Geometry of phylogenetics

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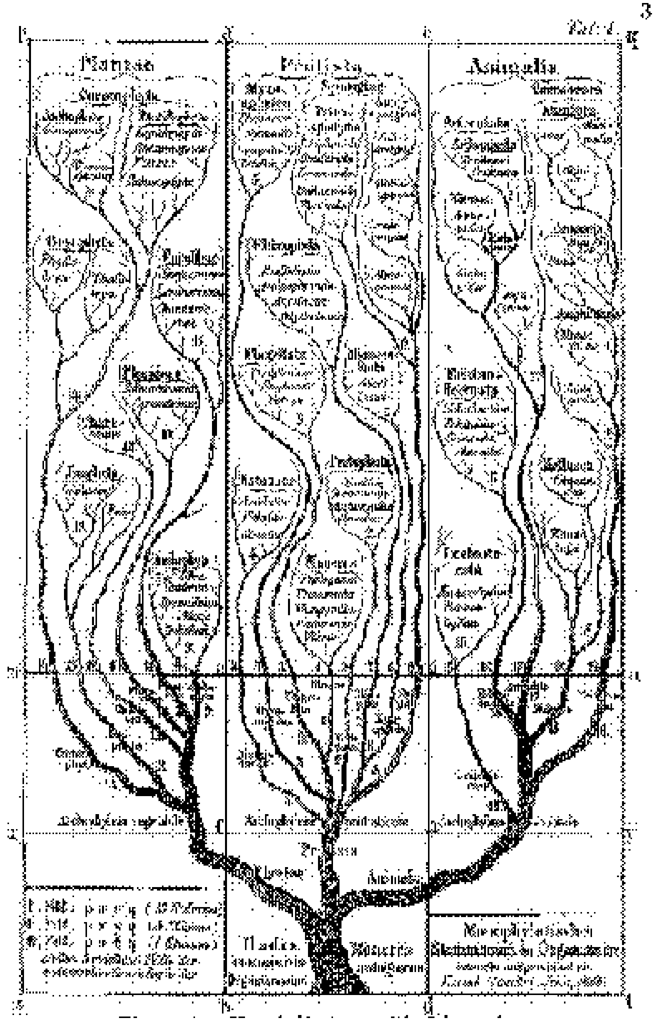
phylogenetics

Phylogenetics: reconstructing historical relation between species by analyzing their *present* features and putting their common ancestors in a diagram which forms a tree. [e.g. Häckel, 1866]



trees, sockets and networks

Consider a tree $\mathcal{T}$ which has $d+1$ leaves $\mathcal{L}$, $d-1$ inner trivalent nodes $\mathcal{N}$ and $2d-1$ edges $\mathcal{E}$; *socket* is a subset of $\mathcal{L}$ which has even number of elements; *path* in $\mathcal{T}$ is a connected union of edges, *network* is a set of non-meeting paths in $\mathcal{T}$ with ends in $\mathcal{L}$

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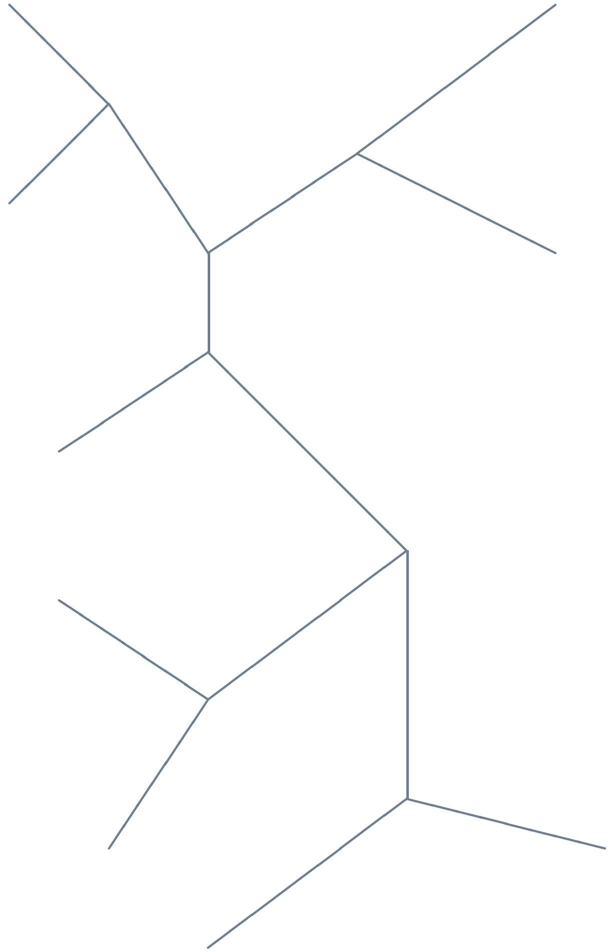

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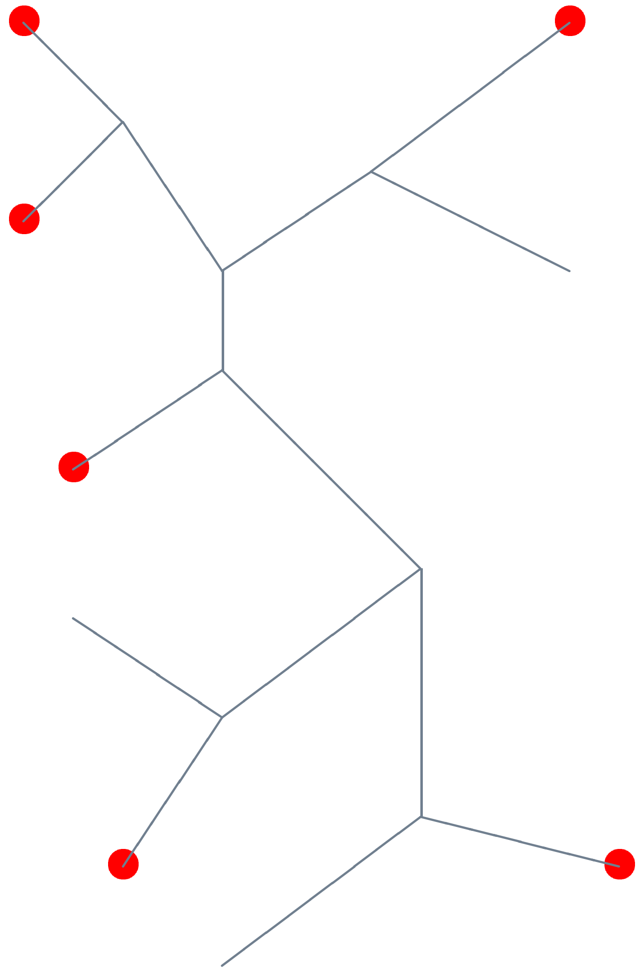

