

ANR-FWF-MOST meeting  
2018-10-30 - Wien

# *Phylogenetic networks: overview, subclasses and counting problems*

Philippe Gambette



# Outline

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- An introduction to phylogenetic networks
- Classes of phylogenetic networks
- Counting problems on phylogenetic networks

# Outline

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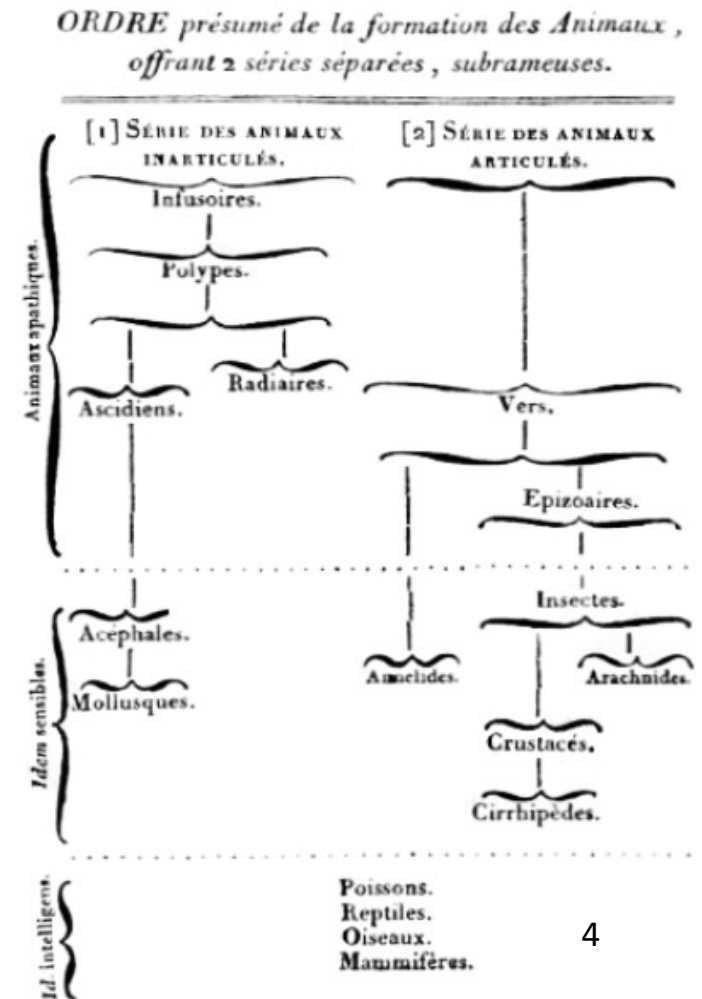
- An introduction to phylogenetic networks
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- Counting problems on phylogenetic networks

# Phylogenetic trees

Phylogenetic tree of a set of species:

- Classify them depending on common characters
- Describe their evolution

classification



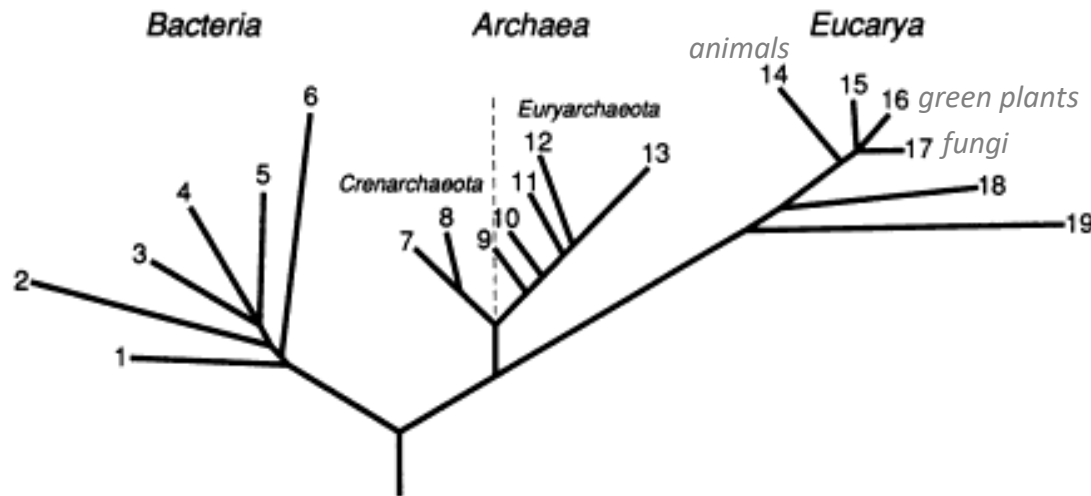
*Lamarck : Histoire naturelle des  
animaux sans vertèbres (1815)*

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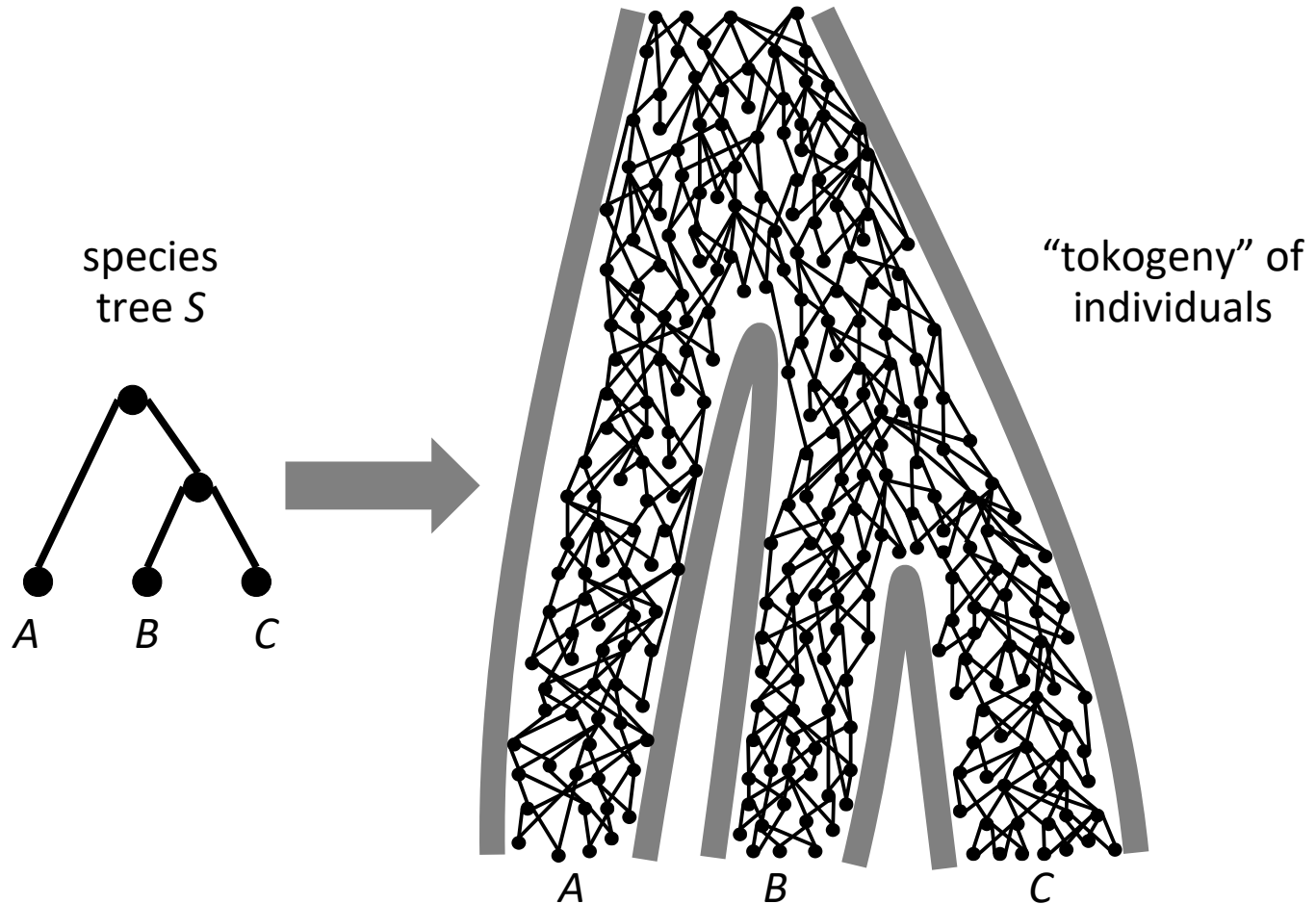
modelization



*Woese, Kandler, Wheelis : Towards a natural system of organisms: proposal for the domains Archaea, Bacteria, and Eucarya, Proceedings of the National Academy of Sciences, 87(12), 4576–4579 (1990)*

# Phylogenetic trees... and networks

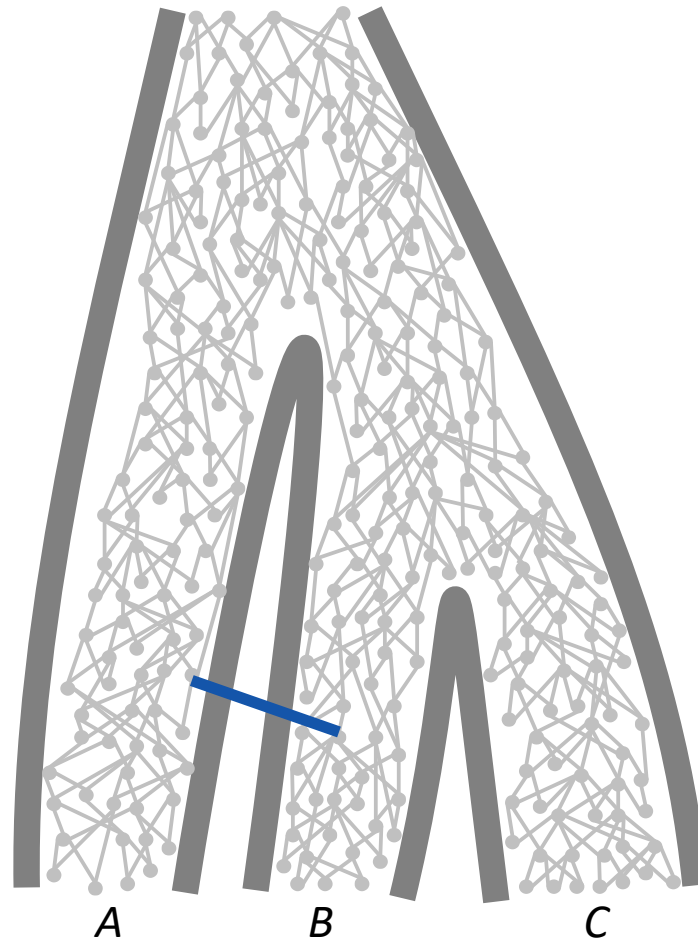
Phylogenetic tree of a set of species



# Genetic material transfers

**Transfers** of genetic material between coexisting species:

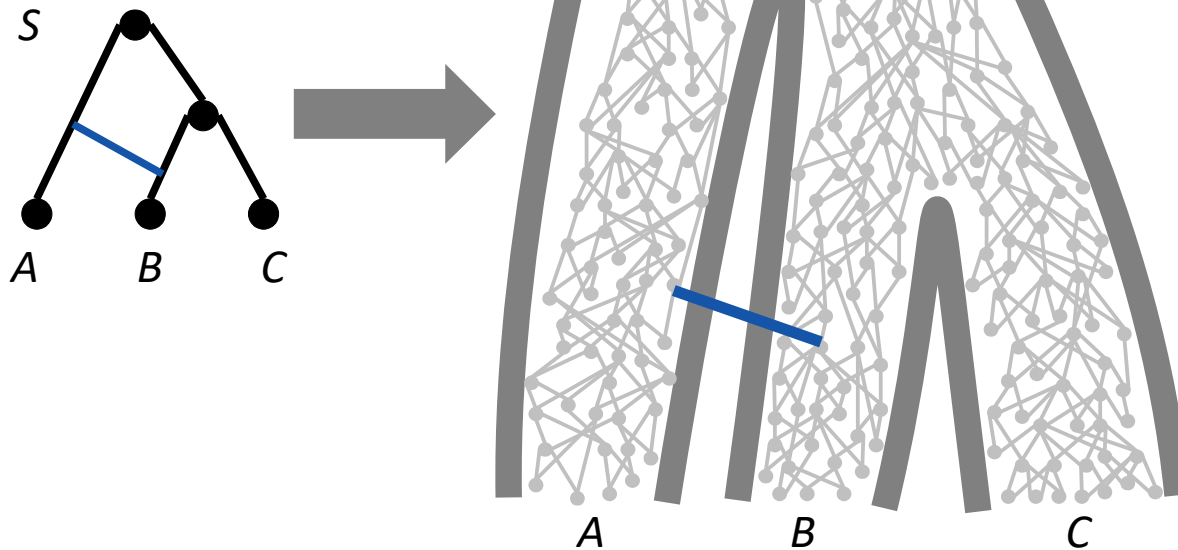
- lateral gene transfer
- hybridization
- recombination



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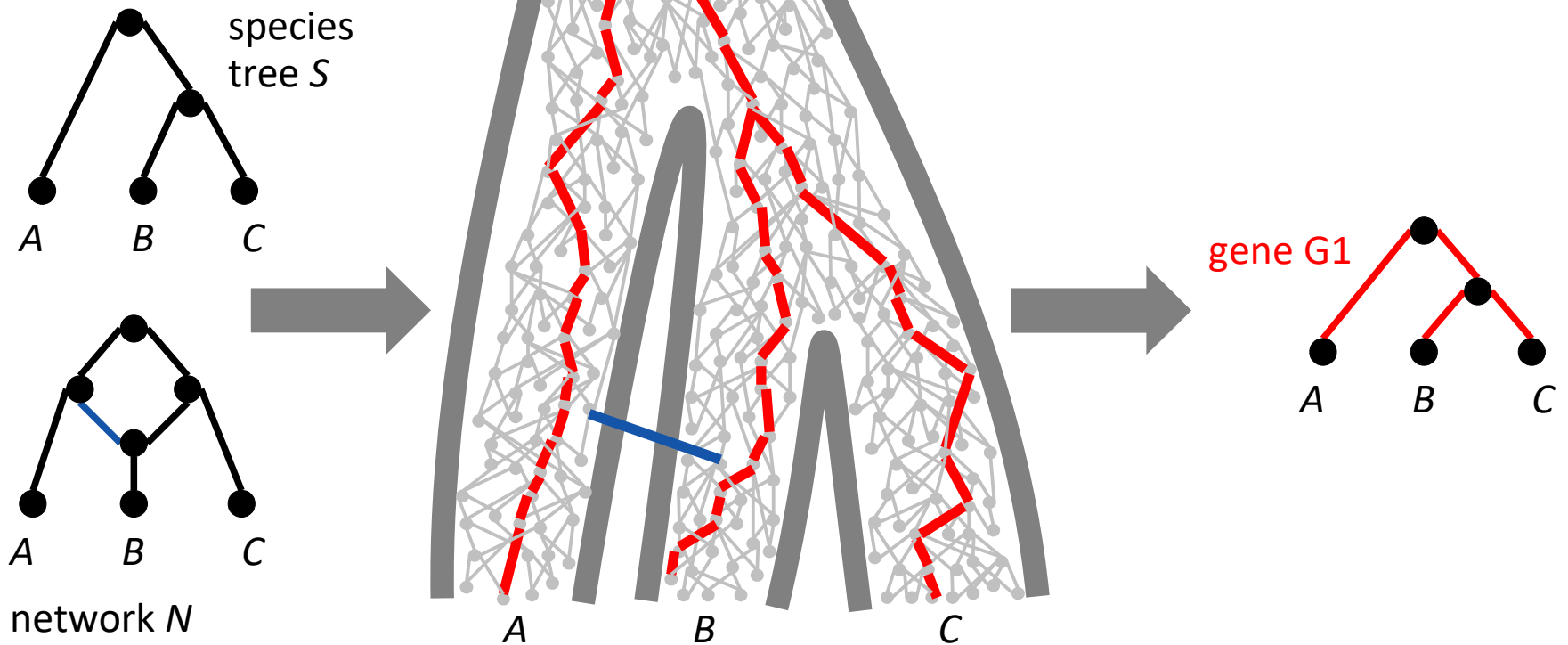




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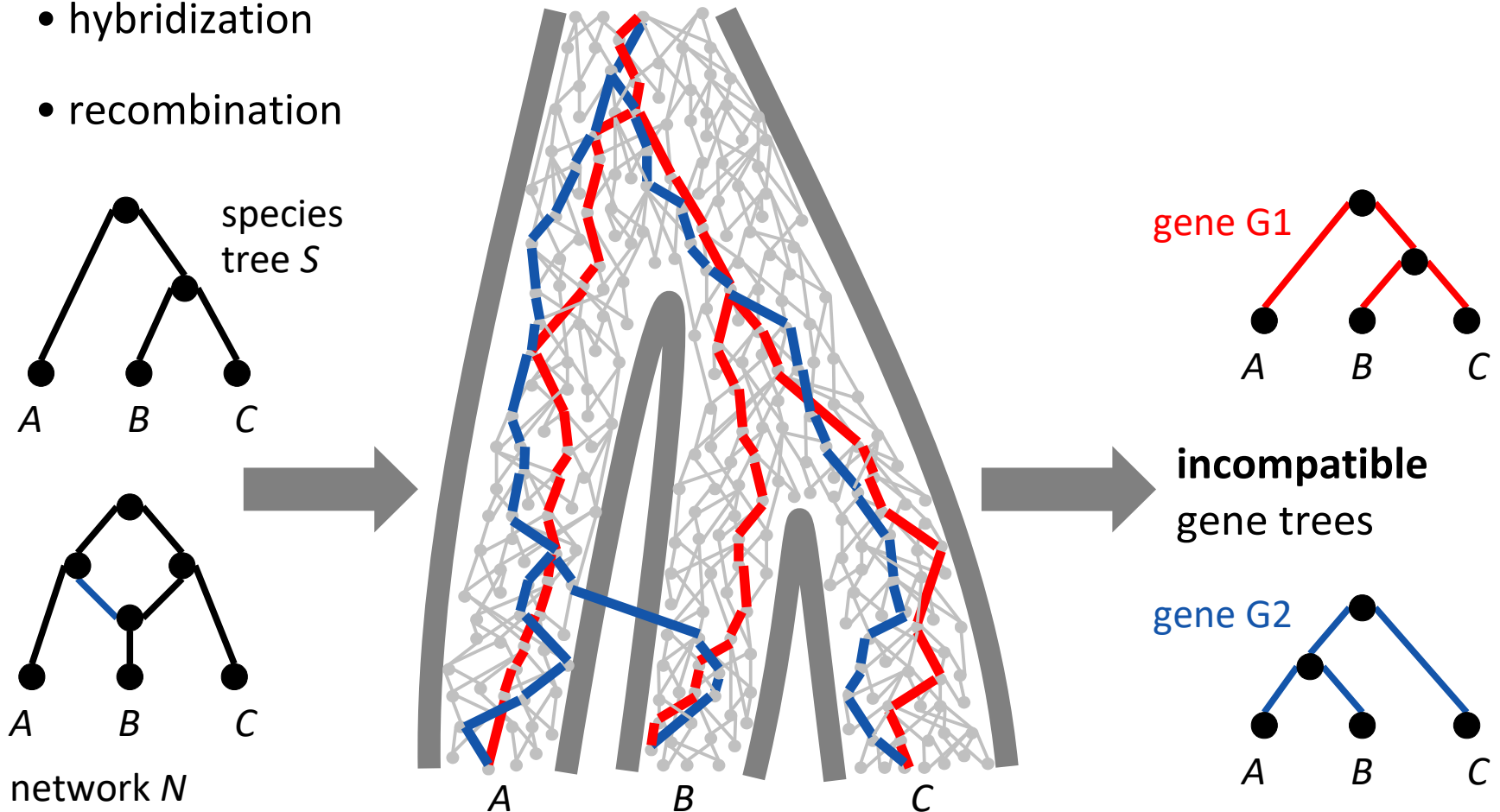
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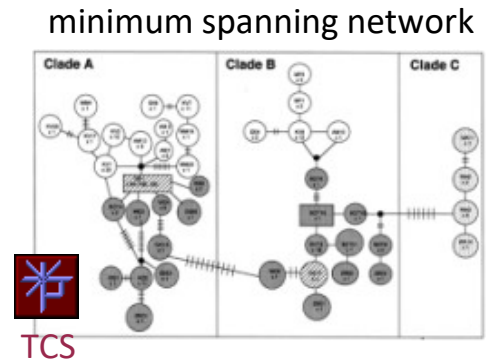
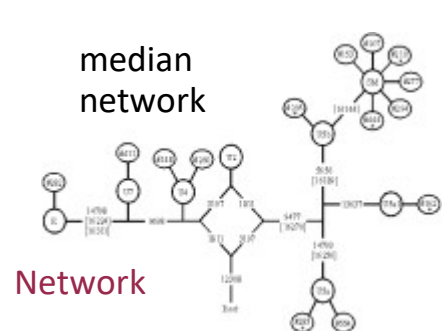
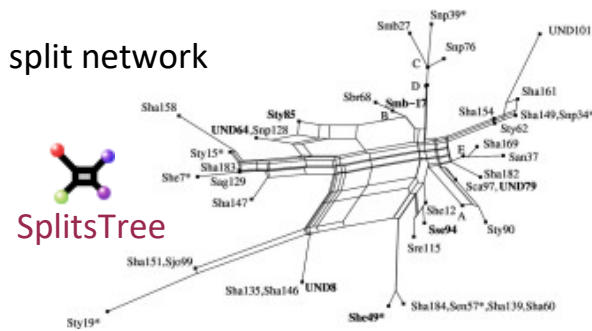
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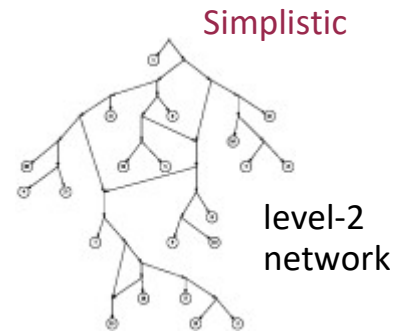
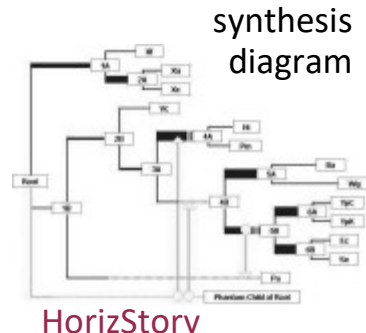
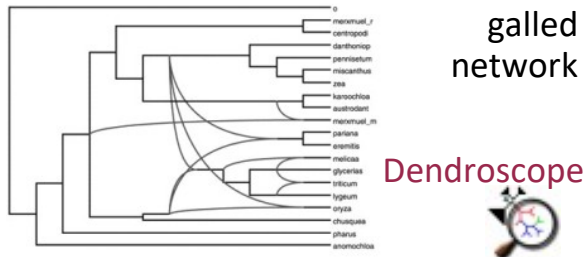
# Phylogenetic networks

