On phylogenetics trees - a geometer's view

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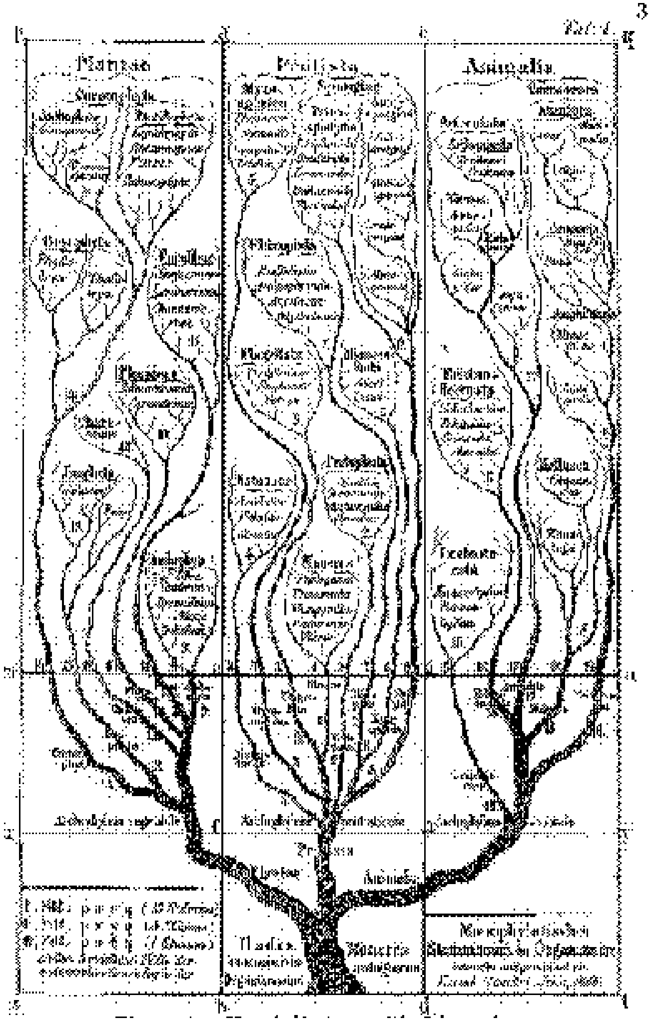
phylogenetics

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]



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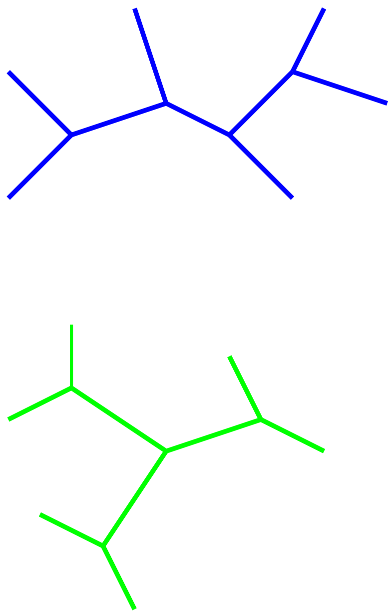
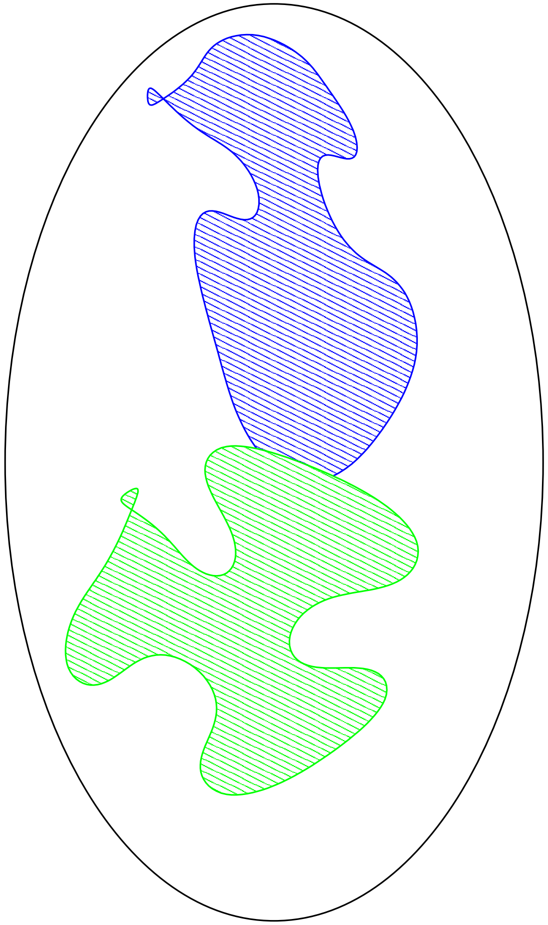
- Data output: the scheme implies constrains
- Algebraic geometry: understand the constrains implied by the assumed scheme
- Statistics: compare what you have with what you should get

