Phylogenetic closure operations and homoplasy-free evolution

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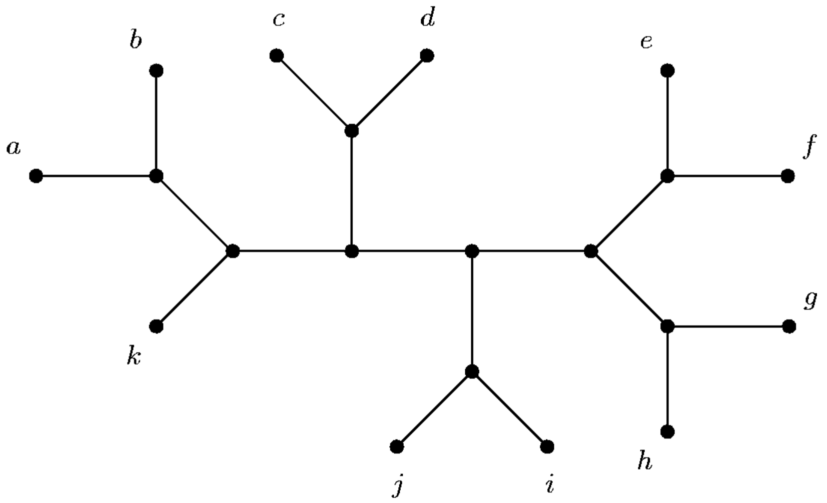
Mike Steel
Allan Wilson Centre for Molecular Biology and Evolution
Biomathematics Research Centre
University of Canterbury, Christchurch, New Zealand

Joint work with…

Phylogenetic trees

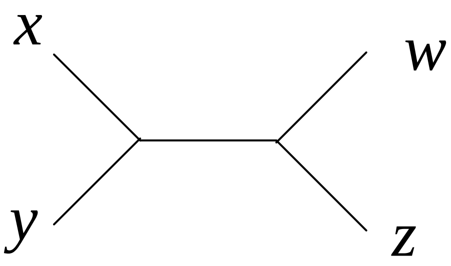
- [Definition] A **phylogenetic X-tree** is a tree *T*=(*V*,*E*) with a set *X* of labelled leaves, and all other vertices unlabelled and of degree $\geq$3.

- If all non-leaf vertices have degree 3 then *T* is **binary**

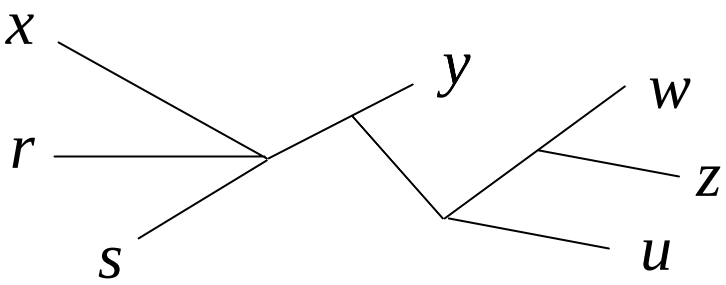


Quartet trees

- A **quartet tree** is a binary phylogenetic tree on 4 leaves (say, *x*,*y*,*w*,*z*) written *xy*|*wz*.



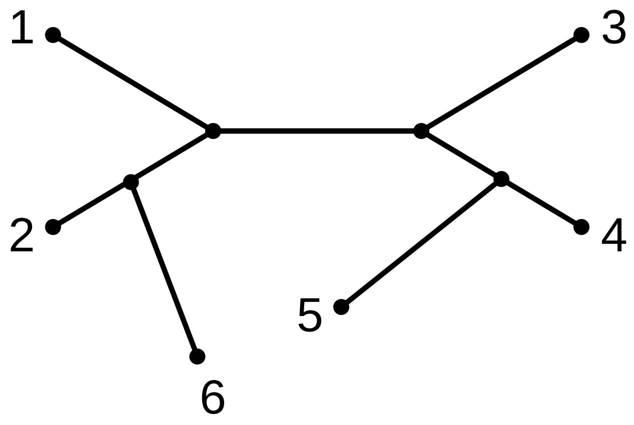
- A phylogenetic X-tree **displays** *xy*|*wz* if there is an edge in *T* whose deletion separates {*x*,*y*} from {*w*,*z*}



Compatibility

A set Q of quartets is compatible if there is a phylogenetic X-tree T that **displays** each quartet of Q

- Example: $Q=\{12|34, 13|45, 14|26\}$



Defining sets

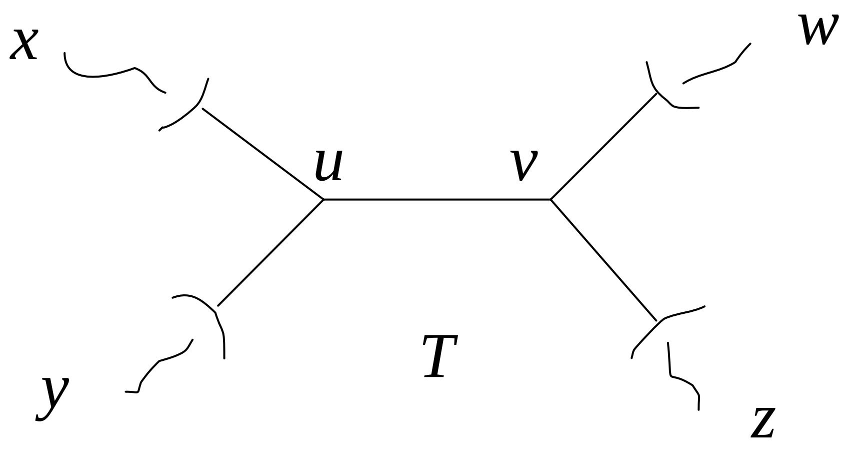
If *T* is the only phylogenetic *X*-tree that displays *Q* (and *X*= L(*Q*)) then we say *Q* **defines** *T* .

- Let *Q*(*T*) be the set of **all** quartets displayed by (any) *T*.

If *T* is binary, then *Q*(*T*) defines *T*.

A necessary condition for Q to define T

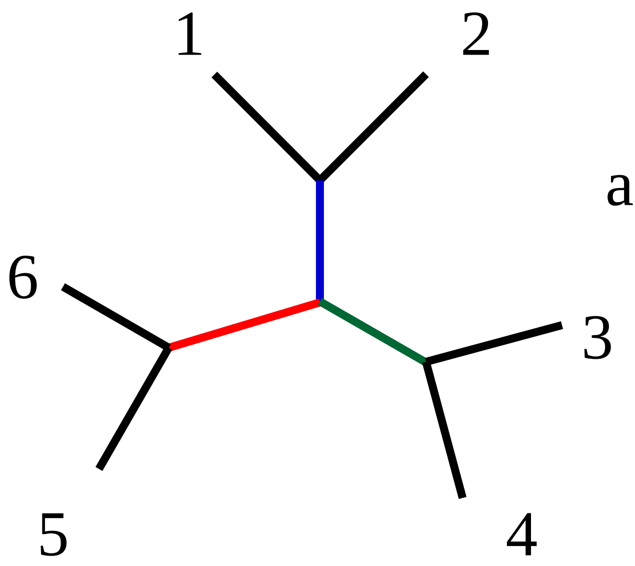
- **Definition:** For a binary phylogenetic tree T, a collection Q of induced quartet trees *distinguishes* an interior edge $\{u,v\}$ of T if there exists a quartet $xy|wz$ in Q that looks like this:



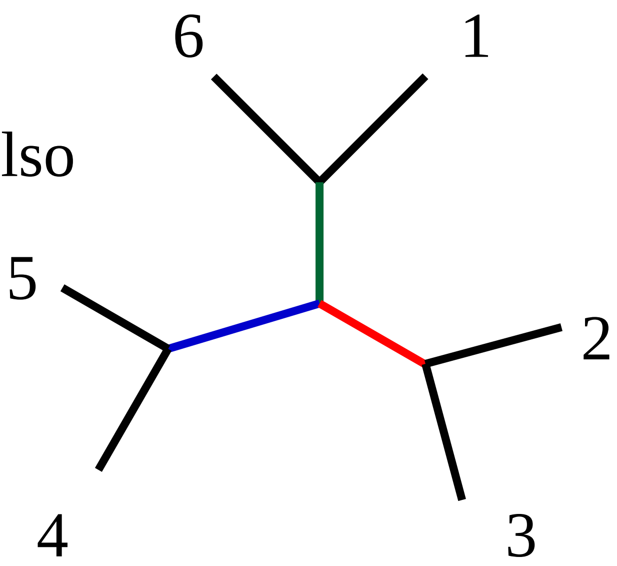
Observation: If Q defines T then T is binary and Q distinguishes every interior edge of T (so $|Q| \geq n-3$).

