Asymptotic and Exact Counting Results for Phylogenetic Networks

(joint with B. Gittenberger and M. Mansouri)

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Evolutionary Biology

Charles Darwin
(1809-1882)

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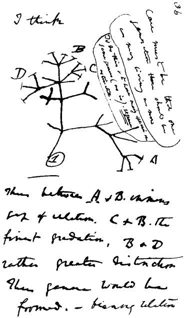
First notebook on Transmutation of Species (1837)



What is a Phylogenetic Tree?

X . . . a finite set

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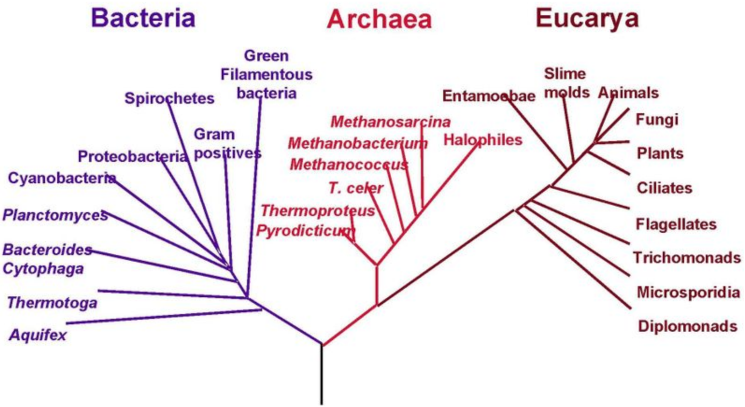

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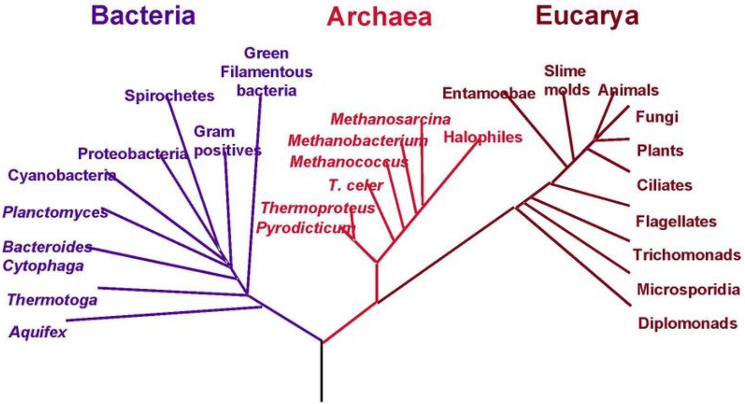

A phylogenetic tree is a rooted, non-plane, binary tree with leaves labeled by X.

What is a Phylogenetic Network?

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(a) *the root has in-degree* 0 *and out-degree* 2;

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(b) *a node with out-degree 0 has in-degree 1 and the number of such nodes is $\mathrm{card}(X)$;*

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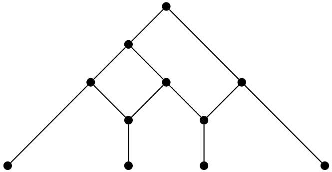
Remark.

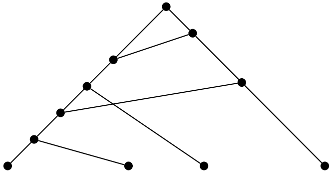
- A leaf-labeled phylogenetic network is a network whose leaves are labeled by X;
- A vertex-labeled phylogenetic network is a network with all nodes labeled.

Two Examples

Example 1: phylogenetic network which is not a tree-child network.



Example 2: tree-child network which is not a normal network.



Some further Notation

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- *A node with out-degree 2 and in-degree 1 is called a tree node;*
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Lemma

The total number of nodes n is odd and we have:

$$\ell + k = t + 2 = \frac{n+1}{2}.$$

Counting Phylogenetic Trees (i)

$\widetilde{\mathcal{T}}_\ell$ ... set of leaf-labeled phylogenetic trees;
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$$\#\widetilde{\mathcal{T}}_\ell = \frac{1}{2}\sum_{k=1}^{\ell-1}\binom{\ell}{k}\left(\#\widetilde{\mathcal{T}}_k\right)\cdot\left(\#\widetilde{\mathcal{T}}_{\ell-k}\right), \qquad (\ell \geq 2),$$

and $|\widetilde{\mathcal{T}}_1| = 1$.

