Linear invariants and the space of phylogenetic mixtures for Felsenstein'81 and other models

Marta Casanellas Rius
(mainly joint work with M. Steel)

Departament de Matemàtiques
Universitat Politècnica de Catalunya

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- First attempts to use invariants: Steel et al. '93, Ferretti-Sankoff '95.
- Main problems: not all invariants known, not clear how to use them, evaluation of fit of model and tree topology at the same time.
- Felsenstein's book: "invariants are worth attention, not for what they do for us now, but what they might lead to in the future".
- Invariants can deal with very general models as GMM (which does NOT assume a stationary distribution, NOR time-reversibility, NOR global homogeneity, NOT even local homogeneity along each edge), mixtures (or fully partitioned model) or the coalescent.
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  - theoretical issues solved for the basic models.
  - widely used in identifiability problems (Allman-Rhodes '06,'07,'12...)
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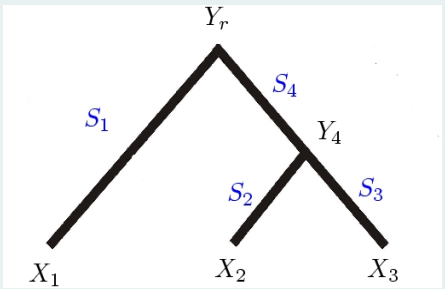
Hidden Markov process

$p_{x_1x_2x_3} = Prob(X_1 = x_1, X_2 = x_2, X_3 = x_3)$ = joint probability of the observed variables X_1, X_2, X_3. Then,



$$p_{x_1x_2x_3} = \sum_{y_4,y_r \in \{\mathtt{A},\mathtt{C},\mathtt{G},\mathtt{T}\}} \pi_{y_r} S_1(y_r, x_1) S_4(y_r, y_4) S_2(y_4, x_2) S_3(y_4, x_3)$$

- Parameters: entries of S_i and π.
- Constraints on S_i and π specify the evolutionary model: (non-homogeneous) JC69, K80, K81, F81, SSM, GMM, ...
- S_i does need to be of type $exp(t_i Q_i)$ (and if it is, the rate matrices Q_i can be different for different branches).
- NO global instantaneous mutation rate matrix assumed $\Rightarrow$ "non-homogeneous across lineages".

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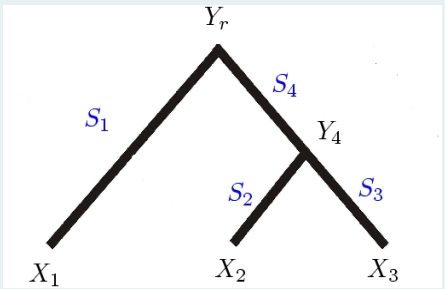

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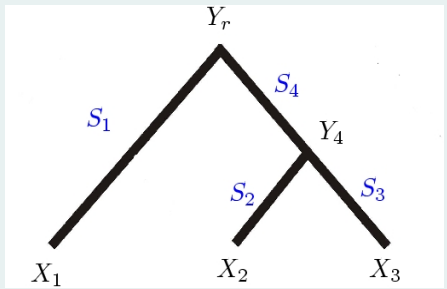

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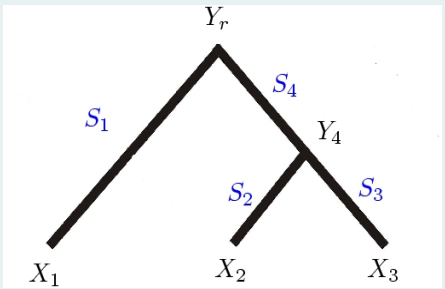

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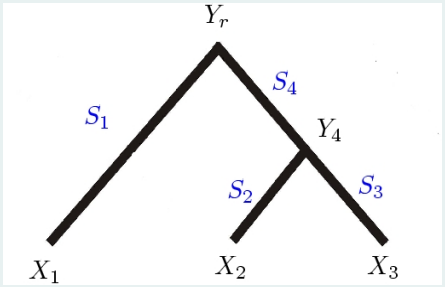