Warning:

Q ={12|45, 56|23, 34|16} distinguishes each interior edge of the tree:



and also



!

Sufficient condition for Q to define T:

- Suppose Q is compatible and distinguishes every interior edge of a binary phylogenetic X-tree T.

Proposition: If there is an element of X that is a leaf of every tree in Q then Q defines T.

Corollary:

There are subsets of $Q(T)$ that define T of size $|X|$-3.

Character data

Type	States	Transitions
Morphology	W(ings), $\neg W$, $-W$	$\neg W \rightarrow W \rightarrow -W$
Sequences	A,C,G,T	$x \leftrightarrow y$
Gene order	$g_1g_2g_3g_4g_5g_6g_7\cdots$	$g_1g_2\boxed{g_5g_4g_3}g_6g_7\cdots$
Gene content	$G = \{g_1,\ldots,g_k\}$	$+g_i/-g_i$
SINEs	$\ldots g \ldots$	$\ldots \rightarrow \ldots g \ldots \rightarrow \ldots ? \ldots$
Oligonucleotides	$\ldots g_1g_2g_3\ldots g_k\ldots = 1$	0 to 1 (once), 1 to 0

Definitions:

- [Character] A character is any function

$$f : X \to S$$

- [Convexity] Given a character $f : X \to S$

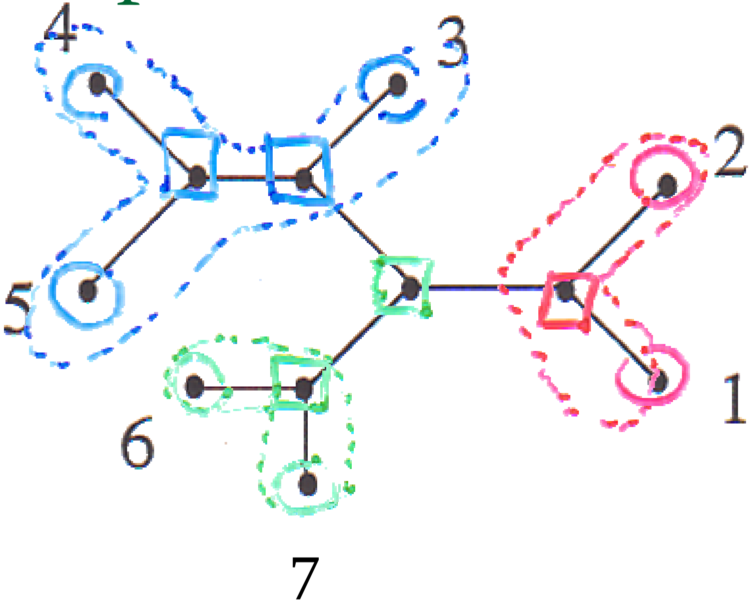
and a phylogenetic *X*-tree *T*=(*V*,*E*), we say *f* is **convex on *T***

if *f* extends to $f':V \to S$

so that $f'| X = f$

and $\{v \in V : f'(v) = s\}$ is connected for all *s* in *S*.

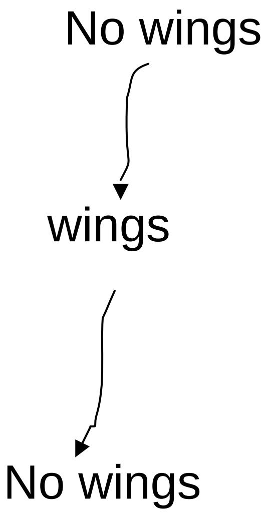
Convexity: example



x	1	2	3	4	5	6	7
$f(x)$	🔴	🔴	🔵	🔵	🔵	🟢	🟢

Biological significance of convexity

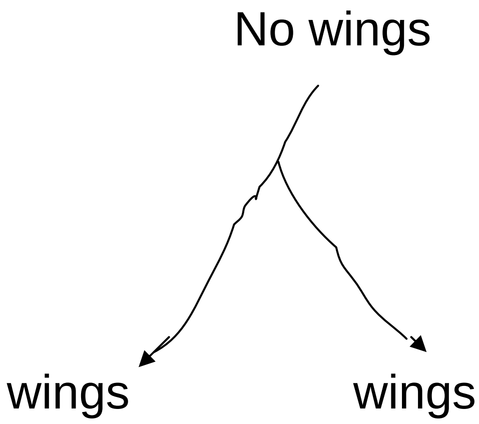
- Lemma: A character χ is convex on a phylogenetic tree T if and only if χ could have evolved on T (from any root vertex) without any **reversals** or **convergent evolution.**



No wings

wings

No wings



No wings

wings

wings

Relevance to genomics

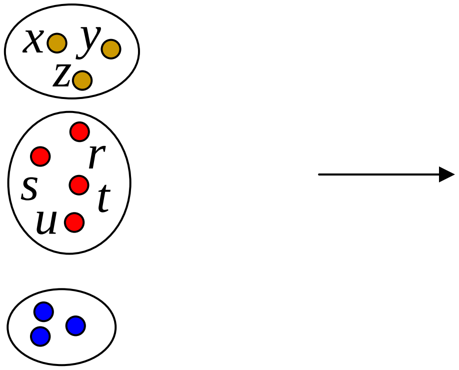
- Eg. gene order rearrangements (*n* species, *L* genes, random inversion model)

$$g_1 g_2 \boxed{g_3 g_4 g_5} g_6 g_7 \cdots \quad \Rightarrow \quad g_1 g_2 g_5 g_4 g_3 g_6 g_7 \cdots$$

$$P[h=0] \geq 1 - \frac{2(2n-3)(n-1)}{L(L-1)}$$

Equivalence of character and quartet compatibility

$$C \rightarrow Q(C)$$



$xy|rs$

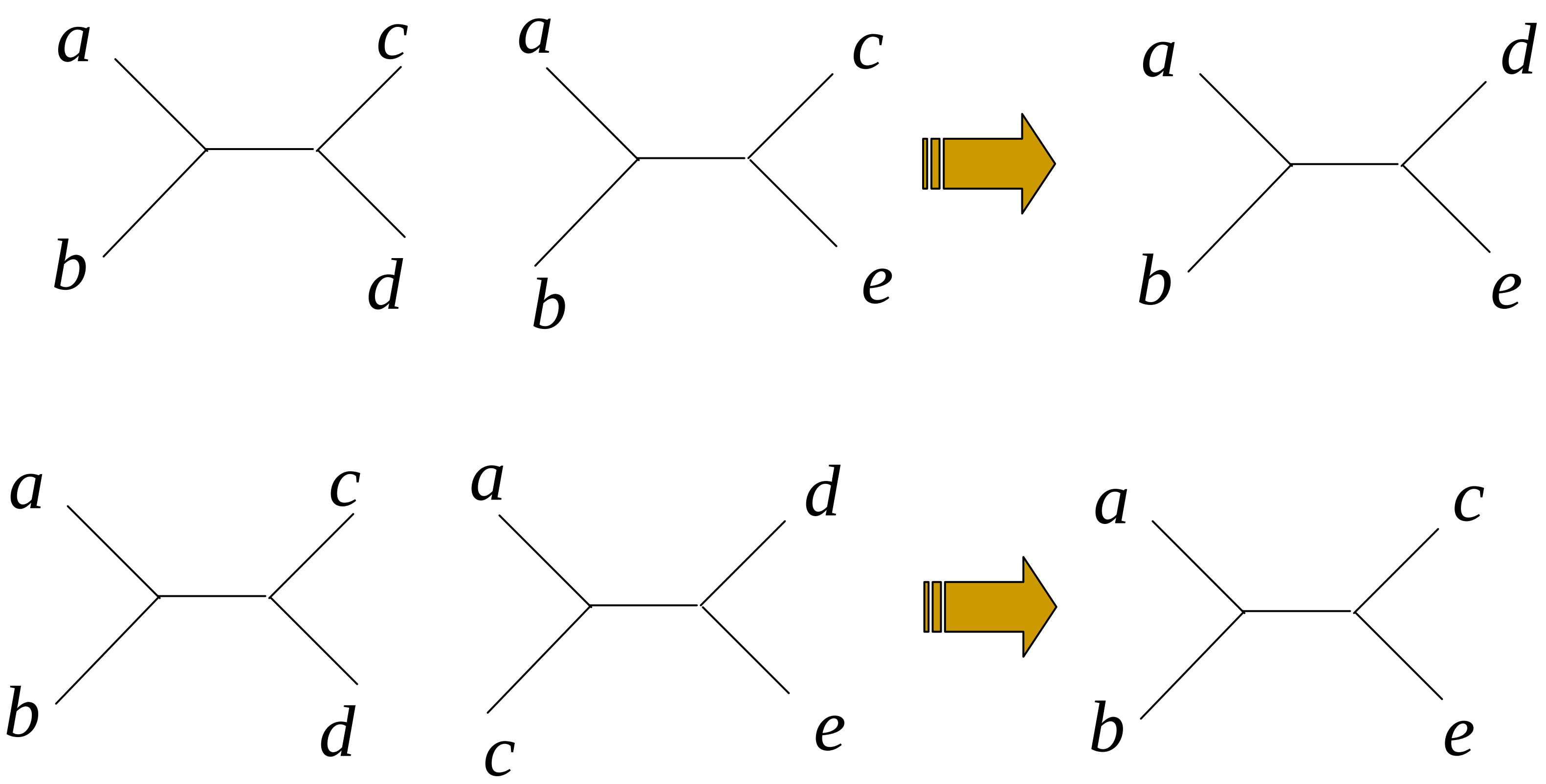
$xz|rs$

$xy|rt$

Lemma: Each character in C is convex on T if and only if T displays all the quartets in $Q(C)$.