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$$T(z) = \sum_{\ell\geq 1}\left(\#\widetilde{\mathcal{T}}_\ell\right)\frac{z^\ell}{\ell!}$$

we obtain that

$$T(z) - z = \frac{1}{2}T(z)^2$$

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we obtain that

$$T(z) - z = \frac{1}{2}T(z)^2 \qquad \Longrightarrow \qquad T(z) = 1 - \sqrt{1-2z}.$$

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Moreover, with $\ell = (n+1)/2$,

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Thus, again by Stirling's formula,

$$\#\mathcal{T}_n \sim \sqrt{2}\,(1-(-1)^n)\left(\frac{\sqrt{2}}{e}\right)^{n} n^{n-1}.$$

Counting Phylogenetic Networks

A less-precise version of the previous result is:

$$\#\widetilde{\mathcal{T}}_\ell = 2^{\ell \log \ell + \mathcal{O}(\ell)}$$

and

$$\#\mathcal{T}_n = 2^{n \log n + \mathcal{O}(n)},$$

where $\log$ denotes the logarithm to base 2.

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Theorem (McDiarmid, Semple, Welsh; 2015)

We have,

$$\#\mathcal{GN}_n = 2^{\frac{3}{2} n \log n + \mathcal{O}(n)}.$$

Tree-Child and Normal Networks

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A tree-child network is called normal network if whenever there is a directed path between two nodes of length at least two, there is no edge between the two nodes.

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Counting Tree-Child and Normal Networks

Theorem (McDiarmid, Semple, Welsh; 2015)

We have,

$$(c_1\ell)^{2\ell} \leq \tilde{N}_\ell \leq \tilde{T}_\ell \leq (c_2\ell)^{2\ell}.$$

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We have,

$$\tilde{N}_\ell = o(\tilde{T}_\ell) \qquad \textit{and} \qquad N_n = o(T_n).$$

Leaves and Reticulation Nodes

Recall that

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Theorem (McDiarmid, Semple, Welsh; 2015)

(i) *For almost all vertex-labeled phylogenetic networks:*

$$\ell = o(n) \qquad \textit{and} \qquad k \sim n/2.$$

(ii) *For almost all vertex-labeled tree-child and normal networks:*

$$\ell \sim n/4 \qquad \textit{and} \qquad k \sim n/4.$$

(iii) *For almost all leaf-labeled tree child and normal networks:*

$$k \sim \ell \qquad \textit{and} \qquad n \sim 4\ell.$$

Counting Vertex-labeled Networks with $k = 1$

$T_{1,n}$ ... # of vertex-labeled tree-child networks with 1 reticulation nodes;
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Theorem (Semple & Steel; 2006)

We have,

$$T_{1,2n+1} = (2n+1)!2^n \left(n4^{-n}\binom{2n}{n} - \frac{1}{2} \right)$$

and

$$N_{1,2n+1} = (2n+1)!2^n \left((n+2)4^{-n}\binom{2n}{n} - \frac{3}{2} \right)$$

Thus,

$$T_{1,n} \sim N_{1,n} \sim \frac{\sqrt{2}}{4}\left(1-(-1)^n\right)\left(\frac{\sqrt{2}}{e}\right)^n n^{n+1}$$

Exact Results for small k and ℓ

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$k \setminus \ell$	2	3	4	5	6	7
1	2	21	228	2805	39330	623385
2		42	1272	30300	696600	16418430
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$k \setminus \ell$	3	4	5	6	7	8
1	3	54	855	14040	248535	4787370
2		48	2310	78120	2377620	70749000
3			1920	184680	11038530	536524830
4				146520	23797302	2217404379

Table: Number of normal networks for small k and ℓ

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Theorem (Zhang; 2019+)

We have,

$$T_{2,2n+1} = (2n+1)!2^{1-n}\sum_{j=1}^{n-3}\binom{2j}{j}\binom{2n-2j-2}{n-j-1}\frac{j(2j+1)(2n-j-3)}{2n-2j-3} + (2n+1)!(n-1)(n-2)2^{n-4} - \frac{(2n+1)!(2n-3)!}{3\cdot 2^{n-2}(n-3)!(n-2)!}.$$

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Zhang asked for a similar exact formula for $N_{2,2n+1}$.

