Open 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

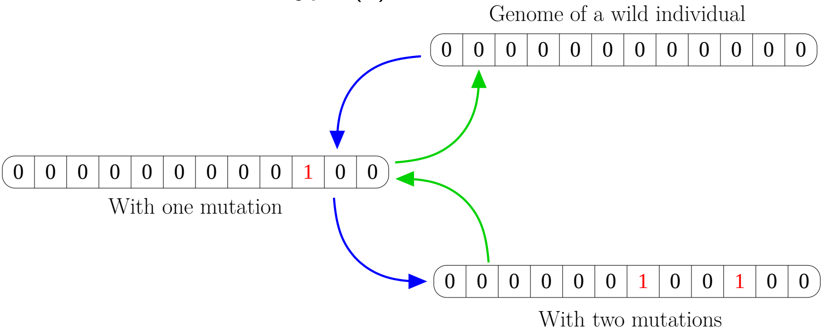
0	0	0	0	0	0	1	0	0	1	0	0

With two mutations

Population with asexual reproduction

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

- There are two viable types (alleles) for each gene: the **wild type** (0) and the **mutated type** (1)

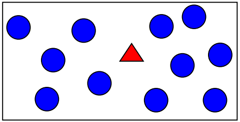


- During reproduction, when a mutation occurs, **only one gene is affected**.

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

Low mutation rate, population not too large

When a mutation occurs,



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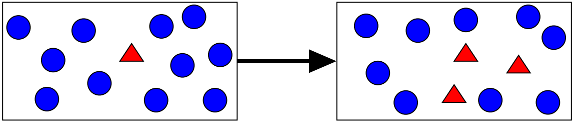

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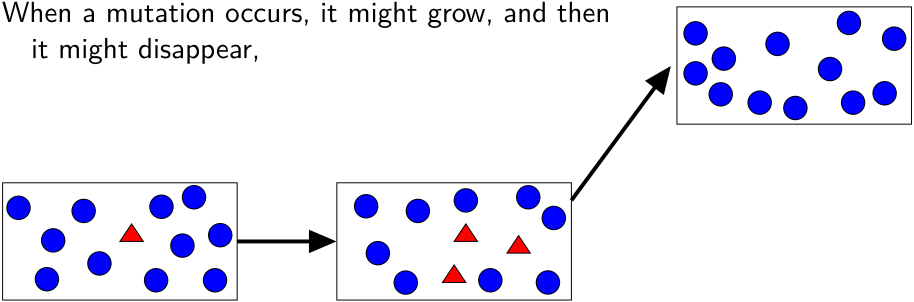

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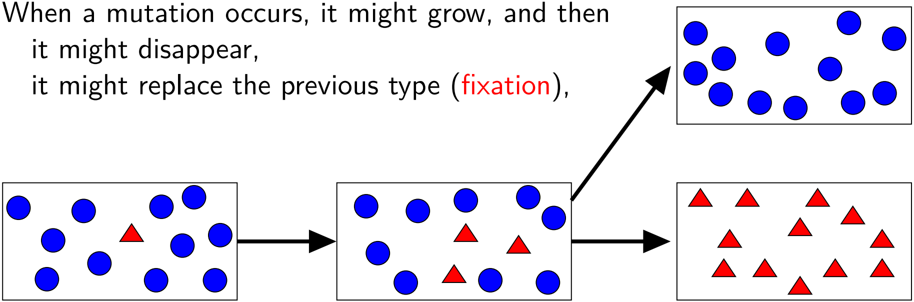
- it might replace the previous type (fixation),