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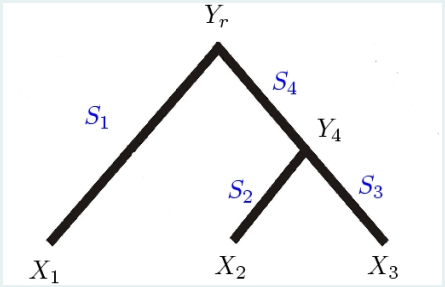

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Example: Jukes-Cantor

- Some relations depend on the model chosen (not on the *tree topology*): $\sum p_{x_1 x_2 \ldots x_n} = 1$ (trivial) and

$$p_{AA\ldots A} = p_{CC\ldots C} = p_{GG\ldots G} = p_{TT\ldots T}$$

$$p_{A\ldots AC} = p_{A\ldots AG} = p_{A\ldots AT} = \cdots = p_{T\ldots TG}$$

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- These are called model invariants (relations satisfied on all tree topologies)
- But some relations depend on the tree topology.

Definition

- Phylogenetic Invariants of a tree T_0: polynomial relations satisfied by any joint distribution that has evolved under an evolutionary model $\mathcal{M}$ on T_0.
- *Topology* invariants: invariants of T_0 that are not satisfied by some joint distributions on some other tree topologies (hence, they could be used to distinguish between different topologies).

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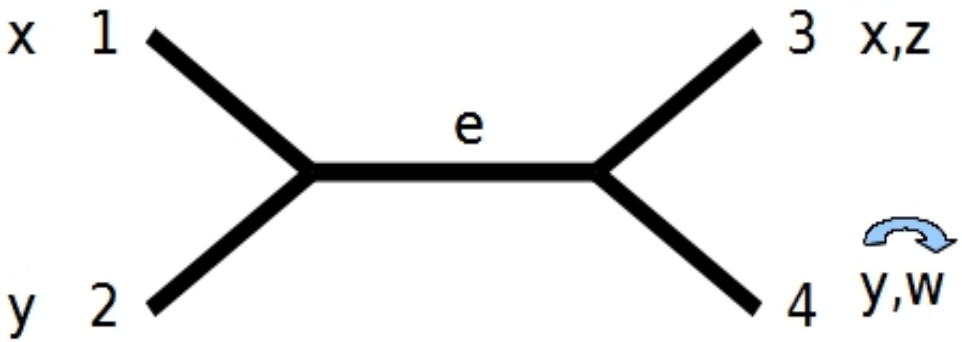
Example: Lake's linear invariants



For the JC60 model on the tree 12|34 the following are linear topology invariants known as Lake's invariants:

$$H_1: \quad p_{xyxy} + p_{xyzw} = p_{xyzy} + p_{xyxw}$$

$$H_2: \quad p_{xyyx} + p_{xywz} = p_{xyyz} + p_{xywx}$$

for any x, y, z, w in $\{A, C, G, T\}$.

- Any other linear topology invariant is a linear combination of these two.
- Degree 1 (linear) ... interesting enough?

Linear invariants can deal with mixtures

- Mixture of Markov processes on a tree T: sites undergo the same model on T (but not with the same instantaneous mutation rates); m partitions in the alignment;
  NO constraint between the substitution matrices of different partitions.