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Theorem (F., Gittenberger, Mansouri; 2019)

There exist a positive constant $c_k > 0$ such that

$$T_{k,n} \sim N_{k,n} \sim c_k \left(1 - (-1)^n\right) \left(\frac{\sqrt{2}}{e}\right)^n n^{n+2k-1}.$$

In particular,

$$c_1 = \frac{\sqrt{2}}{4}; \qquad c_2 = \frac{\sqrt{2}}{32}; \qquad c_3 = \frac{\sqrt{2}}{384}.$$

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In particular,

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Thus, asymptotically almost all vertex-labeled tree-child networks are normal networks.

Colored Motzkin Skeletons and Sparsened Skeletons

Consider a phylogenetic network and do the following:

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Lemma

For a tree-child network with k reticulation nodes, each (colored) Motzkin skeleton is a Motzkin tree with $2k$ unary nodes.

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Sparsened skeleton: ancestor relationship of the green nodes in a Motzkin skeleton.

Motzkin Trees with the Tree-Child Property (i)

Motzkin Tree with TCP:

Motzkin trees where each non-leaf node has at least one child which is not an unary node.

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Set

$$M(z,y) = \sum_{n\geq 1}\sum_{\ell\geq 0} M_{\ell,n} y^{\ell} \frac{z^n}{n!}.$$

Denote by $M_u(z,y)$ and $M_b(z,y)$ all Motzkin trees with TCP whose root is unary and binary.

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Denote by $M_u(z,y)$ and $M_b(z,y)$ all Motzkin trees with TCP whose root is unary and binary.

Then,

$$M_u(z,y) = zy(z + M_b(z,y))$$

Motzkin Trees with the Tree-Child Property (ii)

and

$$M_b(z,y) = \frac{z}{2}((z + M_b(z,y))^2 + 2zy(z + M_b(z,y))^2).$$

Motzkin Trees with the Tree-Child Property (ii)

and

$$M_b(z,y) = \frac{z}{2}((z + M_b(z,y))^2 + 2zy(z + M_b(z,y))^2).$$

Solving gives

$$M_b(z,y) = \frac{1 - \sqrt{1 - 2z^2 - 4yz^3}}{z(1 + 2yz)} - z$$

and

$$M_u(z,y) = u\frac{1 - \sqrt{1 - 2z^2 - 4yz^3}}{1 + 2yz}$$

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and thus

$$\begin{aligned} M(z,y) &= z + M_u(z,y) + M_b(z,y) \\ &= \frac{(1+yz)\left(1 - \sqrt{1 - 2z^2 - 4yz^3}\right)}{z(1+2yz)}. \end{aligned}$$

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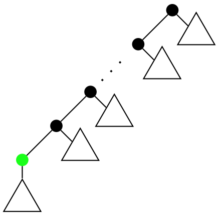

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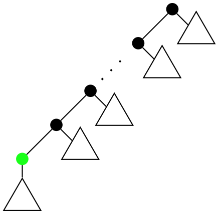

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Edge from g is NOT allowed to point on the subtree attached to g, to any node on the path to x and to the root of subtrees attached to that path.

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where

$$\tilde{M}(z,y) = z + M_b(z,y).$$

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Proposition

We have,

$$N_1(z) = z \frac{\tilde{a}_1(z^2) - \tilde{b}_1(z^2)\sqrt{1 - 2z^2}}{(1 - 2z^2)^{3/2}}.$$

where $\tilde{a}_1(z) = -3z + 2$ *and* $\tilde{b}_1(z) = -z + 2$.

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$$T_1(z) = \frac{1}{2}\frac{\partial}{\partial y}\frac{z\tilde{M}(z,y)}{1 - zM(z,y)}\Big|_{y=0},$$

where

$$\tilde{M}(z,y) = z + M_b(z,y).$$

Proposition

We have,

$$T_1(z) = z\frac{\tilde{a}_1(z^2) - \tilde{b}_1(z^2)\sqrt{1-2z^2}}{(1-2z^2)^{3/2}}.$$

where $\tilde{a}_1(z) = \tilde{b}_1(z) = z$.

