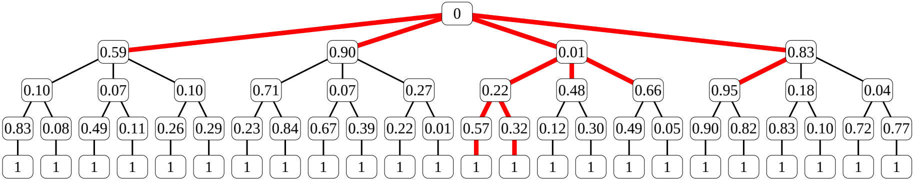

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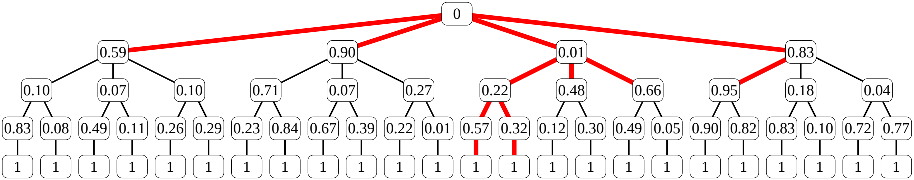

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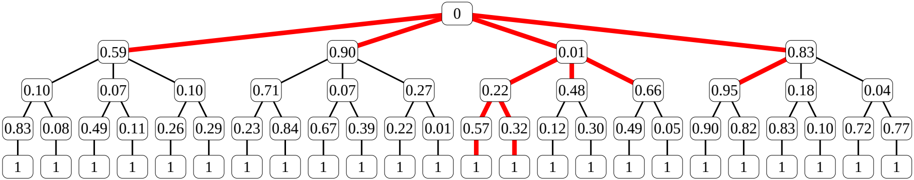

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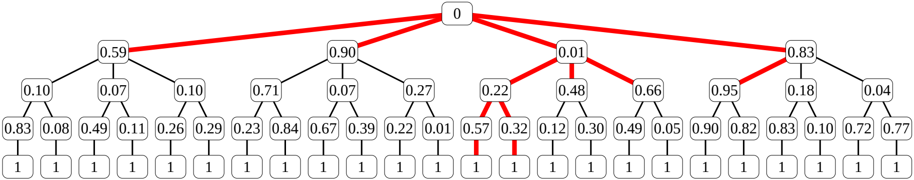
$$G(\lambda, x, L) = \left[x + \int_x^1 \mathrm{d}y\, G(\lambda, y, L-1)\right]^L$$

On the tree



$$\text{(Nb of open paths)} = \sum_{|\sigma|=1} \text{(nb of open paths going through } \sigma\text{)}$$

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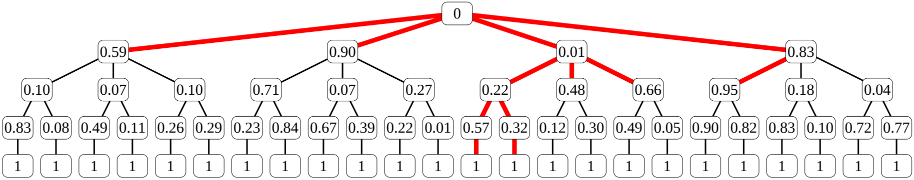

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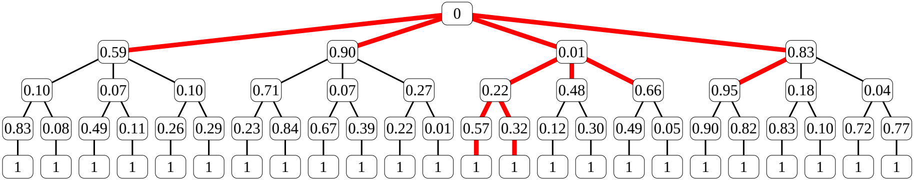
$$\lim_{L\to\infty} G\Big(\frac{\mu}{L}, \frac{X}{L}, L\Big) = ?$$

On the tree, second try



Idea: the first steps determine everything

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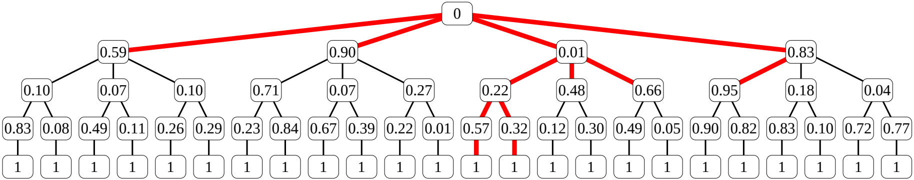