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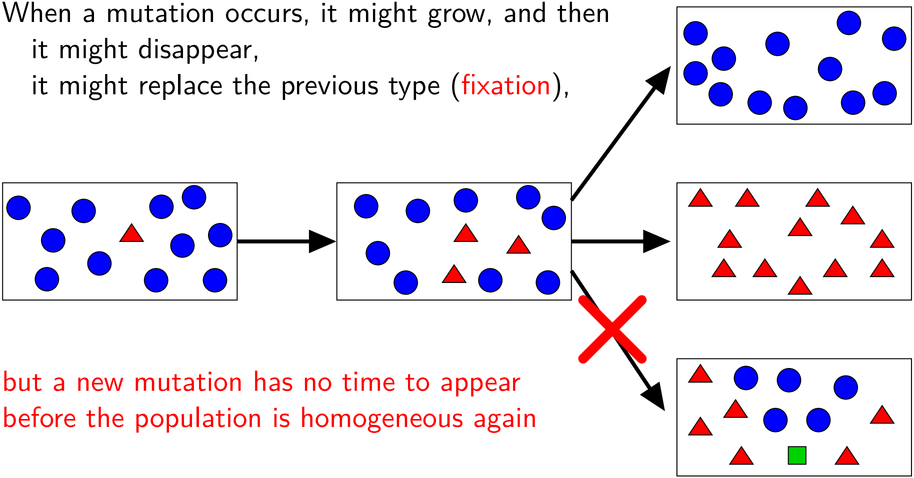
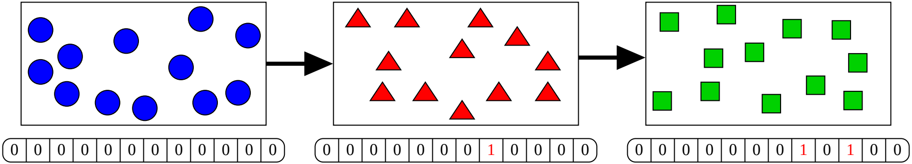


but a new mutation has no time to appear before the population is homogeneous again

Evolutionary paths and Hypercube

Big simplification:



Gillespie 1983, Kauffman Levin 1987

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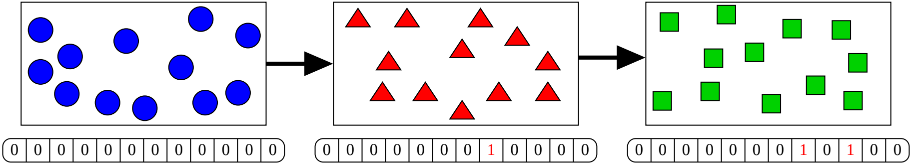
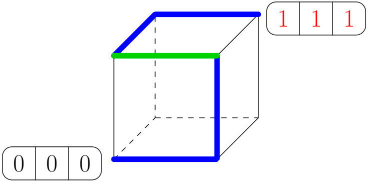


Evolutionary path = walk on the hypercube



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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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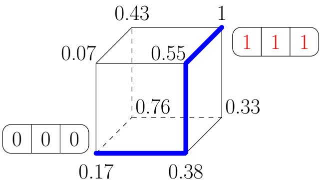
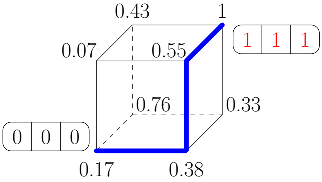
- Assume strong selection
- A transition (= a mutation fixates) may occur only if the fitness value increases



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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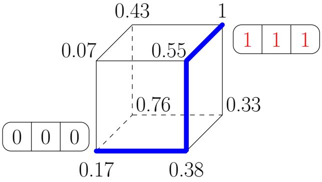

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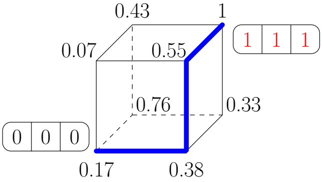

Roughest landscape of all

the House of Cards model

Fitness values are independent random numbers

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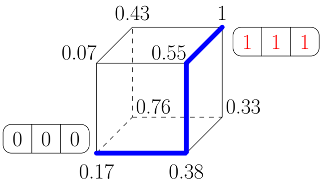

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The question: can the population reach the fittest possible state?

Summary of the model

For an asexual population which is not too large, has low mutation rate and where selection is high, if one assumes that fitness values are distributed according to the House of Cards model, is there an *accessible* or open evolutionary path which leads to the fittest possible genome?

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- Consider a L-hypercube.
- Each site is assigned an independent random value, its fitness.
- A path is said to be open if the fitness values increase along it.
- One starts from site $(0, 0, 0, \dots, 0)$.

Is there an open path to the fittest site ? And how many are there ?