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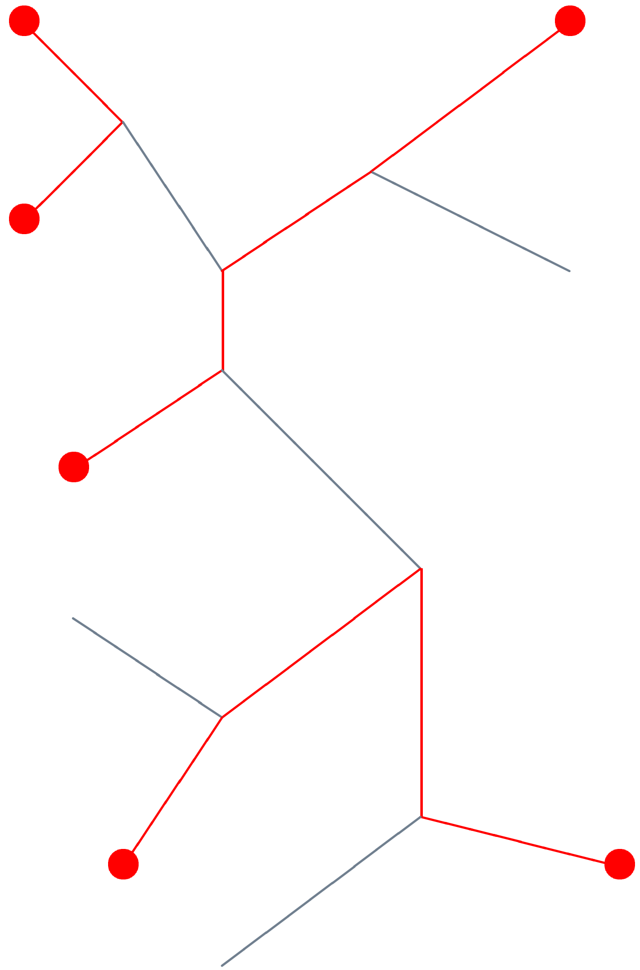

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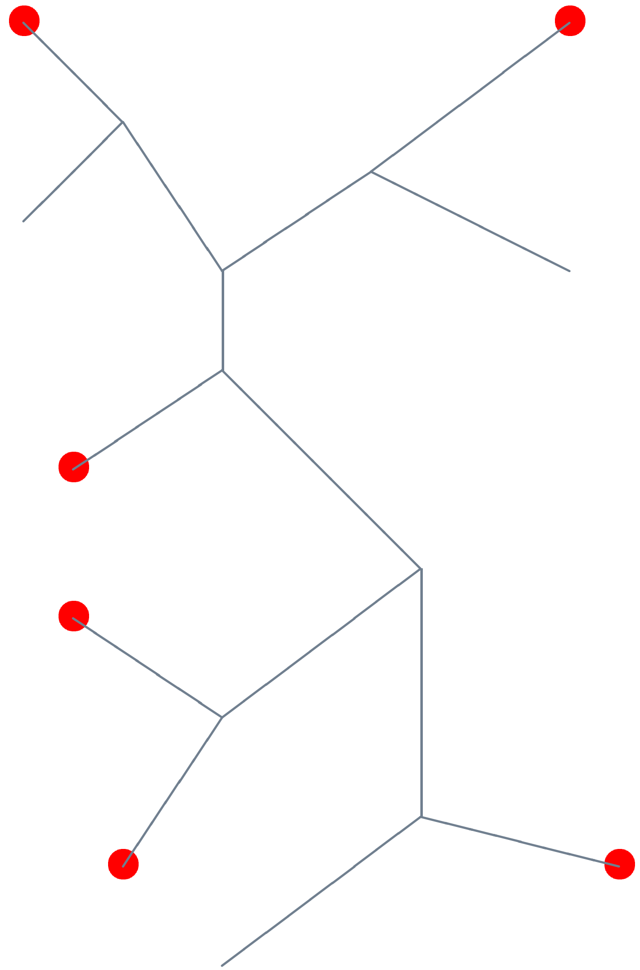

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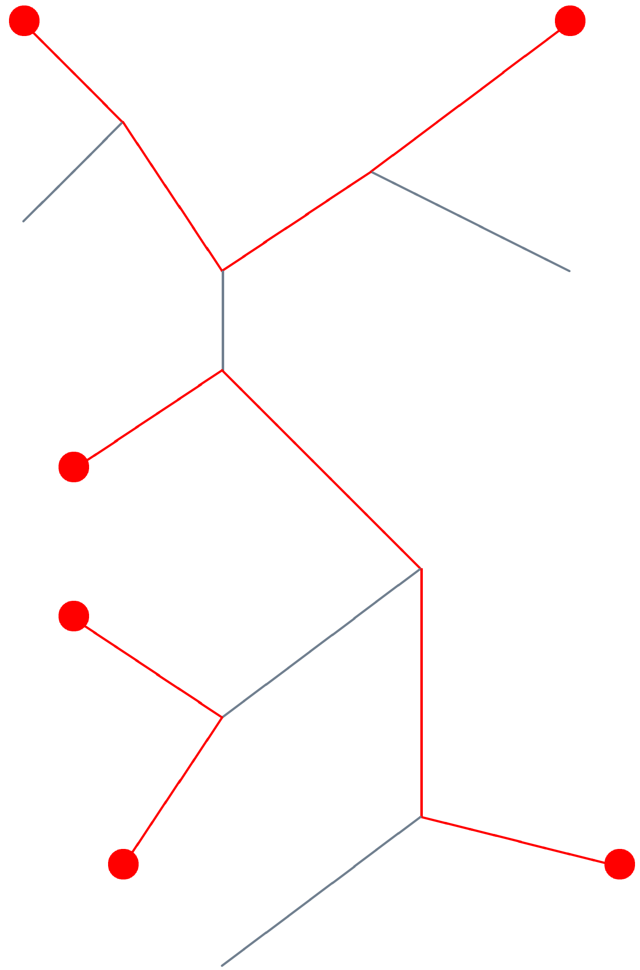

tree $\to$ variety, first view

[lemma] There is a bijection between the set of sockets and networks, that is for every socket σ there exists a unique network $\mu(\sigma)$ whose end points are in σ

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For every edge $e \in \mathcal{E}$ we consider a $\mathbb{P}^1_e$ with homogeneous coordinates $[y^e_0, y^e_1]$. Moreover consider a projective space $\mathbb{P}_\Sigma$ of dimension $2^d - 1$ with homogeneous coordinates $[z_\sigma]$ indexed by sockets of $\mathcal{T}$.

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Define rational map $\prod_{e\in\mathcal{E}} \mathbb{P}^1_e \to \mathbb{P}_\Sigma$ such that

$$z_\sigma = \prod_{e\in\mu(\sigma)} y_1^e \cdot \prod_{e\notin\mu(\sigma)} y_0^e$$

The model of the tree, $X(\mathcal{T}) \subset \mathbb{P}_\Sigma$, is the closure of the image of this map, $\dim X(\mathcal{T}) = 2d - 1$.

first examples

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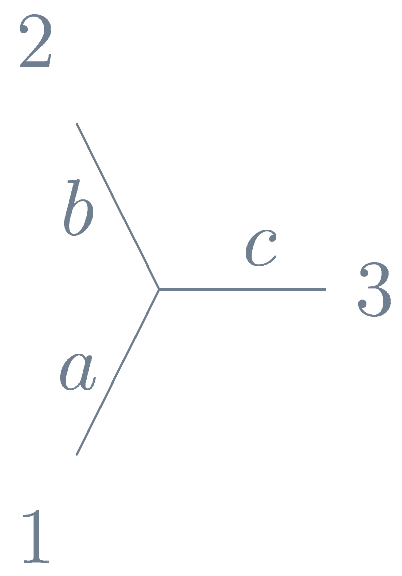
Tripod tree model:

$$\mathbb{P}^1_a \times \mathbb{P}^1_b \times \mathbb{P}^1_c \to \mathbb{P}^3$$

$$z_{000} = y_0^a y_0^b y_0^c \quad z_{110} = y_1^a y_1^b y_0^c$$
$$z_{101} = y_1^a y_0^b y_1^c \quad z_{011} = y_0^a y_1^b y_1^c$$