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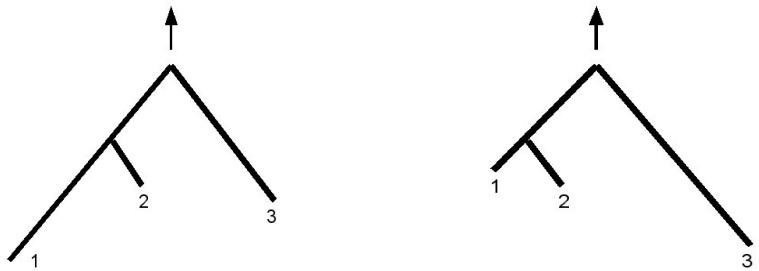

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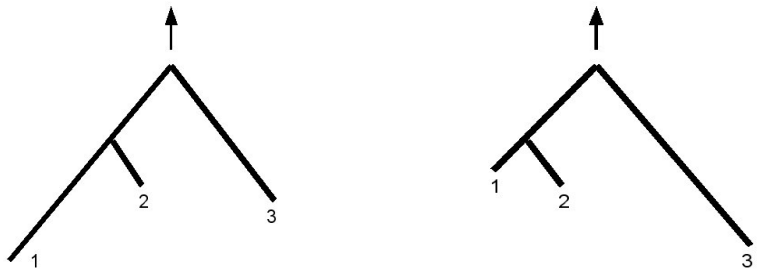

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The space of mixtures for a given model $\mathcal{M}$

Definition

Fix an evolutionary model $\mathcal{M}$. $\mathbb{P}_{T,\Theta}$ = distribution at the tips of of T, T evolving under $\mathcal{M}$ with parameters Θ .
The *space of mixtures on* T is the affine linear variety

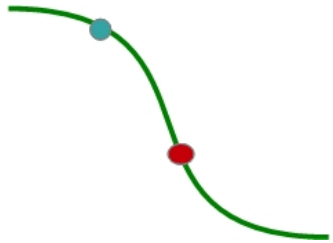
$$\mathcal{D}_T = \left\{ p = \sum_i \lambda_i \mathbb{P}_{T,\Theta_i} \,\middle|\, \sum_i \lambda_i = 1 \right\}.$$

If $\mathcal{T}$ = phylogenetic trees on the set X of taxa, *the space of phylogenetic mixtures* on X is the affine linear variety

$$\mathcal{D} = \left\{ p = \sum_i \lambda_i \mathbb{P}_{T_i,\Theta_i} \,\middle|\, \sum_i \lambda_i = 1\,,\ T_i \in \mathcal{T} \right\}$$

Linear invariants and mixtures

If linear topology invariants exist for the model considered, then the tree topology that generated the mixture is identifiable:



- 2-states, Neyman symmetric model: there are no linear topology invariants (Matsen-Mossel-Steel), so tree topology *cannot* be identified for mixtures on *an arbitrary* number of categories.
- (nonhomogeneous) JC69, K80 have linear topology invariants but K81, SSM and GMM no (tree topology can only be identified for mixtures on a certain number of categories).

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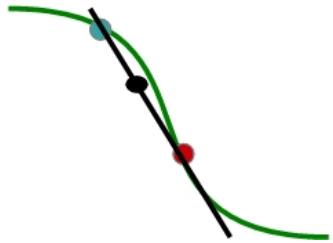

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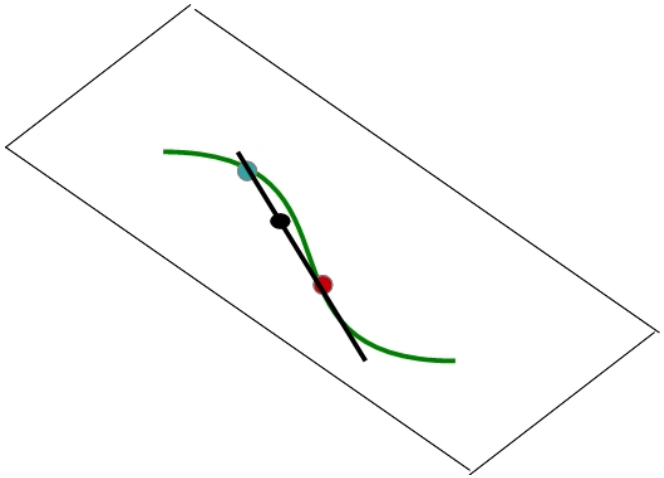