[C is “compatible”, C “defines” T iff $Q(C)$ does]

New quartet trees from old ones



Dyadic rules for quartet trees

(Colonius and Schulze; Dekker)

(**Q1**): $\{ab|cd, ab|ce\} \vdash ab|de$

(**Q2**): $\{ab|cd, ac|de\} \vdash ab|ce, ab|de, bc|de.$

Any phylogenetic X–tree that displays the quartet trees on the left of (**Q1**) or (**Q2**) also displays the corresponding quartet tree(s) on the right.

Dyadic quartet closure

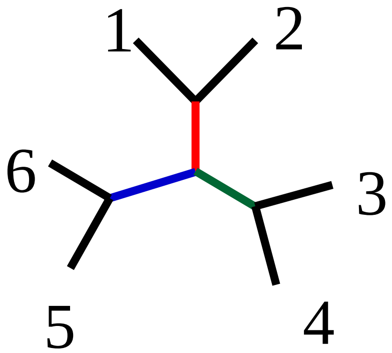
$$\mathcal{Q} = \mathcal{Q}_1 \subseteq \mathcal{Q}_2 \subseteq \cdots \subseteq \mathcal{Q}_m = \mathrm{qcl}_\theta(\mathcal{Q})$$

where $\mathcal{Q}_{i+1}$ consists of $\mathcal{Q}_i$ together with all additional quartets that can be obtained from a pair of quartets in $\mathcal{Q}_i$ by applying the rule(s) allowed by θ.

For $\theta \subseteq \{1, 2\}$, let the dyadic quartet closure under rule θ, $\mathrm{qcl}_\theta(\mathcal{Q})$, denote the minimal set of quartet trees that contains $\mathcal{Q}$ and is closed under rule (**Qi**) for each $i \in \theta$.
We denote these closures with: $\mathrm{qcl}_1(\mathcal{Q}), \mathrm{qcl}_2(\mathcal{Q}), \mathrm{qcl}_{1,2}(\mathcal{Q})$.

Example 1: qcl_2

Definition: If Q distinguishes every interior edge of a binary phylogenetic tree T and we can order Q so that each quartet tree in the ordering introduces precisely one new leaf label, we say Q has a **tight ordering** for $\boldsymbol{T}$.



Example: {12|35, 13|56, 15|34}.

Proposition:

If Q has a tight ordering for T, then $\mathrm{qcl}_2(Q) = Q(T)$

In particular Q defines T.

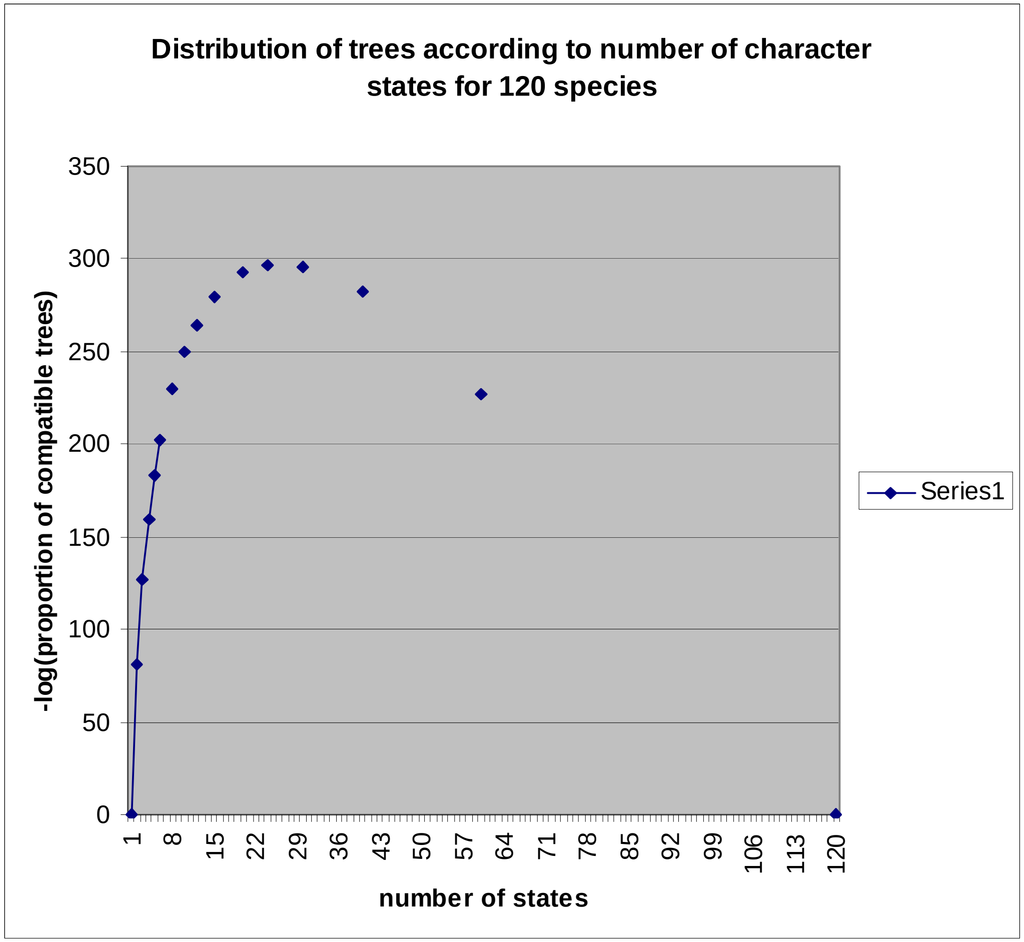
Application: How many characters are needed to define a binary phylogenetic *X*-tree?

- For binary characters we need *n*-3 (*n*=|*X*|).
- For *r*-state characters (*r* fixed) we need at least

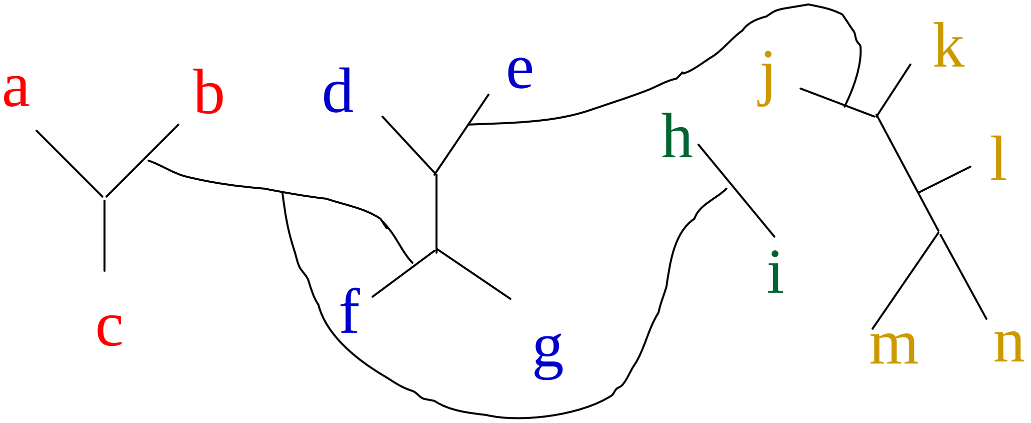
  (*n*-3)/(*r*-1)
- What if *r* is not fixed?

(it is not useful to make *r* too large!)

I(χ) := - log(Pr[χ is convex on random T])



Where do these numbers come from?