Vertex-labeled Normal Networks with $k = 2$ (i)

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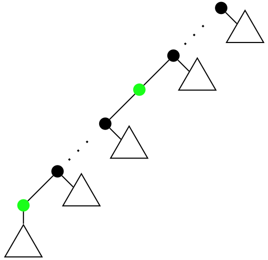
Motzkin skeletons arising when g_1 and g_2 are adjacent:



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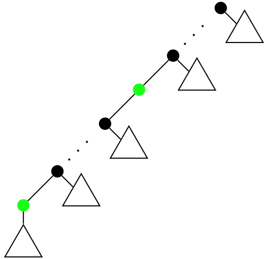

EGF is given by:

$$\partial_{y_1}\partial_{y_2}\frac{z^2\tilde{M}(z,0)}{(1-z\tilde{M}(z,y_1))(1-z\tilde{M}(z,y_1+y_2))}\Big|_{y_1=y_2=0}-\frac{z^7\tilde{M}(z,0)^4}{(1-z\tilde{M}(z,0))^5}.$$

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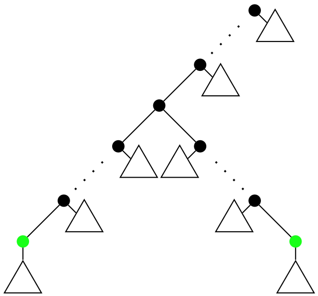

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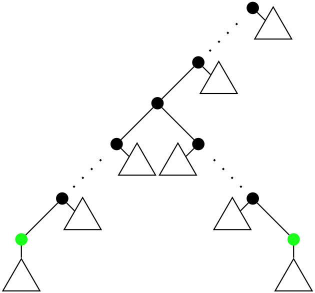

EGF is given by:

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$$+\,\partial_{y_2}\frac{z^5\tilde{M}(z,y_2)^2\tilde{M}(z,0)}{(1-z\tilde{M}(z,y_2))^4}\Big|_{y_2=0}.$$

Vertex-labeled Normal Networks with $k = 2$ (iii)

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where $\tilde{a}_2(z) = 11z^4 - 66z^3 + 50z^2 - 8z$ *and* $\tilde{b}_2(z) = -28z^3 + 42z^2 - 8z$.

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Theorem

We have,

$$N_{2,2n+1} = (2n+1)!\frac{1}{3}\cdot 2^{n-1}(3n-7)\left(\frac{2n(n^2+9n-4)}{(2n-1)4^n}\binom{2n}{n} - 3(n+1)\right).$$

Vertex-labeled Tree-Child Networks with $k = 2$

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where $\tilde{a}_2(z) = -z + 8$ *and* $\tilde{b}_2(z) = 8$.

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Theorem

We have,

$$T_{2,2n+1} = (2n+1)!2^{n-1}(n-1)(n-2)\left(\frac{2n(3n-1)}{3(2n-1)4^n}\binom{2n}{n} - 1\right).$$

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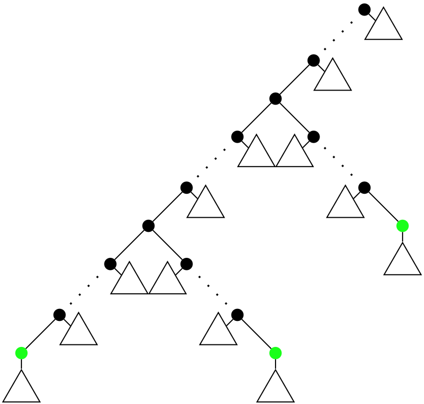
One possible type of Motzkin skeletons:



Generating Paths

If two red nodes are on a path, the tree-child condition must be satisfied.

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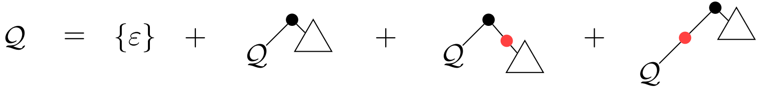

which leads to

$$\mathcal{Q} = \{\varepsilon\} \cup \{\circ\} \times \mathcal{Q} \times \tilde{\mathcal{M}} \cup \{\circ\} \times \mathcal{Q} \times (\{\bullet\} \times \tilde{\mathcal{M}}) \cup \{\circ\} \times (\{\bullet\} \times \mathcal{Q}) \times \tilde{\mathcal{M}},$$

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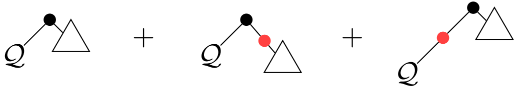

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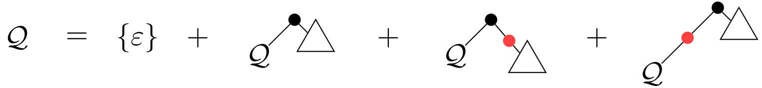