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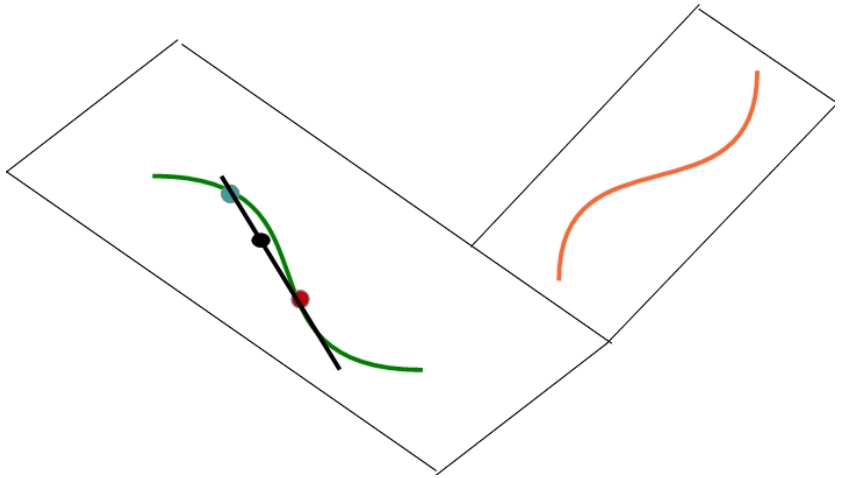

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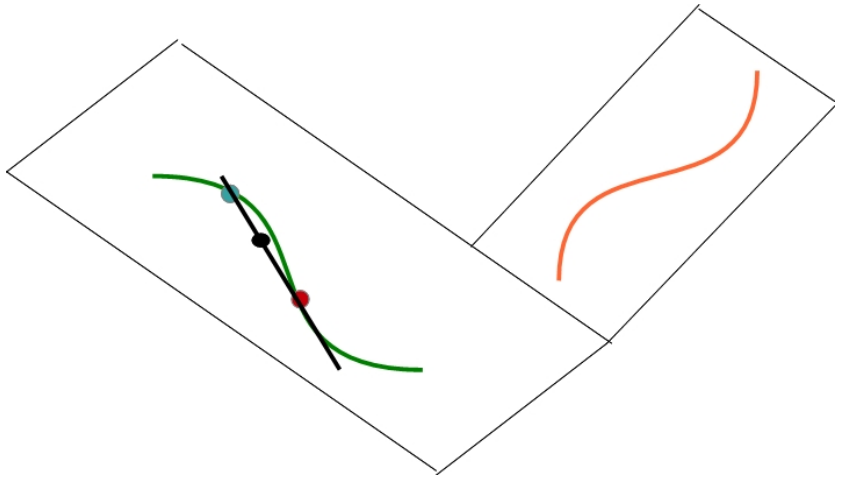

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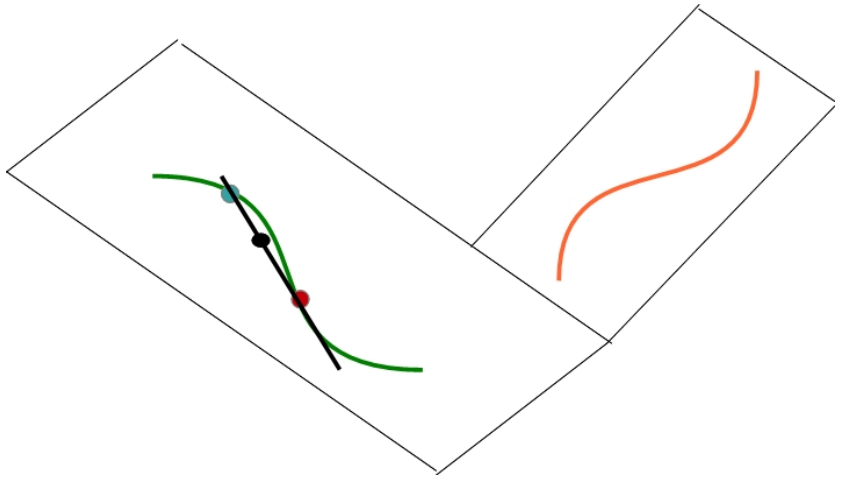

