Distinguishing Convergence Periods on Phylogenetic Networks

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University of Tasmania

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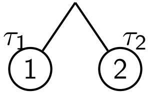
Introduction



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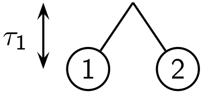

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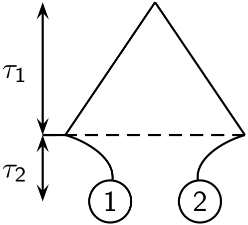

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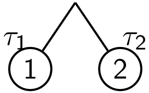

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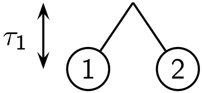

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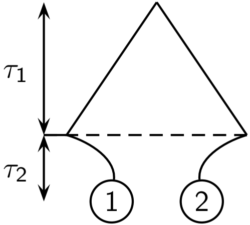

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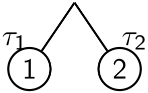

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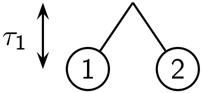

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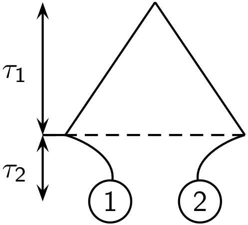

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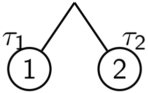

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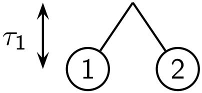

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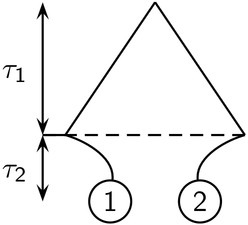

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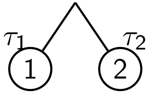

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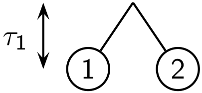

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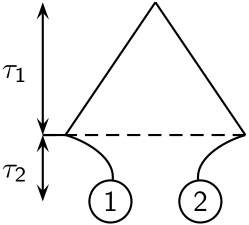

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- Two networks are said to be **distinguishable** if their probability spaces are not identical.

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A three-taxon, five site nucleotide sequence. The set of nucleotides is $\{A,C,G,T\}$.

- Assumption is that the observed frequences are samples from the probability distribution for some model. eg. $p_{CCC} \approx \frac{f_{CCC}}{N} = \frac{1}{5}$.

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- Give preference to tree if tree and convergence network cannot be distinguished.

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- Binary symmetric model is the simplest model and its generators form an abelian (or commutative) group.
- Binary symmetric model can be "diagonalised" with the Hadamard transformation.
- Probability distributions will be given in the Hadamard basis.

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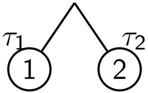
- We will now look at the two and three-taxon cases as examples.

Two-Taxon Networks



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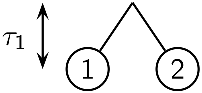

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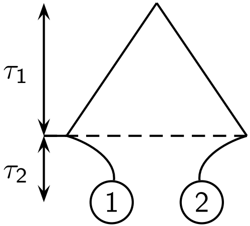

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- In the Hadamard basis, the probability distribution for network 1 is

$$\widehat{P} = \begin{bmatrix} q_{00} \\ q_{01} \\ q_{10} \\ q_{11} \end{bmatrix} = \begin{bmatrix} 1 \\ 0 \\ 0 \\ e^{-(\tau_1+\tau_2)} \end{bmatrix}.$$

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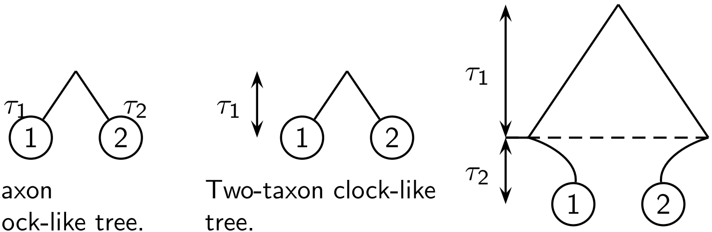

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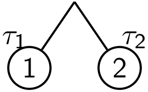

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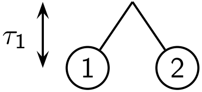

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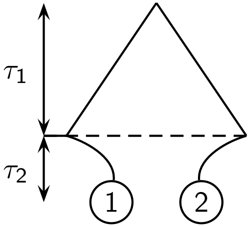

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- In the Hadamard basis, the probability distribution for network 3 is

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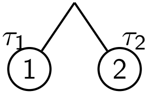

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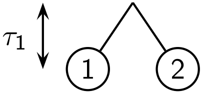

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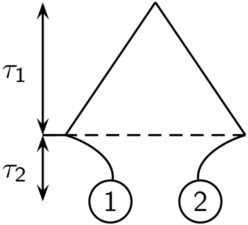

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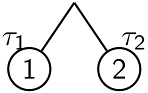

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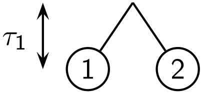

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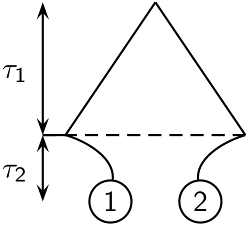