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$$\mathcal{P} = \mathcal{Q} \cup \{\bullet\} \times \mathcal{Q}.$$

Thus,

$$P(z, y, \bar{y}, \tilde{y}, \hat{y}) = \frac{1 + z\hat{y}}{1 - (z + z^2 y + z^2 \bar{y})\tilde{M}(z, \tilde{y})}.$$

$$
\begin{aligned}
&\frac{1}{2}\,\frac{z^5\tilde{M}(z,y_1+y_2)\tilde{M}(z,y_1+y_3)\tilde{M}(z,y_2+y_3)}{1-z\tilde{M}(z,y_1+y_2+y_3)}P(z,0,y_1+y_2,y_1+y_2+y_3,0)\\
&\quad\times P(z,0,y_1+y_3,y_1+y_2+y_3,0)P(z,0,y_2+y_3,y_1+y_2+y_3,0)P(z,0,y_3,y_1+y_2+y_3,0)\\
&+\frac{z^5\tilde{M}(z,y_2)\tilde{M}(z,y_3)\tilde{M}(z,y_2+y_3)}{1-z\tilde{M}(z,y_2+y_3)}P(z,y_1,y_3,y_2+y_3,0)P(z,0,y_2,y_2+y_3,0)P(z,0,y_3,y_2+y_3,0)^2\\
&+\frac{z^5\tilde{M}(z,y_2)\tilde{M}(z,y_3)\tilde{M}(z,y_2+y_3)}{1-z\tilde{M}(z,y_2+y_3)}P(z,y_1,y_2,y_2+y_3,0)\\
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$$

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The three other types of Motzkin skeletons:

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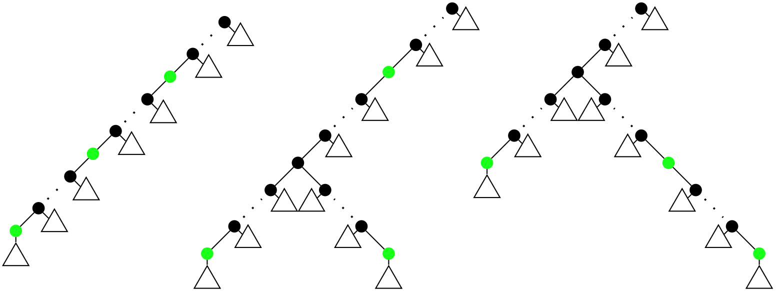

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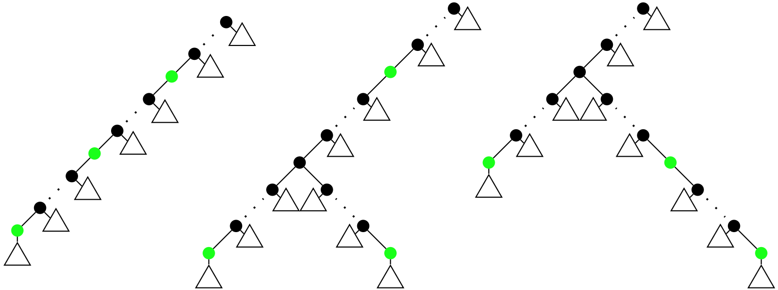

The EGFs have been added up and divided by 8 (since every network is generated exactly 8 times by our method).

Vertex-labeled Tree-Child Networks with $k = 3$

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We have,

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where $\tilde{a}_3(z) = -35z^6 + 175z^5$ *and* $\tilde{b}_3(z) = 34z^6 + 175z^5$.

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Theorem

With $p(n) = (n-4)(n-3)(n-2)$, *we have*

$$T_{3,2n+1} = (2n+1)!\frac{1}{3}\cdot 2^{n-6}p(n)\left(\frac{64n^2(n-1)}{(2n-1)4^n}\binom{2n}{n} - (48n-65)\right).$$

Vertex-labeled Normal Networks with $k = 3$ (iv)

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and

$$N_2(z) = z\frac{\tilde{a}_2(z^2) - \tilde{b}_2(z^2)\sqrt{1-2z^2}}{(1-2z^2)^{7/2}},$$

with suitable polynomials $a_1(z), a_2(z), b_1(z)$ and $b_2(z)$.