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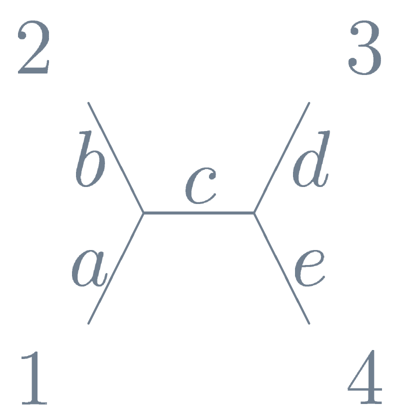
Four leaf tree model in $\mathbb{P}^7$

$$z_{0000} = y_0^a y_0^b y_0^c y_0^d y_0^e \quad z_{1111} = y_1^a y_1^b y_0^c y_1^d y_1^e$$
$$z_{1100} = y_1^a y_1^b y_0^c y_0^d y_0^e \quad z_{0011} = y_0^a y_0^b y_0^c y_1^d y_1^e$$
$$z_{1010} = y_1^a y_0^b y_1^c y_1^d y_0^e \quad z_{1001} = y_1^a y_0^b y_1^c y_0^d y_1^e$$
$$z_{0110} = y_0^a y_1^b y_1^c y_1^d y_0^e \quad z_{0101} = y_0^a y_1^b y_1^c y_0^d y_1^e$$

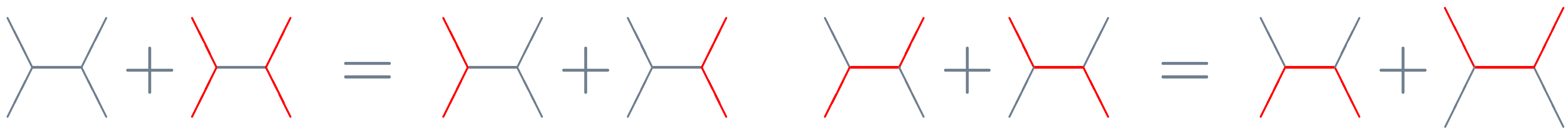


first examples

Leaves of $\mathcal{T}$ are labeled by numbers $1, \ldots, d+1$ and sockets are denoted by $0/1$ of length $d+1$.

Therefore $X(\succ\!\!-) \simeq \mathbb{P}^3$ and $X(\succ\!\!\prec)$ is a complete intersection in $\mathbb{P}^7$:

$$z_{0000} z_{1111} \;=\; z_{1100} z_{0011} \qquad z_{1010} z_{0101} \;=\; z_{1001} z_{0110}$$



binary Markov process on tree

Fix a root r in tree $\mathcal{T}$: this implies a partial order $<$ on the set of vertexes $\mathcal{V} = \mathcal{L} \cup \mathcal{N}$. To each vertex $v \in \mathcal{V}$ assign a random variable ξ_v which takes value in $\{\alpha_1, \alpha_2\}$.

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Variables ξ_v determine a Markov process on $\mathcal{T}$ if (intuitively) the value of ξ_v depends only on the value of ξ_u, where u is the node immediately preceding v.

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and set the probability of the variable ξ_r at the root: $P^r_i = P(\xi_r = \alpha_i)$

from Markov to phylogenetics

For a Markov process on a rooted tree $\mathcal{T}$ as above

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For a Markov process on a rooted tree $\mathcal{T}$ as above and any function $\mathcal{V} \ni v \to \rho(v) \in \{1, 2\}$

$$P(\bigwedge_{v \in \mathcal{V}} \xi_v = \alpha_{\rho(v)}) = P^r_{\rho(r)} \cdot \prod_{e = \langle u, v \rangle \in \mathcal{E}} A^e_{\rho(u)\rho(v)}$$

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where the sum is taken over all $\widehat{\rho} : \mathcal{V} \to \{1, 2\}$ which extend ρ.

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where the sum is taken over all $\widehat{\rho} : \mathcal{V} \to \{1, 2\}$ which extend ρ. Phylogenetics: understand the shape of $\mathcal{T}$ by looking at the distribution of $P(\bigwedge_{v \in \mathcal{L}} \xi_v = \alpha_{\rho(v)})$.

tree → variety, Markov view

Phylogenetics wants to understand the locus of possible probability values of a Markov process on a fixed tree $\mathcal{T}$:

$$\mathcal{X}(\mathcal{T}) :=$$
$$\{\zeta_\rho = P(\bigwedge_{v\in\mathcal{L}} \xi_v = \alpha_{\rho(v)}) : A^e_{ij}, P^r_i \text{ are arbitrary}\}$$

in the simplex with coordinates ζ_ρ where $\zeta_\rho \geq 0$, $\sum_\rho \zeta_\rho = 1$.

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note: these assumptions are very special but then incidently we have

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[theorem: Sturmfels, Sullivant] Then after suitable change of coordinates (and identifying spaces) the varieties $\mathcal{X}(\mathcal{T})$ and $X(\mathcal{T})$ coincide.

tree $\to$ variety, via quotients

On $\mathbb{P}^3$ with homogeneous coordinates $[z_{000}, z_{110}, z_{101}, z_{011}]$ take three actions of $\mathbb{C}^*$ whose weights are determined by socket $0/1$ sequence:

$$\lambda_1(t)[z_{000}, z_{110}, z_{101}, z_{011}] = [z_{000}, tz_{110}, tz_{101}, z_{011}]$$

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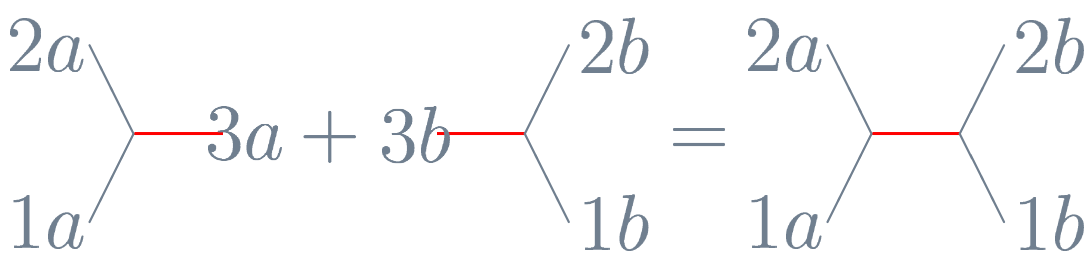
Trivalent trees are built from tripods by identifying edges of leaves:



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Take quotient $\mathbb{P}^3_a \times \mathbb{P}^3_b//(\lambda_{3a} \cdot \lambda_{3b}^{-1})$

$$([z^a_{000}, z^a_{110}, z^a_{101}, z^a_{011}], [z^b_{000}, z^b_{110}, z^b_{101}, z^b_{011}]) \to$$
$$[z^a_{000}z^b_{000}, z^a_{000}z^b_{110}, z^a_{110}z^b_{000}, z^a_{110}z^b_{110}, z^a_{101}z^b_{101},$$
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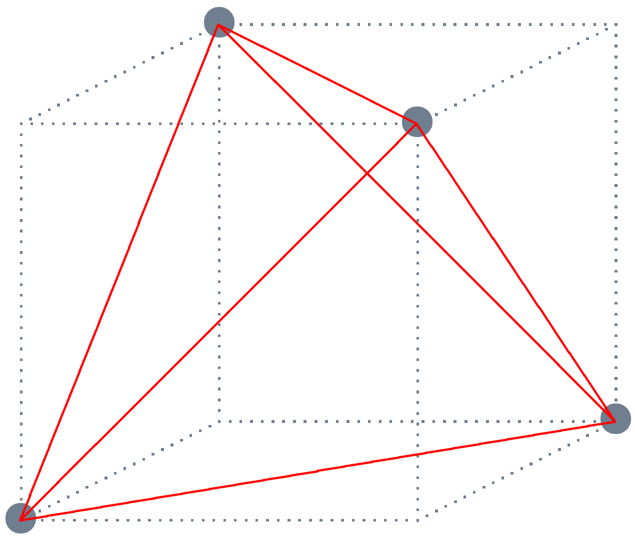
The variety $X(\mathcal{T})$ is obtained as a quotient of product of $\mathbb{P}^3$ indexed by inner nodes by a torus identifying legs of tripods to inner edges of the tree.

tree → variety, toric view

In toric geometry $\mathbb{P}^3$ can be viewed as a tetrahedron inscribed in a cube with the three principal directions of projection representing respective $\mathbb{C}^*$ actions.



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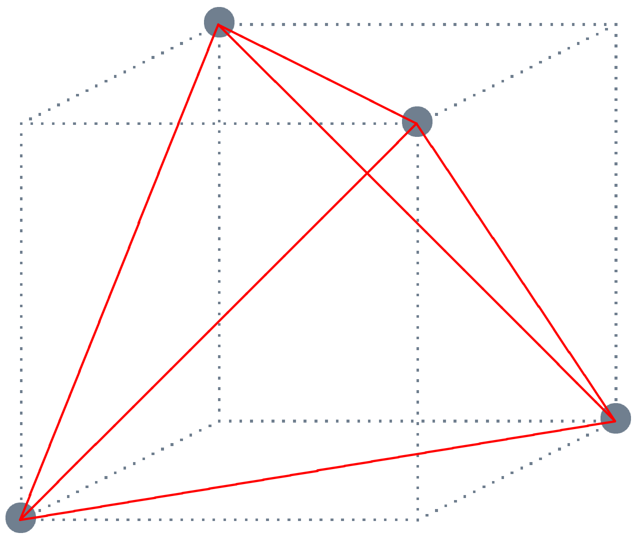

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Thus toric varieties associated to trees can be viewed as the fiber products of such tetrahedra.

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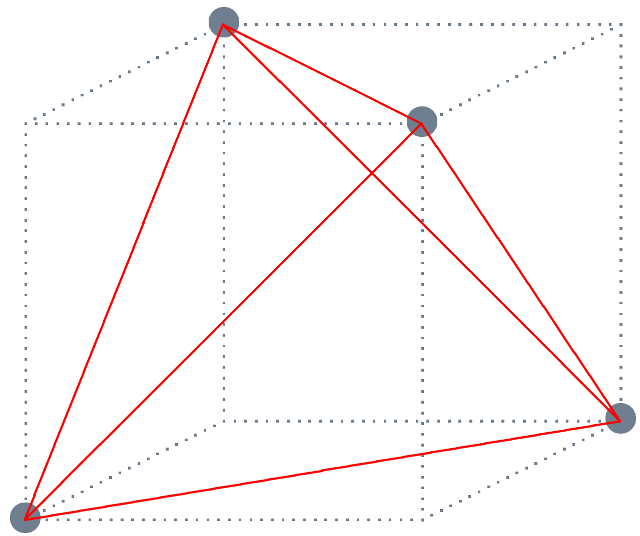

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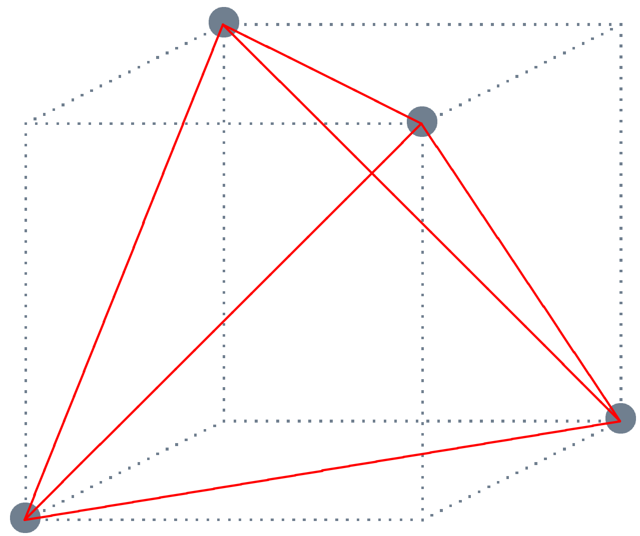

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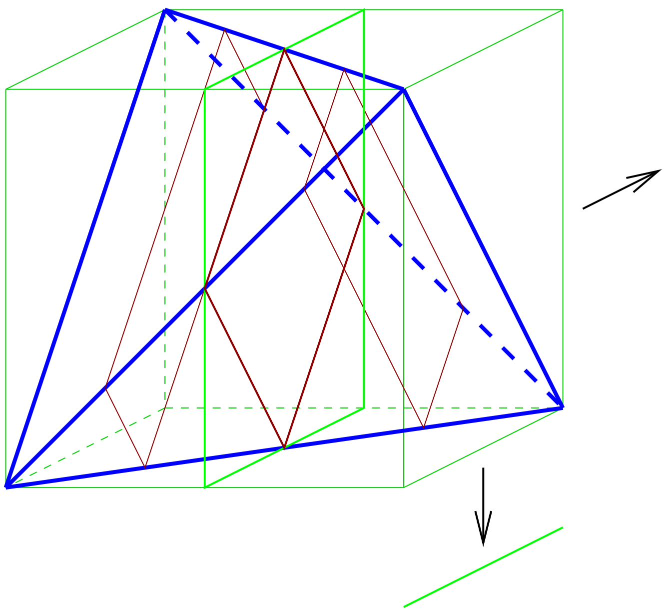
Surprise: Hilbert-Ehrhart polynomial does not depend on the shape of $X(\mathcal{T})$.