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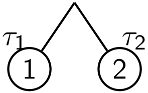

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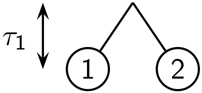

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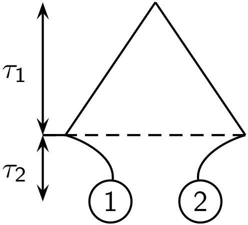

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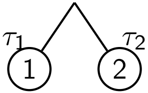

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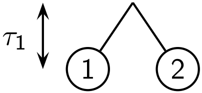

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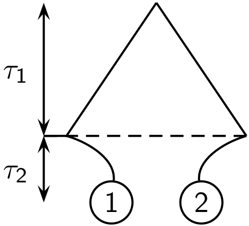

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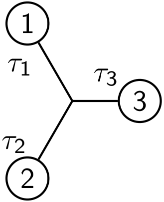
- Networks are not distinguishable.
- No reason to introduce convergence periods for two-taxon trees under our models.

Three-Taxon Networks



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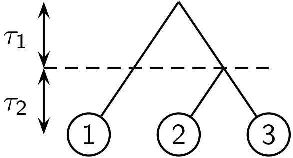

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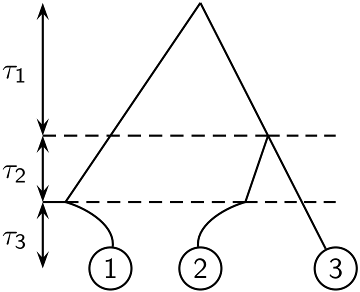

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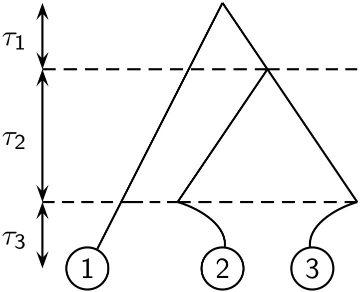

Network 4

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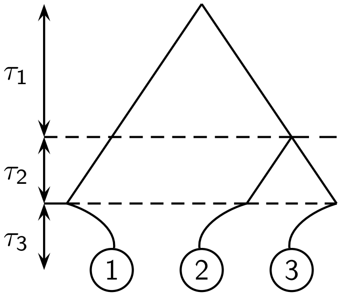

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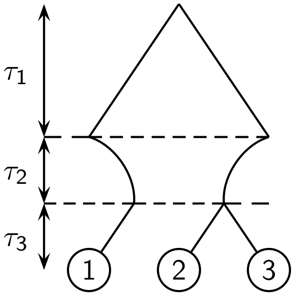

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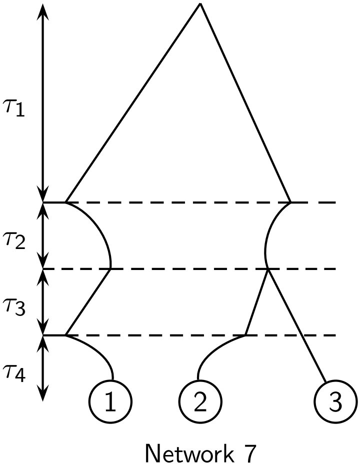

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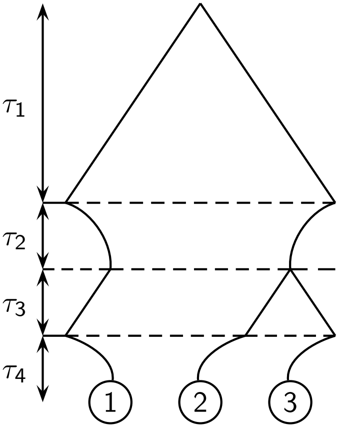
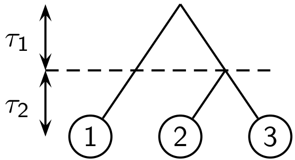


Network 9

An Example: Three-Taxon Clock-Like Tree



Three-taxon clock-like tree with no convergence periods

- In the Hadamard basis, the probability distribution is

$$P = \begin{bmatrix} q_{000} \\ q_{001} \\ q_{010} \\ q_{011} \\ q_{100} \\ q_{101} \\ q_{110} \\ q_{111} \end{bmatrix} = \begin{bmatrix} 1 \\ 0 \\ 0 \\ e^{-2\tau_2} \\ 0 \\ e^{-2(\tau_1+\tau_2)} \\ e^{-2(\tau_1+\tau_2)} \\ 0 \end{bmatrix}.$$

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- Since the τ's are time parameters, $\tau_i \geq 0$ for all i.

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- We can derive probability distributions for other networks in a similar fashion.
- To determine probability spaces, we want to find the constraints on the q's.
- Since we know the constraints on the τ's, solving for the τ's as functions of q's gives (most of) the constraints on the q's.
- Since the τ's are time parameters, $\tau_i \geq 0$ for all i.
- To solve the equations we must first make the substitutions $x_i = e^{-\tau_i}$. This forces all of the probability distribution equations to be polynomial equations in the form

$$q_{i_1 i_2 \ldots i_n} = f\left(x_1, x_2, \ldots x_m\right),$$

where n is the number of taxa and m is the number of time parameters.

