Groupe de travail APR, LIP6
Paris – 18/11/2011

Structure and enumeration of level-k phylogenetic networks

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GASPARD - MONGE - INSTITUT

Outline

- Phylogenetic motivations
- Level-*k* network reconstruction
- Structure of level-*k* networks
- Counting level-1 and 2 networks

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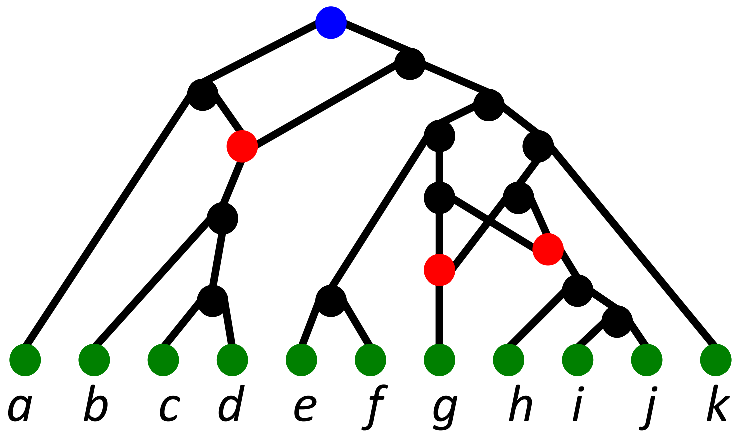
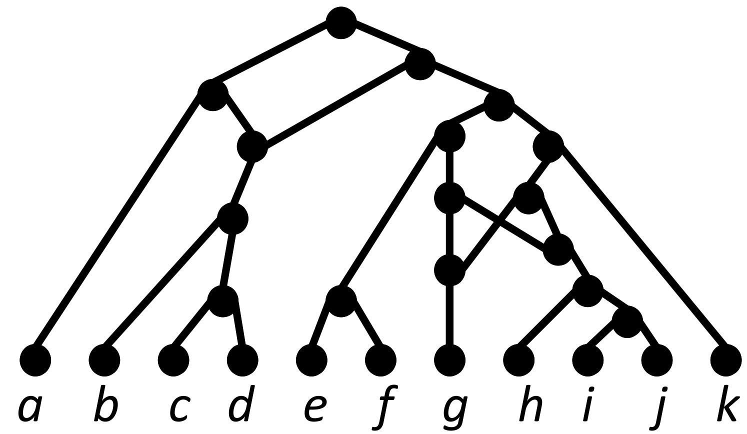
Rooted binary phylogenetic networks



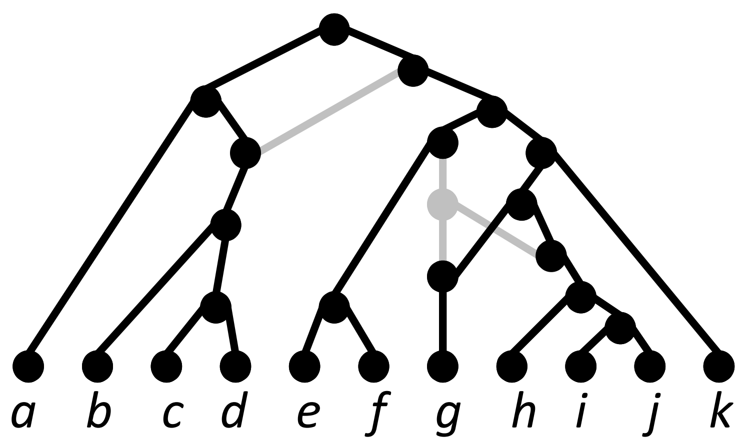
leaves bijectively labeled by current species
+ internal vertices (extinct species) :
- root
- **split vertices** (speciation)
- **hybrid vertices** (hybridization, horizontal gene transfer)

Rooted binary phylogenetic networks

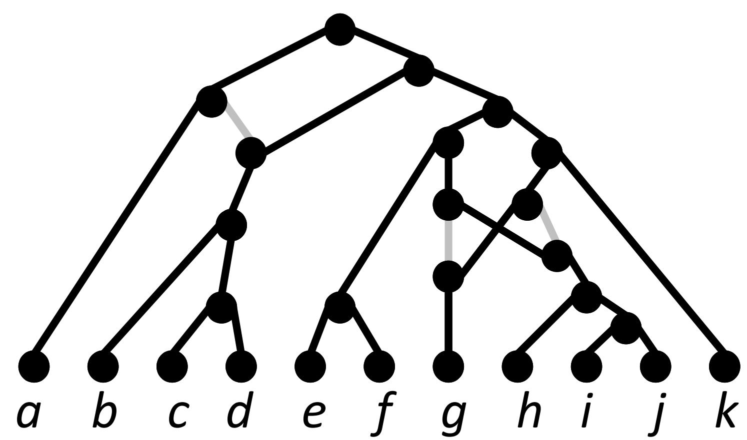


Model: each gene comes from one parent:

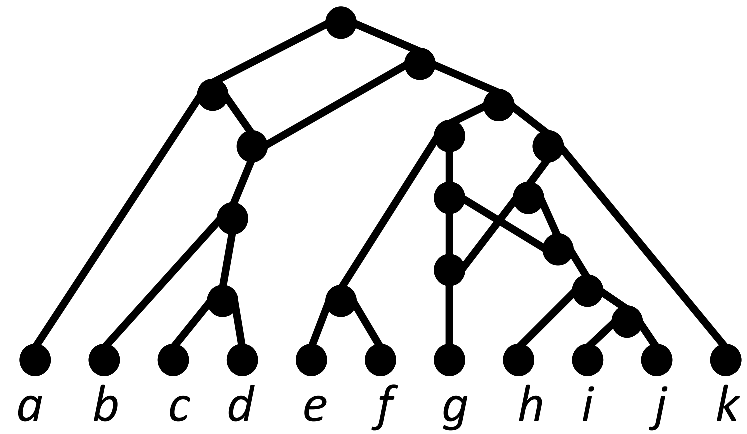
Gene 1



Gene 2



Rooted binary phylogenetic networks



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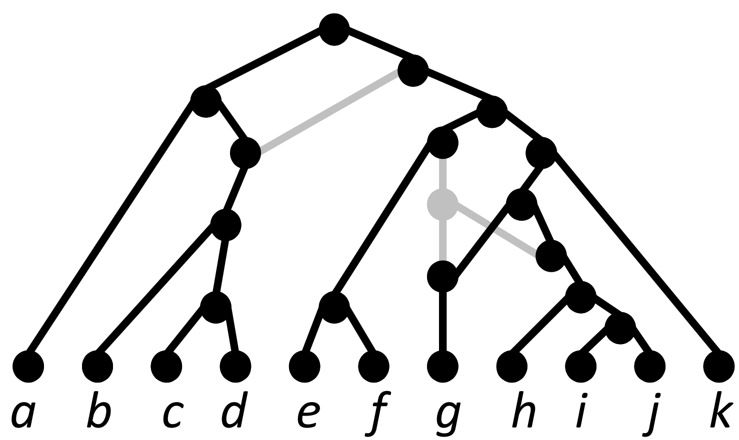
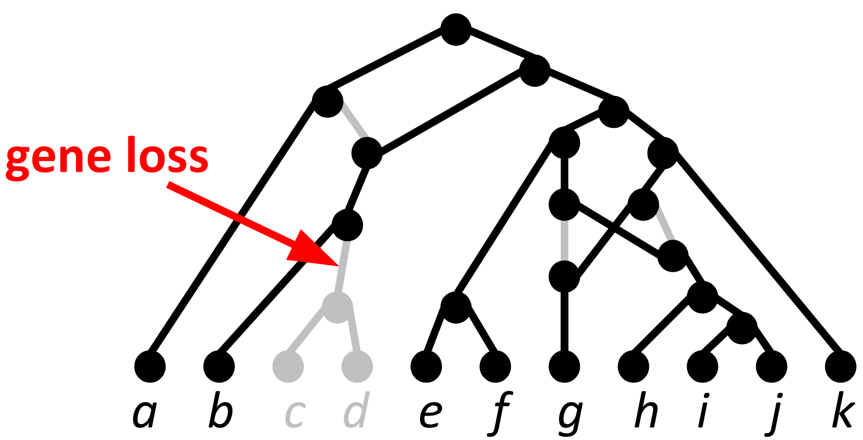