Phylogenetic network: network representing evolution data

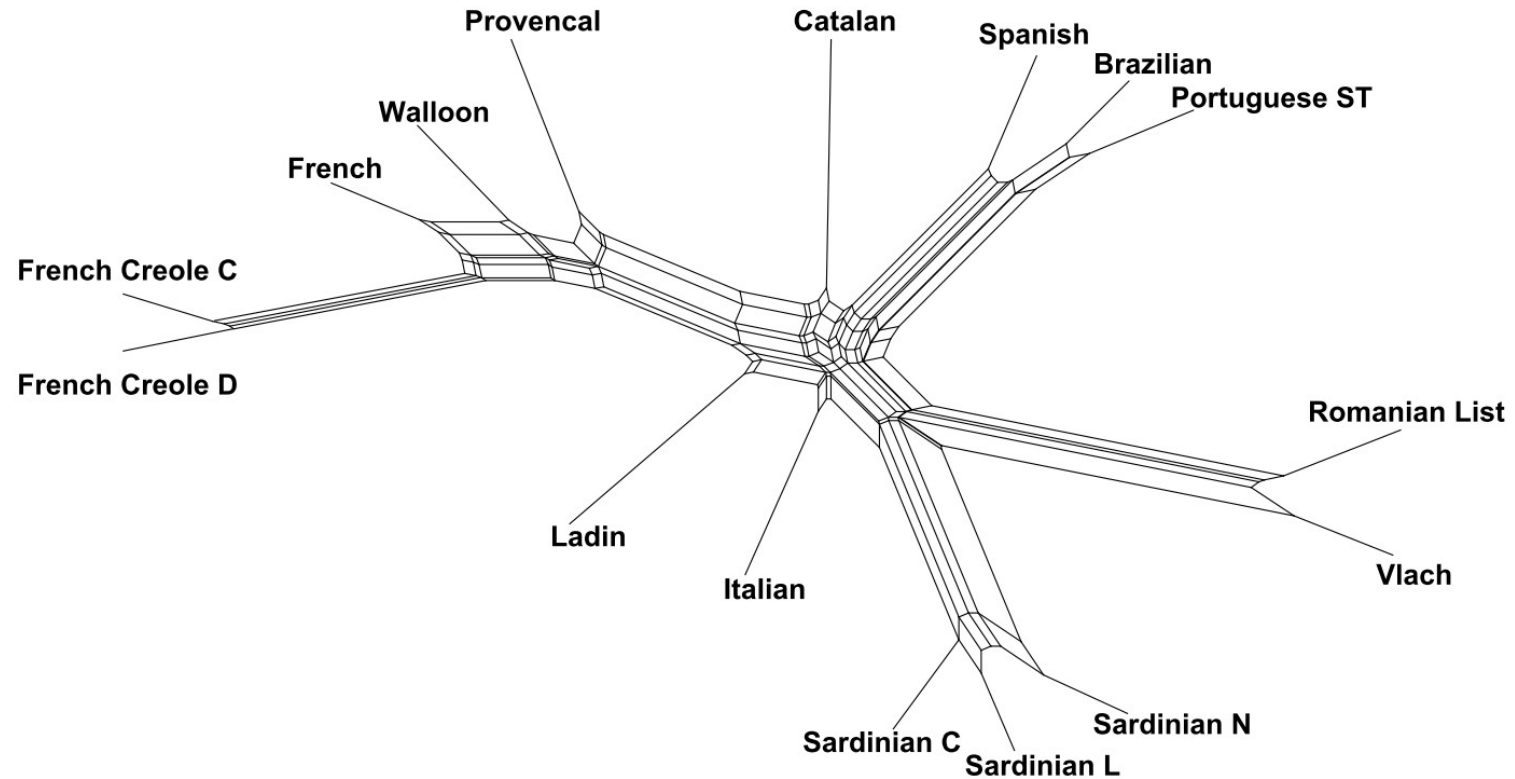
- **abstract / implicit / data-display** phylogenetic networks: to **classify, visualize data**



- **explicit** phylogenetic networks: to **model evolution**

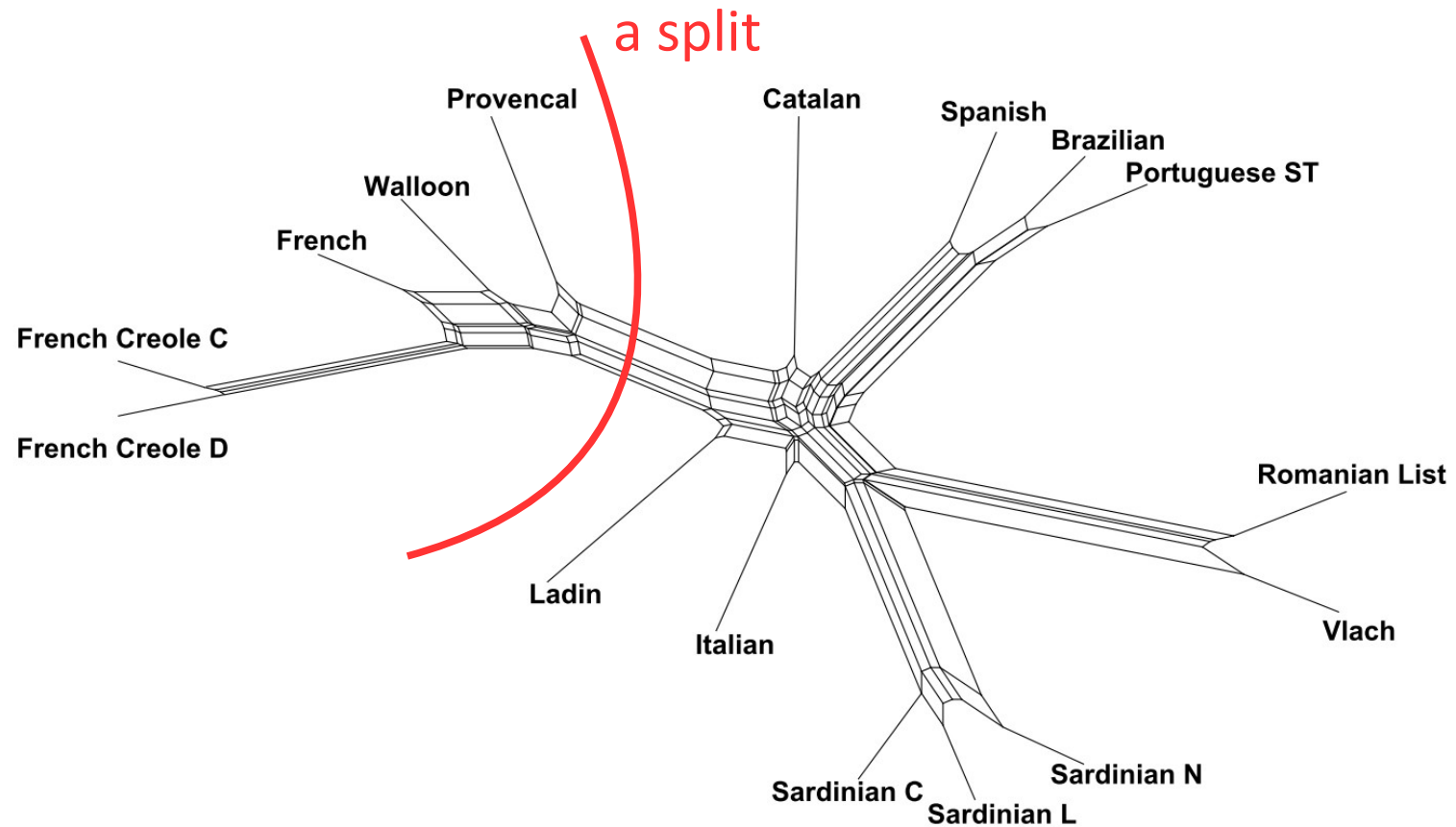


# Abstract phylogenetic networks: split networks



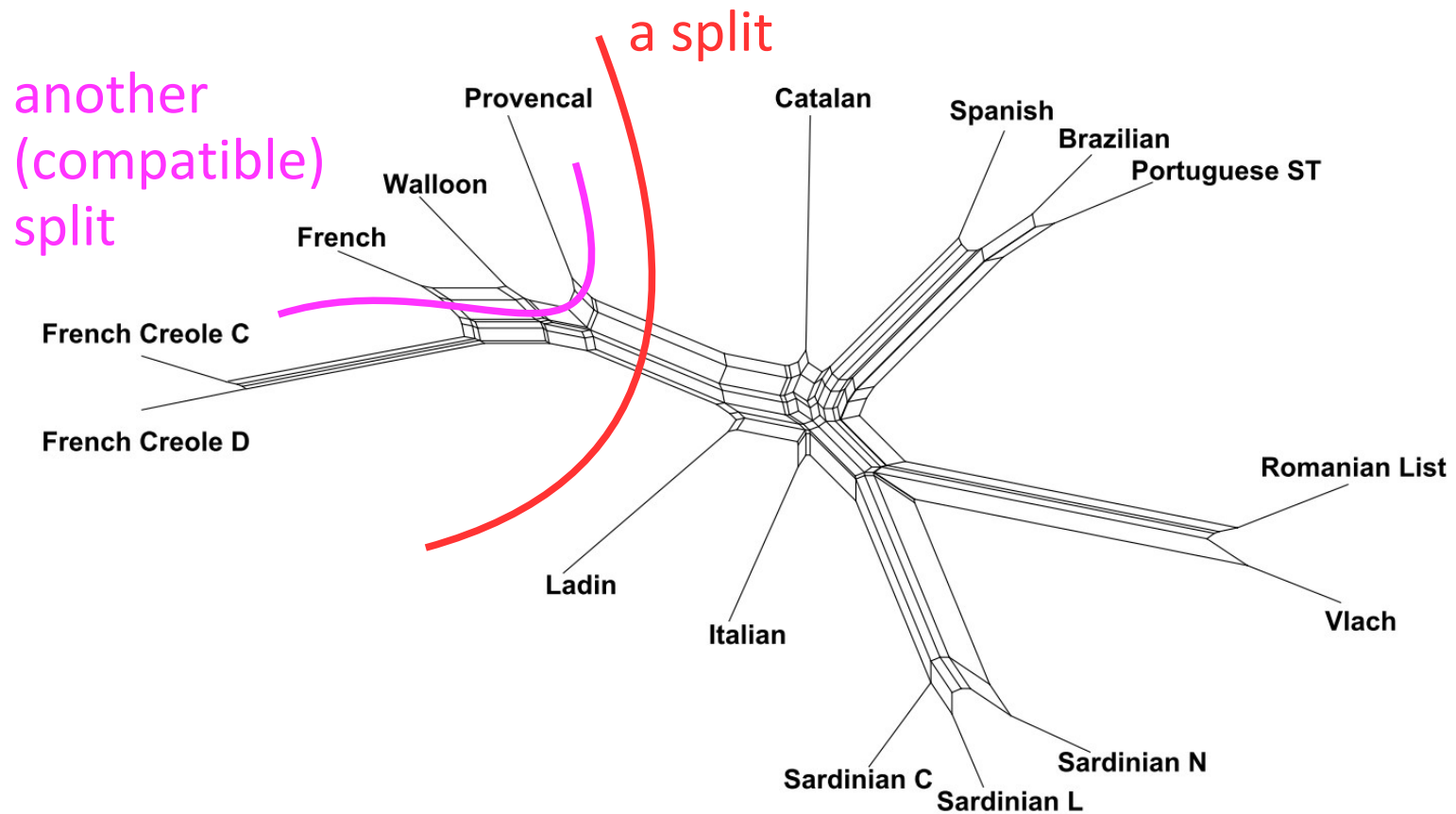
*Willems, M., Lord, E., Laforest, L., Labelle, G., Lapointe, F.-J., Di Sciullo, A. M. & Makarek, V. (2016). Using hybridization networks to retrace the evolution of indo-european languages. BMC Evolutionary Biology, 16(1), 180.*

# Abstract phylogenetic networks: split networks



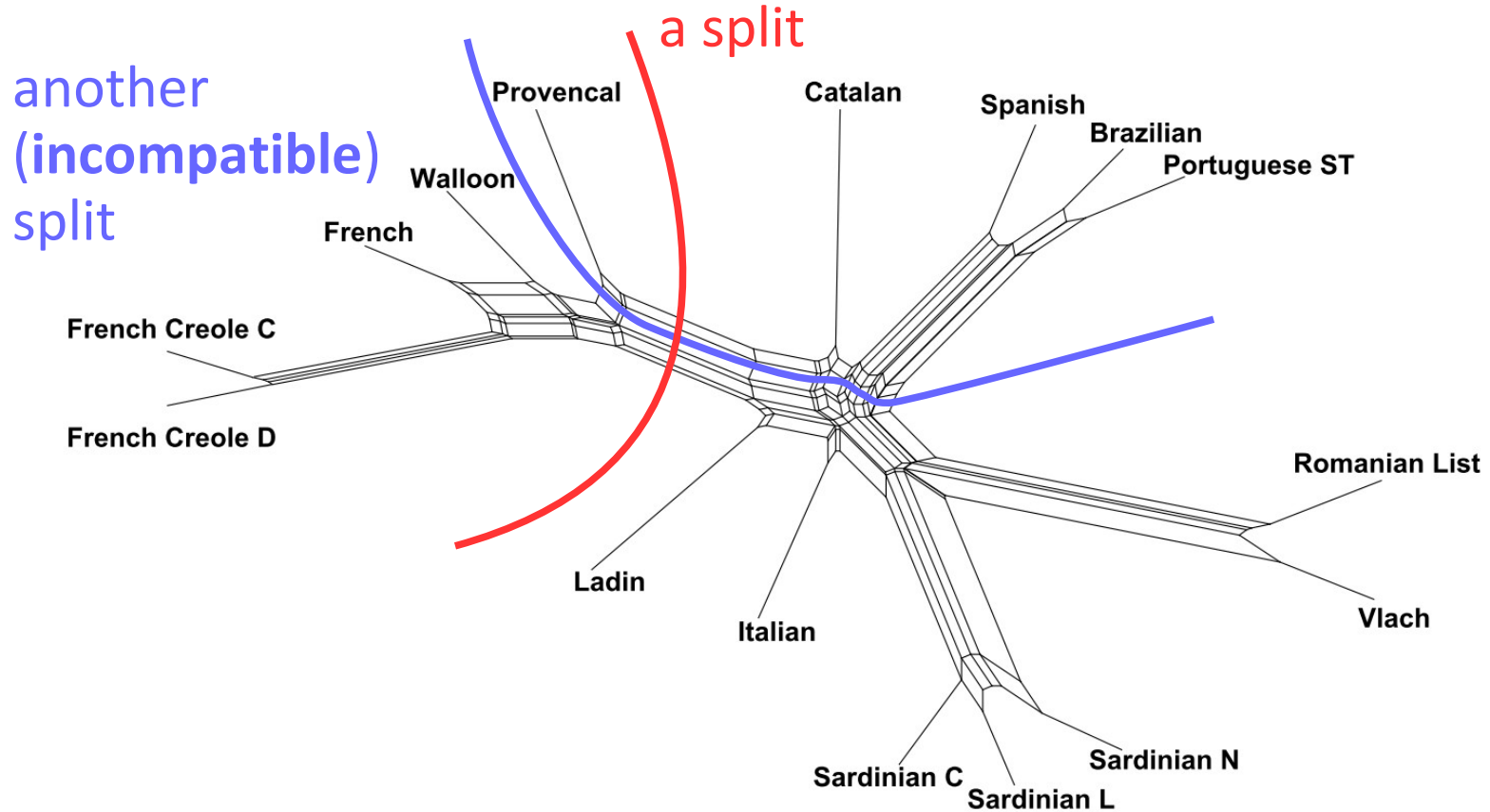
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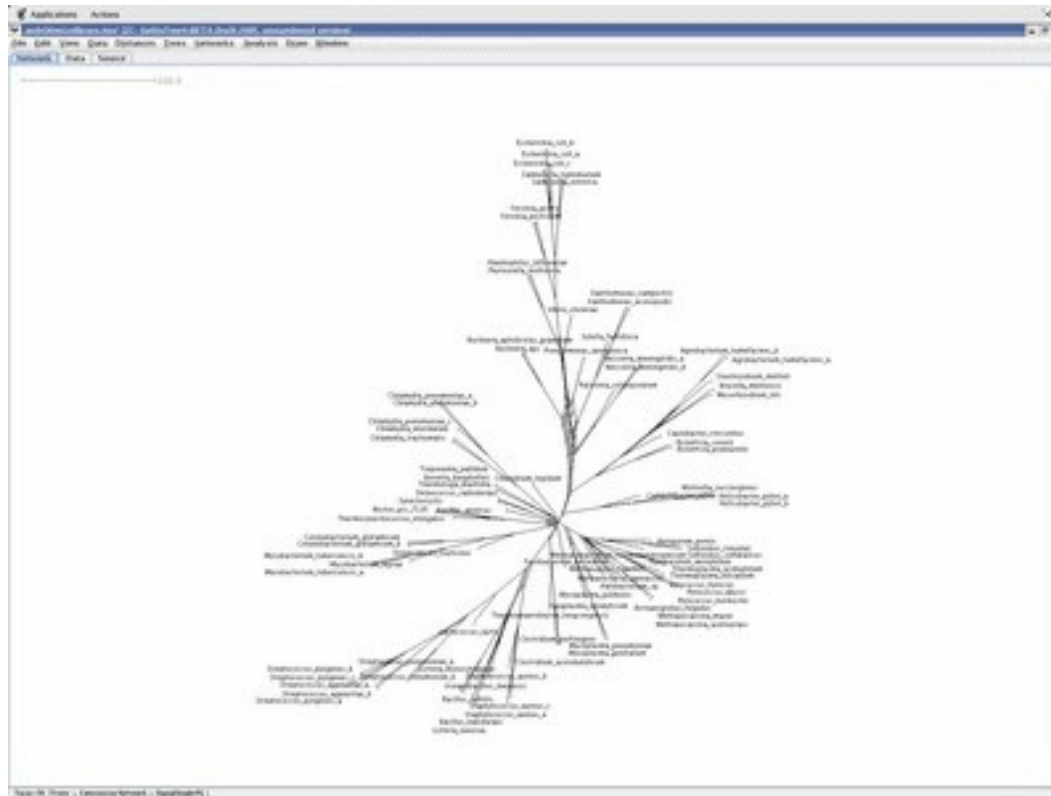


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# Abstract phylogenetic networks: split networks

The “boxes” in split networks: incompatible splits

→ open them as much as possible in SplitsTree!