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- The other sites get independent uniform fitness values between 0 and 1
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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 $(1, 1, 1, \ldots, 1)$

Nowak Krug 2013, Hegarty Martinsson 2012

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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 $a(L) \to \infty$ (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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For large L, when the location of the fittest site is random

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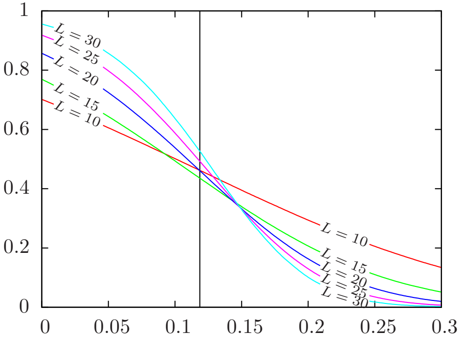
When fittest site is $(1, 1, 1, \ldots, 1)$, critical value is $0.11863\ldots$



Paths with forward and backward mutations

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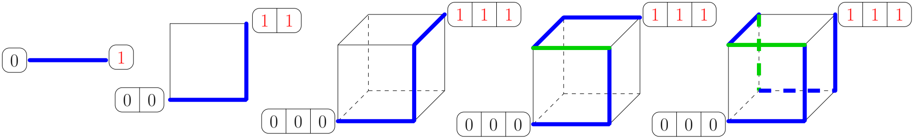

$a_1 = 1, \quad a_2 = 2, \quad a_3 = 18$

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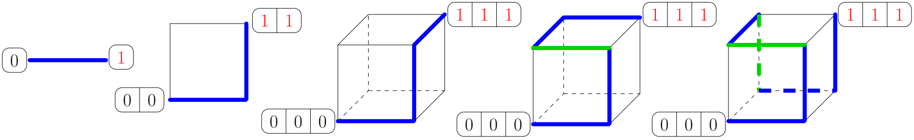

$$a_1 = 1, \quad a_2 = 2, \quad a_3 = 18, \quad a_4 = 6\,432, \quad a_5 = 18\,651\,552\,840$$

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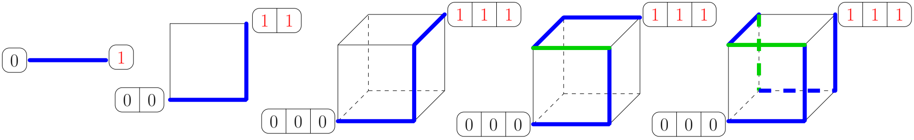
$a_L = a_{L,0} + a_{L,1} + a_{L,2} + \cdots =$ total nb of self-avoiding paths.



$$a_1 = 1, \quad a_2 = 2, \quad a_3 = 18, \quad a_4 = 6\,432, \quad a_5 = 18\,651\,552\,840$$

Asymptotically, $e^{c \times 2^L} \leq a_L \leq e^{c' \times (\ln L) 2^L}$

Paths with forward and backward mutations

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

		nb of self-avoiding paths
0 backstep	length L	$a_{L,0} = L!$
1 backstep	length $L+2$	$a_{L,1} = L! \times \frac{L(L-1)(L-2)}{6}$
2 backsteps	length $L+4$	$a_{L,2} = L! \times \frac{(L-1)(L-2)(5L^4+3L^3+34L^2-264L+180)}{360}$
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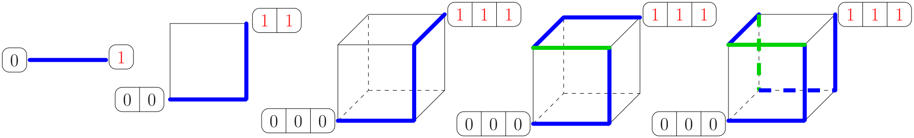

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How many are open ?

Paths with forward and backward mutations

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

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

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

Unproved speculation: $\mathbb{E}^x(\text{nb of open paths}) \sim \phi(x) L \big[\sinh(1-x)\big]^L.$

Generalization and conjecture

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

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Conjecture

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 $(1, 1, 1, \dots, 1)$.

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

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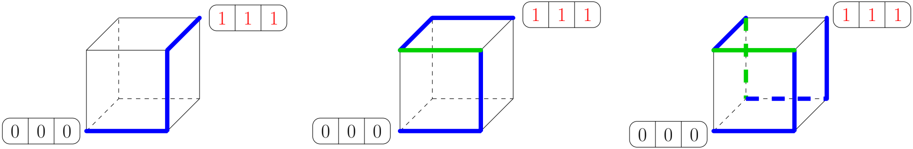
- Code paths as sequence of numbers



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

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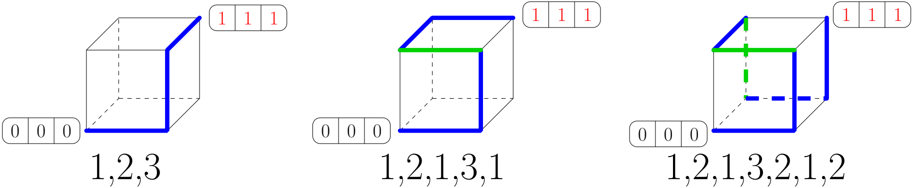