Gene 2



Combinatorial phylogenetic network reconstruction

```
species 1 : AATTGCAG TAGCCCAAAAT
species 2 : ACCTGCAG TAGACCAAT
species 3 : GCTTGCCG TAGACAAGAAT
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```
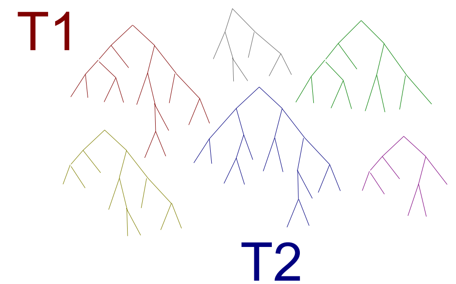

G1 G2

{gene sequences}

↓

{trees}



Phyl-ARIANE

ANR

HOGENOM database
Dufayard, Duret, Penel, Gouy, Rechenmann & Perrière, *BioInf*, 2005

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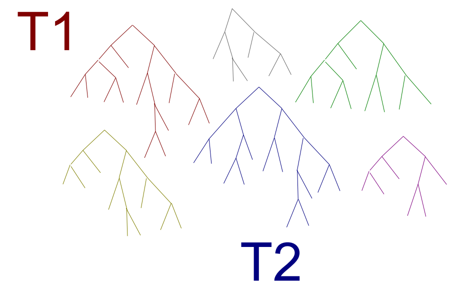

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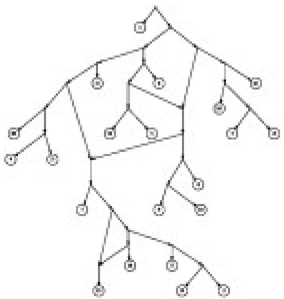

network

contains the trees
+ “optimal”

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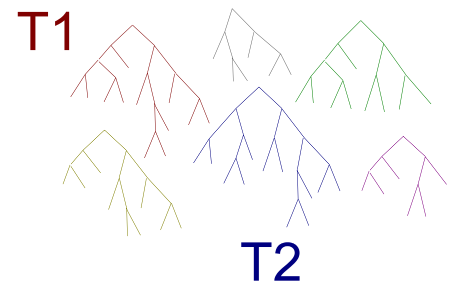

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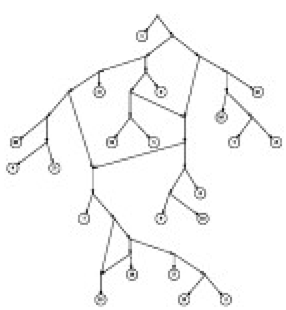

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NP-complete for 2 rooted trees

Bordewich & Semple, *DAM*, 2007

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G1 G2

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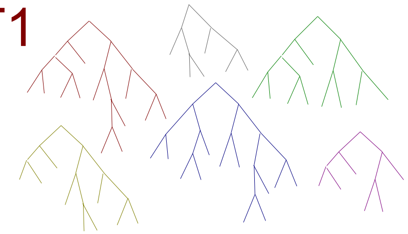
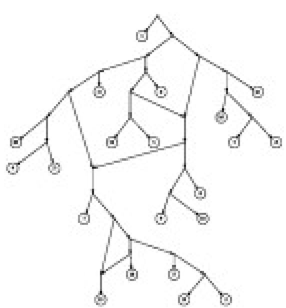
T1



T2

HOGENOM database
Dufayard, Duret, Penel, Gouy, Rechenmann & Perrière, *BioInf*, 2005
> 500 species, >70 000 trees



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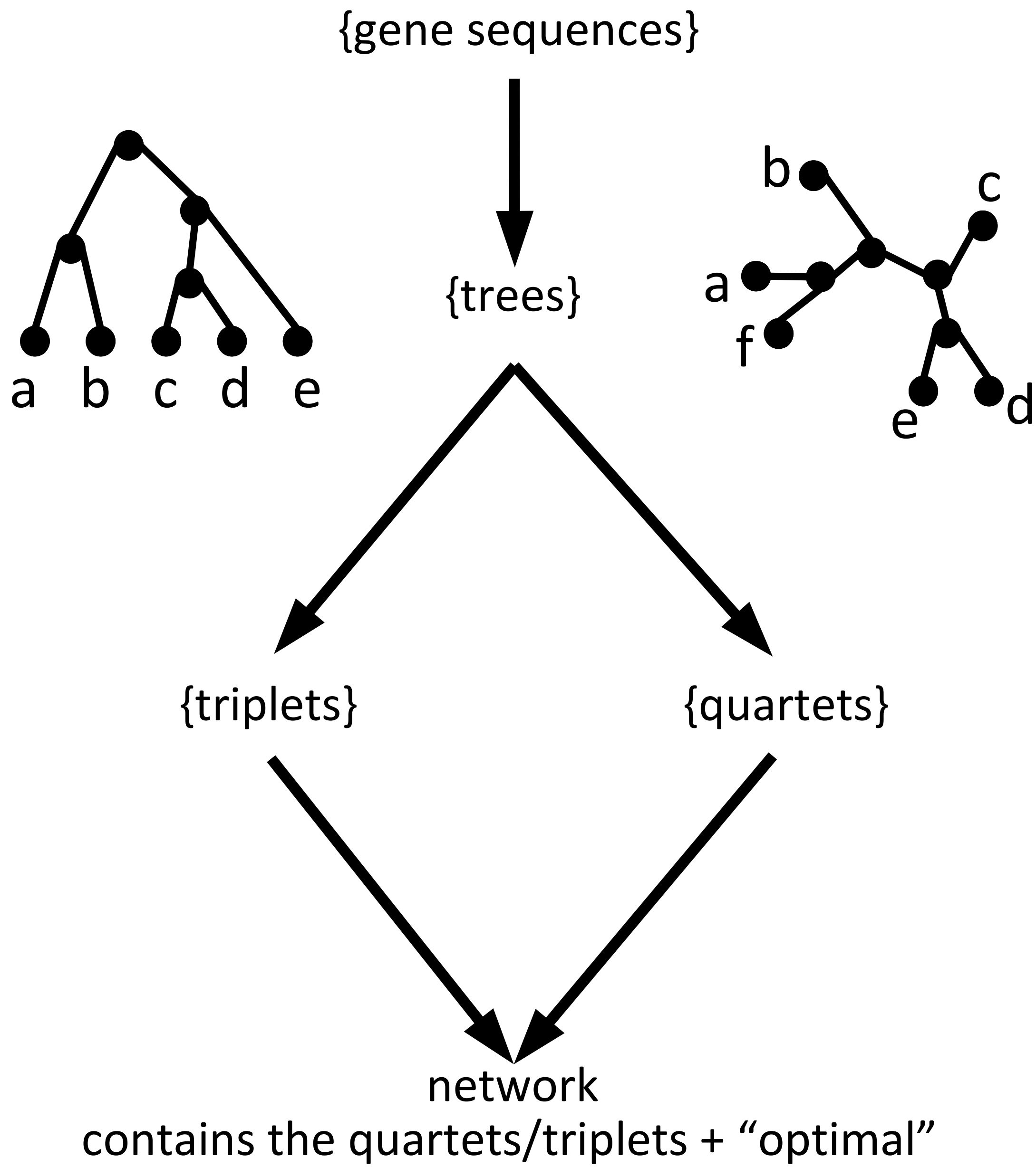
Reconstruction from triplets / quartets



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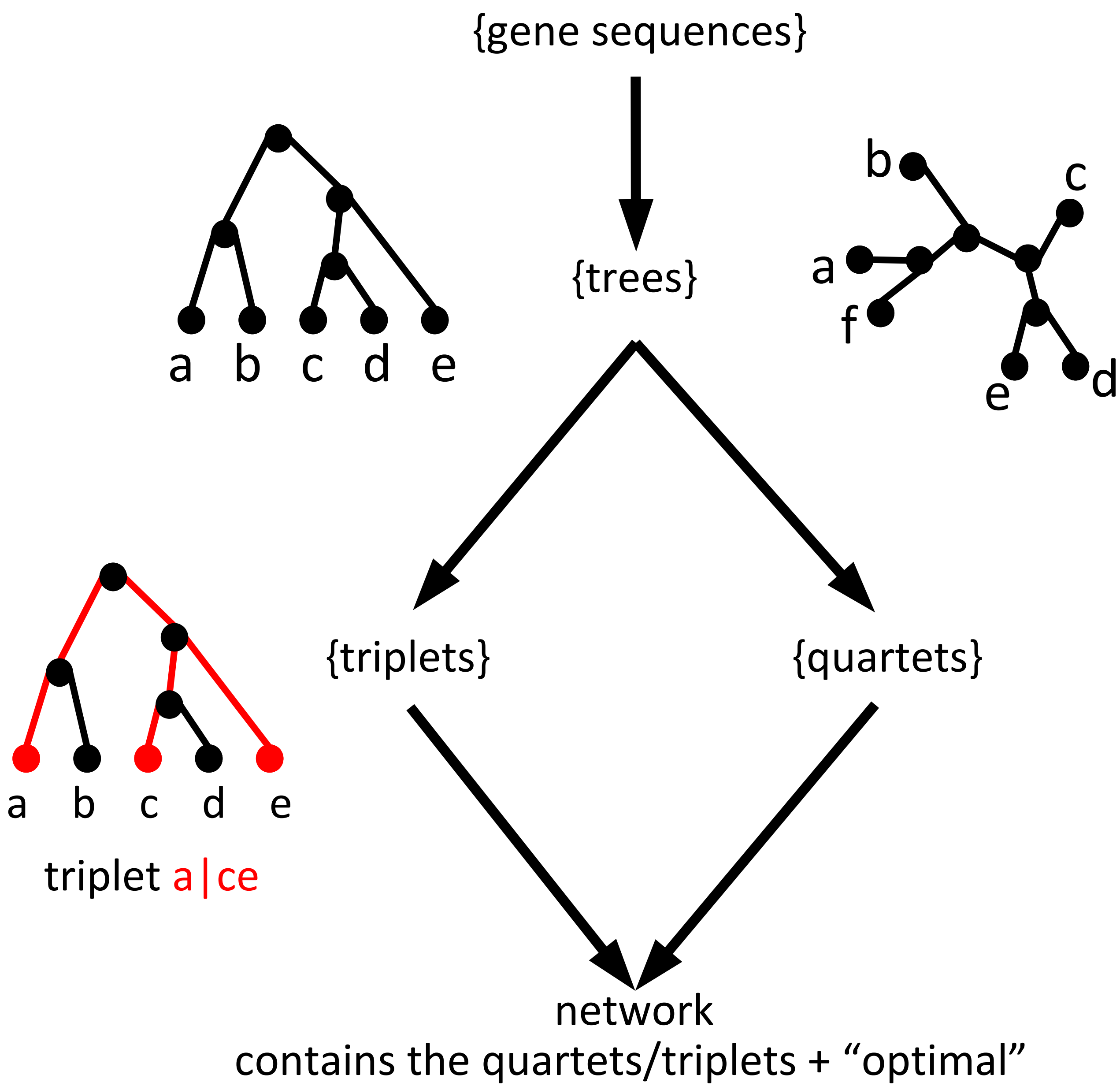

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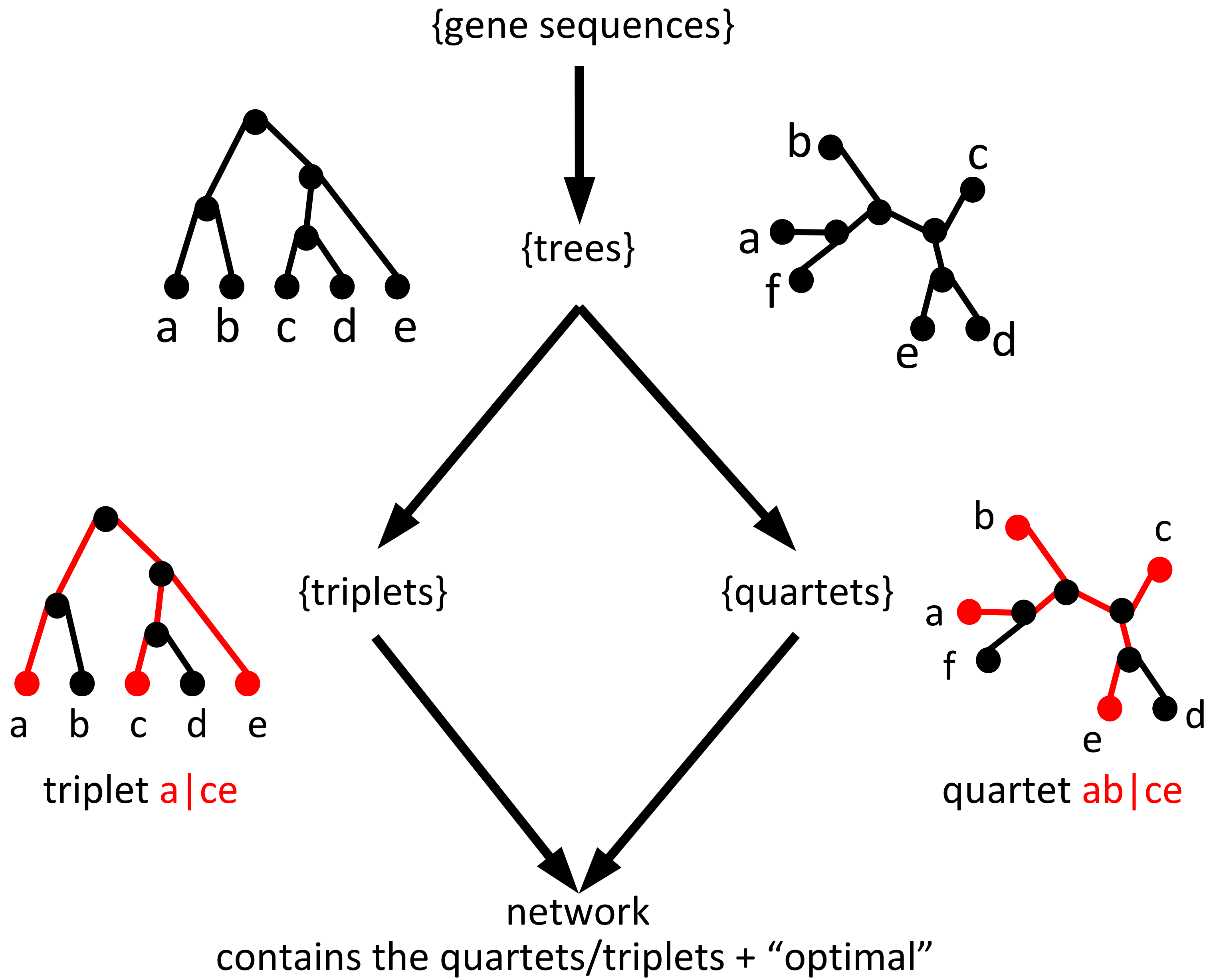

Reconstruction from triplets / quartets

Checking the solution:

Finding **all triplets** of a rooted network: $O(n^3)$

Byrka, Gawrychowski, Huber & Kelk, *JDA*, 2010

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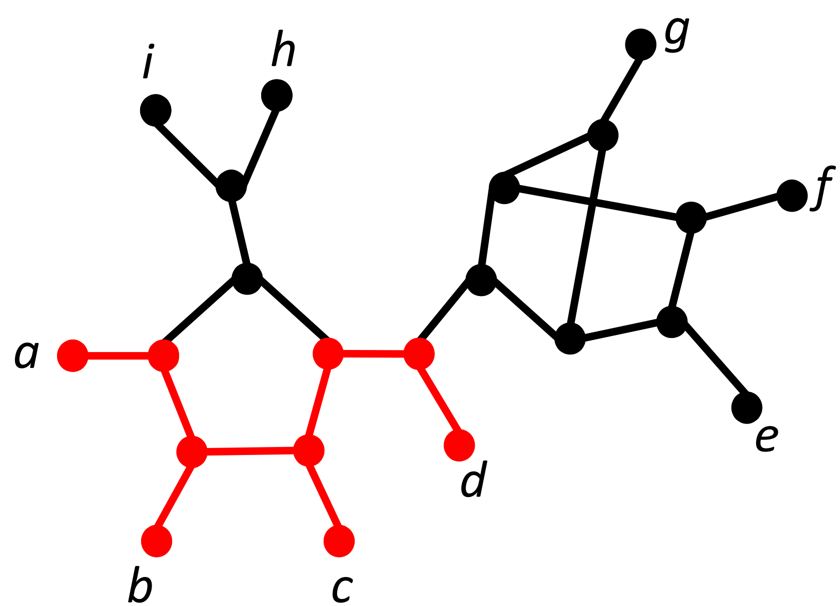
Finding **all quartets** of an unrooted network?

quartet *ab|cd*



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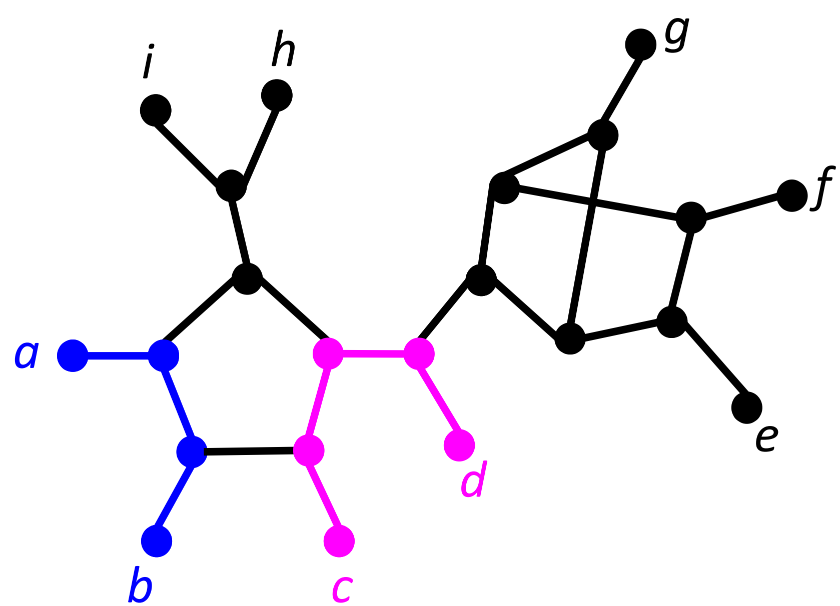
⬍

2-disjoint paths
a-b,*c-d*



Reconstruction from triplets / quartets

Checking the solution:

Finding **all triplets** of a rooted network: $O(n^3)$

Byrka, Gawrychowski, Huber & Kelk, *JDA*, 2010

Finding **all quartets** of an unrooted network: $O(n^6)$

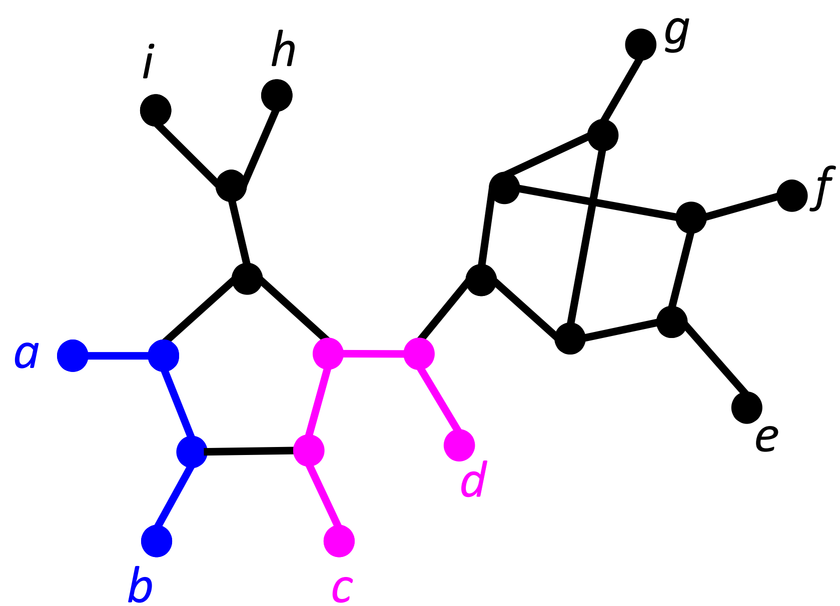
2-Disjoint Paths in a graph of degree ≤3: $O(n(1+\alpha(n,n)))$

Tholey, *SOFSEM'09*, 2009

quartet *ab*|*cd*

⬍

2-disjoint paths
a-b,*c-d*

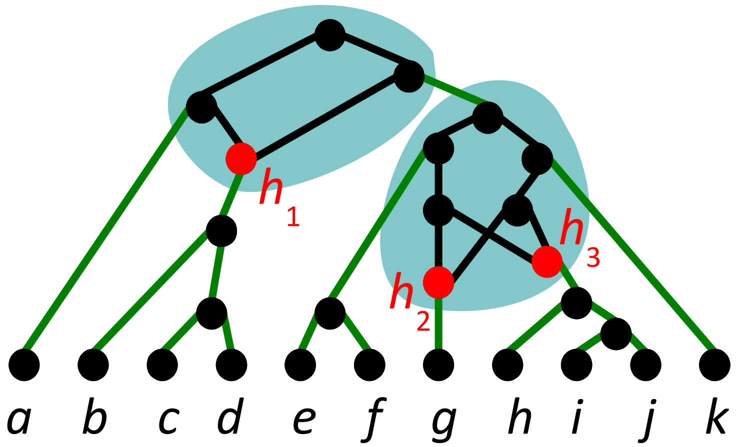


Plan

- Phylogenetic motivations