Hilbert-Ehrhart: $\star$ product

For a positive integer n let $[n] = \{0, \ldots n\}$.
Function $f : [n] \to \mathbb{Z}$ is symmetric if for every $k \in [n]$ it holds $f(k) = f(n-k)$.
By **1** $: [n] \to \mathbb{Z}$ denote the unit function.
If f_1 $f_2 : [n] \to \mathbb{Z}$ are symmetric functions then we define their symmetric product $f_1 \star f_2 : [n] \to \mathbb{Z}$ such that for $k \leq n/2$:

$$(f_1 \star f_2)(k) = 2 \cdot \left(\sum_{i=0}^{k-1} \sum_{j=0}^{i} f_1(i) f_2(k+i-2j) \right) + \left(\sum_{i=k}^{n-k} \sum_{j=0}^{k} f_1(i) f_2(k+i-2j) \right)$$

geometric interpretation of $\star$



Consider the simplex Δ as in the picture

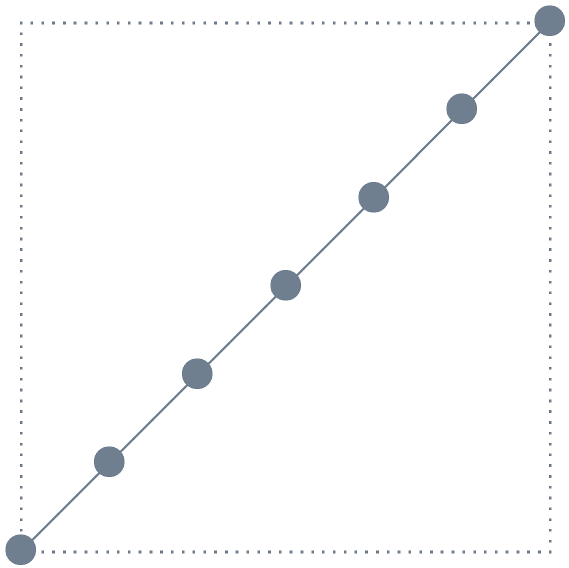
$(f_1 \star f_2)(k)$ is equal to the sum of products of f_1 and f_2 counted over points of lattice spanned by Δ in k-th slice of $n \cdot \Delta$

$(\mathbf{1} \star \mathbf{1})(k) = (k+1)(n-k+1)$ is the number of lattice points in k-th slice of $n \cdot \Delta$ and thus

$\star$ can be used to compute Hilbert-Ehrhart polynomial

travel trough $6 \cdot \Delta$

$$k = 0$$



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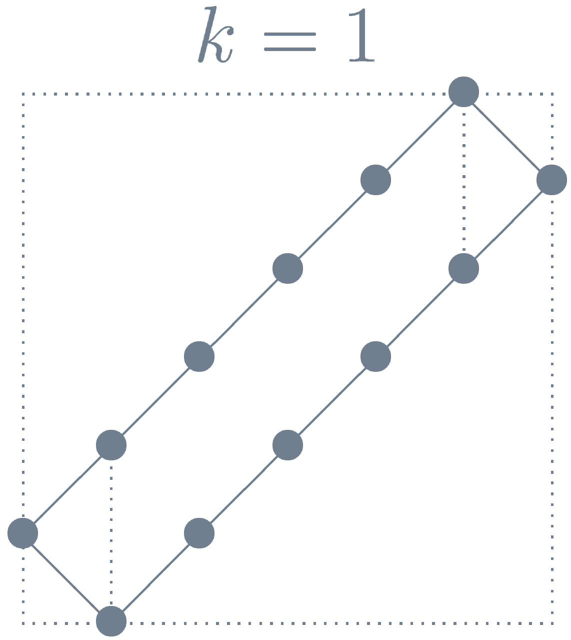

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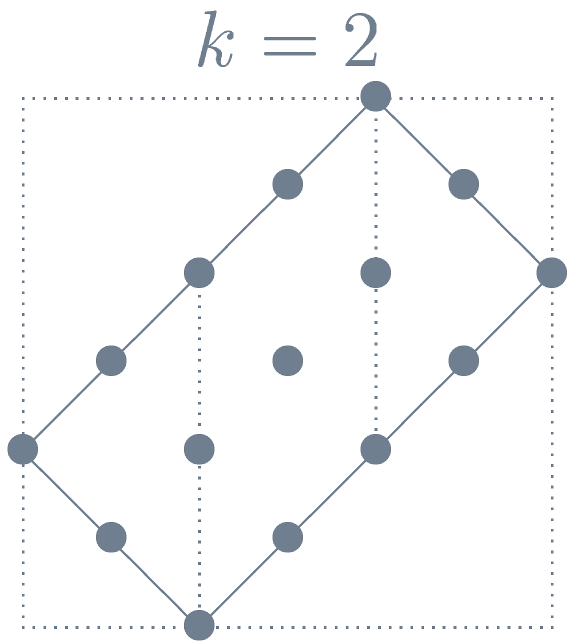

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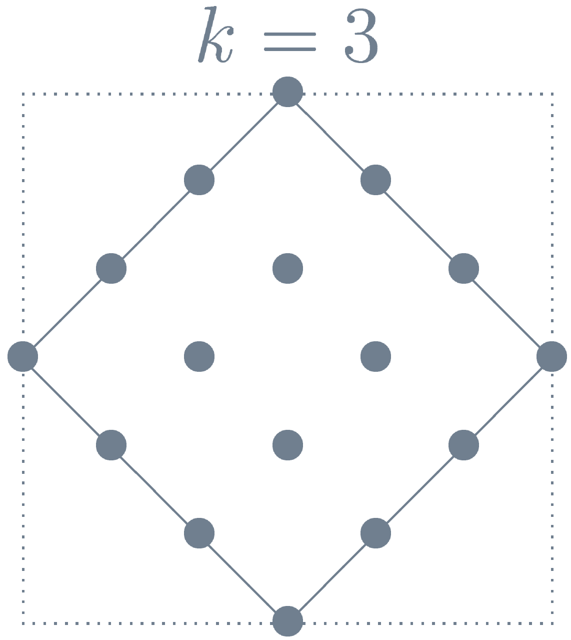

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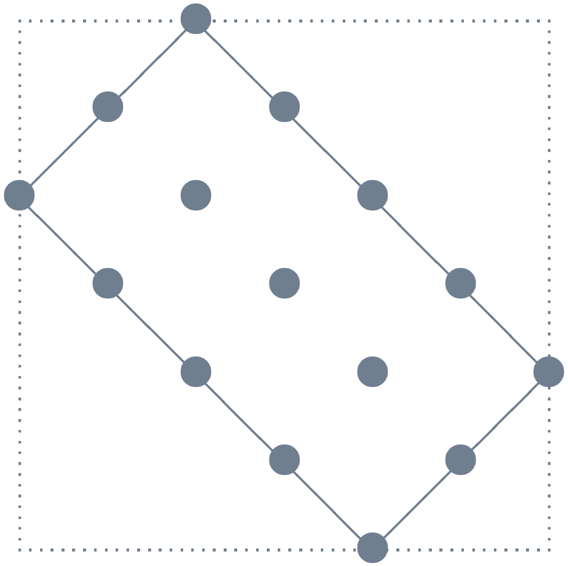
$$k = 4$$



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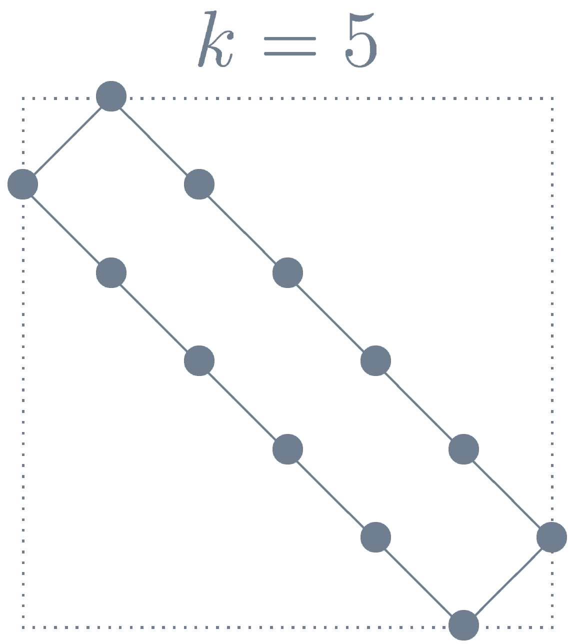