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Space of Mixtures and linear phylogenetic invariants

Relationship between mixtures and linear invariants:

$$\mathcal{D}_T = \underbrace{\left\langle \vec{p} \,\middle|\, p = \mathbb{P}_{T,\Theta} \right\rangle}_{E_T} \cap \{\text{trivial invariant}\}$$

$$\mathcal{D} = \underbrace{\left\langle \vec{p} \,\middle|\, p = \mathbb{P}_{T,\Theta}\ T \in \mathcal{T} \right\rangle}_{E} \cap \{\text{trivial invariant}\}$$

- Linear model invariants: L orthogonal (dual) space to E.
- Linear invariants for a tree T: L_T orthogonal (dual) space to E_T.
- Linear topology invariants: quotient space L_T/L

So far, only linear invariants for models with uniform stationary distribution and 4 states had been studied.

Equal Input model on k-states (EI-model)

- $\pi =$ a stationary distribution on k states; for each edge e, consider a parameter $\theta_e \in [0,1]$ and let conditional probabilities satisfy:

$$Prob(\beta|\alpha, e) = \pi_\beta \cdot \theta_e,$$

  for any states α, β.

- For $k = 4$, this is Felsenstein'81 model:

$$S^e = \begin{pmatrix} 1-(1-\pi_A)\theta_e & \pi_C\theta_e & \pi_G\theta_e & \pi_T\theta_e \\ \pi_A\theta_e & 1-(1-\pi_C)\theta_e & \pi_G\theta_e & \pi_T\theta_e \\ \pi_A\theta_e & \pi_C\theta_e & 1-(1-\pi_G)\theta_e & \pi_T\theta_e \\ \pi_A\theta_e & \pi_C\theta_e & \pi_G\theta_e & 1-(1-\pi_T)\theta_e \end{pmatrix}$$

- Fully symmetric model: π uniform distribution. $k = 4 \rightarrow$ Jukes-Cantor model.
- Coincides with the random cluster model on k states.
- For $k = \infty$: Kimura's infinite alleles model.

$k \geq 4$, Generalizing Lake's invariants

- π fixed (inferred from data?)
- Felsensten'81

$$H_1: \quad \frac{p_{xyxy}}{\pi(x)\pi(y)} + \frac{p_{xyzw}}{\pi(z)\pi(w)} = \frac{p_{xyzy}}{\pi(z)\pi(y)} + \frac{p_{xyxw}}{\pi(x)\pi(w)}$$

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- Generalized to k states $EI-$models, $k \geq 3$ (and more general models).

Model invariants for $EI-$models, π fixed

Set of taxa $[n] = \{1, 2, \ldots, n\}$ $k \geq 2$.

Theorem (C-Steel)

We provide a set of linearly independent points that span the space of mixtures $\mathcal{D}^\pi$ for almost any π . The dimension of $\mathcal{D}^\pi$ equals

$$\sharp\{partitions\ of\ [n]\ of\ size\ \leq k\} - 1$$

(if $k \geq n$ it equals $B_n - 1$ where B_n: Bell number.)

Consequence: easy way to obtain a set of generators for the space of linear model invariants.

- $k = 4$, $dim\mathcal{D}^\pi = \frac{2^{2n-3}+1}{3} + 2^{n-2} - 1$.
- Results are also valid for $k = \infty$, Kimura's infinite alleles model.

Topology invariants for $EI-$models, π fixed

Theorem (C-Steel)

We provide a set of linearly independent points that span the space of mixtures $\mathcal{D}_T^\pi$, for any π fixed, any k, any $n \geq 3$.
The dimension of $\mathcal{D}_T^\pi$ equals $|co(T)| - 1$, where $co(T)$ is the set of partitions of $\{1, \ldots, n\}$ compatible with T.