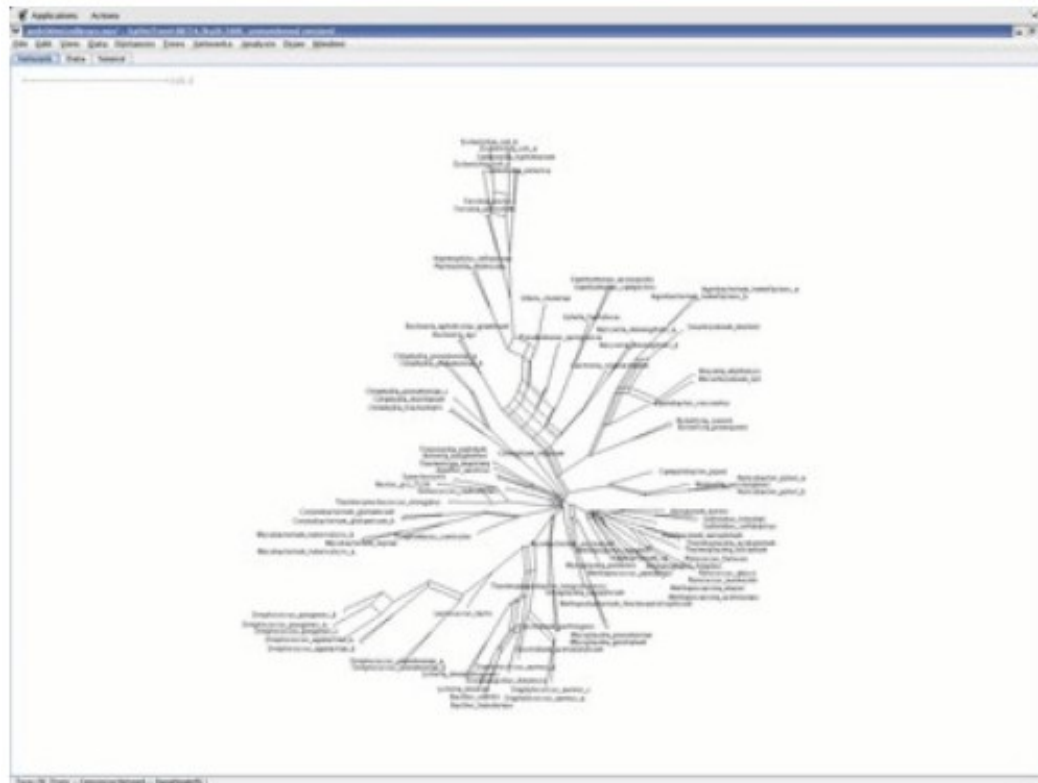




# Abstract phylogenetic networks: split networks

The “boxes” in split networks: incompatible splits

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*Philippe Gambette & Daniel H. Huson, Improved Layout of Phylogenetic Networks, IEEE/ACM TCBB 5(3), p. 472-479*

# Who is who in Phylogenetic Networks?

## Who is Who in Phylogenetic Networks

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### FIND EXPERTS

Find researchers working on a specific topic, in a given country, and find where (journals, conferences) the community publishes or meets.

### EXPLORE RESEARCH

Browse publications, access keyword definitions and find trends in publications on phylogenetic network methods and methodologies.

### DISCOVER SOFTWARE

Locate programs to compute, evaluate, compare or visualize phylogenetic networks, and view how these are linked with each other and input data.

### FOLLOW COMMUNITY

Follow an author, publications tagged with a keyword, or the entire database using the 📡 icon in the menu, on an author's page, or on a keyword's page.

Based on BibAdmin by Sergiu Chelcea  
+ tag clouds, date histograms, journal lists,  
keyword definitions, co-author graphs  
(work of Tushar Agarwal)

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

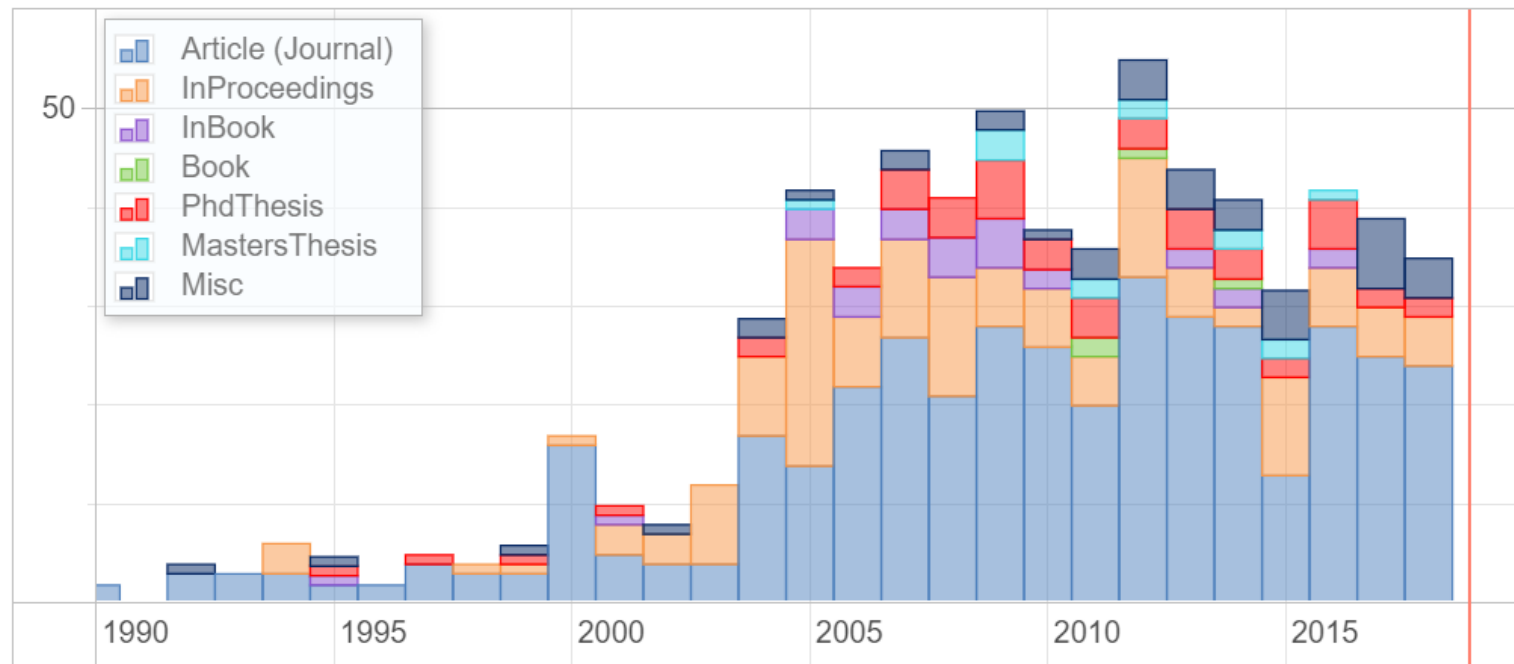
# Who is who in Phylogenetic Networks?

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# Who is who in Phylogenetic Networks?

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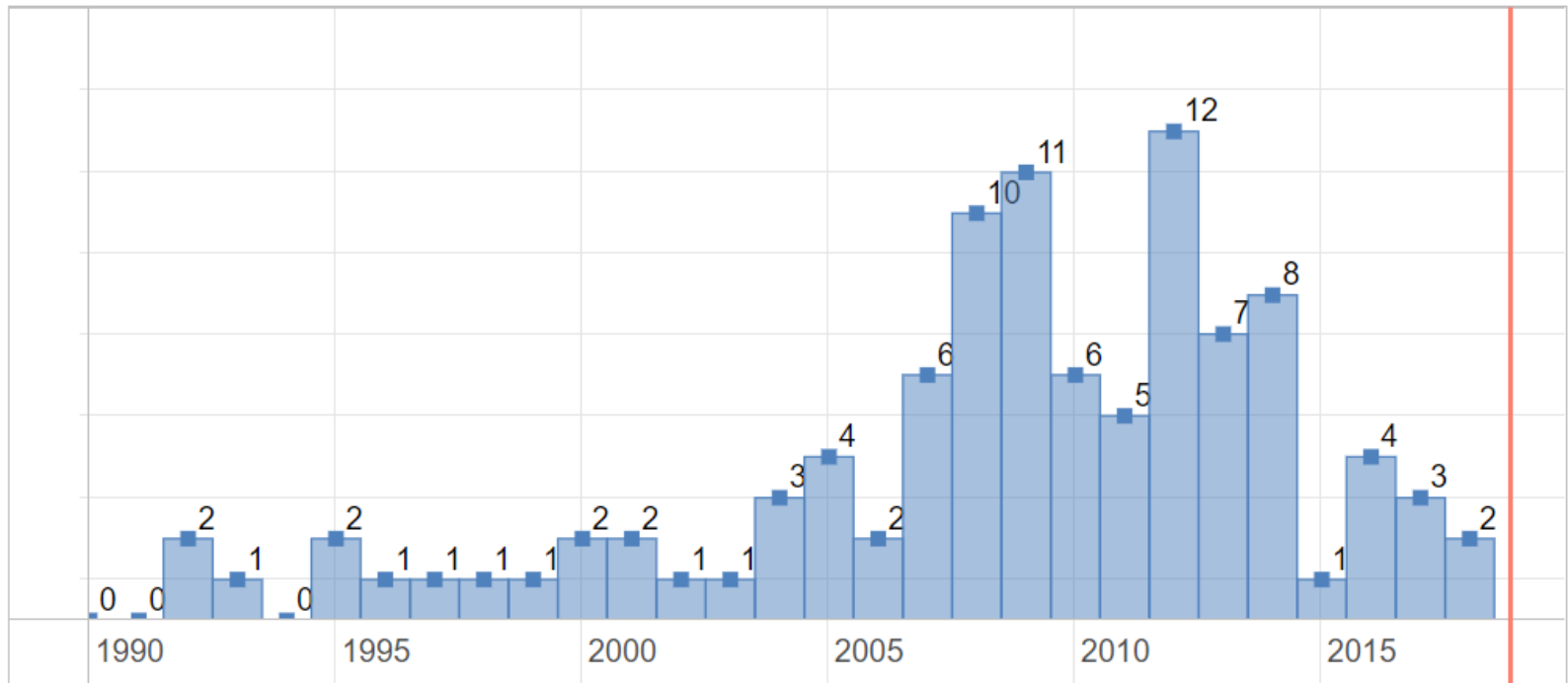
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Browse publications by keyword:

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abstract network

Go

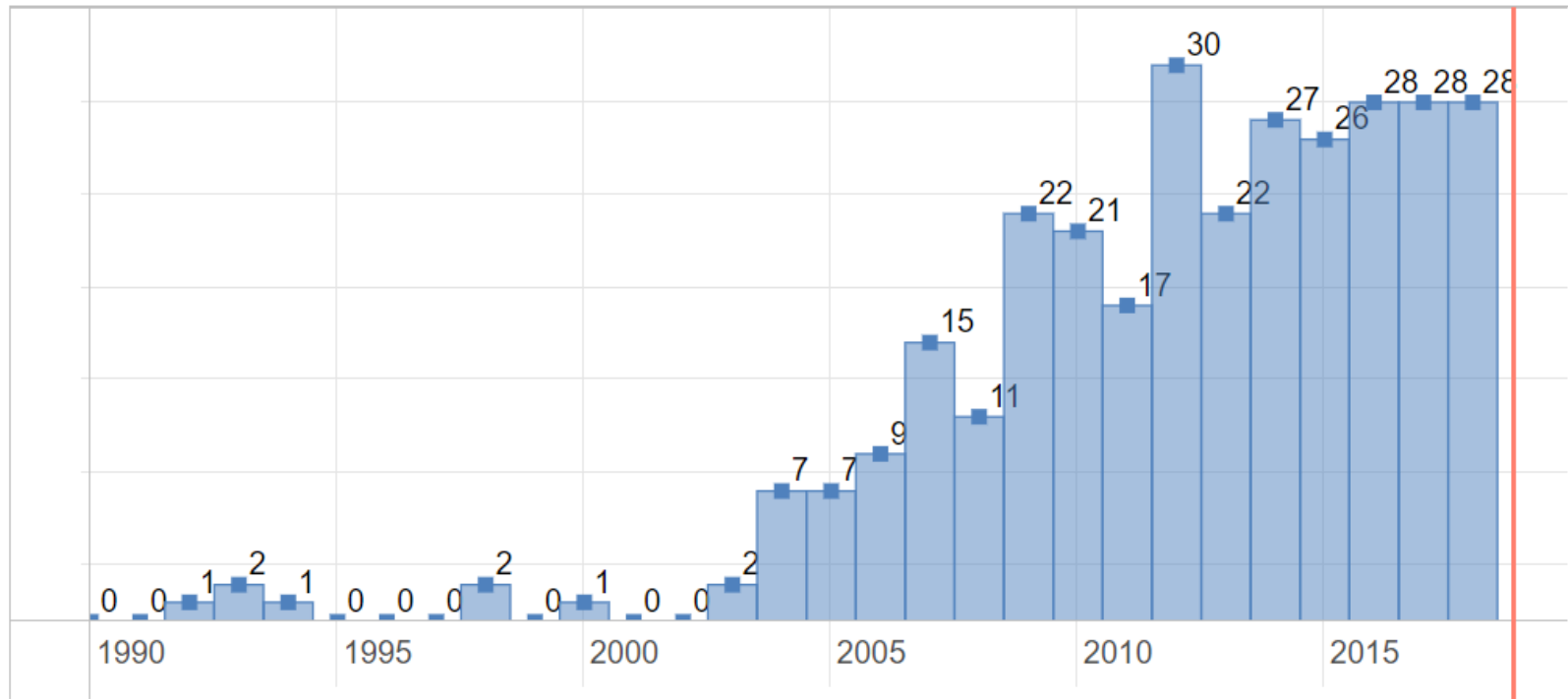


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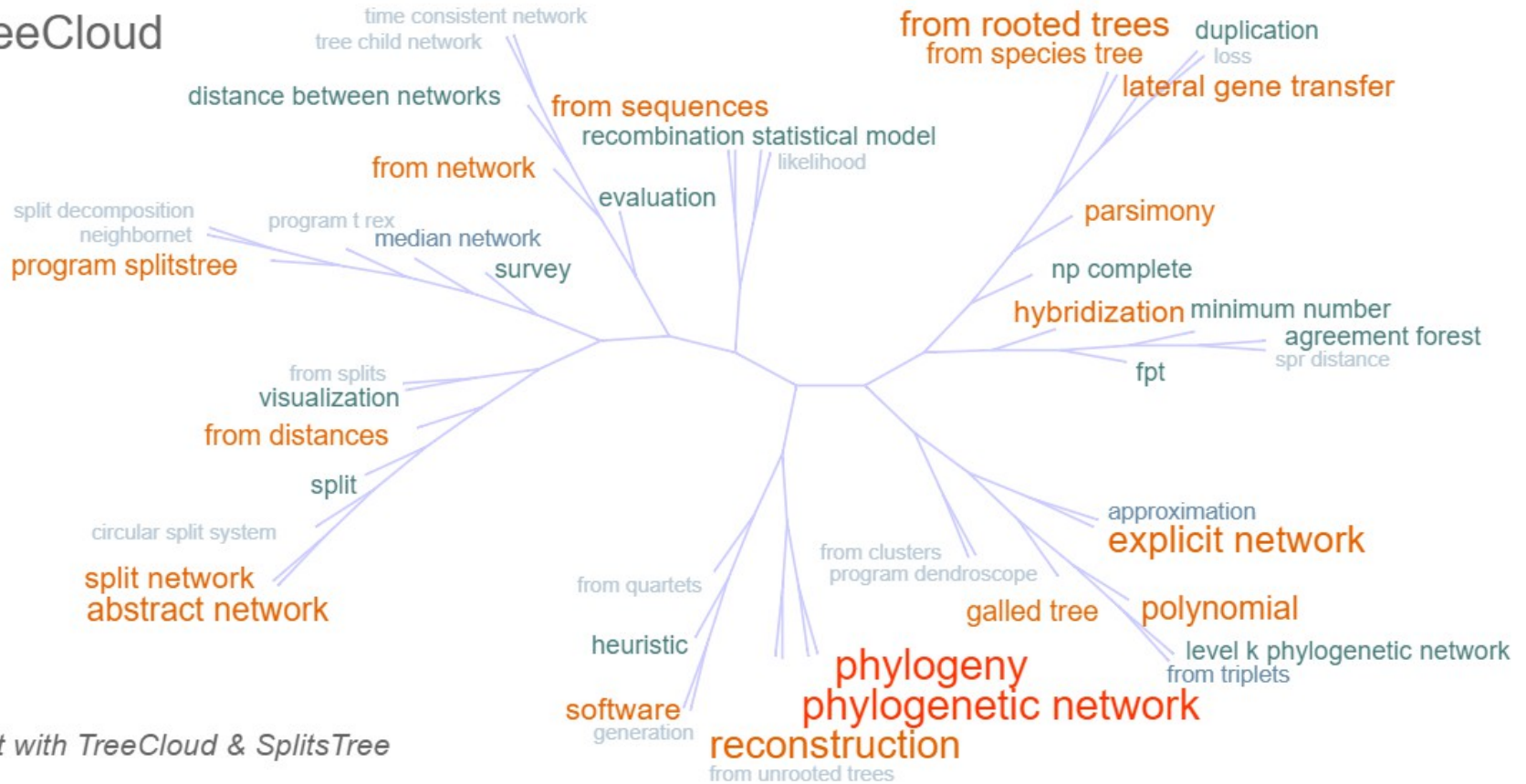
Choose a keyword to see the number of publications containing it over the years.

Browse publications by keyword:



# Keywords about phylogenetic networks

TreeCloud

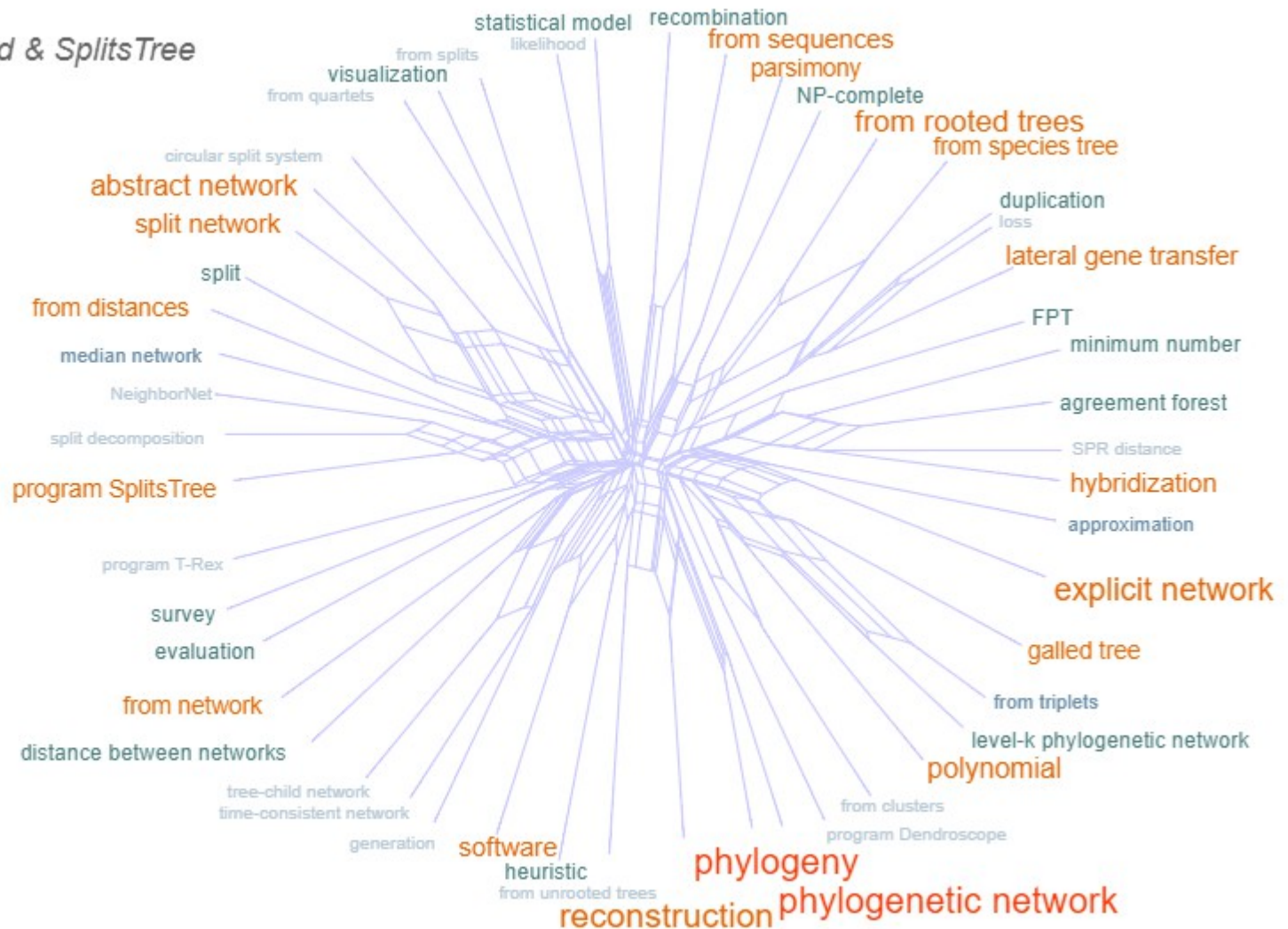


Built with TreeCloud & SplitsTree

# Keywords about phylogenetic networks

NetCloud

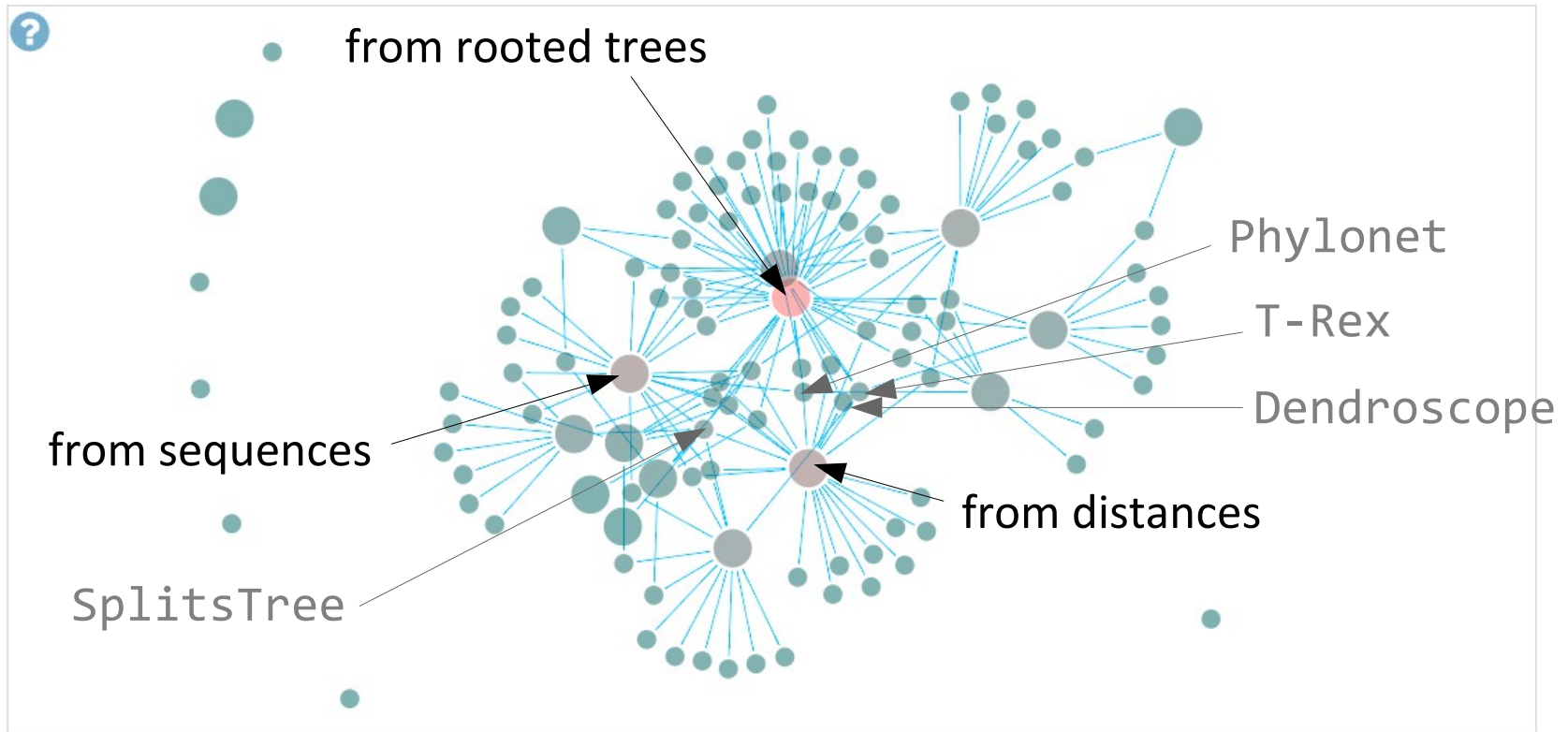
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# Who is who in Phylogenetic Networks? Software!

Hover over or click on a node to see more information.



Based on BibAdmin by Sergiu Chelcea  
+ tag clouds, date histograms, journal lists,  
keyword definitions, co-author graphs  
(work of Tushar Agarwal)

<http://phylonet.univ-mlv.fr/show.php?keyword=programs>



# Who is who in Phylogenetic Networks? Keywords!

**abstract-network(88)** agreement-forest(29) approximation(18) APX-hard(4) ARG(6) bayesian(4) block-realization(1) bootstrap(4) bound(4) branch-and-bound(1) cactus-graph(1) characterization(11) circular-split-system(13) clustering(3) coalescent(10) consensus(8) consistency(2) cophylogeny(1) counting(3) database(1) distance-between-networks(30) diversity(5) duplication(33) dynamic-programming(10) enumeration(4) **evaluation(25)** **explicit-network(191)** exponential-algorithm(6) FPT(31) from-clusters(16) from-continuous-characters(1) from-distances(45) from-gene-order(1) from-multilabeled-tree(9) from-network(39) from-NGS-data(1) from-quartets(16) **from-rooted-trees(122)** from-sequences(51) from-species-tree(46) from-splits(13) from-trees(7) from-trinets(2) from-triplets(24) from-unrooted-trees(16) galled-network(7) galled-tree(38) generation(12) haplotype-network(2) haplotyping(1) heuristic(32) HMM(2) hybridization(52) inapproximability(5) integer-linear-programming(3) isomorphism(3) k-reticulated(1) kernelization(2) labeling(4) lateral-gene-transfer(56) level-k-phylogenetic-network(30) likelihood(16) lineage-sorting(10) loss(16) MASN(4) median-network(16) MedianJoining(2) Minimal-lateral-network(1) minimum-contradiction(2) **minimum-number(33)** minimum-spanning-network(2) model-selection(2) mu-distance(2) **NeighborNet(14)** nested-network(2) netting(3) normal-network(9) NP-complete(33) optimal-realization(3) parsimony(39) pedigree(1) perfect(5) **phylogenetic-network(402)** **phylogeny(387)** **polynomial(70)** population-genetics(5) Program-AdmixTools(1) Program-ALE(1) Program-Angst(2) Program-Arlequin(5) Program-Beagle(3) Program-BIMLR(1) Program-Bio-PhyloNetwork(4) Program-Clustistic(2) Program-CMPT(1) Program-CombineTrees(2) Program-ConsensusNetwork(1) Program-constNJ(1) Program-CycleKiller(3) **Program-Dendroscope(14)** Program-EEEP(3) Program-FastHN(1) Program-FlatNJ(1) Program-Fylogenetica(2) Program-GalledTree(1) Program-GraphDTL(2) Program-HapBound(1) Program-HGT\_simul(1) Program-HiDe(1) Program-HorizStory(2) Program-Hybrid-Lambda(1) Program-HybridInterleave(5) Program-HybridNET(2) Program-HybridNumber(3) Program-Hybroscale(3) Program-JML(1) Program-LatTrans(5) Program-LEV1ATHAN(1) Program-Level1Generator(1) Program-Level2(2) Program-lingpy(1) Program-LNetwork(2) Program-MaafB(2) Program-Marlon(3) Program-MC-Net(1) Program-McKITsch(1) Program-Mowgli(5) Program-MowgliNNI(2) Program-MPNet(1) Program-MY-CLOSURE(1) Program-Nepal(7) Program-NetGen(3) Program-NetTest(1) Program-NetView(1) Program-Network(5) Program-Notung(1) Program-PADRE(7) Program-Phangorn(2) Program-PhippsNetwork(2) **Program-PhyloNet(11)** Program-PhyloNet-HMM(1) Program-PIRN(3) Program-Prunier(2) Program-Pyramids(3) Program-QNet(4) Program-Quartet(1) Program-Quartet-Decomposition(1) Program-QuartetMethods(1) Program-QuartetNet(2) Program-QuasiDec(1) Program-QuickCass(1) Program-RANGER-DTL(4) Program-RecMin(1) Program-Recodon(3) Program-RecPars(1) Program-Reticlad(2) Program-SAGE(2) Program-SAQ-Net(1) Program-Serial-NetEvolve(1) Program-SHRUB(3) Program-Simplistic(3) Program-Sliding-MinPD(1) Program-SNSA(2) Program-Spectronet(4) **Program-SplitsTree(36)** Program-SPNet(5) Program-SPRDist(1) Program-SuperQ(1) **Program-T-REX(13)** Program-TCS(8) Program-TERA(2) Program-TerminusEst(2) Program-TreeFix-DTL(1) Program-TreeMix(1) Program-Treevolve(2) Program-TripNet(2) Program-ultra-Net(1) Program-Ultratnet(1) Program-WeakHierarchies(2) Program-Xscape(1) pyramid(8) quasi-median-network(3) realization(4) **recombination(29)** recombination-detection(4) **reconstruction(255)** regular-network(7) reticulogram(10) serial-evolutionary-networks(1) simulated-annealing(4) simulation(5) site-consistency(1) **software(66)** split(27) split-decomposition(13) split-network(54) SPR-distance(13) spread(2) **statistical-model(32)** statistical-parsimony(3) supernet(4) survey(31) tanglegram(1) time-consistent-network(12) tree-child-network(15) tree-sibling-network(10) tripartition-distance(9) triplet-distance(3) unicyclic-network(3) **visualization(30)** weak-hierarchy(8) weakly-compatible(3)

# Who is who in Phylogenetic Networks? Keywords!

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input

software

# Who is who in Phylogenetic Networks? Keywords!

**abstract-network(88)** agreement-forest(29) approximation(18) APX-hard(4) ARG(6) bayesian(4) block-realization(1) bootstrap(4) bound(4) branch-and-bound(1) cactus-graph(1) characterization(11) circular-split-system(13) clustering(3) coalescent(10) **consensus(8)** consistency(2) cophylogeny(1) **counting(3)** database(1) **distance-between-networks(30)** **diversity(5)** duplication(33) dynamic-programming(10) **enumeration(4)** **evaluation(25)** **explicit-network(191)** exponential-algorithm(6) **FPT(31)** **from-clusters(16)** from-continuous-characters(1) **from-distances(45)** from-gene-order(1) from-multilabeled-tree(9) **from-network(39)** from-NGS-data(1) from-quartets(16) **from-rooted-trees(122)** from-sequences(51) **from-species-tree(46)** from-splits(13) from-trees(7) from-trinets(2) from-triplets(24) from-unrooted-trees(16) galled-network(7) **galled-tree(38)** **generation(12)** haplotype-network(2) haplotyping(1) **heuristic(32)** HMM(2) hybridization(52) inapproximability(5) integer-linear-programming(3) isomorphism(3) k-reticulated(1) kernelization(2) **labeling(4)** lateral-gene-transfer(56) level-k-phylogenetic-network(30) likelihood(16) lineage-sorting(10) loss(16) MASN(4) median-network(16) MedianJoining(2) Minimal-lateral-network(1) minimum-contradiction(2) **minimum-number(33)** minimum-spanning-network(2) model-selection(2) mu-distance(2) NeighborNet(14) nested-network(2) netting(3) normal-network(9) NP-complete(33) optimal-realization(3) parsimony(39) pedigree(1) perfect(5) **phylogenetic-network(402)** **phylogeny(387)** **polynomial(70)** population-genetics(5) Program-AdmixTools(1) Program-ALE(1) Program-Angst(2) Program-Arlequin(5) Program-Beagle(3) Program-BIMLR(1) Program-Bio-PhyloNetwork(4) Program-Clustistic(2) Program-CMPT(1) Program-CombineTrees(2) Program-ConsensusNetwork(1) Program-constNJ(1) Program-CycleKiller(3) **Program-Dendroscope(14)** Program-EEEP(3) Program-FastHN(1) Program-FlatNJ(1) Program-Fylogenetica(2) Program-GalledTree(1) Program-GraphDTL(2) Program-HapBound(1) Program-HGT\_simul(1) Program-HiDe(1) Program-HorizStory(2) Program-Hybrid-Lambda(1) Program-HybridInterleave(5) Program-HybridNET(2) Program-HybridNumber(3) Program-Hybroscale(3) Program-JML(1) Program-LatTrans(5) Program-LEV1ATHAN(1) Program-Lev1Generator(1) Program-Level2(2) Program-lingpy(1) Program-LNetwork(2) Program-MaafB(2) Program-Marlon(3) Program-MC-Net(1) Program-McKITsch(1) Program-Mowgli(5) Program-MowgliNNI(2) Program-MPNet(1) Program-MY-CLOSURE(1) Program-Nepal(7) Program-NetGen(3) Program-NetTest(1) Program-NetView(1) Program-Network(5) Program-Notung(1) Program-PADRE(7) Program-Phangorn(2) Program-PhippsNetwork(2) **Program-PhyloNet(11)** Program-PhyloNet-HMM(1) Program-PIRN(3) Program-Prunier(2) Program-Pyramids(3) Program-QNet(4) Program-Quartet(1) Program-Quartet-Decomposition(1) Program-QuartetMethods(1) Program-QuartetNet(2) Program-QuasiDec(1) Program-QuickCass(1) Program-RANGER-DTL(4) Program-RecMin(1) Program-Recodon(3) Program-RecPars(1) Program-Reticlad(2) Program-SAGE(2) Program-SAQ-Net(1) Program-Serial-NetEvolve(1) Program-SHRUB(3) Program-Simplistic(3) Program-Sliding-MinPD(1) Program-SNSA(2) Program-Spectronet(4) **Program-SplitsTree(36)** Program-SPNet(5) Program-SPRDist(1) Program-SuperQ(1) **Program-T-REX(13)** Program-TCS(8) Program-TERA(2) Program-TerminusEst(2) Program-TreeFix-DTL(1) Program-TreeMix(1) Program-Treevolve(2) Program-TripNet(2) Program-ultra-Net(1) Program-Ultranet(1) Program-WeakHierarchies(2) Program-Xscape(1) **pyramid(8)** quasi-median-network(3) realization(4) **recombination(29)** recombination-detection(4) **reconstruction(255)** regular-network(7) reticulogram(10) serial-evolutionary-networks(1) simulated-annealing(4) simulation(5) site-consistency(1) **software(66)** split(27) split-decomposition(13) split-network(54) SPR-distance(13) spread(2) statistical-model(32) statistical-parsimony(3) supernet(4) survey(31) tanglegram(1) time-consistent-network(12) tree-child-network(15) tree-sibling-network(10) tripartition-distance(9) triplet-distance(3) unicyclic-network(3) **visualization(30)** weak-hierarchy(8) weakly-compatible(3)

input

software

problems



# Who is who in Phylogenetic Networks? Keywords!

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input

software

problems

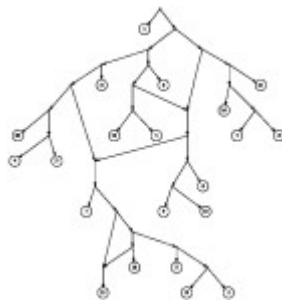
algorithmic results



# Phylogenetic network reconstruction

espèce 1 : AATTGCAG TAGCCCAAAAT  
espèce 2 : ACCTGCAG TAGACCAAT  
espèce 3 : GCTTGCCG TAGACAAGAAT  
espèce 4 : ATTTGCAG AAGACCAAAT  
espèce 5 : TAGACAAGAAT  
espèce 6 : ACTTGCAG TAGCACAAAAT  
espèce 7 : ACCTGGTG TAAAAT

G1 G2



{gene sequences}

## distance methods

*Bandelt & Dress 1992 - Legendre & Makarenkov 2000 -  
Bryant & Moulton 2002 - Chan, Jansson, Lam & Yiu 2006  
- Willems, Tahiri & Makarenkov 2014*

## parsimony methods

*Hein 1990 - Kececioglu & Gusfield 1994 - Jin, Nakhleh,  
Snir, Tuller 2009 - Park, Jin & Nakhleh 2010 - Kannan &  
Wheeler, 2012 - Kelk, Padio, Scornavacca & van Iersel,  
2017*

## likelihood methods

*Snir & Tuller 2009 - Jin, Nakhleh, Snir, Tuller 2009 -  
Velasco & Sober 2009 - Meng & Kubatko 2009*

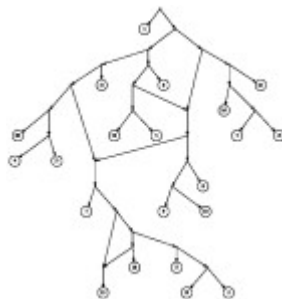
network N

# Phylogenetic network reconstruction

**Problem: methods are usually slow,  
especially with rapidly increasing sequence length.**

espèce 1 : AATTGCAG TAGCCCAAAAT  
espèce 2 : ACCTGCAG TAGACCAAT  
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**G1**    **G2**



{gene sequences}

*distance methods*

*Bandelt & Dress 1992 - Legendre & Makarenkov 2000 -  
Bryant & Moulton 2002 - Chan, Jansson, Lam & Yiu 2006  
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*parsimony methods*

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2017*

*likelihood methods*

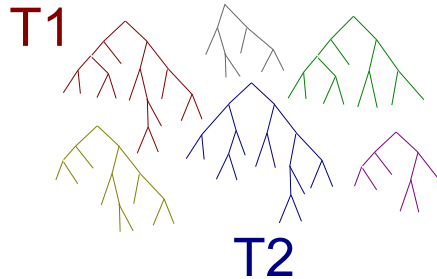
*Snir & Tuller 2009 - Jin, Nakhleh, Snir, Tuller 2009 -  
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network *N*

# Phylogenetic network reconstruction from trees

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G1 G2



{gene sequences}

*Reconstruction of a tree for each gene present in several species*

Guindon & Gascuel, SB, 2003

{trees}

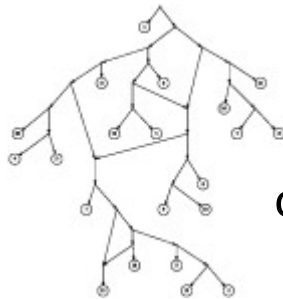
HOGENOM Database



Dufayard, Duret, Penel, Gouy,  
Rechenmann & Perrière, BioInf, 2005

*Tree reconciliation or consensus*

explicit network



optimal super-network  $N$ :

- contains the input trees
- has the smallest number of reticulations



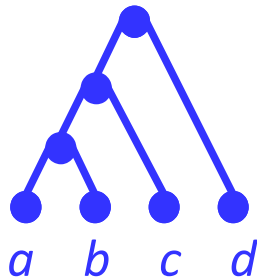
# Phylogenetic network reconstruction from trees

The “**hybridization network**” problem:

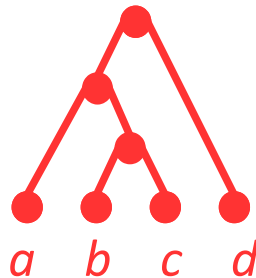
given 2 trees, find the smallest network containing both of them with the minimum number of hybrid vertices

**Easy** to find a network containing the two trees!

*T1*



*T2*



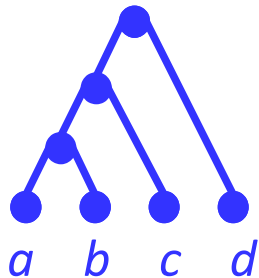
# Phylogenetic network reconstruction from trees

The “hybridization network” problem:

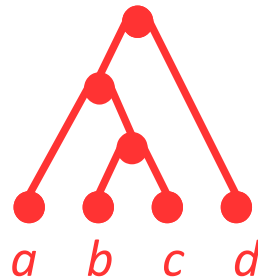
given 2 trees, find the smallest network containing both of them with the minimum number of hybrid vertices

Easy to find a network containing the two trees!

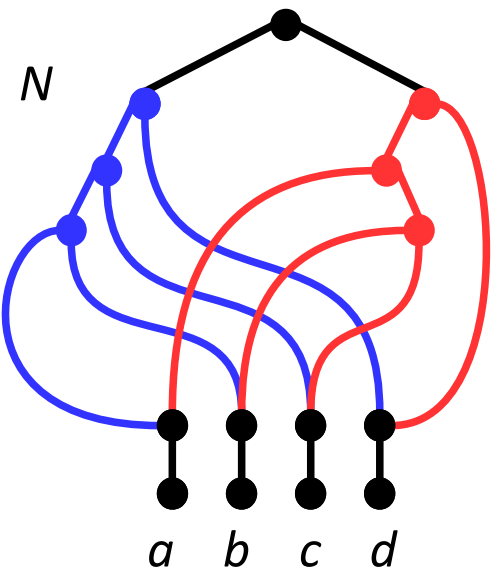
$T_1$



$T_2$



add a root above  
the two trees, glue  
the leaves together



But  $n$  hybrid vertices for trees with  $n$  leaves: not optimal!