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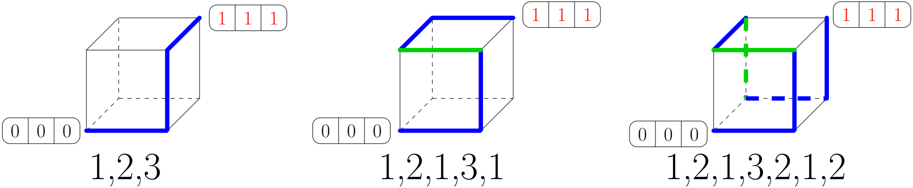

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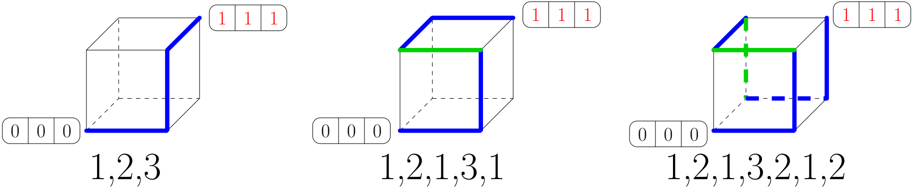

- A path in $a_{L,p}$ has a sequence of length $L + 2p$
- A path reaches $(1, 1, 1, \dots, 1)$ if each number between 1 and L appears oddly many times in the sequence
- A path is self-avoiding if in any non-empty substring, at least one number appears oddly many times

Outline of proof

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

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Example

$m_{3,0}$:	123 132 213 231 312 321
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$m_{3,2}$:	
$a_{3,2}$:	1213212 1312313 2123121 2321323 3132131 3231232
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$(M_{3,1} = 60,\ M_{3,2} = 4920\ldots)$

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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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When only forward steps are allowed

- Forward steps only are allowed
- Fittest site is $(1, 1, 1, \dots, 1)$
- Starting site $(0, 0, 0, \dots, 0)$ 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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One already knows that

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

Hypercube vs Tree

Hypercube is hard; try a tree!

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

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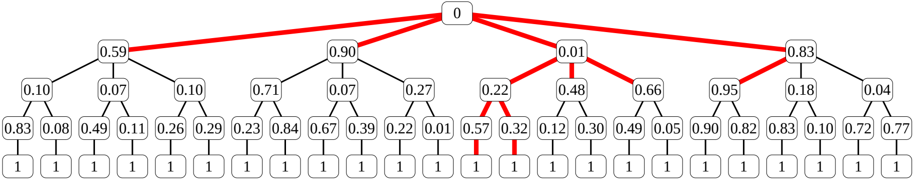

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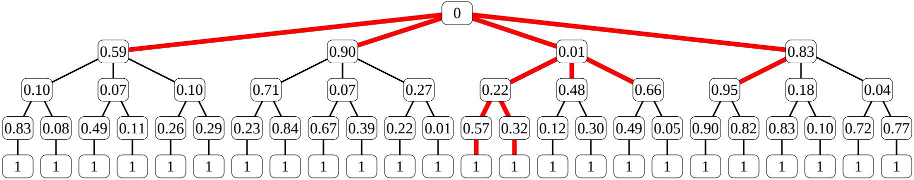

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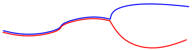
$$\mathbb{E}^{\frac{X}{L}}\left[(\text{nb of open paths})^2\right] \sim \begin{cases} 2L^2e^{-2X} & \text{(tree)} \\ & \end{cases}$$



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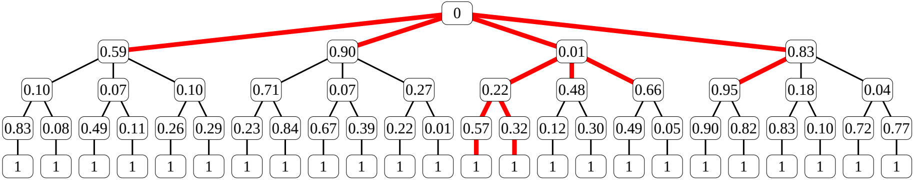
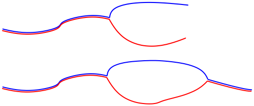
1^{st} step: L choices; 2^{nd} step: $L-1$ choices; 3^{rd} step: $L-2$ choices; ...