Vertex-labeled Normal Networks with General k

Induction on k gives the following result.

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We have,

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From this, an asymptotic expansion can be obtained by singularity analysis.

P. Flajolet and A. M. Odlyzko (1990). Singularity analysis of generating functions, SIAM Journal on Algebraic and Discrete Methods, 3:2, 216–240.

Singularity Analysis

Recall

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This function has two dominant singularities at $z = 1/\sqrt{2}$ and $z = -1/\sqrt{2}$ with singularity expansions

$$N_k(z) \overset{z\to\pm 1/\sqrt{2}}{\sim} \pm\frac{\tilde{a}_k(1/2)}{4^k(1\mp\sqrt{2}z)^{2k-1/2}}.$$

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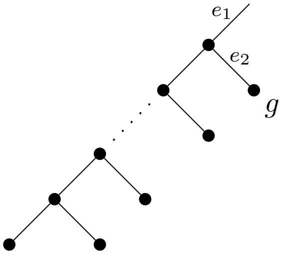
Then,
$$\begin{aligned} n![z^n]N_k(z) &\sim n!\frac{\tilde{a}_k(1/2)}{4^k}\left([z^n]\frac{1}{(1-\sqrt{2}z)^{2k-1/2}} - [z^n]\frac{1}{(1+\sqrt{2}z)^{2k-1/2}}\right) \\ &\sim c_k(1-(-1)^n)\left(\frac{\sqrt{2}}{e}\right)^n n^{n+2k-1}, \end{aligned}$$

where $c_k = \sqrt{2\pi}\tilde{a}_k(1/2)/(4^k\Gamma(2k-1/2))$.

$c_k > 0$ (i)

Consider as Motzkin sekeleton the caterpillar:



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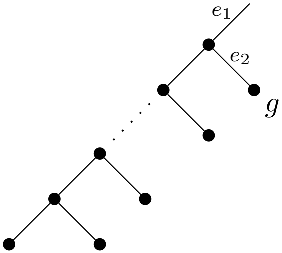

Generate normal networks where g is only allowed to point at e_1 and e_2 and recursively for the other green nodes.

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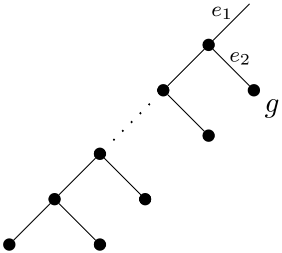

Generate normal networks where g is only allowed to point at e_1 and e_2 and recursively for the other green nodes.

EGF of # of these normal networks has the same shape as that for all normal networks.

$c_k > 0$ (ii)

$C_{k,n}$ ... # of vertex-labeled normal networks with k reticulation nodes arising from the caterpillar skeleton.

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Proposition

There exists a positive constant $d_k > 0$ such that

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This implies that c_k with

$$N_{k,n} \sim c_k \left(1 - (-1)^n\right) \left(\frac{\sqrt{2}}{e}\right)^n n^{n+2k-1}$$

is also positive.

Counting Leaf-labeled Networks with Fixed k

$\tilde{T}_{\ell,n}$ ... # of leaf-labeled tree-child networks with k reticulation nodes;
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Lemma

The descendant sets for any two nodes in a tree-child network (and thus also normal network) are different.

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Theorem

We have,

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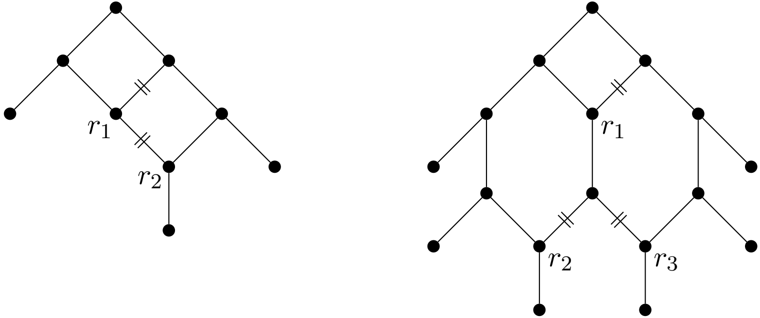
Counting all Networks

Counting all Networks

- Motzkin skeleton does not necessarily have $2k$ unary nodes:



In both cases, a leaf becomes a colored node!