# Phylogenetic network reconstruction from trees

The “**hybridization network**” problem:

given 2 trees, find the smallest network containing both of them with the minimum number of hybrid vertices

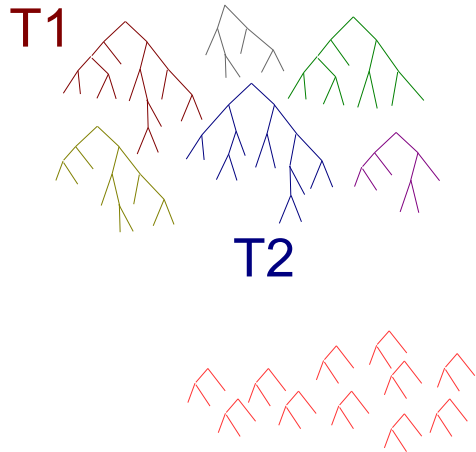
**NP-hard** to minimize the number of hybrid vertices

Bordewich & Semple (2007) Discrete Appl Math

# Phylogenetic network reconstruction from trees

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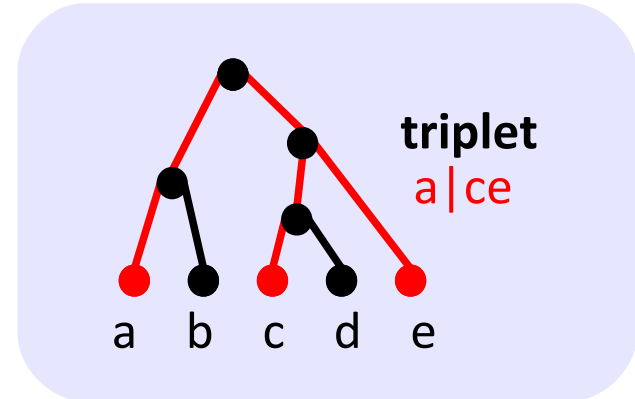
G1 G2



{gene sequences}

{trees}

{triplets}



explicit network



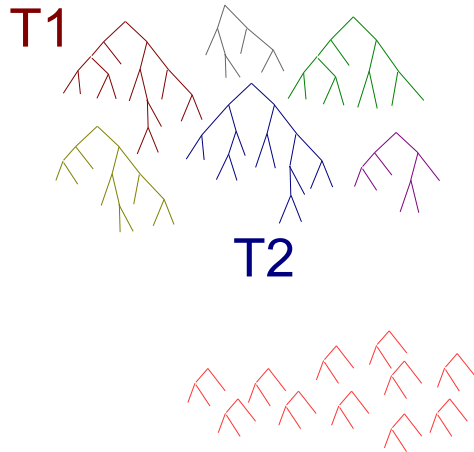
optimal super-network  $N$ :

- contains the input triplets
- has the smallest number of reticulations

# Phylogenetic network reconstruction from trees

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G1 G2

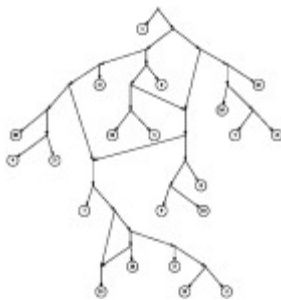


{gene sequences}

{trees}

{triplets}

explicit network



optimal super-network  $N$ :

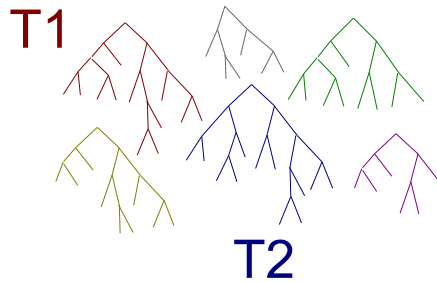
- contains the input triplets
- has the smallest number of reticulations

→ still NP-hard

# Phylogenetic network reconstruction from trees

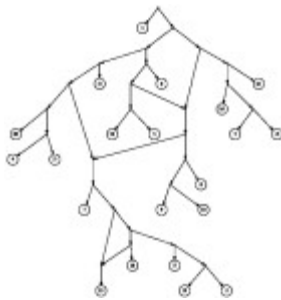
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G1 G2



{triplets} ("dense" set)

explicit network



super-network  $N$ :

- contains the input triplets
- has level at most  $k$  (i.e. close to a tree)

→ polynomial time algorithm for fixed  $k$ :  
Habib & To, CPM 2009, JBCB 2012

{gene sequences}

{trees}

{triplets} ("dense" set)

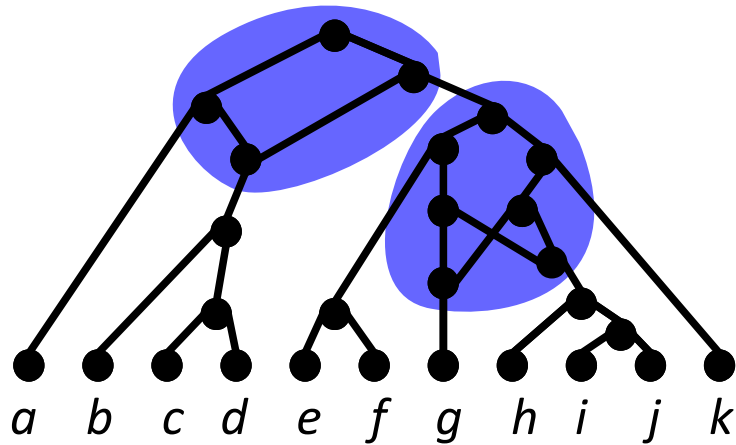
super-network  $N$ :

# Outline

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- An introduction to phylogenetic networks
- **Classes of phylogenetic networks**
- Counting problems on phylogenetic networks

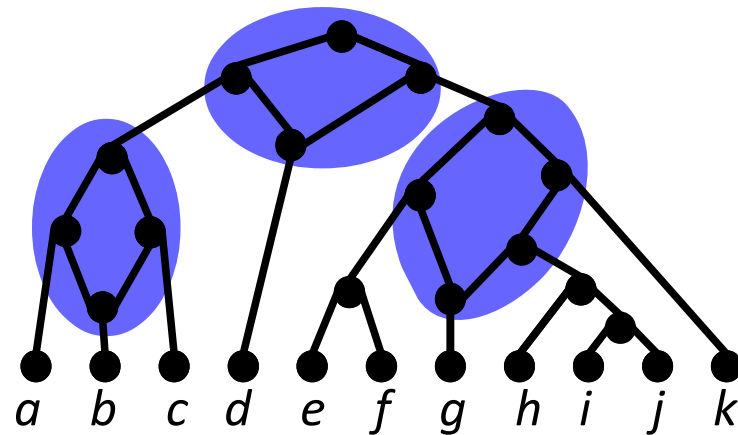
# Classes of phylogenetic networks: level-k networks



level-2 network

**level =**  
maximum number of reticulations  
per **blob** (=bridgeless component  
of the underlying undirected  
graph).

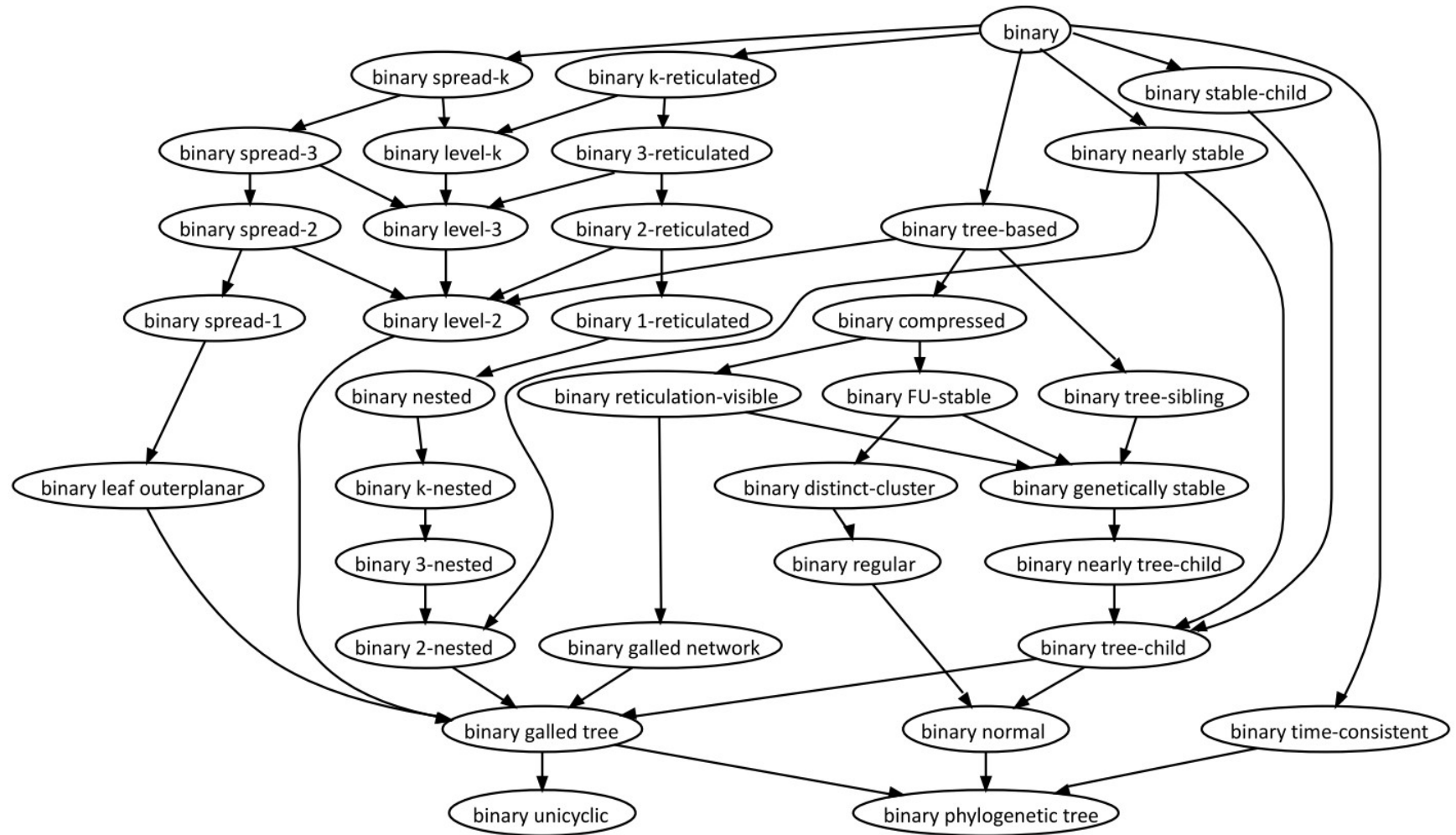
level-1 network  
(*"galled tree"*)





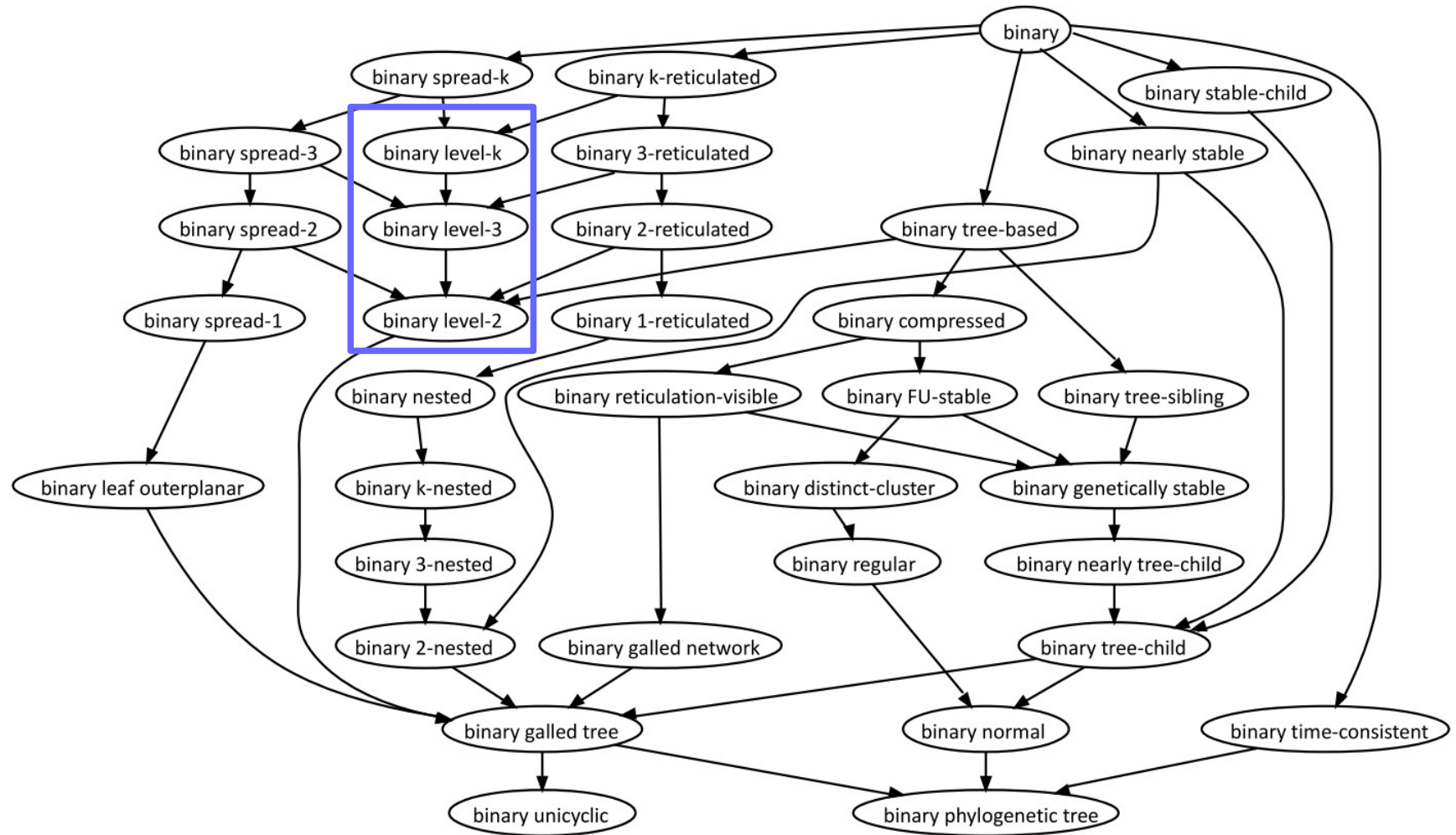
# Classes of phylogenetic networks: ISIPhyNC

## Information System on Inclusions of Phylogenetic Network Classes



# Classes of phylogenetic networks: ISIPhyNC

## Information System on Inclusions of Phylogenetic Network Classes





# Classes of phylogenetic networks: inclusions

<i>binary</i>	unic	gall	tree	nea	gall	gen	reti	tree	con	non	reg	dist	FU	nea	tree	nes	2-n	3-n	level	level	leaf	spr	spr	spr	tim
<u>unicyclic</u>	=	c	c	c	c	c	c	c	c	5	5	5	c	c	c	c	c	c	c	c	c	c	c	c	5
<u>galled tree</u>	6	=	c	c	c	c	c	c	c	5	5	5	c	c	c	c	c	c	c	c	c	c	c	c	5
<u>tree-child</u>	6	7	=	c	c	c	c	c	c	5	5	5	c	c	7	7	7	7	15	15	7	7			5
<u>nearly tree-child</u>	6	7	8	=	8	c	c	c	c	5	5	5	c	8	c	7	7	7	8	15	7	7			5
<u>galled network</u>	2	2	1	1	=	1	c	1	c	1	1	1	14	21	c	7	7	7	18	18	7	7			5
<u>genetically stable</u>	4	4	4	4	4	=	c	c	c	5	5	5	c	8	c	4	4	4	8	15	7	7			4
<u>reticulation-visible</u>	2	2	1	1	4	1	=	1	c	1	1	1	14	8	c	4	4	4	8	15	7	7			4
<u>tree-sibling</u>	4	4	4	4	4	12	12	=	12	5	5	5	12	8	c	4	4	4	8	15	7	7			4
<u>compressed</u>	2	2	1	1	4	1	11	1	=	1	1	1	14	8	c	4	4	4	8	15	7	7			4
<u>normal</u>	7	7	c	c	13	c	c	c	c	=	c	c	c	c	c	7	7	7	15	15	7	7			22
<u>regular</u>	2	2	2	2	13	2	24	2	c	2	=	c	c	8	c	7	7	7	8	15	7	7			22
<u>distinct-cluster</u>	2	2	2	2	13	2	24	2	c	2	9	=	c	8	c	7	7	7	8	15	7	7			22
<u>FU-stable</u>	2	2	1	1	4	1	11	1	c	1	1	1	=	8	c	4	4	4	8	15	7	7			4
<u>nearly stable</u>	2	2	2	2	3	2	3	2	3	2	3	3	3	=	3	7	7	7	3	15	3	3			5
<u>tree-based</u>	2	2	1	1	4	1	12	1	12	1	1	1	12	8	=	4	4	4	8	15	7	7			4
<u>nested</u>	3	3	3	3	3	3	3	3	3	3	3	3	3	19	3	=	20	20	3	16	3	3			5
<u>2-nested</u>	3	3	3	3	3	3	3	3	3	3	3	3	3	c	3	c	=	c	3	16	3	3			5
<u>3-nested</u>	3	3	3	3	3	3	3	3	3	3	3	3	3	19	3	c	19	=	3	16	3	3			5
<u>level-2</u>	4	4	4	4	4	12	12	14	12	4	4	4	12	17	c	4	4	4	=	c	7	7	c	c	4
<u>level-3</u>	2	2	2	2	3	2	3	2	3	2	3	3	3	8	3	4	4	4	3	=	3	3		c	4
<u>leaf outerplanar</u>	4	4	4	4	4	10	10	10	10	4	4	4	10	8	10	4	4	4	8	16	=	c	c	c	4
<u>spread 1</u>	4	4	4	4	4	10	10	10	10	4	4	4	10	8	10	4	4	4	8	16	9	=	c	c	4
<u>spread 2</u>	3	3	3	3	3	3	3	3	3	3	3	3	3	8	3	4	4	4	3	16	3	3	=	c	4
<u>spread 3</u>	3	3	3	3	3	3	3	3	3	3	3	3	3	8	3	4	4	4	3	16	3	3		=	4
<u>time-consistent</u>	3	3	3	3	3	3	3	3	3	3	3	3	3	8	3	7	7	7	3	23	3	3			=

joint work with Maxime Morgado and Narges Tavassoli

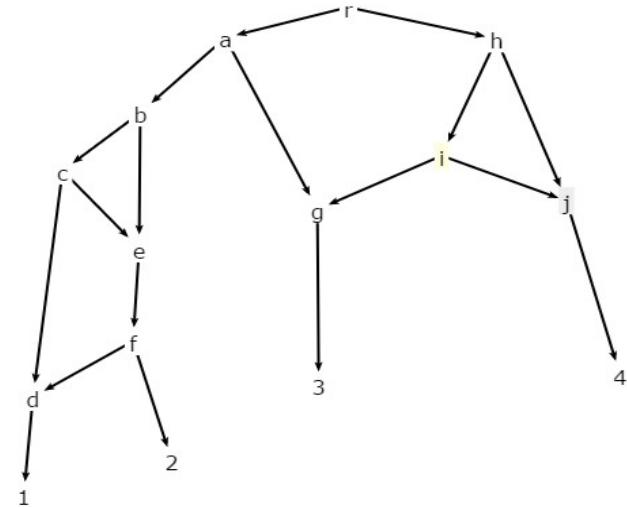
# Classes of phylogenetic networks: inclusions

<i>binary</i>	unic	gall	tree	nea	gall	gen	reti	tree	con	non	reg	dist	FU	nea	tree	nes	2-n	3-n	level	level	leaf	spr	spr	spr	tim
<u>unicyclic</u>	=	c	c	c	c	c	c	c	c	5	5	5	c	c	c	c	c	c	c	c	c	c	c	c	5
<u>galled tree</u>	6	=	c	c	c	c	c	c	c	5	5	5	c	c	c	c	c	c	c	c	c	c	c	c	5
<u>tree-child</u>	6	7	=	c	c	c	c	c	c	5	5	5	c	c	7	7	7	7	15	15	7	7			5
<u>nearly tree-child</u>	6	7	8	=	8	c	c	c	c	5	5	5	c	8	c	7	7	7	8	15	7	7			5
<u>galled network</u>	2	2	1	1	=	1	c	1	c	1	1	1	14	21	c	7	7	7	18	18	7	7			5
<u>genetically stable</u>	4	4	4	4	4	=	c	c	c	5	5	5	c	8	c	4	4	4	8	15	7	7			4
<u>reticulation-visible</u>	2	2	1	1	4	1	=	1	c	1	1	1	14	8	c	4	4	4	8	15	7	7			4
<u>tree-sibling</u>	4	4	4	4	4	12	12	=	12	5	5	5	12	8	c	4	4	4	8	15	7	7			4
<u>compressed</u>	2	2	1	1	4	1	11	1	=	1	1	1	14	8	c	4	4	4	8	15	7	7			4
<u>normal</u>	7	7	c	c	13	c	c	c	c	=	c	c	c	c	c	7	7	7	15	15	7	7			22
<u>regular</u>	2	2	2	2	13	2	24	2	c	2	=	c	c	8	c	7	7	7	8	15	7	7			22
<u>distinct-cluster</u>	2	2	2	2	13	2	24	2	c	2	9	=	c	8	c	7	7	7	8	15	7	7			22
<u>FU-stable</u>	2	2	1	1	4	1	11	1	c	1	1	1	=	8	c	4	4	4	8	15	7	7			4
<u>nearly stable</u>	2	2	2	2	3	2	3	2	3	2	3	3	3	=	3	7	7	7	3	15	3	3			5
<u>tree-based</u>	2	2	1	1	4	1	12	1	12	1	1	1	12	8	=	4	4	4	8	15	7	7			4
<u>nested</u>	3	3	3	3	3	3	3	3	3	3	3	3	3	19	3	=	20	20	3	16	3	3			5
<u>2-nested</u>	3	3	3	3	3	3	3	3	3	3	3	3	3	c	3	c	=	c	3	16	3	3			5
<u>3-nested</u>	3	3	3	3	3	3	3	3	3	3	3	3	3	19	3	c	19	=	3	16	3	3			5
<u>level-2</u>	4	4	4	4	4	12	12	14	12	4	4	4	12	17	c	4	4	4	=	c	7	7	c	c	4
<u>level-3</u>	2	2	2	2	3	2	3	2	3	2	3	3	3	8	3	4	4	4	3	=	3	3		c	4
<u>leaf outerplanar</u>	4	4	4	4	4	10	10	10	10	4	4	4	10	8	10	4	4	4	8	16	=	c	c	c	4
<u>spread 1</u>	4	4	4	4	4	10	10	10	10	4	4	4	10	8	10	4	4	4	8	16	9	=	c	c	4
<u>spread 2</u>	3	3	3	3	3	3	3	3	3	3	3	3	3	8	3	4	4	4	3	16	3	3	=	c	4
<u>spread 3</u>	3	3	3	3	3	3	3	3	3	3	3	3	3	8	3	4	4	4	3	16	3	3		=	4
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joint work with Maxime Morgado and Narges Tavassoli



# Classes of phylogenetic networks: inclusions



## Classes containing this network or not

### Classes which contain this network (with direct proof)

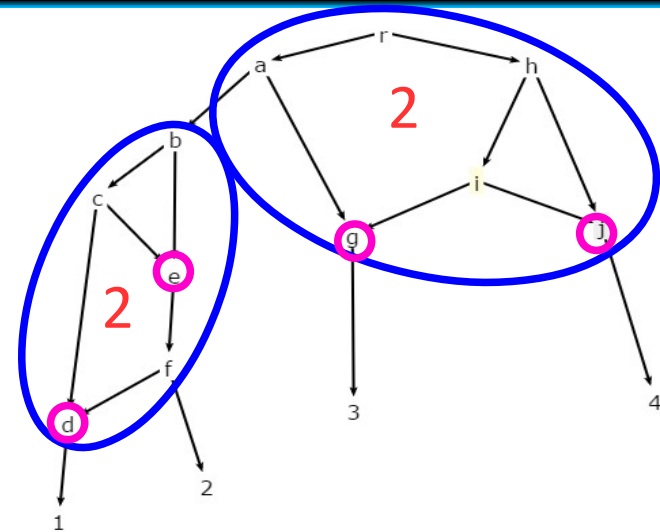
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- binary nearly stable: All vertices except  $c$  and  $i$  (whose unique parent is in both cases stable) are stable.
- binary level-2: Easy to check.
- binary leaf outerplanar: Easy to check.
- binary FU-stable: Easy to check.