idea: tree → variety

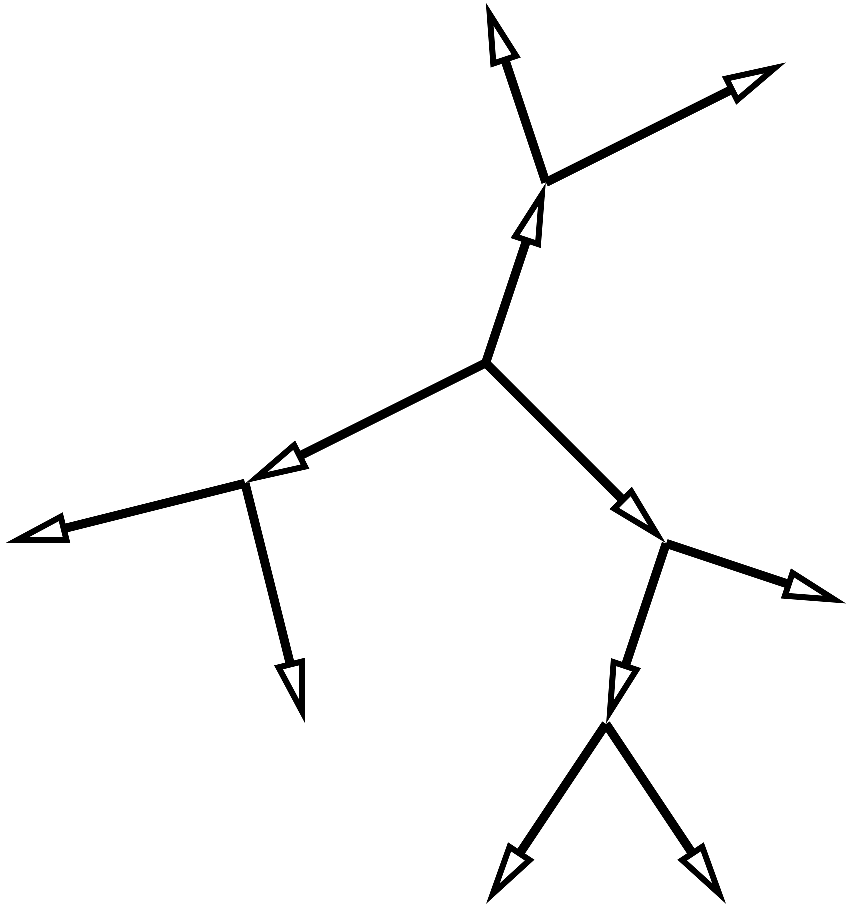
Geometric model of a tree: the locus of probable distribution of the data in the space of all possible distributions — subject to constrains given by the shape of a tree





trees

We consider a tree $\mathcal{T}$ which has $2d-1$ edges in set $\mathcal{E}$, and $2d$ vertices in $\mathcal{V}$ including $d+1$ leaves in $\mathcal{L}$ and $d-1$ inner trivalent nodes in $\mathcal{N}$. Fixing a root r in $\mathcal{T}$ implies a partial order $<$ on the set of vertexes $\mathcal{V} = \mathcal{L} \cup \mathcal{N}$.



binary Markov process on tree

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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For each edge $e = \langle u, v \rangle$ bounded by vertexes $u < v$ define the transition matrix A^e:

$$A^e_{ij} = P(\xi_v = \alpha_j | \xi_u = \alpha_i)$$

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

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

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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 $\to$ variety, definition

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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Baby case: these assumptions are special but convenient to show how algebraic geometry may be used

toric picture

Given tree $\mathcal{T}$ define lattice spanned on its edges $M_0 = \bigoplus_{e\in\mathcal{E}} \mathbb{Z}e$ and identify every $v \in \mathcal{V}$ with a point in the dual lattice N_0:

$$v(e) = \begin{cases} 0 \text{ if } v \notin e \\ 1 \text{ if } v \in e \end{cases}$$

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Think about edges as monomials and vertices as 1-parameter groups whose weights are determined by the incidence relation in $\mathcal{T}$.

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Toric variety defined by $\Delta(\mathcal{T})$ is the model $X(\mathcal{T})$: Fourier transform, [Sturmfels, Sullivant]

trees, sockets and networks

Given a tree $\mathcal{T}$ define: a *socket* is a subset of $\mathcal{L}$ which has even number of elements, a *path* in $\mathcal{T}$ is a connected union of edges and a *network* is a set of non-meeting paths in $\mathcal{T}$ with ends in $\mathcal{L}$

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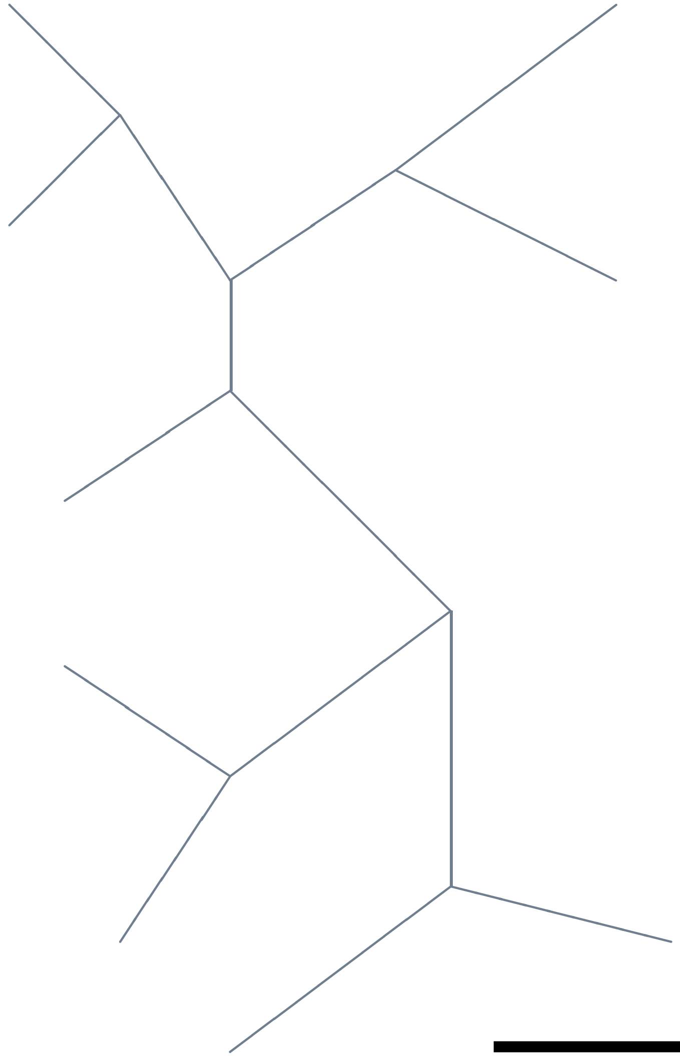