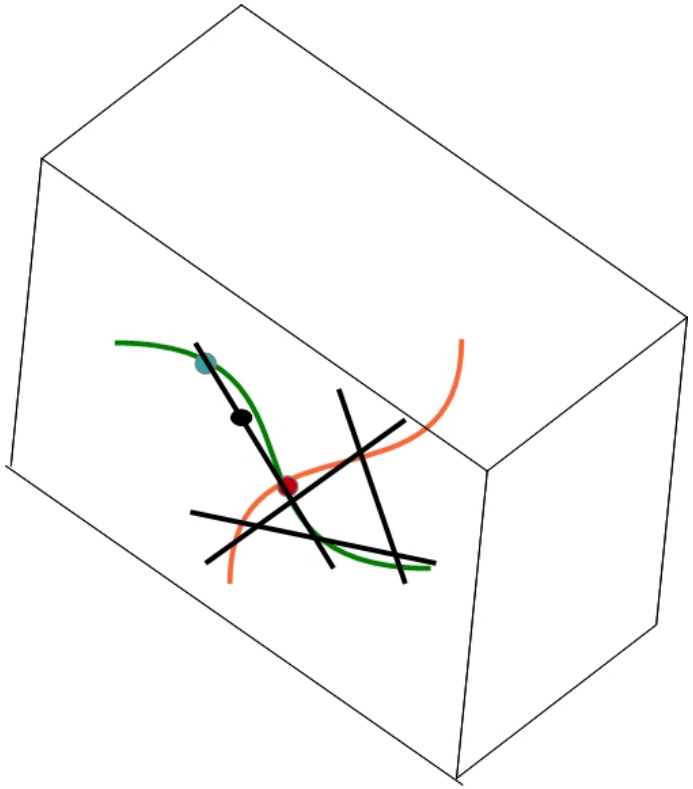
Corollary

Algorithm to obtain a basis of the set of **linear topology invariants** *for the EI model on $n \geq 4$ leaves, any k; dimension $= |\Sigma_k| - |co(T)| =$ number of partitions of $\{1, \ldots, n\}$ of size $\leq k$ incompatible with T.*

Corollary

For $k \geq n$ or for $n = 4$, Lake-type invariants generate all linear topology invariants. For $k < n$, NO.

What if there are NO linear topology invariants?



But still, different models give rise to different linear spaces $\Rightarrow$ use linear **model invariants**.

Why should one care? Model selection:

- Linear model invariants are satisfied by any number of mixtures on (possibly) different topologies.
- They allow to distinguish between different models and can be used for model selection.
- C-Fernández-Sánchez-Kedzierska'12: algorithm that provides all linear model invariants for any number of taxa for JC69, K80, K81, SSM.
- This has been used in `SPIn` (Kedzierska-Drton-Guigó-C, MBE 2012): it tells you wether your data is likely to come from a mixture (possibly on a collection of different tree topologies) of (nonhomogeneous) JC69, K80, K81 or SSM processes.
- Not many models ... but good results compared to `jmodeltest` because we consider nonhomogeneous models across lineages (different instantaneous mutation rates at different lineages) and allow mixtures!