### Classes which do not contain this network (with direct proof)

- binary nearly tree-child: Reticulation vertex  $g$  is stable but none of its parents  $a$  and  $i$  have the tree-path property.
- binary nested: Easy to check.
- binary time-consistent: The redundant arc from  $b$  to  $e$  makes it impossible to build a time-consistent labeling of the vertices.
- binary galled network: Reticulation arc  $(c,e)$  is a common arc of reticulation cycles from  $b$  to  $e$  and from  $c$  to  $d$ .
- binary distinct-cluster: Vertices  $h$  and  $i$  both have the same cluster:  $\{3,4\}$
- binary 1-reticulated: Tree vertex  $b$  can reach 2 reticulation vertices by 2 directed internally vertex-disjoint paths:  $d$  and  $e$ .

# Classes of phylogenetic networks: inclusions

**level** = maximum number of **reticulation vertices** among all **bridgeless components** in the network



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joint work with Maxime Morgado and Narges Tavassoli  
<http://phylnet.univ-mlv.fr/isiphync/network.php?id=4>

# Classes of phylogenetic networks: inclusions

**cluster** = set of **leaves** below a **vertex**  
**distinct-cluster** = all vertices (except reticulation vertices with their child) have distinct clusters

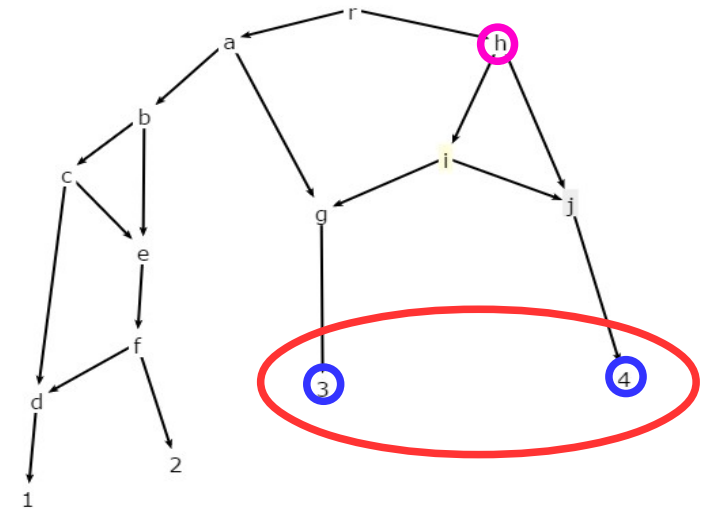
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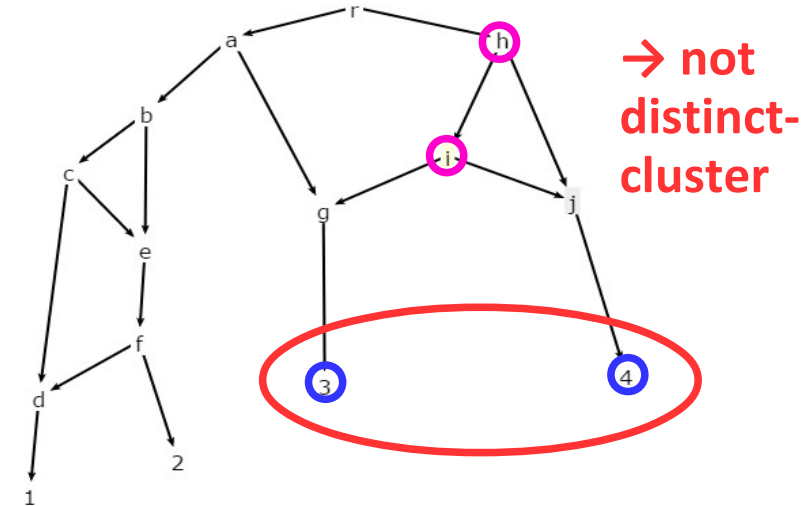
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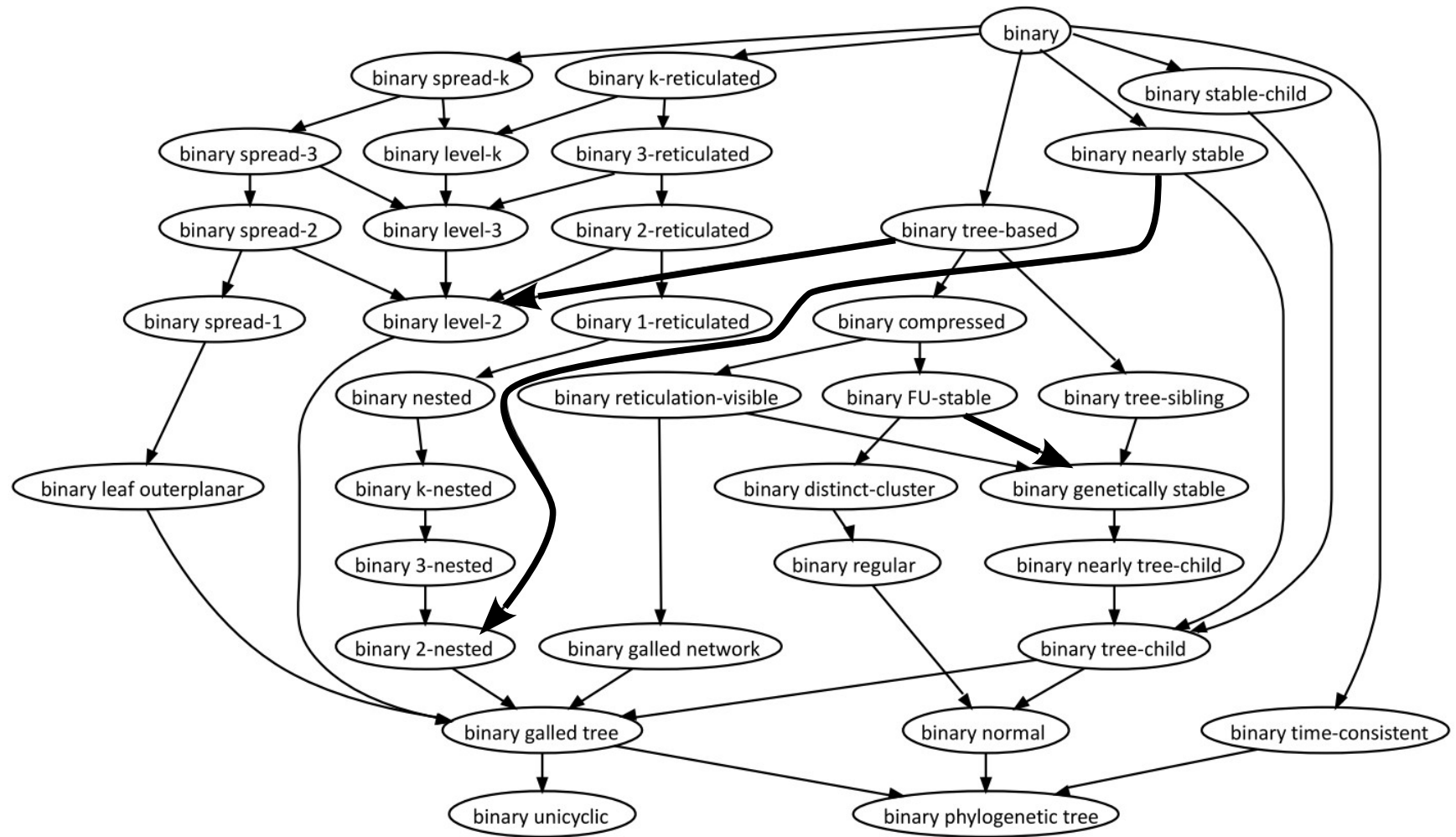
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# Classes of phylogenetic networks: new inclusions



# Who is who in Phylogenetic Networks?

**abstract-network(88)** agreement-forest(29) **approximation(18)** APX-hard(4) ARG(6) bayesian(4) block-realization(1) bootstrap(4) bound(4) branch-and-bound(1) **cactus-graph(1)** characterization(11) **circular-split-system(13)** clustering(3) coalescent(10) **consensus(8)** consistency(2) cophylogeny(1) **counting(3)** database(1) **distance-between-networks(30)** diversity(5) **duplication(33)** dynamic-programming(10) **enumeration(4)** **evaluation(25)** **explicit-network(191)** exponential-algorithm(6) **FPT(31)** from-clusters(16) from-continuous-characters(1) from-distances(45) from-gene-order(1) from-multilabeled-tree(9) from-network(39) from-NGS-data(1) from-quartets(16) **from-rooted-trees(122)** from-sequences(51) from-species-tree(46) from-splits(13) from-trees(7) from-trinets(2) from-triplets(24) from-unrooted-trees(16) **galled-network(7)** **galled-tree(38)** **generation(12)** haplotype-network(2) haplotyping(1) **heuristic(32)** HMM(2) hybridization(52) inapproximability(5) **integer-linear-programming(3)** isomorphism(3) **k-reticulated(1)** kernelization(2) **labeling(4)** **lateral-gene-transfer(56)** **level-k-phylogenetic-network(30)** likelihood(16) lineage-sorting(10) loss(16) MASN(4) **median-network(16)** MedianJoining(2) Minimal-lateral-network(1) minimum-contradiction(2) **minimum-number(33)** minimum-spanning-network(2) model-selection(2) mu-distance(2) NeighborNet(14) **nested-network(2)** netting(3) **normal-network(9)** **NP-complete(33)** optimal-realization(3) parsimony(39) pedigree(1) perfect(5) **phylogenetic-network(402)** **phylogeny(387)** **polynomial(70)** population-genetics(5) Program-AdmixTools(1) Program-ALE(1) Program-Angst(2) Program-Arlequin(5) Program-Beagle(3) Program-BIMLR(1) Program-Bio-PhyloNetwork(4) Program-Clustistic(2) Program-CMPT(1) Program-CombineTrees(2) Program-ConsensusNetwork(1) Program-constNJ(1) Program-CycleKiller(3) **Program-Dendroscope(14)** Program-EEEP(3) Program-FastHN(1) Program-FlatNJ(1) Program-Fylogenetica(2) Program-GalledTree(1) Program-GraphDTL(2) Program-HapBound(1) Program-HGT\_simul(1) Program-HiDe(1) Program-HorizStory(2) Program-Hybrid-Lambda(1) Program-HybridInterleave(5) Program-HybridNET(2) Program-HybridNumber(3) Program-Hybroscale(3) Program-JML(1) Program-LatTrans(5) Program-LEV1ATHAN(1) Program-Level1Generator(1) Program-Level2(2) Program-lingpy(1) Program-LNetwork(2) Program-MaafB(2) Program-Marlon(3) Program-MC-Net(1) Program-McKITsch(1) Program-Mowgli(5) Program-MowgliNNI(2) Program-MPNet(1) Program-MY-CLOSURE(1) Program-Nepal(7) Program-NetGen(3) Program-NetTest(1) Program-NetView(1) Program-Network(5) Program-Notung(1) Program-PADRE(7) Program-Phangorn(2) Program-PhippsNetwork(2) **Program-PhyloNet(11)** Program-PhyloNet-HMM(1) Program-PIRN(3) Program-Prunier(2) Program-Pyramids(3) Program-QNet(4) Program-Quartet(1) Program-Quartet-Decomposition(1) Program-QuartetMethods(1) Program-QuartetNet(2) Program-QuasiDec(1) Program-QuickCass(1) Program-RANGER-DTL(4) Program-RecMin(1) Program-Recodon(3) Program-RecPars(1) Program-Reticlad(2) Program-SAGE(2) Program-SAQ-Net(1) Program-Serial-NetEvolve(1) Program-SHRUB(3) Program-Simplistic(3) Program-Sliding-MinPD(1) Program-SNSA(2) Program-Spectronet(4) **Program-SplitsTree(36)** Program-SPNet(5) Program-SPRDist(1) Program-SuperQ(1) **Program-T-REX(13)** Program-TCS(8) Program-TERA(2) Program-TerminusEst(2) Program-TreeFix-DTL(1) Program-TreeMix(1) Program-Treevolve(2) Program-TripNet(2) Program-ultra-Net(1) Program-Ultratnet(1) Program-WeakHierarchies(2) Program-Xscape(1) **pyramid(8)** **quasi-median-network(3)** realization(4) recombination(29) recombination-detection(4) **reconstruction(255)** **regular-network(7)** reticulogram(10) serial-evolutionary-networks(1) **simulated-annealing(4)** simulation(5) site-consistency(1) **software(66)** split(27) split-decomposition(13) split-network(54) **SPR-distance(13)** **spread(2)** **statistical-model(32)** statistical-parsimony(3) supernet(4) survey(31) tanglegram(1) **time-consistent-network(12)** **tree-child-network(15)** **tree-sibling-network(10)** tripartition-distance(9) triplet-distance(3) unicyclic-network(3) **visualization(30)** weak-hierarchy(8) weakly-compatible(3)

input

software

classes

problems

algorithmic properties

# Classes of phylogenetic networks: problems

## Problems and properties studied on these classes

### Problems

- **Tree Containment:** Does the input network contain the input tree on the same set of leaves?
- **Cluster Containment:** Does the input network contain the input subset of leaves as a softwired cluster?
- **Phylogenetic Network Isomorphism:** Are the two input phylogenetic networks isomorphic?

### Properties

- **Upper bound on the number of vertices:** The number of vertices is bounded by the number of leaves.
- **Unbounded number of vertices:** The number of vertices is not bounded by the number of leaves.
- **Completeness for reconstruction from trees:** There exists a network in this class which displays all binary rooted phylogenetic trees on  $n$  leaves.

### Database content

73 classes of phylogenetic networks including 35 classes of binary phylogenetic networks (defined in a total of 20 bibliographic references), 51 inclusion relationships proved directly between classes (including some found in a total of 9 bibliographic references), 21 networks (65 memberships to a class, 53 non-memberships to a class), 3 problems considered, 3 properties considered, 33 theorems proved directly (including some found in a total of 15 bibliographic references) including 23 positive results (which can be extended to subclasses) and 10 negative results (which can be extended to superclasses).



# Classes of phylogenetic networks: problems

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Problem **easy to solve** on class A  $\rightarrow$  **easy to solve** on **subclass** B  
**Hard to solve** on class B  $\rightarrow$  **hard to solve** on **superclass** A  
(similar to ISGCI)

# Phylogenetic network reconstruction from trees

Recall the **“hybridization network”** problem:

given 2 trees, find the smallest network containing both of them with the minimum number of hybrid vertices

Even **checking a solution** is **hard!**

# The Tree Containment Problem (T.C.P.)

---

**Input:** A binary phylogenetic network  $N$  and  
a tree  $T$  over the same set of taxa.

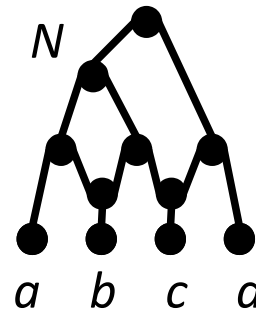
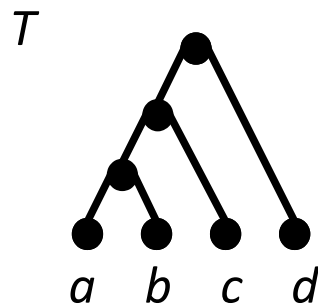
**Question:** Does  $N$  display  $T$ ?

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→ Can we remove one incoming arc, for each vertex with  $>1$  parent in  $N$ , such that the obtained tree is equivalent to  $T$ ?



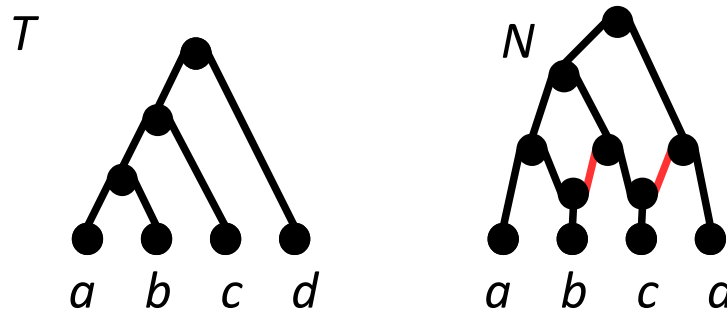


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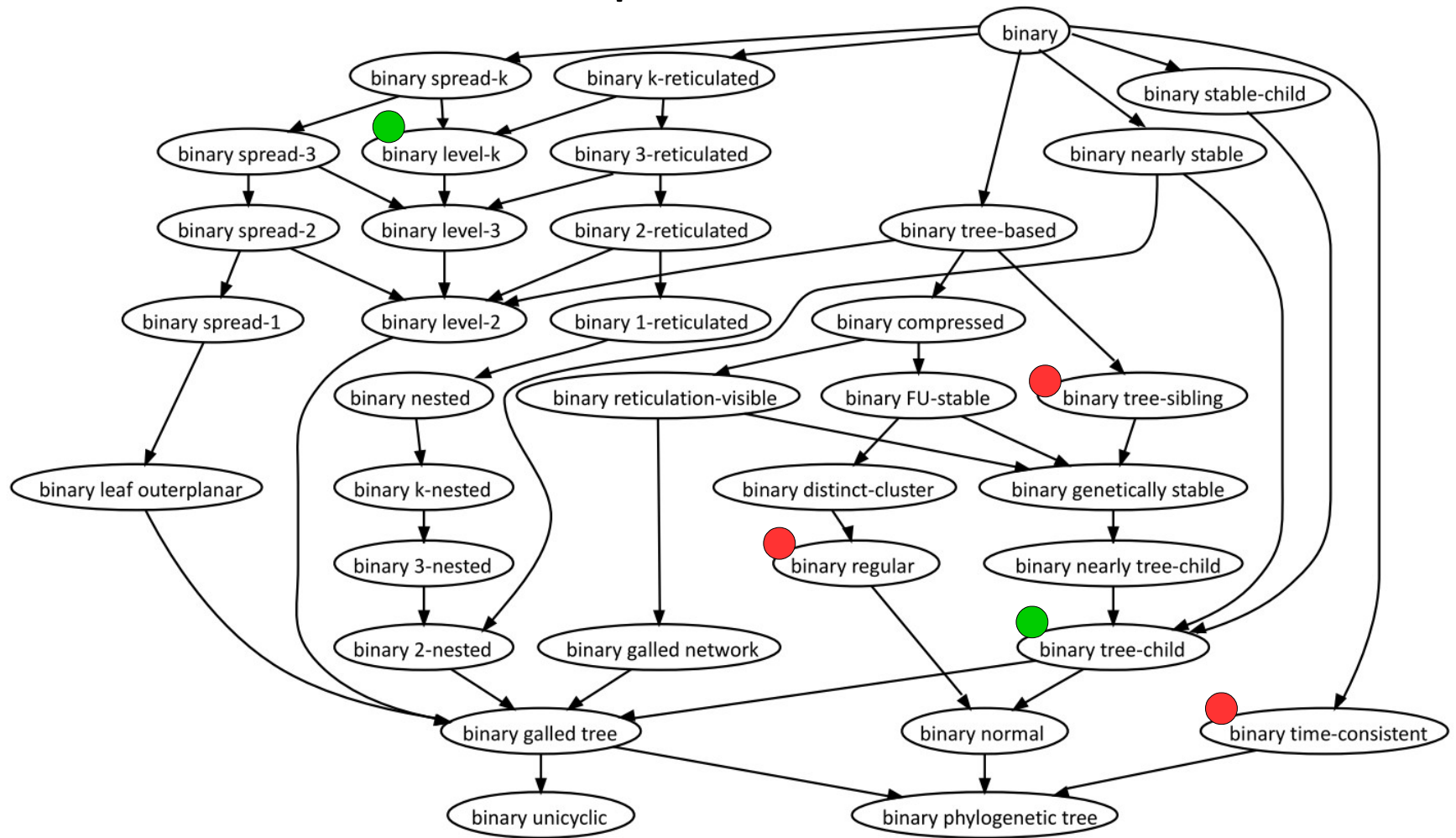
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- **NP-complete** in general (Kanj, Nakhleh, Than & Xia, 2008)
- **NP-complete** for tree-sibling, time-consistent, regular networks (Iersel, Semple & Steel, 2010)
- **Polynomial-time solvable** for normal networks, for binary tree-child networks, and for level- $k$  networks (Iersel, Semple & Steel, 2010)