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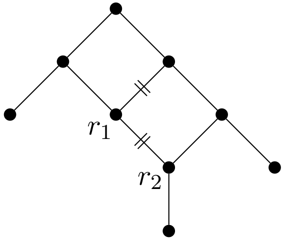

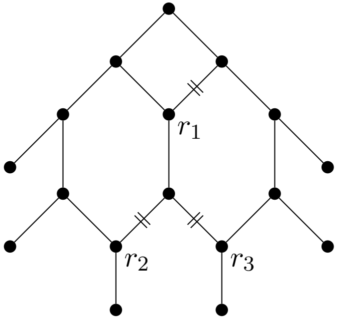

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One needs consider more types of Motzkin skeleton for the counting.

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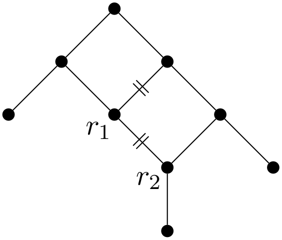
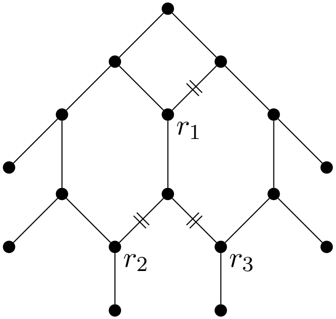
- Motzkin skeleton does not necessarily have $2k$ unary nodes:





In both cases, a leaf becomes a colored node!

One needs consider more types of Motzkin skeleton for the counting.

- For the leaf-labeled case, one has to cope with symmetries.

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- Results for tree-child and normal networks:
  - *M. Fuchs, B. Gittenberger, M. Mansouri (2019). Counting phylogenetic networks with few reticulation vertices: tree-child and normal networks, Australas. J. Combin., 73:2, 385–423.*
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- Results for general networks:
    - *M. Mansouri. Counting general phylogenetic networks with few reticulation vertices, preprint.*

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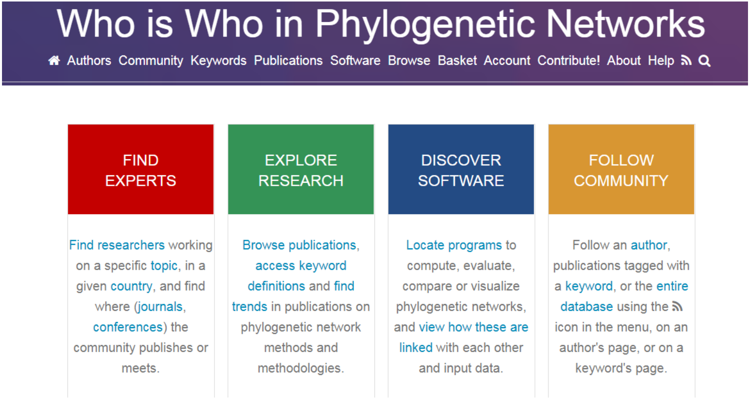
- Results for general networks:
  - *M. Mansouri. Counting general phylogenetic networks with few reticulation vertices, preprint.*
- Other classes of phylogenetic networks have also been counted recently, e.g.,
  - *M. Bouvel, P. Gambette, M. Mansouri. Counting phylogenetic networks of level 1 and 2, ArXiv::1909.10460.*

There are many more classes of phylogenetic networks:

http://phylnet.univ-mlv.fr/



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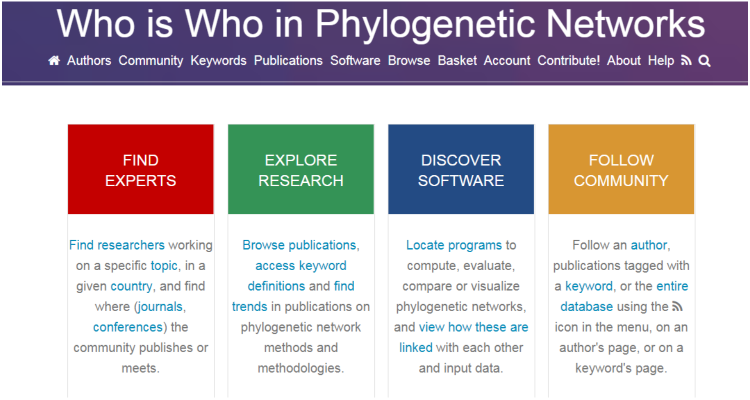

Thanks for your attention!