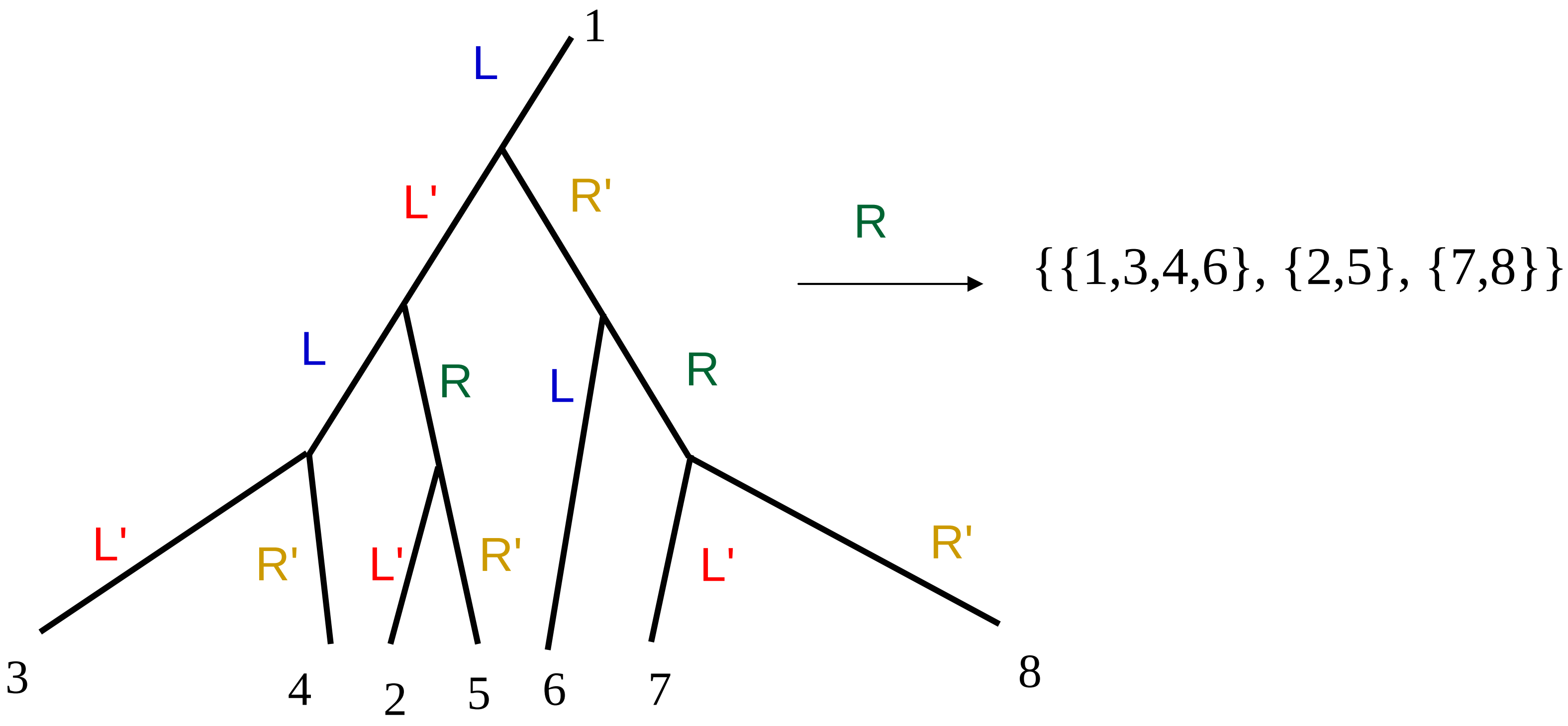


Carter *et al.* (1990); Erdös & Székely (1993).

# binary phylogenetic trees with n leaves, $b(n) = 1\times 3\times\cdots\times(2n-5)$

# of these on which χ is convex = $b(n)\prod_{i=1}^{r} b(a_i+1) \Big/ b(n-r+2)$

Edge-colouring a tree by $Z_2 \times Z_2$



{{1,3,4,6}, {2,5}, {7,8}}

Theorem (Huber, Moulton, S, 2003)

Q(*C*) contains a subset with a tight ordering for *T*.

Thus for any tree there is a set of just ***four*** characters that defines *T*.

Distances or characters?

- $d_C(i,j)$ = # characters in C on which i and j differ

If C is compatible is d_C tree-like?

C binary – yes.
C non-binary no.

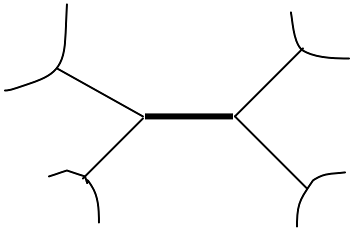
Theorem [Huson and S, 2003]:

For any two trees T_1, T_2 there is a set of multi-state characters C such that

- C defines T_1 (i.e. C homoplasy-free only on T_1) yet
- d_C is tree-like (and ultrametric!), but only on T_2.

Application 2: "Short" quartets

- $Q_{\text{short}}(T)$



- **Theorem** (Erdös *et al.* 1997)

$Q_{\text{short}}(T)$ contains a subset that has a tight ordering for T (and so $\text{qcl}_2(Q_{\text{short}}(T)) = Q(T)$).

- The number of characters required to reconstruct (wp >1-ε) a binary phylogenetic tree with n leaves from binary characters generated under a finite Markov process is (for almost all trees) at most

$$k \geq \frac{c_\varepsilon (\log(n))^{d(p)}}{a^2}$$

A further application involving qcl$_2$:

We say Q is **excess-free** if |L(Q)|-3-|Q| = 0.

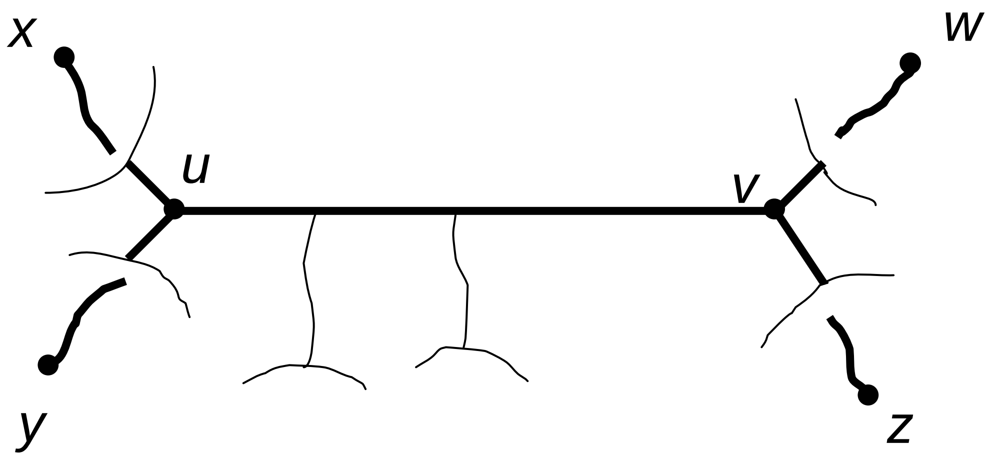
- **Proposition:** Suppose a subset Q of $Q(T)$ contains an excess-free subset Q_0 that defines T. Then qcl$_2$(Q)=Q(T).

- Why? Let us say a set Q of quartet trees is “good” if (i) Q defines a phylogenetic tree, and (ii) exc(Q)=0.

  Theorem [Bocker, Dress 1999] Any good set of ($\geq$2) quartets is the disjoint union of precisely two good sets.

Example 2: qcl_1

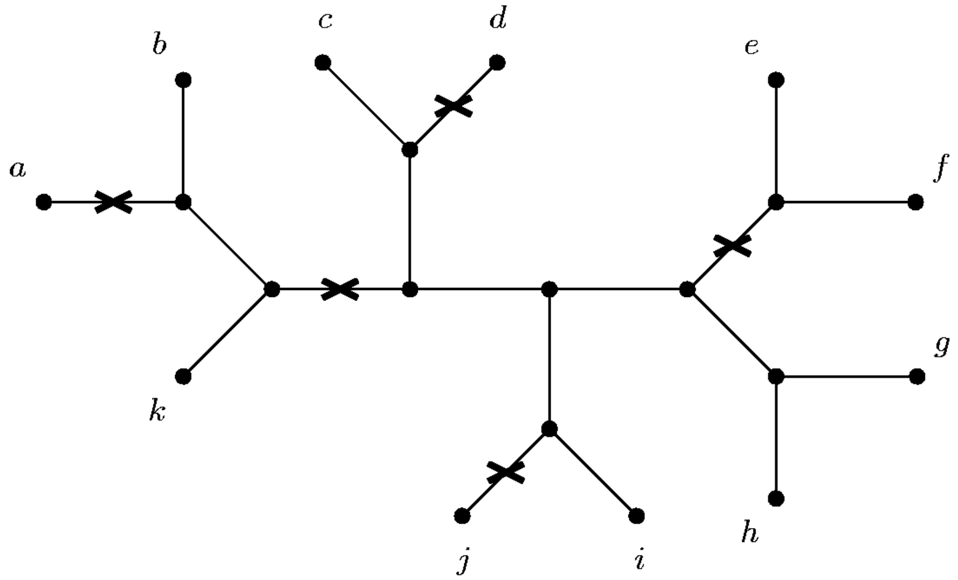
- **Definition:** For a binary phylogenetic tree *T*, a collection *Q* of displayed quartet trees is a *generous cover* for *T* if for all pairs *u*,*v* of interior vertices of *T*, we have a quartet *xy*|*wz* in *Q* that looks like this:



Theorem (Dezulian + S, 2003): If *Q* is a generous cover for *T*, then $\mathrm{qcl}_1(T) = Q\ (T)$. Thus *Q* defines T.