Comparing Probability Spaces

- We now rearrange the equations to evaluate to zero on the model,

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- We then extract the polynomials, $f(x_1, x_2, \ldots x_m) - q_{i_1 i_2 \ldots i_n}$, from the polynomial equation and make them the generating polynomials of an ideal.
- Now that we have an ideal generated by polynomial equations we can solve these polynomial equations.

Comparing Probability Spaces

Definition

For any set of polynomials, $f_1, f_2, \ldots, f_s \in \mathbb{F}[x_1, x_2, \ldots, x_m]$, we can define the set $I = \langle f_1, f_2, \ldots, f_s \rangle$, as follows:

$$I = \langle f_1, f_2, \ldots, f_s \rangle = \left\{ \sum_1^s h_i f_i : \quad h_1, h_2, \ldots, h_s \in \mathbb{F}[x_1, x_2, \ldots, x_m] \right\}.$$

A key result is that $I = \langle f_1, f_2, \ldots, f_s \rangle$ meets the definition of an *ideal* for *any* polynomials $f_1, f_2, \ldots, f_s \in \mathbb{F}[x_1, x_2, \ldots, x_m]$. For the three-taxon clock-like tree, our set of generating polynomials is $\{x_2^2 - q_{011}, x_1^2 x_2^2 - q_{101}, x_1^2 x_2^2 - q_{110}\}$, which forms the ideal $I = \left\langle x_2^2 - q_{011}, x_1^2 x_2^2 - q_{101}, x_1^2 x_2^2 - q_{110} \right\rangle$.

Comparing Probability Spaces

- Definition (Gröbner Basis)

  Fix a monomial order. A finite subset $G = \{g_1, \ldots, g_t\}$ *of an ideal* I *is said to be a* **Gröbner basis** *(or* **standard basis***) if* $< LT(g_1), \ldots, LT(g_t) >=< LT(I) >$.

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  - By transforming our ideal into the Gröbner basis with lex order the system still has the same solutions and can be solved for the τ's using back-substitution.
  - By applying the constraints on the τ's, we can find all of the constraints on the q's.

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- Going back to our example, the system of equations (after turning them into polynomials) was $\{x_2^2 - q_{011} = 0, x_1^2 x_2^2 - q_{101} = 0, x_1^2 x_2^2 - q_{110} = 0\}$.

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- We will now compare some three-taxon examples.

Three-Taxon Networks

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Network(s)	$q_{101} = q_{110}$ (Y/N)	$q_{011} \geq q_{101}$ (Y/N)	$q_{011}(1 - q_{110})^2 \geq (q_{011} - q_{101})^2$ (Y/N)
1	N	N	N
2, 4, 5, 6, 8, 9	Y	Y	N
3, 7	N	Y	Y

Summary of network constraints which must be met.

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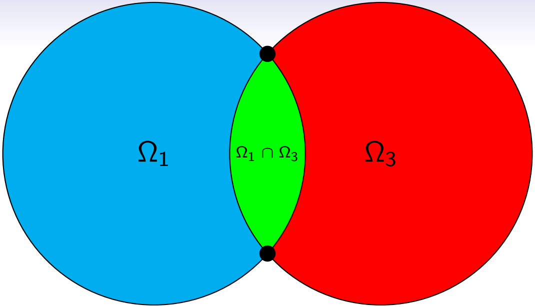
- In addition, the non-clock-like tree (network 1) must meet the constraints
  $\{q_{011} \geq q_{101}q_{110}, q_{101} \geq q_{011}q_{110}, q_{110} \geq q_{011}q_{101}\}$.



Probability spaces of the networks. The probability space for network 2 is the two black dots where the probability spaces for networks 1 and 3 intersect.

Colour	Probability Space	Constraints
Blue	Ω_1	$\{q_{011} \geq q_{101}q_{110}, q_{101} \geq q_{011}q_{110}, q_{110} \geq q_{011}q_{101}\}$
Red	Ω_3	$\{q_{011} \geq q_{101}, q_{110} \geq q_{101}, q_{011}(1-q_{110})^2 \geq (q_{011}-q_{101})^2\}$
Green	$\Omega_1 \cap \Omega_3$	$\{q_{011} \geq q_{101}, q_{110} \geq q_{101}, q_{101} \geq q_{011}q_{110}\}$
Black	$\Omega_1 \cap \Omega_2 \cap \Omega_3$	$\{q_{101} = q_{110}, q_{011} \geq q_{110}\}$

Summary of network constraints which must be met in the region of the probability space.

- In summary, there are four distinct regions in the probability space of the networks. The probability space either belongs to the non-clock-like tree exclusively, the clock-like network with convergence exclusively, either of the non-clock-like tree or the clock-like network with convergence, or all three networks.

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- Consequently, the three-taxon clock-like network with convergence is a viable model of evolution.
- Next step is to compare the fit of the three networks to a given dataset.
- Further work could involve extending the results to more taxa or to more complicated Abelian models beyond the binary symmetric model.