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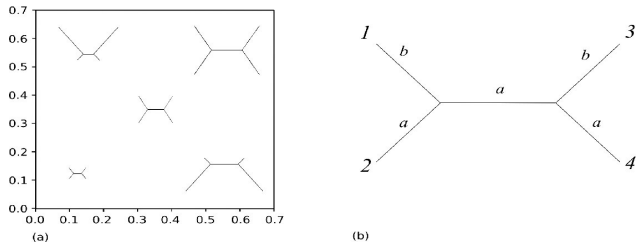
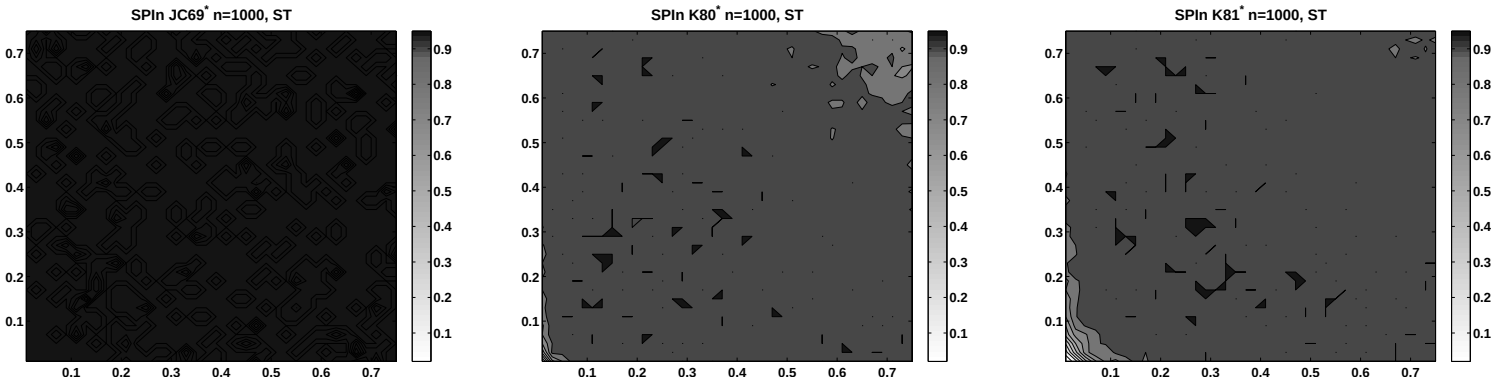
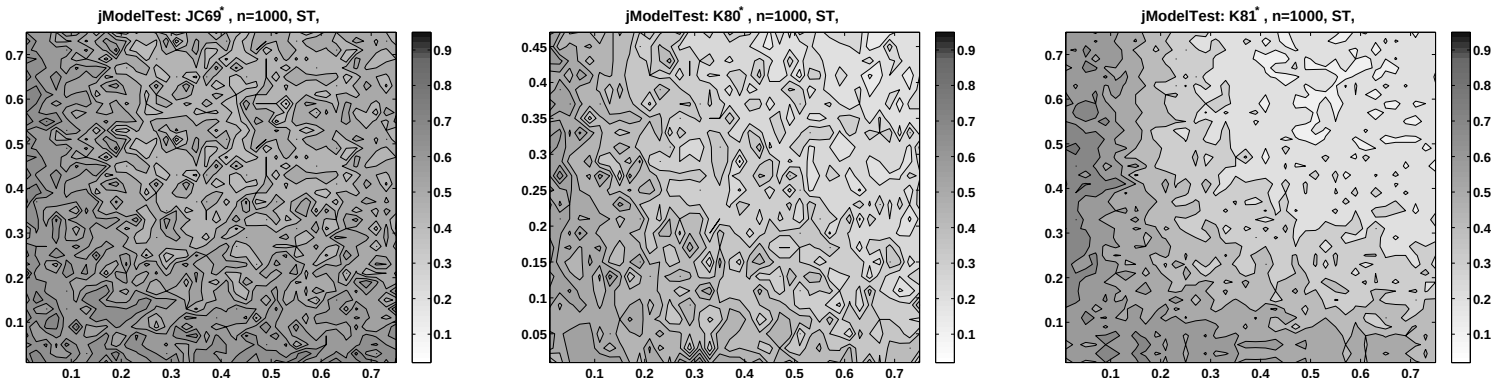
Results on simulated (unmixed) data