Application: the random cluster model

Random process on a phylogenetic tree $\mathcal{T}$. Independently cutting edges with probability $p(e)$ generates , by connectivity, random characters on $\mathcal{T}$.



Cutting the marked edges yields the character $\{a|bk|cghi|d|ef|j\}$.

Reconstructing *T* from *k* independent characters (bounds and phase transition)

- Theorem (Mossel and S, 2003) For random cluster model, if
- $0 < a \leq p(e) \leq p < 0.5$, every binary phylogenetic tree with *n* leaves can be reconstructed with probability at least 1-ε from *k* indep. characters if

$$k \geq \frac{c_{p,\varepsilon} \log(n)}{a}$$

- A fast (polynomial-time) algorithm to reconstruct *T* from the characters.
- Proof uses generous cover result. Doesn't require i.i.d.
- Lower bound: log(*n*) needed (not trivial) and polynomial (*n*) if p>0.5.
- *cf.* finite-state $k \geq \frac{c_\varepsilon (\log(n))^{d(p)}}{a^2}$

Relevance to finite-state space?

Corollary:

Random walk on group with generating set of size

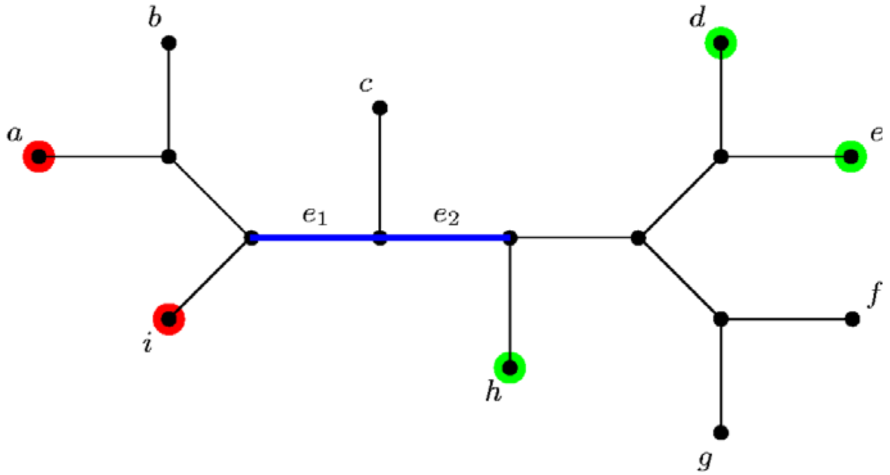
$$d \geq c_\varepsilon n^2 \log(n)$$

then *T* can be reconstructed w.p. > 1-ε with a Θ(log(n)) number of characters

Application 3: qcl_1, qcl_2, $\mathrm{qcl}_{1,2}$

[Definition] A **partial X-split** $A|B$ is a partition of a subset into two non-empty sets, A,B. $A|B$ is **displayed** by T if we can remove an edge from T to separate A from B.

Example: {a,i}|{d,e,h} is displayed by T.



Meacham‘s dyadic rules for splits (1983)

(**M1**): If $A_1 \cap A_2 \neq \emptyset$ and $B_1 \cap B_2 \neq \emptyset$ then

$$\{A_1|B_1, A_2|B_2\} \vdash A_1 \cap A_2 | B_1 \cup B_2, A_1 \cup A_2 | B_1 \cap B_2.$$

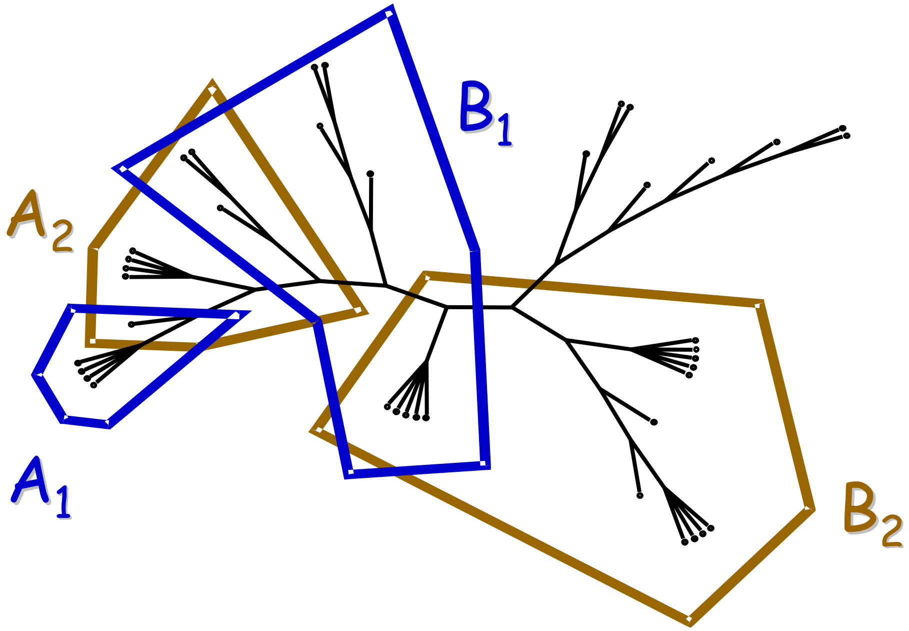
(**M2**): If $A_1 \cap A_2 \neq \emptyset$ and $B_1 \cap B_2 \neq \emptyset$ and $A_1 \cap B_2 \neq \emptyset$ then

$$\{A_1|B_1, A_2|B_2\} \vdash A_2|B_1 \cup B_2, A_1 \cup A_2|B_1.$$

Any phylogenetic X–tree that displays the partial X–splits on the left of (**M1**) or (**M2**) also displays the corresponding partial X–splits on the right.

Illustration of (M2)

$$\frac{A_1}{B_1} \quad \frac{A_2}{B_2} \longrightarrow \frac{A_1}{B_1 \cup B_2} \, , \quad \frac{A_1 \cup A_2}{B_2}$$



Dyadic split closure

$$\Sigma = \Sigma_1 \subseteq \Sigma_2 \subseteq \cdots \subseteq \Sigma_m = \mathrm{spcl}_\theta(\Sigma)$$

where Σ_{i+1} consists of Σ_i together with all additional splits that can be obtained from a pair of splits in Σ_i by applying the rule(s) allowed by θ.

For $\theta \subseteq \{1, 2\}$, let the dyadic split closure under rule θ, $\mathrm{spcl}_\theta(\Sigma)$, denote the minimal set of splits that contains Σ and is closed under rule (**Mi**) for each $i \in \theta$.
We denote these closures with: $\mathrm{spcl}_1(\Sigma), \mathrm{spcl}_2(\Sigma), \mathrm{spcl}_{1,2}(\Sigma)$.

The (almost) happy marriage

$$\begin{tikzcd}
\Sigma \arrow[r, "\mathcal{Q}"] \arrow[d, "\mathrm{spcl}_\theta"'] & \mathcal{Q}(\Sigma) \arrow[d, "\mathrm{qcl}_\theta"] \\
\mathrm{spcl}_\theta(\Sigma) \arrow[r, "\mathcal{Q}"] & (*)
\end{tikzcd}$$

?