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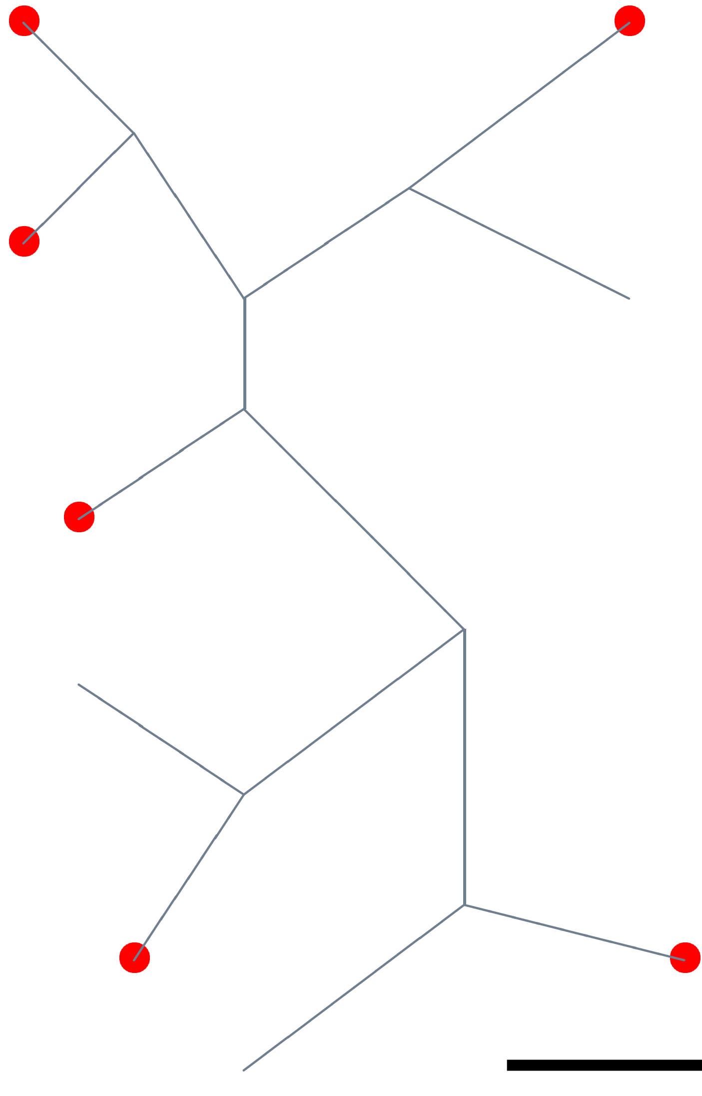

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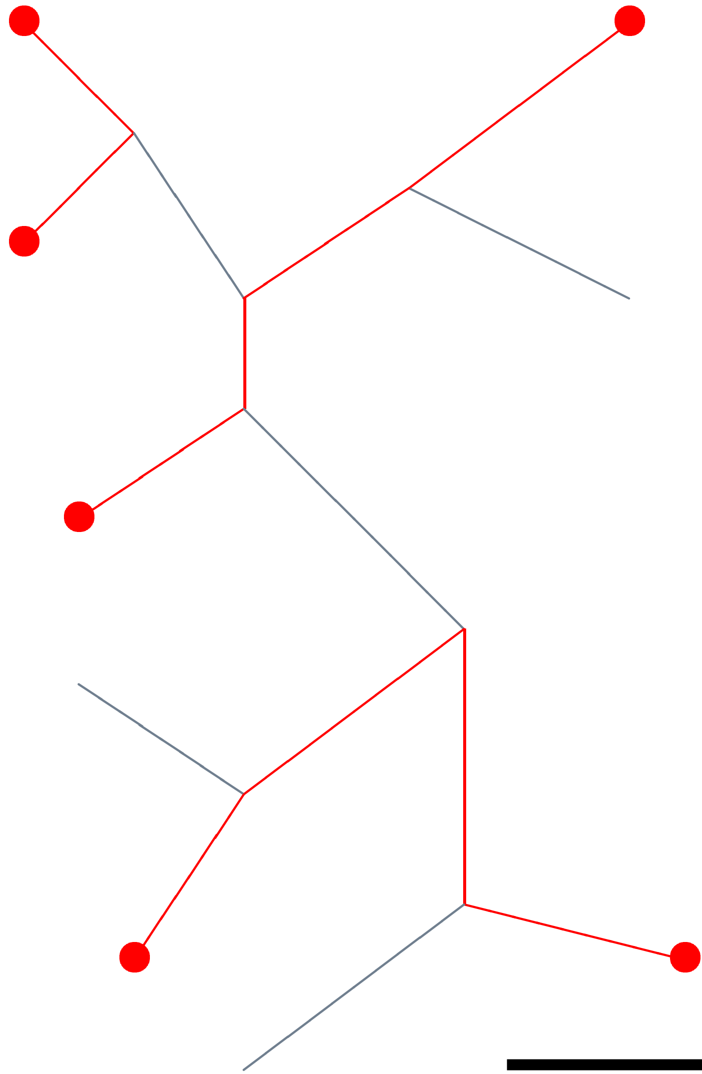

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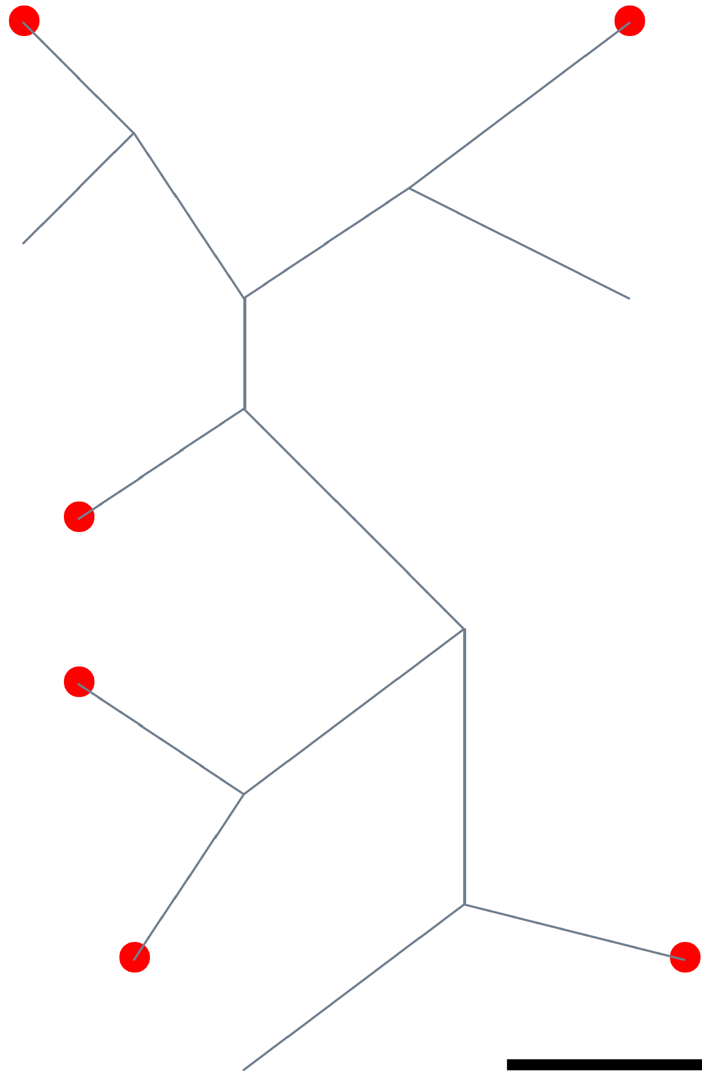