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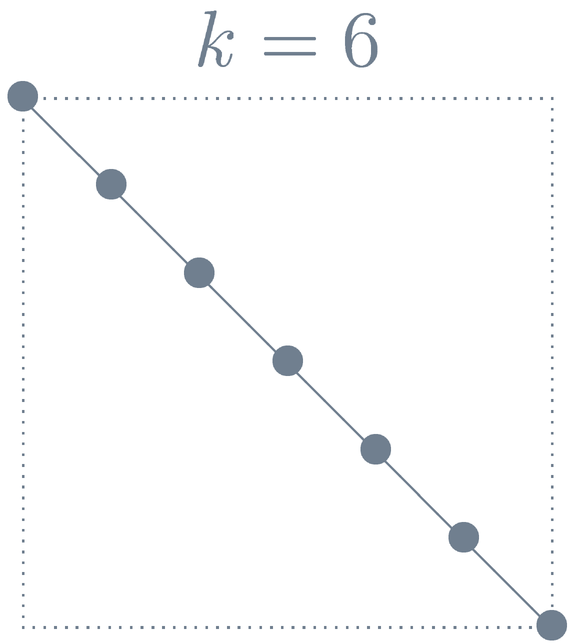

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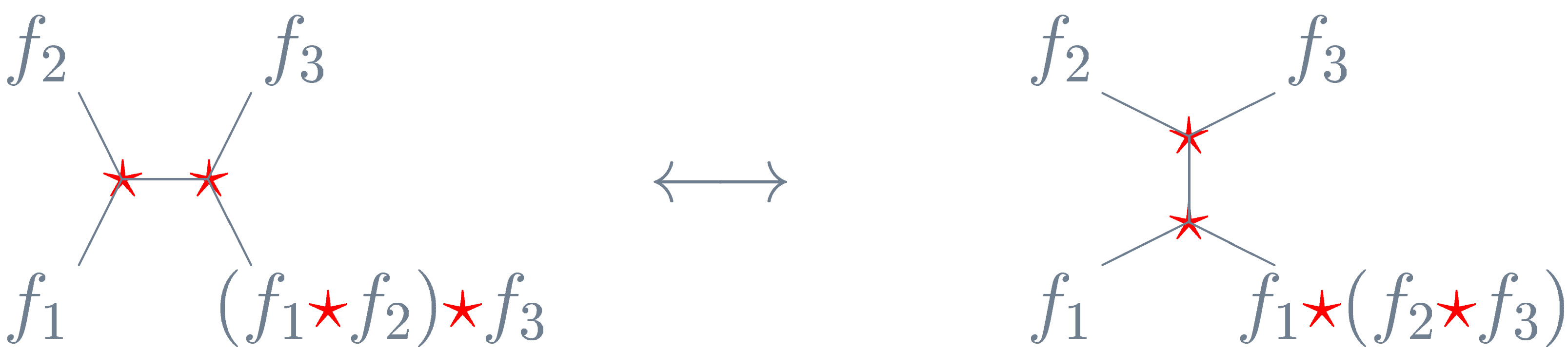

deforming $X(\mathcal{T})$ within $\mathbb{P}_\Sigma$

Recall that leaves of $\mathcal{T}$ can be labeled by numbers $1, \ldots, d+1$ or, equivalently, given $d+1$ points we can make them leaves of a (non-unique) tree $\mathcal{T}$.

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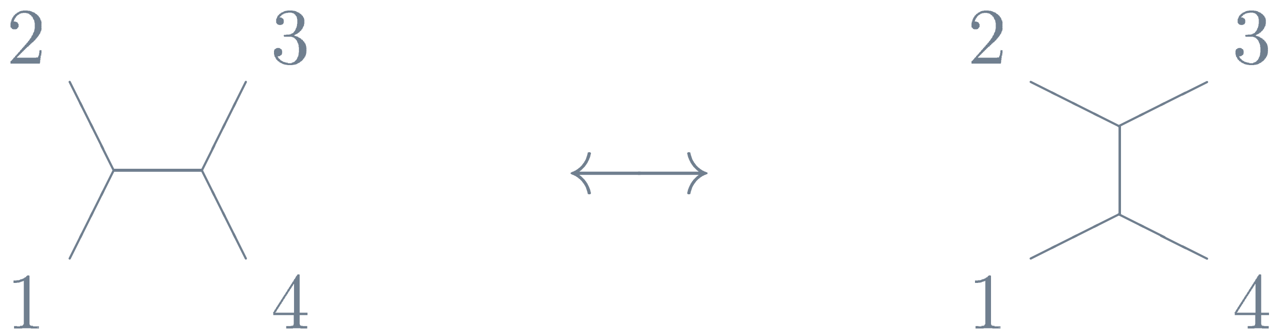

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Thus, all varieties representing different labeled trees can be embedded in a fixed $\mathbb{P}_\Sigma$
These varieties can be non-isomorphic (one can check it), however they are in the same connected component of the Hilbert scheme of $\mathbb{P}_\Sigma$, that is

deforming $X(\mathcal{T})$ within $\mathbb{P}_\Sigma$

Recall that leaves of $\mathcal{T}$ can be labeled by numbers $1, \ldots, d+1$ or, equivalently, given $d+1$ points we can make them leaves of a (non-unique) tree $\mathcal{T}$.
Thus, all varieties representing different labeled trees can be embedded in a fixed $\mathbb{P}_\Sigma$
[theorem] $X(\mathcal{T}_1)$ can be deformed to $X(\mathcal{T}_2)$ if only $\mathcal{T}_1$ and $\mathcal{T}_2$ have the same number of leaves.

proof: working dictionary

Translate the original problem into toric geometry

proof: working dictionary

Translate the original problem into toric geometry

tree

proof: working dictionary

Translate the original problem into toric geometry

tree variety

proof: working dictionary

Translate the original problem into toric geometry

tree polytope variety

proof: working dictionary

Translate the original problem into toric geometry

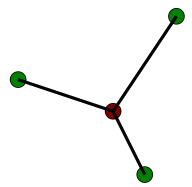
tree polytope variety

understand the basic objects

proof: working dictionary

Translate the original problem into toric geometry

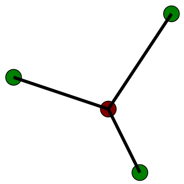
tree polytope variety



proof: working dictionary

Translate the original problem into toric geometry

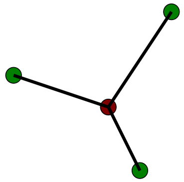
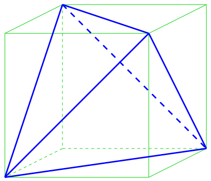
tree | polytope | variety



$\mathbb{P}^3$

proof: working dictionary

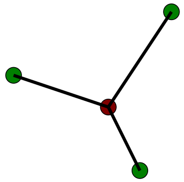
Translate the original problem into toric geometry