- Level-*k* network reconstruction
- Structure of level-*k* networks
- Counting level-1 and 2 networks

Level-*k* networks

level: how "far" is the network from a tree ?
small level ➡ tree structure ➡ fast algorithms



level-2 network

level =
maximum number of hybrid vertices by bridgeless component (*blob*) of the underlying undirected graph.

Choy, Jansson, Sadakane & Sung, *TCS*, 2005

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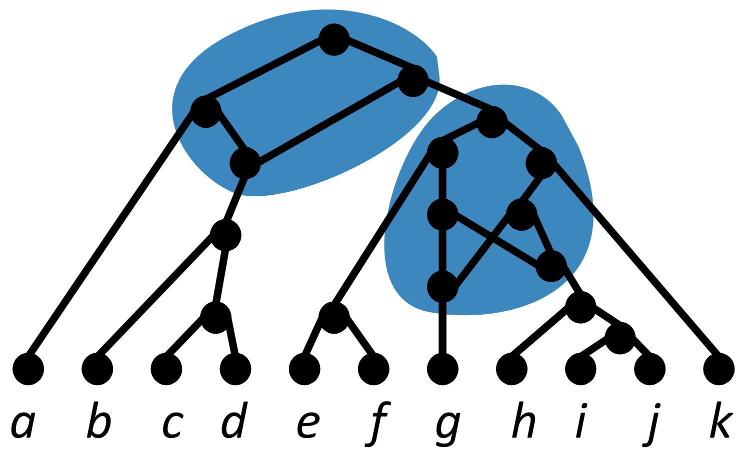
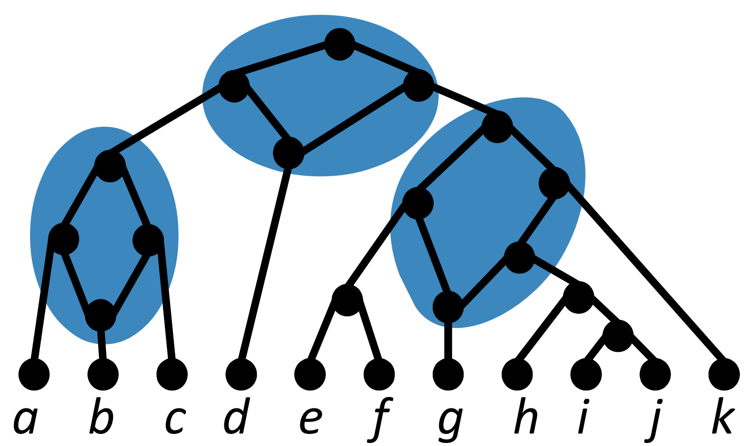


level-2 network

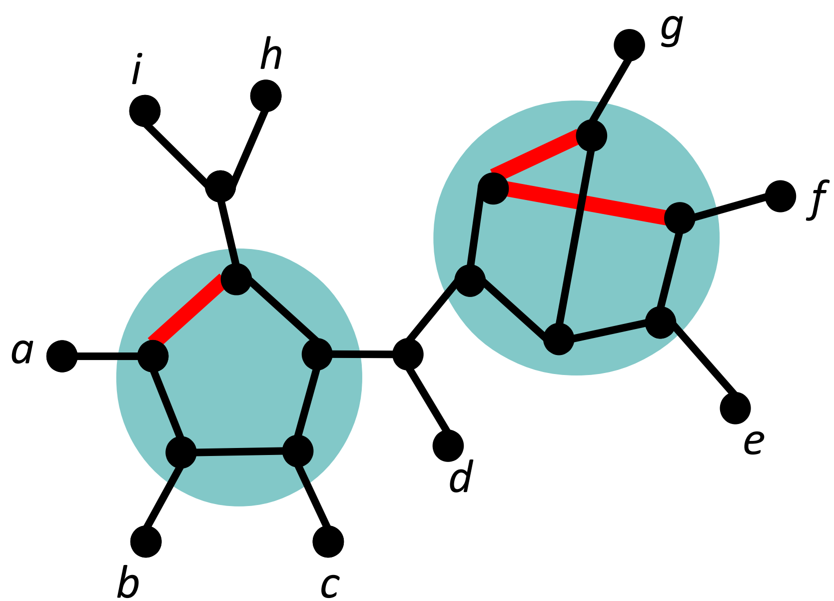
level =
maximum number of hybrid vertices
by *blob*.

level-1 network
("*galled tree*")



Unrooted level-*k* networks

level: how “far” is the network from an unrooted tree ?
small level ➡ tree structure ➡ fast algorithms



unrooted level-2 network

level =
maximum number of edges to remove, by *blob*, to obtain a tree.

Gambette, Berry & Paul, manuscript, 2011

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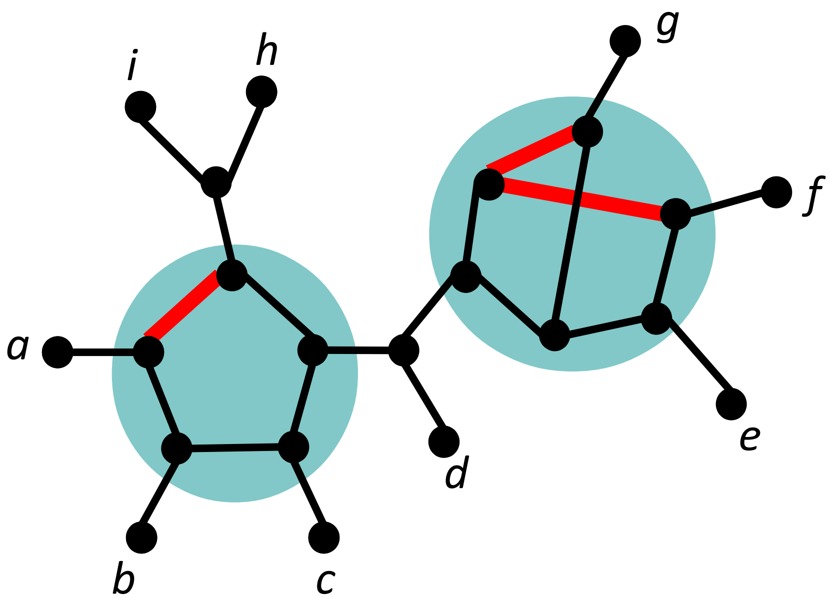

unrooted level-2 network

level =
maximum number of edges to remove, by *blob*, to obtain a tree.
= maximum ***cyclomatic number*** of the blobs

Unrooted level-*k* networks

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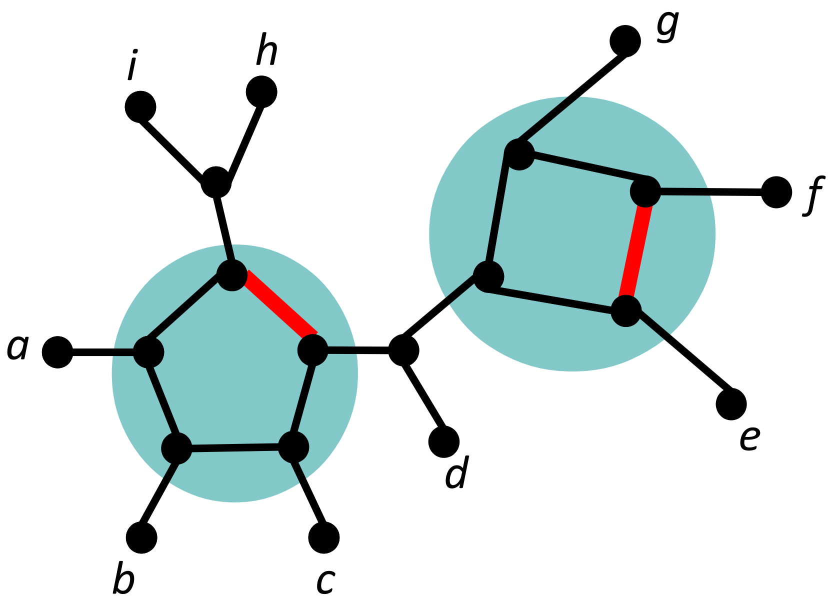
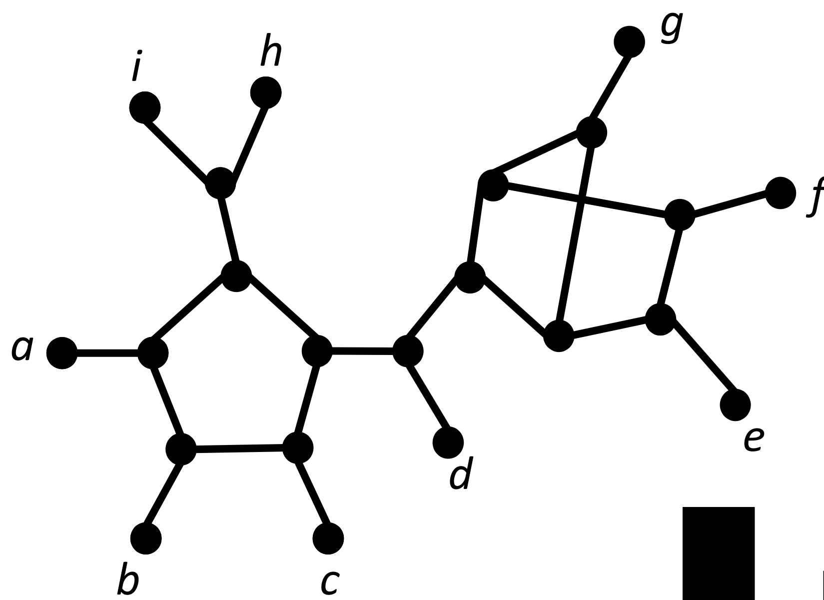
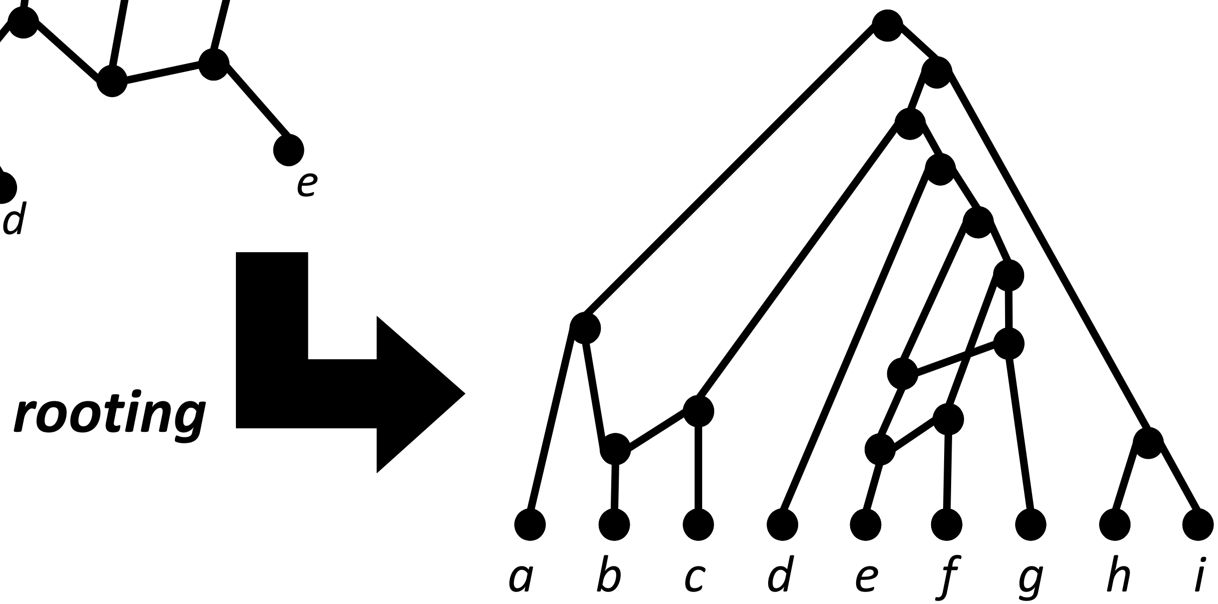


level =
maximum number of edges to remove, by *blob*, to obtain a tree.

unrooted level-1 network ➡ tree of cycles
(unrooted galled tree)

Equivalence between rooted and unrooted level





Rooting:
- choosing a root
- choosing an orientation for the edges

Gambette, Berry & Paul, manuscript, 2011

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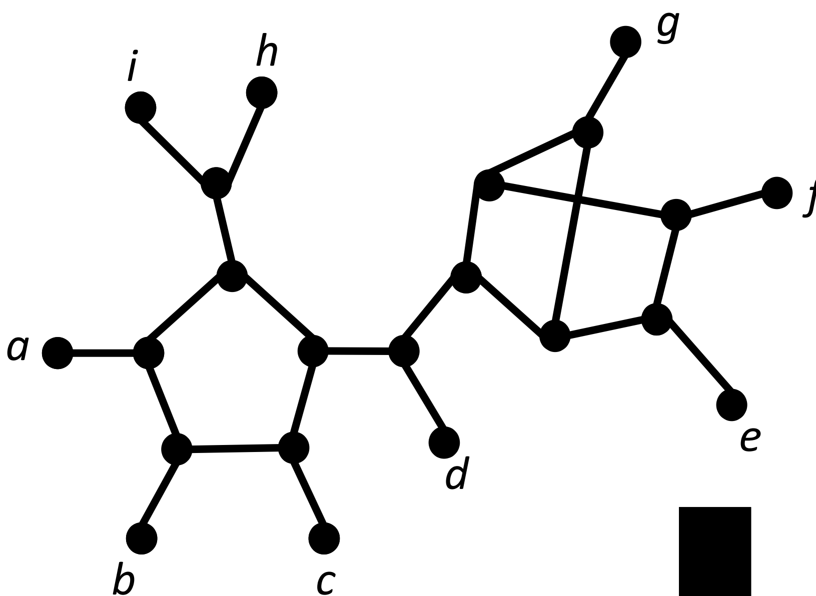

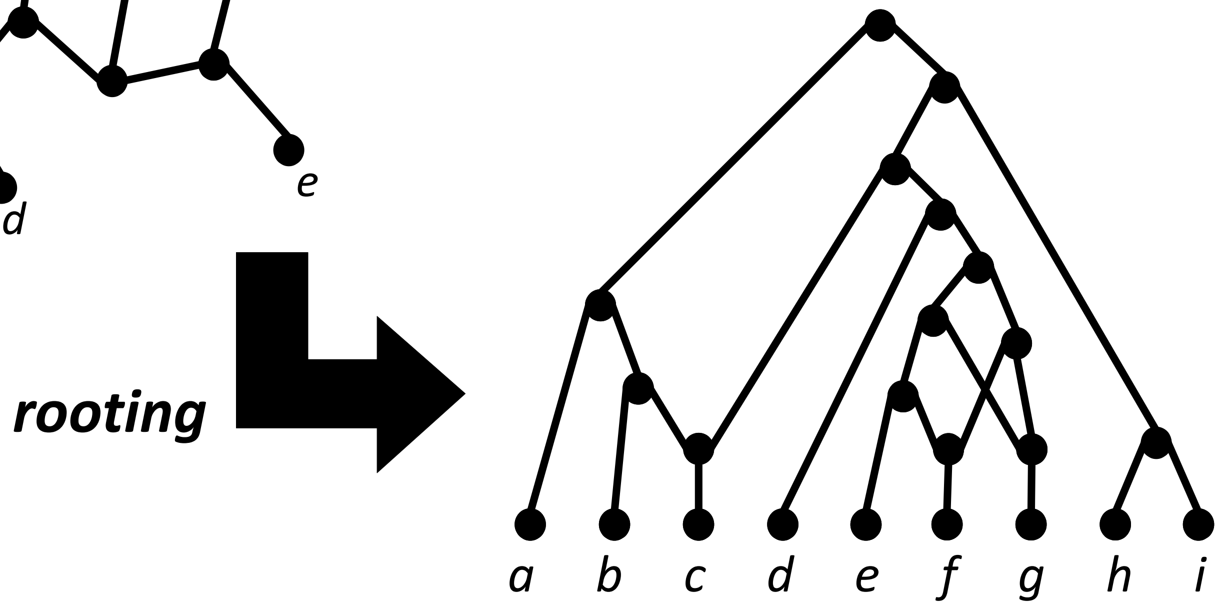

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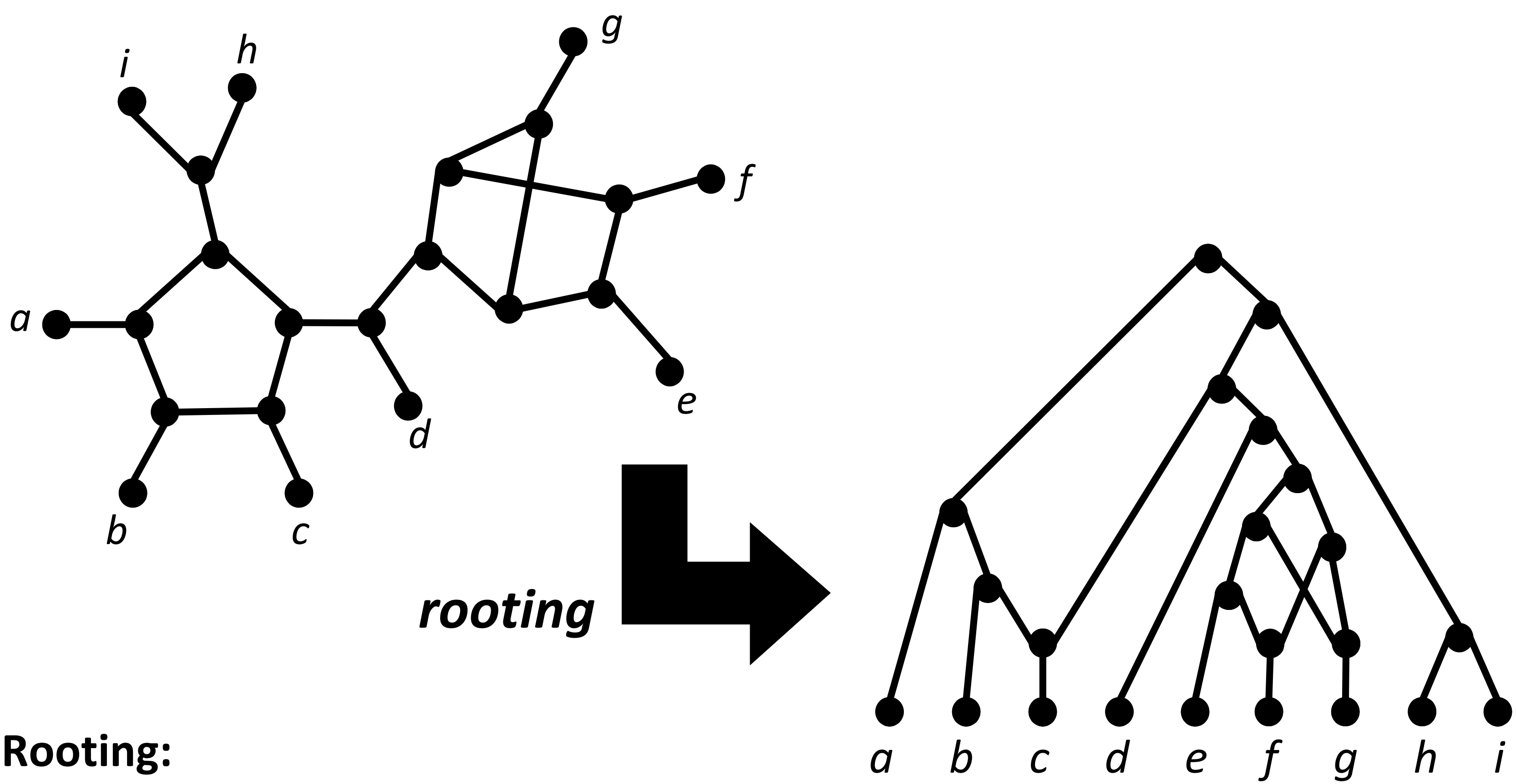
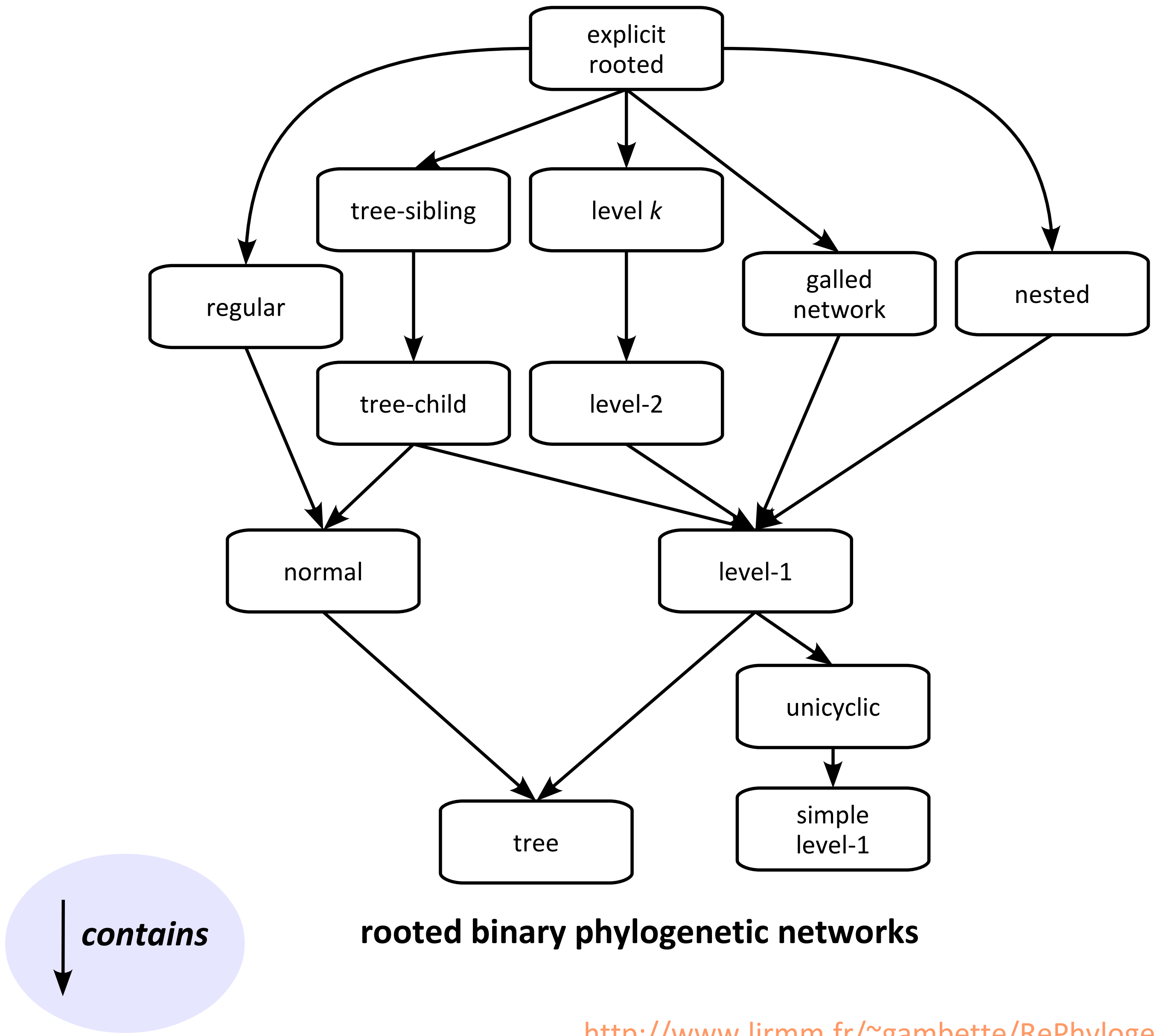


Rooting:
- choosing a root
- choosing an orientation for the edges

- **many** possible rootings (possibly exponential in the level)
- **same level** (invariant)

Gambette, Berry & Paul, manuscript, 2011

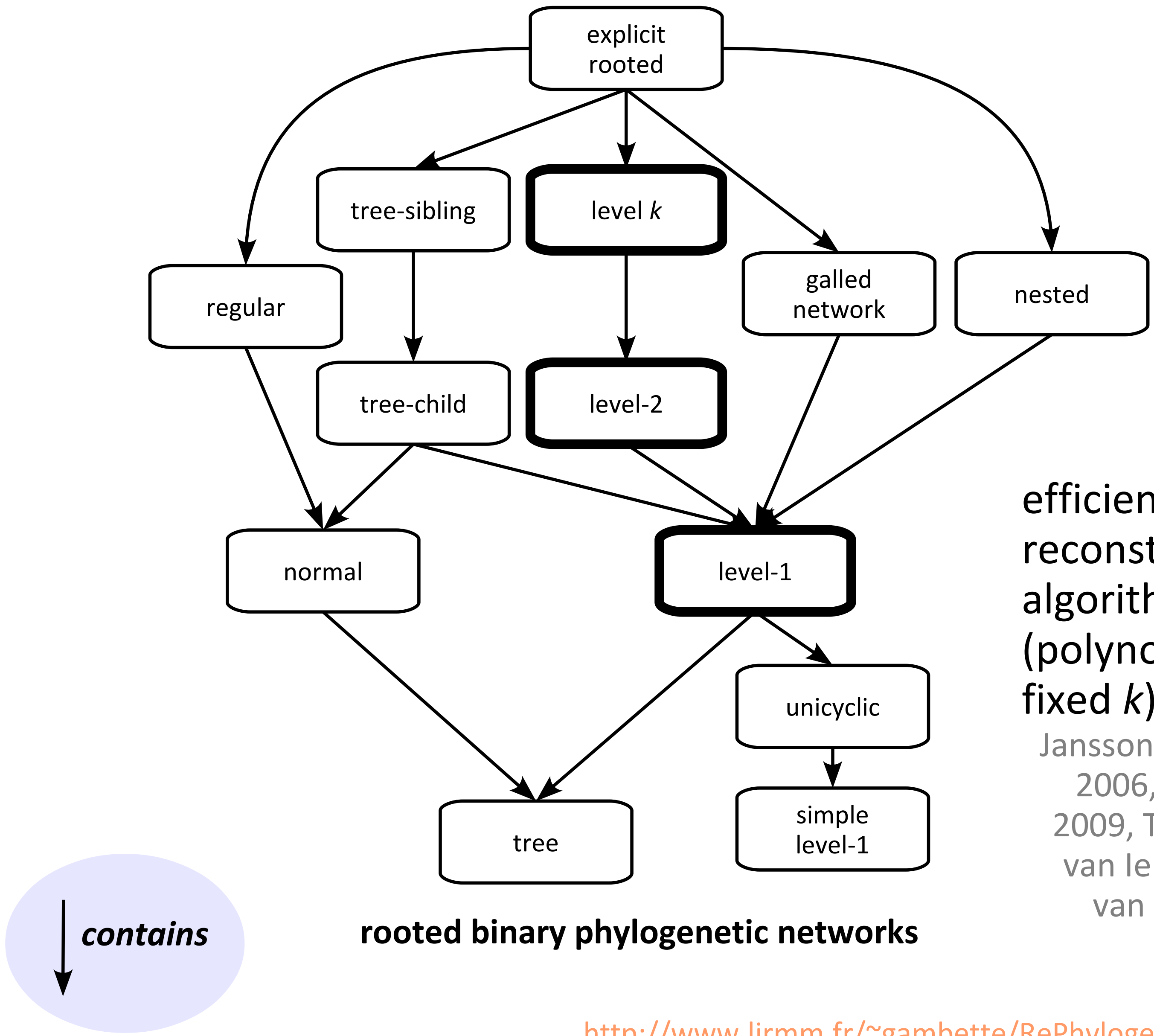
Phylogenetic network subclass hierarchy



rooted binary phylogenetic networks

http://www.lirmm.fr/~gambette/RePhylogeneticNetworks.php

Phylogenetic network subclass hierarchy



rooted binary phylogenetic networks

efficient reconstruction algorithms (polynomial for fixed *k*)