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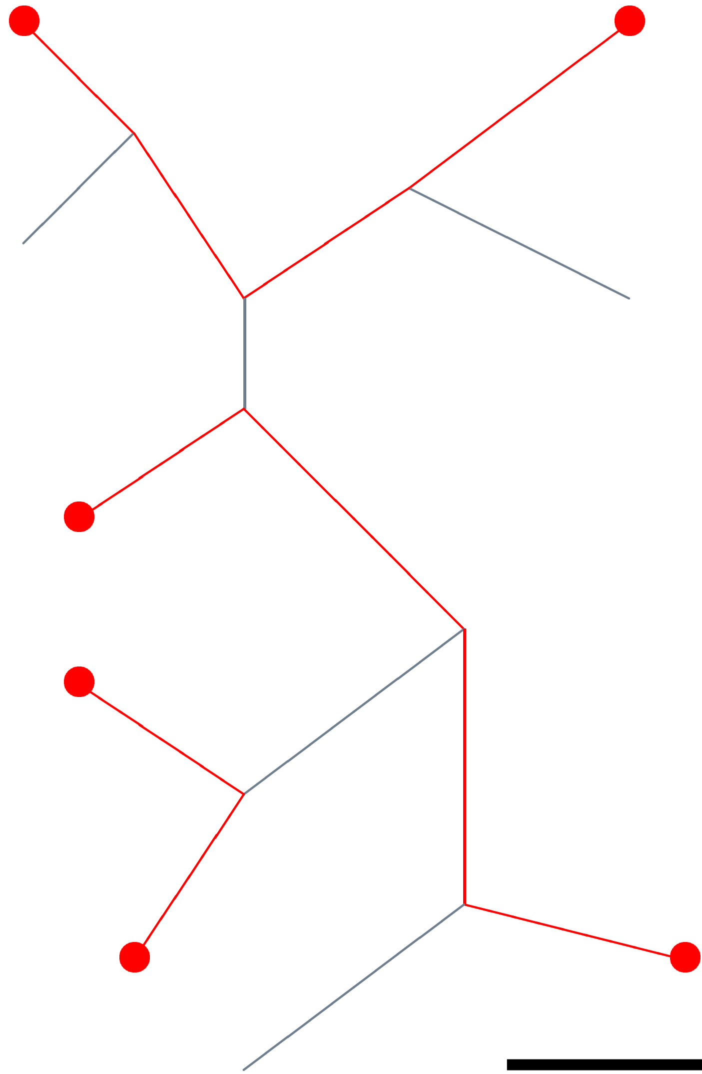

tree $\rightarrow$ variety, 2nd definition

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 $[y_0^e, y_1^e]$. 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 $\prod_{e\in\mathcal{E}}\mathbb{P}^1_e \rightarrow \mathbb{P}_\Sigma$ such that

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

Then $X(\mathcal{T}) \subset \mathbb{P}_\Sigma$, is the closure of the image of this map.

first examples

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

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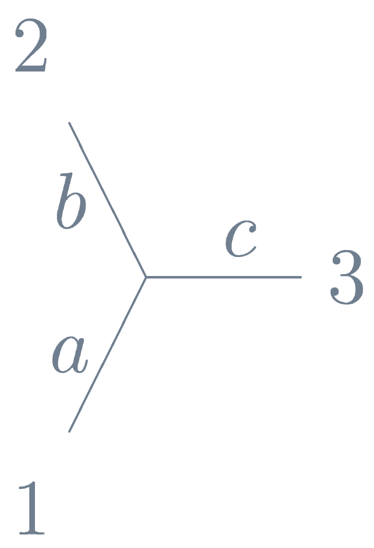
Tripod tree model:

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

$$z_{000} = y^a_0 y^b_0 y^c_0 \quad z_{110} = y^a_1 y^b_1 y^c_0$$
$$z_{101} = y^a_1 y^b_0 y^c_1 \quad z_{011} = y^a_0 y^b_1 y^c_1$$



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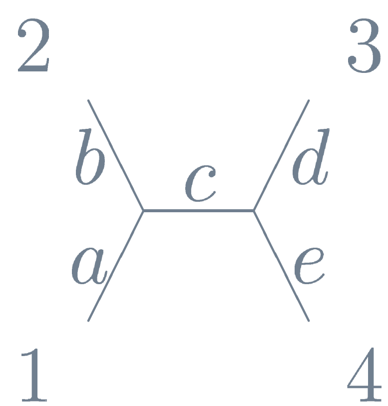
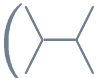
Four leaf tree model in $\mathbb{P}^7$

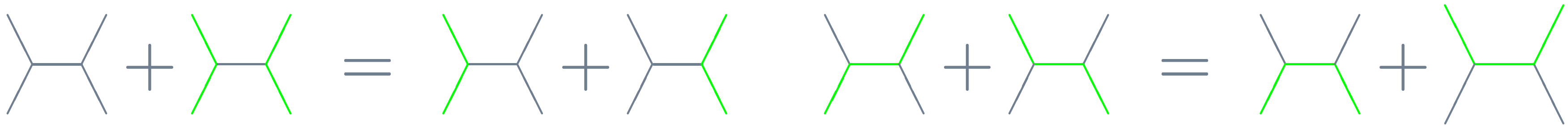
$$
\begin{aligned}
z_{0000} &= y_0^a y_0^b y_0^c y_0^d y_0^e & z_{1111} &= y_1^a y_1^b y_0^c y_1^d y_1^e \\
z_{1100} &= y_1^a y_1^b y_0^c y_0^d y_0^e & z_{0011} &= y_0^a y_0^b y_0^c y_1^d y_1^e \\
z_{1010} &= y_1^a y_0^b y_1^c y_1^d y_0^e & z_{1001} &= y_1^a y_0^b y_1^c y_0^d y_1^e \\
z_{0110} &= y_0^a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



first examples

Leaves of $\mathcal{T}$ are labeled by numbers $1, \ldots, d+1$ and sockets are denoted by $0/1$ sequence of length $d+1$. Edges are labeled by letters. Therefore $X($$) \simeq \mathbb{P}^3$ and $X($$)$ is a complete intersection in $\mathbb{P}^7$:

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



tree $\rightarrow$ variety, 3rd definition

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

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

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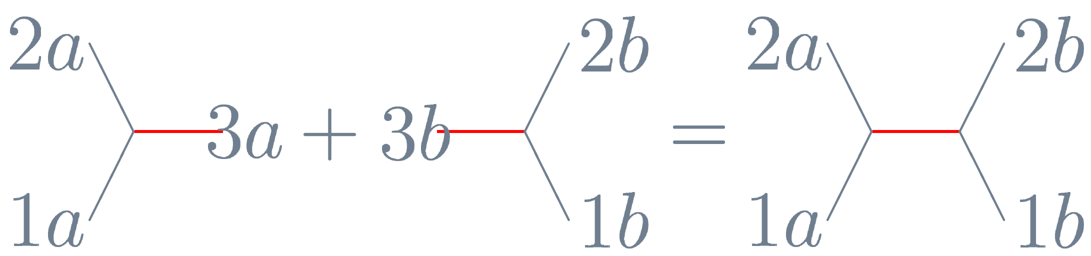
Trivalent trees can be built from tripods (here denoted by letters) by identifying edges of leaves:



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

$$([z^a_{000}, z^a_{110}, z^a_{101}, z^a_{011}], [z^b_{000}, z^b_{110}, z^b_{101}, z^b_{011}]) \to$$
$$[z^a_{000}z^b_{000}, z^a_{000}z^b_{110}, z^a_{110}z^b_{000}, z^a_{110}z^b_{110}, z^a_{101}z^b_{101}, z^a_{101}z^b_{011}, z^a_{011}z^b_{101}, z^a_{011}z^b_{011}]$$

different $X(\mathcal{T})$ in $\mathbb{P}_\Sigma$

We let leaves of $\mathcal{T}$ be labeled by numbers $1, \ldots, d+1$, equivalently, given $d+1$ points can be made leaves of a (non-unique) tree $\mathcal{T}$.

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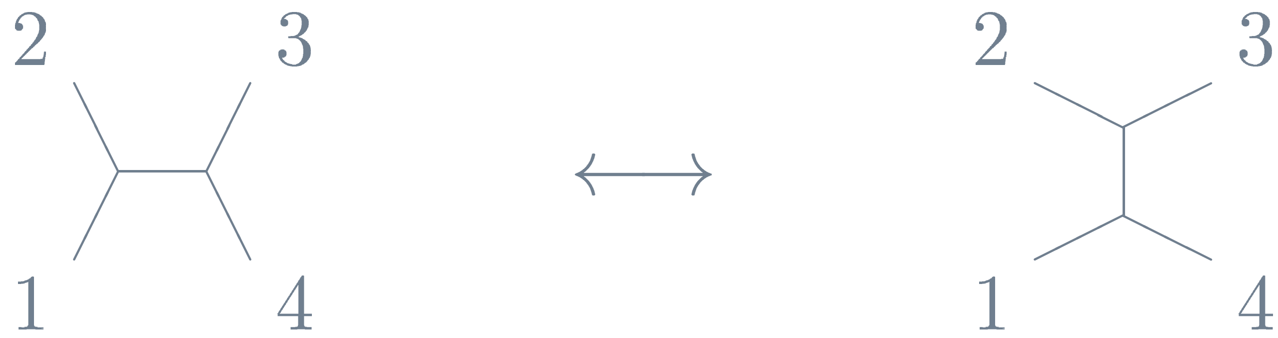