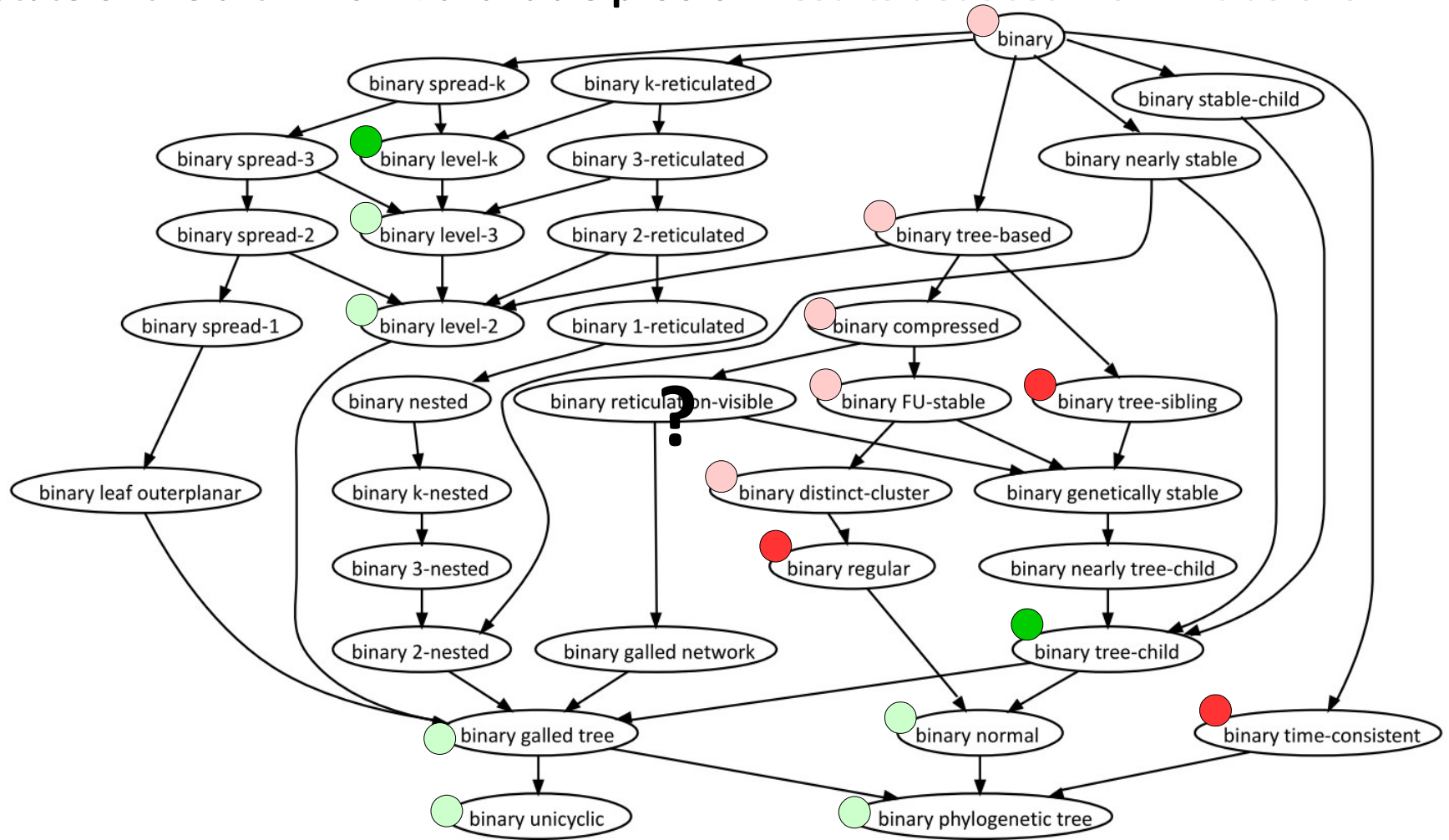
# Classes of phylogenetic networks and the T.C.P.

State of the art in 2011: available proofs

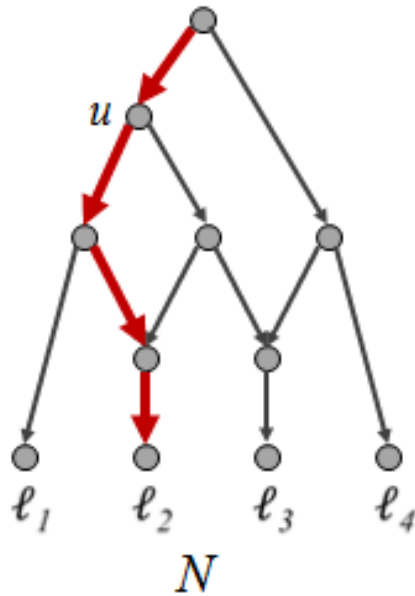


# Classes of phylogenetic networks and the T.C.P.

State of the art in 2011: available proofs + results deduced from inclusions

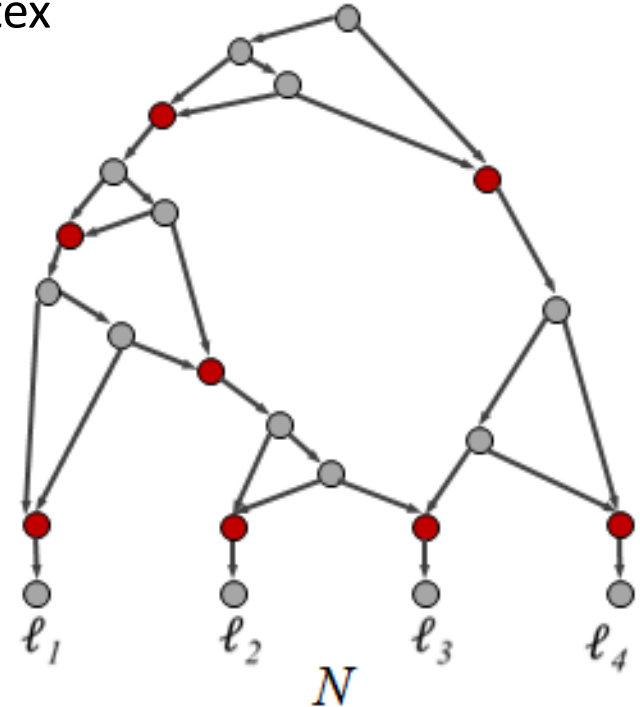


# Reticulation-visible and nearly-stable networks



A vertex  $u$  is **stable** if there exists a leaf  $l$  such that all paths from the root to  $l$  go through  $u$ .

A phylogenetic network is **reticulation-visible** if every reticulation vertex is stable.



A phylogenetic network is **nearly-stable** if for each vertex, either it is stable or its parents are.

# Strategy to get a quadratic time algorithm for T.C.P.

Given  $N$ , a phylogenetic network with  $n$  leaves and the input tree  $T$  of the T.C.P.

**Theorem 1:** If  $N$  is reticulation-visible then:  $\#\{\text{reticulation vertices of } N\} \leq 4(n-1)$   
 $\#\{\text{vertices of } N\} \leq 9n$

**Theorem 2:** If  $N$  is nearly-stable then  $\#\{\text{reticulation vertices of } N\} \leq 12(n-1)$

**Theorem 3:** Considering a longest path in  $N$  (nearly stable), it is possible, in constant time:

- either to realize that  $T$  is not contained in  $N$
- or to build a network  $N'$  with less arcs than  $N$  such that  $T$  contained in  $N$  if and only if  $T$  contained in  $N'$

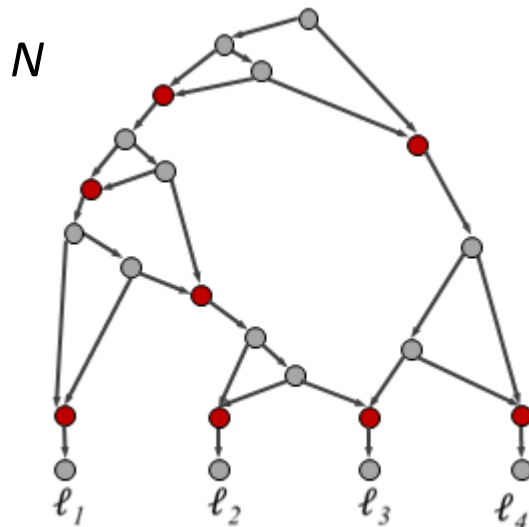
# Number of reticulations of a reticulation-visible network

Decompose  $N$  into  $2n-2$  paths:

- remove one reticulation arc per reticulation, ensuring we get no « dummy leaf », to get a tree  $T$  with  $n$  leaves
- summarize  $T$  into a rooted binary tree  $T'$  with  $n$  leaves... and  $2n-2$  arcs

We can prove (technical) that:

**each path contains at most 2 reticulation vertices**







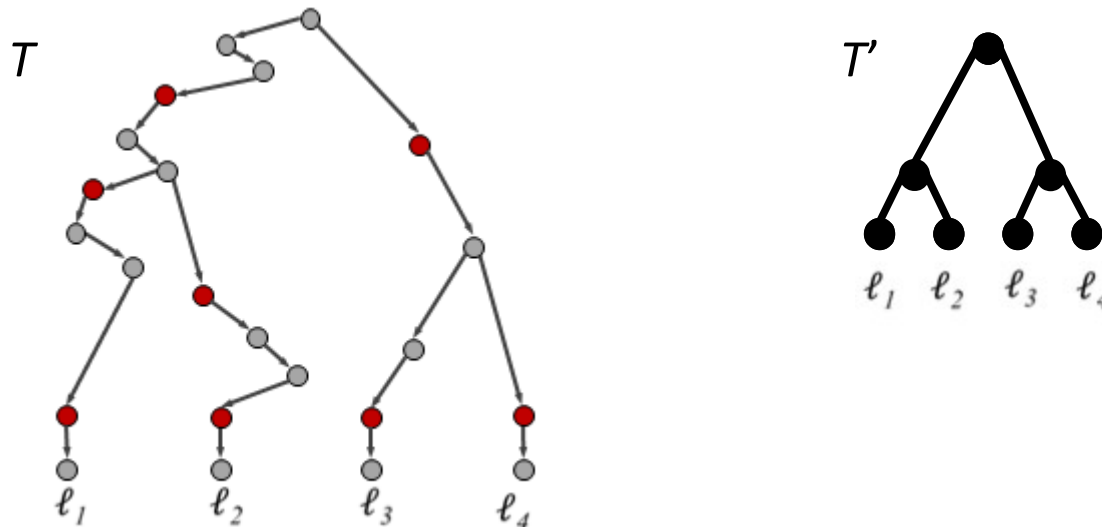
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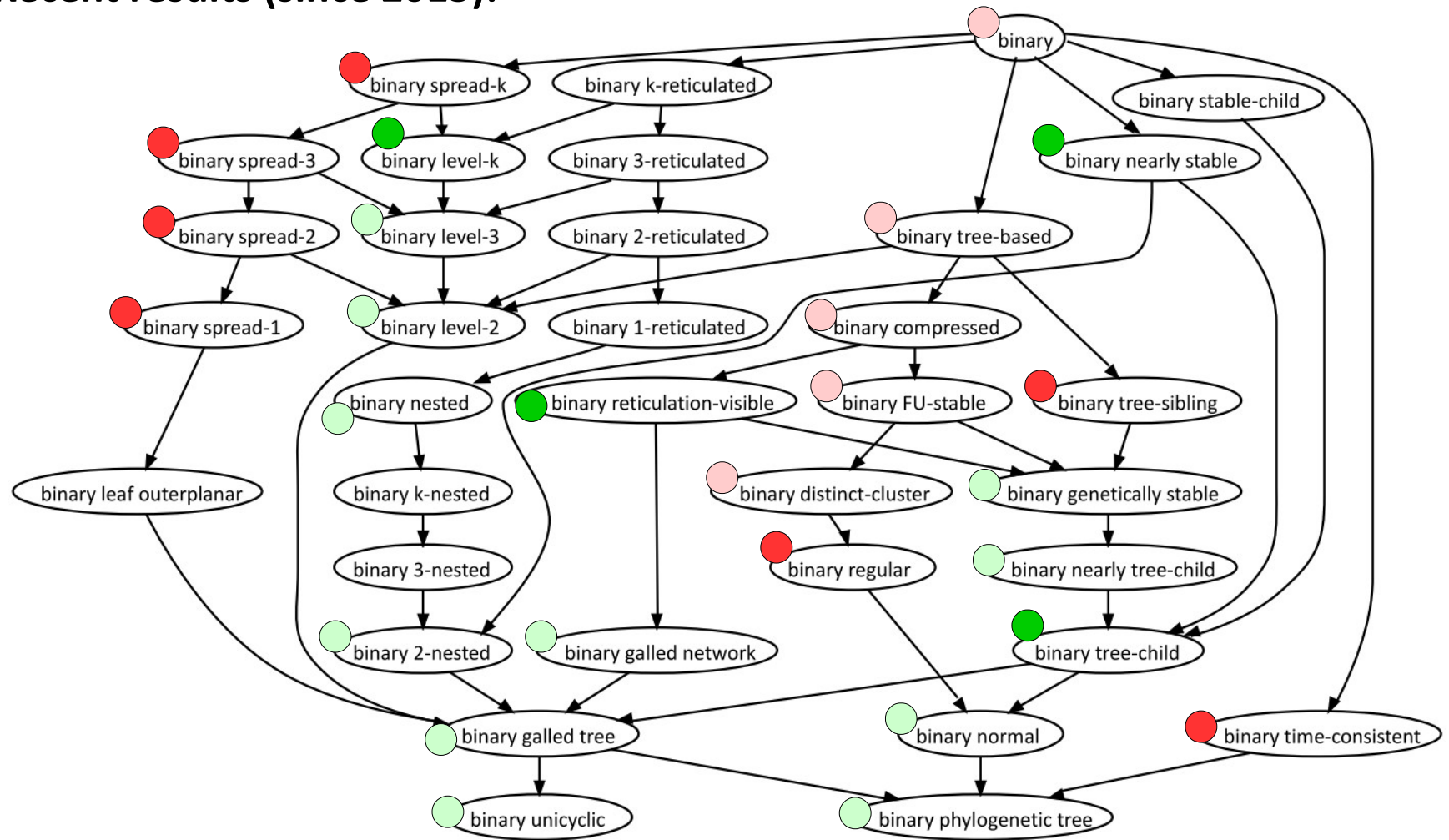
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**→  $N$  contains at most  $4(n-1)$  reticulation vertices**

# Classes of phylogenetic networks and the T.C.P.

Recent results (since 2015):



Bordewich & Semple, *Advances in Applied Mathematics*, 2016  
Gunawan, DasGupta & Zhang, RECOMB 2017  
Gunawan, AlCoB 2018  
Weller, RECOMB-CG 2018

# Fête de la Science at UPEM (science festival)



*Photos : Campus numérique de l'UPEM*

# Outline

- An introduction to phylogenetic networks
- Classes of phylogenetic networks
- Counting problems on phylogenetic networks

## Publications tagged with keyword(s)

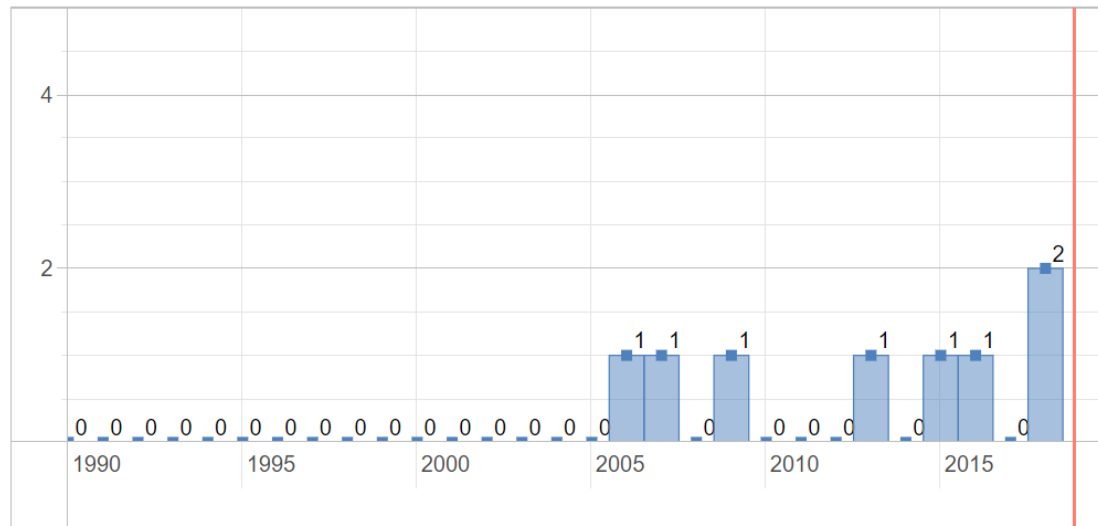
Choose a keyword to see the number of publications containing it over the years.

counting

Browse publications by keyword:

abstract network

Go



# Outline

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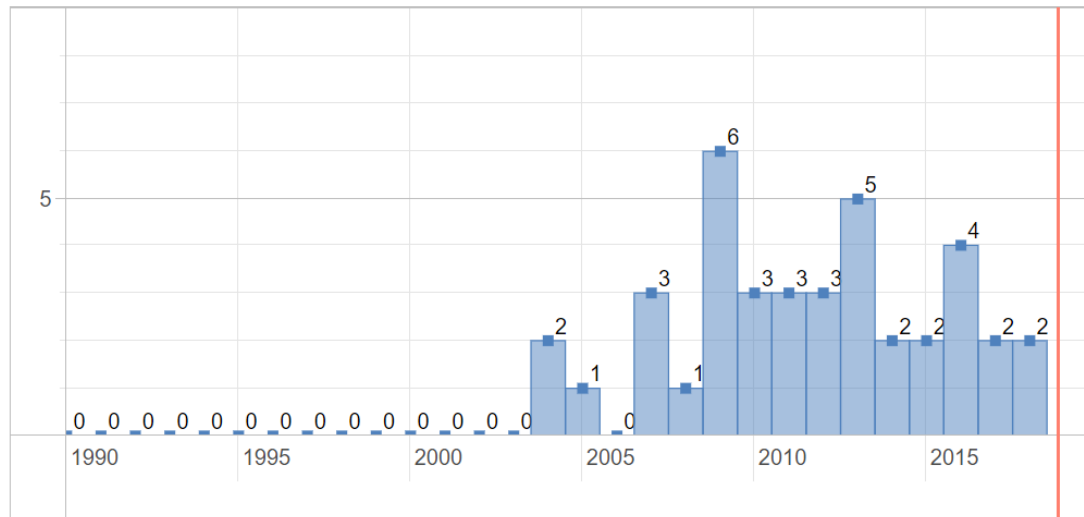
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FPT

Browse publications by keyword:

abstract network

Go



# Counting labeled unrooted level-1 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:

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## Pointing + bijection:

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



# Counting labeled unrooted level-1 networks

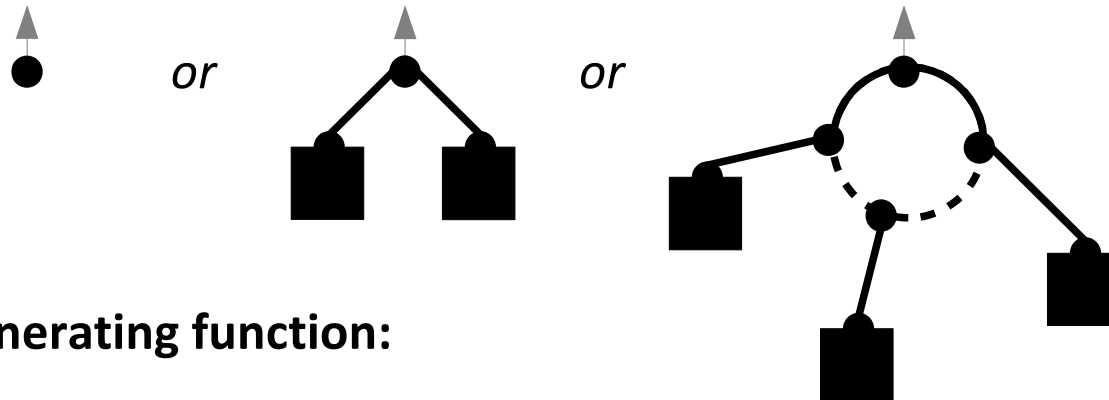
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## Recursive decomposition of pointed level-1 networks with $n$ leaves:



## Exponential generating function:

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

# Counting labeled unrooted level-1 networks

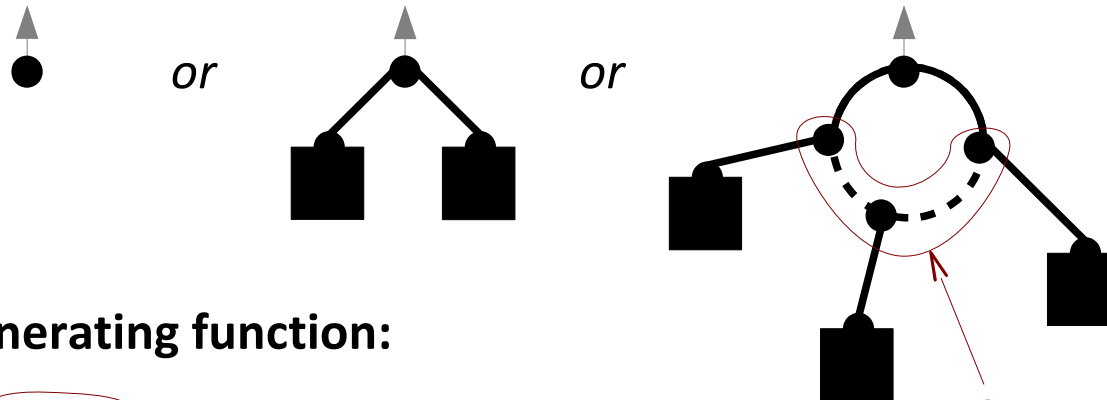
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$\text{Seq}_{\geq 2}$ , any direction

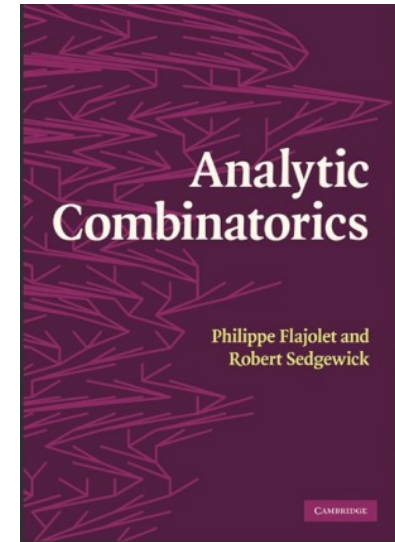
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Using the Singular Inversion Theorem (Theorem VI.6 of

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



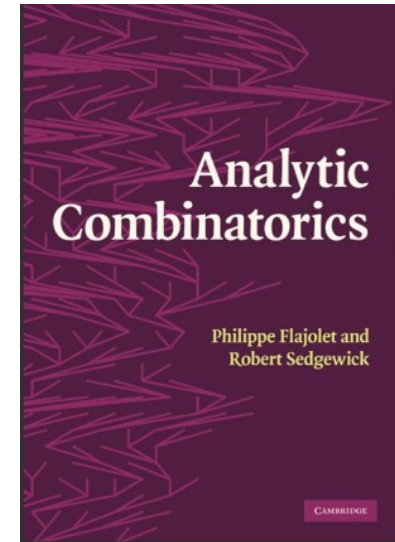
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**Proof :**

We write  $G = z \varphi(G)$ , with  $\varphi(z) = \frac{1}{1 - \frac{1}{2} z (1 + 1/(1-z))}$

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

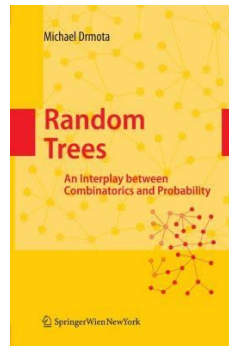
# Counting labeled unrooted level-1 networks

## Multivariate generating function:

$G(z, x, y) = \sum_{n,k,m} \frac{g_{n,k,m}}{n!} z^n x^k y^m$ , where  $g_{n,k,m}$  is the number of unrooted level-1 networks with  $n + 1$  leaves,  $k$  cycles, and  $m$  inner edges, satisfies

$$(\star_G) \quad G(z, x, y) = z + \frac{1}{2}G(z, x, y)^2 + \frac{1}{2}xy^3 \frac{G(z, x, y)}{1 - yG(z, x, y)}.$$

Using Theorem 2.23 of



**Proposition 4.4.** *Let  $X_n$  (resp.  $Y_n$ ) be the random variable counting the number of cycles (resp. inner edges) in unrooted level-1 networks with  $n + 1$  leaves. Both  $X_n$  and  $Y_n$  are asymptotically normally distributed, and more precisely, we have*

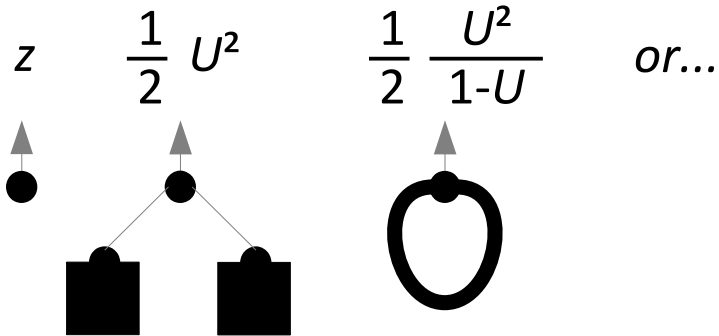
$$\mathbb{E}X_n = \mu_X n + O(1), \quad \text{Var}X_n = \sigma_X^2 n + O(1) \quad \text{and} \quad \frac{X_n - \mathbb{E}X_n}{\sqrt{\text{Var}X_n}} \xrightarrow{d} \mathcal{N}(0, 1),$$

$$\mathbb{E}Y_n = \mu_Y n + O(1), \quad \text{Var}Y_n = \sigma_Y^2 n + O(1) \quad \text{and} \quad \frac{Y_n - \mathbb{E}Y_n}{\sqrt{\text{Var}Y_n}} \xrightarrow{d} \mathcal{N}(0, 1),$$

where  $\mu_X \approx 0.46$ ,  $\sigma_X^2 \approx 0.18$ ,  $\mu_Y \approx 1.61$  and  $\sigma_Y^2 \approx 1.44$ .

# Counting labeled unrooted level-2 networks

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




— Seq<sub>≥1</sub>, any direction

■ Seq<sub>≥2</sub>, any direction

→ Seq<sub>≥1</sub>

➡ Seq<sub>≥2</sub>

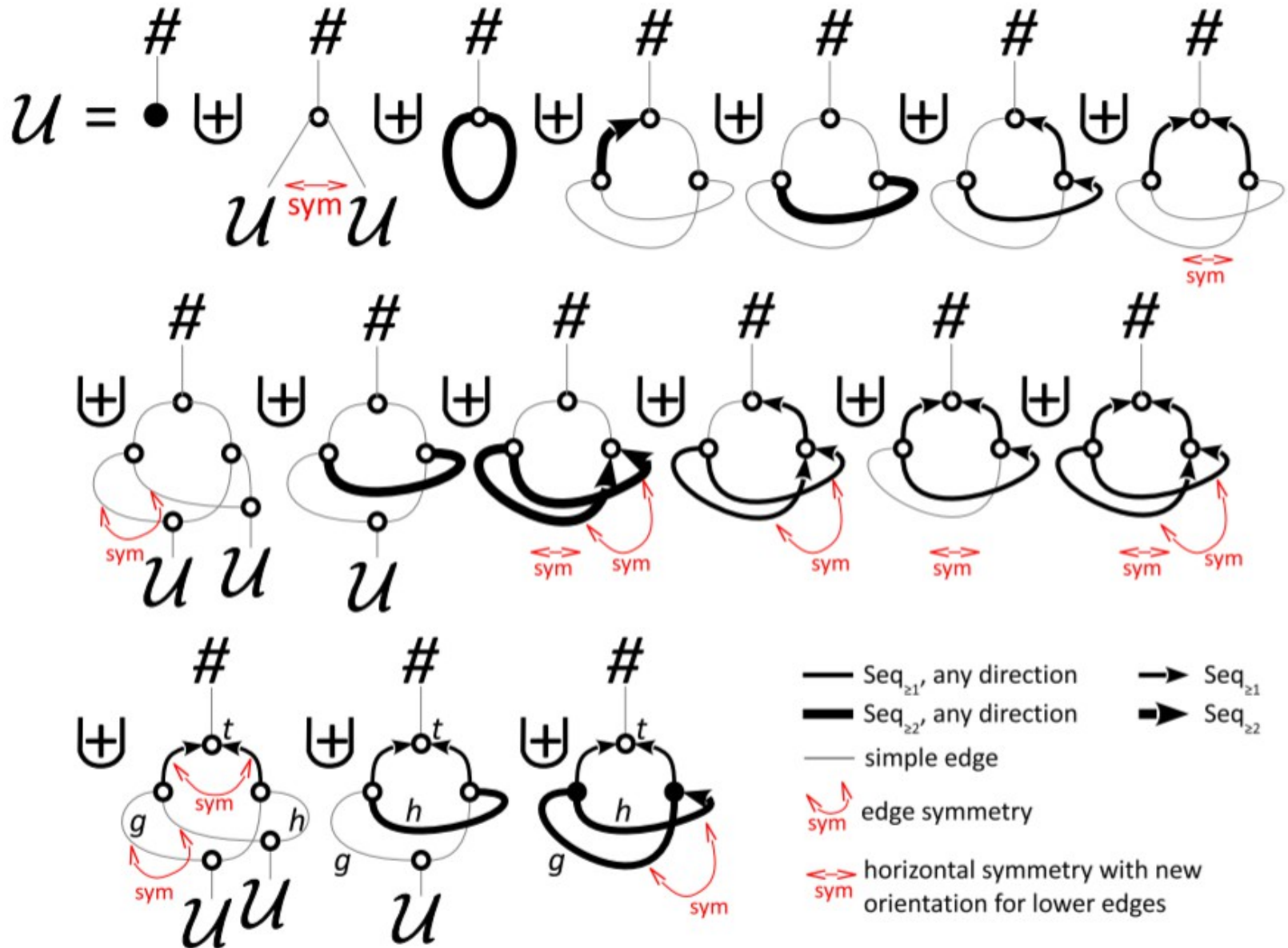
— simple edge

 edge symmetry



horizontal symmetry with  
new orientation for lower  
edges

# Counting labeled unrooted level-2 networks





# Counting labeled unrooted level-2 networks

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

$$\begin{aligned} U &= z + \frac{U^2}{2} + \frac{U^2}{2(1-U)} + \frac{U^2}{1-U} + \frac{U^2}{2(1-U)} + \frac{U^2}{(1-U)^2} + \frac{U^2}{2(1-U)^2} \\ &+ \frac{U^2}{2} + \frac{U^3}{2(1-U)} + \frac{U^4}{4(1-U)^2} + \frac{U^3}{2(1-U)^3} + \frac{U^3}{2(1-U)^2} + \frac{U^4}{2(1-U)^3} \\ &+ \frac{U^4}{4(1-U)^2} + \frac{U^5}{2(1-U)^3} + \frac{U^6}{4(1-U)^4} \end{aligned}$$

Rewrite:

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

# Counting labeled unrooted level-2 networks

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

$$\begin{aligned}
 U &= z + \frac{U^2}{2} + \frac{U^2}{2(1-U)} + \frac{U^2}{1-U} + \frac{U^2}{2(1-U)} + \frac{U^2}{(1-U)^2} + \frac{U^2}{2(1-U)^2} \\
 &+ \frac{U^2}{2} + \frac{U^3}{2(1-U)} + \frac{U^4}{4(1-U)^2} + \frac{U^3}{2(1-U)^3} + \frac{U^3}{2(1-U)^2} + \frac{U^4}{2(1-U)^3} \\
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Lagrange inversion:

$$u_n = n![z^n]U(z) = \frac{n!}{n}[z^{n-1}]\phi^n(z)$$

Taylor expansions of  $\varphi^n(z)$ :

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

# Counting labeled unrooted level-2 networks

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

$$\begin{aligned}
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$$u_n = n![z^n]U(z) = \frac{n!}{n}[z^{n-1}]\phi^n(z)$$

Taylor expansions + Newton formula

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

# 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:  $\approx 0.207 (1.890)^n n^{n-1}$

## 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

# Counting labeled level- $k$ networks

**Open problem on level-1 networks = galled trees:**

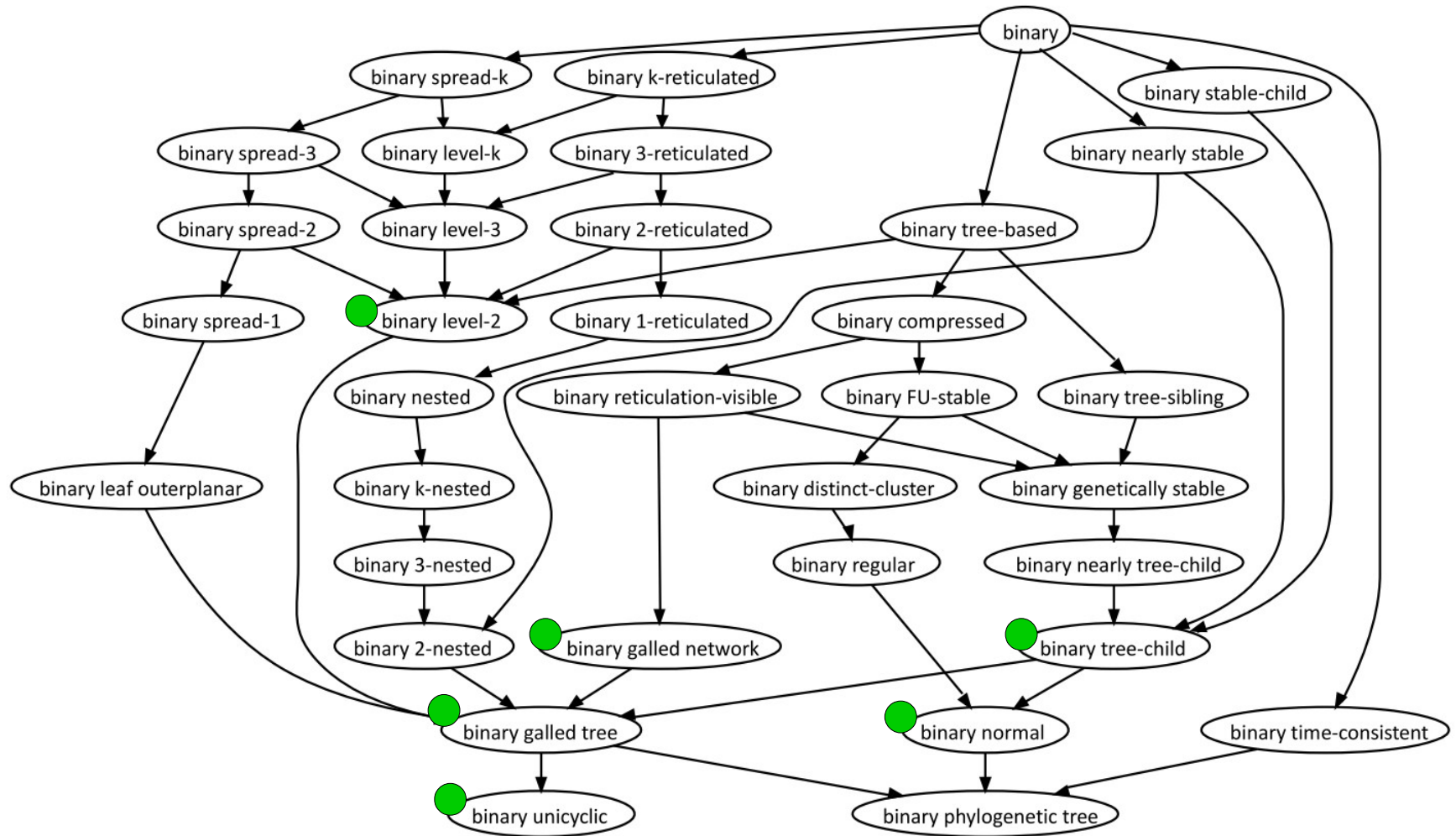
Counting galled tree “shapes” (= unlabeled networks)

Upper bound

Chang, Hon & Thankachan, Data Compression Conference 2018

Upper levels...

# Other phylogenetic network counting results

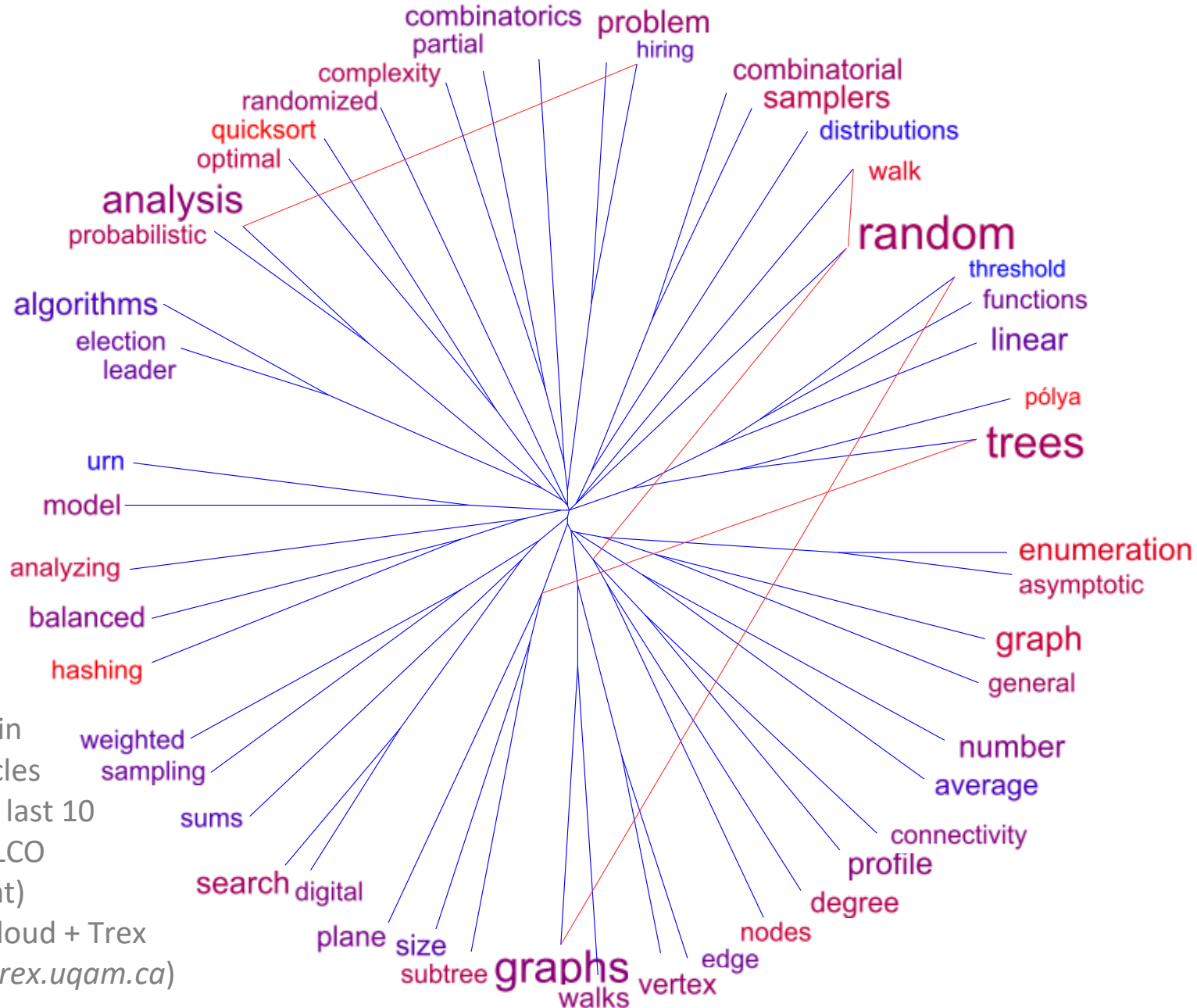


**Tree-child, normal networks:** McDiarmid, Semple & Welsh 2015

Fuchs, Gittenberger & Mansouri 2018

**Galled networks:** Louxin Zhang 2018

# Thank you for your attention!



Reticulogram  
of the 100 most  
frequent words in  
the titles of articles  
published in the last 10  
editions of ANALCO  
(red: most recent)  
Built with TreeCloud + Trex  
([treecloud.org](http://treecloud.org), [trex.uqam.ca](http://trex.uqam.ca))