Jansson, Nguyen & Sung 2006, van Iersel *et al.* 2009, To & Habib 2009, van Iersel & Kelk 2010, van Iersel *et al.* 2010

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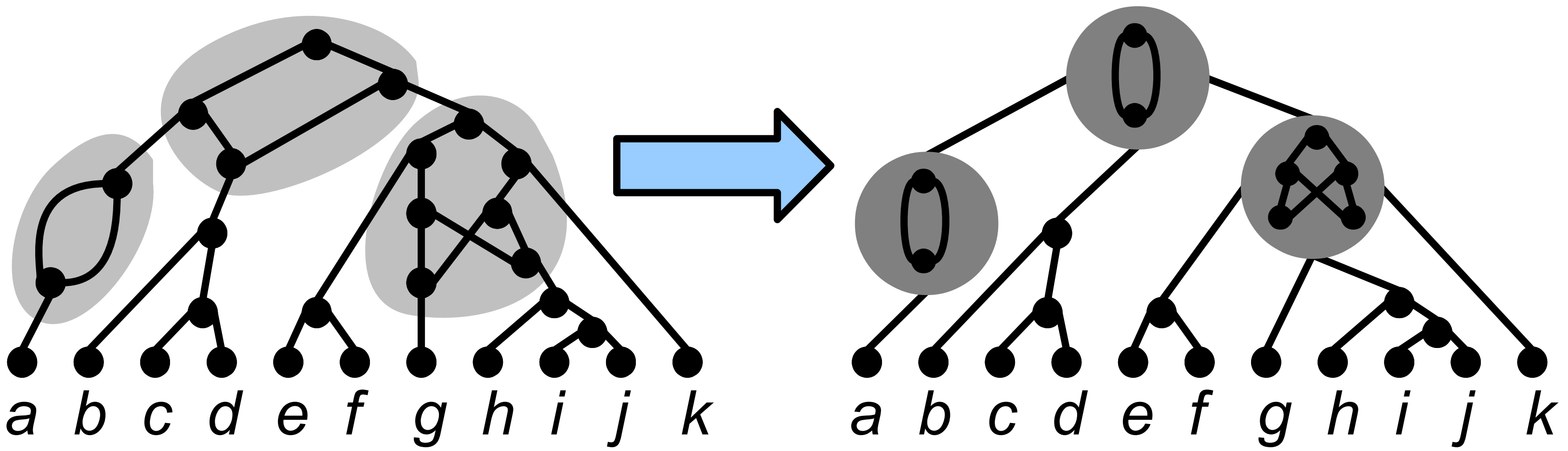
Decomposition of level-*k* networks

We formalize the decomposition into blobs:



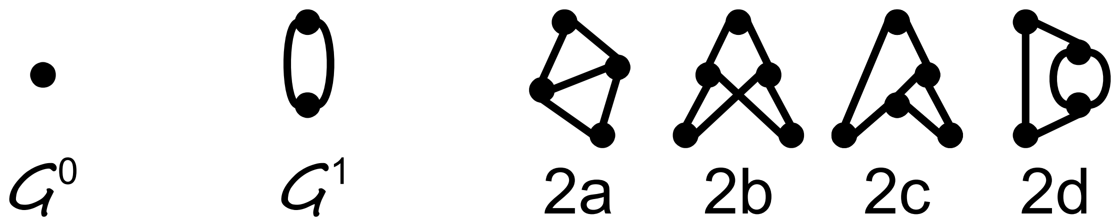
N, level-*k* network.

N decomposed as a **tree** of simple graph patterns: **generators**.

Generators introduced by van Iersel & al (Recomb 2008) for the restricted class of simple level-*k* networks.

Level-*k* generators

A **level-*k* generator** is a level-k network with no cut arc.



The **sides** of the generator are:
- its arcs
- its reticulation vertices of outdegree 0

Decomposition theorem of level-*k* networks

N is a level-k network

iff

there exists a sequence $(l_j)_{j\in[1,r]}$ of r locations

(arcs or reticulation vertices of outdegree 0)

and a sequence $(G_j)_{j\in[0,r]}$ of generators of level at most k, such that:

- $N = \text{Attach}_k(l_r, G_r, \text{Attach}_k(\ldots \text{Attach}_k(l_2, G_2, \text{Attach}_k(l_1, G_1, G_0))\ldots))$,
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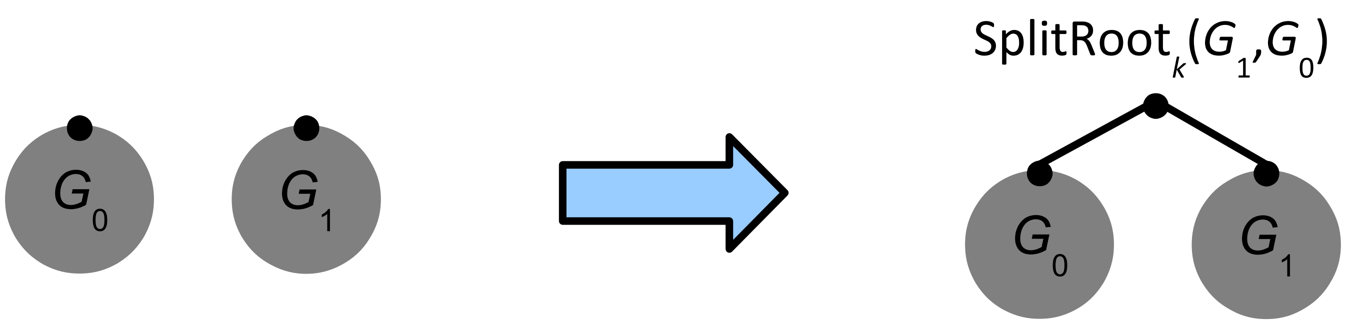

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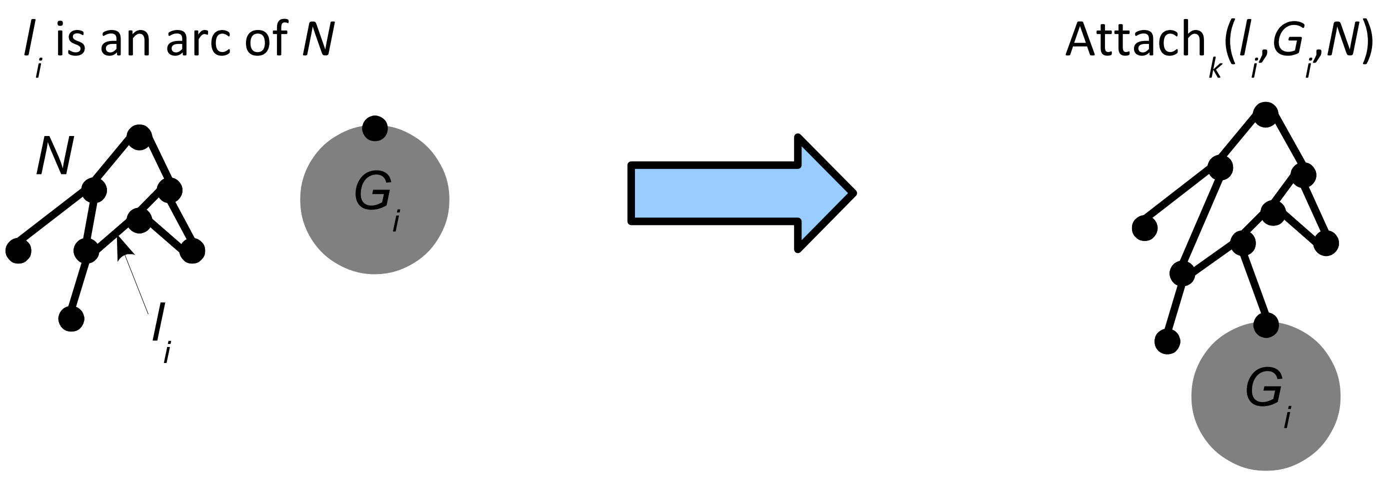

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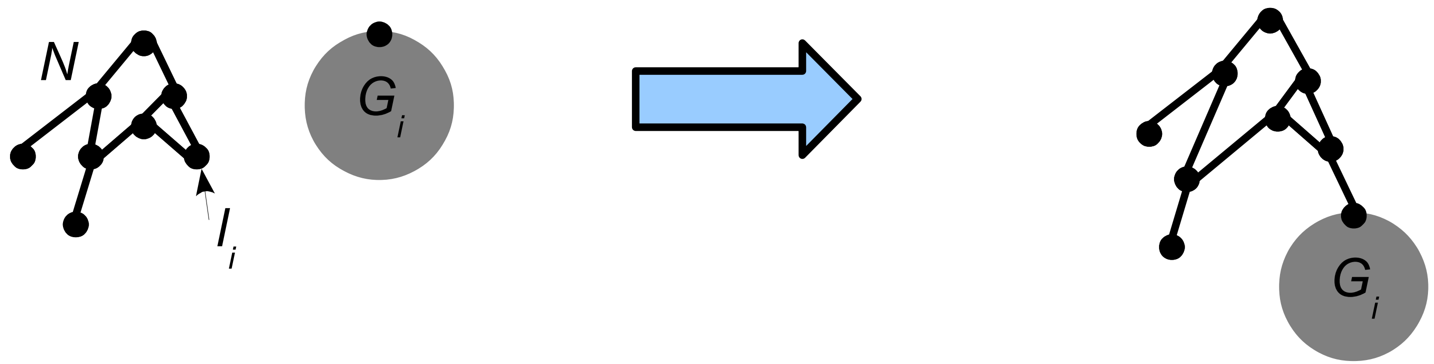
l_i is a reticulation vertex of N

$\text{Attach}_k(l_i,G_i,N)$



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This decomposition is **not unique!**

recursive decomposition later, for level-1...

Construction of level-*k* generators

Case analysis by van Iersel & al to find the 4 level-2 generators
Exponential algorithm by Steven Kelk to find the 65 level-3 generators.

AT&T Integer Sequences RESEARCH

Greetings from The On-Line Encyclopedia of Integer Sequences!

1,4,65 | Search | Hints

Search: **1, 4, 65**

Displaying 1-2 of 2 results found. page 1

Format: long | short | internal | text Sort: relevance | references | number Highlight: on | off

A041119 Denominators of continued fraction convergents to sqrt(68). +20 2

1, 4, 65, 264, 4289, 17420, 283009, 1149456, 18674305, 75846676, 1232221121, 5004731160, 81307919681, 330236409884, 5365090477825, 21790598321184, 354014663616769, 1437849252788260, 23359602708228929 (list; graph; listen)

OFFSET	0,2
CROSSREFS	Cf. A041118. Sequence in context: A138835 A119601 A058438 this_sequence A015475 A025585 A048828 Adjacent sequences: A041116 A041117 A041118 this_sequence A041120 A041121 A041122