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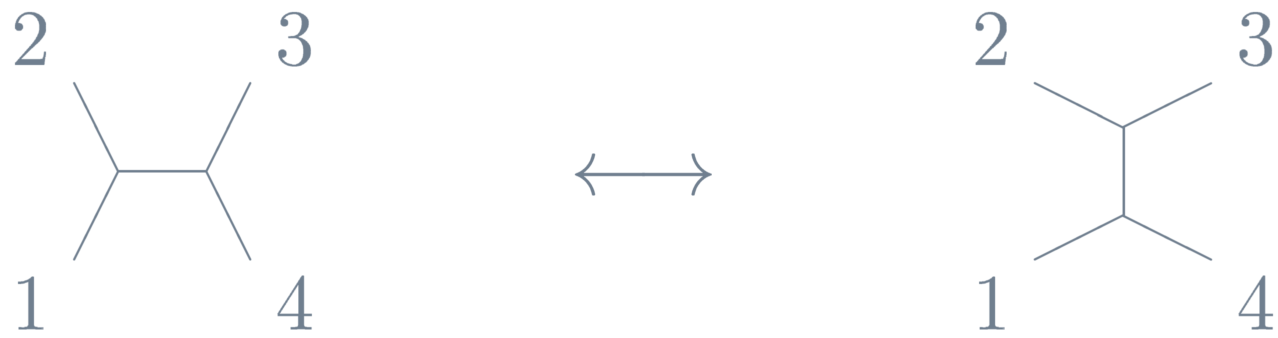
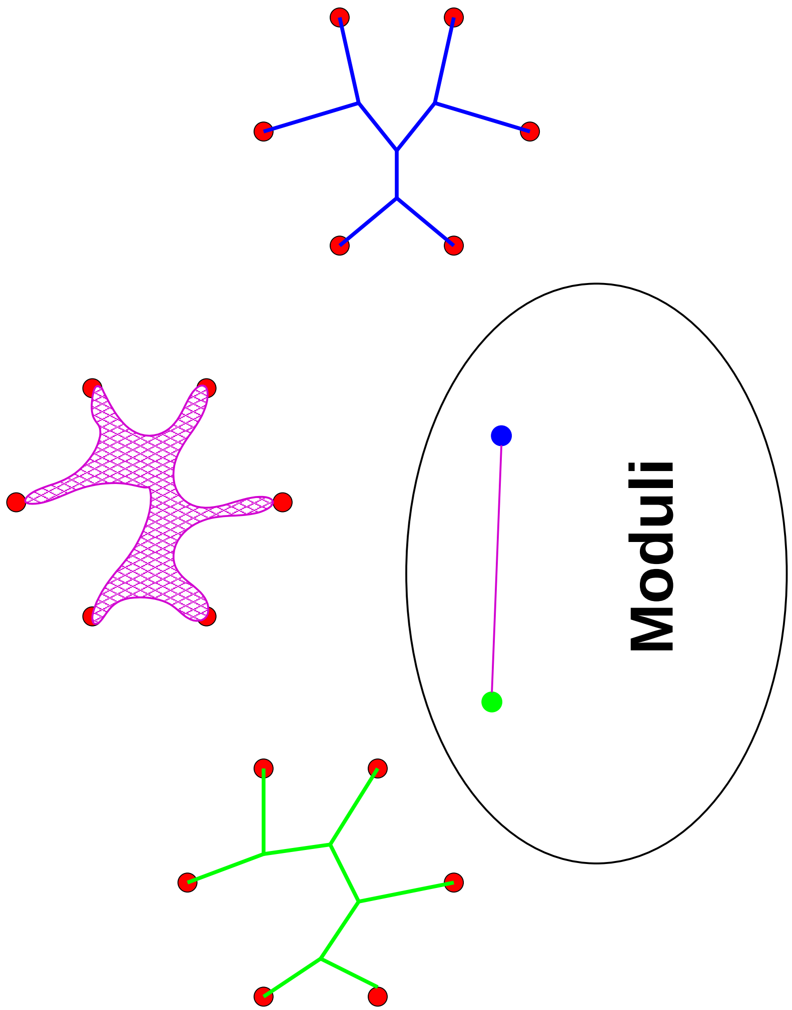


Thus, all the varieties representing different labeled trees are in a fixed $\mathbb{P}_\Sigma$.

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

The varieties $X(\mathcal{T})$ can be non-isomorphic (can be checked) for different $\mathcal{T}$, but [theorem] they are in the same connected component of the Hilbert scheme of $\mathbb{P}_\Sigma$, that is $X(\mathcal{T}_1)$ can be deformed to $X(\mathcal{T}_2)$ if only $\mathcal{T}_1$ and $\mathcal{T}_2$ have the same number of leaves.



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- What is the meaning of the moduli space?

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Classical algebraic geometry: Plücker embedding of $G = \mathrm{Grass}(2, d+1)$.

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In $\mathbb{P} = \mathbb{P}(\wedge^2 \mathbb{C}^{d+1})$ consider coordinates $[x_{ij}]$ where $1 \leq i < j \leq d+1$ then G is given by equations

$$x_{ij} \cdot x_{kl} - x_{ik} \cdot x_{jl} + x_{il} \cdot x_{jk} = 0$$

where $1 < i < j < k < l \leq d+1$

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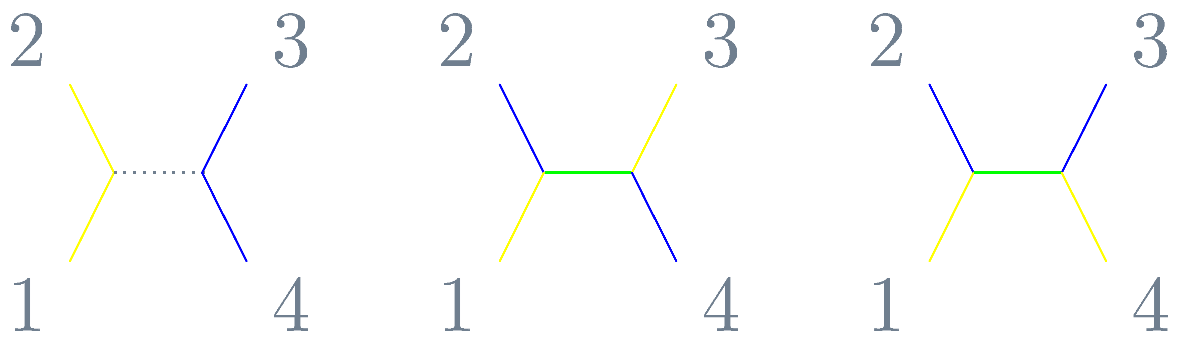

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$$\Delta = \Delta(i, j, k, l) := \delta(i, j) + \delta(k, l) + 2\widehat{\delta}(i, j, k, l) = \delta(i, k) + \delta(j, l) = \delta(i, l) + \delta(j, k)$$

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Given a tree $\mathcal{T}$ label its leaves by $1, \ldots, d+1$ so that for any $1 \leq i < j < k < l \leq d+1$ paths $\langle i, k \rangle$ and $\langle j, l \rangle$ meet. Consider diagonal action of $\mathbb{C}^*$ on $\mathbb{P}$ such that $t(x_{ij}) = t^{-\delta(i,j)} \cdot x_{ij}$.

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and its limit as $t \to 0$ is a toric variety the cone over which is an affine standard coordinate set for $X(\mathcal{T})$, [Speyer-Sturmfels, Gonciulea-Lakshmibai, Howard-Manon-Millson].

Nagata action and its degenerations

Take the Nagata action of $\mathbb{C}^+$ on $\mathbb{C}[x_1, \ldots, x_{d+1}, y_1, \ldots, y_{d+1}]$ given by the formula

$$t(x_i) = x_i, \;\; t(y_i) = y_i + tx_i$$

Nagata action and its degenerations

Take the Nagata action of $\mathbb{C}^+$ on $\mathbb{C}[x_1, \ldots, x_{d+1}, y_1, \ldots, y_{d+1}]$ given by the formula

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The ring of invariants of this action is the coordinate ring of $\mathrm{Grass}(2, d+2)$ with $(d+1)(d+2)/2$ generators x_i and $x_i y_j - x_j y_i$, $i \neq j$.