Idea: the first steps determine everything

$\Theta = (\text{nb of open paths})$, $\quad \Theta_k = \mathbb{E}(\Theta|\mathcal{F}_k)$, $\quad \mathcal{F}_k = (\text{info up to level } k)$

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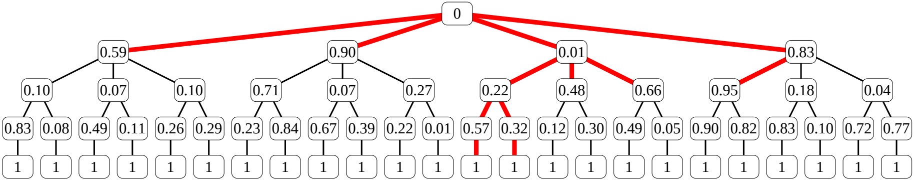

Idea: the first steps determine everything

$\Theta =$ (nb of open paths), $\quad \Theta_k = \mathbb{E}(\Theta|\mathcal{F}_k), \quad \mathcal{F}_k =$ (info up to level k)

$$\Theta_k = \sum_{|\sigma|=k} \mathbb{1}_{\{\sigma \text{ open}\}} \underbrace{(L-k)(1-x_\sigma)^{L-k-1}}_{\substack{\text{expected nb of open} \\ \text{paths through } \sigma}}$$

$$\Theta_1 = 3(1-0.59)^2 + 3(1-0.90)^2 + 3(1-0.01)^2 + 3(1-0.83)^2 = 3.5613$$
$$\Theta_2 = 2(1-0.22)^1 + 2(1-0.48)^1 + 2(1-0.66)^1 + 2(1-0.95)^1 = 3.38$$

On the tree, second try

$\Theta = (\text{nb of open paths})$, $\quad \Theta_k = \mathbb{E}(\Theta|\mathcal{F}_k)$, $\quad \mathcal{F}_k = (\text{info up to level } k)$

Intuitively, $\Theta_k \approx \Theta$ if $\quad \text{Var}(\Theta|\mathcal{F}_k)$ is small

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But (sum over pairs of paths):

$$\lim_{L\to\infty} \mathbb{E}^{\frac{X}{L}}\left[\text{Var}\left[\frac{\Theta}{L}\Big|\mathcal{F}_k\right]\right] = \frac{e^{-2X}}{2^k}$$

In the $L \to \infty$, $k \to \infty$ limit, Θ/L and Θ_k/L have the same distribution

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We want to write a generating function.

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One can then prove that $F_k(\mu, X) = \lim_{L\to\infty} G_k(\frac{\mu}{L}, \frac{X}{L}, L)$ exists and

$$F_k(\mu, X) = \exp\Big[-\int_X^\infty \mathrm{d}Y\,\big(1 - F_{k-1}(\mu, Y)\big)\Big], \quad F_0(\mu, X) = \exp\big(-\mu e^{-X}\big)$$

F_k is the generating function of $\lim_{L\to\infty} \frac{\Theta_k}{L}$ when starting fron $\frac{X}{L}$.

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On the tree, starting from $x=\frac{X}{L}$, $\qquad \frac{\Theta}{L}\xrightarrow[L\to\infty]{\text{in law}} e^{-X}\times\mathcal{E}$

Back to the hypercube

Same trick:

$$\Theta_k = \mathbb{E}(\Theta|\mathcal{F}_k), \qquad \mathcal{F}_k = (\text{info in the } k \text{ first and } k \text{ last levels})$$

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The expectation of the conditional variance can be computed and it works.

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$$\Theta_k = \sum_{|\sigma|=k}\ \sum_{|\tau|=L-k} n_\sigma m_\tau \mathbb{1}_{\{\tau \text{ reachable from } \sigma\}} \mathbb{1}_{\{x_\sigma < x_\tau\}} (L-2k)(x_\tau - x_\sigma)^{L-2k-1}$$

n_σ =nb of open paths from $(0,\dots,0)$ to σ; m_τ =nb from τ to $(1,\dots,1)$

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$\tilde\Theta_k/L$ and Θ_k/L have the same distribution for large L.

Back to the hypercube

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First factor: beginning of the hypercube. Second factor: end of the hypercube. Terms are independent and symmetrical if $X = 0$.

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Intuition: with k fixed and $L \to \infty$, loops become negligible, and the beginning of the hypercube looks like the beginning of the tree. So ϕ_k and Θ_k^{tree}/L have the same large L distribution.

Thank you !