The (almost) happy marriage

$$\begin{tikzcd}
\Sigma \arrow[r, "\mathcal{Q}"] \arrow[d, "\mathrm{spcl}_\theta"'] & \mathcal{Q}(\Sigma) \arrow[d, "\mathrm{qcl}_\theta"] \\
\mathrm{spcl}_\theta(\Sigma) \arrow[r, "\mathcal{Q}"] & (*)
\end{tikzcd}$$

Theorem 2.1. *Let Σ be a collection of partial X–splits. Then,*

$$\mathrm{qcl}_\theta(\mathcal{Q}(\Sigma)) = \mathcal{Q}(\mathrm{spcl}_\theta(\Sigma))$$

for $\theta = \{1\}$ and $\theta = \{1, 2\}$. For $\theta = \{2\}$ we have

$$\mathrm{qcl}_\theta(\mathcal{Q}(\Sigma)) \subseteq \mathcal{Q}(\mathrm{spcl}_\theta(\Sigma))$$

and containment can be strict.

The closure of a set of quartets

For a compatible set $\mathcal{Q}$ of quartet trees, the *closure* $\mathrm{cl}(\mathcal{Q})$ is defined as

$$\mathrm{cl}(\mathcal{Q}) = \bigcap_{\mathcal{T} \in \mathrm{co}(\mathcal{Q})} \mathcal{Q}(\mathcal{T})$$

where $\mathrm{co}(\mathcal{Q})$ is the set of phylogenetic trees that display each of the trees in $\mathcal{Q}$.

Thus $\mathrm{cl}(\mathcal{Q})$ consists of precisely those quartet trees that are displayed by every phylogenetic tree that displays $\mathcal{Q}$.

- Rules of order $<p$ (for any fixed p) do not suffice compute cl(Q).

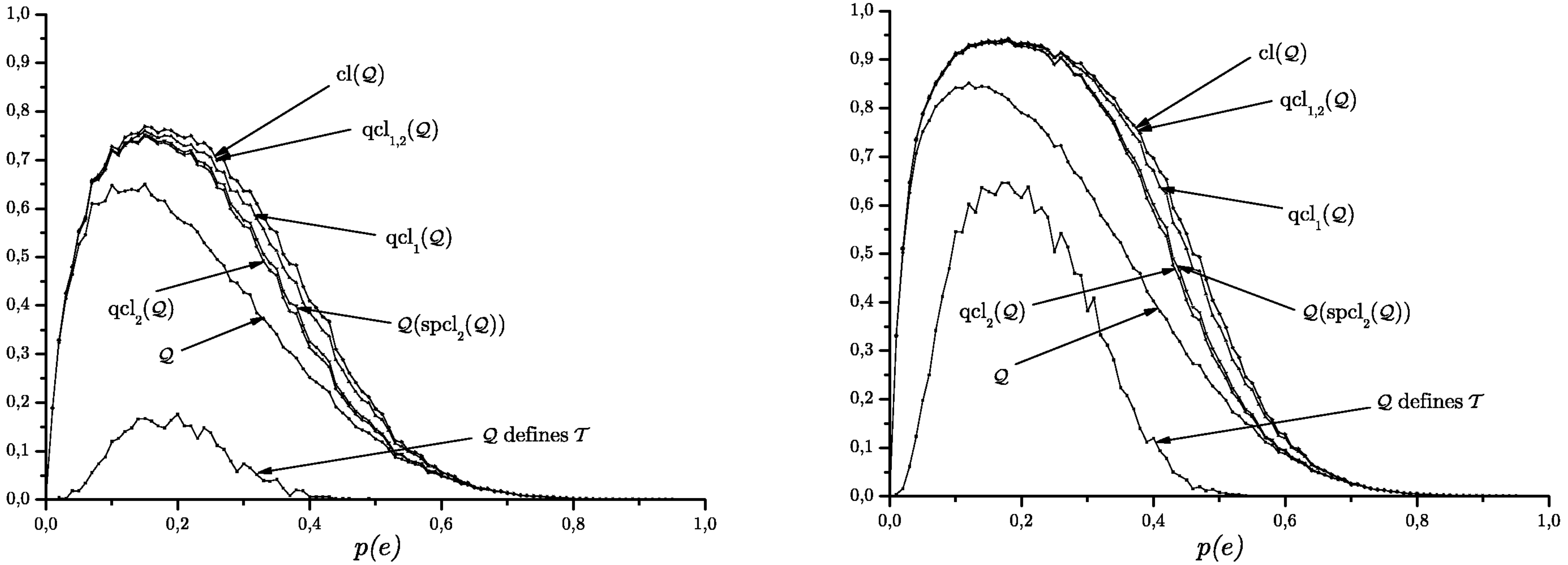
- There is a set Q that is incompatible but every strict subset Q' is compatible and satisfies cl(Q')=Q'

Simulation study

- Random cluster model for binary trees on $n=8$ leaves.

- *Main question:* How much of cl(Q) does qcl$_\theta$(Q) provide? (for $\theta=\{1\}, \{2\}, \{1,2\}$).

Simulations 1 (n=8, k=16,32): absolute quartet closure gains

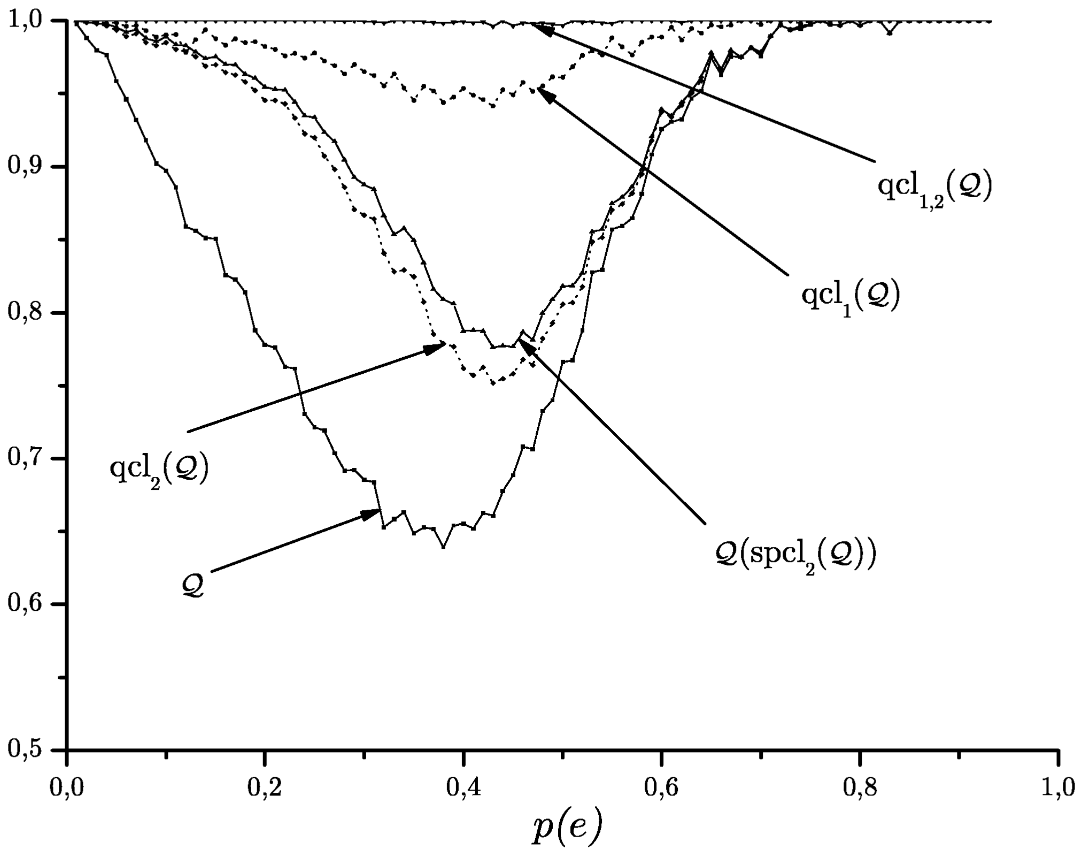


(a) The case $k = 16$.

(b) The case $k = 32$.