Nagata action and its degenerations

Take the Nagata action of $(\mathbb{C}^+)^2$ on $\mathbb{C}[x_1, \ldots, x_{d+1}, y_1, \ldots, y_{d+1}]$ given by the formula

$$\begin{aligned} t_1(x_i) &= x_i, \quad t_1(y_i) = y_i + t_1 x_i \\ t_2(x_i) &= x_i, \quad t_2(y_i) = y_i + a_i t_2 x_i \end{aligned}$$

where a_i are general.

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where a_i are general.

[Castravet, Tevelev] The ring of invariants is the coordinate ring of a projective variety of dimension $2d - 1$ in a projective space whose coordinates are indexed by *odd* cardinality subsets of $\{1, \ldots, d+1\}$.

Nagata action and its degenerations

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where a_i are general.

[conjecture — Castravet] Castravet-Tevelev varieties can be specialized to $X(\mathcal{T})$.

⋆ product of functions

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 $\mathbf{1} : [n] \to \mathbb{Z}$ denote the unit function.

$\star$ product of functions

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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 $k \leq n/2$:

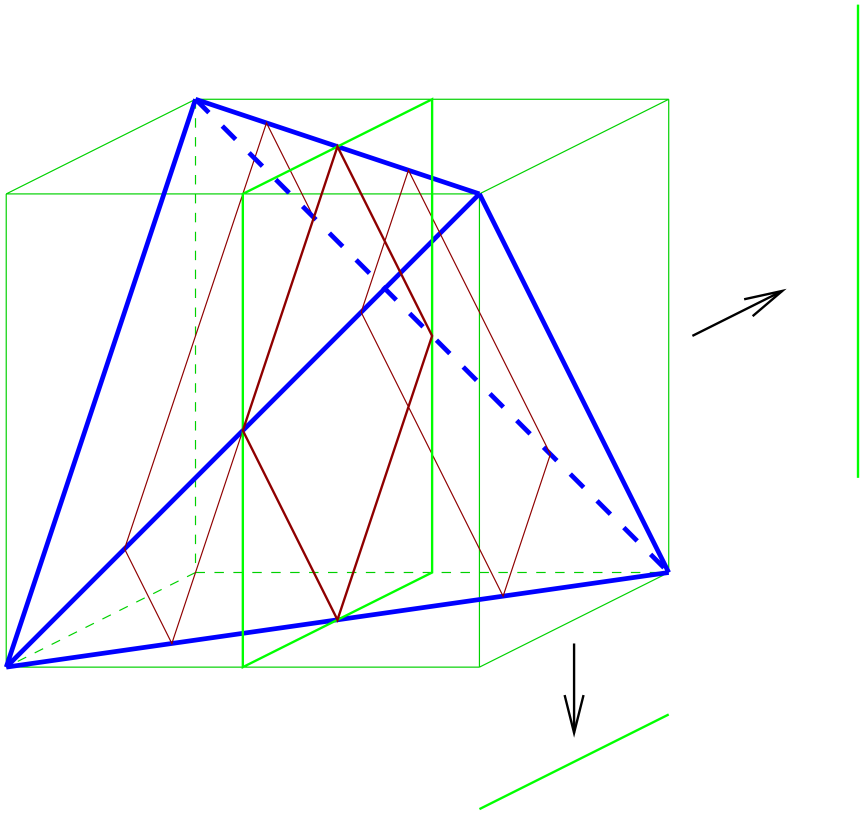
$$(f_1 \star f_2)(k) = 2 \cdot \left(\sum_{i=0}^{k-1} \sum_{j=0}^{i} f_1(i) f_2(k+i-2j) \right) + \left(\sum_{i=k}^{n-k} \sum_{j=0}^{k} f_1(i) f_2(k+i-2j) \right)$$

geometric interpretation of $\star$

Consider the simplex Δ as in the picture

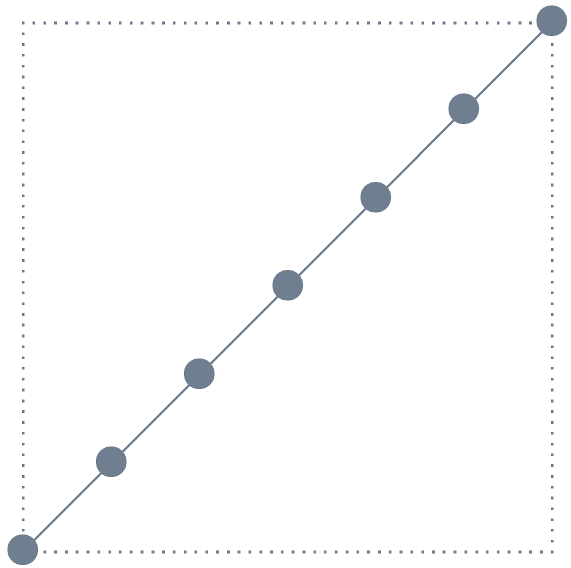
$(f_1 \star f_2)(k)$ is equal to the sum of products of f_1 and f_2 counted over points of lattice spanned by Δ in k-th slice of $n \cdot \Delta$