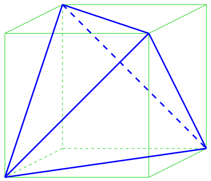
tree	polytope	variety
		$\mathbb{P}^3$

proof: working dictionary

Translate the original problem into toric geometry

tree | polytope | variety



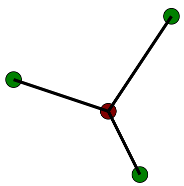
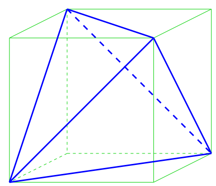


$\mathbb{P}^3$

a leaf

proof: working dictionary

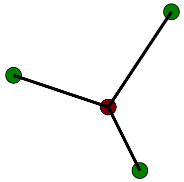
Translate the original problem into toric geometry

tree	polytope	variety
		$\mathbb{P}^3$
a leaf	projection	

proof: working dictionary

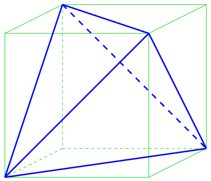
Translate the original problem into toric geometry

tree



a leaf

polytope



projection

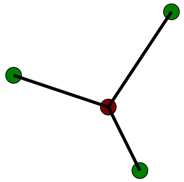
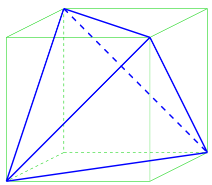
variety

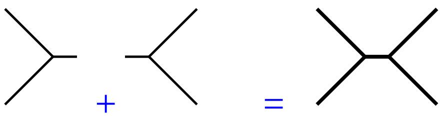
$\mathbb{P}^3$

$\mathbb{C}^*$ action

proof: working dictionary

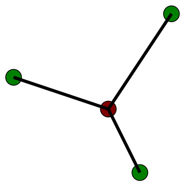
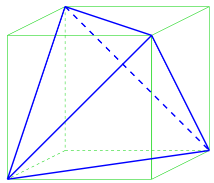
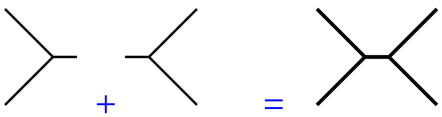
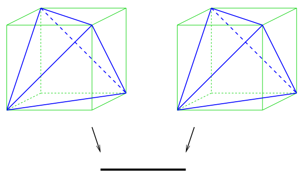
Translate the original problem into toric geometry

tree	polytope	variety
		$\mathbb{P}^3$
a leaf	projection	$\mathbb{C}^*$ action



proof: working dictionary

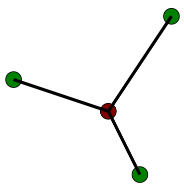
Translate the original problem into toric geometry

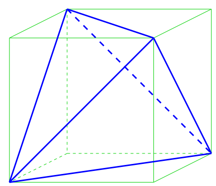
tree	polytope	variety
		$\mathbb{P}^3$
a leaf	projection	$\mathbb{C}^*$ action
		

proof: working dictionary

Translate the original problem into toric geometry

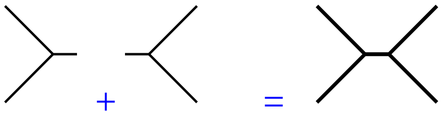
tree | polytope | variety

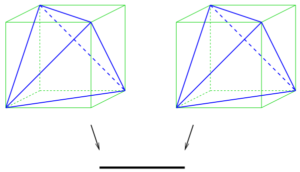




$\mathbb{P}^3$

a leaf | projection | $\mathbb{C}^*$ action

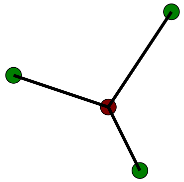
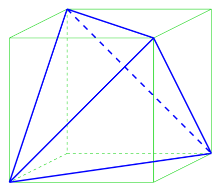
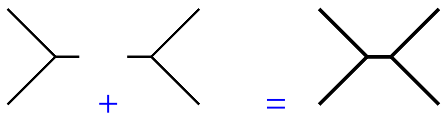
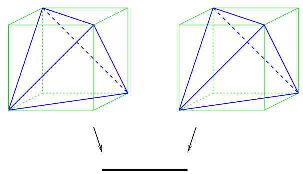




GIT quotient

proof: working dictionary

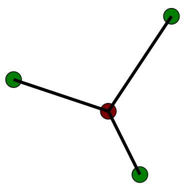
Translate the original problem into toric geometry

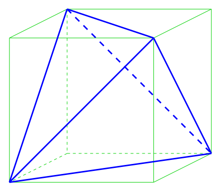
tree	polytope	variety
		$\mathbb{P}^3$
a leaf	projection	$\mathbb{C}^*$ action
 		GIT quotient