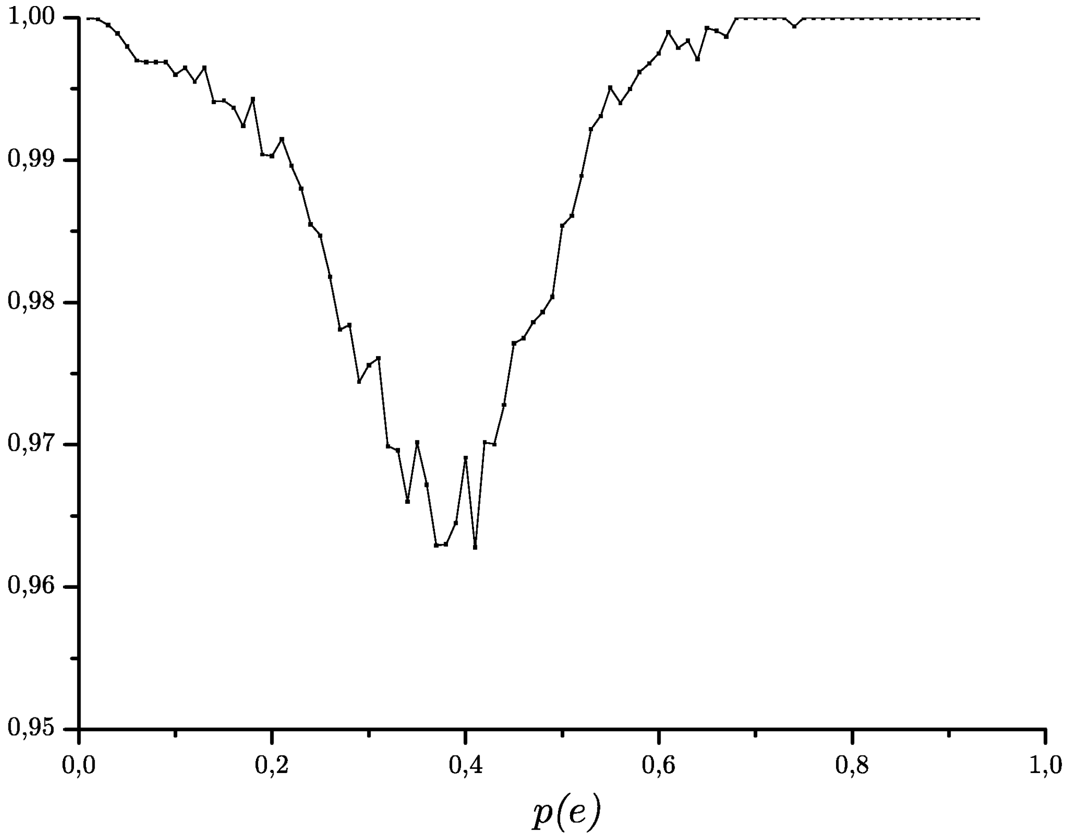
$$\frac{|\mathcal{Q}|}{\binom{n}{4}}, \frac{|\mathrm{qcl}_1(\mathcal{Q})|}{\binom{n}{4}}, \frac{|\mathrm{qcl}_2(\mathcal{Q})|}{\binom{n}{4}}, \frac{|\mathcal{Q}(\mathrm{spcl}_2(\mathcal{Q}))|}{\binom{n}{4}}, \frac{|\mathrm{qcl}_{1,2}(\mathcal{Q})|}{\binom{n}{4}}, \frac{|\mathrm{cl}(\mathcal{Q})|}{\binom{n}{4}}$$

Simulations 2: Relative quartet closure gains



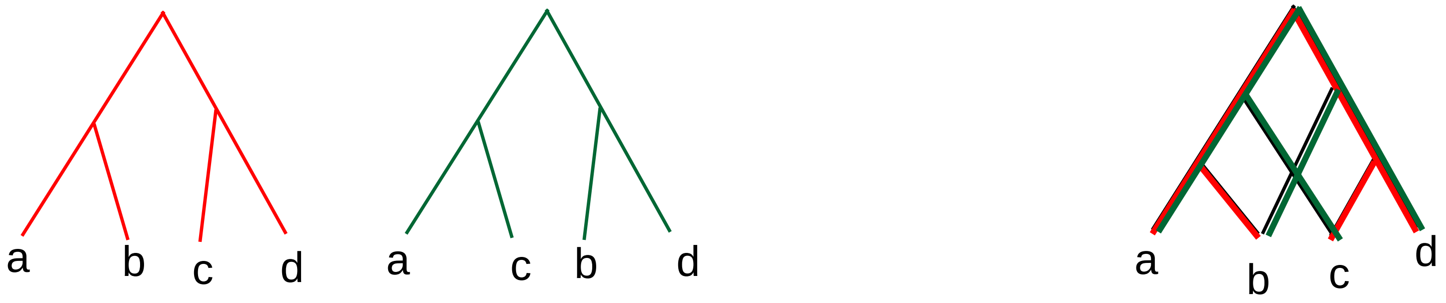
$$\frac{|\mathcal{Q}|}{|\mathrm{cl}(\mathcal{Q})|}, \frac{|\mathrm{qcl}_1(\mathcal{Q})|}{|\mathrm{cl}(\mathcal{Q})|}, \frac{|\mathrm{qcl}_2(\mathcal{Q})|}{|\mathrm{cl}(\mathcal{Q})|}, \frac{|\mathcal{Q}(\mathrm{spcl}_2(\mathcal{Q}))|}{|\mathrm{cl}(\mathcal{Q})|}, \frac{|\mathrm{qcl}_{1,2}(\mathcal{Q})|}{|\mathrm{cl}(\mathcal{Q})|}$$

Simulations 3: dyadic closure of splits and quartets comparison



$$\frac{|\mathrm{qcl}_2(\mathcal{Q})|}{|\mathcal{Q}(\mathrm{spcl}_2(\mathcal{Q}))|}$$ graphed against $p(e)$

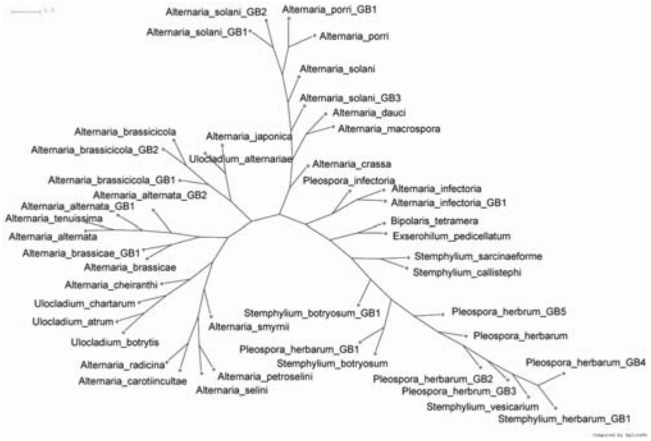
An application of spcl$_2$

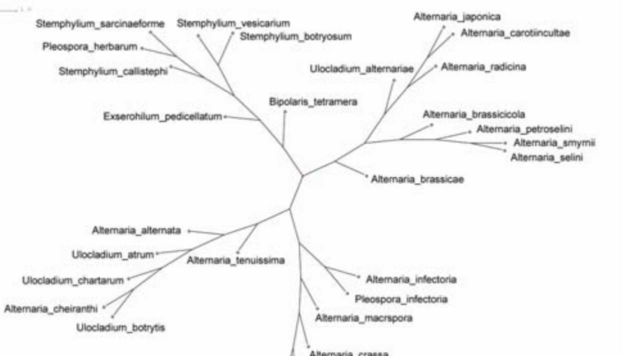


Networks can represent:

- Reticulate evolution (eg. hybrid species)
- Phylogenetic uncertainty (i.e. possible alternative trees)

Approach: *Given* $T_1, \ldots, T_k$ on overlapping sets of species,
let $\Sigma = \Sigma(T_1) \cup \cdots \cup \Sigma(T_k)$
construct spcl$_2$(Σ) and construct the
'splits graph' of the resulting splits that are 'full'.


Alternaria_solani_GB2
Alternaria_porri_GB1
Alternaria_solani_GB1
Alternaria_porri
Alternaria_solani
Alternaria_solani_GB3
Alternaria_dauci
Alternaria_macrospora
Alternaria_brassicicola
Alternaria_japonica
Alternaria_brassicicola_GB2
Ulocladium_alternariae
Alternaria_crassa
Alternaria_brassicicola_GB1
Pleospora_infectoria
Alternaria_infectoria
Alternaria_alternata_GB2
Alternaria_infectoria_GB1
Alternaria_alternata_GB1
Alternaria_tenuissima
Bipolaris_tetramera
Alternaria_alternata
Exserohilum_pedicellatum
Alternaria_brassicae_GB1
Stemphylium_sarcinaeforme
Alternaria_brassicae
Stemphylium_callistephi
Alternaria_cheiranthi
Ulocladium_chartarum
Stemphylium_botryosum_GB1
Pleospora_herbrum_GB5
Ulocladium_atrum
Alternaria_smyrnii
Pleospora_herbarum
Ulocladium_botrytis
Pleospora_herbarum_GB1
Stemphylium_botryosum
Pleospora_herbarum_GB4
Alternaria_radicina
Alternaria_petroselini
Pleospora_herbarum_GB2
Alternaria_carotiincultae
Alternaria_selini
Pleospora_herbrum_GB3
Stemphylium_vesicarium
Stemphylium_herbarum_GB1