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



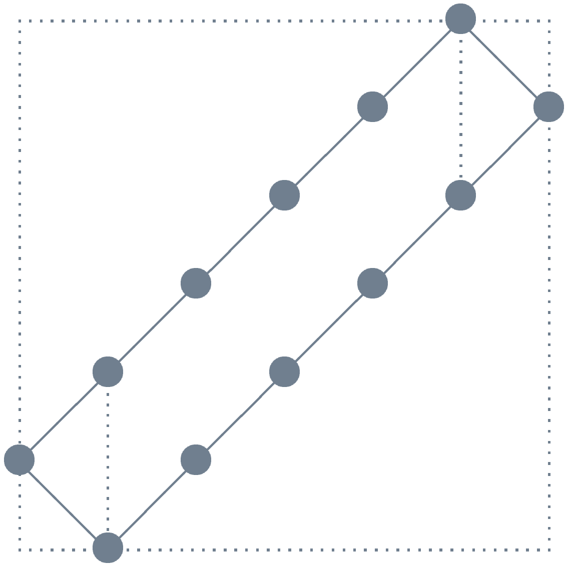
travel trough $6 \cdot \Delta$

$$k = 0$$

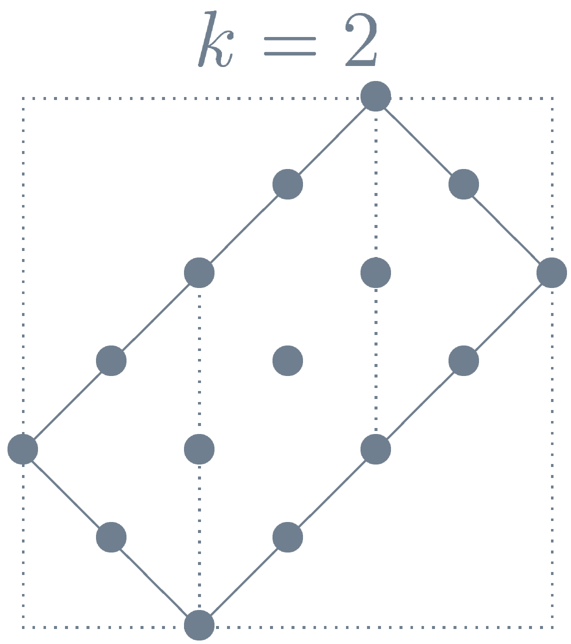


travel trough $6 \cdot \Delta$

$k = 1$



travel trough $6 \cdot \Delta$



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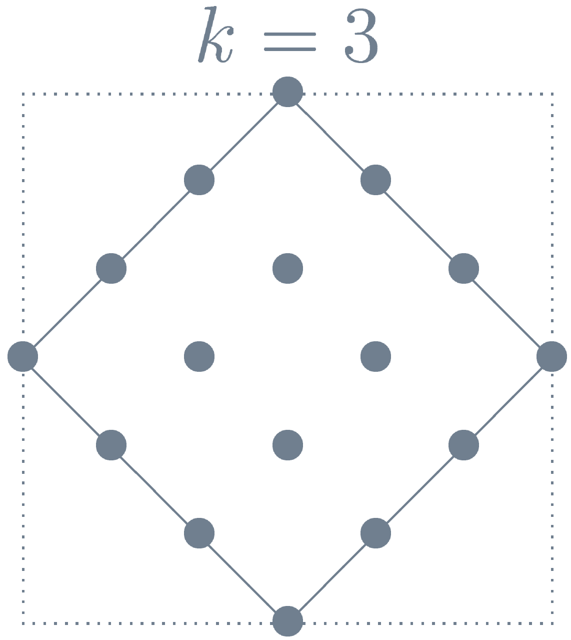

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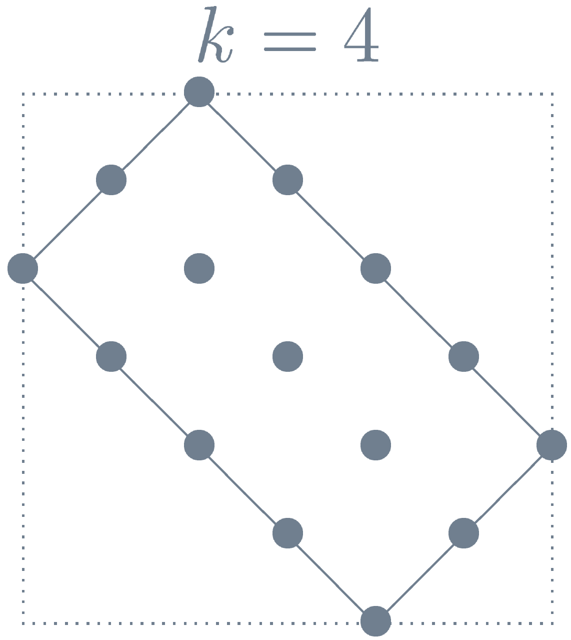
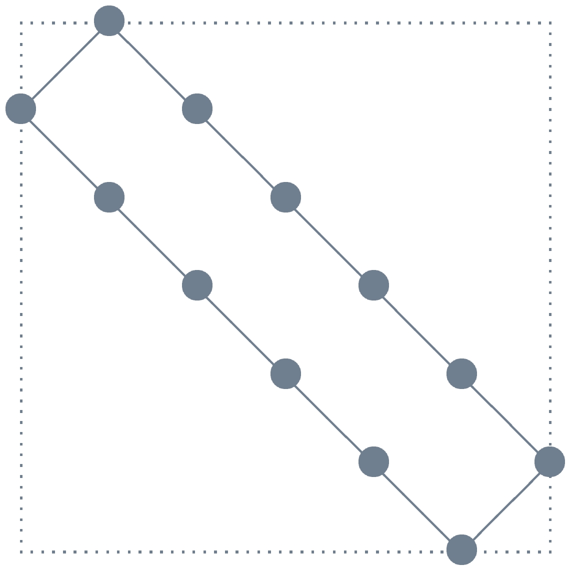
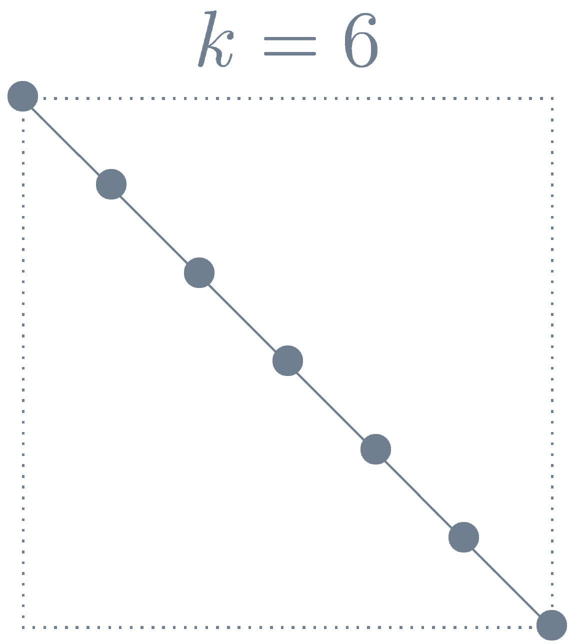


travel trough $6 \cdot \Delta$

$k = 5$



travel trough $6 \cdot \Delta$



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