KEYWORD	nonn,cofr,easy
AUTHOR	njas

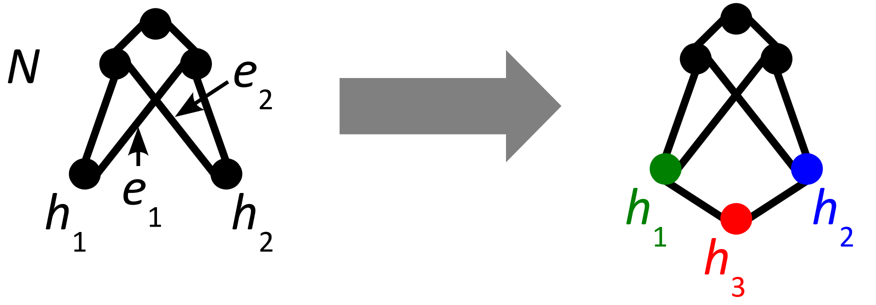
A015475 q-Fibonacci numbers for q=4. +20 1

0, 1, 4, 65, 4164, 1066049, 1091638340, 4471351706689, 73258627454030916, 4801077413298721817665, 1258573637505038759624004676, 1319710110525284599824799048959041 (list; graph; listen)

OFFSET	0,3
FORMULA	a(n) = 4^(n-1) a(n-1) + a(n-2).
CROSSREFS	Sequence in context: A119601 A058438 A041119 this_sequence A025585 A048828

Construction of level-k generators

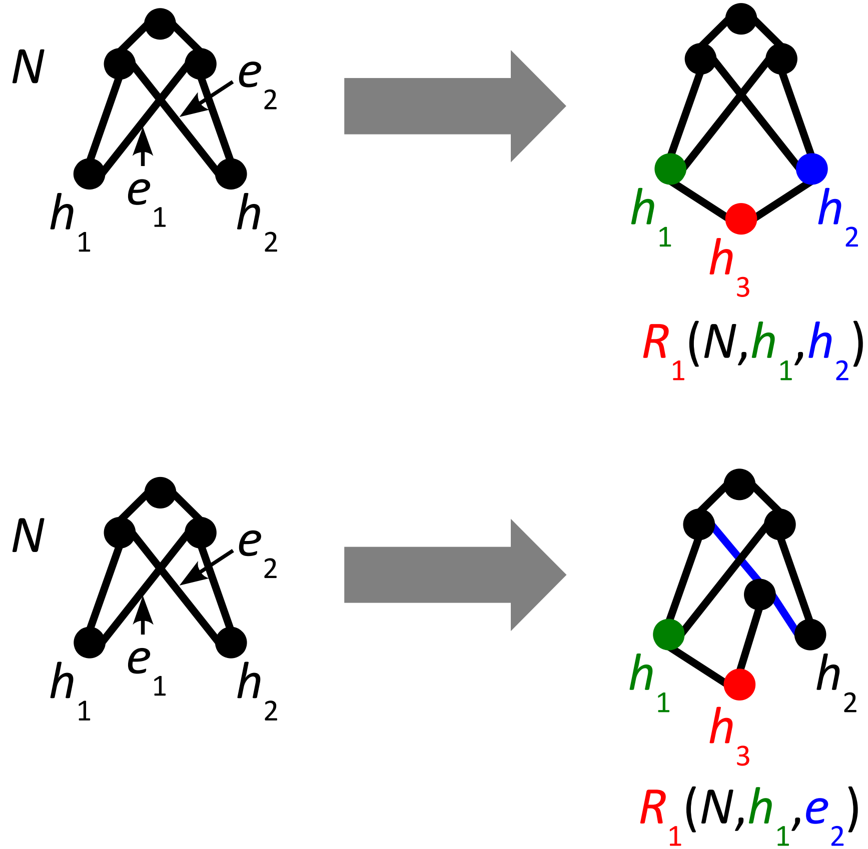
Construction rules of level-(k+1) generators from level-k generators



$R_1(N,h_1,h_2)$

Construction of level-*k* generators

Construction rules of level-(k+1) generators from level-k generators



Construction of level-k generators

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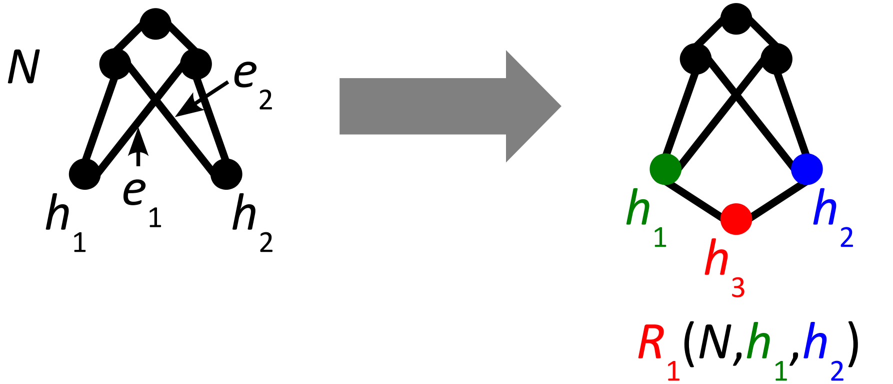
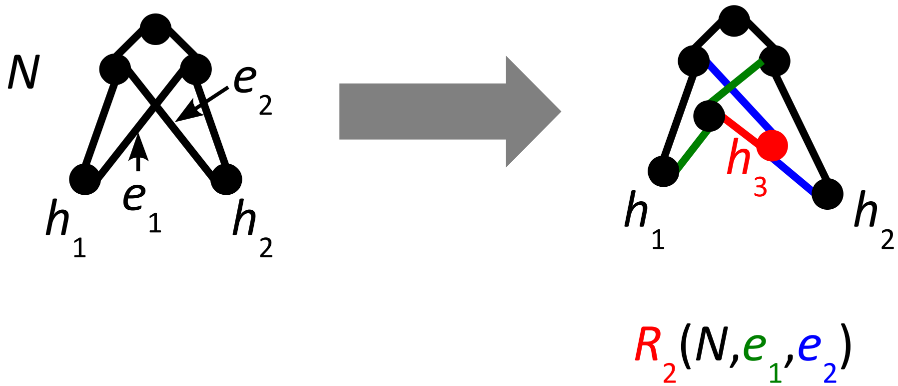




Gambette, Berry & Paul, CPM 2009

Upper bound on the number of level-k generators

R_1 and R_2 can be applied at most on all pairs of sides
A level-k generator has at most $5k$ slides:

$$g_{k+1} < 50\, k^2\, g_k$$

Upper bound:

$$g_k < k!^2\, 50^k$$

Theoretical corollary:
There is a polynomial algorithm to build the set of level-(k+1) generators from the set of level-k generators.
→ polynomial time algorithms to reconstruct level-k networks with fixed k

Kelk, Scornavacca & van Iersel, *TCBB*, 2011

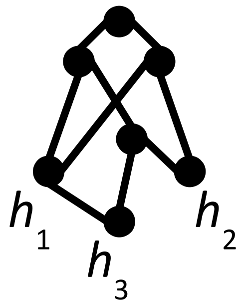
Practical corollary:

$$g_4 < 28350$$

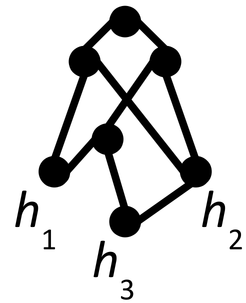
→ it is possible to enumerate all level-4 generators.

Construction of level-*k* generators

Problem:
Some of the level-(k+1) generators obtained from level-k generators are **isomorphic**!



$R_1(N,h_1,e_2)$



$R_1(N,h_2,e_1)$

→ difficult to count

→ possible generation up to level 5 :
1, 4, 65, 1993, 91454

AT&T Integer Sequences RESEARCH

Greetings from The On-Line Encyclopedia of Integer Sequences!

1,4,65,1993 Search Hints

Search: **1, 4, 65, 1993**

I am sorry, but the terms do not match anything in the table.

Gambette, Berry & Paul, CPM 2009
http://www.lirmm.fr/~gambette/ProgGenerators.php

Lower bound on the number of level-k generators

Lower bound:

$$g_k \geq 2^{k-1}$$

There is an **exponential number** of generators!

Idea:
Code every number between 0 and $2^{k-1}-1$ by a level-k generator.

Lower bound on the number of level-*k* generators

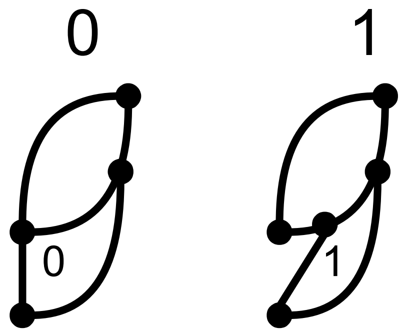
Lower bound:

$$g_k \geq 2^{k-1}$$

There is an **exponential number** of generators!

Idea:
Code every number between 0 and 2^{k-1}-1 by a level-*k* generator.

$k = 1$



Lower bound on the number of level-k generators

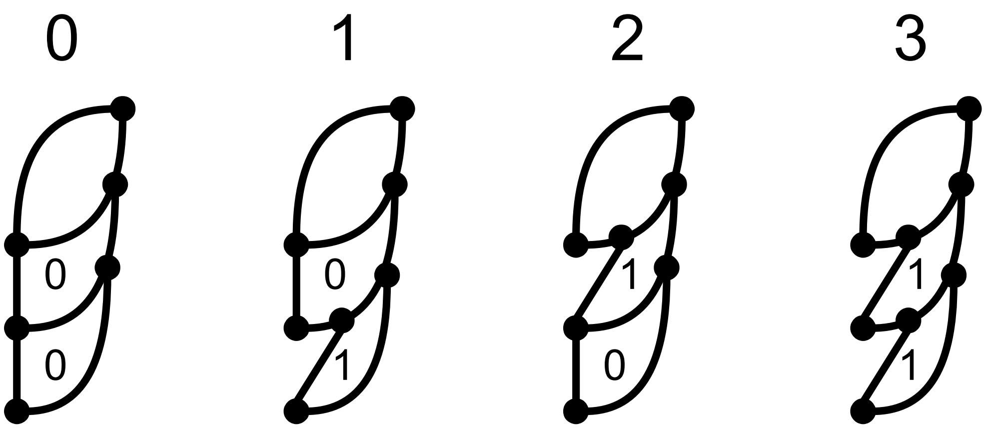
Lower bound:

$$g_k \geq 2^{k-1}$$

There is an **exponential number** of generators!

Idea:
Code every number between 0 and 2^{k-1}-1 by a level-k generator.

$k = 2$



Lower bound on the number of level-*k* generators

Lower bound:

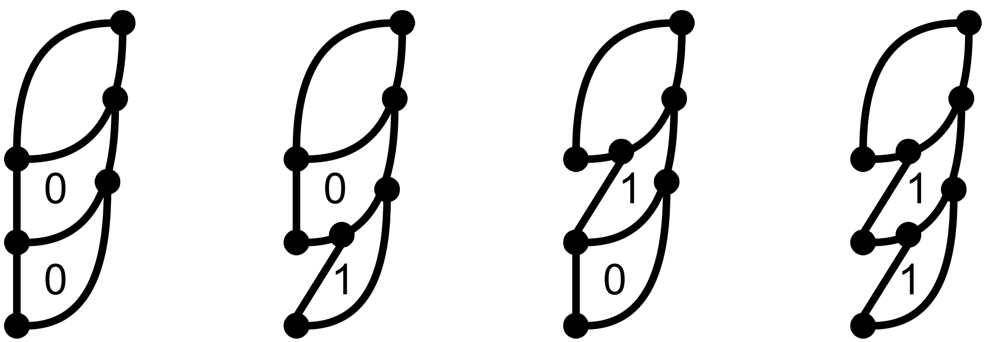
$$g_k \geq 2^{k-1}$$

There is an **exponential number** of generators!

Idea:
Code every number between 0 and 2^{k-1}-1 by a level-*k* generator.

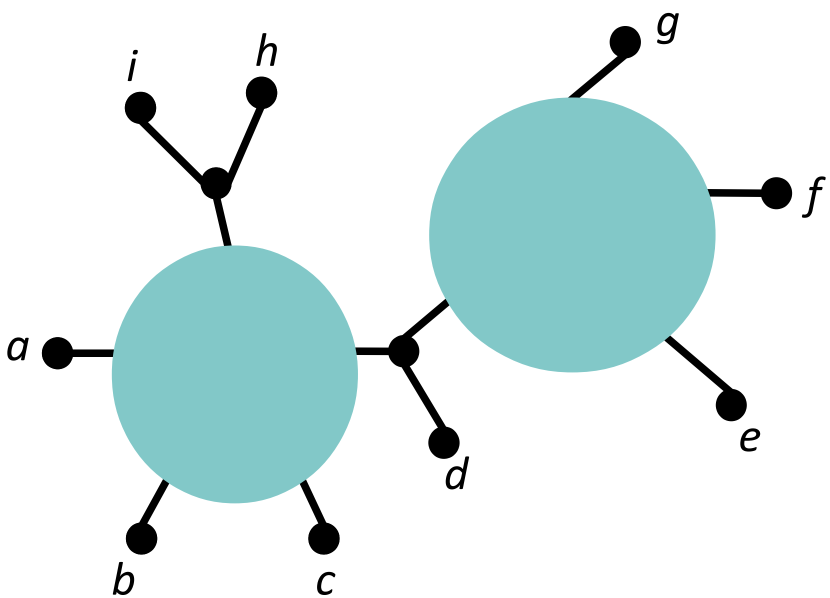
0 1 2 3

k = 2



Practical corollary:
Phylogenetic reconstruction algorithms based on generators are not practical.

Unrooted level-*k* networks

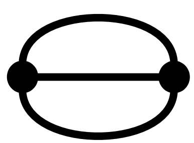


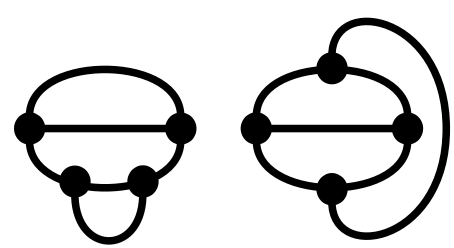
level =
maximum number of edges to remove, by *blob*, to obtain a tree.

unrooted level-*k* network ➡ tree of blobs

➡ tree of **generators** of level ≤*k*

Unrooted level-*k* generators: bridgeless loopless 3-regular multigraphs with 2*k*-2 vertices

level-2 generator 

 level-3 generators

Berry, Bouvel, Gambette & Paul, manuscript, 2011

Plan

- Phylogenetic motivations
- Level-*k* network reconstruction
- Structure of level-*k* networks
- Counting level-1 and 2 networks

Counting labeled level-k networks

Unrooted level-1 networks:
explicit formula for n leaves, c cycles, m edges involved in the cycles.

Semple & Steel, *TCBB*, 2006

Counting labeled unrooted level-1 networks

Unrooted level-1 networks:
explicit formula for n leaves, c cycles, m edges involved in the cycles.

Pointing + bijection:
Bijection between labeled unrooted level-1 networks with $n+1$ leaves and labeled pointed level-1 networks with n leaves.

Semple & Steel, *TCBB*, 2006

Counting labeled unrooted level-1 networks

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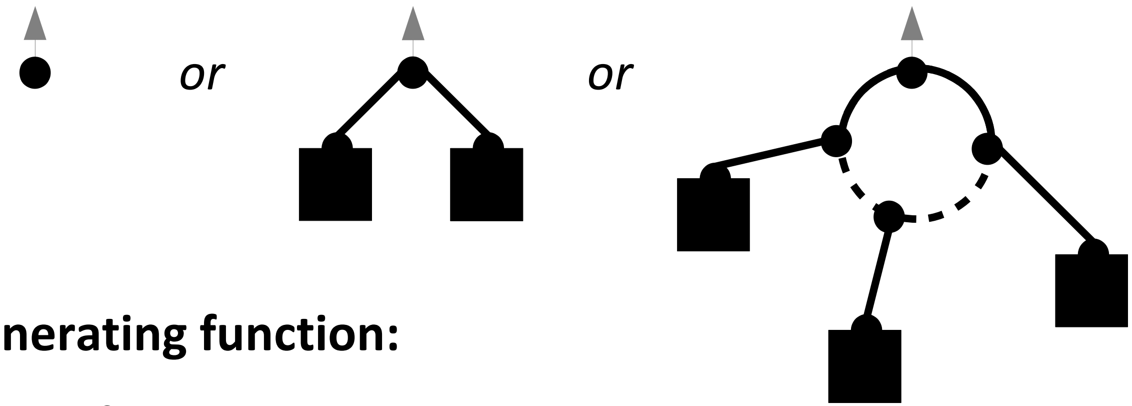
Recursive decomposition of pointed level-1 networks with *n* leaves:



Exponential generating function:

$$G = x + \frac{1}{2}G^2 + \frac{1}{2}\frac{G^2}{(1-G)}$$

Semple & Steel, *TCBB*, 2006

Counting labeled unrooted level-1 networks

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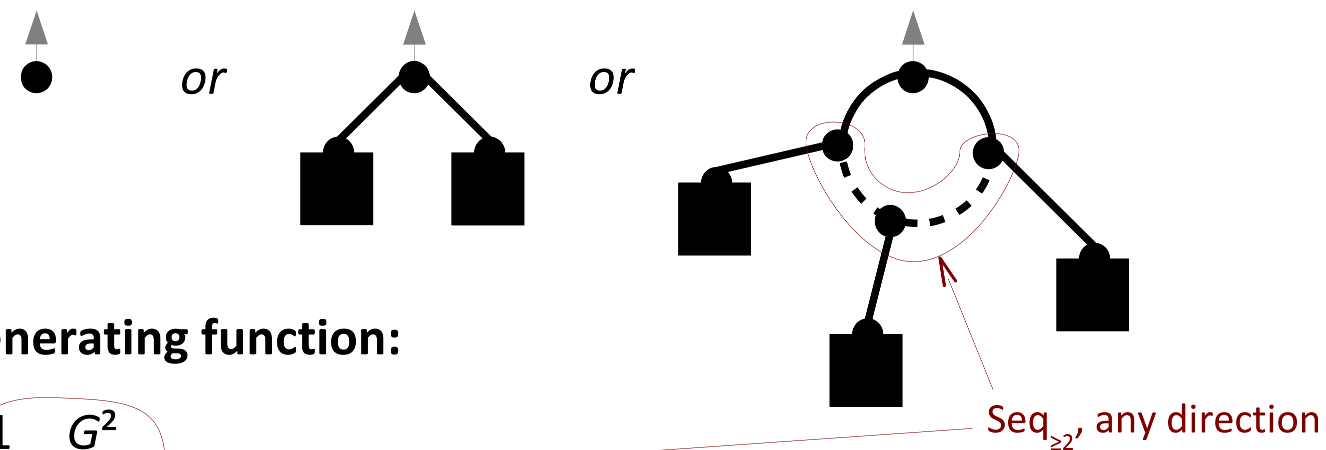

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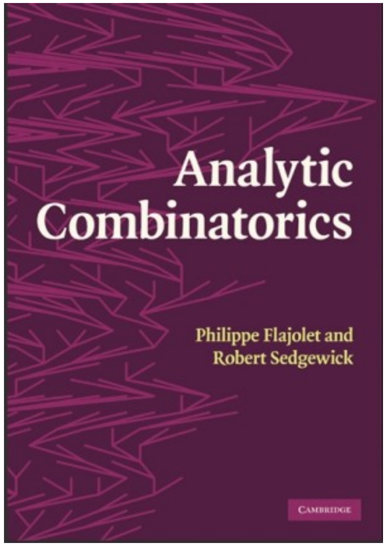
Semple & Steel, *TCBB*, 2006

Counting labeled unrooted level-1 networks

Exponential generating function:

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

Using the Singular Inversion Theorem (Theorem VI.6 of 

):

$g_n \approx 0.2074\ (1.8904)^n\ n^{n-1}$

Maplesoft sage

Berry, Bouvel, Gambette & Paul, manuscript, 2012

Counting labeled unrooted level-1 networks

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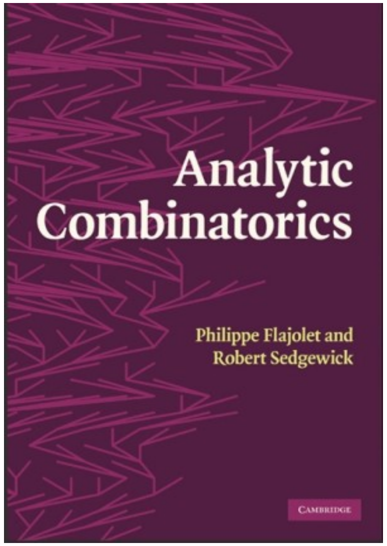
Using the Singular Inversion Theorem (Theorem VI.6 of 

):

$$g_n \approx 0.2074\,(1.8904)^n\, n^{n-1}$$

Proof :
We write $G = z\,\varphi(G)$, with $\varphi(z) = \dfrac{1}{1 - ½\, z\,(1+1/(1-z))}$

Then $g_n \approx n! \sqrt{\dfrac{\varphi(\tau)}{2\varphi''(\tau)}}\, \dfrac{\rho^{-n}}{\sqrt{\pi\, n^3}}$, with $\rho = \tau / \varphi(\tau)$
and τ is the solution of $\varphi(z)\text{-}z\varphi'(z)\text{=}0$

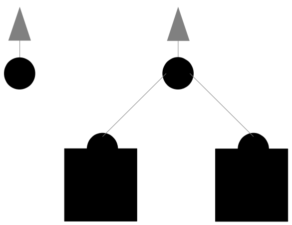
Maplesoft sage

Berry, Bouvel, Gambette & Paul, manuscript, 2012

Counting labeled unrooted level-2 networks

Recursive decomposition of pointed level-2 networks with *n* leaves:

z $\qquad \frac{1}{2} R^2 \qquad \frac{1}{2}\frac{R^2}{1-R}$ $\qquad$ *or...*



Seq$_{\geq 1}$, any direction
Seq$_{\geq 2}$, any direction

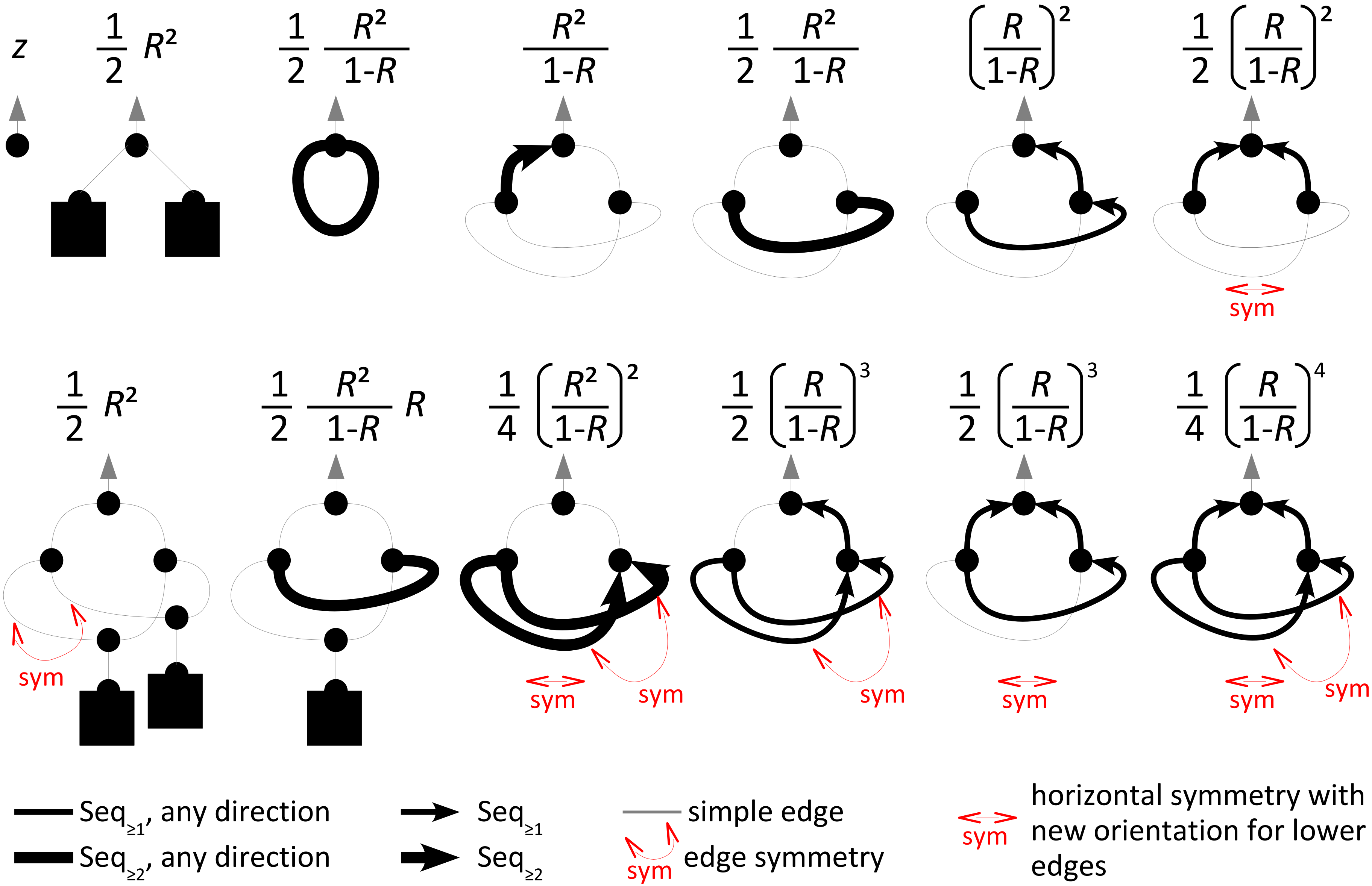
Seq$_{\geq 1}$
Seq$_{\geq 2}$

simple edge
sym edge symmetry

sym horizontal symmetry with new orientation for lower edges

Counting labeled unrooted level-2 networks

Recursive decomposition of pointed level-2 networks with *n* leaves:



Counting labeled unrooted level-2 networks

Recursive decomposition of pointed level-2 networks with *n* leaves:

$$R = z + \frac{R^2}{2} + \frac{R^2}{2(1-R)} + \frac{R^2}{1-R} + \frac{R^2}{2(1-R)} + \frac{R^2}{(1-R)^2} + \frac{R^2}{2(1-R)^2} + \frac{R^2}{2} + \frac{R^3}{2(1-R)} + \frac{R^4}{4(1-R)^2} + \frac{R^3}{2(1-R)^3} + \frac{R^3}{2(1-R)^3} + \frac{R^4}{4(1-R)^4}$$

Rewrite:

$$R = z\phi(R) \text{ where } \phi(R) = \frac{1}{1 - \frac{3r^5 - 20r^4 + 46r^3 - 46r^2 + 18r}{4(r-1)^4}}$$

Berry, Bouvel, Gambette & Paul, manuscript, 2011

Counting labeled unrooted level-2 networks

Recursive decomposition of pointed level-2 networks with *n* leaves:

$$R = z + \frac{R^2}{2} + \frac{R^2}{2(1-R)} + \frac{R^2}{1-R} + \frac{R^2}{2(1-R)} + \frac{R^2}{(1-R)^2} + \frac{R^2}{2(1-R)^2} + \frac{R^2}{2} + \frac{R^3}{2(1-R)} + \frac{R^4}{4(1-R)^2} + \frac{R^3}{2(1-R)^3} + \frac{R^3}{2(1-R)^3} + \frac{R^4}{4(1-R)^4}$$

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Lagrange inversion:

$$r(n) = n![z^n]R(z) = \frac{n!}{n}[\lambda^{n-1}]\phi^n(\lambda),$$

Taylor expansions of $\varphi_n(\lambda)$:

number of leaves	2	3	4	5	6	7