Stemphylium_sarcinaeforme
Stemphylium_vesicarium
Alternaria_japonica
Stemphylium_botryosum
Alternaria_carotiincultae
Pleospora_herbarum
Stemphylium_callistephi
Ulocladium_alternariae
Alternaria_radicina
Bipolaris_tetramera
Exserohilum_pedicellatum
Alternaria_brassicicola
Alternaria_petroselini
Alternaria_smyrnii
Alternaria_selini
Alternaria_brassicae
Alternaria_alternata
Ulocladium_atrum
Alternaria_tenuissima
Ulocladium_chartarum
Alternaria_infectoria
Alternaria_cheiranthi
Pleospora_infectoria
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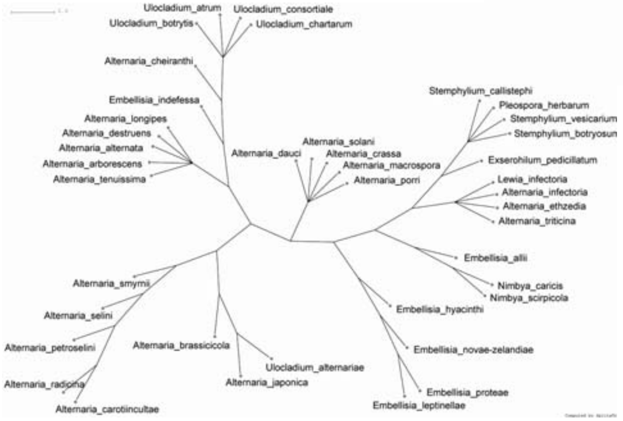
Alternaria_solani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Alternaria_destruens
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Alternaria_crassa
Alternaria_arborescens
Alternaria_macrospora
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Alternaria_tenuissima
Alternaria_porri
Lewia_infectoria
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Embellisia_allii
Alternaria_smyrnii
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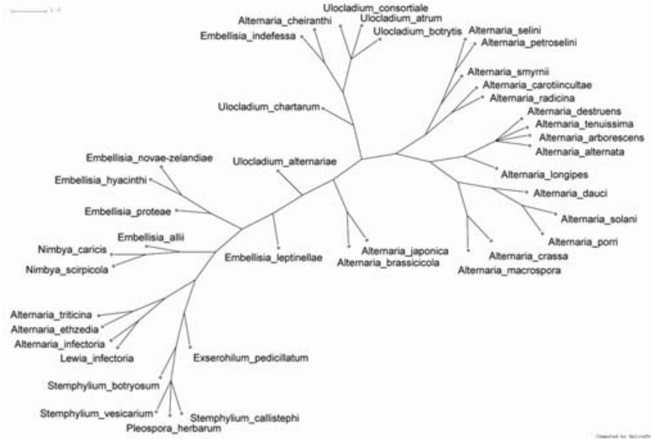
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Alternaria_ethzedia
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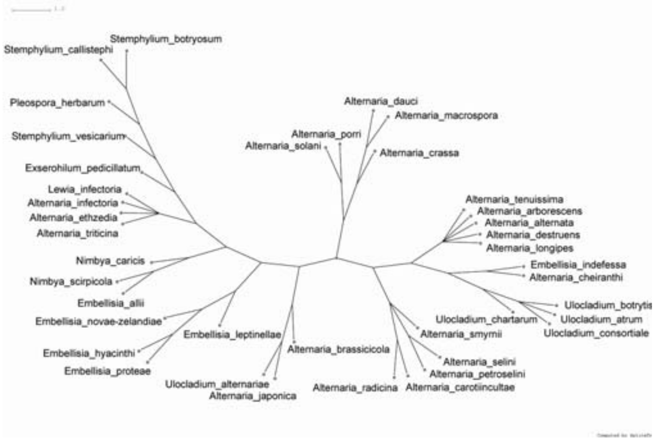
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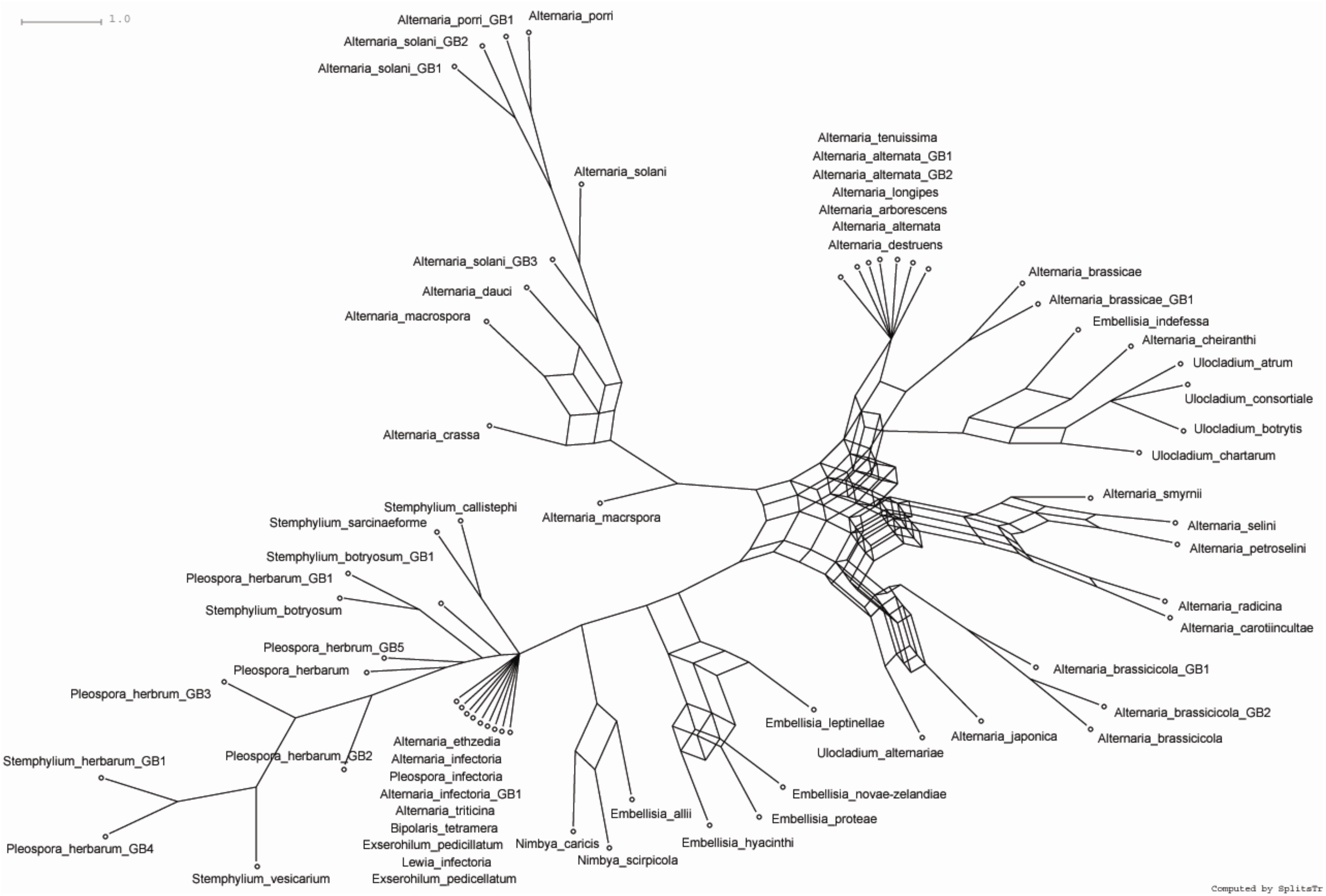
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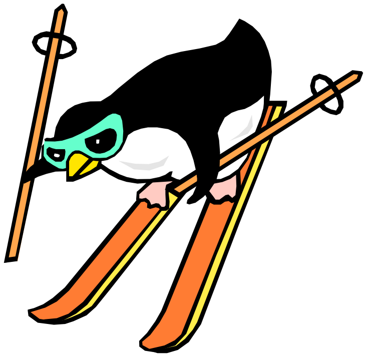

The end

Further details

- A phase transition for a random cluster model on phylogenetic trees. E. Mossel and M. Steel, *Mathematical Biosciences*, 187 (2004), 189-203.
- Phylogenetic closure operations, and homoplasy-free evolution, T. Dezulian and M. Steel *Proceedings of the International Federation of Classification Societies*, Chicago, 2004.
- Four characters suffice to convexly define a phylogenetic tree. K. Huber, V. Moulton and M. Steel (2003). Submitted.
- How much can evolved characters tell us about the tree that generated them? E. Mossel and M. Steel, Book chapter (Oxford University Press).
- Phylogenetic super-networks from partial trees. D. H. Huson, T. Dezulian, T. Kloepper and M. A. Steel, To appear in *WABI 2004*.