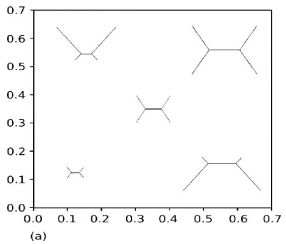
SPIn

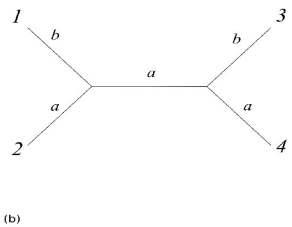


jModelTest



Mixture data





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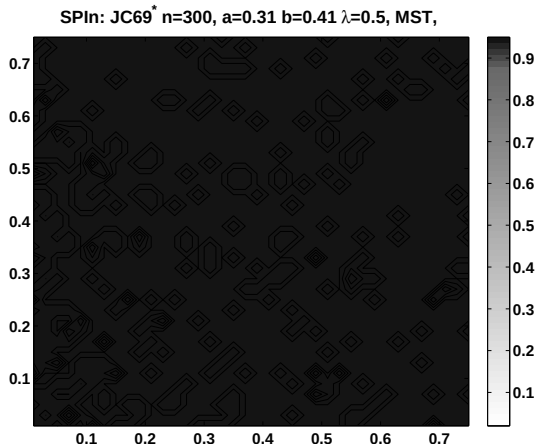

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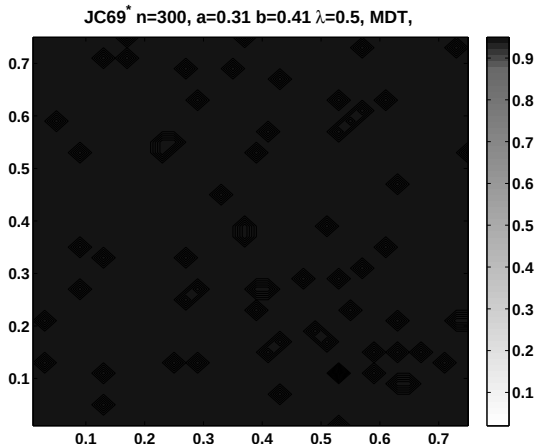
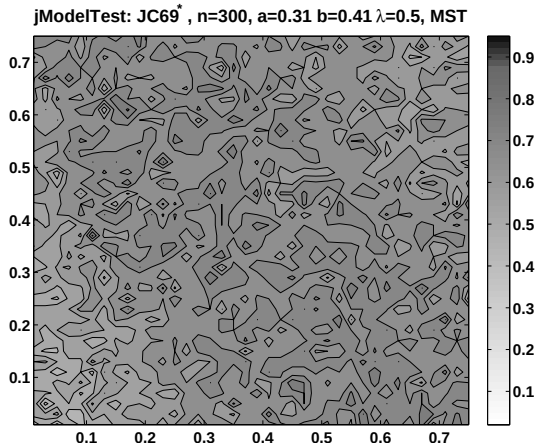
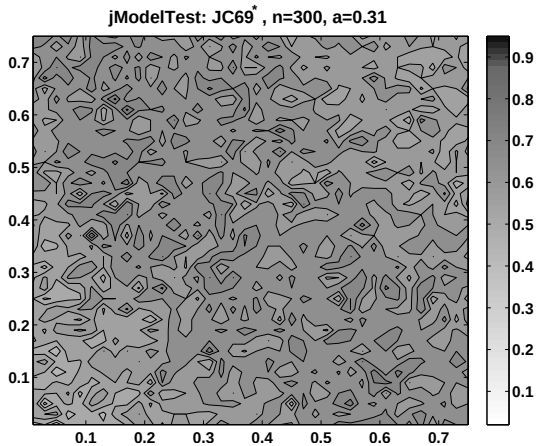


jModelTest



2 categories, 1 tree

jModelTest



2 categories, 2 trees

Thank you for your attention!

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ALGEBRAIC AND COMBINATORIAL PHYLOGENETICS

whole MONTH research program

Barcelona June 12th - July 10th (approx.) 2017.

A WORKSHOP + COURSES by:

Mike Steel

Arndt von Haeseler

Piotr Zwiernik

Some funding available for participants, check the "webpage" (coming soon...)