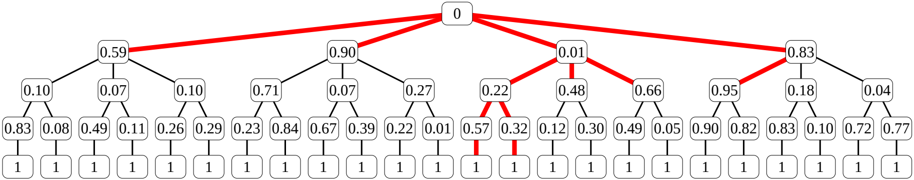


$$\mathbb{E}^{\frac{X}{L}}\big[\text{nb of open paths}\big] = L(1-x)^{L-1} \sim Le^{-X}$$ same for tree or hypercube!

$$\mathbb{E}^{\frac{X}{L}}\big[(\text{nb of open paths})^2\big] \sim \begin{cases} 2L^2e^{-2X} & \text{(tree)} \\ 4L^2e^{-2X} & \text{(hypercube)} \end{cases}$$



On the tree



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

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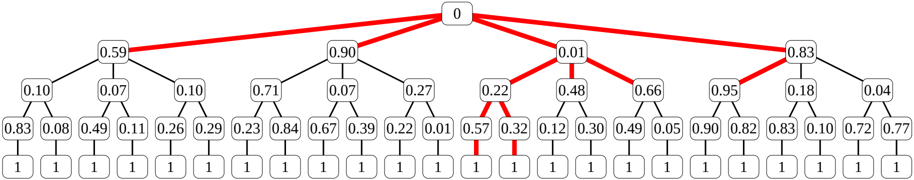

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Sum of uncorrelated terms (because it is a tree), generating function

$$G(\lambda, x, L) := \mathbb{E}^x\left(e^{-\lambda(\text{nb of open paths})}\right)$$

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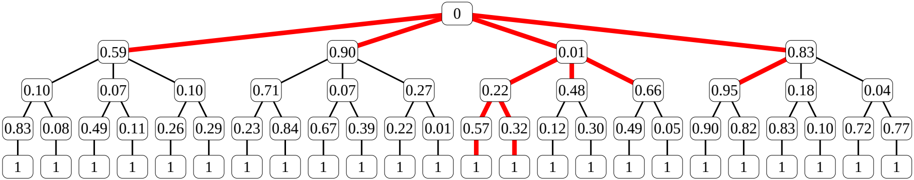

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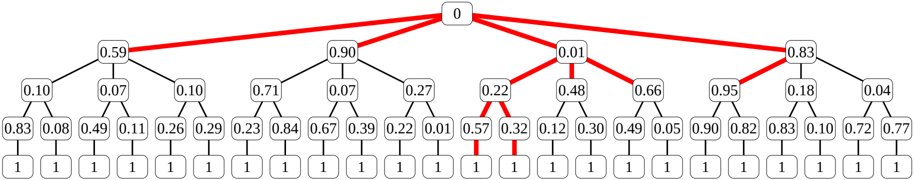

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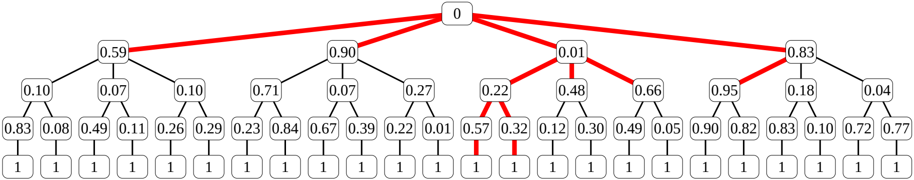

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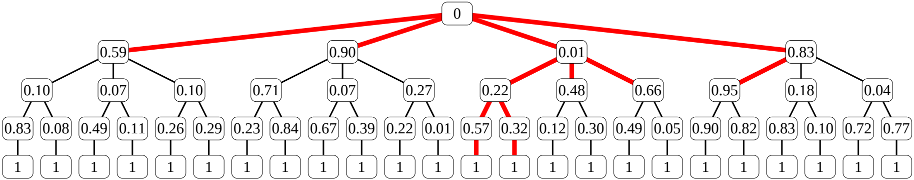