unrooted level-2	-	9	282	14 697	1 071 750	100 467 405

Berry, Bouvel, Gambette & Paul, manuscript, 2011

Counting labeled unrooted level-2 networks

Recursive decomposition of pointed level-2 networks with *n* leaves:

$$R = z + \frac{R^2}{2} + \frac{R^2}{2(1-R)} + \frac{R^2}{1-R} + \frac{R^2}{2(1-R)} + \frac{R^2}{(1-R)^2} + \frac{R^2}{2(1-R)^2} + \frac{R^2}{2} + \frac{R^3}{2(1-R)} + \frac{R^4}{4(1-R)^2} + \frac{R^3}{2(1-R)^3} + \frac{R^3}{2(1-R)^3} + \frac{R^4}{4(1-R)^4}$$

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Lagrange inversion:

$$r(n) = n![z^n]R(z) = \frac{n!}{n}[\lambda^{n-1}]\phi^n(\lambda),$$

Taylor expansions + Newton formula:

$$r(n) = (n-1)! \sum_{\substack{0\le s\le q\le p\le k\le i\le n-1 \\ j=n-1-i-k-p-q-s\ge 0 \\ i\neq 0}} \binom{n+i-1}{i}\binom{4i+j-1}{j}\binom{i}{k}\binom{k}{p}\binom{p}{q}\binom{q}{s} \times \left(\frac{-3}{20}\right)^s \left(\frac{9}{2}\right)^i \left(\frac{-23}{9}\right)^k (-1)^p \left(\frac{-10}{23}\right)^q.$$

Berry, Bouvel, Gambette & Paul, manuscript, 2011

Counting labeled level-k networks

Unrooted level-1 networks:
explicit formula for n leaves, c cycles, m edges involved in the cycles

Semple & Steel, *TCBB*, 2006

+ asymptotic evaluation for n leaves: $\approx 0.207 \dfrac{n^{n-1}}{1.890^n}$

Rooted level-1 networks :
Explicit formula for n leaves, c cycles, m edges across cycles
+ asymptotic evaluation for n leaves: $\approx 0.134\ 2.943^n\ n^{n-1}$

Unrooted level-2 networks :
Explicit formula for n leaves : $$(n-1)! \sum_{\substack{0\leq s\leq q\leq p\leq k\leq i\leq n-1\\ j=n-1-i-k-p-q-s\geq 0\\ i\neq 0}} \binom{n+i-1}{i}\binom{4i+j-1}{j}\binom{i}{k}\binom{k}{p}\binom{p}{q}\binom{q}{s}\left(\frac{-3}{20}\right)^s\left(\frac{9}{2}\right)^i\left(\frac{-23}{9}\right)^k(-1)^p\left(\frac{-10}{23}\right)^q$$

number of leaves	2	3	4	5	6	7
unrooted level-1	-	2	15	192	3 450	79 740
rooted level-1	3	36	723	20 280	730 755	32 171 580
unrooted level-2	-	9	282	14 697	1 071 750	100 467 405

Berry, Bouvel, Gambette & Paul, manuscript, 2011

Thank you for your attention!

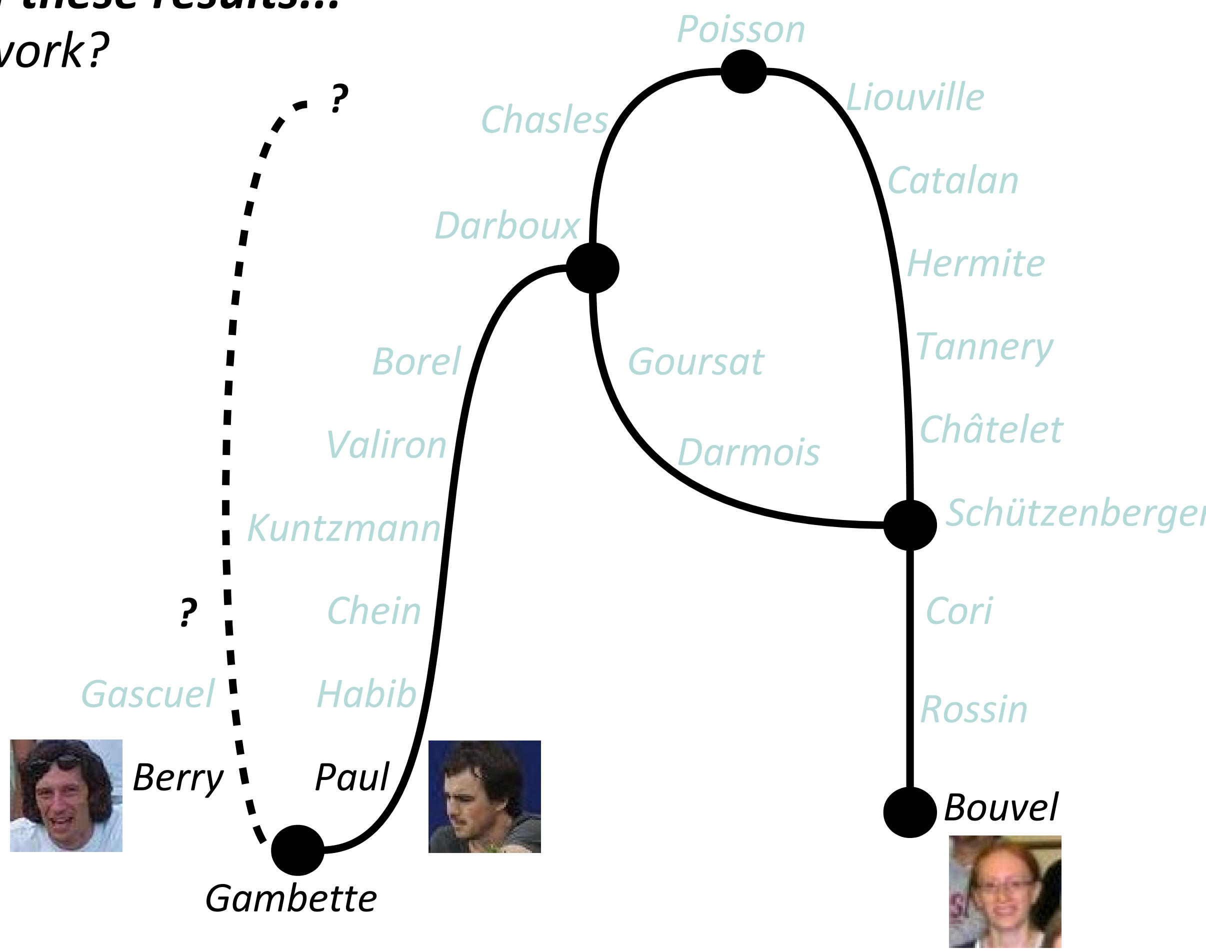
Co-authors of these results

Vincent Berry & Christophe Paul (LIRMM, Montpellier)
Mathilde Bouvel (LABRI, Bordeaux)

Thanks to the LABRI for their *Junior Guest* grant in April 2011!

Thank you for your attention!

Co-authors of these results...
A level-2 network?

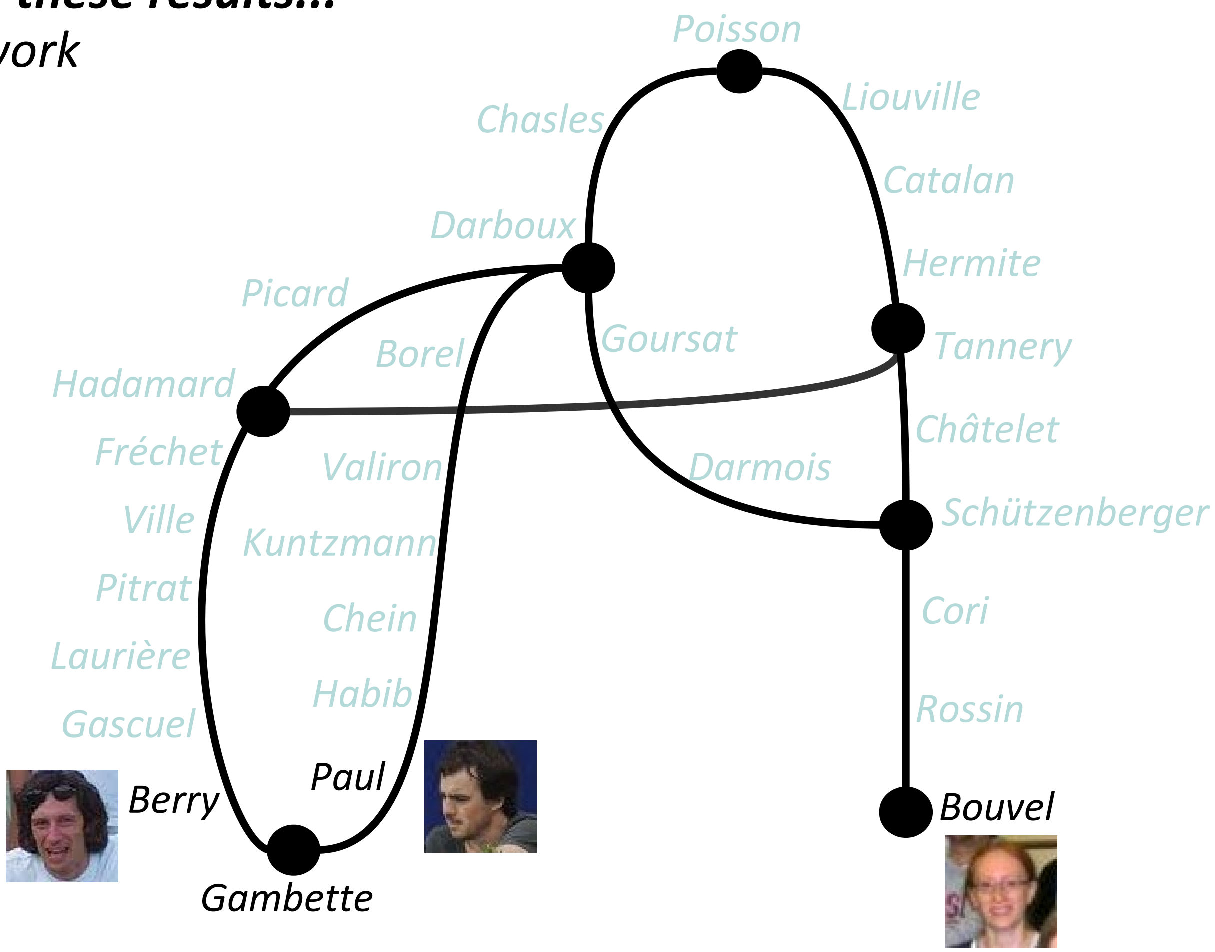


The Mathematics Genealogy

Thank you for your attention!

Co-authors of these results...

A level-3 network



The Mathematics Genealogy