proof: working dictionary

Translate the original problem into toric geometry

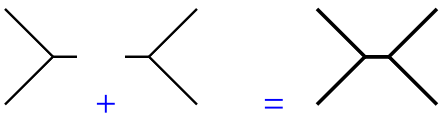
tree | polytope | variety

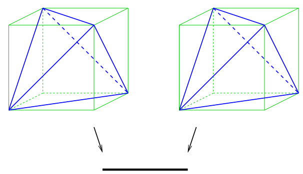




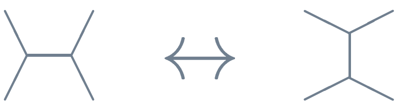
$\mathbb{P}^3$

a leaf | projection | $\mathbb{C}^*$ action





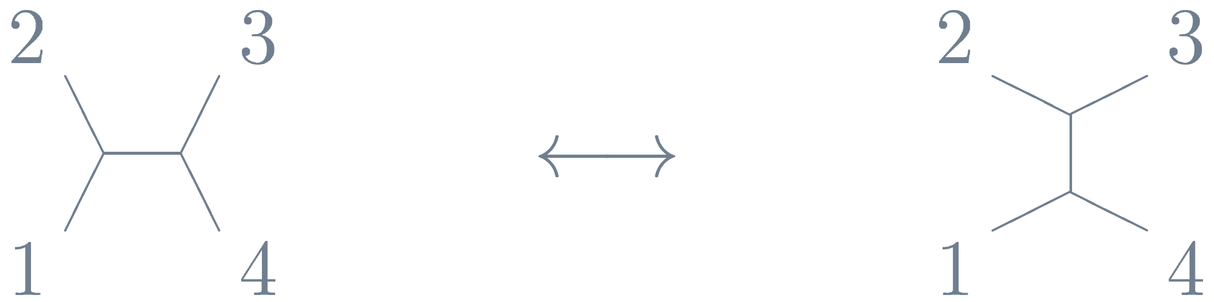
GIT quotient



deformation

proof: the idea

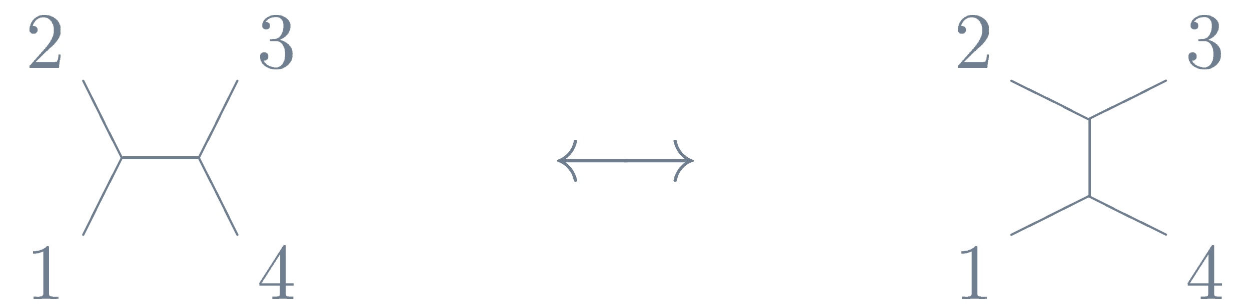
The mutation of a 4-leaf tree



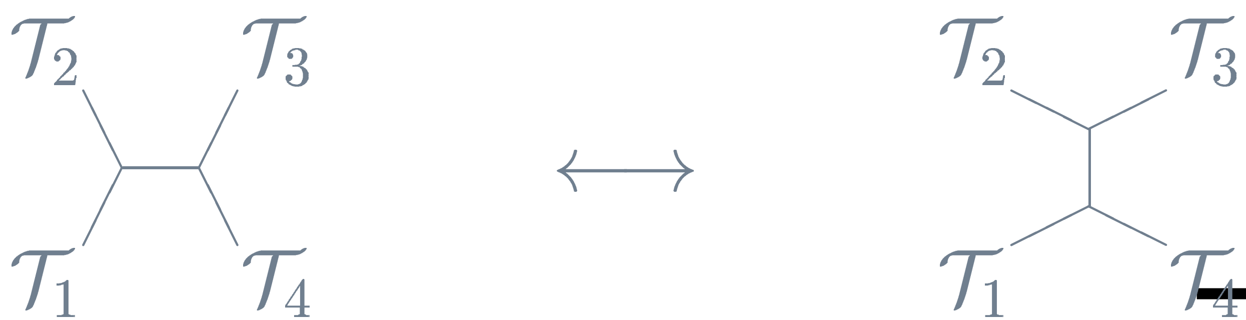
can be explicitly written as deformation which preserves the action of $\mathbb{C}^*$ groups associated to leaves,

proof: the idea

The mutation of a 4-leaf tree



can be explicitly written as deformation which preserves the action of $\mathbb{C}^*$ groups associated to leaves, thus via GIT quotient it can be extended to a mutation of any tree along any inner edge

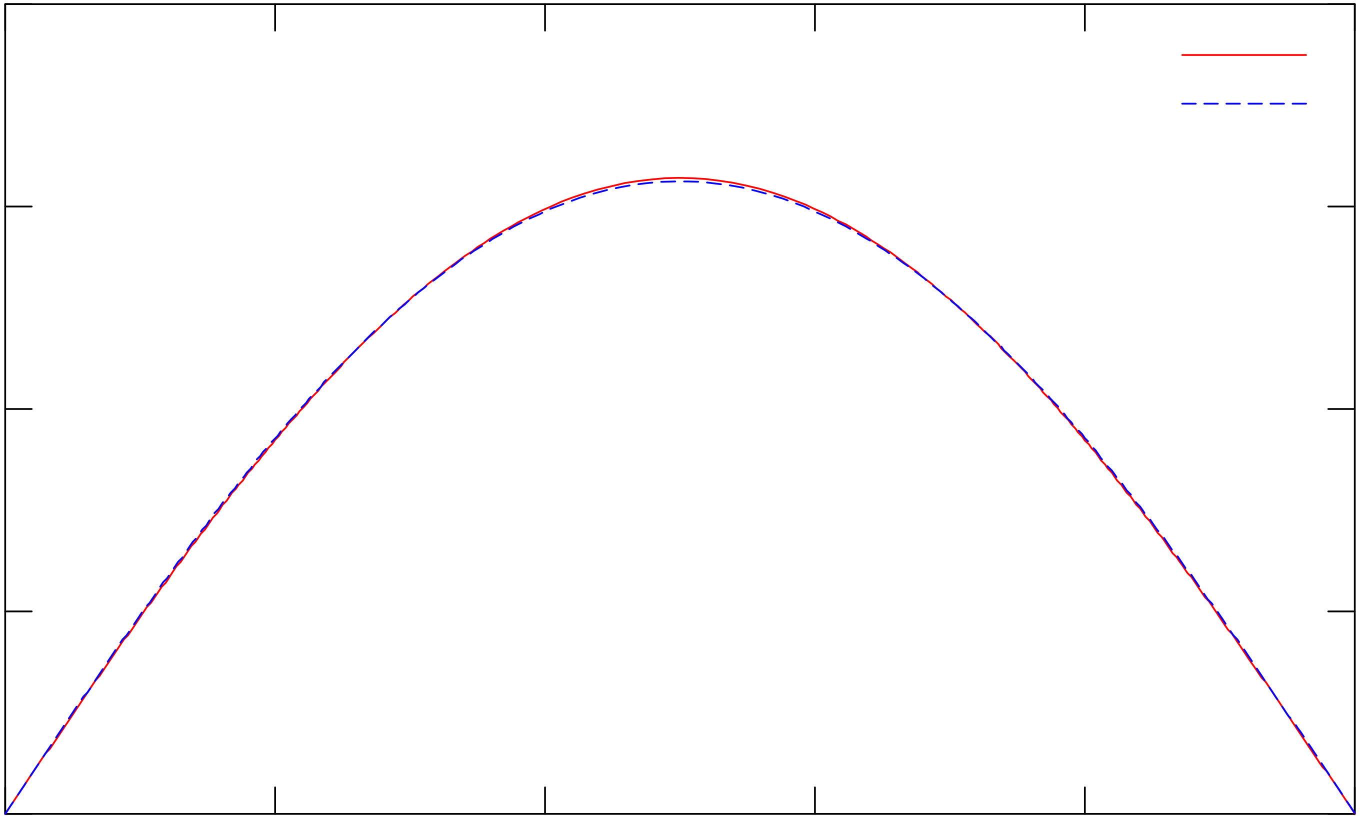


a problem to think about (1)

can one see the size a tree by looking at a leaf?

a problem to think about (1)

can one see the size a tree by looking at a leaf?



a problem to think about (2)

a symmetric model of four state system ACTG

a problem to think about (2)

a symmetric model of four state system ACTG with transition matrix

$$\begin{pmatrix} a & b & c & d \\ b & a & d & c \\ c & d & a & b \\ d & c & b & a \end{pmatrix}$$

a problem to think about (2)

a symmetric model of four state system ACTG

0	0	0	0	0	0	0	0	0	|	1	0	0	1	0	0	0	0	0
1	0	0	0	0	0	1	0	0	|	0	0	0	1	0	0	1	0	0
0	1	0	0	1	0	0	0	0	|	0	1	0	0	0	0	0	1	0
0	0	0	0	1	0	0	1	0	|	0	0	1	0	0	1	0	0	0
0	0	1	0	0	0	0	0	1	|	0	0	0	0	0	1	0	0	1
1	0	0	0	1	0	0	0	1	|	1	0	0	0	0	1	0	1	0
0	1	0	1	0	0	0	0	1	|	0	1	0	0	0	1	1	0	0
0	0	1	1	0	0	0	1	0	|	0	0	1	0	1	0	1	0	0

a problem to think about (3)

the strand model of four state system ACTG

a problem to think about (3)

the strand model of four state system ACTG with transition matrix

$$\begin{pmatrix} a & b & c & d \\ e & f & g & h \\ h & g & f & e \\ d & c & b & a \end{pmatrix}$$