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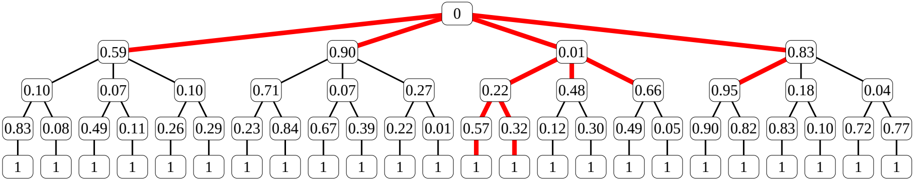

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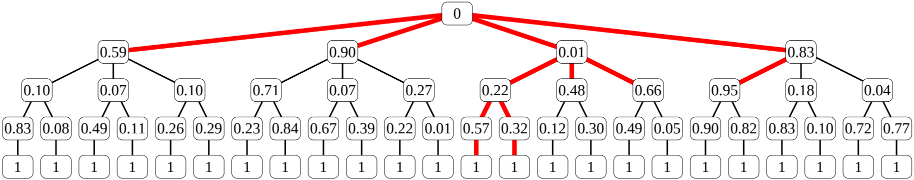
$$\lim_{L\to\infty} G\left(\frac{\mu}{L}, \frac{X}{L}, L\right) = ?$$

On the tree, second try



Idea: the first steps determine everything

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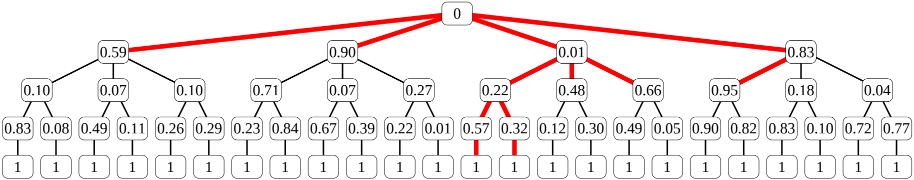

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$\Theta = (\text{nb of open paths})$, $\qquad \Theta_k = \mathbb{E}(\Theta|\mathcal{F}_k)$, $\qquad \mathcal{F}_k = (\text{info up to level } k)$

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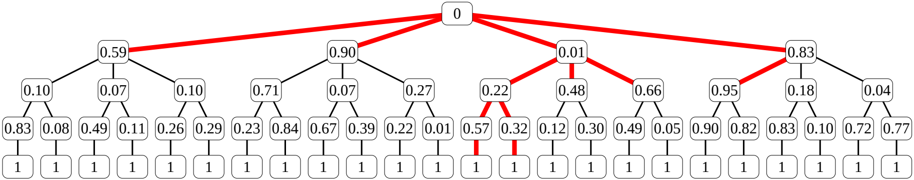

Idea: the first steps determine everything

$\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

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

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

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But (sum over pairs of paths):

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

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

On the tree, second try

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

We want to write a generating function.

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

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

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

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

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

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$$\lim_{L\to\infty} \mathbb{P}^{\frac{X}{L}}\left[\frac{\Theta}{L} < z\right] = \lim_{k\to\infty}\lim_{L\to\infty} \mathbb{P}^{\frac{X}{L}}\left[\frac{\Theta_k}{L} < z\right] \text{ if } \lim_{k\to\infty}\lim_{L\to\infty} \mathbb{E}^{\frac{X}{L}}\left[\operatorname{Var}\left[\frac{\Theta}{L}\middle|\mathcal{F}_k\right]\right] = 0$$

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

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

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

$$\tilde{\Theta}_k := \sum_{|\sigma|=k}\ \sum_{|\tau|=L-k} n_\sigma m_\tau\ L(x_\tau - x_\sigma x_\tau)^{L-2k-1}$$

Back to the hypercube

Same trick:

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$\tilde{\Theta}_k > \Theta_k$, but not that much: $\lim_{L\to\infty} \mathbb{E}^{\frac{X}{L}}\left[\frac{\Theta_k}{L}\right] = \lim_{L\to\infty} \mathbb{E}^{\frac{X}{L}}\left[\frac{\tilde{\Theta}_k}{L}\right]$

Back to the hypercube

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

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$\tilde{\Theta}_k/L$ and Θ_k/L have the same distribution for large L.

Back to the hypercube

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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 $X = 0$.

Back to the hypercube

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Last step: prove that

$$\phi_k := \sum_{|\sigma|=k} n_\sigma (1 - x_\sigma)^{L-2k-1} \xrightarrow[L\to\infty \text{ then } k\to\infty]{\text{in law}} e^{-X}\mathcal{E}$$

Back to the hypercube

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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

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